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Front cover. Indri (*Indri indri*) at Perinet (= Andasibe), Madagascar. Members of this one group have been observed almost daily for decades. 1994. Photo by Russell A. Mittermeier.

# A Word from the Editors

We are pleased to present the second of our catch-up issues intended to bring *Primate Conservation* up-to-date for the first time in six years. This issue covers the period 1993-1994, and includes individual articles as well as selected presentations from a symposium on Population Viability Analysis held at the XV Congress of the International Primatological Society in Bali, Indonesia, in August 1994. This important symposium, unfortunately poorly attended because of scheduling conflicts, included a number of key presentations on endangered primate species, and highlighted the importance of Population Viability Analysis (PVA) in long-term primate conservation endeavors. Robert C. Lacy of the Department of Conservation Biology of the Chicago Zoological Society, Brookfield, Illinois, organized the symposium in Bali, and was kind enough to edit the papers in this issue and provide a guest editorial as well. This focus on using current technologies to assess the long-term status of primates and to develop the most appropriate approaches to conserving them in the wild is one that the PSG hopes to use much more in the future. Indeed, such a case study approach of the most endangered species will be one of the two main objectives of a two-day symposium on "Primate Conservation in the 21st Century", which we are currently organizing for the XVI Congress of the International Primatological Society in Madison, Wisconsin, USA, in August 1996.

This issue also illustrates how we would like to use *Primate Conservation* to publish the results of important meetings such as that for Primate PVA's. Number 8 (1987) included a section for the Proceedings of the Conservation Symposium of the XI Congress of the International Primatological Society in Göttingen, Germany, July 1986. Likewise, the regional newsletters can be a vehicle for publishing the results of conservation and ecology-oriented meetings. The results of a two-day symposium on the Brazilian lion tamarins (*Leontopithecus* spp.), for example, were published in a supplementary issue of Volume 2 (1994) of *Neotropical Primates*. If you are preparing symposia on any aspect of primate conservation and need a venue to publish the results, please contact us about the possibility of putting them into either *Primate Conservation* or one of the regional newsletters.

As always, we need your input as to how we can make this journal and the regional newsletters more effective tools for achieving our primate conservation objectives. Please feel free to contact either one of us at the addresses given on page 64, and continue to send us your articles, field reports, short news items, announcements, etc. for possible inclusion in our five different publications. Addresses for the regional newsletter editors are given at the back of this journal (page 65), and the instructions for contributors are on page 65. We thank you for your continued support.

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Editor, *Primate Conservation*

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# Status and Conservation of Chimpanzee and Gorilla in Cameroon

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Despite their relative abundance, the Pongidae of Cameroon are relatively poorly known and their number is thought to be declining. This paper presents new information on the distribution and status of chimpanzee and gorilla in Cameroon as well as a survey of existing literature. Recommendations are made to enhance the protection of these species.

## Introduction

Cameroon is characterized by a particularly rich wildlife, comprising over 9,000 plant species, 297 mammal species, and 848 species of birds (Ministère de l'Environnement et des Forêts 1994). This diversity is mainly due to the geography of the country, which extends from Lake Tchad in the north to the dense forests in the south. The country has an Atlantic coast, estuaries, mountains reaching 4,000 m, and extensive areas of savanna. More than 44% of the territory is covered with dense forests that are mainly found in the southern part of the country between the Nigerian border to the west and the south-east borders with Equatorial Guinea, Gabon and Congo (Gartlan 1989).

This rich zone of rain forest is inhabited by one of the most important populations of lowland gorilla *Gorilla gorilla gorilla* Savage and Wyman 1847 (Fig. 1) and chimpanzee *Pan troglodytes* Blumenbach 1779 (Fig. 2). Population sizes have been estimated to be between 6,000 and 10,000 for chimpanzees (Teleki 1991) and about 1,500 for gorillas (Gartlan 1980, in Lee *et al.* 1988) in Cameroon. Despite their relative abundance, the Pongidae of Cameroon are relatively poorly known and their numbers are thought to be declining (Lee *et al.* 1988; Wolfheim 1983).

In February 1993, the Jardin zoologique du Québec and the Metro Toronto Zoo organized a joint expedition to Cameroon, in collaboration with the Cameroon Department of Environment and Forests, in order to obtain information on the status of chimpanzees and gorillas in this Central African country. Two weeks were spent visiting the Dja, Mvongame, Campo, Douala-Edea and Korup areas, including field trips and meetings with local authorities. The Limbe Zoo and the Mvog Betsi Zoo in Yaoundé were also visited.

Here field observations are combined with a thorough survey

of the literature, and results are presented for each of the four general areas of Cameroon where great apes are found.

## The Central South and South-East

### Dja Wildlife Reserve

Chimpanzees and Gorillas were once present near the capital, Yaoundé. Hunting and deforestation have exterminated them from the most populated areas. These animals are currently found south of Yaoundé, in and around the Dja Wildlife Reserve (Bergmans



Fig. 1. Gorilla disrupted distribution area in Cameroon

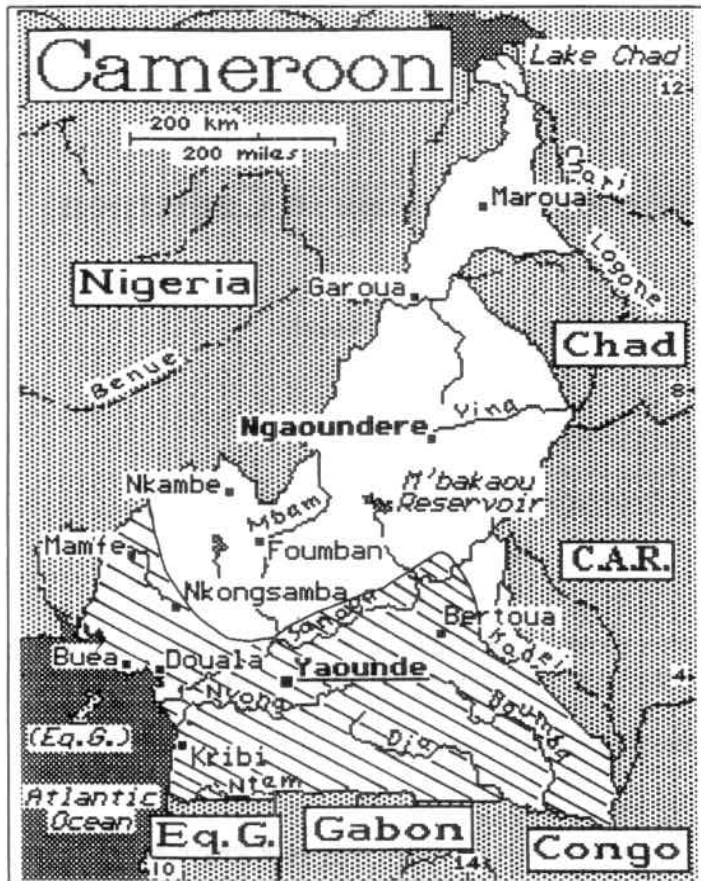


Fig. 2. Chimpanzee disrupted distribution area in Cameroon.

1994). Founded in 1950, the Dja reserve was given the status of a World Biosphere Reserve in 1981, and it is planned to create a National Park there. It is currently the site of a major European Union-funded conservation project (part of the Central African ECOFAC program) including wildlife inventories (J. M. Froment pers. comm. 1994). One conservator and three game wardens share the responsibility of protecting the reserve covering an area of 526,000 hectares of dense lowland rain forest. Elephants, water chevrotains, Bates' antelopes, duikers, buffaloes, bongos, leopards and numerous primate species are found there (Bergmans 1994).

A population of 5,000-7,000 people live within or in proximity to the reserve (Moamosse 1990; van der Zon and Nkemi undated). This population is scattered among 20 small villages and encampments that are connected by a 60 km track (suitable for motor vehicles). The reserve is crisscrossed by tens of kilometers of pathways. The local population lives off hunting, fishing and cultivation (Moamosse 1990).

The cultivations are regularly visited by chimpanzees and gorillas (as well as elephants), especially during the dry season when food is otherwise scarce. The frequency of damage is clearly declining when compared to the situation that prevailed 20-25 years ago. This may be an indication of a decrease in the great ape populations in this area (Moamosse 1990). Apes generally visit the plantations at night. Local people have taken to hunting these animals to protect their plantations and to obtain fresh meat. Hunting gorillas may be dangerous and an average of one casualty or accident per year is reportedly caused by the counter-attack of an injured gorilla.

Gorilla meat is appreciated for its curative properties. Villag-

ers also believe that a vigorous child will be conceived if the mother attaches a gorilla digit to her hips. A similar effect is believed to result if the bone of a gorilla is put on the plate of the child or if a gorilla digit is attached around his hips. Gorilla hairs are also thought to protect the land owners from the spells of the sorcerers or to protect their fields from the sorcerers who may try to steal the fertility of a plantation to the benefit of their own fields (Moamosse 1990).

In the northern part of the reserve, Theodore Lee, an ancient from the village of Etou, kills yearly one or two chimpanzees and half a dozen *Cercopithecus* monkeys using crossbows and poisoned arrows. Our Pygmy tracker also demonstrated his skill at tracking and calling chimpanzees. Apes are mainly hunted during the rainy season when the wet ground muffles the footsteps of the hunters. In this season, groups of apes may also converge on fruit bearing trees (Gartlan and Struhsaker 1972). Most of the time, the meat is shared by the hunter with the members of his family and the other villagers. Caliber 12 or 16 shotguns, rifles, steel traps and snares are also used to acquire bushmeat. On a single morning we have picked up 20 snares in an area frequented by chimpanzees. Chimpanzee meat is highly appreciated by local people. We have estimated that about 40 chimpanzees are killed annually in the area; twice as many as gorillas (Moamosse 1990).

There is also an ongoing illegal trade of young chimpanzees and gorillas. In 1985 and 1988, the park's conservator confiscated two gorilla infants from poachers who had killed their mothers. Young gorillas are occasionally brought to the Yaoundé Zoo but none have yet survived. At the time of our visit, the Mvog Betsi Zoo in Yaoundé housed seven chimpanzees (three females of four, 10 and 17 years old, and four males of four, 18, 18 and 20 years of age). Most of these animals had been brought to the zoo by private owners or local authorities. The Atlantic Beach Hotel in Limbe also housed two male and a female adult chimpanzees in a small barred cage, and the Limbe Zoo had one 3-4 year old female. In Douala, in 1992, at least three chimpanzees were kept by private owners including a six-year-old female obtained from poachers at the age of approximately two weeks (mother probably killed by poachers) and a three-year-old male bought in a local market at the age of 6-7 months (E. Toscano pers. comm. 1992). In July 1995 two six-month old chimpanzees were displayed to the public at the Hotel Le Ranch in Ebolowa, and three juvenile



Fig. 3. Poacher's shelter in the Campo Reserve. Photograph by Jacques Prescott.



chimpanzees were kept at the Hotel de la Plage in Kribi. One young live chimpanzee and the head of an adult specimen were offered for sale on a Yaoundé street (J. Prescott pers. obs).

Between 1970 and 1980, when a ferry across the Dja allowed the circulation of motor vehicles inside the reserve from Somalomo, the subsequent establishment of numerous villages and the development of agriculture within the reserve have forced the gorillas to take refuge in a remote area at the center. It must be noted, however, that during this relatively prosperous period, the villagers could sell their crops more easily and the hunting pressure was a little less marked.

Gorilla groups of up to 20 individuals are occasionally seen in more humid areas near the center of the reserve, over 15 km from the nearest villages. In Etou, the last gorilla was seen in 1978. Gorillas are also regularly reported in the northwestern part of the reserve. A few days prior to our visit in February 1993, a small group was observed by Pygmies near Somalomo, north of the Dja river. Chimpanzees seem to be only slightly more common near Etou and Somalomo. We have heard about twenty individuals on both sides of the Dja river.

In 1990, an expedition organized by the Garoua Wildlife College in the south-east of the Dja reserve near Lomié confirmed the presence of great apes. Gorilla skulls were observed in the villages and traces of chimpanzee activity were noted (Thal *et al.* 1990). Similar observations were made south of Lomié in January 1994 and near Mékas in 1992 (H. Planton pers. comm. 1994).

Further to the east, chimpanzees are known to occur in the Nki and Boumba Bek forests as well as within the future Lobeke Lake Wildlife Reserve (H. Planton pers. comm. 1993). The presence of gorilla in the Lobeke Lake area has been regularly confirmed by H. Planton in the past few years (pers. comm. 1994) though their presence was considered doubtful in this area in 1980 (Gartlan 1980, in Lee *et al.* 1988).

North of Yaoundé, the presence of gorillas was noted within the Pangar Djerem Wildlife Reserve in 1970 (Lee *et al.* 1988) but their continuing presence as well as that of chimpanzees could not be confirmed in the present study.

#### *Mvangame Area*

The area between Mvangame and the border with Gabon is covered by dense rain forests. A 25,000 ha reserve is planned in this area. In close proximity to the villages of Bitche and Bikou'ou (near Akoabas), we counted about 20 gorilla nests distributed in three distinct groups along a 2 km transect line. In 1986, "fresh gorilla tracks" were noted almost every 3 km along two transects totaling 32 km (Belinga 1987), and the presence of gorillas was confirmed again in 1991 (Mengang Mewondo and Ndo Nkoumou 1991) near Amvom a few kilometers to the west. In Bikou'ou, villagers use scarecrows to frighten gorillas from their plantations. In 1987, a villager was badly hurt by a gorilla whose hand had been cut off by one of his snares. Villagers do know of (but insist that they no longer follow) the traditional uses of gorilla hair and digits noted in the Dja reserve.

Chimpanzees are regularly heard by villagers, and their presence was confirmed in 1986 when 16 temporary nests were observed (Belinga 1987). Many other primate species are found in this area including potto, galago, mandrill, Diana monkey, De Brazza's guenon, white-nosed monkey, crowned monkey, black



Fig. 4. Traditional hunting weapons are being replaced by firearms (Theodore Lee and his crossbow in Etou). Photograph by Jacques Prescott.

and white colobus, moustached monkey, and dwarf guenon. It would be highly desirable to carry out an exhaustive survey of gorillas as well as the other threatened primate species in this zone in order to support the Gorilla reserve project planned by the Cameroon Government.

#### **The South-East**

##### *Campo Wildlife Reserve*

In the southwest, 89 km from Kribi, the Campo Wildlife Reserve, created in 1932, covers 300,000 ha. Along the Atlantic coast, the vegetation is mainly shrubby but towards the interior stands a dense low-altitude rain forest inhabited by a rich fauna. The presence of chimpanzees and gorillas is regularly noted by the conservator and the four game wardens, despite having only one motorbike to survey the entire reserve. In 1980, the number of gorillas was estimated to be between 200-300 (Calvert 1980, in Lee *et al.* 1988). From 1984 to 1988, J. Hoshino carried out a study of the ecology and behavior of chimpanzees using an artificial feeding station. The study was abandoned after several animals were killed by poachers in 1985 (MESRS 1987).

Dipikar Island, which is isolated from the northern part of the reserve by the northern branch of Ntem river, is considered an exceptional habitat for great apes. This island was logged in 1969. It is still connected to the northern part of the reserve by a presently disused bridge. We have counted five gorilla nests and traces of feeding activity along a 500 m transect line near the Ntem river. Chimpanzees, mandrills, buffaloes and elephants are also found in this area, which could be viewed as an excellent site for scientific studies.

Logging is the main threat for great apes within the reserve. The French company "La Forestière de Campo" holds a 25-year exploitation permit and has been in the reserve since 1968, despite the legal status "protecting" it (Gartlan 1980, in Lee *et al.* 1988). In 1993, there was no indication that this activity would cease. About twenty truckloads of timber leave the reserve daily. We have estimated that the company has opened more than 2,000 km of forestry roads that split up the habitat and allow the local populations to reach further into the forest. Despite some local habitat degradation, many old logging roads return to forest after a few

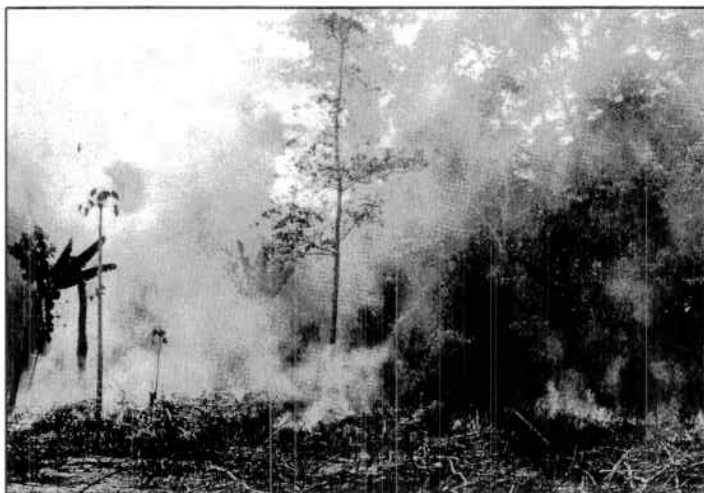


Fig. 5. Slash-and-burn in the Dja Reserve. Photograph by Jacques Prescott.

years without people settling along them (Toornstra *et al.* 1994).

The 4,000 people living in the Campo Reserve mainly live off hunting and traditional agriculture. Many of them work for the logging company. A population of 356 people are settled in six small villages deep in the reserve. Some of the Pygmies offer their services as trackers to hunters coming from outside the region. In December 1992, more than 26 hunting encampments were destroyed by the authorities within the reserve. We also noted that the foresters actively hunt the wildlife and sell the bushmeat that they do not use.

#### *Douala-Edea Wildlife Reserve*

The Douala-Edea Wildlife Reserve, created in 1932, covers 160,000 ha. It includes mangroves, but the main part consists of dense rain forest. Elephants, buffaloes, bongos and several primate species, including a small number of chimpanzees, are found there (Struhsaker 1972). Gorillas probably no longer occur in the reserve, but in 1992, one was seen crossing the Edea-Douala highway 30 km from Edea. That year, in the same area, authorities confiscated the arm of a gorilla that was offered for sale on the roadside (J. Liombe pers. comm. 1993). The reserve is protected by only one conservator and a single game warden, and hunting is particularly intensive in the area. There is also considerable com-

merce of bushmeat. A survey of the villagers living around Tisongo Lake recorded more than 50 firearms. Five villages are established within the reserve and bushmeat accounts for a major part of the local income. Numerous hunters come from Douala and Yaoundé on weekends, and city dwellers currently provide ammunition and firearms to local hunters in order to obtain fresh bushmeat.

An important concession has been granted to the Société Africaine Forestière et Agricole du Cameroun which has been logging in the northern part of the reserve since 1985. Authorities currently plan to declassify this sector.

### **The Central-West**

#### *Korup National Park*

The Korup National Park, created in 1962, covers an area of 125,000 ha of dense rain forests. The western part of the park is bordered by Nigeria. Chimpanzees are frequently observed in the northern part of the park as well as within the Ejagham, Takamanda, Nta Ali, Banyang Mbo and Mawne river Forestry Reserves. To the south, their presence has been noted in Barombi Mbo and Mount Koupe Forestry Reserves as well as in the Mount Cameroon and Nlonako area (H. Planton pers. comm. 1993). A survey undertaken in 1992 confirmed the presence of chimpanzees around Mount Koupe, Mwenzekong and Mwendelengo mountains as well as in the Mungo valley (King 1994). Gartlan and Struhsaker (1972) also noted their presence in the South Bakundu forestry reserve between 1966 and 1968. Their current status is unknown in this zone.

Gorillas are absent from the region, with the exception of a small population (estimated at 60 individuals by Cousins in 1978) still living in the 50,000 ha Takamanda Forestry Reserve on the Nigerian border (Fay 1987, in Lee *et al.* 1988; Z. Akum pers. comm. 1993). This population is important in that it is completely isolated from the southern populations, though it probably connects with remnant populations in Nigeria. Its genetic distinctiveness needs investigation.

Chimpanzees and the few remaining gorillas are also hunted in this region by the local population. According to Ruitenbeek (1990, in MEF 1992), 25% of the rural revenue comes from



Fig. 6. Gorilla nest in the Mvangan area. Photograph by Jacques Prescott.



Fig. 7. Pygmy village near Somalomo (Dja area). Photograph by Jacques Prescott.

bushmeat, and according to Infield (1988) 80% of the wild game killed in the Korup area is used for commerce rather than subsistence. King (1994) reported that the commercial value of a chimpanzee may reach 11,500-15,000 CFA (20-25 US\$) and even up to 50 US\$ (H. Planton pers. comm. 1994). Local population eat the meat and use chimpanzee pelts for decoration. Chimpanzee bones are also valued for their therapeutical qualities: the bone corresponding with the damaged part of the patient is boiled in water and the liquid applied to the skin. Chimpanzee skulls are sometimes sold to traders from Nigeria where they are used in connection with magic (King 1994). In order to limit the trade and commerce of bushmeat and stop the decline of great ape population, the Korup Project, financed by WWF, is currently trying to develop alternative sources of income for the populations living around the park. The Korup Forest Research Project (funded by US-Aid and the New York Zoological Society) has recently tried to implement a number of measures to prevent poaching in the area.

## Conclusions

In Cameroon, current gorilla and chimpanzee populations can be roughly estimated at about 1,000 and 6,000, respectively. They are subject to hunting and habitat loss due to logging and habitat destruction. In December 1993, a new legislation replaced Article 69 of Bill 81-13 relating to forest, wildlife and fisheries management giving full protection to great apes. Despite this protection, great ape meat is in great demand amongst the local populations because of its taste and alleged therapeutical properties. Great apes are also killed when they raid plantations. In the past, traditional hunting techniques using crossbows and snares had only limited impact on great ape populations. However, since the 1960's the increasing use of firearms and access to ammunition have taken an increasing toll on these species. It must be noted that most hunters do not own the firearm they use. These are provided by upper class city dwellers, who would be expected to know the current wildlife legislation. These people negotiate their markets in the cities and make their requests to local hunters according to the demand (Moamosse 1990). A considerable internal and international illegal traffic in young apes still exists. When young apes are captured, their parents and other group members are killed, further contributing to the decline in numbers. Cameroon is a signatory of CITES but this convention limits international trade only. The national government should take appropriate measures to enforce its legislation and strictly prohibit capture of great apes.

Wildlife agencies suffer acutely from a lack of personnel, communication equipment, vehicles, firearms and ammunition. Consequently, they cannot prevent poaching activities that are going on throughout all social classes with any efficiency. Their relations with local populations are often tense because of the economic interests at stake. In the Dja, a hunter may earn annually between 100,000 and 300,000 CFA Francs (170-520 US\$) (Moamosse 1990).

In southern Cameroon, between 80,000 and 150,000 ha are logged annually. Logging occurs near densely populated areas, mostly around urban centers and along roads. Deforestation reduces areas of gorilla and chimpanzee habitats and facilitates the poachers' access to the richest areas. It is caused mainly by

slash-and-burn cultivation, logging, road development and urbanization. A similar situation prevails in the country's western highlands (MEF 1992).

The survival of gorillas and chimpanzees in Cameroon is dependent upon the willingness of the government to 1) establish and maintain a network of protected areas encompassing the territories where these species are still present, 2) to enforce the policies, legislation and regulations which guarantee the sustainable use of forestry and wildlife resources, and 3) to instigate and promote a participatory approach to local land use and wildlife management.

## Specific Recommendations

### *Dja Wildlife Reserve*

- Provide game wardens with appropriate equipment including: motorbikes, camping gear, uniforms, shoes, firearms and ammunition.
- Develop and implement landscape management and zoning within the reserve.
- Reestablish the ferry-boat, reopen the road between Somalomo and Ekom and establish a control station in Somalomo in order to promote the development of agriculture and ecotourism and alleviate hunting pressure.
- Establish a research center to study and monitor wildlife populations and determine hunting quotas for game species.
- Develop an environmental education public program linked to a health care program.

### *Campo Wildlife Reserve*

- Elaborate a zoning plan including the full protection of Dipikar Island and of the southernmost area of the reserve and establish controlled hunting areas around this zone.
- Develop the tourist potential of easily accessed areas (e.g., the German constructions, the beaches).
- Implement selective logging based on resource inventory and minimal diameter.

### *Mvangame Area*

- Carry out an exhaustive inventory of gorilla populations and of other threatened primates and create a fully protected ecological or wildlife reserve.

### *Douala-Edea Wildlife Reserve*

- Determine the presence of gorillas by means of an appropriate survey.
- Educate the local populations regarding the need to protect the most vulnerable species including chimpanzee, manatee and possibly gorilla.
- Develop fisheries and tourism (beach, ecotourism).



- Increase the number of game wardens and provide them with appropriate land vehicles and motorboats.
- Modify the zoning of the reserve and establish a fully protected core area surrounded by peripheral exploitation zones.

#### Korup National Park

- Continue to support the on-going Korup project in order to develop an alternative economy for the benefit of local populations.

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# A Survey of the Lemurs of Ambatovaky Special Reserve, Madagascar

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Madagascar is regarded as one of the world's prime targets for conservation efforts because of the high level of endemism among most of its faunal groups and the severe human pressure on natural habitats, in particular the extensive slash-and-burn clearance of the rainforests of eastern Madagascar for *tavy* (shifting cultivation). Half of the country's rainforest disappeared in this way between 1950 and 1985, at a rate of more than 1,000 km<sup>2</sup> per year, with the lowest-elevation forest on the flattest ground suffering the greatest losses (Green and Sussman 1990). Most of the rainforest now remaining is in areas of low population density - often on steeper slopes. These rainforests contain the greatest biodiversity on the island (see IUCN/UNEP/WWF 1987).

Ambatovaky Special Reserve is the largest lowland rainforest reserve in Madagascar. It was created by presidential decree in 1956, and out of a total area of 60,050 ha, 51,050 ha (85%) was reported by Nicoll and Langrand (1989) to be in the 'Eastern [floristic] Domain' (equivalent to lowland rainforest), representing the largest discrete area of lowland rainforest within the protected area network. Prior to the survey reported here, virtually nothing was known about the reserve except that satellite images indicated that large areas of forest still existed (G. Green, in Nicoll and Langrand 1989). It appeared to have never been visited by scientists due to its remoteness and difficulty of access, and for similar reasons (as well as lack of money) the government had not been able to assign any forest guards to protect it, at least in recent decades. Moreover, Ambatovaky was a large, unsurveyed gap in the zoogeography of the Madagascan rainforests, since its forests lie part-way between two rainforest areas (also nature reserves) where faunal surveys have been carried out in recent years and for which past records existed (see Fig. 1). However, the extent of lower-elevation Eastern Domain forest is much larger in Ambatovaky than in the mainly mid-altitude forest of 'Sihanaka Forest' and Zahamena Strict Nature Reserve, 70 km to the south (Thompson *et al.* 1987), or than in Marojejy Strict Nature Reserve, 200 km to the north (Safford and Duckworth 1990) where there are only 12,030 ha of Eastern Domain forest (Nicoll and Langrand 1989). Consequently Nicoll and Langrand (1989) listed Ambatovaky as a priority area for a baseline biological survey.

A revised reserve map was compiled for this study, based on

the 1:50,000 topographic maps published by the Institut Géographique National (Paris - Centre à Madagascar) and Foiben-Taosarintanin'i Madagasikara in 1972 and 1977 (which were based on aerial photographs from 1957, checked on the ground between 1969 and 1974), superimposed with the reserve boundary from the 1956 sketch map prepared when the reserve was declared (Direction des Eaux et Forêts files). Figure 2 is based on these sources. The reserve lies between 16°57'S and 16°36'S and between 49°04'E and 49°25'E. The area of the reserve was re-estimated from the new map as approximately 61,500 ha, in very close agreement with the original estimate upon gazettelement. However, ground surveys as part of this study revealed that much of the south-eastern part of the reserve, below 500 m, is now deforested.

The aim of the lemur survey was to compile a species list for the reserve, with particular emphasis on searching for and obtaining information on species considered to be globally threatened by IUCN (Harcourt and Thornback 1990). Investigations were concentrated at two study sites within the Reserve, referred to henceforth as Site 1 and Site 2, and described below.

