



## Demography and Life History of Free-Ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar

Patricia C. Wright<sup>1</sup>

Received November 21, 1994; revised March 3, 1995; accepted April 12, 1995

I conducted the first long-term study of the life history patterns of *Propithecus diadema edwardsi*—Milne-Edward's sifaka—in the rain forests of southeastern Madagascar, beginning in 1986. I report behavioral observations on a total of 33 individuals from three groups over a 9-year span. We captured, marked, and released 21 individuals. Individual group size ranged from three to nine sifakas. Two breeding females lived in groups I and II until 1993. A newly formed group (III) had one breeding female. Age at first reproduction is 4 years for females and 5 years for males. Gestation length is 179 days ( $n = 2$ ). Most births occurred in June ( $n = 17$ ), but infants were also born in May ( $n = 2$ ) and July ( $n = 2$ ). Nine of 21 (43%) infants born died before the age of 1 year, and 15 (67%) died before the age of reproduction. One female bred in her natal group after the death of the resident male and the immigration of an adult male. Another two females disappeared at 4 and 5 years of age; they could have emigrated or died. All 5-to-6-year-old males ( $n = 4$ ) have emigrated from their natal groups to adjacent groups. Two have committed infanticide. Five or more individuals were killed by *Cryptoprocta ferox*. Despite high mortality and offspring dispersal, the number of individuals in the two main groups remained nearly the same over the 9-year study.

**KEY WORDS:** *Propithecus diadema edwardsi*; life history; infanticide; *Cryptoprocta ferox* predation.

<sup>1</sup>Department of Anthropology, SUNY at Stony Brook, Stony Brook, New York 11794.

0164-0291(199510)16:5:1-0

## INTRODUCTION

Detailed data from populations of marked subjects, monitored over decades, is crucial to our understanding of population dynamics and the evolution of behavior. Although long term studies on identifiable individuals began in the 1960s and 1970s for anthropoid primates (Altmann, 1980; Goodall, 1986; Fossey, 1982; Glander, 1980, 1992), counterparts were lacking for prosimian primates. During the last 10 years, long-term demographic studies have begun in the dry forests of western Madagascar on *Lemur catta* and *Propithecus verreauxi* (Sussman, 1991, 1992; Richard *et al.*, 1991).

The study that I describe is the first continuous long-term study of the demography and life history of a Malagasy rain forest primate. I collected data on a free-ranging population of *Propithecus diadema edwardsi* (sifaka), the largest primate in Ranomafana National Park in southeastern Madagascar. This research provides information on life history traits such as age of first reproduction, gestation length, lactation length, and estimates of life span. I present demographic data, including migration patterns, interbirth intervals, mortality patterns, and rates of population growth. Predation by the large, viverrid carnivore, *Cryptoprocta ferox*, and infant killing by immigrant males affect the demography of the Ranomafana sifaka population.

## STUDY SITE

I conducted research in southeastern Madagascar at the Ranomafana National Park (RNP), located at 21°16'S latitude and 47°20'E longitude, about 25 km east of Fianarantsoa (Fig. 1). My study began in 1986, before the 41,000-ha area was designated a national park in 1991 (Wright, 1992).

The Ranomafana National Park ranges in altitude from 500 to 1500 m. I focused on the 5-km<sup>2</sup> Talatakely Trail System (TTS) (Fig. 2), which is at an altitude of 1000 m. TTS was selectively logged in 1986 and 1987. The forest within RNP is classified as submontane rain forest. It contains more stems per hectare than found in Gabon or in most plots in the South American forests (Gentry, 1990; Schatz and Malcomber, 1993). The most common plant family is Monimiaceae (an understory group). The plant families that occupy the most basal area in Ranomafana botanical plots are Lauraceae, Myrtaceae, Elaeocarpaceae, Sterculiaceae, Cunoniaceae, Moraceae, and Sapotaceae (Schatz and Malcomber, 1993). The canopy ranges from 20 to 25 m in height, with some gaps created by selective logging. Large lianas are less common than in comparable tropical forests

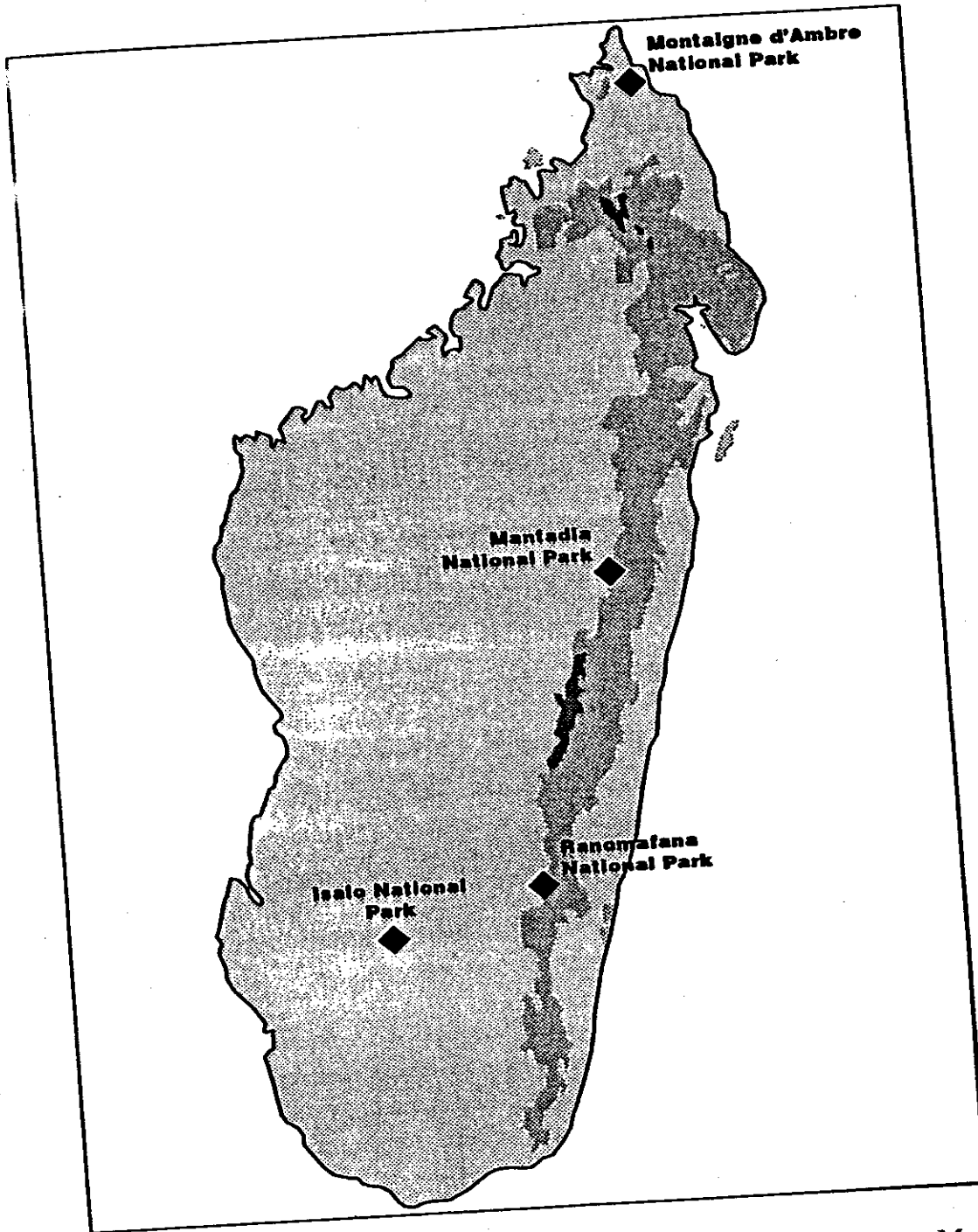
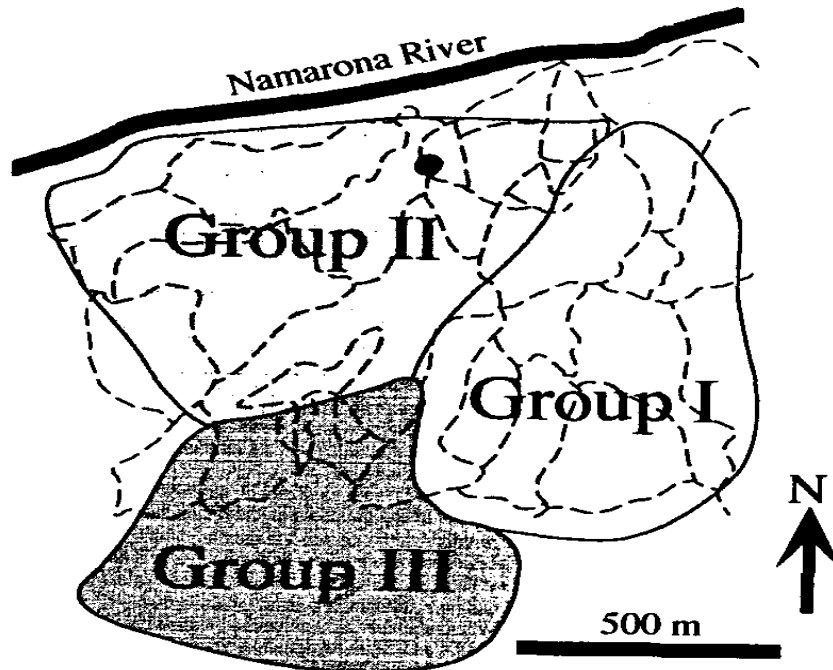