## Site 1 (centred on 16°51'S, 49°08'E)

This study area was based at a camp about 6 km west of Iampirano village, by the Iampirano river at about 530 m altitude. Surveys took place from 5 February to 1 March 1990. The camp was in a valley bottom in Primary Lowland Rainforest (we follow White's [1983] terms and definitions when referring to forest-types) near the limit of the patches of regenerating and grazed *tavy* which extend up the valley from Iampirano village. The area of detailed studies covered about 6 km<sup>2</sup>. Below about 700 m was Primary Lowland Forest with a high canopy (over 30 m), and in the valley bottoms relatively little undergrowth. Above this altitude, a ridge trail and slopes from about 700 to 950 m were regularly visited and comprised primary Moist Montane Forest with a lower canopy (20-25 m) and more undergrowth; the low starting altitude for this habitat is due to the exposed nature of ridgetops. At about 950 m there was a relatively sudden transition to Sclerophyllous Montane Forest extending to the highest summits in the reserve at approximately 1,100-1,200 m. An extension to an existing trail was

cut by the expedition to a peak just south of the main peak (1,174 m) of the Ambatovaky massif. This Sclerophyllous Montane Forest had a lower canopy of about 10–15 m (down to 4–5 m on the summit) and dense undergrowth, with trees covered in mosses, lichens and epiphytes.

The long climb to the Sclerophyllous Montane Forest area meant that relatively little time was spent in this zone. An altitude of 950 m is relatively low for the start of Sclerophyllous Montane Forest, but in the section of the rainforest belt occupied by Ambatovaky there are no mountains above 1,200 m, and these low summits are, therefore, relatively exposed, so that habitat zones are compressed and found at lower altitudes compared, for example, with higher massifs such as Marojejy (Safford and Duckworth 1990), an example of the 'Massenerhebung effect' (see Whitmore 1984).

#### Site 2 (centred on 16°51'S, 49°16'E)

This study area was based around a camp approximately 6 km north of Amberomanitra, and about 2 km within the southern boundary of the reserve, in an area of *tavy* at about 380 m altitude by the Antsanavavy river. Immediately north of this river was a narrow band of secondary forest fringing primary lowland forest. Surveys took place between 4 and 25 March 1990. The study area comprised Primary Lowland Forest over steep-sided ridges at 450–485 m and narrow valley bottoms at 340–400 m. The valley bottom forests were similar to those at Site 1, although apparently better drained with a somewhat lighter, sandier soil, which was not as swampy and humus-rich. The ridges, although at low altitude, supported forest with a slightly lower canopy (up to 25 m) and considerably more undergrowth than the valley bottoms. All of the threatened lemur species found at this site occurred on these ridges but very few were recorded in the valley bottoms. However, this may have been an observational artefact since the bushy understorey found on the better-lit and more open ridgetops attracted lemurs down from the canopy, making them perhaps more visible/detectable to observers on the ground.

Observer activity was concentrated on a patch of about 4 km<sup>2</sup> at this study area, which comprised about half of the area in this altitudinal range within the reserve south of the Sandrangato river, and a substantial part of the remainder of this zone had already been degraded or cleared of forest. The team was able to work from a dense network of existing trails which provided access to

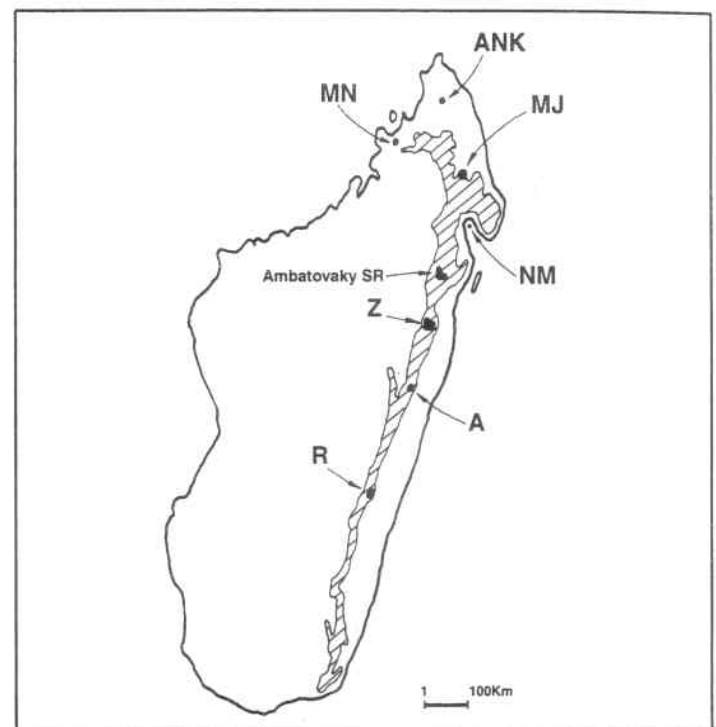


Fig. 1. Madagascar, showing rainforest and important locations mentioned in text. Key. ANK = Ankarana Special Reserve, MJ = Marojejy Strict Nature Reserve, MN = Manongarivo Special Reserve, NM = Nosy Mangabe Special Reserve, R = Ranomafana National Park, Z = Zahamana Strict Nature Reserve, SR = Special Reserve. The shaded part is the area of remaining rain forest (after Green and Sussman 1990).

isolated areas of active *tavy*.

#### Methods

No rigorous quantitative survey work was undertaken on lemurs, given the short duration of the study and the multiple faunal groups investigated. All incidental, diurnal observations of lemurs were recorded while carrying out other aspects of the faunal surveys. All members of the team contributed records, gathered during 24 days of fieldwork at Site 1 and 22 days at Site 2. When lemurs were encountered, the following information was noted (where possible): date, time, locality, size of group, age/sex of individuals, activity, reaction to human presence, identity of food items, and any other interesting behaviour.

Night-torching was carried out on some nights specifically to locate nocturnal lemurs. While walking along trails, head-torches were used to locate eye-shine and the animal would then be lit with a more powerful torch and watched with binoculars whenever possible. Some night-torching followed a structured procedure: the same path was used for outward and return journeys from the camp; a slow, constant pace of walking was attempted; and any time spent stationary and watching each lemur was deducted from 'total time spent night-torching', along with a 30-minute period of rest in the dark at the end of the outward journey (to allow animal activity along the path to recover from observer disturbance - loop trails were rarely available for walking).

All signs of hunting and trapping of lemurs were noted and discussions with the local (Betsimisaraka) people provided information on the animals (including local names) and the extent of

Table 1. Frequencies of different group sizes of lemurs encountered in the Ambatovaky Special Reserve, Madagascar<sup>1</sup>.

| Species                    | Group size |    |    |   |   | Total encounters | Mean group size |
|----------------------------|------------|----|----|---|---|------------------|-----------------|
|                            | 1          | 2  | 3  | 4 | 5 |                  |                 |
| <i>Cheirogaleus major</i>  | 13         |    |    |   |   | 13               | 1.0             |
| <i>Microcebus rufus</i>    | 7          | 1  |    |   |   | 8                | 1.1             |
| <i>Avahi laniger</i>       | 3          | 2  |    |   |   | 5                | 1.4             |
| <i>Indri indri</i>         | 4          | 11 | 15 | 3 | 1 | 34               | 2.6             |
| <i>Propithecus diadema</i> |            | 7  | 2  | 4 |   | 13               | 2.8             |
| <i>Haplemys griseus</i>    |            | 4  |    |   | 1 | 5                | 2.6             |
| <i>Lemur fulvus</i>        |            |    | 4  |   |   | 4                | 3.0             |
| <i>Lemur rufiventer</i>    | 1          | 13 | 2  |   |   | 16               | 2.1             |
| <i>Varecia variegata</i>   | 15         | 46 | 14 | 9 |   | 84               | 2.2             |

<sup>1</sup>Duplication (repeated encounters with the same group) has not been taken into account in the table. In a few cases group size will have been underestimated by missing some group members, but the table excludes encounters where the group size was known to be larger than the number actually counted.



hunting and trapping, as well as any taboos with respect to lemurs.

## Results - Species Accounts

IUCN threat status (Harcourt and Thornback 1990) is given after the species' name, where relevant.

### *Cheirogaleus major*, Greater Dwarf Lemur

**Status in the Reserve:** This was the second-most common nocturnal lemur seen. *Cheirogaleus* was positively identified 14 times by night-torching. Its presence at Site 2, where little night-torching was done, was not confirmed. All were solitary individuals (Table 1) in Primary Lowland Rainforest (550-600 m). The encounter rate (on a limited sample) appeared almost identical to that of another survey (earlier in the season, using the same methods) at another rainforest site at about double the altitude of Ambatovaky (Analamazaotra Special Reserve, see Table 2).

**Reaction to humans:** One was watched feeding 6.5 m above the observer, under powerful illumination, and did not react to the observer; all other observations were at longer range and no disturbance of behaviour was noted.

**Notes on biology:** Nine out of 11 individuals were high in the forest canopy and two were in the mid-storey (at least one of these in the crown of a sub-canopy tree), at heights of 8-25 m above the ground. One *Cheirogaleus* was observed feeding on a large, stocky insect, probably a cicada, and another fed on a similar-sized insect or fruit, in both cases by holding the food item with both hands whilst perched on its hind legs on a horizontal branch. The condition of the base of the tail was noted in three animals - on all three the hairless pink underside looked stout and swollen, as if packed with fat.

### *Microcebus rufus*, Brown mouse lemur

**Status in the Reserve:** Night-torching revealed *Microcebus* to be reasonably common in bushy secondary growth in old tavy clearings in Primary Lowland Rainforest at both sites, venturing up to 20 m away from the forest edge. Animals were watched climbing about in wild ginger *Aframomum* stands and also on *Harungana madagascariensis* saplings.

**Reaction to humans:** On being 'torched', the animal would freeze initially then slowly turn away, climb down the plant and jump to another stem away from the observer. In one case the observer got within touching distance of a torch-dazzled animal, when the brown upperparts, creamy white underside and narrow,

black eye-ring were noted.

**Notes on biology:** Most animals were solitary (Table 1), and were recorded at 1-3 m above the ground.

### *Avahi laniger*, Woolly lemur

Vulnerable, Betsimisaraka name: *ampongy*

**Status in the Reserve:** Recorded at both sites on a total of seven occasions by night-torching. All were in Primary Lowland Rainforest at 300-550 m. The encounter rate (on a limited sample) appeared higher than that of another survey earlier in the season at another rainforest site (Analamazaotra Special Reserve), at about double the altitude of Ambatovaky (see Table 2).

**Notes on biology:** This species was found clinging to vertical stems in the shrub layer and mid-storey vegetation. Two pairs and three individuals were noted (Table 1); two of the three solitary animals were moving whereas both pairs were resting. One pair rested with heads 15-30 cm apart whilst the other pair appeared to be in bodily contact; both were 2-3 m above ground.

### *Indri indri*, Indri

Endangered, Betsimisaraka name: *babakoto*

**Status in the Reserve:** 'Song' was heard daily at both sites, with up to five different groups heard per day at Site 1 and four per day at Site 2. Records came from Primary Lowland Forest at 350-850 m.

**Reaction to humans:** At both sites *Indri* almost invariably alarm-barked at humans when encountered, likewise lip-smacking followed by an exhalation through the open mouth was common. At Site 1 they rarely retreated, even when an observer was directly below them, but at Site 2 instances of immediate retreat/dispersal when a human appeared were common - such groups would then stop to watch the observer and eventually relax, although remaining very watchful. However, at both sites an observer could sometimes approach closely to 10-15 m range, although unlike all other diurnal lemur species at Ambatovaky, there were no instances of *Indri* approaching observers in apparent curiosity. No *fady* (taboo) against killing *Indri* was reported at Site 2, and a dead, trapped individual was seen there.

**Notes on biology:** Groups ranged in size from single individuals to five animals (average group size was 2.6, see Table 1). Three different groups of three comprised an adult pair and one young of approximately half-to-two-thirds adult size, and one of a group of four was also "not fully grown". In these groups, the young one was carried on the back of an adult. The individuals in a group of *Indri* were usually in different trees, often quite dispersed with up to 50 m or more between animals. *Indri* would often join in alarm calls started by other lemurs, especially *Varecia*. Self-grooming was noted on three occasions as *Indri* scratched ears, muzzle and chin with a hind foot or licked a fore leg. When feeding, branches were pulled closer to the body and the leaves inspected; red, young leaves were picked off with the mouth.

The *Indri* of Ambatovaky were blackish overall, being whitish-grey only on the flanks, hindquarters and chest. Some brown fur was noted on the shoulders and back of the neck above the very prominent black dorsal stripe.

**Records outside the Reserve:** A total of about 11 different groups were heard while the expedition was traversing the c.16 km of mostly unbroken Primary Lowland Forest at 400-500 m between

Table 2. Encounter rates for two nocturnal lemurs in two evergreen forest reserves in eastern Madagascar.<sup>1</sup>

| Species                   | Data                       | Ambatovaky <sup>2</sup> |              | Analamazaotra <sup>2</sup> |  |
|---------------------------|----------------------------|-------------------------|--------------|----------------------------|--|
|                           |                            | Feb-Mar 1990            | Oct-Nov 1988 |                            |  |
| <i>Cheirogaleus major</i> | Minutes night-torching     | 446                     | 390          |                            |  |
|                           | Number of animals seen     | 10                      | 9            |                            |  |
|                           | Encounter rate (animals/h) | 1.35                    | 1.38         |                            |  |
| <i>Avahi laniger</i>      | Minutes night-torching     | 446                     | 390          |                            |  |
|                           | Number of animals seen     | 4                       | 2            |                            |  |
|                           | Encounter rate (animals/h) | 0.54                    | 0.31         |                            |  |

<sup>1</sup> Table only includes data gathered following controlled night-torching procedure described in the section on methods.

<sup>2</sup> This study

<sup>3</sup> Data from Safford and Duckworth (1990: 167-168).

Andratambe and Antara on 4 February, and at least five groups were heard in the c.9 km walked between Antara and Iampirano on the reserve boundary on 5 February. Between Site 2 and Vatomora on 16 March, an individual was seen in a small, almost isolated stand of trees in a relatively open landscape where the original forest had been severely fragmented by *tavy*.

*Propithecus diadema diadema*, Diademed sifaka

Endangered, Betsimisaraka name: *simpona*

**Status in the Reserve:** This subspecies was recorded at both sites at 400-800 m, with two groups at Site 1 and two to four groups at Site 2.

**Reaction to humans:** Animals at both sites showed little fear of humans. Although they nearly always gave the sneeze-like 'viff' alarm call initially, followed by a sucking noise, after 5-15 minutes they would relax and resume other activities or move off. In six out of 13 encounters, *Propithecus* moved closer to the observer (down to 4 m) and remained in the immediate area for periods exceeding an hour in four cases and 30 minutes in another three cases. In a male-female pair, the male approached closer to the observer on both occasions where this was recorded.

**Notes on biology:** Groups of 2-4 were recorded (average 2.8 animals, see Table 1). Two individuals in a group of four were watched playing for over 20 minutes and were presumably fully grown young - they had brown muzzles and no white pelage on their faces, unlike the presumed adults with them. No infants or sub-adult-sized animals were seen. Inter-individual distance was usually 5-20 m, but could be up to 50 m. Other vocalizations included: a rather lowing growl-purr when quite close to humans (c.10 m); a quiet clicking; and a series of loud, raucous, growling roars accompanied by looking around up at the canopy and sky (presumably an alarm call against bird predators [see Goodman 1994]).

As with *Indri*, *Propithecus* was selective about the leaves it ate. Feeding high in the canopy on young, red leaves and clusters of fruit, *Propithecus* moved lower to rest and digest. Animals often self-groomed while resting and were much 'troubled' by horseflies (Diptera: Tabanidae) which were common in the forest at both sites due to the practise of cattle-rearing in abandoned *tavy* clearings. The lemurs warded off the flies by frequently shaking their hands and feet and peering around their body, looking for settling flies.

The local people consider *Propithecus* to be the dominant lemur in any inter-specific interactions, even over the larger *Indri*, but no interactions with other species were noted during the survey.

*Daubentonia madagascariensis*, Aye-aye

Endangered, Betsimisaraka name: *hay-hay*

**Status in the Reserve:** No animals were seen, but feeding traces of two types indicated the presence of this species, at both sites.

1.Characteristically gnawed nuts of *Canarium* sp. (Burseraceae; a large canopy tree, called *aramy* locally, with green fruit and large, hard nuts) were found commonly at both sites in Primary Lowland Forest at 400-600 m, very similar to illustrations and descriptions of damage to *Canarium* nuts gnawed by captive aye-ayes (Iwano and Iwakawa 1988) and to presumed damage to such nuts by wild

aye-ayes (Duckworth 1990). Aye-ayes have been watched feeding on *Canarium* nuts in the wild at Ankarana Special Reserve (Hawkins *et al.* 1990), and it seems certain that aye-ayes were involved at Ambatovaky. The damage was reported by local people to be made by rodents (*antsangy*: *Eliurus* spp. and/or *Nesomys rufus*) but the incisor-groove width (1-3 mm) was too large for any Malagasy rainforest rodent.

2.Characteristic pits gnawed into a dead tree trunk at Site 2 in Primary Lowland Forest at 400 m - similar to known aye-aye damage at Nosy Mangabe Special Reserve and at Parc Tsimbazaza in Antananarivo (MIE pers. obs.). The upright tree trunk, with a diameter at breast height of 12-15 cm, had snapped off at 2.5 m above ground, with about 2 m of the fallen trunk lying adjacent on the ground. Both the free-standing and the fallen wood was solid but dry-rotted and light, and riddled with the tunnels of large, wood-boring grubs. At least ten pits had been gnawed into the wood surface (one pit measured 4 cm long by 2.5 cm wide by 2 cm deep), with numerous, large incisor-grooves visible (their apparent width was about 3.5 mm, but the fibrous, friable wood did not leave a clear record of the true incisor-width). This feeding technique is well known for aye-ayes, and no other animal is known in Madagascar which could leave feeding traces such as those described here.

Examples of both types of feeding traces have been deposited in the Mammal Section of the Natural History Museum (London). The closest documented records of aye-aye are probably those from the Mananara area to the north-east and the Mahambo area to the south-east (IUCN/UNEP/WWF 1987). Perhaps unusually, local people at Site 2 said that the aye-aye was not a *fady* animal, and that it was not necessary to kill it if one was found.

**Records outside the Reserve:** Gnawed *Canarium* nuts, similar to those described above, were found in excellent Primary Lowland Forest at 400-500 m at several different locations along the main 16-km-path between Andratambe and Antara on 4 February.

*Haplemur griseus griseus*, Grey bamboo lemur

Rare, Betsimisaraka name: *bokombola*

**Status in the Reserve:** Animals were found at 400-1000 m in Primary Lowland Forest, Moist Montane Forest and Sclerophyllous Montane Forest, making this the most widespread lemur species in the reserve, although not the most frequently recorded. At Site 1 there were only three sightings, of one to two individuals. It was commoner at Site 2 where groups of two to five were sighted six times (mean group size, where all individuals were definitely counted, was 2.6; see Table 1). Compared with Marojejy Strict Nature Reserve and with Analamazaotra Special Reserve, numbers and densities seemed low (Duckworth 1990; MIE pers. obs.), perhaps due to the apparent rarity of bamboo at Ambatovaky compared to these sites (only slender, clambering species were seen at Ambatovaky, and then only rarely).

**Reaction to humans:** Encounters with *Haplemur* began with characteristic low-intensity alarm calls, being similar to alarm-grunts given by *Lemur fulvus* but shorter and higher-pitched. Other vocalizations included quiet, purring grunts and an explosive yowl produced with a wide open mouth which appears to signify a higher level of alarm or fear than the grunting call (MIE pers. obs.). The tail would be swished back and forth whilst giving alarm calls. At Site 1 an individual and a pair approached the observer, but a pair



Fig. 2. Location of Ambatovaky Special Reserve, eastern Madagascar. The shaded area is the Ambatovaky Special Reserve. The limits to the Reserve on the western boundary (dashed line) were established prior to a proper mapping of the area and do not correspond to the topography. The dotted lines are the main paths used for the surveys. 1 = Site 1 and 2 = Site 2 (see text). Key. F = Fotsialanana, Amt = Ambatabe, Amb = Amberomanitra, And = Andratambé, Ant = Antara, Iam = Iamparino, Ran = Ranomena II, Vat = Vatomora.

in Sclerophyllous Forest were more circumspect, possibly because a pair of red-bellied lemurs were nearby. At Site 2, animals were more fearful: either retreating if encountered closely, with much 'yowling' and grunting, or staying their ground only if the observer was detected at long range (40-50 m away).

**Notes on biology:** No infants were seen, although the birth season appears to be January and February (IUCN/UNEP/WWF 1987). A group were watched unawares as they ate leaves of a slender, clambering bamboo (stem diameter 0.5-1 cm) in the shrub layer of Primary Lowland Forest, moving around on the ground and up to 2 m above; a similar bamboo species was in the vicinity of at least two other groups when sighted. A group at Site 2 grunted at the observer for ten minutes until two nearby ruffed lemurs *Varecia varecia* made a loud roaring call, whereupon the group immediately turned to face the calling and fell silent, and then silently and rapidly descended to the shrub layer, perhaps to avoid the ruffed lemurs.

#### *Hapalemur* sp., Bamboo lemur

Subfossil remains and nineteenth-century specimen records of the broad-nosed bamboo lemur *Hapalemur simus* are widely, if rarely, distributed in north, north-west, east and central Madagascar. Although presently the species is known only from one small area east of Fianarantsoa in east-central Madagascar, there is a post-1870 record from near Mananara (IUCN/UNEP/WWF 1987), 85 km north-east of Ambatovaky.

Discussions with local people indicated that there existed until recently a lemur which fed on giant bamboo along the Sandrangato and/or Marimbona rivers, known as *alakoto* or *halokoto*, and usually described as larger than the grey bamboo lemur. However, the details of its size and the rest of its appearance, habits, and present status were vague and sometimes contradictory, no doubt due to our inability to converse freely in Malagasy. Giant bamboo, upon which broad-nosed bamboo lemur is apparently dependent (IUCN/UNEP/WWF 1987), did not occur in our two study sites but does still exist in small stands along the Marimbona and Sandrangato

rivers, for example, near Vatomora where all the original forest vegetation has been cleared from the facing hillsides except for the riverine stands of giant bamboo, and where it is much used for house construction and water vessels. Reports that giant bamboo is a 'secondary' or 'successional' species or species-group, originally confined to naturally disturbed areas such as the banks of large rivers (IUCN/UNEP/WWF 1987), appear to be confirmed by observations at Ambatovaky and at Marojejy (Safford and Duckworth 1990; MIE pers. obs.) and Ranomafana (PMT pers. obs.). The flat land, rich soils and natural lines of communication have probably made larger river valleys a natural focus for human exploitation, habitat destruction, and disturbance ever since Madagascar was first settled, thus providing a convincing explanation for the decline of broad-nosed bamboo lemurs (IUCN/UNEP/WWF 1987).

Circumstantial evidence indicates, therefore, that further searches for broad-nosed bamboo lemurs might not be worthless or in vain. River-side areas which have yet to be explored and which appear to be very thinly populated and to have natural forest up to their banks include (1) the Marimbona river north of the trail between Andratambé and Antara, an area where an extension to the reserve has been suggested (Thompson and Evans 1991); (2) the Marimbona river upstream of Antara (reserve boundary); and (3) the Sandrangato river north and west of Site 2 (inside the reserve). The identity of the giant bamboo at Ambatovaky is not known; broad-nosed bamboo lemurs are dependent on *Cephalostachium viguieri* at its only known locality.

#### *Lemur fulvus*, Brown Lemur

Betsimisarakana name: *varikosy*

**Status in the Reserve:** This species' status was surprising. Firstly, this was the rarest diurnal lemur: only one group was sighted and a different one was heard (one time each) at Site 1, and there were three sightings of one group at Site 2 (it was also heard several times at night during a full moon). All records came from Primary Lowland Rainforest at 400-750 m. This species is the commonest diurnal lemur at several other sites in the eastern rainforest such as Zahamena, Analamazaotra and Marojejy (Thompson *et al.* 1987; Safford and Duckworth 1990). Secondly, all individuals showed characteristics of the nominate subspecies, which was perhaps unexpected given the published distribution of the races (Tattersall 1982; Harcourt and Thornback 1990). There is a population of *L. f. fulvus* north and east of the Betsiboka river in western Madagascar from south of Ambato-Boeny through Analalava and Manongarivo Special Reserve to a site east of the Galoka Mountains or south of Beramanja (Tattersall 1982; Quansah 1988; N. Quansah pers. comm.). Isolated from these animals by the now deforested central highlands is a second population of the nominate subspecies in eastern Madagascar (the limits of which are not known), which has been recorded at Analamazaotra Special Reserve and south of Lac Alaotra (Tattersall 1982), c.190 km from Ambatovaky. *L. f. albifrons* is claimed to occur in the forests between the eastern population of *L. f. fulvus* and Ambatovaky - for example at Zahamena Strict Nature Reserve (Tattersall 1982). However, a more recent survey of Zahamena recorded animals showing the characteristics of *L. f. fulvus* (Thompson *et al.* 1987; PMT pers. obs.). In addition, there are specimen records of *L. f. albifrons* from along the north-east coast of Madagascar south to



Toamasina (i.e., from both north and south of Ambatovaky), suggesting that these two subspecies formerly met along an extensive contact zone, running north of and inland from Toamasina.

The following composite description of the Ambatovaky animals is based on the records of all observers: males had a black face and ears, no white patches above the eyes, cheeks and side of the muzzle were white, upper body was grey-brown being especially grey on the haunches, along the dorsal line there was a dark brown stripe, chin and throat were beige, and undersides were pale; the fur on the hands, feet, the base of the tail and the back of the neck was more rufous. Females were similar, except that the face was greyer, the dorsal stripe less obvious, and white spots were present by the eyes.

Hunting and trapping pressure cannot explain the scarcity of this species since this pressure was observed to be relatively low and other diurnal lemurs were common and approachable. The high density of ruffed lemurs in Ambatovaky may contribute to the scarcity of the brown lemur (through competition?), since we do not know of any sites where both are common: brown lemurs are common at Marojejy, where ruffed lemurs are inexplicably absent (Duckworth 1990) and, likewise, brown lemurs are common in Zahamena where ruffed lemurs are scarce; in fact the latter were not recorded during an extensive survey in 1985 (Thompson *et al.* 1987).

**Reaction to humans:** Upon detecting the observer, the group at Site 1, approached and spent 17 minutes calling and mobbing at close range (3 m) before moving away, the male leading; behaviour suggesting very little experience of humans or hunting. At Site 2 one group moved off silently when encountering humans, but others continued to groom or forage warily before quietly moving off.

**Notes on biology:** Group size was three in all sightings (Table 1). The group at Site 1 (two males, one female) was feeding on the pale orange, cherry-like drupes of a ridgetop tree. At Site 1 a group was heard 'throttle-calling' between 20h30 and 21h30 on a moonlit night in forest near Iampirano.

#### *Lemur rubriventer*, Red-bellied lemur

Vulnerable, Betsimisaraka name: *halomena*

**Status in the Reserve:** Not uncommon at both sites at 400-950 m. It was recorded six times at Site 1 and ten times at Site 2. We were surprised to find this species as low as 400 m since it appears to be generally confined to higher altitudes in Madagascar at present (Tattersall 1982). At Marojejy in 1988 it was only observed above 900 m (Duckworth 1990) and far from villages, but local people reported that 12-16 years earlier it could be found down to 300 m in dense Primary Lowland Forest (Durbin 1990), implying that human disturbance of habitat and/or hunting had caused its disappearance at lower altitudes, from where it was not excluded purely on ecological grounds. Hence this species' relative abundance at low altitude in Ambatovaky might indicate an unusually low level of hunting pressure and human disturbance.

**Reaction to humans:** At Site 1, animals showed little fear, preferring to mob observers (even when the latter were directly below them) rather than flee. At Site 2, this species was much more wary, fleeing to 40-50 m range, or mobbing from c.50 m range and fleeing if approached closer.

**Notes on biology:** This species was usually seen in twos (all being male-female pairs, except for two males on one occasion).

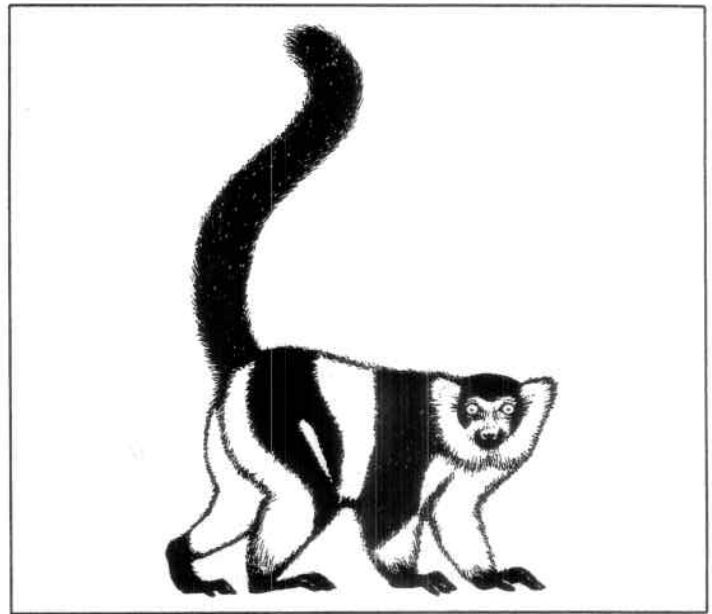


Fig. 3. Ruffed lemur, *Varecia variegata variegata*, from Ambatovaky Special Reserve Madagascar, resembling 'type C' morph of Tattersall (1982) and Harcourt and Thornback (1990). (Illustration: Stephen D. Nash)

On three occasions a pair were with young (Table 1). One pair had twins, only previously noted in captivity (Harcourt and Thornback 1990). When mobbing humans, a high-pitched grunt ending in a high squeak was used, easily separable from the squeak-less grunting of brown lemur.

Apparent interspecific food competition was noted at Site 1 on 23 February. A male-female pair of red-bellied lemurs were feeding on the fruit of a palm, *Vonitra* sp. (Arecaceae), in the mid-storey of the forest, cracking open the fruit on one side of the jaw and then chewing and eating the kernel. After about 10 minutes a pair of ruffed lemurs approached the palms directly and fairly rapidly, possibly first attracted by the red-bellied lemur's quiet calls, and giving low growl-calls. The red-bellied lemurs immediately stopped feeding and hurriedly departed, scrambling tree-to-tree through the sub-canopy and sometimes looking back at the approaching ruffed lemurs. At one point the red-bellied lemurs made a long downward jump spanning up to 3 m horizontal distance or more, remarkable not least because the female was carrying her 25%-adult-size infant cross-ways across her back. She only attempted the jump after much hesitation and rapid intention movements or feints, suggesting that she was being forced into doing something she would not normally attempt. The ruffed lemurs meanwhile arrived at the palm and immediately began to feed on the nuts.

#### *Lepilemur* sp., Sportive lemur

Insufficiently known

Local people reported that a lemur called *fitsidika* occurred in the reserve, but that it was difficult to see and/or rare. This name is used for *Lepilemur* by the Betsimisaraka people at Marojejy (Durbin 1990) and also by Tsimihety people at Manongarivo (Quansah 1988); the word comes from *tsidika* - to watch (Durbin 1990) - and possibly describes this species' characteristic habit of sometimes sitting at the entrance to its tree-hole roost during the day, watching the outside world. Its presence in Ambatovaky is

expected (see maps in Tattersall 1982 and in Harcourt and Thornback 1990). The most likely species is *L. mustelinus*.

#### *Varecia variegata variegata*, Ruffed lemur

Endangered, Betsimisaraka name: *varikandra*

**Status in the Reserve:** This subspecies was the most commonly encountered lemur, being recorded in Primary Lowland Forest at 350–800 m with up to four to five groups heard or seen daily at both sites (84 sightings, see Table 1).

The *Varecia* in Ambatovaky resemble the form described by Tattersall (1982) and Harcourt and Thornback (1990) as 'type C', but with consistent, minor differences. Ambatovaky *Varecia* were mainly black, except for white on the ears, throat and cheek-hair tufts; white hairs on the muzzle below the eyes; a transverse white band extending across the back and flanks behind the shoulders; a white band across the rump, extending down the posterior aspect of the thighs to the lateral aspect of the lower legs; white patches on the outer, distal portion of the forearms; a large brown 'saddle' behind the white band extending over the lower back on to the hindquarters (see Fig. 3). The key difference is the brown 'saddle', ranging from 'café-au-lait' to chestnut to blackish. Although the shoulders were very dark, verging on black in most individuals seen at Site 1, others seen at Site 2 had brown shoulders. Also, at least two animals had indistinct white rings on the distal portion of the tail, also noted on 'type C' individuals on Nosy Mangabe in 1988 (MIE pers. obs.).

It is worth noting that comparatively little variation in markings was seen within the Ambatovaky populations, compared with the great variety of patterns seen in wild-caught, captive animals kept at Ivoloia (near Toamasina). These *Varecia* are thought to have been collected in the Toamasina region (A. Katz pers. comm.). If pelage pattern really is fixed for a particular locality, and if the geographic distribution of pelage patterns can be determined, this would allow original localities to be identified for the confiscated wild animals currently used in breeding programmes.

**Reaction to humans:** At both sites, animals showed little fear of humans, although animals at Site 2 tended to bark (in alarm?) at observers more than at Site 1. No instances of immediate and obvious retreat from humans were noted at either site, and in some instances animals approached observers (to c.10 m) in apparent curiosity, suggesting little direct hunting.

**Notes on biology:** *Varecia* was found to be active throughout the morning and from 15h00 until dusk. Most animals were in groups of two, presumably male-female pairs, and five of the groups (overall, at both sites) included one or two young, which were approximately two-thirds of adult size. Most observations were of animals moving swiftly through the canopy or resting there, when much self-grooming occurred. *Varecia* used a hind foot to scratch the ears, muzzle and chin. Considerable attention was paid to the hands and feet, opening out the digits to lick between them. Allogrooming was noted on three occasions, where one animal would initiate by pulling another closer to be able to reach the head; grooming would alternate between partners or become mutual. *Varecia* at rest would lie stretched on their front on horizontal branches (chin flat on branch) or recline against another branch on their back, with dangling limbs and tail.

The nine observations of feeding all concerned green fruit: a

palm *Vonitra* (Arecaceae) plus the fruit of two to four other unidentified trees or lianes. They were also reported by local people to feed on the fruit of *aramy* (*Canarium* sp., see account for aye-aye above) and the fruit of the *voandrozana* tree (literally 'palm nuts', but the green fruit pointed out to MIE as having this name, while resembling palm-nuts, came from a dicotyledonous tree). A pair revisited a fruiting liane in the canopy at Site 1 every few days, obviously harvesting the fruit as they ripened. One in a *Ravenala madagascariensis* inspected the fruit but did not try it, instead appearing to drink from the base of a frond.

Possible feeding dominance over *Lemur rubriventer* was noted (*q.v.*) and the species' presence possibly caused avoidance behaviour in *Haplemur griseus* (*q.v.*). Despite this species' large canines and size, local people said that it did not use these in encounters with other species, and ruffed lemurs were seen resting immediately adjacent to both indri and diademed sifaka without interaction.

The presence of two raptors, the Madagascar harrier-hawk (*Polyboroides radiatus*) and Henst's goshawk (*Accipiter henstii*), elicited much alarm barking - suggesting that predation by raptors occurs, or occurred (Goodman 1994).

## Discussion

Ambatovaky Special Reserve represents an important refuge for lemurs and considerable populations exist there. Ten species were confirmed in the reserve: nine were observed by the expedition, and the presence of aye-aye can be inferred from distinctive feeding traces. In addition, the presence of a *Lepilemur* sp. was reliably reported by local people (making 11 species). There is a fair chance that two more lemur species may be discovered within the reserve, given more fieldwork: the very rare hairy-eared dwarf lemur *Allocebus trichotis* was recently discovered in lowland rainforest near Mananara (Meier and Albignac 1989), only 85 km to the north-east, and the fork-marked dwarf lemur *Phaner furcifer* occurs in rainforest less than 200 km to the north and south of Ambatovaky (Mittermeier *et al.* 1992). There is also a remote possibility that *Haplemur simus* may occur in the reserve.

Eight of the 11 species are considered to be globally threatened with extinction by IUCN (Harcourt and Thornback 1990), including the 'Endangered' indri and aye-aye. Although no quantitative assessment of lemur population densities was possible, the team's comparative experience of lemurs in at least eight other rainforest sites in Madagascar, plus reference to published density figures (in IUCN/UNEP/WWF 1987), suggested that all of the threatened species observed were present at high densities, except for grey bamboo lemurs which seemed to be at a relatively low density compared to some other sites (where secondary/degraded, bamboo-rich habitat is more common).

At Site 1, all diurnal lemur species were remarkably tolerant of humans, tending to approach and mob observers at close range or to simply ignore them. Hunting pressure on lemurs and other animals in this area was low and was a lesser threat than forest clearance. The trails were simple through-routes and did not have the widespread, anastomosing pattern characteristic of heavily hunted areas. Only one (inactive) lemur trap was found and none of the few people encountered were carrying hunting equipment or were accompanied by dogs. However, free-ranging cattle in

abandoned agricultural clearings were hindering the regrowth of forest in these areas. Local people also collected plants and wild honey from the forest.

At Site 2, some diurnal species (diademed sifaka and ruffed lemur) appeared tolerant and little afraid of humans, although not to the degree shown at Site 1. Some other species, however (indri, grey bamboo lemur, brown lemur and notably red-bellied lemur) showed higher levels of alarm at human presence. Hunting pressure was relatively high in the area. Each ridge trail had a number of lemur traps of typical design, with 1-5 per km of trails, although most appeared to be inactive at the time of the survey. However, there appeared to be no *fady* on killing any lemur species here, and one indri was seen to be trapped and killed, and a diademed sifaka was reported to have been trapped during our visit. Hunting with dogs and catapults for lemurs, as well as pigs, tenrecs and birds, was observed on several occasions. This hunting pressure resulted from the much higher human population density bordering the study area compared with Site 1. Despite the higher hunting pressure and human population density, and an extensive and anastomosing path system, lemur species overall did not occur at lower density than at Site 1 (perhaps even at higher densities for some species). Hence the hunting (which appears to be for subsistence only, and not for commercial reasons) may be occurring at a sustainable level for the moment.

However, a growing human population and a change to the use of more powerful weapons than sling-shots could change this situation, for instance through the development of unregulated commercial hunting with hired guns, as has occurred at Marojejy (Safford and Duckworth 1990). At Site 2 continuing deforestation already threatens a key area of Primary Lowland Forest with a notably diverse and dense lemur population, including some species at lower altitudes than in most of their ranges. Cattle, which were free-ranged in areas of abandoned *tavy*, did not penetrate more than 50 m into primary forest at this study site, but some areas of *tavy* (holding cattle) were found well within the forest on the slopes by the Sandrangato river. During the survey, all of the active *tavy* in this part of the reserve were being used for growing hill rice and maize. No tree crops appeared to have been planted, and buildings were only occupied during the growing season, these perhaps being indications of very recent, 'pioneer' invasion of the area by humans.

The recently published action plan for the conservation of Madagascar's lemurs during the period 1993-1999 (Mittermeier *et al.* 1992) lists Ambatovaky as one of 12 protected areas which are of the highest priority for the immediate establishment of programs for conservation action. The plan identifies hairy-eared dwarf lemur, aye-aye, indri, diademed sifaka, ruffed lemur, and fork-marked dwarf lemur as the taxa of highest priority for any species-directed actions within the reserve, and indicates that US\$195,000 will be needed to support lemur conservation there. Specifically, \$15,000 is needed for immediate, more detailed surveys of the population sizes and trends of lemurs in the reserve and the status of its forests, \$110,000 for the establishment and running of a reserve headquarters, and \$70,000 to support long-term studies there (\$10,000 per year). However, the appropriate funding has not yet been found for this program, and the reserve is not so far included in Madagascar's 'Environment Program 1', the first five-year stage of a 15-20-year National Environmental

Action Plan (Mittermeier *et al.* 1992).

The reserve is highly deserving of preferential treatment, however, since it is the largest lowland rainforest reserve in Madagascar, with all that this entails in terms of supporting the maximum diversity of viable populations of animals and plants at all trophic levels. Our relatively brief and 'shallow' inventory also discovered at least 11 vertebrate taxa new to science (a shrew-tenrec, *Microgale*, plus ten reptiles and amphibians), as well as the most diverse herpetofaunal community yet found in Madagascar (86 species), and seven globally threatened birds (Evans and Thompson 1992) including several extremely rare species such as Madagascar serpent-eagle (Raxworthy and Colston 1992), red-tailed newtonia (Evans 1991) and white-breasted mesite (Evans and Raxworthy in prep.).

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## Conservation of Lemurs in Ambohitantely Special Reserve, Madagascar

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The Ambohitantely Special Reserve represents one of the few surviving fragments of native forest on the Central Plateau of Madagascar (Battistini and Verin 1972; Nicoll and Langrand 1989). It is situated about 130 km north-west of Antananarivo in Antananarivo Province (Fig. 1), and lies between 1448 and 1662 m altitude at latitude 18° 04'-18° 14' S, and longitude 47° 12'-47° 20' E. Ambohitantely covers 5,600 ha but most of this area comprises plantations and grassland, and only some 1,700 ha are native forest (Nicoll and Langrand 1989). This forest may be under threat. Cattle have been reported in the reserve for many years and human induced savannah fires continue to diminish the remnant forest cover (Bastian 1964; Nicoll and Langrand 1989). Very little is known of the fauna of this threatened reserve.

Between August 1988 and March 1990, ten visits were made to the largest remaining forest block in Ambohitantely. During a total of 36 days, diurnal and nocturnal walks were made randomly within the reserve to survey the primate fauna. At night, torches and headlamps were used to detect nocturnal lemurs by eye-shine.

Three species of lemur were encountered in the reserve. Two troops of brown lemur, *Eulemur* (= *Lemur*) *fulvus fulvus*, were observed during the daytime. One troop of five individuals was encountered in the north-west of the forest in November 1988. The second troop comprised more than seven individuals and was seen in the south of the forest in October 1989. Given the time interval between observations, this may have been the same troop observed twice. Brown lemurs are usually very vocal, probably using their call to maintain distance between coexisting troops (Harrington 1975). However, troops were never heard calling in Ambohitantely. This may be due to a low density of this lemur in the reserve. In other parts of Madagascar, population densities of *E. f. fulvus* have been estimated at 40-170 individuals per km<sup>2</sup> (see Harcourt and Thornback 1990). Although we have insufficient data to calculate total numbers in Ambohitantely, the population would appear to be lower than at any other study site. *E. f. fulvus* has a wide range in eastern and western forests, but it is considered "Rare" by IUCN (Harcourt and Thornback 1990).

Solitary individuals of the mouse lemur, *Microcebus rufus*, were frequently observed at night at the forest edge. This species is widespread in eastern forests and is frequently encountered in sec-

ondary vegetation, and is probably one of the least threatened lemurs (Harcourt and Thornback 1990).

The nocturnal woolly lemur, *Avahi laniger laniger*, was recorded on the forest edge as well as deep within the reserve. This subspecies is considered "Vulnerable" (Harcourt and Thornback 1990). Solitary individuals were usually recorded, although, in October 1989, one pair was found during the daytime roosting in a tree with their infant. Although *Avahi laniger laniger* is generally restricted to eastern rain forests, fossil evidence indicates that it formerly occupied forest on the Central Plateau (Tattersall 1982). The animals at Ambohitantely may represent a relict population.

A preliminary survey of Ambohitantely (Seguier-Guis 1988) also revealed the presence of only three lemur species. The present study, therefore, confirms that primate species richness in Ambohitantely is lower than in most other protected areas surveyed in Madagascar (Mittermeier *et al.* 1992). This probably accounts for the fact that, although two of the three lemurs are threatened nationally by habitat loss (Harcourt and Thornback 1990), the reserve is not considered a priority protected area for lemur conservation (Mittermeier *et al.* 1992). However, there are a number of potential threats to the lemurs of Ambohitantely.

Throughout the forest there is vegetation damage and soil disturbance consistent with the foraging of both wild boar (*Potamochoerus larvatus*) and domestic livestock. Cattle damage was particularly evident in the north-west of the forest, adjacent to a vehicle trail. The physical damage caused by these ungulates hinders the development of the understorey and prevents natural regeneration (Bastian 1964). Measures need to be implemented to remove both species from the reserve. Interpretive information could perhaps be provided to dissuade local people from allowing their cattle into the forest. Clear signposts at the reserve boundaries may be adequate, if warnings are subsequently enforced by forestry officials. Although intensive hunting using traditional methods may be able to reduce wild boar numbers, it has been suggested that snaring may be more effective in eradicating this pest (Anderson and Stone 1993).

Some lemurs may be under direct human pressure. Harcourt and Thornback (1990) report that hunting of brown lemurs has been observed in the reserve. Although illegal, lemurs are trapped



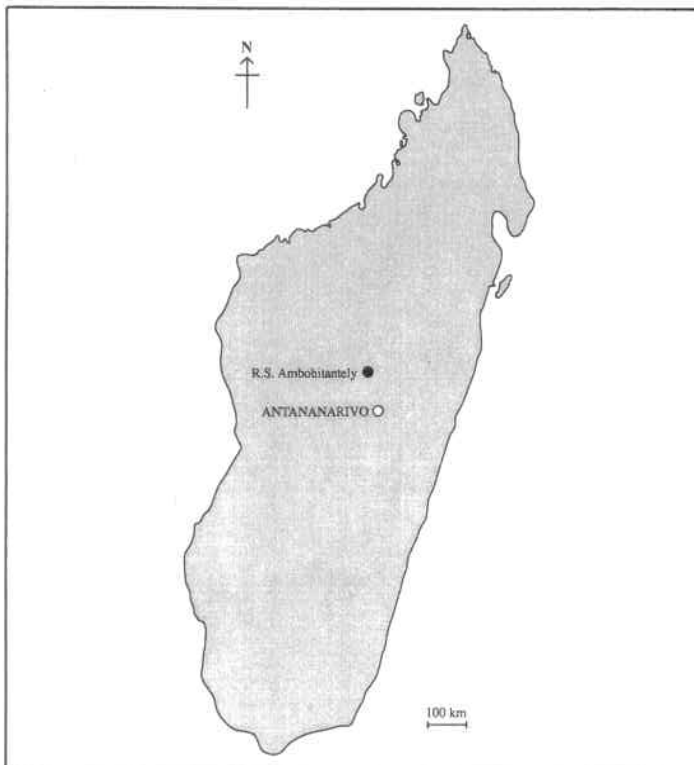


Fig. 1. Map of Madagascar showing the location of the Ambohitantely Special Reserve.

for food in many Malagasy forests (e.g., Thompson *et al.* 1987; Raxworthy and Stephenson 1988). No evidence of hunting was uncovered in the present study but any direct killing would exacerbate the problems facing the small population.

The greatest threat to the fauna and flora of Ambohitantely forest is the regular burning of surrounding savannah. This has occurred for many years, destroying vegetation, preventing regeneration, and causing forest cover to diminish (Bastian 1964; Nicoll and Langrand 1989). Firebreaks have been created in the south and west of the reserve but are absent in the north (Nicoll and Langrand 1989). A solution to this problem is less easy to identify as it will involve changes in land-use practices by local communities. Creating plantations adjacent to native forest might help by acting as a buffer zone, as well as providing additional foraging habitat for brown lemurs (Ganzhorn 1987).

Since Ambohitantely forest is surrounded by grassland, lemurs in the reserve have no opportunity for interbreeding with animals in contiguous forest blocks. Such isolation can often lead to species extinctions (see Soulé and Wilcox 1980). Predicting the probability of any of the three lemur populations dying out is difficult without more data, but the apparently low density of brown lemurs may be indicative of the effects of isolation.

Although none of the lemurs in the reserve are among the most threatened in Madagascar (Mittermeier *et al.* 1992), their demise would reflect a general loss of biodiversity within one of the few remaining plateau forests. There is therefore urgent need for an on-going survey of the lemurs of Ambohitantely in order to monitor changes in population densities over time and to determine the long-term effects of isolation. In the meantime, the reserve could be better safeguarded by eradicating introduced ungulates and creating a forest buffer zone.

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# Primate Population Viability Analysis Symposium

## Editorial

Guest Editor: Robert C. Lacy

The concept and techniques of Population Viability Analysis (PVA) have been developed only in the past 15 years, with most of the development and the term PVA itself occurring during the past decade. Yet already PVA has been used to help assess population status, identify threats to persistence, and guide conservation planning for many primate species in Asia, Africa (including Madagascar), and South and Central America. Because PVA is so new and rapidly evolving, there is considerable interest in using the approach, but there is also considerable uncertainty or confusion regarding what PVA is and how it can be used to assist conservation. For that reason, a number of primatologists had urged that a symposium and workshop on PVA be included in the XVth Congress of the International Primatological Society, held in Bali, Indonesia, in August 1994.

The purpose of the symposium was four-fold: to provide an overview of the concept and techniques of PVA; to have presented some of the PVA analyses that have been conducted on primate species; to provide a forum for discussions about the strengths, limitations, concerns, and hopes for PVAs of primates; and to offer a demonstration of some of the PVA computer modeling tools that are available. To meet the first of these purposes: Jeanne Altmann (University of Chicago and Chicago Zoological Society) introduced the workshop; Russell Mittermeier (Conservation International) provided an overview of primate diversity and the conservation needs that might be addressed in part with PVA; Robert Lacy (Chicago Zoological Society) gave an overview of what PVA encompasses and how it is used to assist with conservation; and Timothy O'Brien and Margaret Kinnaird (NYZS/Wildlife Conservation International) described some of the techniques and the difficulties of obtaining the necessary parameter estimates from field data on primate populations. Four talks then summarized PVAs that have been completed on some primate species: Jatna Supriatna (University of Indonesia) and Kunkun Gurmaya (University of Padjajaran) presented PVAs conducted on Javan gibbons and langurs; Warren Brockelman (Mahidol University) described a PVA of Thai gibbons; Anthony Rylands (Conservation International) presented PVAs on the four taxa of lion tamarins in Brazil; and Widodo Ramono (Indonesia PHPA) presented results of a PVA on orang utans. Following these talks, Jeanne Altmann chaired a lively discussion among the workshop speakers and a number of participants from the audience. In the afternoon, Robert Lacy demonstrated the VORTEX computer simulation modeling program for conducting PVAs.

At the IPS workshop, it was recommended that as much as possible of the material presented there be made available to all those interested in primate conservation. I am grateful to the editor of *Primate Conservation* for providing this opportunity. Four papers from the IPS symposium are included in this issue; they present an overview of PVA and examples of its use in the study and conservation of primates in South America, Africa, and Asia. I also must express my appreciation to Jeanne Altmann for assistance in instigating, organizing, and conducting the symposium, and for her valuable review of papers. In addition to the four papers from the symposium, included here is a paper reporting a PVA on another endangered primate, the muriqui. I thank Karen Strier (University of Wisconsin) for contributing her paper on Population Viability Analysis.

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# What is Population (and Habitat) Viability Analysis?

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## Some History of Concepts, Terms, and Approaches

The papers presented in this symposium refer both to "Population Viability Analysis (PVA)" and to "Population and Habitat Viability Analysis (PHVA)." In the conservation literature, one can find reference also to "Population Vulnerability Analysis", "Population Viability (or Vulnerability) Assessment", and other variants on the name. This diversity of terminology has caused some confusion among practitioners of the PVA (or PHVA) approach, and probably even more confusion among conservationists and wildlife managers who have tried to understand what analysis was being described, and whether it could be a useful tool in their efforts to conserve biodiversity. The diversity of perceptions about the PVA approach is not limited to its name. Different people mean different things by PVA, and the definitions and practice of PVA are constantly evolving. It is not the case, as has sometimes been suggested, that some people are doing PVA correctly, and others incorrectly, but rather that people are using different (if related) kinds of analyses and labelling them with the same (or similar) terms. What analysis is correct depends on the need and the application. In this paper, I will attempt to clarify what PVA is, by suggesting a more consistent terminology and by describing the features that characterize the application of the PVA approach to conservation. The perspective I offer is necessarily biased by my experiences in conservation. I will not attempt an exhaustive historical account of this field.

Population viability analysis originally described methods of quantitative analysis to determine the probability of extinction of a population. Shaffer (1981) identified multiple factors that can threaten viability or persistence of a population. He usefully categorized these factors into demographic stochasticity, environmental variability, catastrophic variation, and genetic drift and inbreeding. Any or all of these factors could threaten the persistence of a population that falls below a "minimum viable population size", or MVP. Each of these factors entails a stochastic, or random probabilistic, process which causes small populations to undergo fluctuations and possibly further decline. The smaller and more erratic is the size of a population, the greater the probability that the number will, by chance, hit zero — the extirpation of the local

population, or ultimate extinction if the local population was all that remained of the taxon. Gilpin and Soulé (1986) stressed that the destabilizing stochastic processes are synergistic: various of demographic, environmental, and genetic processes can exacerbate the instability caused by other factors, causing what has been depressingly referred to as "extinction vortices". Shaffer (1981) first defined an MVP as the size at which a population has a 99% probability of persistence for 1000 years, but it might be more meaningful biologically to consider it to be the size below which a population's fate becomes determined largely by the stochastic factors that characterize extinction vortices.

One concept of population viability analysis is any methodology used to determine an MVP. Shaffer (1981) had suggested several ways to determine an MVP. Perhaps the most rigorous method, and the one that would produce the most defensible estimates, would be an empirical observation of the stabilities and long term fates of a number of populations of various sizes. Berger (1990) presented a good example of this approach, in which he observed that populations of bighorn sheep in the mountains of the western USA persisted only when the populations consisted of more than 100 animals. More empirical studies are needed, but the time and numbers of populations required for such studies are precluded in the cases of most species threatened with extinction — exactly those for which estimates of MVP are most urgently needed. A more elegant and general approach to PVA is to develop analytical models of the extinction process that will allow calculation of the probability of extinction from a small number of measurable parameters. Goodman's (1987) model of demographic fluctuations, and applications to conservation of the classic population genetic models of loss of genetic diversity by genetic drift (Franklin 1980; Soulé *et al.* 1986; Lande and Barrowclough 1987) are valuable efforts in this direction. Kinnaird and O'Brien (this issue) describe the use of some of these models in a PVA of the Tana River crested mangabey (*Cercocebus galeries galeries*).

Unfortunately, our understanding of population biology is not yet sufficient to provide fully adequate analytical models of the extinction process. For example, none of the existing analytical models incorporate all three of demographic, environmental, and genetic fluctuations, and thus they do not begin to model the array



of extinction vortices described by Gilpin and Soulé (1986). Moreover, the analytical models make extremely simplifying assumptions about a number of the intricacies of population structure. For example, social groupings or preferences are often assumed to be invariant or lacking, resulting in random mating; and dispersal is usually assumed to be random between all sites (the "island model") or only to occur between adjacent sites (the "stepping stone model"). Much more work is needed either to develop more complex and flexible models or to demonstrate that the simple models are sufficient to provide guidance for conservation.

A third method of estimating an MVP described and demonstrated by Shaffer (1981) is the use of computer simulation modeling to project the probability distribution of possible fates of a population. Simulation models can incorporate a very large number of threatening processes and their interactions, if the processes can be described in terms of quantitative algorithms and parameterized. The flexibility of such models is both a strength and a weakness of the approach (Lacy 1993a; Lindenmayer *et al.* 1993a). The extinction process is exceedingly complex (Clark *et al.* 1990), and it can be difficult to focus on the key threatening processes when using a model that allows for testing of almost everything (Lacy and Clark 1990; Maguire *et al.* 1990; Lindenmayer *et al.* 1991, 1993a, 1993b).

Shaffer's (1981) original term "minimum viable population" (MVP) has fallen into disfavor (Soulé 1987), even as the PVA approach has risen in popularity. Shaffer stressed that an MVP was an estimate of the population size below which the probability of extinction was unacceptably high, that different populations would have different MVPs, and that the MVP determined for a population would depend on the threatening factors that were considered. However, the term implied to some people that there was a well-defined number below which extinction was certain and above which persistence was assured. Re-emphasizing the probabilistic nature of the extinction process, a number of conservation biologists have focused on methods for estimating the probability of extinction over defined time periods for a designated population exposed to a specific scenario of environmental conditions, threats to persistence, and future management actions and other foreseeable events (Brussard 1985; Starfield and Bleloch 1986; Soulé 1987; Simberloff 1988; Gilpin 1989; Shaffer 1990; Boyce 1992; Burgmann *et al.* 1993; Lacy *in press*). Thus, "Population Viability Analysis" (or the synonymous "Population Viability Assessment" and "Population Vulnerability Analysis") came to describe any of the array of methods for quantifying the probability of extinction of a population. Although PVA has been extended by some to encompass a broader approach to conservation (see below), the term "Population Viability Analysis", or PVA, should perhaps be reserved for its original, yet still rather broad, meaning.