Fig. 1. Location of Ranomafana National Park (RNP) in southeastern Madagascar.

(Schatz and Malcomber, 1993). The rainfall varies from 2300 to 4000 mm, with most of the rain between December and March (Overdorff, 1991, 1993; Hemingway, 1995). The highest ambient temperatures also occurred

COPIED FROM THE ORIGINAL DOCUMENT



**Fig. 2.** The home ranges of the three study groups of *Propithecus diadema edwardsi* within the Talatakely Trail System (TTS) in RNP. Note the location of the RNP Research Cabin and Laboratory (black dot). The Vatoharanana Trail System is 5 km south, and the forest is continuous.

during these months. Average annual temperature is 21°C, with low recordings from June to September (4–12°C).

There are 12 sympatric species of primates in the Ranomafana National Park. *Propithecus diadema edwardsi* is the largest, (5.8 kg). The other 11 species are *Hapalemur aureus*, *Hapalemur simus*, *Hapalemur griseus*, *Eulemur rubriventer*, *Eulemur fulvus rufus*, *Varecia variegata variegata*, *Microcebus rufus*, *Cheirogaleus major*, *Avahi laniger*, *Lepilemur* sp., and *Daubentonia madagascariensis* (Wright, 1992; Glander *et al.*, 1992).

## METHODS

During May 1987, May 1988, May 1991, January 1993, and June 1994, we captured 2–5 adjacent groups (21 subjects) of *Propithecus diadema edwardsi* within the 5-km<sup>2</sup> Talatakely Trail System (TTS) (Fig. 2). We used the Pneu-dart system, whereby disposable nonbarbed darts with a 9-mm needle are delivered via a gun powered by carbon dioxide. The capture drug is Telazol, at a dosage of 20 mg/kg, with the tranquilizing drug Zolazepam HCl (Glander *et al.*, 1992). We fitted each individual with a colored

nylon collar with a tag of a different color and shape. The combination of collar and tag colors signified the individual, for example, Purple Yellow had a purple collar and a yellow tag. In 1987, some individuals wore suede collars, which we replaced with nylon in 1988, due to color changes. In 1987 we tried plastic ear tags as double markings, but by 1988 the sifakas had removed them. We did not use radio collars.

We captured all individuals from a group and carried them to the research cabin to be weighed with portable spring scales and measured. While they were tranquilized, we recorded the following information: body weight and measurements, reproductive state, internal body temperature, hair samples, special marks such as scars, dental condition, testicular length and width, and ectoparasites (Glander *et al.*, 1992). In 1993 and 1994, we took dental impressions for comparisons to estimate tooth wear patterns and age.

With research assistants, I made behavioral observations on two adjacent groups (I and II) from 1986–1994. From June 1992 to October 1994 we observed group III, which held a territory south of and adjacent to those of I and II (Fig. 2). For 3 months in 1986, we took scan samples (Altmann, 1974) on group members' activities every 5 min: 5 days each month on group I and intermittent days on group II. Beginning in 1987, we followed groups I and II simultaneously for five full-day follows once per month. We chose a focal individual for each group each day and recorded its activity, height, and nearest neighbors every 5 min. We also recorded all occurrences of grooming, aggression, infant development, displacement, traveling order, playing, and copulations. Plant parts eaten were identified by local guides and collected for later identification by botanists.