Beginning in about 1989 (Lacy *et al.* 1989; Seal and Lacy 1989; Seal *et al.* 1990), it became increasingly recognized that PVA can often be most usefully incorporated into a strategy for the conservation of a taxon if it is part of, and often central to, a conservation workshop that mobilizes collaboration among the array of people with strong interest in or responsibility for a conservation effort (e.g., governmental wildlife agencies, conservation NGOs, and the local people who interact with the species or its habitat) or with particular expert knowledge about the species, its habitats, or the

threats it faces (e.g., academic biologists, conservation professionals, other wildlife biologists, experts on human demographics and resource use). Conservation problems are almost always multifaceted, involving not only complex dynamics of biological populations, but also interactions with human populations, the past, present, and future impacts of humans on habitats, and human political, social, and economic systems (Alvarez 1993; Bormann and Kellert 1991; Clark 1989, 1993). Many people need to contribute knowledge, expertise, and ideas in order to achieve the recovery of threatened species. Population viability analyses can provide a framework for incorporating the many needed kinds of knowledge into species conservation efforts, because PVAs do allow the assessment of many kinds of factors that threaten the persistence of populations (Lacy 1993a; Lindenmayer *et al.* 1993a).

The Conservation Breeding Specialist Group (CBSG, formerly called the Captive Breeding Specialist Group) of the IUCN Species Survival Commission especially has advocated and used workshops centered on PVAs to provide guidance to conservation assessment and planning (e.g., Seal *et al.* 1990; Ellis *et al.* 1992a; Foose *et al.* 1993). Over the past few years, the PVA workshop as an approach to species conservation has expanded considerably beyond the quantitative analysis of extinction probabilities as advanced by Shaffer (1981, 1990), Soulé (1987), Gilpin (1989), Clark *et al.* (1991), Boyce (1992), and others. PVA workshops have incorporated consideration of resource use and needs by local human populations (Seal *et al.* 1991), education programs for the local human populations (Odum *et al.* 1993), trade issues (Foose *et al.* 1993), and trends in human demographics and land use patterns (Walker and Molur 1994). Recognizing that the conservation assessment workshops increasingly incorporated more than just the population biology modeling (which still formed a core organizing and analysis framework for the workshop), the CBSG has more recently termed their workshops *Population and Habitat Viability Analyses* (PHVA) (e.g., Ellis *et al.* 1992a; Odum *et al.* 1993). I would recommend that the term *Population and Habitat Viability Analysis* (PHVA) be used to describe the collaborative workshop approach to species conservation that centers on, but encompasses more than, a *Population Viability Analysis* (in the narrow sense). The concept of a PHVA continues to expand and evolve, as it should considering the need for more holistic and flexible approaches to conservation (e.g., Ruggiero *et al.* 1994; and see the debates in almost any issue of *Conservation Biology*). Thus, in the usage I recommend, PVA is a quantitative analysis of the probability of population persistence under defined sets of assumptions and circumstances. PHVA is a workshop process that brings to bear the knowledge of many people on species conservation, eliciting and assessing multiple options for conservation action, principally by using the tool of PVA as a way evaluate present threats to population persistence and likely fates under various possible scenarios. In the IPS symposium on the application of P(H)VAs to primate conservation, there were presented discussions and examples of PVAs, in the narrow sense (e.g., Kinnaird and O'Brien this volume), and PHVAs, in the broadest sense (e.g., Rylands this volume; Brockelman this volume).

### Population Viability Analysis (PVA)

Two defining characteristics of a PVA are an explicit model of

the extinction process and the quantification of threats to extinction. These features set PVA apart from many other analyses of the threats facing species, including, for example, the IUCN Red Books of Threatened Species published in the past. As a methodology to estimate the probability of extinction of a taxon, PVA necessarily must start with an understanding, or model, of the extinction process (Clark *et al.* 1990).

Generally, the model of extinction underlying a PVA considers two categories of factors: deterministic and stochastic. Deterministic factors, those that can shift species from long-term average population growth to population decline include the well-known threats of over-harvest, habitat destruction, pollution or other degradation of environmental quality, and the introduction of exotic predators, competitors, and diseases. Singly or combined, these forces have driven many wildlife populations to low numbers and, for some, to extinction. Once a population becomes small, and isolated from conspecific populations that might serve as sources for immigrants that could stabilize demographics and genetics, its dynamics and fate can become dominated by a number of random or stochastic processes (as outlined above and by Shaffer 1981). Thus, even if the original deterministic causes of decline are stopped or reversed, the instability caused by stochastic processes acting on small populations can cause the extinction of a population.

In nature, most threatening processes have both deterministic and stochastic features. For example, a high level of poaching might be seen as a deterministic factor driving a wildlife population toward extinction, but whether an individual animal is killed might be largely a matter of chance. In a PVA, poaching might be modelled as a deterministic process by killing a determined proportion of the animals, or it might be modelled as a stochastic process by giving each animal that probability of being killed but allowing the exact numbers killed to vary over time. If the population is large and the percent of animals killed is high, then these two ways of modelling the effects of poaching will yield the same results: the deterministic component of poaching dominates the population dynamics. If the population is small or the percent age of animals killed is very low, then the numbers killed in a stochastic model (and in nature) might vary substantially from year to year: the stochastic nature of poaching further destabilizes the population.

Which of the various deterministic and stochastic factors are important to consider in a PVA will depend on the species biology, the present population size and distribution, and the threats it faces. For example, orang utans may be threatened by forest destruction and other largely deterministic processes, but inbreeding and randomly skewed sex ratios resulting from highly stochastic processes are unlikely to be problems, at least not on a species-wide basis. On the other hand, even if the remnant Atlantic coastal rainforest of Brazil is secured for the future, the populations of golden lion tamarins (*Leontopithecus rosalia*) which can persist in that remnant forest are not sufficiently large to be stable in the face of stochastic threats (Seal *et al.* 1990; Rylands this volume). The identification of the primary threats facing a taxon via a comprehensive PVA is important for conservation planning. For example, tamarin populations might be stabilized by the translocations and reintroductions that are underway and planned, but the orang utan PHVA recognized that releases of confiscated "pet" orang utans are unlikely to have a conservation benefit for those populations

which are facing habitat destruction, not stochastic fluctuations and inbreeding. For many species, such as the whooping crane (*Grus americana*), the temporarily extinct-in-the-wild black-footed ferret (*Mustela nigripes*), and the Puerto Rican parrot (*Amazona vittata*), only a single population persisted in the wild. Although those populations may have been maintained or even increased for a number of years, the principal threat was that a local catastrophe (e.g., disease epidemic, severe storm) could decimate the population (Clark 1989; Lacy *et al.* 1989; Mirande *et al.* 1991). The primary recovery actions therefore needed to include the establishment of additional populations. Tragically, some taxa, such as the Florida panther (*Felis concolor coryi*) and the eastern barred bandicoot (*Perameles gunnii*) in Victoria, Australia, are critically threatened simultaneously by deterministic factors, stochastic processes, and the possibility of catastrophic loss (Seal and Lacy 1989; Lacy and Clark 1990).

PVA is formally an assessment of the probability of extinction, but PVA methods often focus on other indicators of population health. Mean and variance in population growth (Lindenmayer and Lacy 1995a, 1995b, 1995c), changes in range, distribution, and habitat occupancy (Hanski and Gilpin 1991), and losses of genetic variability (Soulé *et al.* 1986; Lande and Barrowclough 1987; Seal 1992; Lacy and Lindenmayer 1995) can be analyzed and monitored. Although not yet common, monitoring of population health could also utilize measures of developmental stability (Clarke 1995), physiological parameters such as body condition (Altmann *et al.* 1993) or levels of the hormones related to stress and reproduction (Sapolsky 1982, 1986), or the stability of behavior and the social structure of the population (Samuels and Altmann 1991).

The interactions and synergism among threatening processes will often cause numerical, distributional, physiologic, behavioral, and genetic responses to concordantly reflect species decline and vulnerability. It remains important, however, to understand and target the primary causal factors in species vulnerability. The recent proposal to base IUCN categories of threat on quantified criteria of probability of extinction, or changes in such indicators as species range, numbers, and trends (Mace and Lande 1991; Mace *et al.* 1992; Mace and Stuart 1994; IUCN Species Survival Commission 1994) reflects the increased understanding of the extinction process that has accompanied the development of PVA, and simultaneously demands that much more progress be made in developing predictive models, gathering relevant data on status and threats, and applying the PVA techniques.

### Population and Habitat Viability Analysis (PHVA)

Population and Habitat Viability Analysis is a multi-faceted process or framework for assisting conservation planning, rather than a singular technique or tool. It is often interwoven with other techniques for managing complex systems, such as decision analysis (Maguire 1986; Maguire *et al.* 1990). Even when viewed as "the" PHVA workshop, all such conservation workshops involved and required substantial pre-workshop and post-workshop activities. Some PHVA workshops have been extended into multiple workshops and less formal, smaller collaborative meetings, often focused on subsets of the larger problems of species conservation.

Although PHVAs are diverse and not well defined, the PHVA



process contains a number of critical components (Lacy in press), many of which were illustrated well in the PHVA workshops described in this symposium. First, it is essential to gather an array of experts who have knowledge of the species or problem. A PHVA is not required to bring together experts, but it often facilitates such sharing of expertise because the collective knowledge of many is essential for a useful PVA (in the narrow sense) to be completed. In addition to a diversity of people, a PHVA workshop also requires and therefore facilitates the involvement of a number of agencies and other concerned organizations. For example, the PVA on the two endemic primates of the Tana River Primate Reserve in Kenya (Seal *et al.* 1991) was convened by the Kenya Wildlife Service, facilitated by the IUCN SSC Captive Breeding Specialist Group, benefitted from the expertise contributed by members of the IUCN SSC Primate Specialist Group, and was sponsored by the World Bank. The involvement of many agencies and interested parties is critical to endangered species recovery.

An early requirement, or prerequisite, of a PHVA workshop is to determine the conservation problem to be addressed, and to state the goals of the management plan. Many endangered species programs have not clearly identified their goals. For example, at a PHVA and Conservation Assessment and Management Plan workshop on the forest birds of the Hawaiian islands (Ellis *et al.*, 1992a, 1992b), it became apparent that the agencies responsible for the conservation of Hawaii's bird fauna had not determined whether their goal was to prevent species extinctions, prevent taxa (species or subspecies) from becoming extirpated on any of the islands they presently inhabit, preserve species in sufficient numbers and distribution to allow them to continue to fill ecological roles in the biological communities, or the restoration of taxa to most or all parts of the original ranges. The management actions required to achieve these various levels of conservation are quite different.

PHVA workshops facilitate the assembly of all available data. Often, important information is found in the field notes of researchers or managers, in the heads of those who have worked with and thought about the problems of the species, and in unpublished agency reports, as well as in the published scientific literature. A pending PHVA can be the impetus that encourages the collection of data in anticipation of presentation, review, and analysis at the workshop. For example, a Sumatran Tiger PHVA helped stimulate the systematic collection of data on sightings and signs of tigers in protected areas throughout the island of Sumatra, and collation and integration with a Geographic Information System (GIS) map of habitats and human pressures on those habitats.

It is important to specify the assumptions that underlay a PHVA, and any consequent management recommendation. For example, the Hawaiian bird conservation efforts are constrained by a belief that no birds bred outside of the islands should ever be brought back to the islands for release. While this position derives from a reasonable concern for disease transmission (much of the decline of Hawaii's native birds is thought to be due to introduced avian diseases) as much as from any political or philosophical stand, any justification for the restriction must be questioned in light of the fact that wildlife agencies import and release, without quarantine, 1000s of exotic gamebirds onto the islands annually.

Once experts are assembled, problems stated and goals set, data gathered, and assumptions specified, then the PHVA process can proceed with what I describe as PVA in the narrow sense: estima-

tion of the probability of population persistence. The available data are used to estimate the parameters that are needed for the model of population dynamics to be applied. Often, data are not available from which to estimate certain key parameters. In those cases, subjective and objective, but non-quantified, information might be solicited from the assembled experts, values might be obtained from data on related species, or a factor might simply be omitted from the model. While such a non-precise process might consist simply of intuitive judgements made by experts, it is important to specify how values for the parameters in the model were obtained. The resulting limitations of the analyses should be acknowledged, and a decision made if, how, by whom, and when the missing data would be collected so that more refined analyses could be conducted. With the PVA model, projections of the most likely fate, and distribution of possible fates, of the population under the specified assumptions are made.

Because so much of a PVA - the data, the model, and even the interpretation of output - is uncertain, a PVA that provides an estimate of the probability of extinction under a single scenario is of very limited usefulness. An essential component of the PHVA process, therefore, is sensitivity testing. Ranges of plausible values for uncertain parameters should be tested, to determine what effects those uncertainties might have on the results. In addition, several different PVA models might be examined at a PHVA workshop, or the same general model tested under different structural assumptions. Different participants in the process should assess and interpret the results. Such sensitivity testing reveals which components of the data, model, and interpretation have the largest impact on the population projections. This will indicate which aspects of the biology of the population and its situation contribute most to its vulnerability and, therefore, which aspects might be most effectively targeted for management. In addition, uncertain parameters that have a strong impact on results are those which might be the focus of future research efforts, to better specify the dynamics of the population. Close monitoring of such parameters might also be important for testing the assumptions behind the selected management options and for assessing the success of conservation efforts.

Closely parallel to the testing of uncertainties in the present situation is the testing of options for management. PVA modeling allows one to test the expected results of any given management action, under the assumptions of the model and within the limitations of present knowledge, on the computer before implementation in the field. This process can guide selection of the management options most likely, given current knowledge, to be effective, and will define target recovery goals that should be obtained if our knowledge is adequate and the recommended actions are followed. A PHVA workshop on the Black Rhinoceros in Kenya's 11 rhino sanctuaries (Foose *et al.* 1993) suggested that periodic movement of rhinos between fenced sanctuaries to reduce inbreeding and demographic fluctuations would be necessary to stabilize the populations in the smaller parks. Moreover, the modeling provided estimates of the rate at which the larger populations would be able to provide surplus animals for translocation.

It would be an error to assume that any PVA model incorporates everything of interest (Lacy in press). A PVA simulation program can only include those processes that are known to the programmer. This will likely be a subset of what might be known

to the field biologists, which in turn will definitely be a subset of those processes that impact natural populations. A number of variables affecting population dynamics and viability are not yet commonly examined in PVA models. These include: social and ecological determinants of dispersal; complex social processes, such as the role of non-breeders in group stability and the impacts of other aspects of the social environment on reproductive success and survival; competitive, exploitative, or mutualistic interactions with other species experiencing their own population dynamics; and the effects of changes in the global environment. To date, most PVA models treat organisms as independent actors in spatially homogeneous physical, biotic, and social environments. There is tremendous opportunity and need for elaboration of PVA models, and it is likely that increasingly sophisticated models will also become more specific to the individual taxa and environments under study.

PHVA workshops must incorporate consideration of the assumptions of the PVA model used and the biases or limitations in interpretation that could result. PHVAs consider only those threatening processes of which we have knowledge, for which we can develop algorithms for modeling or other methods for analysis, and for which we have some data. As a result, it is likely that PVAs will underestimate the extinction vulnerability of most populations, and that PHVA workshops will be less comprehensive than is desirable. We need always to be cognizant of the limits of our understanding of wildlife populations, and to include appropriate margins for error in our conservation strategies.

PVA is, by definition, an assessment of the probability of persistence of a population over a defined time frame. Yet, persistence of a population, while a necessary condition for effective conservation of natural systems, is often not sufficient. Prevention of extinction is the last stand of conservationists, but the goals should be higher: conservation of functional biological communities and ecosystems. PVA usually ignores the functional role of a species in a community, but a PHVA workshop should consider much more than the prevention of the final biological extinction of the taxon. A species, such as the American Bison (*Bison bison*), can be functionally extinct in terms of no longer filling its original role in nature, even as it is praised as a conservation success story and would, by PVA, be considered safe from extinction and viable.

The use of the PHVA process to help guide conservation decisions is not a singular event, in which an analysis can be completed, management actions recommended and implemented, and conservation thereby assured. The many uncertainties in the process mandate that PVA be used as a tool in an adaptive management framework, and a PHVA workshop is just one stage of an effective conservation strategy. In adaptive management, the lack of knowledge adequate to predict with certainty the best course of action is recognized, management actions are designed in such a way that monitoring will allow testing of the adequacy of our model and understanding, and corrective adjustments to management plans are made whenever the accumulating data suggest that the present course is inadequate to achieve the goals and that a better strategy exists (Holling 1978). The urgency of the biodiversity crisis will not permit us ethically to refrain from aggressive conservation action until we have scientifically sound understanding of all the factors that drive population, community, and ecosystem

dynamics. PHVA provides a forum for making use of the information we do have, in a well-documented process that is open to challenge and improvement. PHVA workshops can, therefore, assist wildlife managers in the very difficult and important job of using science to safeguard the future of wildlife populations.

## Summary

Population Viability Analysis (PVA) and Population and Habitat Viability Analysis (PHVA) refer to an array of interrelated and evolving techniques for assessing the survival probability of a population and possible conservation actions. I suggest that it might be useful to restrict the term PVA to its original meaning - the use of quantitative techniques to estimate the probability of population persistence under a chosen model of population dynamics, a specified set of biological and environmental parameters, and enumerated assumptions about human activities and impacts on the system. PHVA refers to a workshop approach to conservation planning, which elicits and encourages contributions from an array of experts and stakeholders, uses PVA and other quantitative and non-quantitative techniques to assess possible conservation actions, and strives to achieve consensus on the best course of action from competing interests and perspectives, incomplete knowledge, and an uncertain future.

Many of the components of PVAs and PHVAs, even when used in isolation, can be effective educational and research tools. To be a useful framework for advancing the conservation of biodiversity, however, PHVA must incorporate all of: (1) collection of data on the biology of the taxon, status of its habitat, and threats to its persistence, (2) quantitative analysis of available data, (3) input of population status and identifiable threats to persistence into analytical or simulation models of the extinction process, (4) assessment of the probability of survival over specified periods of time, given the assumptions and limitations of the data and model used, (5) sensitivity testing of estimates of extinction probability across the range of plausible values of uncertain parameters, (6) specification of conservation goals for the population, (7) identification of options for management, (8) projection of the probability of population survival under alternative scenarios for future conservation action, (9) implementation of optimal actions for assuring accomplishment of conservation goals, (10) continued monitoring of the population, (11) reassessment of assumptions, data, models, and options, and (12) adjustment of conservation strategies to respond to the best information available at all times. There are many uncertain aspects of population dynamics, especially of endangered taxa, including few data on species biology and habitats, uncertain political and social climate for implementing conservation actions, and the unpredictability inherent in small populations due to the many stochastic forces that drive population dynamics.

The rapid development of PVA as a research and management tool, and the concurrent but not always parallel expansion of the scope of what conservation threats, options, and actions are considered in PHVA workshops, has led to confusion. Different people can describe rather distinct kinds of analyses with the same terminology, while others use different terms to describe nearly identical approaches. The ever-changing concepts of PVA and PHVA



are confusing, but the flexibility of the processes is also their strength. Current tools are inadequate to address fully the challenges of stemming the losses of biodiversity. The PVA/PHVA framework allows and encourages rapid application of new tools, data, and interpretations into increasingly effective conservation programs.

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## Population Viability Analyses and the Conservation of the Lion Tamarins, *Leontopithecus*, of South-East Brazil

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There are four species of lion tamarins, all endemic to the Atlantic coastal forest of Brazil. Three of them, the golden lion tamarin, *Leontopithecus rosalia*, the golden-headed lion tamarin, *L. chrysomelas*, and the recently discovered black-faced lion tamarin, *L. caissara*, occur in coastal regions, in the states of Rio de Janeiro, Bahia, and Paraná/São Paulo. The fourth, the black lion tamarin, *L. chrysopygus*, occurs inland in the state of São Paulo. All are extremely endangered, with very reduced distributions in the wild resulting principally from the widespread and continuing destruction of the Atlantic forests they occupied in the past (Coimbra-Filho 1969, 1976; Coimbra-Filho and Magnanini 1968; Coimbra-Filho and Mittermeier 1973). Populations today are minimal and very highly fragmented.

A Population Viability Workshop (PVA) was held for these species in Belo Horizonte, Brazil, in June of 1990 (Seal *et al.* 1990). It was organized by the World Conservation Union (IUCN) Species Survival Commission (SSC) Conservation Breeding Specialist Group (CBSG) in conjunction with the Fundação Biodiversitas, World Wildlife Fund (WWF), Conservation International (CI), the Jersey Wildlife Preservation Trust (JWPT), and the Brazilian Federal Institute for the Environment and Renewable Natural Resources (Ibama). It involved two components: the first an evaluation of the status of the species in captivity and the wild, with the elaboration of specific recommendations for future action; and the second an evaluation through computer simulation of the viability of the wild populations in protected areas, based on genetic aspects and population parameters, potential and current threats, and the known or estimated size of the populations.

All of the species, excepting the black-faced lion tamarin, *L. caissara* discovered only in 1990, had been subject to varying degrees of research and conservation efforts during the previous 10 years, and so a limited amount of information was available concerning the principle parameters used for the PVA. These included main threats, their occurrence in protected areas, distributions, population sizes, densities, and group sizes. Estimations of reproductive parameters and group sizes in the wild depended mainly on the information available for the golden lion tamarin in Rio de Janeiro.

### International Management Committees

An important aspect to note is that at the time of the PVA Workshop there existed International Management Committees for the captive populations of *L. rosalia*, *L. chrysomelas* and *L. chrysopygus* (see Mallinson 1986, 1987, 1989, 1994a, 1994b). These committees have played a fundamental role in the interactive management of the captive and wild populations, and in 1991 a fund-raising program administered by the Committees was established specifically for lion tamarin research and conservation, "The Lion Tamarins of Brazil Fund", a direct result of the 1990 Lion Tamarin PVA Workshop (Mallinson 1994b).

The committee for *L. rosalia* arose from a PVA-style workshop, "The Golden Marmoset Conference", held at the National Zoological Park, Washington, D.C., in February of 1972 (Bridgwater 1972). The Wild Animal Propagation Trust, based in Wheeling, West Virginia, responsible for the meeting, had been monitoring the captive population since 1966 to assess its status, rationalize breeding efforts, and stimulate conservation action. In 1971, there were approximately 90 animals in captivity in about 38 institutions worldwide, but second generation breeding was reported as infrequent and problematic. The 1972 National Zoological Park meeting resulted in documents providing recommendations concerning husbandry and research priorities. In 1974, Devra G. Kleiman (National Zoological Park, Washington, D.C.) took over the studbook and established a very successful management committee. The captive population is now being maintained at approximately 500 animals in 125 institutions (Ballou 1993). The Committee was formerly recognized by the Brazilian Institute for the Environment (Ibama) in 1990 (Ibama Edict No. 2342, 28 November 1990). Conservation measures in the natural range of the species have involved, since the early 1980's, a reintroduction program, coordinated by Benjamin Beck, along with a research program coordinated by Devra Kleiman and James Dietz, and an environmental education program, coordinated by Lou Ann Dietz, in and around the Poço das Antas Biological Reserve in Rio de Janeiro, all part of the Golden Lion Tamarin Conservation Program run by the Smithsonian Institution (Beck *et al.* 1986, 1991; Dietz *et al.* 1986, 1994a, 1994b; Dietz and Nagagata 1986; Kleiman



*et al.* 1986, 1991; Peres 1986, 1989, 1991; Pinder 1986).

An insignificant number of golden-headed lion tamarins, *L. chrysomelas*, were held in captivity prior to 1972. At this time there was just one breeding colony in what is today the Rio de Janeiro Primate Center (CPRJ/FEEMA). The International Committee for this species arose as a result of concern over the illegal export of 50-60 animals to Belgium and Japan in 1983/84 (Konstant 1986; Mallinson 1986, 1987, 1989). The Brazilian Institute for the Environment (Ibama) invited Jeremy Mallinson (Jersey Wildlife Preservation Trust) and Ademar F. Coimbra-Filho (Rio de Janeiro Primate Center) to set up a committee for the recovery of these animals, eventually formalized in 1990 (Ibama, Edict No.1204, 18 July 1990) (Mallinson 1989). The recovery was highly successful, and the Committee established a breeding program and studbook for the species (Ballou 1989; De Bois 1993, 1994). The 1993 studbook, coordinated by Helga de Bois (Royal Zoological Society of Antwerp), reported 575 animals in 49 institutions, and efforts are underway to reduce the growth of the population (De Bois 1993, 1994; Van Elsacker *et al.* 1994).

The creation of an International Committee for the black lion tamarin, *L. chrysopygus*, was an obvious step following the establishment of those for *L. rosalia* and *L. chrysomelas*. It was set up on the initiative of the São Paulo State Forestry Institute in 1986 due to the imminent demise of approximately 35 animals with the flooding of part of the Morro do Diabo State Park by the construction of the Rosana Hydroelectric dam (Valle and Rylands 1986). It was formerly recognized by Ibama in 1990 (Ibama, Edict No.1203, 18 July 1990), and is currently chaired by Faical Simon (São Paulo Zoological Park) and Devra G. Kleiman.

By 1990, therefore, both *L. rosalia* and *L. chrysomelas* had sizeable and well-managed captive populations, and that for *L. chrysopygus* was under management and growing, albeit slowly. All are being monitored and managed using the most up-to-date software for viability analyses. A significant step taken on the occasion of the Lion Tamarin PVA Workshop in 1990 was the formal recognition of the three management committees by Ibama as consultative committees for *all* matters concerning the species, expanding, therefore, their role to include conservation and management in the wild. The PVA Workshop also resulted in the creation (Ibama Edict No.106/92-N, 30 September 1992) of an International Committee for the then very recently discovered black-faced lion tamarin, *L. caissara* Lorini and Persson 1990, under the leadership of Admiral Ibsen Câmara (Brazilian Foundation for the Conservation of Nature - FBCN, Rio de Janeiro), and Jeremy Mallinson. No captive population has been established for this species.

All four species of lion tamarins, therefore, have International Management Committees for the conservation of both wild and captive populations. They meet every year under the auspices of the Brazilian Institute for the Environment (Ibama). The document which arose from the PVA Workshop provides the general and specific guidelines for the priorities and actions of these Committees.

### Lion Tamarin PVA Workshop

The 1990 PVA Workshop counted on the participation of the large majority of people involved in the coordination of the cap-

tive breeding programs, in field research and conservation efforts for lion tamarins. It was run by Ulysses Seal (IUCN/SSC Conservation Breeding Specialist Group), and the aim was examine the viability of the captive and wild populations, and to develop conservation strategies to assure with a high probability the continued survival of the *Leontopithecus* species. Analytical procedures were used to estimate the probabilities of the species going extinct, given the various conditions and scenarios drawn up by the participants. The goal of the analyses was a greater than 98% probability of survival of each species over 100 years, dependent on action in four major areas: 1) securing and protecting habitats; 2) inventorying and protecting wild populations; 3) the scientific maintenance and management of wild and captive populations; and 4) the restocking of wild populations in suitable habitat.

The PVA Workshop demonstrated well that each species differs in terms of its status in the wild and captivity, and in the socioeconomy of the regions where they occur, and, as a result, the scenario in which conservation action can be taken. I will give here some examples of the recommendations for conservation action resulting from the PVA which have, in the subsequent four years, born fruit.