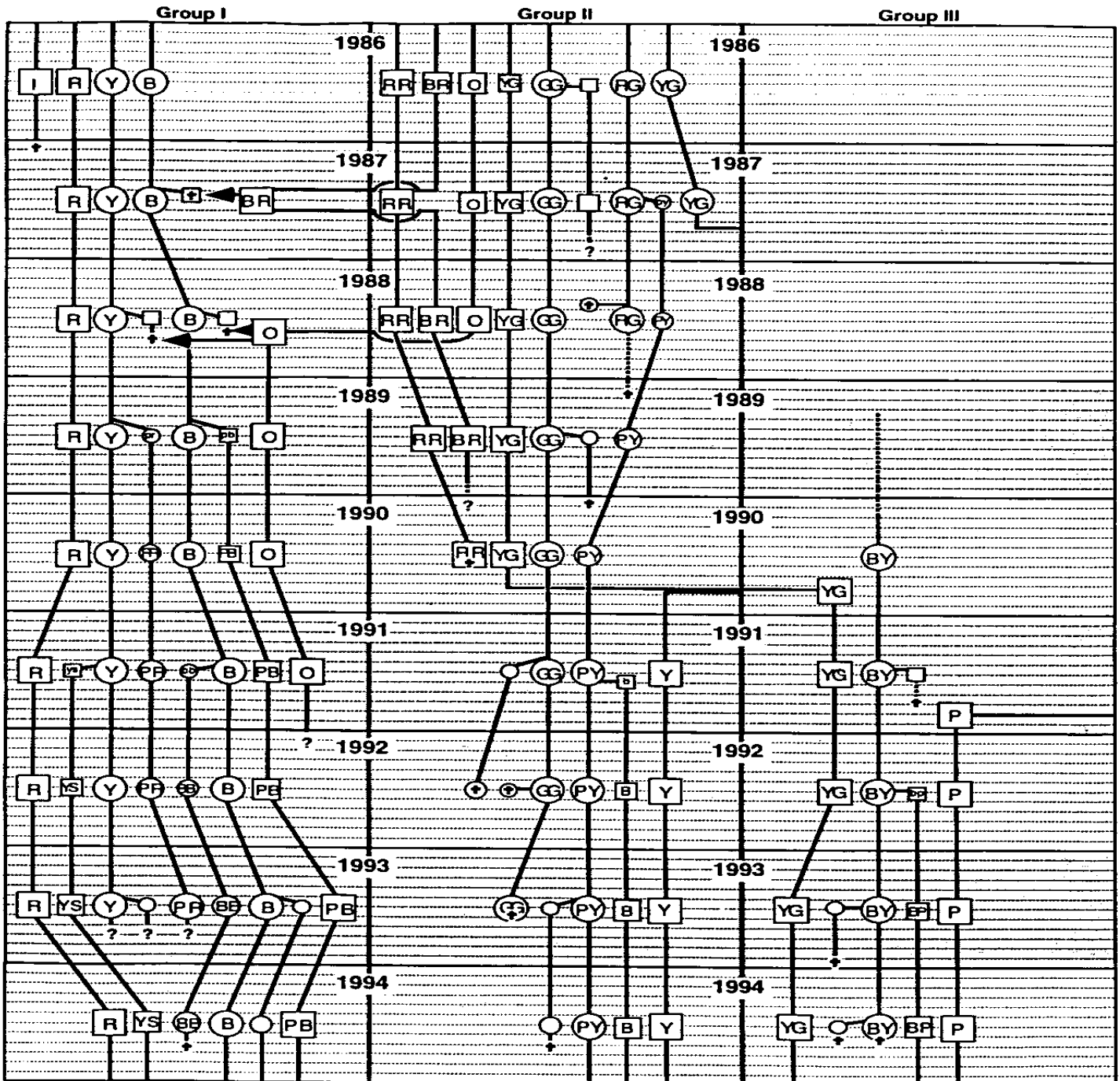
Over the 9-year period, the groups were under observation for 75 months, during which we witnessed three infanticides, eight emigrations, six immigrations, six copulations, determination of the birthdays of 12 infants within 2 days, observations of sick individuals, and three carcasses recently eviscerated by fossas (*Cryptoprocta ferox*).

## RESULTS

### Group Size

In Fig. 3, I present the history of the three study groups. Group size ranged from three to nine individuals. Group I increased from three to nine individuals in 6 years, with two breeding females and two breeding males. Group II decreased from nine to three in 5 years, because of several factors including subadult emigration and deaths of two adult females and one adult male.

*Propithecus diadema edwardsi*



**Fig. 3.** A 9-year history of the three study groups of *Propithecus diadema edwardsi* within the Talatakey Trail System (TTS) in RNP. Squares represent males and circles represent females. Letters represent the collar of the individual; for example, RR is red-red male. Each year has 12 spaces representing the 12 months, and deaths and births are placed according to month of event. Infanticides are represented by arrows, and crosses represent deaths.

In 1990 we observed a new group form with a 6-year-old from group II, Yellow Green (YG-male), joining a single adult Blue Yellow (BY-female). With the birth of an infant 8 months later, and a second adult Pink (P-male) joining, this group consisted of four individuals. However, the infant disappeared. In 1992 a surviving infant, Blue Purple (BP-male), was born. By 1993 a second surviving infant increased the group size to five. In 1994 BY-female and her 3-month-old infant were probably killed by a *Cryptoprocta ferox* (fossa). The group of three males remained in the group III territory for about 2 weeks. For 1 week the adult YG-male slept all morning and fed in the afternoons, recovering from the bite wounds resulting from the above incident. Two weeks after BY-female and infant disappeared, YG-male suddenly traveled 4 km south to Vatoharanana Trail System (Overdorff, 1993) but has not been observed accepted into another group. The nonbreeding male from group III (P-male) left group III territory a few days after YG-male left, and P-male attempted to enter group I with severe aggression and chasing by resident R-male. Within 3 days P-male followed group II. He remained in group II, but aggression between him and resident Y-male continued for almost a 3-month period, with Y-male bitten on the thighs near the testicles by the immigrant P-male. The 2-year-old BP-male remained alone in group III territory for at least 3 months.

### Group Composition

There were two breeding females in groups I and II and one breeding female in the newly formed group III (Fig. 3). The relatedness of the two breeding females in group I and in group II is unknown, but tooth wear is consistent with age differences suggesting mother and daughter. There were two adult males in groups I and III. The second male in group I immigrated from group II and was not closely related to the resident male. The second male in group III was only a year or two younger than the breeding male. Group II had one adult male for at least 6 consecutive years but has two unrelated adult males presently. In each group only one male has been observed to mate, and in each case, it is the older male. The ratio of males:females:infants:juveniles is 1:1.2:0.6:1.3. Infant sex ratio at birth is not significantly different from 1:1.

### Migration Between Groups

At 4 or 5 years of age, natal females either disappeared from their groups ( $n = 2$ ) or gave birth therein ( $n = 1$ ). In September 1987, a nul-

liparous, adult Yellow Green (YG-female) estimated to be 5 years old disappeared from group II. YG-female received repeated aggression from the dominant female Green Green (GG-female) beginning in July, and this aggression increased until YG-female disappeared in September (Wright, 1988). All adjacent groups were searched, but she has not been sighted since. In September 1993 Purple Red (PR-female), a 4 year old born into group I, disappeared from her natal group and was not seen again. The fact that females cannot be found in neighboring groups implies that, like some monogamous birds, female sifakas may migrate farther than male sifakas (Greenwood *et al.*, 1978; Greenwood, 1980). An obvious alternative hypothesis is that the females died before joining or forming another group.

Young males emigrate from their natal groups by 5–6 years of age ( $n = 4$ ). All four males transferred to an adjacent group. In two cases the males moved two to four times. Blue Red (BR-male) from group II moved to group I in May 1987 and killed Blue's (B-female's) infant. The resident R-male watched without attempting to defend B-female, but the second adult Y-female, without an infant, chased the immigrant male, while the mother moved down to the forest floor where the wounded infant lay vocalizing. The infant died within several hours. After daily aggression by both adult females toward BR-male for 2 months whenever he attempted to get close to them, BR-male returned to his natal group. He stayed a year in his natal group and then migrated again in 1989 to a group 4 km away.

In 1988, Orange (O-male) emigrated from group II, entered group I, and within 3 days fatally slashed Y-female's 2-month-old infant across the abdomen with his canine. O-male remained in the group and often attempted to approach B-female with her dependent infant. B-female was continuously alert and moved away from him. One month later, in September, O-male approached B-female while she was unaware and feeding with a clinging 3-month-old infant. O-male bit the infant's elbow. The startled infant turned, and O-male slashed it across the abdomen. The infant fell to the ground and died. During this month the resident male R-male never behaved aggressively toward the immigrant male but instead, mutually groomed with O-male often and slept in the same tree with him every night. O-male remained in the group for 3 years, until December 1991. We have not sighted O-male since. Four infants were born into this group during his tenure.

In October 1990, Yellow Green (YG-male) from group II emigrated to join an adult Blue Yellow (BY-female) whose territory is adjacent to those of the two study groups (Fig. 2). In 1991, this new group (group III) was joined by a second male, Pink (P-male) of unknown origin.



In October 1990 Y-male immigrated into group II. Copulations occurred between Green Green (GG-female) and Y-male. The year following the arrival of each of these males, surviving offspring were born into the groups.

In October 1994, after the death of the only resident female in group III (BY-female), the YG-male moved south towards a group at Vatoharana trail system (Overdorff, 1993). On March 30, 1995, YG-male was alone in an area bordering both Group I and Group II's territory. He did not join either group. The second adult male (P-male) attempted to join group I and then succeeded in joining group II, though he did not mate with the adult female. The 2-year-old Blue Purple (BP-male), son of BY-female, did not emigrate from his natal territory, and remained alone, often giving lost calls for three months. He has been sighted alone in group I territory in May 1995.

## REPRODUCTION

### Copulation

Copulations were observed on 4 occasions. On December 1, 1990, GG-female copulated with Y-male. There was no other male in that group.

On December 14, 1993, BY-female copulated three times (at 0736, 1142 and 1608) with YG-male, a resident. At 0612 the second male in the group (P-male) harassed YG-male and BY-female when they attempted to mate. BY-female walked away from the two males. I did not observe P-male mate with BY-female on this or succeeding days. YG-male approached the female, groomed her for 1 min, then mounted her for the first two copulations, and she approached him for the late afternoon mating. All copulations were single mount. There was additional harassment by the second adult male at the time of the 1142 copulation. The 1.5-year-old juvenile (BP-male) did not harass or approach the mating couple. Tooth wear indicates that the second adult P-male is younger than YG-male, and P-male was submissive to YG-male in most interactions. During 5-day samples between October 1993 and May 1994, YG-male slept next to BY-female in the evenings 25% of nights and with her juvenile (BP-male) 75% ( $n = 32$ ). BY-female never slept next to the P-male. On the night of the copulation day, the female slept next to the juvenile with the two adult males sleeping together 17 m away.

The next observations of copulations were on January 5 and 6, 1995. In group II the resident Y-male bred with PY-female once late on January 5 and again early on January 6. The male that had immigrated from group

III (P-male) to join group II in October did not breed with PY-female but overmarked the scent marks of PY-female during the copulation days. The resident (Y-male) was aggressive toward the immigrant male during the copulation days. The groups were followed before and after the days of breeding, and it appears that copulations occur within a 24-hr estrous interval only.

### Gestation Length

Births resulting from the first two copulations occurred on May 26, 1991 and June 14, 1994. The gestation lengths are 176 and 182 days, respectively. The mean of 179 days (6 months) is 1 month more than for *Propithecus verreauxi* (Haring *et al.*, 1988) and *P. tattersalli* (Meyers, 1993).

### Weaning

Infants ( $n = 6$ ) traveled independently 80% of the time by the seventh month (Wright, 1990; Tan and Wright, 1995) and received more than half their nourishment from foods other than milk by the sixth month of age (Meyers and Wright, 1993). By the twelfth month the infants ceased suckling from their mothers during the day. Secretion of milk during capture from mothers with 1.5-year-old juveniles suggests the possibility that suckling may occur during the night for an additional year. Mothers consistently sleep with offspring up to 2 years of age. Facultative lactation may occur, since during a subsequent year, milk was not secreted from the nipples of three captured mothers with year-old offspring.

### Birth Rate, Infant Mortality

Birthrates were relatively low, with a mean of 0.48 per year per female for the 9 years. Infant mortality was high, and 9 of 21 infants (43%) died before the age of 1 year. Five infants died at <3 months; three from infanticide and two probably from *Cryptoprocta ferox*. Fifteen of the 21 infants (67%) born into the three groups over the 9 years died before reproductive age. It should be noted (Fig. 3) that GG-female, estimated to be < 20 years old in 1993, lost all of her offspring that were born between 1986 and 1994. PY-female, a 4-year-old female, gave birth 1.5 months later than most births, yet her infant (B-male) survived. Females can reproduce every year, but on average, intervals after surviving offspring are  $\geq 2$  years. These data indicate that during the first 2 years of life sifakas have a low survivorship.

### Juvenile and Adult Mortality

Adult mortality rates are difficult to determine because missing animals may have emigrated, not died. Between 1986 and 1995 two adults (one male and one female) died as evidenced by their corpses, but there are four additional adults (one male and three females) that are presumed dead. Accordingly, maximum yearly mortality of adults is 12%.

Mortality from attacks by *Cryptoprocta ferox* (7–12 kg) is highly probable in five cases. The resident adult male from group II (RR-male) disappeared in July 1990. The next day, remaining group members lingered over the area where there were entrails (Goodman *et al.*, 1993). Group II was on the ground eating dirt 5–10 m from this site several days before the death. Two months later, 300 m from the kill site, there was a chewed collar, with assorted limb bones including two femora with their epiphyses gnawed and tooth marks. *Cryptoprocta ferox* eviscerates prey (Albignac, 1970, 1973), so the entrails indicated that a fossa killed the adult male *Propithecus*.

In September, 1993, the older adult Y-female and her 3-month-old infant disappeared overnight from group I and were never seen again. There was no evidence for cause of disappearance, though it is highly improbable that a dominant adult female with an infant would emigrate.

On August 1, 1994 the adult BY-female and 2-month-old infant from group III disappeared, and the adult YG-male, which often slept with this pair, was severely wounded. YG-male had long gashes on his back and head, suggesting that a large carnivore had attacked him. Although sleeping most of the 2 days following the injuries, YG-male recovered and returned within a week to the two remaining males in the group. The carcasses of BY-female and infant have not been found, but the wounds of the YG-male suggest that the fossa might have attacked them in the night at the sleeping tree.