#### *Leontopithecus rosalia*

As mentioned earlier, *Leontopithecus rosalia* is the best known of the four species due to it being the first to be subjected to active management and research in captivity and due to the Conservation Program of the Smithsonian Institution involving research on wild populations, and programs for reintroduction and environmental education. The captive population, chaotic and unproductive in the 1960's, is now highly organized by the Management Committee for the species. The studbook is maintained by Jonathan D. Ballou and Devra G. Kleiman at the National Zoo, Washington, D.C. The population grew from about 100 individuals in the 1960's, to somewhat less than 200 by 1980, and in 1985 and 1986 it was levelled off at a little over 500 animals through active management to curb breeding. About a third of these animals are reproducing (Ballou 1993). Currently, the most significant problem being faced involves balancing the need for zero population growth with the maintenance of genetic diversity and the interest of zoos to hold breeding pairs. About 40 pairs need to breed each year to maintain zero population growth, but genetic diversity is rapidly lost if only a few pairs produce offspring. The strategy, therefore, is to have many pairs breeding but with each producing only a few litters. In 1992 alone, over 120 animals were moved among zoos (Ballou 1993). Pedigree analyses have indicated that the current population has retained about 96% of its original heterozygosity, this based on 46 founders, eight of which were still alive in 1992. Founder representation, however, is highly skewed with a few founders being heavily represented today, and many contributing only a very small fraction of the genes in the living population. This can be corrected to some extent by careful husbandry, but without new founders it does represent a genetic bottleneck (Ballou 1993). This aspect is discussed by Mansour and Ballou (1994), who demonstrated clearly the importance of establishing a good and well-managed founder population from the start, to assure not only the genetic health of the captive population but also to minimize the economic cost of the program. Mansour and Ballou (1994) showed that a higher genetic diversity amongst the founder popu-

lation means that a smaller population can be maintained, say two to three hundred instead of five hundred individuals, in order to guarantee a similar genetic reservoir. This obviously has a very significant impact on the economics of a captive breeding program, and is especially relevant to the black lion tamarin program where the captive population is on the verge of rapid expansion, with plans now underway to increase considerably the number of participating institutions (see below). The demographic and genetic analyses of the captive population involved in the PVA have allowed for the determination of the genetic minimum viable population size, and the reproductive objectives for the population as a whole and of each individual. Reproductive management is based on the concept of "target founder contribution", or corrective measures to shift the existing founder representation to one which is most favorable in terms of genetic diversity (Ballou 1993).

While the captive population of golden lion tamarins is under active management and being restrained from explosive growth, the population in the wild is declining drastically. The 5,500 ha Poço das Antas Biological Reserve is the only conservation unit protecting the species. About 2,900 ha of the reserve contains forests occupied by the lion tamarins. Estimates made during the PVA Workshop indicated a carrying capacity of about 290 individuals in the reserve as it is, and 508 if the reserve was entirely forested. The current effective population size for the reserve, estimated from population studies over the last 10 years is 94 (Kleiman *et al.* 1990). In 1990, very little information was available for the wild population outside of Poço das Antas (Kleiman *et al.* 1990). Only four other areas of forest of significant size were identified within the species' distribution. They totalled 5,150 ha. A carrying capacity of 844 lion tamarins was calculated for the Poço das Antas Reserve and the four additional forests. This means that the only significant forests remaining within the golden lion tamarin's current distribution could maintain less than half of a minimum viable population of 2,000. The PVA for this species resulted in nine specific recommendations, all of which were or are now being carried out (see Table 1).

A survey of all remaining forest and the species' distribution was carried out in 1992/93 by Kierulff (1993a, 1993b; Kierulff *et al.* in press). An analysis of satellite images indicated approximately 299,000 ha of forest below 700 m altitude remaining within the species's known range. Half of these forests, however, are comprised of areas of less than 500 ha, and only approximately 30% were found to be adequate for lion tamarins. The total wild population was calculated at 559 individuals in 103 groups, with a minimum of 470 and maximum estimate of 631. They are concentrated in four areas, including the Poço das Antas reserve, with 12 groups in isolated and small fragments. This gives a picture which is similar to that portrayed during the PVA workshop. PVA analyses using the Vortex software were carried out on each of the populations, and none of them were found to have an effective population size sufficient to avoid fatal inbreeding and genetic drift in the short term. The Poço das Antas Biological Reserve offered the best hopes, estimated to contain a population with an 88% probability of survival over a 100 years, maintaining 87% heterozygosity. Importantly, the study also demonstrated variable habitats for the remaining populations in terms of both vegetation and climate. These aspects might well alter PVA analysis predictions, based entirely on the population parameters from the Poço

das Antas population, due to differences in breeding rates, densities and group sizes.

This work led to the identification of five variables which need to be managed in order to guarantee the survival of the wild populations. The first is reducing the likelihood of catastrophes, remembering that, for a population as fragmented and small as that of the golden lion tamarin, forest destruction or habitat loss is a catastrophe not just a reduction in population size. The second is habitat restoration. The third is introduction, reintroduction or translocation. The fourth is monitoring the habitats tamarins occupy to understand how habitat characteristics influence survival and population parameters, and the fifth is permanent monitoring of the populations surviving. These are specific recommendations based in part on the conclusions of the PVA analyses and on an understanding of the population size and distribution, and they point to the importance of ecological aspects which influence population parameters. The ecology of the species in the different forests and climates within its distribution is still poorly known even for the Poço das Antas population, despite 10 years of research there.

Further recommendations which have been acted upon include a reforestation program to increase the area of forest in the Poço das Antas Biological Reserve along with a floristic inventory (Pessamílio 1994), and the establishment of a protected area where isolated groups identified in Kierulff's survey are being translocated (Kierulff and Oliveira 1994). Long-term research on the wild groups in the Poço das Antas Biological Reserves continues (Baker *et al.* 1993; Boinski *et al.* 1994; Dietz and Baker 1993; Dietz *et al.* 1994b; Halloy and Kleiman 1994). By September 1992, 112 lion tamarins had been reintroduced, 39 of which were still alive, and with 53 surviving offspring (Beck *et al.* 1986, 1991; Beck pers. comm. in Mallinson 1994a). The ongoing environmental education program has as one of its main aims incentives for the permanence of the forest patches on private lands (Dietz and Nagagata 1986; Dietz *et al.* 1994a; Padua *et al.* 1990).

#### *Leontopithecus chrysomelas*

In dealing with the golden-headed lion tamarin, *L. chrysomelas*, the 1990 PVA workshop resulted in 21 specific recommendations in five major aspects concerning protected areas, potential protected areas, environmental education, captive breeding and reintroduction (summarized in Table 2). As with the golden lion tamarin, nearly all are being tackled, and a number of the recommendations have been fulfilled.

The captive population rose from 297 animals in 25 institu-

**Table 1.** Principal recommendations for action for the conservation of *Leontopithecus rosalia* arising from the PVA Workshop on lion tamarins in 1990.

1. Surveys of all remaining forest within the species distribution.
2. Measures for the protection of the remaining forests containing golden lion tamarins.
3. Land purchase.
3. Measures for the prevention of possible catastrophic events such as fires, and pollution.
4. Reforestation of the degraded protected areas.
5. Increase the number of founders in the captive population.
6. Invest further in environmental education.
7. Continue and expand the reintroduction program.
8. Implement a program for the genetic and demographic management of the captive and wild populations.

Sources: Seal *et al.* (1990), Kleiman *et al.* (1990).



tions in 1990, to 575 animals in 49 institutions recorded in the 1993 studbook, and efforts are now underway to curb the growth of the population (De Bois 1993, 1994; Van Elsacker *et al.* 1994). The founder representation is considerably better than for the golden lion tamarin, having 154 contributing founders, but there are also problems concerning skewed representation.

The VORTEX computer simulation analyses at the 1990 Workshop indicated that the Una Biological Reserve contained the only population of lion tamarins which had some guarantee of survival over 100 years. However, the population estimate of 466 animals was based on projections involving group sizes which were larger and home ranges which are evidently smaller than has been evidenced through recent work by Dietz *et al.* (1994c). They have found the home range to be as large as 90 ha, double that used in the Vortex simulations, and it is probable that halving the total population estimate for the reserve would place the population into the category of doomed over the next 100 years. To counteract this, however, recommendations of the PVA Workshop concerning this Reserve involved its expansion, and measures have been taken to achieve this. Land purchase since 1989 has increased the size of the Reserve by 18% or 1,717 ha to 7,059 ha, including the widening of a narrow corridor of forest connecting the two forest blocks which had comprised the Reserve since its creation in 1980 (Mallinson 1989, 1994a; Coimbra-Filho *et al.* 1993).

The second aspect tackled since the PVA Workshop was a survey of the remaining populations outside of the Una Biological Reserve (Pinto 1994; Pinto and Tavares 1994; Pinto and Rylands in press). The survey, carried out during 1992/1993, identified a geographic distribution of 37,500 km<sup>2</sup> and demonstrated a highly fragmented population, evidently under severe decline due to ongoing and widespread deforestation. The population was estimated to be between 6,000 and 14,000 individuals. Pinto (1994) also identified home ranges which were larger than those used in the 1990 VORTEX simulation. Tackling other recommendations, his study identified a number of areas with potential for the expansion of the reserve network for this animal, although specific action has yet to be taken.

There is a long-term environmental education program coor-

**Table 3.** Principal recommendations for action for the conservation of *Leontopithecus chrysopygus* arising from the PVA Workshop on lion tamarins in 1990.

1. A survey and census of populations outside the Morro do Diabo State Park and Caetetus State Biological Reserve.
2. A census of the population in the Caetetus State Biological Reserve.
3. Increase in support for the Rio de Janeiro Primate (CPRJ), the principal breeding center for the species.
4. Measures to control forest fires in the protected areas.
5. Development of a masterplan for the management of the captive population.
6. Environmental education in the vicinities of the protected areas.
7. Habitat restoration in the protected areas.
8. Increase funding for surveillance guards and park wardens.
9. Define the limits of the Morro do Diabo State Park.
10. Develop management plans for the protected areas.
11. Create buffer zones around the protected areas.
12. Continue ecological, behavioral and demographic fieldwork.
13. Identify potential areas for restocking.

Sources: Seal *et al.* (1990), Valladares-Padua *et al.* (1990)

inated by Alves (1991; Padua *et al.* 1990; Nagagata 1994), which has included the recent construction of a Nature Center and a temporary holding facility for locally confiscated or donated animals. Dietz *et al.* (1994c) have begun a long term research program on the populations and ecology of golden-headed lion tamarins in the Una Reserve. The distribution survey and the observations of Dietz *et al.* (1994c) in the Reserve are showing that group sizes and population densities may vary between different parts of the geographic range, along with differing habitats in terms of forest structure, composition, and seasonality of food resources. Ecological studies examining these aspects are fundamental for a more realistic appraisal through PVA analyses. A reintroduction program is believed to be unnecessary at the present, mainly because there are still sufficient numbers in the wild, although forest destruction continues, there is not yet sufficient protected habitat for a reintroduction, and the causes of the decline have not yet been controlled (Kleiman 1990; Kleiman *et al.* 1994; see Pinto and Rylands in press).

### *Leontopithecus chrysopygus*

A single and small population of black lion tamarins, *Leontopithecus chrysopygus*, has been maintained in the Rio de Janeiro Primate Center since the early 1970's, but, with the influx of approximately 20 animals, the São Paulo Zoo and the Jersey Wildlife Preservation Trust have also become involved, and the 1992 studbook recorded 81 individuals in these three institutions. The growth of the captive population has not been as rapid as it has for *rosalia* and *chrysomelas*, but following the recommendations of the PVA workshop, a number of other zoos will be included in the program in the near future, and it is expected that the captive population will reach 500 animals in only a few years. There is a serious problem regarding the small founder population for this species, as pointed out by Mansour and Ballou (1994). Viability analyses have shown that the present situation with only 18 founders will demand the maintenance of something over 600 animals in order to minimize loss of heterozygosity. This is recognized as unacceptable in terms of financial costs and the use of zoo space. The options of abandoning the breeding program and concentrating heavily on the protection and management of the five wild populations surviving or of increasing the number of founders by 25 or 30 animals were discussed at the 1994 meeting of the International Committees. The addition of founders is ur-

**Table 2.** Principal recommendations for action for the conservation of *Leontopithecus chrysomelas* arising from the PVA workshop on lion tamarins in 1990.

1. Measures to increase the number, size, and effectiveness of existing protected areas. Includes the removal of squatters, improvement of the infrastructure, acquisition of land, a lion tamarin population survey, and a study of the possibilities of restoration of degraded land in the Una Biological Reserve. Also measures to secure the protected status of two smaller areas; the forested part of the Lemos Maia Experimental Station and the Canavieiras Experimental Station under the administration of the Regional Cocoa Growing Authority (CEPLAC).
2. Concerning potential protected areas. Includes a vegetation survey, a survey of the distribution and status of *L. chrysomelas*, the identification of potential areas, studies on forest regeneration and abandoned cocoa plantations, and a study of the rates and causes of deforestation in the region.
3. Environmental education. Includes targeting landowners with proposals for the creation of private reserves, reduction of regional and national trade in these animals, and the involvement of local institutions such as the University of Santa Cruz.
4. Captive breeding. Expansion of the network of institutions involved in the program, measures to facilitate exchange between institutions, the transfer of confiscated animals held captive at the Una Biological Reserve, and the construction of a local facility for the temporary maintenance of confiscated animals.
5. Reintroduction. The identification of areas for future reintroductions.

Sources: Seal *et al.* (1990), Rylands *et al.* (1990).



**Table 4.** Principal recommendations for action for the conservation of *Leontopithecus caissara* arising from the PVA Workshop on lion tamarins in 1990, and the subsequent emergency action plan drawn up by the International Committee.

1. Increase the size of the Superagüi National Park to include the entire island, except for the areas containing traditional local communities.
2. The creation of protected areas throughout the continental part of the species' distribution.
3. Improve the surveillance and protection of current reserves.
4. The elaboration of a research program on the ecology, behavior and demographics of the species.
5. The development of an effective environmental education program.
6. Examination of the potential and needs for translocation of threatened subpopulations and for the purposes of management.
7. The establishment of at least two captive breeding colonies.
8. The elaboration of a management plan for the Superagüi National Park.

Sources: Seal *et al.* (1990), Teixeira (1990), Câmara (1993a, 1993b, 1994), Câmara *et al.* (1990).

gent considering the current increase in the captive population.

The 1990 PVA analysis was carried out on the only two areas where the animal was known to exist at the time. They are both reserves: the Morro do Diabo State Park is the largest of any of the protected areas containing lion tamarins, totalling 34,156 ha, and was estimated to contain between 80 and 350 animals; and the Caetetus State Biological Reserve of 2,178 ha was estimated to contain between 8 and 30 animals (Valladares-Padua *et al.* 1990). Despite the size of the Morro do Diabo State Park, the PVA analysis demonstrated that the population of black lion tamarins did not meet the extinction tolerance criteria even for a period of 20 years. The lion tamarins in the Caetetus Reserve were found to have a 78% chance of extinction by the year 2000 (Seal *et al.* 1990). The reason for the low viability of these populations comes from the observation that the groups are smaller and the home ranges are very much larger, reaching over 100 ha, in black lion tamarins when compared to *rosalia* and *chrysomelas* (see Rylands 1993).

A considerable amount of research has been carried out on the black lion tamarin since the 1990 PVA Workshop, principally by Valladares-Padua and his team (Valladares-Padua *et al.* 1994). The total population estimate has been increased to about 1,000, with the finding of four new isolated populations, all however too small to be viable. With a better understanding of the ecology of the species, Valladares-Padua *et al.* (1994) are currently proposing a metapopulation management program involving translocation and monitoring of the wild groups. The program is based on the findings of the PVA analyses. An ongoing and successful environmental education program, centered on the Morro do Diabo State Park, was begun 1988/89 (Padua *et al.* 1990; Padua and Jacobsen 1993; Padua 1994).

#### *Leontopithecus caissara*

Recommendations for the conservation of the black-faced lion tamarin, *Leontopithecus caissara* arising from the 1990 PVA Workshop are summarized in Table 4. This species still lacks a captive breeding program. Conservation efforts on behalf of this animal have been restricted to date to the establishment of an International Committee in 1992, the elaboration of an emergency action plan (most importantly arguing primarily for the need for an effective protection of the Superagüi National Park) (Câmara 1993a, 1993b, 1994), its listing as an endangered species by the Brazilian Government (Ibama Edict No.045/92N, 27 April 1992), and an exhaustive search to define the total population size and its

distribution in the wild (Lorini and Persson 1994a, 1994b; Persson and Lorini 1993, 1994; Martuscelli and Rodriguez 1992; Rodriguez *et al.* 1992). The threats to this species are numerous, and include the fact that the extremely reduced populations are isolated and divided into two blocks (island of Superagüi and the continent), the highly precarious situation of the Superagüi National Park, the existence of groups on part of the island not covered by the Park, tourism, local human populations on the island (including activities threatening the integrity of the Park, such as buffalo ranching and extractivism), the naturally slow recovery of the coastal, sandy-soil vegetation (*restinga*), local trade in the animals, and the lack of a captive breeding program (Câmara 1993a, 1993b; Câmara *et al.* 1990; Teixeira 1990).

The known distribution to date does not exceed 300 km<sup>2</sup> and the total population on the island of Superagüi and on the mainland is believed to be around 250 animals (Lorini and Persson 1994a, 1994b; Persson and Lorini 1993, 1994; Martuscelli and Rodriguez 1992; Rodriguez *et al.* 1992). A PVA analysis was carried out on the population estimated for the Superagüi National Park, the island where it was discovered. The model used the golden lion tamarin population parameters for 165 animals in the Park, and indicated an extinction probability of more than 99% over 100 years. Two teams of researchers are completing surveys which include careful descriptions of the habitats. One of them is also attempting an ecological study of wild groups, but as yet with little success. *L. caissara* is the southernmost of the callitrichids, and the evidence to date suggests very low population densities.

**Table 5.** Summary of the status in captivity and in the wild of the four lion tamarins, *Leontopithecus rosalia* (GLT), *L. chrysomelas* (GHLT), *L. chrysopygus* (BLT), and *L. caissara* (BFLT)

| Captive Population     | GLT  | GHLT                  | BLT              | BFLT |
|------------------------|--|-----------------------|------------------|------|
| Size                   | 500+<br>(stabilized)   | 500+<br>(stabilizing) | 80+<br>(growing) | None |
| Institutions           | 125  | 49                    | 4                | -    |
| Founders               | 43   | 154                   | 18               | -    |
| <b>Wild Population</b> | <b>GLT - <i>Leontopithecus rosalia</i> - Critically Endangered</b>   |                       |                  |      |
| Distribution           | c. 105 km <sup>2</sup> (actual occurrence)   |                       |                  |      |
| Total Population Size  | c. 559 (470-631)   |                       |                  |      |
| Protected Area         | Poço da Antas Biological Reserve (5,500 ha), pop. = c. 360   |                       |                  |      |
| Other Areas            | 5 (privately owned) + 12 isolated groups in 9 areas  |                       |                  |      |
| <b>Wild Population</b> | <b>GHLT - <i>Leontopithecus chrysomelas</i> - Endangered</b>   |                       |                  |      |
| Distribution           | 37,500 km <sup>2</sup> (geographic range)  |                       |                  |      |
| Total Population Size  | 6,000-14,000   |                       |                  |      |
| Protected Areas        | Una Biological Reserve (7,059 ha), pop. = c. 416<br>Lemos Maia Experimental Station (240 ha), pop. = c. 17<br>Djalma Bahia Experimental Station (270 ha), pop. = c. 14<br>Canavieiras Experimental Station, pop. = c. 24 |                       |                  |      |
| Other Areas            | Numerous   |                       |                  |      |
| <b>Wild Population</b> | <b>BLT - <i>Leontopithecus chrysopygus</i> - Critically Endangered</b>   |                       |                  |      |
| Distribution           | c. 286 km <sup>2</sup> (actual occurrence)   |                       |                  |      |
| Total Population Size  | c. 1000  |                       |                  |      |
| Protected Areas        | Morro do Diabo State Park (34,156 ha), pop. = c. 821<br>Caetetus State Ecological Station (2178 ha), pop. = c. 69  |                       |                  |      |
| Other Areas            | 4, pop. = c. 28  |                       |                  |      |
| <b>Wild Population</b> | <b>BFLT - <i>Leontopithecus caissara</i> - Critically Endangered</b>   |                       |                  |      |
| Distribution           | c. 300 km <sup>2</sup> (geographic range)  |                       |                  |      |
| Total Population Size  | c. 260   |                       |                  |      |
| Protected Areas        | Superagüi National Park (21,400 ha), pop. = c. 121<br>Jacupiranga State Park (150,000 ha), pop. = ?  |                       |                  |      |

Sources: For captive populations: GLT - Ballou (1993), GHLT - De Bois (1993, 1994), BLT - Valladares-Padua and Simon (1992); For wild populations: GLT - Kierulff (1993a, 1993b), GHLT - Pinto (1994), Pinto and Tavares (1994), Pinto and Rylands (in press), BLT - Valladares-Padua *et al.* (1994), Valladares-Padua and Cullen Jr. (1994), BHLT - Lorini and Persson (1994a, 1994b).

Resources or temperatures may be critical for this species and, as suggested by Carlos Peres (pers.comm.), may under any circumstances be resulting in periodic localized extinctions throughout its distribution.

## Discussion

To summarize, we can see that the four lion tamarin species are in different situations regarding their status in captivity and in the wild. Captive populations have reached over five hundred in *rosalia* and *chrysomelas*, with *chrysomelas* having the healthiest population in terms of the highest number of founders. The captive population of *chrysopygus*, the black lion tamarin, is beginning to grow but urgently requires new founders (Table 5). The importance of the PVA analyses for the captive management of these species is unquestionable.

In the wild, the golden lion tamarin, the black lion tamarin, and the black-faced lion tamarin, all fall within the threatened category of "critical" as defined in the new Mace-Lande method for the categorization of threatened species adopted by the World Conservation Union (IUCN) (Mace and Stuart, 1994; Rylands *et al.* in press). *L. chrysomelas* is the most numerous of the species, but it is endangered due the fragmentation of the populations and forest destruction.

The use of PVA analyses has channeled and oriented conservation efforts over the last few years and is a fundamental tool when dealing with such reduced and fragmented populations which demand active management. In the simplest terms, perhaps one of the most important results is the fact that the PVA analyses have formally refuted the prospects for long-term survival of the populations in the various protected areas. This has been most significant in discouraging complacency with regard to their protection and management, and the creation of further conservation units. Likewise PVA analyses have, as argued earlier, brought into question the validity of running the analyses as if all four species were identical in their population parameters. This has underlined the need to understand the basic ecology of these animals, something which, despite nearly twenty years of research and conservation efforts is surprisingly still lacking. Feeding ecology and information on the distribution and abundance of food resources in space and time, aspects which affect population size, population density, group size, home range size, and reproduction, are only now beginning to be studied. The best and worst scenarios can be modelled, but the power of these analyses will lie in the extent to which they can analyze *reality*. These real scenarios depend on the quality and range of studies on the populations and ecology of the species.

Information obtained since 1990 has indicated that it is probably unreal to use the population parameters obtained from just one population of one of the species. It is highly likely that population parameters are different for the different populations of the same species, and certainly for the different species under highly different ecological conditions. Certainly the eastern (more coastal) populations of *chrysomelas* and *rosalia* will be different from those in the west of their geographical distributions. Likewise, it would seem that the group sizes, home ranges, population densities, and reproductive rates of *chrysopygus* and *caissara* are very different

from those of *rosalia* and *chrysomelas* (see Rylands 1993).

PVA analysis used as an ongoing process of perfecting the data base and as a means of providing a consistent and periodic re-evaluation of conservation status has proved to be an important tool for guiding the conservation measures and research priorities for the four lion tamarin species.

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# Viability Analyses of an Isolated Population of Muriqui Monkeys (*Brachyteles arachnoides*): Implications for Primate Conservation and Demography

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## Introduction

The utility of population viability analyses (PVAs) for assessing extinction risks for endangered primates has recently been challenged on both practical and scientific grounds (Harcourt 1995). In addition to the practical difficulties of obtaining accurate demographic data for long-lived primates, PVA programs make assumptions about demographic processes that may not apply uniformly to all species (Walters 1991; Reed and Dobson 1993). Little is known, for example, about the actual effects of inbreeding depression in the wild (Caughley 1994), or about the degree to which rules of thumb that emphasize reproductive variables such as female age at first reproduction or reproductive rates can be generalized across primates with different life histories (Dobson and Lyles 1989; Soulé 1987). Demographic models also need to more fully integrate the effects of ecological variables on primate populations (Shaffer 1987; Lande 1988; Boyce 1992). As Harcourt (1995) notes, in most cases this involves incorporating the effects of habitat disturbance or loss into primate viability models. In some instances, however, modeling improvements in habitat availability and size may be more appropriately justified.

Despite these caveats, PVAs can still be productive first steps in the process of understanding how endangered primate populations may respond to specified demographic events. By comparing observed and hypothetical demographic parameters for particular populations that have been monitored closely over time, PVAs can also help to identify species-specific rules of thumb for evaluating data from censuses or short-term field studies.

This paper examines the viability of one population of muriqui monkeys (*Brachyteles arachnoides*) inhabiting the 800 ha forest at the Estação Biológica de Caratinga (EBC), located at Fazenda Montes Claros in Minas Gerais, Brazil (Strier 1991, 1992). The demographic and life history data, compiled over a 12-year period, are also used to evaluate some fundamental assumptions that may affect the reliability of PVAs for muriquis, and possibly other primates, and to identify key demographic variables that can be readily obtained from census data at other sites.

Muriquis meet established criteria for critically endangered species (IUCN 1994), largely because deforestation throughout their

Atlantic forest habitat in southeastern Brazil has led to a highly fragmented distribution with small population sizes. In 1987, muriquis were known to occur at only 11 locations (Mittermeier *et al.* 1987). Although recent reports of additional localities in the states of Espírito Santo (Mendes and Chiarelli 1993) and São Paulo (Martuscelli *et al.* 1994) have nearly tripled the number of forests now known to support muriquis, estimates of the size of most of these populations are alarmingly low. The absence of long-term demographic and life history data for all but the EBC muriquis imposes severe limitations on the wider application of these viability analyses for the species (Soulé 1987; Soulé and Kohn 1987). Nonetheless, data derived from this population provide a basis for assessing both the future of the EBC muriquis and the critical variables that may affect the viability of muriquis at other sites.

Muriquis are also ideally suited for evaluating the presumed importance of inbreeding depression, female age at first reproduction, and reproductive rates to demographic models of population viability. For example, although demographic models and captive data indicate that inbreeding has deleterious effects on reproduction and survival, particularly among infants and juveniles (Ralls *et al.* 1986), there have been few supporting data from wild populations until recently (Pettersson 1985; Charlesworth and Charlesworth 1987; O'Brien *et al.* 1987; Shaffer 1987; Wildt *et al.* 1987; Boyce 1992; Caro and Laurenson 1994; Caughley 1994; Jiménez *et al.* 1994; Keller *et al.* 1994; Merola 1994; Vrijenhoek 1994; Fitzsimmons *et al.* 1995; Harcourt 1995).

The failure to consider the evolutionary history of species such as muriquis can also obfuscate extrapolations from theory to reality. Like other endemic Atlantic forest fauna, muriquis have a long evolutionary history of population fragmentation due to the expansion and contraction of the Atlantic forest during the Pleistocene glaciations (Kinzey 1982). The isolation of populations within Pleistocene refugia suggests that muriquis may have survived multiple genetic bottlenecks and repeated bouts of inbreeding and loss of genetic heterogeneity in their evolutionary past. It is unclear, however, how such a history of genetic isolation has affected their fitness, or whether such episodes in the past differ markedly from the fragmentation of their habitat due to human activities over the last quarter century (Strier 1992). If current



conditions of fragmentation resemble those induced by climatic changes during the marmoset's evolutionary history, then the deleterious effects of inbreeding on their viability may not be as evident as demographic models might predict (Soulé and Kohn 1987; Lande 1988; Boyce 1992; Caughley 1994). Comparing extinction probabilities and projected population sizes under simulated inbreeding conditions may provide indirect evidence into the relative importance of considering a species' evolutionary history when evaluating its future viability (Strier in press a).

The demographic patterns of the EBC marmosets show no evidence that inbreeding has had deleterious effects on their survival or fecundity, despite the geographic and genetic isolation of these marmosets for at least the last 40 years. The main study group at this site has increased at a steady rate from 22 to 51 individuals between June 1982 and August 1993 due to extremely low mortality rates and correspondingly high birth rates (Strier 1991, 1993, in press b). With one exception, all females have transferred from their natal group at adolescence (5-7 years of age), and emigrations by natal females have been offset by female immigrations from one of the other two marmoset groups in the forest (Strier *et al.* 1993). Births have been strongly female-biased throughout the study period, and the interbirth interval, estimated at  $36.37 \pm 4.3$  mos (median = 36.00 mos) from 19 successive births involving 11 females has remained stable (Strier in press b). Age at first reproduction, based on the only female known to have reproduced in her natal group, is estimated at 7.5 years, well within the three interbirth intervals identified by Dobson and Lyles (1989) in their comparative data on expanding primate populations (Strier 1991).