On September 6, 1994, during a 5-day sample, the 1-year-old female in group II, which was alive and sleeping with her mother PY-female the previous evening, was dead at the base of the sleeping tree at 0635. She was torn open from chest to neck, with the heart, lungs, and liver gone, but the stomach and intestines remained intact. The vertebral column was gone and the skull was attached only via the skin. The skull and most of the skeleton were complete. It is probable that the fossa was interrupted by researchers just after the kill, since at 0815 a fossa with a very distended abdomen returned to the kill site. Later dissection of the mandible of the *Propithecus* revealed canine punctures through the right and left lower corpora (angular processes), suggesting that the killing bite was to the throat.

On September 12, 1994, 3-year-old Brown-Blue (BB-female) from group I was dead and eviscerated. The heart, lungs, spleen, and liver were gone, and only the stomach, pancreas, small, and large intestine remained. The frontal bone of the skull with canine punctures was near its nylon collar. The maxilla was nearly intact, but with canine punctures above the premolar roots on the right and left sides. The spinal column was gone, and only the gnawed remains of the left and a right ilia remained of the pelvis. The ends of all the long bones were gnawed off and only the distal shafts of the humeri, the tibiae, and the femora remained. This evidences that *Cryptoprocta ferox* killed BB-female.

Additional evidence that the fossa is a major predator of lemurs is scatological. Feces of *Cryptoprocta ferox* containing *Eulemur rubriventer* bone fragments, occurred at Vatoharanana (the trail system 5 km south of the Talatakely trail system) in July 1994 (Overdorff and Strait, 1995). In August 1994, within the territory of group III, there were scats of *Cryptoprocta ferox* containing hairs of *Haplemur griseus* or *Haplemur simus* (Kim Heckscher and Amy Dunham, personal observation). In 1991, hairs of *Eulemur fulvus* were defecated by a *Cryptoprocta ferox* captured in group II's territory (Gavin Naylor, personal observation).

There is one case of mortality possibly resulting from illness and old age. The aged GG-female, estimated to be >20 years old, had health problems, probably stemming from dental abscesses. In June and July 1990, the right side of her face was swollen, her feeding bouts decreased, and she was last during progressions. She recovered in September 1990. We captured her in January 1993, and noted that her broken right second lower molar was associated with a healed abscess. In June 1993, GG-female's eye and face swelled, her feeding bouts decreased, and she disappeared from the group for 3-day intervals. After July, GG-female was never seen again. The death could have been caused by a new tooth abscess, infection, and starvation. It is also possible that a fossa killed her. We found no carcass.

## DISCUSSION

*Propithecus diadema edwardsi* has a long life span with a high infant mortality. Gestation length, lactation length, age at first reproduction, and life span are similar to those in monkey species of the same body size.

Comparative data on long term studies of monkey populations indicate that infant mortality (43%) is higher in *Propithecus diadema edwardsi* than in most rain-forest monkeys. For example, in a 15-year study of *Alouatta seniculus* there was 18–21% infant mortality (Crockett and Pope, 1993). Over a 14-year span, in two groups of *Macaca fascicularis* in

Ketambe, Sumatra, 20% of the infants died before 1 year of age (van Noordwijk *et al.*, 1993). Infant mortality rates for *Cebus olivaceus* in Venezuela are 18.2% for males and 21.6% for females (O'Brien and Robinson, 1993). A 10-year study of *Brachyteles arachnoides* in southeastern Brazil, where the large predators have been eliminated, indicates a very low infant mortality (Strier, 1992). A 4-year study of *Ateles paniscus* in the Manu National Park, Perú (with a full community of predators), revealed 33% infant mortality (MacFarland Symington, 1988).

In Madagascar, long-term studies of lemurs in dry forests show that infant mortality is 40–70% (Jolly *et al.*, 1982; Sussman, 1991; Sauther, 1991; Richard, 1978; Richard *et al.*, 1991). The data from my rain-forest study of *Propithecus* show high infant mortality figures, similar to the dry-forest lemur mortality. However, the lemur mortality is not higher than mortality rates of nonprimate mammals (Bartlett *et al.*, 1993). In general, it appears that large and medium sized monkey species that live in rain forests have a lower rate of infant mortality than lemurs of the same size.

There are many factors that can explain mortality: predation (Terborgh, 1983; Cheney and Wrangham, 1987; Janson and van Schaik, 1993), disease (DeRousseau, 1994; Lovell, 1990; Zihlman *et al.*, 1990), environmental stress (drought, cyclones) (Boyce, 1979), or decreasing performance (tooth wear) (Kilgore, 1989), and injuries resulting from aggression (Hrdy, 1977; Fossey, 1983; Goodall, 1986). Understanding the cause of the high infant mortality may explain much of life history variation in relation to ecology.

In all tropical forests, primates have three categories of major predators other than humans: felids (Emmons, 1987; Isbell, 1990; Boesch, 1991), raptors (Rettig, 1978; Struhsaker and Leakey, 1990; Janson and van Schaik, 1993), and reptiles (Galdikas and Yeager, 1984; Yeager, 1991; Wright and Martin, 1995). In Madagascar, the felid-like fossa preys on large lemurs (Goodman *et al.*, 1993), and large hawks and eagles can take large-bodied lemurs (Goodman *et al.*, 1991). The predators of small, nocturnal prosimians—*Microcebus rufus*, *M. murinus*, *Cheirogaleus major*, and *Avahi laniger*—include *Buteo* (a buzzard), *Polyboroides* (a hawk), *Tyto* and *Asio* (owls), *Galidea elegans* (a viverrid), and *Sanzinia madagascariensis* (a boa constrictor) (Goodman *et al.*, 1993; Wright and Martin, 1995).

In Ranomafana National Park the fossa, *Cryptoprocta ferox*, appears to be the main predator on its largest lemur, *Propithecus diadema*. The probable toll includes one adult male, one or two adult females, one 3-year-old female, a female yearling, and one or two infants that died with their mothers. These data indicate that *Cryptoprocta ferox* may be an equal opportunity predator, taking from all age–sex classes. It should also be noted that in fossa predatory incidents that occurred in the same year, vic-

tims were eaten from different, but adjacent groups. These groups of *Propithecus* varied in size from four to six, and there is no indication that smaller groups were more vulnerable to predation than larger groups were (van Schaik, 1983). The fossa may be an "ambush" predator, and more "eyes and ears" may not be helpful (Hamilton, 1971). In three incidents, the sifakas were killed at night in their sleeping trees. These nocturnal attacks occurred during the darkest phase of the moon.

Although few data are available, it has been estimated that each individual *Cryptoprocta* requires a minimum range of 1 km<sup>2</sup> (Albignac, 1970, 1973). *Cryptoprocta* are rarely sighted at Ranomafana, and it is possible that their ranges are much bigger than 1 km<sup>2</sup>. One fossa's range may include from four to six groups of *Propithecus*, but we need more data on their ranging and feeding patterns. Of the 12 species of lemurs at Ranomafana National Park, feces show that the fossa eats at least 4 of the 7 diurnal lemur species. The national park, created on May 31, 1991, has protected the lemurs from the effects of further habitat destruction or logging. Perhaps the killing of four *Propithecus* from the three study groups in 1994 was a result of habitat destruction outside the park diminishing the range of *Cryptoprocta*. We know that some predators on primates, such as leopards and chimpanzees, can remain in one area for enough time to impact negatively on the prey population (Cheney and Wrangham, 1987; Stanford *et al.*, 1994), but we have no long-term data on the behavior of fossa.