The rapid and steady increase in the size of this group has also resulted in a shift in the group's composition. The proportion of adult females (>7 years, see below) to immature females declined from 67% in 1982 to 54% in 1993, and there is some indication that the group may be approaching a stable age distribution in which the proportion of individuals in each age class remains constant (Emlen 1984). Both the skewed age distribution, which included a total absence of juvenile females, and the small group sizes suggest that the population had experienced a bottleneck prior to 1982 due to an unknown catastrophe from which it has been

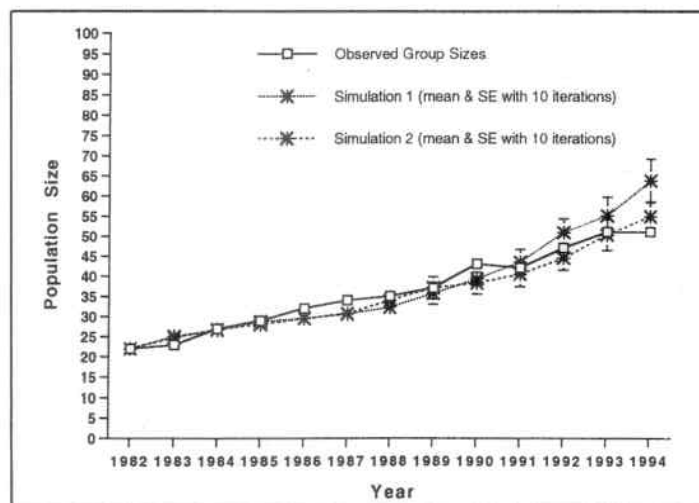


Fig. 1. Comparison of VORTEX trial simulations and observed group sizes. No difference between observed and expected (simulations) was detected. See text for explanation.

recovering ever since. Evaluating simulated effects of catastrophes on reproduction and survival, as well as differences in female age at first reproduction and infant sex ratios, can provide insights into the ways that these demographic variables affect population viability.

Unlike many other endangered primates, marmosets at the EBC have been well-protected. Prohibitions against hunting were in effect prior to the onset of the study, and large feline predators such as jaguars, which are known to prey on marmosets at other locations (e.g., Olmos 1994), are not present at this site, or, in the case of ocelots, have only recently begun to return (Strier pers. obs.). Selective logging has persisted in the forest, but comparative data from other study sites indicate that secondary and regenerating habitats created by such extraction actually support higher marmoset densities than the more floristically pristine forests (Fonseca 1985; Stalling and Robinson 1991; Strier 1992; Pinto *et al.* 1993; Stuart *et al.* 1993). The perimeter of the forest at the EBC has also expanded over the past decade as pasture and cultivated land have been allowed to regenerate. Consequently, both the effective forest size and marmoset carrying capacity at this site have been increasing. The effects of habitat improvement and variance in carrying capacity may thus be especially relevant ecological variables for assessing the future viability of marmosets at this and other privately-owned forests where disturbances due to human activities occur.

## Methods

The demographic and life history data compiled for the EBC marmosets were adapted to meet the parameters required by VORTEX v.6 (Lacy 1993; Lacy *et al.* 1993). VORTEX was selected because of its widespread use in species' action plans for other endangered primates, but like all such programs, it makes specific assumptions that may not necessarily apply to all primates. To evaluate the appropriateness of VORTEX for marmosets, two trial

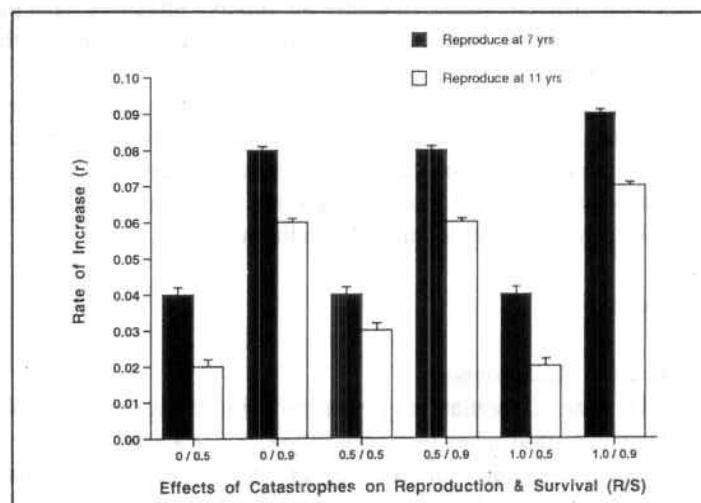


Fig. 2. Effects of catastrophes on rates of population increase (mean and SE). A stable K and no inbreeding depression were modeled here. Effects of catastrophes on reproduction were modeled as 0 (total reproductive failure in years of catastrophes), 0.5 (50% loss in reproduction), and 1.0 (100% reproduction). Effects of catastrophes on survival were modeled as 0.5 and 0.9 (50% and 90% survival in catastrophic years). Paired comparisons between female first reproduction at 7 versus 11 years were significant ( $t = 11.00$ ,  $df = 5$ ,  $p < 0.001$ ).

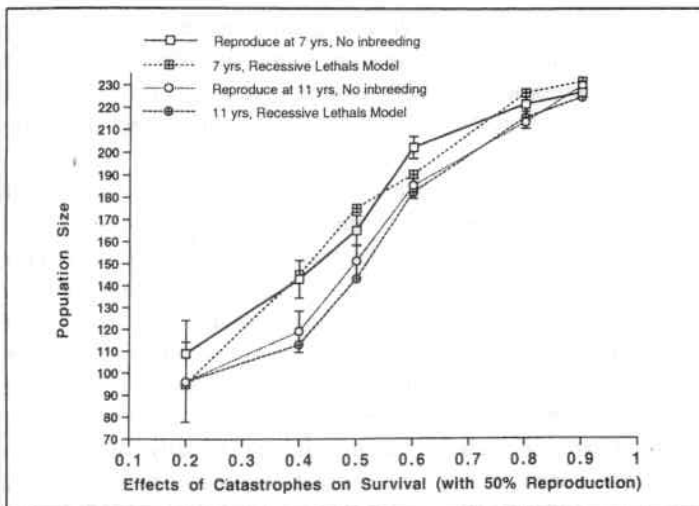


Fig. 3. Effects of survival in catastrophic years on population sizes at 100 years (mean and SE). A stable  $K$  was modeled here. Effects on catastrophes on survival were varied to range from 0.2–0.9 (only 20–90% of the population survived catastrophic years).

simulations with 10 iterations were run for the same 12-year period for which actual data are available. These trials used the 1982 age distribution and the life history and ecological parameters compiled during this period from one of the three muriqui groups now inhabiting this forest.

Both trial simulations yielded annual group sizes nearly identical to the actual group sizes observed during the same 12-year period ( $r = 0.997$ ,  $p < 0.001$ , Fig. 1). Standard errors for each set of 10 iterations were minimal until the final years of the trial. These results suggest that VORTEX can provide credible estimates of group size with the demographic parameters observed during the study period.

The same demographic parameters calculated from the main study group were adopted in the extended simulations. Some of the variables in the VORTEX program were quantitatively derived from the actual 1982–1993 data base; others could only be estimated or anticipated. In both cases, multiple simulations were run with different values to assess the relative effects of each parameter. Variable values and their rationales are provided in the Appendix.

Extended simulations were run for 100 years with 100 iterations each. Means and standard errors based on the 100 iterations are presented. Rates of increase ( $r$ ), extinction probabilities, and population sizes at 10 year intervals and at 100 years were compared under different simulated conditions.

## Results

### Effects of Catastrophes

The rate of population growth proved to be insensitive to the effects of catastrophes (estimated to occur at a rate of 1 per 15 years; see Appendix) on reproduction, even when total reproductive failure occurred in catastrophic years ( $R = 0$ ; Fig. 2). Rates of population growth were, however, highly sensitive to the effects of survival during catastrophic years: higher survivorship (0.90, or 90%, in catastrophic years) also resulted in larger population sizes at 100 years than did lower survivorship (50%), whereas differing effects of catastrophes on reproduction were not detectable.

Both  $r$  and population size at 100 years (Fig. 3) increased with survivorship during catastrophic years. Extinction probabilities were inversely related to survivorship, and were less than 10% when at least 50% of the population survived catastrophes. Extinction probabilities did, however, increase dramatically when survivorship dropped below 50%.

### Effects of Age at First Reproduction

Rates of population increase were consistently and significantly lower when females began reproducing at 11 years of age than when they began reproducing at 7 years (Fig. 2). Across the different effects of catastrophes modeled, age at first reproduction did not correspond to significant differences in population sizes at 100 years when deleterious inbreeding was absent and  $K$  was held constant, or when  $K$  increased without inbreeding depression or with the recessive lethals model of inbreeding. Population sizes at 100 years were significantly smaller when females delayed reproduction until 11 years only when both a constant carrying capacity and the recessive lethal model of inbreeding depression were specified (Figure 3). Extinction probabilities did not differ for early or late age at first reproduction across any of the varying inbreeding or  $K$  conditions.

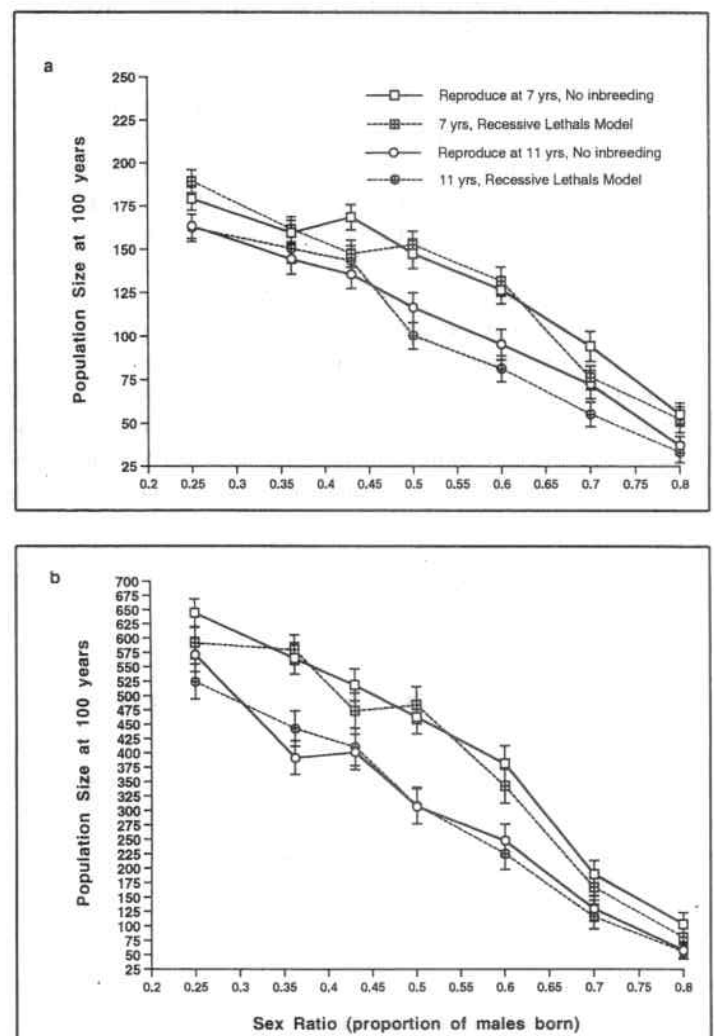


Fig. 4a and b. Effects of sex ratios and constant carrying capacity on population sizes at 100 years (mean and SE). No reproduction and 50% survival in catastrophic years were specified. a)  $K$  is modeled at a constant 240 individuals; b)  $K$  is modeled to increase 5% for 50 years.

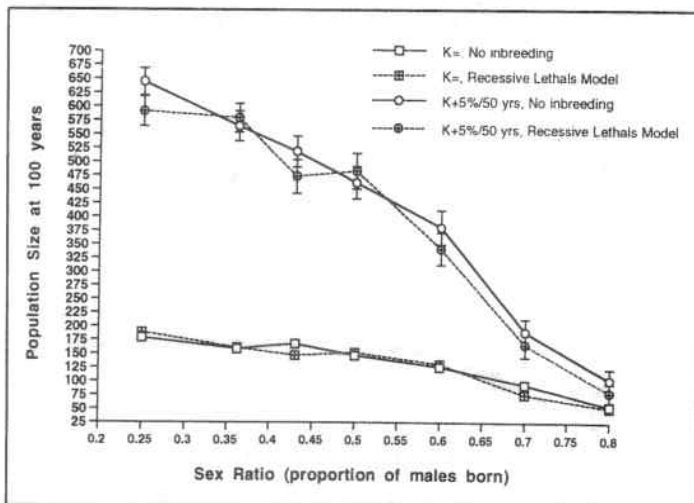


Fig. 5. Effects of varying sex ratios and carrying capacities on population sizes at 100 years (mean and SE).  $K$  is modeled at a constant 240 individuals ( $K=$ ) or permitted to increase 5% for 50 years ( $K+5\%/50$  yrs). Female first reproduction at 7 years and no reproduction and 50% survival in catastrophic years were specified. No inbreeding depression and the recessive lethals model of inbreeding depression are compared.

#### Infant Sex Ratios

Varying the sex ratio of infants had similar effects on population sizes at 100 years independent of whether  $K$  was constant (Fig. 4a) or increased (Fig. 4b). Female-biased sex ratios resulted in consistently larger population sizes at 100 years than did male-biased sex ratios. Extremely male-biased sex ratios (0.80) led populations under expanding  $K$  conditions to converge on the smaller population sizes when  $K$  was held constant (Fig. 5). By 20–30 years into the simulation, populations with infant sex ratios of 0.50 or higher plateaued or began to decline (Fig. 6). The probability of extinction increased as sex ratios increased when  $K$  was held constant and when  $K$  expanded.

#### Inbreeding Models

There were no significant differences between any pairwise comparisons of inbreeding conditions when mean  $r$ , extinction probabilities, and population size at 100 years were compared for the six sets of catastrophic effects when  $K$  was held constant and permitted to increase 5% over 50 years. Population sizes were larger with no inbreeding depression, intermediate with the recessive lethals model, which assumes that each offspring inheriting homozygote lethals is immediately eliminated, and smaller for six of the 10-year intervals with the heterosis model of inbreeding using the default, median value of lethal equivalents supplied by VORTEX (Lacy 1993). Nonetheless, final population sizes at 100 years converged for each condition (Fig. 7).

#### Effects of Carrying Capacity ( $K$ )

The effects of catastrophes on reproduction and survival were consistent and proportionate across varying models of carrying capacity. The reproductive consequences of catastrophes were undistinguishable, while higher survival in catastrophic years resulted in larger population sizes. Greater increases in  $K$  always resulted in larger population sizes at 100 years.

Population sizes at 100 years were more than 50% larger when  $K$  was permitted to increase under severe catastrophic effects (no

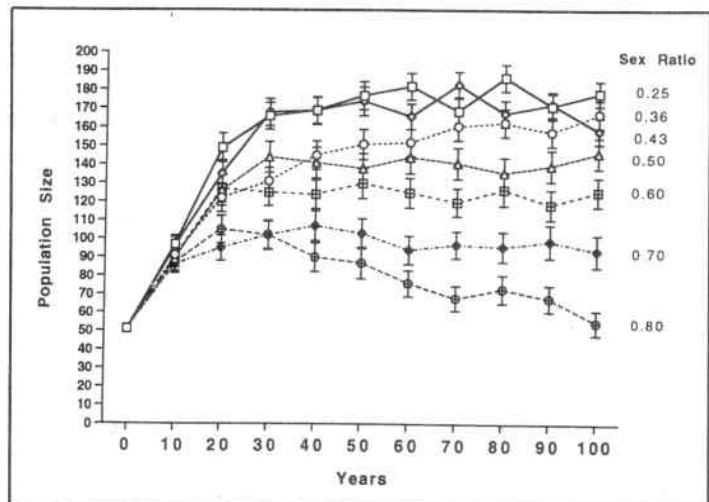


Fig. 6. Effects of varying sex ratios on population sizes at 10 year intervals (mean and SE). Female first reproduction at 7 years, constant  $K$  of 240 individuals, no inbreeding depression, and no reproduction and 50% survival in catastrophic years were specified.

individuals reproduced and 50% survived) than when  $K$  was held constant under the most benign catastrophic conditions. Furthermore, under severe catastrophic conditions, population sizes were much more sensitive to the effects of increasing  $K$  than to inbreeding depression. For both early and delayed age at first reproduction, even populations modeled to experience inbreeding depression began to diverge between 20–30 years, or roughly 2–3 muriqui generations, when  $K$  was permitted to expand (Fig. 8a and b).

#### Effects of Environmental Variance

Differences in environmental variance resulted in significantly different population sizes at 100 years across the various catastrophic conditions. Population sizes were generally larger when the variance in  $K$  was low ( $SD = 10\%$ , or 24 individuals) than when it was high ( $SD = 50\%$ ). Under severe catastrophic conditions, population sizes deviated significantly at 10 year intervals before ultimately converging (Fig. 9). Consistent with the effects of increased  $K$ , the greatest differences from environmental variance occurred 20–30 years into the simulation. The mean probability of extinction was twice as high when environmental variance was 50% ( $0.08 \pm 0.03$ ) than when it was 10% ( $0.04 \pm 0.02$ ), but first population extinction occurred at 43 years in both cases. Indeed, although the number of extinctions caused solely by environmental variance is small compared to other causes in these simulations, the population is nonetheless vulnerable to environmental effects.

#### Discussion

##### Variables Affecting the Viability of the EBC Muriquis

The simulations presented here indicate that the EBC muriquis have a low probability of extinction during the next 100 years. This optimistic assessment is based on the unrealistic assumption that the extraordinarily low mortality, high fecundity, and female-biased sex ratios documented over the last 12 years will persist in the future (see Ginzburg *et al.* 1990). While there is no evidence to date that reproduction is density dependent, it is likely that this situation will change as population size increases unless the carry-



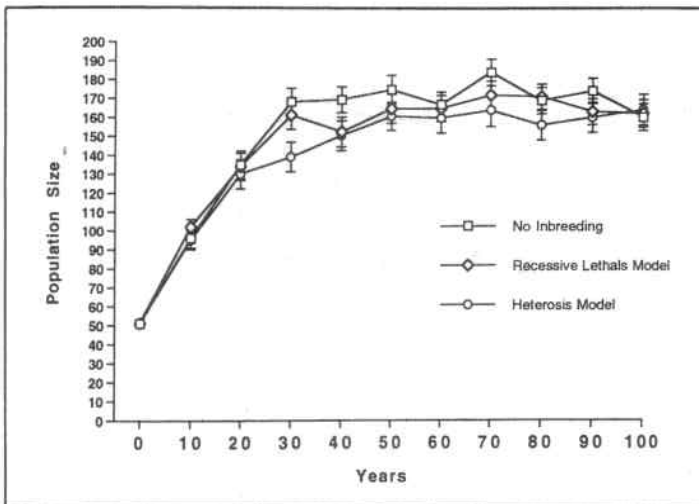


Fig. 7. Effects of inbreeding depression on population size at 10 year intervals (mean and SE). A constant K, female first reproduction at 7 years, and no reproduction and 50% survival in catastrophic years were modeled here. Both models of inbreeding depression in the VORTEX v.6 program are used.

ing capacity of this forest can be increased beyond the monkeys' capacity to populate it (Boyce 1992). Similarly, the strongly female-biased sex ratio is likely to be a stochastic phenomenon (Gabriel *et al.* 1991; Caughley 1994). Increasingly male-biased sex ratios, in addition to higher mortality rates, would have profound effects on the population's viability, as demonstrated by the higher extinction probabilities when sex ratios were simulated at  $\geq 0.50$  and survivorship in catastrophic years dropped below 50%. The importance of continued monitoring of these variables in the EBC muriquis is strongly indicated.

The fact that rates of population increase, extinction probabilities, and population sizes at 100 years were not affected by reproductive failure during catastrophic years may be a consequence of the muriquis' long interbirth intervals. Because only about a third of mature females reproduce in any year, the consequences of a bad year for reproduction are proportionately lower than they would be for a species that reproduced at shorter intervals (Belovsky 1987). More frequent catastrophes that led to total reproductive failure could, nonetheless, inhibit population recovery (Gabriel *et al.* 1991), making continued monitoring of female reproductive success imperative. Similarly, although female age at first reproduction did not alter extinction probabilities, delayed reproduction did result in slower rates of growth. In contrast to Dobson and Lyles' (1989) rule of thumb, however, population growth was still positive when female age at first reproduction was 11 years, and therefore greater than 3 interbirth intervals under the existing female-biased infant sex ratio.

Among the most striking findings to emerge from these simulations is that inbreeding depression, at least as it is modeled in VORTEX v. 6, does not appear to be a serious concern for the EBC muriquis in the next 100 years. This may reflect the fact that muriqui numbers at this site are presently above some critical size, that 100 years is insufficient time for inbreeding depression to affect population size with the muriquis long generation lengths, or that their high birth rate and low mortality rate permit population size to increase above this level fast enough to compensate for losses due to inbreeding (Caughley 1994). Behavioral patterns in which female muriquis do not mate with their sexually active sons,

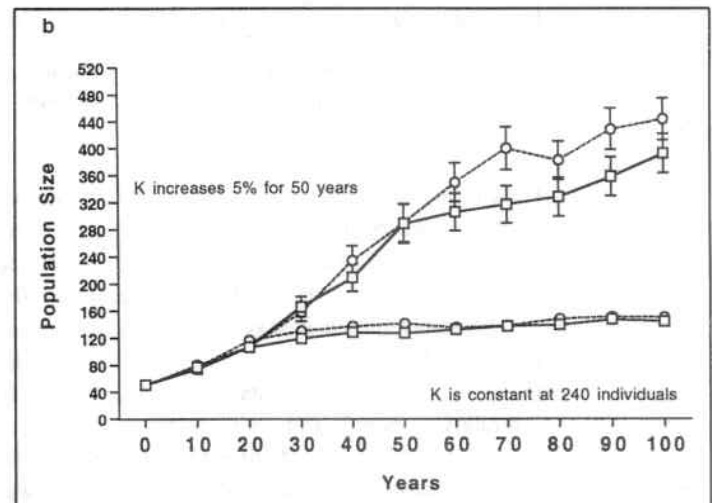
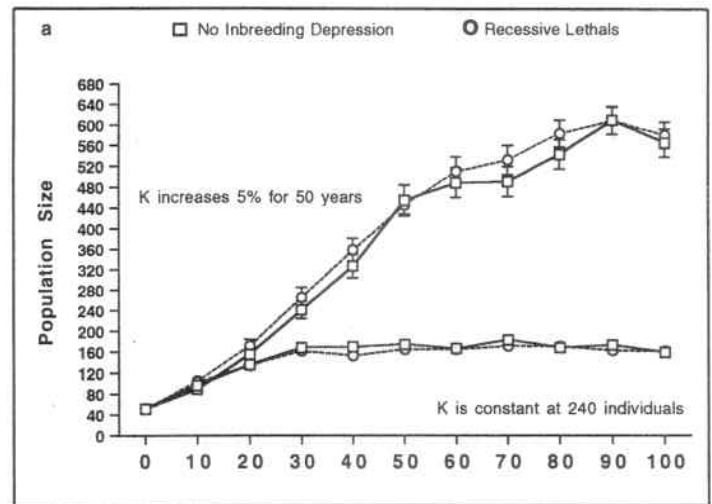


Fig. 8a and b. Effects of changes in carrying capacity on population size at 10 year intervals when a) female first reproduction is 7 years, and b) when female first reproduction is 11 years. No inbreeding depression and the recessive lethals model of inbreeding depression are compared with K is constant or increases 5% for 50 years. No reproduction and 50% survival in catastrophic years were modeled here.

and daughters emigrate from their natal groups during adolescence may also limit the opportunities for inbreeding between close relatives (Strier in press c). The effects of inbreeding depression might become more evident if the number of muriquis at this site dropped due to severe mortality in response to catastrophes or strongly male-biased sex ratios that lower overall fecundity or restrict the availability of unrelated mates (Soulé and Kohn 1989; Boyce 1992).

While it is not possible to control mortality rates or infant sex ratios, the simulations indicate that even a modest increase in the carrying capacity at this site could help buffer this population from catastrophic or stochastic demographic events (Harcourt 1995). Expanding the available habitat now, while mortality rates and sex ratios are still low and birth rates are still high, would permit the population to increase to the point that its long-term viability would not be jeopardized by temporary declines in survival or reproduction.

Increasing carrying capacity and reducing environmental variation in K should lead to larger populations within 20-30 years under the current demographic conditions specified in the simula-

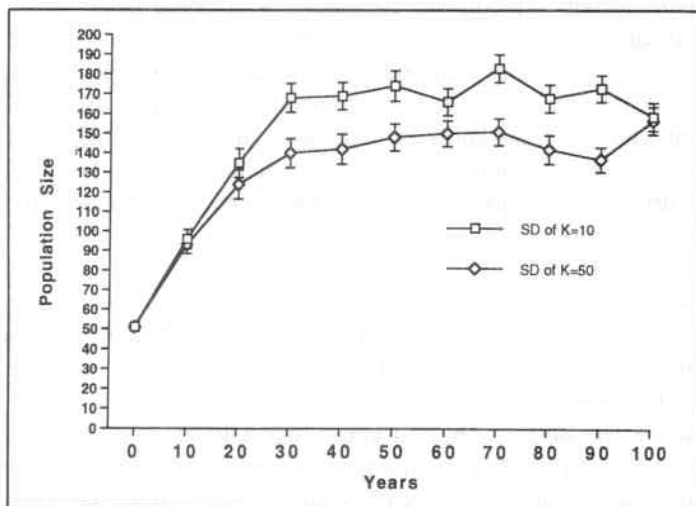


Fig. 9. Effects of environmental variance ( $SD(K)$ ) on population size at 10 year intervals. A stable  $K$ , female age at first reproduction of 7 years, and no inbreeding depression were modeled here. See appendix for explanation of environmental variance. No reproduction and 50% survival in catastrophic years were modeled here. Paired comparisons across the 10 year intervals between  $SD(K) = 1.0\%$  and  $SD(K) = 5.0\%$  were significantly different ( $t = 5.50$ ,  $df = 9$ ,  $p < 0.001$ ).

tions. The fact that 20–30 years into the simulations is also the point at which the effects of higher infant sex ratios on population size become apparent further emphasizes that action to ensure habitat expansion during the next 2–3 murrelet generations will be critical to their long-term viability at this site.

The minimum impact that inbreeding depression appears to have on extinction probabilities and population size at 100 years also supports the argument that translocations to increase genetic diversity are not yet warranted for these murrelets (Strier 1991, 1992). The relatively long generation length for murrelets permits time to develop an informed response to increases in mortality or sex ratios that may ultimately lead to population decline, but immediate attention to habitat recovery and expansion will help to insulate this population from such demographic shifts (Goodman 1987).

#### Implications for Murrelets at Other Sites

The protected status, habitat expansion, and increase in murrelet numbers at the EBC make extrapolations from the present PVA to murrelets at other sites extremely tenuous (Reed and Dobson 1993). It is questionable whether the life history parameters calculated from the long-term data at the EBC are applicable to other populations of murrelets, particularly when the morphological and genetic evidence supporting the distinction of murrelets into northern (*Brachyteleus arachnoides hypoxanthus*) and southern (*B.a. arachnoides*) subspecies are considered (Vieira 1944; Lemos de Sá and Glander 1993). Despite the successful interbreeding of individuals from these regions in captivity (Coimbra-Filho *et al.* 1993, 1994), it is not known whether the earlier ages at first reproduction for both females and males and the shorter interbirth intervals from captivity reflect subspecific or populational variability, or their release from social and/or ecological stresses that may affect wild animals (Strier in press b).