What is the effect of immigrant male infanticide on demography? Infanticide has been described as a reproductive strategy of advantage to males when they migrate into a new group, and that it has been favored by sexual selection (Hrdy 1974; Hausfater and Hrdy, 1984). In the classic cases, the female victim of infanticide immediately comes into estrus and copulates with the infanticidal male (Sugiyama, 1965; Hausfater and Hrdy, 1984). Male newcomers gain an earlier opportunity to sire the female's next infants.

In Malagasy lemurs, an infanticidal male may not be able to breed when he commits infanticide because a female does not come immediately into estrus. Female breeding is triggered by photoperiodicity (Evans and Goy, 1968; Rasmussen, 1984), and after an infant killing, the seasonally breeding females come into estrus as soon as they can, 3–6 months later. Testicular size and development also increase seasonally beginning three months before the breeding season (Pereira and Weiss, 1991; Glander *et al.*, 1992). The reproductive advantage of an infanticidal tactic increases if breeding opportunities are so restricted.

Some breeding relationships of *Propithecus diadema edwardsi* may remain stable over 6–10 years. If adult mortality is low, a young male may have difficulty obtaining a breeding position in a group. Even though si-

fakas are long-lived, female reproductive output is low. A combination of constraints, including strict seasonality of estrus and large territory size, may make it difficult for a male to find and to mate with more than two females per year. A good strategy in this species may be for a male not to delay breeding, but to move into a new group and to kill infants to ensure the receptivity of two females that year. However, contrary to prediction (van Schaik and Kappeler, 1993), resident males do not defend against infanticide, nor has male-male aggression been observed before or after the killing. We are investigating the paternity of infants born the following year to determine whether there were different fathers for the two offspring or the father was the resident male or the immigrant. The few copulations observed suggest that the resident male may be the only breeder.

Female dominance, which has been documented in all species of *Propithecus*, does not prevent infanticide. The immigrant males follow the females with infants, in one instance for over a month, until they can catch the mother off guard and attack her infant. In one case, it took the immigrant male weeks before the dominant females whose infants had been killed would mutually groom with him. In another case, the females refused to groom with the immigrant male, and he left the group and returned to his natal group. The sample size of infants killed by immigrant males is small ( $n = 3$ ). As our demographic database increases, we hope to establish more fully how infanticide impacts on the population (Bartlett *et al.*, 1993).

Males transfer alone from their natal groups. No groups of *P. diadema edwardsi* fissioned. When groups reached a larger size ( $n = 9$ ), subadult individuals emigrated. Most males transferred into adjacent groups, but some males were in groups 2-4 km from their natal groups. Females disappeared from their natal groups at 4 or 5 years of age, but were not found in adjacent groups. In one case the female stayed in her natal group and became the dominant female. Her father, the resident male, died when she was 4 years old and the natal female bred with an immigrant male, which took over the group 3 months later. Small group size seems to be an active part of sifaka society, and the emigration of both male and female subadults may be key to maintaining the system. (A. Jolly, personal communication)

Over the 9 years of studies of these groups of *Propithecus diadema edwardsi*, exclusive territories were maintained with little overlap or expansion. Group size increased and decreased, but the boundaries were maintained. This pattern of maintenance of boundaries over time with turnover in group membership occurs in other primates (Terborgh, 1983) and indicates that each piece of property (a mosaic of rain forest) contains enough year-round food for maximum group size. It also implies that large group size is not necessary to defend a high-quality or adequate territory.

What does this high rate of infant mortality in wild populations of lemurs mean? A high rate of infant mortality is correlated with low birth weight, but not necessarily low adult mortality and long life span (Promislow and Harvey, 1990; Ross, 1992). Lemurs have lower birth weights than anthropoids of the same size do, though lemurs do not necessarily grow proportionally faster (Rasmussen and Tan, 1992). Moreover, milk is dilute and low in lipids and protein in most lemur species (Tilden, 1993). Collectively, these facts indicate that lemurs have a relatively low investment in their infants. Interestingly, in my study 8 of 10 deaths of offspring were due to predators and infanticide, and it does not appear that an increase in investment—higher quality of milk or increased length of lactation—would necessarily decrease the probability of offspring mortality from predation or infanticide. Thus, there may be increased selection pressure for mothers to keep some resources in reserve (bet hedging), so that a female will be in sufficiently good health to produce an infant at the next cycle, if she loses an offspring. Further, by keeping some resources in reserve, she probably can extend her total reproductive life span.

Recent long-term studies of primates released from predation pressure show expanding populations (Strier *et al.*, 1993). In contrast, primate communities with a full complement of predators, do not increase substantially (Terborgh, 1983). This trend seems to be supported by my study in Ranomafana National Park. As we monitor the RNP primate population over time, drastic changes such as deforestation of part of the fossa's territory can have heavy implications on the survival of the lemurs, even if the lemur's territory and the trees within it are not cut down.

### ACKNOWLEDGMENTS

The author gratefully acknowledges the permission and assistance of the government of the Democratic Republic of Madagascar, especially the Ministry of Higher Education, the Department of Waters and Forests, and the National Association for the Management of Protected Areas. I am grateful to Benjamin Andriamihaja and the Ranomafana National Park Project staff for their logistical assistance. This study would not be possible without the research assistance of George Rakotonirina, Emile Rajiarison, Loret Rasabo, Pierre Talata, Richard Randriapiona, William Rakotonirina, Albert Telo, Raymond Ratsimbazafy, Remy Rakotovao, Edmond Randrianandrasana, N. Asquith, L. Balko, A. Clemente, T. Crockett, M. Curtis, P. Daniels, A. Dehgan, L. Dew, C. Dina, A. Dunham, M. Erdmann, H. Ferrette, E. Fox, S. Foxman, M. Hale, D. Haring, K. Heckscher, C. Hemingway, J. Jernvall, E. Kappeler, P. Kappeler, A. Kemmerer, L. Martin,



W. Martin, E. McGuinness, A. Merenlender, D. Meyers, D. Overdorff, S. Palez, K. Petras, J. Powzyk, J. Ratsimbazafy, H. Rasamimanana, L. Santini, O. Schwaner-Albright, N. Shah, S. Strong, P. Szatanek, C. Tan, M. Todd, N. Vesey, M. Welch, M. Willis, A. Wright, and M. Yochelson. I am also grateful to K. Glander, A. Merenlender, and L. Rasabo for capturing and marking the subjects. Special thanks go to Jukka Jernvall for the graphics in Fig. 3. C. Janson, J. Fleagle, C. Yeager, C. Hemingway, B. Sussman, J. Jernvall, and two anonymous reviewers are thanked for comments on the manuscript. My work was supported by the Douroucoul Foundation, Duke University Research Funds, SUNY at Stony Brook, the John. D. and Catherine T. MacArthur Foundation, the Explorer's Club, USAID, and the National Geographic Foundation.

### REFERENCES

- Albignac, R. (1970). Notes ethologiques sur quelque carnivores Malgaches: Le *Cryptoprocta ferox* (Bennett). *Terre Vie* 24: 395-402.
- Albignac, R. (1973). *Faune de Madagascar*. No. 36. *Mammifères Carnivores*, OSTOM/CNRS, Paris.
- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour* 49: 227-267.
- Altmann, J. (1980). *Baboon Mothers and Infants*, Harvard University Press, Cambridge, MA.
- Bartlett, T. Q., Sussman, R. W., and Cheverud, J. M. (1993). Infant killing in primates: A review of observed cases with specific reference to the sexual selection hypothesis. *Am. Anthropol.* 95: 958-990.
- Blesch, C. (1991). The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour* 117: 220-242.
- Boyce, M. S. (1979). Seasonality and patterns of natural selection for life histories. *Am. Nat.* 114: 569-583.
- Cheney, D. L. and Wrangham R. W. (1987). Predation. In Smuts, B. B., Cheney, D. L., Seyfarth, R.M., Wrangham, R. W., and Struhsaker. T. T. (eds.), *Primate Societies*. University of Chicago Press, Chicago, pp. 227-239.
- Crockett, C. M., and Pope, T. R. (1993). Consequences of sex differences in dispersal for juvenile red howler monkeys. In Pereira, M. E., and Fairbanks, L. A. (eds.), *Juvenile Primates*, Oxford University Press, New York, pp. 104-118.
- DeRousseau, C. J. (1994). Primate gerontology: An emerging discipline. In Crews, D. E., and Garruto, R. M. (eds.), *Biological Anthropology and Aging*, Oxford University Press, New York, pp. 127-153.
- Emmons, L. H. (1987). Comparative feeding ecology of felids in a neotropical rainforest. *Behav. Ecol. Sociobiol.* 20: 271.
- Evans, C. S., and Goy, R. W. (1968). Social behavior and reproductive cycles in captive ringtailed lemurs (*Lemur catta*). *J. Zool. Lond.* 156: 181-197.
- Fossey, D. (1982). Reproduction among free-living mountain gorillas. *Am. J. Primatol.* 1: 97-104.
- Fossey, D. (1983). *Gorillas in the Mist*. Houghton Mifflin, Boston.
- Galdikas Birute, M. F., and Yeager, C. P. (1984). Crocodile predation on a crab-eating macaque in Borneo. *Am. J. Primatol.* 6: 49-51.
- Gentry, A. H. (1990). Floristic similarities and differences between Central America and upper Central Amazonia, In Gentry, A. H. (ed.), *Four Neotropical Rainforests*, Yale University Press, New Haven, CT, pp. 141-157.

- Glander, K. E. (1980). Reproduction and population growth in free-ranging mantled howling monkeys. *Am. J. Phys. Anthropol.* 53: 25-36.
- Glander, K. E. (1992). Dispersal pattern in Costa Rican mantled howling monkeys. *Int. J. Primatol.* 13: 415-436.
- Glander, K. E., Wright, P. C., Daniels, P. S., and Merenlender, A. (1992). Morphometrics and testicle size of rainforest lemur species from southeastern Madagascar. *J. Hum. Evol.* 22: 1-17.
- Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of behavior*, Harvard University Press, Cambridge, MA.
- Goodman, S. M., Creighton, G. K., and Raxworthy, C. (1991). The food habits of the Madagascar long-eared owl *Asio madagascariensis* in southeastern Madagascar. *Bonn. Zool. Beitr.* 42: 21.
- Goodman, S. M., O'Connor, S., and Langrand, O. (1993). A review of predation on lemurs: Implications for the evolution of social behavior in small, nocturnal primates. In Kappeler, P. M., and Ganzhorn, J. N. (eds.), *Lemur Social Systems and Their Ecological Basis*, Plenum Press, New York, pp. 51-66.
- Greenwood, P. J. (1980). Mating systems, philopatry, and dispersal in birds and mammals. *Anim. Behav.* 28: 1140-1162.
- Greenwood, P. J., Harvey, P. H., and Perrins, C.H. (1978). Inbreeding and dispersal in the great tit. *Nature* 271: 52-54.
- Hamilton, W. D. (1971). Geometry for the selfish herd. *J. Theor. Biol.* 31: 295-311.
- Haring, D. M., Wright, P. C., Izard, M., and Simons, E. L. (1988). Conservation of Madagascar's sifakas (*Propithecus*) in captivity and in the wild. In Dresser, B. (ed.), *Proceedings of the Fifth World Conference on Breeding Endangered Species in Captivity*, Cincinnati, pp. 67-81.
- Hausfater, G., and Hrdy, S. B. (1984). *Infanticide: Comparative and Evolutionary Perspectives*, Aldine, Hawthorne, NY.
- Hemingway, C. A. (1995). *Feeding and Reproductive Strategies of the Milne-Edwards' Sifaka, Propithecus diadema edwardsi*, Unpublished Ph.D. dissertation, Duke University, Durham, NC.
- Hrdy, S. B. (1974). Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu. *Folia Primatol.* 22: 19-58.
- Hrdy, S. B. (1977). *The Langurs of Abu*, Harvard University Press, Cambridge, MA.
- Isbell, L. A. (1990). Sudden short-term increase in mortality of vervet monkeys *Cercopithecus aethiops* due to predation in Amboeseli National Park, Kenya. *Am. J. Anthropol.* 21: 41-52.
- Janson, C. H., and van Schaik, C. P. (1993). Ecological risk aversion in juvenile primates: Slow and steady wins the race. In Pereira, M. E., and Fairbanks, L. A. (eds.), *Juvenile Primates: Life History, Development and Behavior*, Oxford University Press, New York, pp. 57-76.
- Jolly, A., Gustafson, H., Oliver, W. L. R., and O'Connor, S. M. (1982). *Propithecus verreauxi* population and ranging at Berenty, Madagascar, 1975 and 1980. *Folia Primatol.* 39: 124-144.
- Kilgore, L. (1989). Dental pathologies in ten free-ranging chimpanzees from Gombe National Park, Tanzania. *Am. J. Phys. Anthropol.* 80: 219-227.
- Lovell, N. C. (1990). Skeletal and dental pathology of free-ranging mountain gorillas. *Am. J. Phys. Anthropol.* 81: 399-412.
- McFarland Symington, M. (1988). Demography, ranging patterns, and activity budgets of black spider monkeys (*Ateles paniscus chamek*) in Manu National Park, Peru. *Am. J. Primatol.* 15: 45-67.
- Meyers, D. M. (1993). *Conservation Status of the Golden-Crowned Sifaka (Propithecus tattersalli)*, Unpublished Ph.D. thesis, Duke University, Durham, NC.
- Meyers, D. M., and Wright, P. C. (1993). Resource tracking: Food availability and *Propithecus* seasonal reproduction. In Kappeler, P. M., and Ganzhorn, J. U. (eds.), *Lemur Social Systems and Their Ecological Basis*, Plenum Press, New York, pp. 179-192.