The demographic parameters calculated from the EBC murrelets are even less likely to apply to murrelets inhabiting ecologically different forests. Forest size and composition, degree of human

disturbance, sympatric food competitors, and predator pressures are known to vary widely (Fonseca 1985; Stalling and Robinson 1991; Strier 1992; Pinto *et al.* 1993; Stuart *et al.* 1993). It will only be possible to assess the degree to which these factors affect forest carrying capacity and murrelet demography and viability when comparative data become available. Indeed, even in the present analyses where the relevant demographic variables are well-documented, the constant  $K$  of 240 individuals estimated is subject to doubt (see also rationale in Appendix). The density of 0.3 individuals/ha may be an overestimate of the actual carrying capacity at EBC because sympatric brown howler monkeys (*Alouatta fusca*) and capuchin monkeys (*Cebus apella*) may deplete or compete with murrelets for shared food sources (Mendes 1989; Rímoli in prep.). Conversely, it may underestimate EBC carrying capacity because the extreme heterogeneity of the forest, which includes primary as well as secondary and regenerating forest (Hatton *et al.* 1983), may provide essential microhabitats that can support more murrelets than forests where no primary forest vegetation occurs.

Larger, less disturbed forests support uniformly lower murrelet densities than the smaller disturbed forests like EBC (e.g., Pinto *et al.* 1993), but the suggestion that these differences are due to the absence of abundant secondary and regenerating food resources in the pristine areas remains a hypothesis (Strier 1992). The impact of predation on murrelet mortality rates, which is likely to be greater at large, less disturbed forests where predators are more abundant, also requires further comparative data to evaluate.

Despite these limitations, the EBC data provide potential insights into assessing the viability of murrelets at other localities. First, small populations, with fewer than 50 individuals, are predictably more vulnerable to extinction than larger populations (see Franklin 1980). Enhancing the size of these remnant populations by introducing murrelets would only be warranted, however, in well-protected areas where carrying capacity can be reasonably estimated and the impact of murrelets on other sympatric species can be monitored. Based on the consistent patterns of female dispersal and male philopatry among the EBC murrelets, such introductions should involve only females, but even then, the risks of exposing individuals with parasitic infections to naive hosts must be weighed (Boyce 1992; Strier 1993; Stuart *et al.* 1993).

Populations with more than 50 individuals may prove to be viable and capable of recovering without costly or risky intervention programs provided that they and their habitats are well-protected and that mortality rates are low and birth rates are high. While it is difficult to estimate mortality and birth rates from census data, it is possible to calculate sex ratios from counts of unhabituated animals. Visual determination of sex is relatively easy in murrelets because both males and females have pendulous genitalia that are distinguishable within a few months of birth. Inferring from the present study, populations with infant sex ratios lower than 0.5 are expected to have a higher probability of recovery than those with male-biased sex ratios (Caughley 1994).

The results of the present analyses imply that even small murrelet populations surviving in disturbed habitats merit conservation efforts. The evidence that small-scale disturbances that increase the heterogeneity of these forests may actually increase forest carrying capacity also suggests that controlled, sustainable extraction programs in collaboration with the private owners of these forests

may be beneficial to muriquis as well.

#### *Implications for Interpreting PVAs on Other Primates*

The indistinguishable effects of inbreeding depression on muriqui extinction probabilities and population sizes suggest that the deleterious effects of inbreeding may be overrated in demographic models or that the inbreeding depression modeled in VORTEX is inappropriate for a variety of reasons. Indeed, VORTEX assumes that inbreeding impacts only juvenile survival, and that all animals are initially unrelated. The fact that at least some of the EBC muriquis are known relatives (parent-offspring or siblings), as is likely to be the case in other closed primate populations, suggests that inbreeding projections simulated in VORTEX may not always apply. In addition, because the recessive lethals model of inbreeding assumes that homozygotes are eliminated from the population, there are few ways in which lethals can accumulate in populations such as that of the EBC muriquis, where females migrate between groups within a single, related population (Charlesworth and Charlesworth 1987). Finally, it is possible that although inbreeding had minimal effects on final population sizes at 100 years in the present simulations, populations with different starting sizes may have higher extinction probabilities (Bowman and Falconer 1960).

It is also possible that other aspects of muriqui life histories or demography compensate or override the effects of inbreeding, including their behavioral avoidance of matings between close relatives (Strier in press c). Alternatively it is possible that inbreeding may affect different species to different degrees depending on their evolutionary history (Walters 1991; O'Brien 1994). Mutation rates and genetic heterogeneity are known to vary widely across primates (Caughley 1994), and these differences may be important to consider when applying inbreeding models to viability analyses (Allendorf 1986; Soulé and Kohn 1989; Boyce 1992).

The effects of infant sex ratios on muriqui viability also suggest significant implications for other primates. The finding that EBC muriquis continue to exhibit population growth even when female age at first reproduction exceeds 3 interbirth intervals may be a consequence of their strongly female-biased sex ratio. Evaluating the effects of skewed sex ratios on other primates may lead to refinements in the demographic models used to assess population viability (Gabriel *et al.* 1991; Boyce 1992; Caughley 1994).

Population sizes were consistent in diverging from one another between 20-30 years into simulations comparing different sex ratios, carrying capacities, and environmental variance. If these projections, which correspond to 2-3 muriqui generations, also apply to other primates, they present a paradox for conservation strategies. Species with long generation lengths are generally considered to be more vulnerable to extinction because of their slower reproductive rates (Belovsky 1987). Yet, the same 20-30 years that appear to be critical for ensuring the viability of muriquis may be too long for species with shorter generations. Greater insights into the interactions between generation length and extinction risks are clearly needed.

While it is unadvisable to extend the results from viability analyses of a single population to other populations of the same species or to other species (Gilpin and Soulé 1986), the popular adoption of PVAs by policy makers make evaluating the reliability of PVAs an urgent concern. The limited contributions of female age at first

reproduction, reproductive consequences of catastrophes, and inbreeding depression to muriqui viability in the present analyses support suggestions that models emphasizing these variables may not be widely applicable to wild populations (Thomas 1990). At the same time, the apparent importance of infant sex ratio, catastrophic survival, and carrying capacity to the viability of the EBC muriquis provide examples of alternative variables that may merit closer scrutiny.

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## Appendix

### VORTEX variables and rationales for values entered

|                        |   |
|------------------------|---|
| Number of iterations:  | 100 (10 for trial simulations)            |
| Number of years:       | 100 (12 for trial simulations)            |
| Extinction reports:    | 10 years (annually for trial simulations) |
| Number of populations: | 1   |

**Rationale:** All demographic data were derived from one of the three murequins groups now inhabiting the EBC forest. It is assumed that these data represent this entire population. The group was modeled as a single population owing to the lack of validity of generalizing the demographic parameters from this site to others.

Inbreeding depression: Varied (No for trial simulations)

**Rationale:** The lack of evidence of deleterious effects of inbreeding on the EBC murequins over the past 12 years justified specifying no inbreeding in the trial simulations. However, simulations comparing population viability without inbreeding depression and with both the recessive lethals model and the heterosis model were run holding K constant with female age at first reproduction of 7 years. All other simulations were run without inbreeding depression and with the recessive lethals model of inbreeding depression. The recessive lethals model was used because it assumes that all lethal alleles are removed by natural selection when homozygous and that each founder member of the population carries a single recessive lethal and non-lethal allele. The fact that the population appeared to be recovering from a bottleneck that eliminated nearly the entire juvenile class at the onset of the study provided justification for the assumption that lethal equivalents were low at the onset of the simulations. Survivors are expected to be highly homogeneous. See Charlesworth and Charlesworth (1987) and Lacy (1993) for further details.

Number of types of catastrophes: 1 (0 for trial simulations)

**Rationale:** Any of several possible catastrophes (e.g., drought, fire, epidemic) could occur, but each is assumed to affect reproduction and survivorship similarly.

Probability of catastrophe: 6.67%

**Rationale:** The estimated probability of catastrophes of 1 per 15 years (0.0667) is based on the assumption that a catastrophe had occurred prior to the onset of the study in 1982 when the original group size was small and group composition highly skewed toward adults. A fire that burned roughly 30 ha of forest in 1990 occurred beyond the murequins' home range, but by 1994 the murequins had begun to exploit this regenerating area.

Breeding system: Polygynous

**Rationale:** Determined from data (Strier 1986, 1987, 1992).

Age females begin breeding: Varied (7 years for trial simulations)

**Rationale:** Female age at first reproduction was determined from data to be 7.5 years (Strier 1991). This estimate was based on a single female who reproduced in her natal group. She was an infant in June 1982 and gave birth to her first offspring in September 1989. This may be younger than the age that most females who emigrate from their natal groups reproduce. Indeed, the average age of migration is 72 mos ( $\pm 5.5$  mos; Strier in press b), and the estimated age that immigrant females begin reproducing is 9 years ( $\pm 2$  years; Strier in press b). Thus, extended simulations using 7 and 11 years for female first reproduction were compared.

Age males begin breeding: 7

**Rationale:** Determined from data (Strier in press b). Much younger males have achieved successful fertilizations in captivity (Coimbra-Filho *et al.* 1993), suggesting that social and/or ecological factors may delay the onset of reproductive maturity in the wild.

Age of senescence: 35

**Rationale:** There are no data on senescence in murequins, but dental examination of wild murequins at another site led to an estimated age of >29 years for one female (Lemos de Sá and Glander 1993).

Proportion of males at birth: Varied (0.366 for trial simulations)

**Rationale:** Of a total 35 infants born in the study group from 1983-1993 and the 6 infants that were present in the group in 1982, 26 were females and 15 were males. The sex of one of a set of twins was not determined prior to its death and is not included among the 41 infants on which this ratio is based. The only other infant mortality documented, a male, is included in this ratio. The female-biased sex

ratio may be atypical for these muriquis, or may reflect female age or reproductive experience (Strier in press b). To examine the effects of variation in sex ratios, simulations were also run using ratios from 0.25 (strongly female-biased) to 0.80 (strongly male-biased).

Maximum Litter Size: 2

Rationale: One set of twins was born during the study period (Strier 1991).

Is reproduction density dependent: No

Rationale: There is currently no evidence that reproduction in this group has been affected by group size or density.

Percent of females producing litter sizes (SD) of

0: 69.5 (19.8)

1: 29.7 (20.5)

2: 0.8 (2.9)

Rationale: Calculations are based on all infants born between 1983-1993. Interbirth intervals average roughly 3 years (see text; Strier in press b), so in most years, females are associated with a single infant. Of the 35 births between 1983-1993, 97.14% involved single infants. An average SD of 20 was calculated based on the average 3-year interbirth interval, with 31% of the females reproducing annually from 1982-1993.

| Age-specific mortality (mean and [SD]): | Age | Females    | Males     |
|---|-----|------------|-----------|
|   | 0-1 | 0 (0)      | 0 (0)     |
|   | 1-2 | 0 (0)      | 0 (0)     |
|   | 2-3 | 0 (0)      | 0 (0)     |
|   | 3-4 | 6.3 (17.7) | 10 (22.4) |
|   | 4-5 | 0 (0)      | 0 (0)     |
|   | 5-6 | 0 (0)      | 0 (0)     |
|   | 6-7 | 0 (0)      | 0 (0)     |
|   | >7  | 0 (0)      | 3.4 (8.1) |

Rationale: Determined from data. Mean mortality rates and SD for each age-class were calculated by obtaining the proportion of individuals that died for each year interval, summing these proportions, and dividing them by the number of years in which there were entries for those age classes. For example, there were 5 years in which males fell or should have fallen into the 3-4 year age class. Four of these years had 0% mortality, in one year, 1 of 2 males, or 50% of the 3-4 year old males disappeared and is presumed dead. The total mortality, 50%, was divided by the 5 years in which this age class was represented to yield an average of 10% mortality and an SD of 22.4%. Two of the 11 years in which males were classified in the >7 year age class suffered 25% and 12.5% mortalities (2/8 and 2/7, respectively); the other 9 years included 0% mortalities among adult males. Female disappearances from 5 years of age are treated as emigrations with 0% mortality based on confirmation of their successful integration into new groups. Note that with such low mortality rates, it may be inappropriate to distinguish age and sex specific mortality values.

Do all adult males breed: Yes

Rationale: Determined from data (Strier 1994, in press c).

Stable age distribution: No

| Age | Females (1993) | Males (1993) | Females (1982) | Males (1982) |
|-----|----------------|--------------|----------------|--------------|
| 1   | 2              | 2            | 4              | 2            |
| 2   | 6              | 2            | 0              | 0            |
| 3   | 1              | 1            | 0              | 0            |
| 4   | 2              | 0            | 0              | 0            |
| 5   | 1              | 2            | 0              | 0            |
| 6   | 3              | 1            | 0              | 2*           |
| 7   | 0              | 1            | 0              | 0            |
| 8   | 1              | 2            | 8*             | 6*           |
| 9   | 0              | 0            |                |              |
| 10  | 5              | 0            |                |              |
| 11  | 0              | 0            |                |              |
| 12  | 2              | 2            |                |              |
| 13  | 0              | 0            |                |              |
| 14  | 0              | 0            |                |              |
| 15  | 1              | 0            |                |              |
| 16  | 1              | 0            |                |              |

| Age | Females (1993) | Males (1993) | Females (1982) | Males (1982) |
|-----|----------------|--------------|----------------|--------------|
| 17  | 0              | 1            |                |              |
| 18  | 0              | 0            |                |              |
| 19  | 8*             | 4*           |                |              |
| ≥20 | 0*             | 0*           |                |              |

Rationale: Age distributions were determined from actual situation at the onset of the study in 1982 for the trial simulations and as of August 1993 for the extended simulations. All adults at the onset of the study were assigned a minimum age of 8 years. Asterisks indicate that these are estimated values that may underestimate true age.

Carrying capacity: 240 (100 in trial simulations)

Rationale: Carrying capacity was estimated based on the highest reported density for muriquis, where 12 individuals occupied a 40 ha forest (Lemos de Sá and Glander, 1993). A density of 0.3 individuals per ha at EBC yields a K of 240 muriquis in this 800 ha forest. See text for further qualifications.

SD in K due to EV: Varied (10% in trial simulations)

Rationale: Environmental variance was estimated to be 10%, equal to 24 individuals in the extended simulations and 10 individuals in the trial simulations. Extended simulations were also run with an EV of 50%, equal to 120 individuals. The EV of 10% reflects the highest mortality observed for any age class, but otherwise there is no empirical basis for this or the higher estimated value.

Trend in K? Varied (Yes in trial simulations)

Rationale: Habitat regeneration along the perimeter of the forest during the 12-year study period has resulted in an increase in K. The muriquis have extended their home range to include these regenerating areas where greater heterogeneity in vegetation increases food supplies (Strier *et al.* 1993). Extended simulations were run holding K constant at 240 individuals and increasing K to various degrees.

Years K changes: Varied (12 in trial simulation)

Rationale: K was permitted to increase over 25 and 50 years in some extended simulations. See below.

Percent increase in K: Varied (5% in trial simulations)

Rationale: Extended simulations in which K showed a trend compared the effects of increasing K 2% over 50 years, 5% over 25 years, and 5% over 50 years. The 5% increase in K over 50 years is likely to be an underestimate of the actual transformation of regenerating forest into exploitable food sources, particularly because some pasture areas that previously isolated the EBC forest from neighboring forests are regenerating into corridors that make neighboring forests accessible to muriquis.

No harvesting or other manipulation of population during this period were modeled.



# Estimation of Parameters in Population Viability Analysis: A Case Study of the Tana River Crested Mangabey

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Population viability analysis (PVA) can be thought of as a species' risk assessment. Soulé (1987) defines a PVA as the systematic evaluation of the relative importance of factors that place populations at risk of extinction. The objective of PVA therefore is to evaluate the genetic and demographic health of populations. Some risk factors have obvious effects. Catastrophic habitat destruction may cause density independent population responses such as the elimination of entire populations or forced migrations. Other factors are more subtle, such as loss of reproductive potential due to inbreeding (Ralls *et al.* 1979). Sometimes several factors may interact to affect populations.

There are fundamental problems in conducting PVAs for little-known, long-lived species such as primates. Usually databases for primate species are limited. Most primate studies are of short duration, normally one to two years, and study a single group (Dobson and Lyles 1989). Most primate species however live at least 10 years and as long as 40 years. Estimates of age-specific survival require long-term data on known animals, or a short-term census on a large sample. Reproductive parameters such as birth sex ratio, interbirth interval, and age at first reproduction usually require several years of data collection (Robinson 1988). Finally, many demographic parameters cannot be estimated with confidence from a single group.

One solution to the problem of sparse datasets is to use data from captive groups to fill in blanks in demographic information. This is particularly useful for reproductive parameters and longevity data, but we must recognize that some species do better in captivity and the parameters do not always reflect the wild state. Another solution is to use the data available as a first approximation, acknowledging that better data are needed. The best solution, however, is to design studies for PVAs such that they maximize the return on information for the time invested.

Ideally, a short study should focus intensively on three or more groups, and should collect population data on as many additional groups as possible. A major weakness of many PVAs to date has been the lack of suitable data for use in the modelling process. Frequently the research objective was social behavior and few demographic data were collected. Often, group counts were not rep-

licated over time, limiting their usefulness for analyzing population trends.

In this paper, we use a study of the Tana River crested mangabey (*Cercocebus galerritus galerritus*) as an example of a short-term primate study that generated data sufficient for population viability analysis. We were interested in projecting future population trends for this rare primate to use as guides to actions necessary for conservation. Using mangabey data, we describe techniques that allow for estimation or simulation of a number of demographic parameters useful in PVA analysis. We explore a number of genetic and demographic models and check for consistency in results. PVA is an exploratory process that helps clarify relationships between parameters and processes. Examining several models therefore is a useful and cautious approach to PVA. Many of the results discussed here have been published previously (Kinnaird and O'Brien 1991).

## The Tana River Crested Mangabey

The Tana River crested mangabey (Figure 1) is a species experiencing many factors that contribute to endangerment. It has a small population size, estimated in 1989 at 725 individuals in 32 to 35 social groups (Kinnaird and O'Brien 1991). It is a forest primate restricted in range to approximately 25 small patches of gallery forest bordering the lower Tana river in eastern Kenya (Figure 2). The mangabey population has declined despite the creation of a reserve for the protection of the mangabey and Tana River red colobus (*Colobus badius rufomitratus*). Kinnaird *et al.* (1990) speculated that the decline resulted from forest destruction and fragmentation due, in part, to agricultural expansion.

The mangabeys have been the subject of two research projects conducted by Homewood in 1975 (Homewood 1978) and Kinnaird in 1987 (Kinnaird 1990a). Both studies were approximately two years long, both censused the entire population, and both collected detailed data on several mangabey groups (Table 1). Life history data from Homewood (1978), Kinnaird (1990a, 1990b) and Kinnaird and O'Brien (1991) form the basis for parameter estimates used in modelling.

## Choice of Models

There are two very different approaches to the problem of estimating viable populations: genetic and demographic. Genetic models are concerned with the effective population size,  $N_e$ , and the loss of genetic variation through inbreeding and genetic drift (Lande and Barrowclough 1987). Genetic models also are used to address problems of population fragmentation (metapopulations) and isolation (Gilpin and Hanski 1991). For example, Wright's island model and linear stepping stone models (Wright 1943; Kimura and Weiss 1964) may be used to assess spatial isolation in fragmented populations.

The demographic approach, on the other hand, is concerned with extinction of populations through random demographic events. Random demographic events include population bottlenecks, catastrophic population declines, and disease outbreaks. These models are concerned with estimates of rates of increase, environmental variance and the impact of density independent catastrophic events. Models incorporating environmental stochasticity have been developed by Leigh (1981) and Goodman (1987). Models based on probability of a catastrophic event are also available (Shaffer 1983). Models such as VORTEX (Lacy *et al.* 1993) have attempted to combine genetic and demographic aspects by following individuals through simulated life histories and then pinpointing times when genetic or demographic factors become significant. In general, demographic factors more often lead to extinction than genetic factors (Lande 1988; Caughley 1994).

## Genetic Models

The effective population size,  $N_e$ , is the size of an ideal population that would undergo the same amount of random drift as the actual or census population (Wright 1931).  $N_e$  generally is used as a measure of the risk of losing genetic variation. Estimates of  $N_e$  provide first approximations of the magnitude of potential genetic problems and the range of genetic loss likely to take place. If estimation of  $N_e$  is an objective of a population survey, censuses should be repeated for at least two years and accurate estimates of group composition collected. At its simplest, maximum effective population size is twice the breeding population size (Wright 1931).  $N_e$ , however, is affected by breeding sex ratio, variance in progeny number, variance in reproductive success, fluctuations in population size, overlapping generations, and population subdivision (Chepko-Sade *et al.* 1987).

**Table 1.** Age/sex composition of seven crested mangabey groups from Kinnaird (1990a) with comparative means from Homewood (1976; 4 groups).

| Forest    | AM   | SAM  | AF   | SAF  | JM | JF   | IM | IF   | Total |
|-----------|------|------|------|------|----|------|----|------|-------|
| Mchelelo  | 1    | 0    | 6    | 0    | 5  | 3    | 1  | 1    | 17    |
| Congolani | 2    | 1    | 6    | 2    | -  | 6    | 3  | 1    | 28    |
| Mnazini K | 2    | 0    | 4    | 0    | 3  | 4    | 3  | 1    | 17    |
| Mnazini   | 2    | 0    | 4    | 0    |    | 3    |    | 2    | 15    |
| Mnazini N | 2    | 1    | 7    | 0    |    | 11   |    | 3    | 24    |
| Guru      | 2    | 1    | 5    | 0    |    | 6    |    | 4    | 18    |
| Baomo     | 2    | 1    | 8    | 0    |    | 12   |    | 2    | 25    |
| Mean      | 1.85 | 0.57 | 5.85 | 0.29 |    | 8.57 |    | 3.00 | 20.5  |
| 1975 Mean | 3.25 | 3.50 | 9.75 |      |    | 6.00 |    | 2.50 | 26.5  |

Key: AM = adult males; SAM = subadult males; JM = juvenile males; AF = adult females; SAF = subadult females; JF = juvenile females; IM = infant males; and IF = infant females



**Fig. 1.** Tana River crested mangabey.

Variance in lifetime reproductive success (RS) is especially important in estimates of  $N_e$  (Wade 1979). Because RS can take a generation to measure empirically, lifetime RS for males and females can be estimated by simulation using data on reproductive lifespan, breeding sex ratio, birth sex ratio, survival estimates, interbirth interval, and male tenure time. We must caution, however, that simulation results are only as good as the parameter estimates used.

In order to calculate  $N_e$  for minimum and maximum estimated populations of mangabeys (Table 2) we obtained estimates of the demographic variables that impact  $N_e$  (Lande and Barrowclough 1987). Unequal sex ratios were based on group composition for seven groups. Bounds on population fluctuation were set by using population estimates from 1975 and 1989. Variance in RS for males and females were simulated by bootstrapping (Efron and Tibshirani 1986) reproduction by females conditional on their survival to each reproductive event, survival of infants, and sex ratio of offspring. Because we lacked data on male breeding opportunities, we used three estimates of male RS based on the likelihood of obtaining breeding tenure in a group one, two or three times, and on surviving through each reproductive year (Table 2). The final range of  $N_e$  after adjusting for fluctuating population size was 87 to 135; this range of values incorporates the best and worst case scenarios. If the underlying data are weak, are short-term, or involve simulation, the most conservative approach is to present a range of results that reflect the uncertainty in the data.

Estimates of  $N_e$  can be further refined by considering the spatial structure of the population. Isolated subpopulations limit the opportunity for gene flow and influence the effective population size. Tana mangabeys are distributed in a linear system of forest patches, separated by a major river. We expected gene flow east to west to be disrupted by the river and gene flow north to south to be impeded by distance and isolation between patches.

We assessed the degree of isolation between forest patches on the same river bank using a stepping stone model (Kimura and Weiss 1964) and between east and west river banks using Wright's island model (Wright 1943). We evaluated the amount of genetic differentiation among forests with the fixation index  $F_{st}$ .  $F_{st}$  values are based on the level of migration within a population. Migration rates may be estimated directly by measuring rate of movement into study groups or estimated by the ratio of males produced

in a population and available for migration (e.g., capable of breeding) to the number of breeding positions in adjacent populations. We estimated short-distance migration for mangabeys using the ratio of males available for migration. Long distance migration was estimated as equal to the mutation rate, as suggested by Kimura and Weiss (1964).

Our  $F_{st}$  estimates suggest that mangabeys on each side of the river are not isolated by forest patchiness, and that migration along the river banks provides adequate mixing (Table 3). The genetic consequences of the demographic structure in the models would predict that only four to five percent of the genetic variance appears due to differentiation among the forests. The demographic structure of the population is such that little genetic divergence would develop among mangabey groups in forest patches on each side of the river.

Gene flow across the river occurs during times of major flooding when river meanders break and entire forests shift from one side of the river to the other. These are uncommon events, happening every 50 to 80 years.  $F_{st}$  values indicate that for each flooding scenario, approximately 50 to 60% of genetic differentiation was predicted to be due to isolation by the river (Table 3). We conclude from this that the river forms a major impediment to gene flow and that isolated subpopulations probably exist on each side of the river. This isolation means that the effective population size of interest is for two subpopulations rather than the entire population. Effective population sizes for the east and west bank of the river average around 36 individuals each. Such small subpopulations may not protect against loss of genetic material.

### Demographic models

Demographic models provide a fundamentally different approach to PVA. The demographic approach is concerned with com-

Table 2. Parameter values for population and estimates of effective population size for male tenure in one, two and three groups (Kinnaid and O'Brien 1991)

| Parameter     | 1975    |         | 1989    |         |
|---------------|---------|---------|---------|---------|
|               | Minimum | Maximum | Minimum | Maximum |
| N             | 1245    | 1511    | 683     | 225     |
| $N_m$         | 47      | 57      | 32      | 35      |
| $N_f$         | 458     | 556     | 193     | 205     |
| $K_f$         | 2.57    | 2.57    | 2.57    | 2.57    |
| $V_f$         | 1.84    | 1.84    | 1.84    | 1.84    |
| $N_e$         | 514     | 624     | 216     | 230     |
| 1 male tenure |         |         |         |         |
| $K_m$         | 7.41    | 7.41    | 4.45    | 4.45    |
| $V_m$         | 44.13   | 44.13   | 15.88   | 15.88   |
| $N_{em}$      | 28      | 34      | 20      | 22      |
| $N_e$         | 107     | 129     | 74      | 80      |
| 2 male tenure |         |         |         |         |
| $K_m$         | 11.85   | 11.85   | 7.13    | 7.13    |
| $V_m$         | 56.37   | 56.37   | 20.41   | 20.41   |
| $N_{em}$      | 36      | 43      | 26      | 28      |
| $N_e$         | 133     | 162     | 93      | 99      |
| 3 male tenure |         |         |         |         |
| $K_m$         | 15.75   | 15.75   | 9.47    | 9.47    |
| $V_m$         | 60.32   | 60.32   | 21.82   | 21.82   |
| $N_{em}$      | 40      | 48      | 28      | 31      |
| $N_e$         | 148     | 179     | 99      | 108     |

Key: N = population size;  $N_m$  = number of adult males;  $N_f$  = number of adult females; K = number of progeny for adult males and females; V = variance in progeny for males and females;  $N_e$  = effective population size;  $N_{em}$  = effective number of males;  $N_{ef}$  = effective number of females.

Table 3. Estimates of  $F_{st}$

| Forests                                 | $F_{st}$ | Model          |
|---|----------|----------------|
| East bank (10 forest patches)           | 0.036    | Stepping stone |
| West bank (13 forest patches)           | 0.048    | Stepping stone |
| East and West (considered as 2 patches) |          |                |
| 80-year floods                          | 0.597    | Island         |
| 50-year floods                          | 0.495    | Island         |

plete extinction of a population through random demographic events. A number of generic demographic and analytical models are available (e.g., RAMAS, VORTEX). The choice of models often depends on the amount of information required and that which is available for the species of concern.

The Tana mangabey population has declined from approximately 1500 to 725 in 15 years (Kinnaid and O'Brien 1991; Marsh 1986). The simplest estimate of time to extinction assumes that a declining population will continue on the same trajectory unless there is a change in the present conditions. Extinction time is calculated by projecting the trend until the population disappears. If the Tana mangabey continues to decline approximately 50% every 15 years the population is expected to go extinct in 150 years.

Many estimates of persistence, or time to extinction, depend on the per capita rate of increase,  $r$ . These methods require estimates of variance in the rate of increase, which in practice are difficult to obtain. If a life table is available for the population, variance in  $r$  can be generated using bootstrapping techniques (Dobson *et al.* 1991). Belovsky (1987) and Caughley (1994) discuss methods for estimating variance in  $r$  with limited data. Once  $r$  and variance of  $r$  are calculated, we can ask 'what if' questions. What if a population has a positive mean  $r$ , but the confidence limits on  $r$  include negative values? As variance in  $r$  increases, the probability that  $r$  will be negative also increases along with the chance of population decline.

For the Tana mangabey, we estimated  $r$  using Cole's (1954) equation and compared it to an estimate of  $r$  derived from the observed exponential rate of increase ( $\lambda$ ) for the three main study groups. Both methods gave an estimate of  $r = 0.11$ . We used Belovsky's (1987) recommendations for estimating variance in  $r$  to arrive at a variance = 0.20. We used these values to generate a distribution for  $r$  and then calculated the probability of  $r$  being negative. Negative  $r$  occurred 42% of the time; therefore,



Fig. 2. Aerial view of the Tana River National Primate Reserve showing patchy distribution of the riverine forests.



mangabeys have a 0.42 probability of going extinct given this distribution of  $r$ . We can determine the probability of going extinct within 100 years by finding the value of  $r$  at which the population goes extinct in exactly 100 years; for all values of  $r$  less than this, the population will go extinct sooner. For the distribution generated above, the population will go extinct within 100 years when  $r$  is -0.06 or less. This occurs in 38% of the trials, giving a probability of extinction within 100 years of 0.38.

We also examined a demographic extinction model developed by Leigh (1981) and modified by Goodman (1987). This model calculates persistence time based on the assumption that populations are subject to environmental variance. We used mean  $r$  and variance in  $r$  as calculated above and the maximum population size from the mid 70s and late 80s to estimate mean persistence time. Results show that the mean persistence time declined from 400 years to 200 years between the 70s and 80s. Mean persistence time in this model, however, is distributed as an asymmetric, negative exponential with the fattest tail closest to zero. The majority of populations with a mean persistence time of 200 years will in fact go extinct in less than 200 years.

Using Goodman's model, we generated distributions of persistence times to determine the probability of Tana mangabey extinction within four time periods. We used mean persistence times of 200, 400, 1000, and 2000 years. The results show for a persistence time of 200 years the probability of going extinct within 100 years is again approximately 0.40. To be 95% certain of survival during the next 100 years, would require a mean persistence time of 2000 years or a population size of nearly 8000 individuals (see Kinnaird and O'Brien 1991, for details).

Models that incorporate life history and demography often require larger populations than those based on genetic considerations alone. Demographic and genetic models, however, look at different aspects of population viability. Random demographic and environmental fluctuation may require a larger population size as a buffer against extinction. Models such as Goodman's have been criticized as being overly simplistic and dependent on a few hard to measure variables (but see Caughley 1994). They predict rigid responses to environmental variance; adaptable species may persist at smaller population sizes.

Application of data for Tana mangabeys to both genetic and demographic models, however, result in similar population requirements. Given the relationship between 1989 population size and  $N_e$ , a census population of approximately 9000 is required for an  $N_e$  of 500, a figure often cited as necessary to maintain genetic variability. These requirements are very similar to the demographic model requirements for a 95% probability of persistence over the next 100 years. The similarities may be fortuitous, but the important point is that all the methods make similar predictions; the present Tana mangabey population is at risk both of loss of genetic variance and possible extinction given its present size of approximately 725 individuals.

### Cautionary Measures

When conducting a PVA, it is important to investigate several models and check for consistency in results. Consider carefully the quality of the parameter estimates and the variance of these

parameter estimates. Whenever possible, study populations and avoid single group studies. Investigate several groups intensively and monitor as many others as possible. Such a strategy will allow calculation of variance estimates and prevent bias due to idiosyncrasies of a single group. If it is not feasible to study more than one group, be extremely careful with data interpretation. Be cautious; always consider minimum and maximum values so that optimistic as well as pessimistic scenarios may be presented. Finally, consider the possibility that a PVA may not be appropriate if the requisite data are not available or if management solutions cannot be found or implemented (Caughley 1994). It is not enough to know that a species will be driven to extinction if there is no initiative for recovery. As Caughley (1994) rightly points out, determination of factors that lead to endangerment of a species or population is not of much use if action is not taken to safeguard the population at risk. The Sumatran rhinoceros PVA and management program serves as an excellent warning of good intentions gone astray; an expenditure of nearly three million dollars resulted in no visible improvement in rhino protection and an unsuccessful captive breeding effort (Rabinowitz 1994). Risk assessment therefore should not be the sole objective of a PVA; a PVA should be used as an indicator of gaps in present knowledge of a species and as a guide for urgent management.

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# PHVA Workshop: Learning to Help the Gibbons of Thailand

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In January of 1992, the deputy director-general of the Royal Thai Forest Department issued an invitation to the Co-coordinator of the American Zoo and Aquarium Association (AZA) Gibbon Species Survival Plan (SSP) Committee (Dr. Ronald Tilson) to conduct a workshop in Thailand to "prepare a set of national guidelines governing the rehabilitation of captive gibbons and their re-introduction into the wild or semi-wild state," and also to help improve the quality of zoos in Thailand in general. The IUCN/SSC Conservation Breeding Specialist Group (CBSG) was enlisted to help plan, coordinate and conduct a Population and Habitat Viability Analysis (PHVA) workshop, which was implemented during 26-29 April, 1994, in Khao Yai National Park, one of the primary gibbon conservation areas of Thailand (Fig. 1). The workshop attracted over 90 local and foreign participants, including representatives of the Forest Department, Thai Zoological Parks Organization, conservation NGOs, animal welfare NGOs and university scientists. The majority of people concerned with gibbons there probably had little, if any, prior understanding of PHVA, and overall, the meeting was an important educational event.

According to the executive summary of the PHVA report (Tunhikorn *et al.* 1994) the AZA's Gibbon Species Survival Plan had been requested to "prepare and conduct a PHVA workshop to assess the risks of extinction in the wild populations and to resolve the growing crisis of too many captive gibbons in Thailand." The CBSG of course realizes that the primary goal of captive management is to supplement and support the extant wild populations as much as possible, and that any program for the captive population of an endangered species must be based on careful evaluation of the condition of natural populations. From the Thai perspective, however, the "gibbon problem" - how to manage all those gibbons in zoos and in private hands - was the main issue of immediate concern. As stated early in the report, there has been a growing crisis of too many captives in Thailand, due largely to continuing poaching, the popularity of baby gibbons as pets, and a continuing ban on primate exports imposed by the Forest Department. Many of the people who attended the workshop were not primarily concerned with wild gibbon populations at all. This fact led to some ambiguity about the aims of the workshop.

In the following sections I will briefly outline the contents of

the workshop and the report (Tunhikorn *et al.* 1994) which followed, and then comment on some of the problems of implementing a gibbon action plan for Thailand. In my opinion, the computer program used in the PHVA workshop has not dealt effectively with the complexity of the problems facing wild gibbon populations. Failure to address this problem adequately has led to some simplistic or insufficiently qualified conclusions. I will therefore discuss some problems inherent in the CBSG's methodology in its current PHVA approach to species conservation, and suggest some remedies. I must share the blame for any deficiencies of the workshop as I was an integral part of it, and helped to shape the draft report as well. The comments about PHVA methodology were developed largely in hindsight, and are intended to be used constructively to help improve future workshops.

## The Workshop

### *Problem Statement*

This initial section included an excellent overview of the "gibbon problem" in Thailand, followed by discussion of the meaning of Population and Habitat Viability Analysis, and the specific objectives of the workshop. The goal of PHVA is the recovery of endangered species and the reduction of the risk of extinction. The goal is placed in the context of the metapopulation (without using the term): "In widely distributed species, local populations may be lost, but are readily re-established from adjacent populations... The goal of recovery is to extract a population out of the extinction vortex by returning its numbers, range and diversity to such levels that normal population dynamics, including temporary extinctions, preclude the extinction process."

It is not clear to me how well this population concept applies to gibbons; it seems more applicable to animals with higher reproductive rates in less stable environments. I suspect that gibbon population fluctuations follow very long-term habitat changes and climate shifts, and that we need to look at an historical time scale extending to up to as long as a million years to see such dynamic changes. They are probably not important within the time frames relevant to the modeling exercises and to our management options.





Fig. 1. Wild gibbon in a fig tree in Khao Yao National Park, Thailand.

This section established two perspectives common to population viability analysis: (1) almost exclusive concentration on modeling factors affecting small populations, and (2) a primary concern with species preservation. These concerns have often been highly justifiable, but they may be less so in the present case. In the case of still widespread and relatively common species such as many of the gibbons, the two concerns seem incompatible.

#### *Habitat and Population Status*

Estimates of areas of broad-leaved evergreen forest were taken from the MASS data base on species, habitats and protected areas of Thailand maintained at the Center for Conservation Biology, Faculty of Science, Mahidol University. A summary of the distribution of contiguous forest areas ("Effective Conservation Units") had already been prepared by Brockelman and Baimai (1993), which greatly facilitated the analysis.

Gibbon densities in Thailand have been crudely estimated from spot surveys or censuses in many protected areas, mostly by myself and S. Srikosamatara over the last 15 years (e.g., Brockelman and Srikosamatara 1993). Some core areas remote from human settlements contain as many as 4 groups per km<sup>2</sup>, but most areas where hunting has occurred have densities closer to 1 group per km<sup>2</sup> or less. Perimeter areas near protected area boundaries were

discounted, as they suffer from more poaching and human disturbance.

Occupied *Hylobates lar* gibbon habitat was found to total about 17,000 km<sup>2</sup> and contain about 110,000 gibbons. *H. pileatus* habitat, in southeast Thailand, totals roughly 5,000 km<sup>2</sup> and contains approximately 30,000 gibbons.

The effective areas of habitat are highly fragmented, and both species are characterized by a few large viable populations and a larger number of smaller ones of questionable long-term viability. For example, the estimated population sizes of *H. lar* range from 100 to 43,000, and of *H. pileatus*, from 150 to 9,000.

#### *Life History and VORTEX Analysis*

The set piece of PHVAs facilitated by the CBSG is an evolving simulation model for personal computer, the VORTEX program, that incorporates very explicit genetic, demographic and ecological assumptions and mimics the dynamic changes that a population may follow for a preset period of time. The brief introduction explains that "The VORTEX program is a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental and genetic stochastic events on wildlife populations." It was run 500 times for each set of conditions programmed. The important result is the proportion of times the population becomes extinct within the preset period; this is regarded as the probability of extinction within the time period.

The program requires reliable life history and demographic data about the populations to be modelled. The relevant data for Thai gibbons were as follows:

|                            |  |
|----------------------------|--|
| Age at first reproduction: | 8 years (females) to 10 years (males)                                  |
| Litter size:               | 1 young/birth  |
| Interbirth interval:       | 3 years  |
| Males breeding:            | all, with monogamy   |
| Mortalities:               | 5% per year for all age classes  |
| Inbreeding:                | none, or else the equivalent of one lethal mutation per diploid genome |

The starting population carrying capacities, frequency and severity of catastrophes, and the rate of extra mortality due to poaching were also varied in the simulations.

It is not possible to summarize all the results here. At the risk of some oversimplification, some of the important conclusions were as follows.

1. The potential (base) growth rate of the population was 2.6 % per year.
2. Obviously, a harvest mortality of more than 2.6 % per year will eventually result in the extinction of all populations.
3. For small populations of 200-1000 individuals, zero risk of extinction can be achieved only if harvest mortality is less than 1% per year.
4. Critically small populations (50-200 individuals) cannot always withstand harvest, and may suffer inbreeding depression.
5. Populations in habitats with low carrying capacities (as opposed to those small populations well below the carrying capacity of the habitat) will suffer more from inbreeding depression.

sion and will require more genetic intervention.

6. It was concluded that 16 of the 31 *H. lar* populations and 6 of 8 of the *H. pileatus* populations are over 1000 individuals and should not require management efforts other than protection.
7. The population growth rates are highly sensitive to changes in the age at first reproduction and the interbirth interval, and so attempts should be made to estimate these parameters more accurately, for both expanding populations and those at carrying capacity. Increase in the age at first reproduction for females to 10 years, or increase in the birth interval to 4 years, will nearly stabilize a population. Based on data (unpublished) for the *H. lar* study population in Khao Yai Park, which is approximately at carrying capacity, I believe that such changes in the birth schedule, rather than changes in mortality, are what result in natural population regulation.

#### *Human Demography and Community Participation*

The small working group on this topic came up with the interesting conclusions that Thai human population growth has been reduced to nearly replacement and is no longer a factor in the decline of gibbon habitat or populations around Khao Yai National Park and most other areas. Rather, there is a greater need for modifying the behavior of people around protected areas where hunting and encroachment still occur.

#### *Genetic Aspects of Gibbon Management*

Genetic management is destined to become important in monitoring the genetic variability of captive and small natural populations. Individual genotyping should be carried out on individuals to be used for breeding programs and for reintroduction (Woodruff 1990, 1992).

Of particular importance in Thailand is the identification of differences, if any, between the subspecies of *H. lar* (*carpenteri*, *entelloides*), and the geographically separated populations of *H. pileatus* (Woodruff 1993). We still do not know if outbreeding depression will result from matings in captivity between individuals from geographically distant *H. lar* populations, and some of these (such as northern Thai *H. lar*) are already endangered. Non-invasive methods of genotyping Thai gibbons have recently been introduced (Garza and Woodruff 1992; Woodruff 1993).

#### *Captive Gibbon Populations in Thailand*

Attempts have been made to census the captive gibbons in zoos, Forest Department facilities, and private collections, and homes. Since 1992 the Forest Department has required registration of all captive gibbons, and about 1800 privately held animals, nearly all *H. lar*, have been registered. There are 377 known animals in zoos, both public and private. Although Forest Department officials regard compliance with the law to be in excess of 75%, NGO representatives believe that at least 50% of private captive gibbons are still unregistered. Thus, the number of captive gibbons in Thailand is probably in the range of 2500-3600.

Although it is believed that the rate of entry of wild gibbons into the captive population is declining, an increasing number have been coming through the cross-border trade from Cambodia, Laos

and Myanmar. The most accessible gibbon populations in Thailand have long been hunted out.

#### *Captive Management*

The working group on captive management covered such topics as transport of gibbons, quarantine, cage design, restraint methods, exhibit and holding facilities, introduction, diseases, diet and record keeping. The group sought to bring Thai practices up to international zoo standards. As the majority of captives in Thailand are held privately by people who know little about how to feed and care for them, improving the way gibbons are treated overall presents considerable challenges. It is cage space, not gibbons, that is in short supply in Thai zoos, and most zoos would like to find a way to get rid of their excess animals. Indeed, many private owners and even large zoos have released large numbers of gibbons in forest areas and abandoned them simply to get rid of them. Such behaviorally abnormal animals have little chance of survival, and most such releases have never been monitored.

#### *Gibbon Diseases*

This working group discussed the state of the art in diagnosing diseases of live animals and in performing proper necropsies. Proper diagnosis is important in animals destined for breeding or reintroduction programs.

#### *Reintroduction*

The process of reintroduction of captive gibbons into the wild was discussed in considerable detail. Proper reintroduction requires attention to the following steps: selection of suitable animals, "rehabilitation" to more natural-like behaviors, medical examination, pair-bond formation prior to release of a breeding pair, selection of release area, public relations near the release area, supervised release, follow-up observations. This is clearly a procedure that requires considerable planning, expertise, and effort to accomplish with much success.

Even though the workshop concluded that intervention in the form of release was not justified by natural population numbers, it was felt that a limited, long-term release program should be carried out as a research project to establish feasibility and to gain additional experience.

#### *Problems Remaining*

##### *Implementation of the Action Plan*

The Thai Gibbon Action Plan at the end of the report succinctly summarizes the results of the workshop in the form of general recommendations. The plan recommends that "This captive management program should be under the direction of the Zoological Parks Organization of Thailand (ZPO), and should have the participation of the gibbons being held by the RFD at long-term holding facilities or sites." This seems reasonable because the ZPO has trained veterinarians and has a better capability for caring for gibbons, even though it does not have facilities for handling the majority of those in captivity. It is the Royal Forest Department, however, that has responsibility for protected area conservation, international trade restrictions and registration of captives. But the RFD does not have sufficient manpower and exper-

tise to implement forest surveys, reintroduction programs, genetic analysis, and research on ecology and behavior. Most expertise in these areas lies in universities, though Thai and foreign academic researchers often engage in collaborative projects with the RFD. The RFD has been somewhat wary of collaborating with zoos, because it has perceived that the mission and interests of zoos do not always coincide with their own. Thai zoos still have to demonstrate that they have a significant role to play in wildlife conservation. Often, ZPO and RFD conservation officials have different views about what are the most important conservation problems in Thailand, and how to solve them.

It will be difficult to implement a management plan for gibbons in Thailand, because there is no single authority with responsibility for management of the diverse aspects that a comprehensive program will call for. The ZPO and RFD lines of authority are separate at government cabinet level, and universities fall under still another government bureau. There is no official who could order such a plan to be implemented. For this reason, species management plans such as gibbon action plans have been discussed, planned and proposed for years but never seriously initiated. Throw into this confusion the diverse interests of highly vocal Thai NGOs, and you have a sure formula for inaction.

Thus, a prerequisite for implementing an action plan for Thailand will be to somehow create a central management authority. This problem has been recognized by insiders for many years, but was considered outside the purview of the workshop, and the mandate of the CBSG. Undoubtedly the problem exists in other countries as well.

#### *The Gibbon Problem*

The problem of excessive numbers of captive gibbons in Thailand was addressed only within the framework of the PHVA protocol, and the conclusion was that the conservation of gibbons in Thailand does not call for vigorous breeding or reintroduction programs. They are not yet endangered. There are several problems with this conclusion. The first is that they certainly *are* endangered within many habitat areas, and have been extirpated from many parts of their range. The global perspective of the CBSG sometimes fails to come to grips with local problems. Secondly, by the time all populations are critically endangered, it may be too late to implement an effective reintroduction program. The expertise and facilities will not be available, and there may not be enough gibbons surviving in captivity for such a program.

Thirdly, even though the excessive captive population is not perceived as a conservation problem, it is still a management problem needing a solution. The solution should be affordable locally, without the need for large international conservation grants that only highly endangered species normally can attract. Some local NGOs, in fact, have raised funds to help house and feed gibbons for the Forestry Department.

#### *What Kind of Population Biology?*

The following is the first conclusion of the Thai Gibbon Action Plan, under the heading "Recommendations for wild Thai gibbon populations":

"The current combined subpopulations of *Hylobates lar* in each of the 4 regions of Thailand are sufficiently large not to require

exchange of individuals between the regions or the addition of captive bred individuals for either genetic or demographic support or augmentation of the population over the next 100 years."

The succeeding recommendations under the heading are based on the outputs of the VORTEX analysis which have been summarized above. This section of the action plan is prefaced by the statement that "The simulations for gibbon populations assumed that there would be no future loss of protected habitat and considered varying levels of removal." By "*levels of removal*" is meant, in the present example, poaching. The quoted conclusion, however, appears to imply that poaching will not be a problem, although I know that this was not the deliberate intention of the authors.

In fact, the poaching problem is the reason why the above conclusion, taken at face value, will likely turn out to be completely false. The statement was simply a "safe" conclusion based on the VORTEX results. I now come to the point, namely that the VORTEX models, and the thrust of the entire PHVA process, are based on threats facing *small* populations, and pay little attention to those facing *large* populations. The fact that large populations exist in all 4 regions of the country does not mean that they are safe, but only that the problems facing them are probably different. (In fact, we ought to be careful about assuming that they really *are* large populations, and not internally fragmented in some way that we are not aware of. Adequate surveys have not been made.)

Poaching pressure is in the process of reducing large populations to small ones in most regions of the country. The major challenge to conservation is to prevent large populations from being reduced to small ones, not simply to save small populations which are about to blink out of existence. Ecosystem conservation efforts and protected area management in fact have the effect of doing this, but species conservation efforts have become fixated on saving small populations. This is highly appropriate when a species has become reduced to a single or very few endangered populations. But when PHVA attempts to deal with species that are fragmented into an array of both large and small populations, it tends to regard the species as safe or not threatened due to the existence of the large populations, and ignore the needs of the small populations because they are not essential to the survival of the species.

On the contrary, we should analyze and tackle the problems facing large populations, and develop programs for saving small populations wherever they are. The global perspective fosters an overriding concern for saving "species" on the earth, but from a local perspective, all populations are equally important. The tragedy is the same when a population disappears, whether the whole species is endangered or not. The Species Survival Commission (SSC) is coming to realize that the threatened categories may be applied to any level of taxon or population, and Mace and Stuart (1994) use the term "taxon" in place of "species" in discussing threatened status. In my view, the CBSG should assume a more local perspective on population conservation when conducting a local workshop. Evolutionary biologists are generally less confident than they used to be about the distinctions between local populations, subspecies and species, and the differences are not uniform throughout the animal kingdom.

The CBSG, which came into existence in response to the need



to promote breeding of small captive populations, then turned its talents to the problems of managing small captive *and* wild populations, now might complete its evolution and develop a protocol for dealing with the biological problems facing *all* populations. The preoccupation of conservation biology theory with small population biology has been discussed by Caughley (1994) in an article which strikes at the core of the issue. Caughley argued that the "large population paradigm" requires development of a better theoretical framework in order to better serve conservation, and my suggestion here is that the PHVA workshops attempt to pioneer in such a development, as they have pioneered in the application of small population biology to conservation. In order to do this they will need increased collaboration from population ecologists and increased inputs from members of the SSC with their more field-oriented expertise. There is little doubt that the CBSG could develop computer models to analyze the threats facing large populations if these were clearly defined, and if we asked the right questions about such populations.

## Conclusions

### *The Workshop*

The gibbon PHVA Workshop was admirably comprehensive in its coverage of gibbon management, and an impressive number of experts participated. Many topics, especially those relating to natural populations, still need to be analyzed in greater depth. By being so comprehensive, the workshop suffered somewhat by lacking a clear focus and purpose.

### *Action Plan*

The gibbon action plan, in its present and very general form, could not be implemented by any single agency. The best strategy is probably to break it down into components for particular agencies or groups of researchers. In fact, in recent years progress has been made along several fronts: (1) university scientists have carried out baseline surveys of some wild populations, developed census methods, and continued long-term study of ecology, social behavior and life history; (2) foreign researchers have pioneered in the genetic typing of Thai gibbon populations; (3) the Forest Department has made progress in censusing the captive population and in reducing the illegal trade in pets; (4) a local NGO, the Wild Animal Rescue Foundation, has provided support and volunteers to help the Forest Department cage and care for confiscated animals; (5) a pilot gibbon rehabilitation and release project has been initiated with volunteer NGO help on Phuket Island, southern Thailand. Thus, there has been some action on gibbon conservation and management, but little coordination, and inadequate funding. The workshop provided an opportunity for persons involved in these efforts to meet and exchange information.

### *The VORTEX Model*

The major biological innovations incorporated in the VORTEX model deal with the threats facing small or endangered populations, although some threats which may face large populations also, such as poaching and catastrophes, are included. PHVA workshops, however, are assigned to deal with species level taxa. The model does not yet deal effectively with the threats facing

large populations and does not have the metapopulation structure that would be required to deal with most species taxa. In my view, there is excessive attention focused at the species level by the SSC and CBSG, and more attention should be focused on saving individual populations of various sizes, or groups of populations connected by dispersal events. Overall, there needs to be a clear connection between modeling efforts and plans to save particular populations. Follow-up meetings or workshops will be required to deal with these problems in more detail.

### *Field Research and Surveys*

If the VORTEX model is to produce meaningful results, accurate life history and population data must be incorporated. For the sake of demonstration and experimentation with parameters, however, we must often settle for simply the best available 'guesstimates' and assumptions. Often, parameters of considerable importance have not been sought in field studies. It is essential that modelers and field workers interact so that information which is important but still poorly known is identified. Field ecologists will also have to help model the declines in *large* populations, and develop appropriate survey and long-term monitoring techniques. Questions that might be asked about large populations include the following:

1. Is the habitat homogeneous or are there barriers to movement and variations in habitat suitability or occupancy?
2. Do poaching and other threats occur throughout the area or are they concentrated in certain areas or around the edges?
3. Is there dispersal out of or into the population or is it completely isolated?
4. Is the population at carrying capacity throughout the area?
5. Are the population's food and water sources stable, or are they threatened?
6. Are migration routes threatened?
7. How does poaching affect the social structure and movements of the population?

Some of the above questions suggest that a large population model will need to have spatial structure, and provision of certain types of heterogeneity. It is likely that such modeling attempts will not leave us too sanguine about the long-term survival chances of large populations.

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

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Homewood, K. M. 1976. Ecology and Behaviour of the Tana Mangabey (*Cercocebus galerritus galerritus*). Unpubl. Ph.D. thesis, University College, London.

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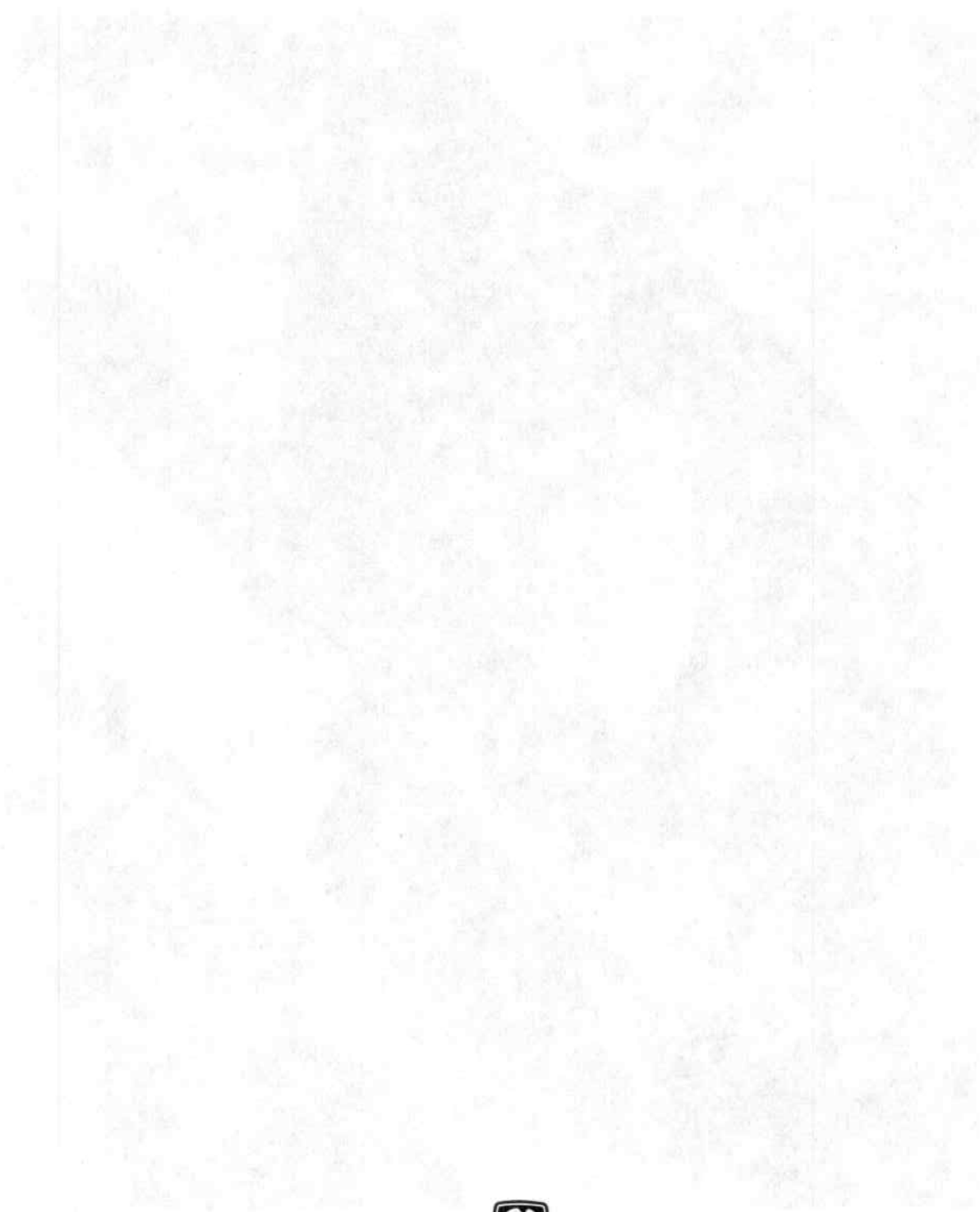
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