- O'Brien, T. G., and Robinson, J. G. (1993). Stability of social relationships in female wedge-capped capuchin monkeys. In Pereira, M.E., and Fairbanks, L. A. (eds.), *Juvenile Primates*, Oxford University Press, New York, pp. 197-210.
- Overdorff, D. (1991). *Ecological Correlates to Social Structure in two Prosimian Primates in Madagascar*. *Eulemur fulvus rufus* and *Eulemur rubriventer* in Madagascar, Unpublished Ph.D. thesis, Duke University, Durham, NC.
- Overdorff, D. (1993). Similarities, differences, and seasonal pattern in the diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana National Park, Madagascar. *Int. J. Primatol.* 14: 721-753.
- Overdorff, D., and Strait, S. G. (1995). Life-history and predation in *Eulemur rubriventer* in Madagascar. *Am. J. Phys. Anthropol.* 20(321): 164-165.
- Pereira, M. E., and Weiss, M. L. (1991). Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behav. Ecol. Sociobiol.* 28: 141-152.
- Promislow, D. E. L. and Harvey, P. H. (1990). Living fast and dying young: A comparative analysis of life-history variation among mammals. *J. Zool. Lond.* 220: 417-437.
- Rasmussen, D. T. (1984). A comparative study of breeding seasonality and litter size in eleven taxa of captive lemurs (*Lemur* and *Varecia*). *Int. J. Primatol.* 6: 501-517.
- Rasmussen, D. T., and Tan, C. L. (1992). The allometry of behavioral development: Fitting sigmoid curves to ontogenetic data for use in interspecific allometric analyses. *J. Hum. Evol.* 23: 159-181.
- Rettig, N. (1978). Breeding behavior of the harpy eagle *Harpia harpyja*. *Auk* 95: 629-643.
- Richard, A. F. (1978). *Behavioral Variation: A Case Study of a Malagasy Lemur*, Bucknell University, Lewisburg.
- Richard, A. F., Rakotomanga, P., and Schwartz, M. (1991). Demography of *Propithecus verreauxi* at Beza Mahafaly, Madagascar: Sex ratio, survival, and fertility, 1984-1988. *Am. J. Phys. Anthropol.* 84: 307-322.
- Ross, C. (1992). Environmental correlates of the intrinsic rate of natural increase in primates. *Oecologia* 90: 383-390.
- Sauther, M. L. (1991). Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *Am. J. Phys. Anthropol.* 84: 463-477.
- Sauther, M. L., and Sussman, R. W. (1993). A new interpretation of the social organization and mating system of the ringtailed lemur (*Lemur catta*). In Kappeler, P. M., and Ganzhorn, J. U. (eds.), *Lemur Social Systems and Their Ecological Basis*, Plenum Press, New York, pp. 111-122.
- Schatz, G.E., and Malcomber, S. T. (1993). Botanical Research at Ranomafana National Park: Baseline Data for Long-term Ecological Monitoring. *Ranomafana National Park Biodiversity Symposium Volume*, Stony Brook, NY.
- Stanford, C. B., Wallis, J., Matama, H., and Goodall, J. (1994). Patterns of predation by chimpanzees on red colobus monkeys in Gombe National Park. *Am. J. Phys. Anthropol.* 94: 213-228.
- Strier, K. B. (1992). *Faces in the Forest: The Endangered Muriqui Monkeys of Brazil*, Oxford University Press, New York.
- Strier, K. B., Mendes, F. D. C., Rímoli, J., and Rímoli, A. (1993). Demography and social structure of one group of muriquis (*Brachyteles arachnoides*). *Int. J. Primatol.* 14: 513-526.
- Struhsaker, T. T., and Leakey, M. (1990). Prey selectivity by crowned hawk-eagles on monkeys in the Kibale Forest, Uganda. *Behav. Ecol. Sociobiol.* 26: 435.
- Sugiyama, Y. (1965). On the social change of hanuman langurs (*Presbytis entellus*) in their natural conditions. *Primates* 6: 213-247.
- Sussman, R. W. (1991). Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. *Am. J. Phys. Anthropol.* 84: 43-58.
- Sussman, R. W. (1992). Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). *Int. J. Primatol.* 13: 395-413.
- Tan, C., and Wright, P.C. (1995). Feeding behavior of female *Propithecus diadema edwardsi*: Implications for the evolution of female social dominance in Malagasy lemurs. *Am. J. Phys. Anthropol. Suppl.* 19.

- Terborgh, J. (1983). *Five New World Primates: A Study in Comparative Ecology*, Princeton University Press, Princeton, NJ.
- Tilden, C. D. (1993). *Reproductive Energetics of Prosimian Primates*, Unpublished Ph.D. dissertation, Duke University, Durham, NC.
- van Noordwijk, M. A., Hemelrijk, C. K., Herremans, L. A. M., and Sterck, E. H. M. (1993). Spatial position and behavioral sex differences in juvenile long-tailed macaques. In Pereira, M. E., and Fairbanks, L. A. (eds.), *Juvenile Primates: Life History, Development, and Behavior*, Oxford University Press, New York, pp. 77-85.
- van Schaik, C. P. (1983). Why are diurnal primates living in groups? *Behaviour* 87: 120-144.
- van Schaik, C. P., and Kappeler, P. M. (1993). Life history, activity period and lemur social systems. In Kappeler, P.M., and Ganzhorn, J. U. (eds.), *Lemur Social Systems and Their Ecological Basis*, Plenum Press, New York, pp. 241-260.
- Wright, P. C. (1988). Social behavior of *Propithecus diadema edwardsi* in Madagascar. *Am. J. Phys. Anthropol.* 75: 289.
- Wright, P. C. (1990). Patterns of paternal care in primates. *Int. J. Primatol.* 11: 89-102.
- Wright, P. C. (1992). Primate ecology, rainforest conservation, and economic development: Building a national park in Madagascar. *Evol. Anthropol.* 1: 25-33.
- Wright, P. C., and Martin, L. B. (1995). Predation, pollination and torpor in two nocturnal prosimians (*Cheirogaleus major* and *Microcebus rufus*) in the rain forest of Madagascar. In Alterman, L., Doyle, G. A., and Izard K. (eds.), *Creatures of the Dark: The Nocturnal Prosimians*, Plenum Press, New York, pp. 45-60.
- Yeager, C. P. (1991) Proboscis monkey (*Nasalis larvatus*) social organization: intergroup patterns of association. *Am. J. Anthropol.* 23(2): 73-86.
- Zihlman, A. L., Morbeck, M. E., and Goodall, J. (1990). Skeletal biology and individual life history of Gombe chimpanzees. *J. Zool. Lond.* 221: 37-61.