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Demography of *Propithecus verreauxi* at Beza Mahafaly, Madagascar: Sex Ratio, Survival, and Fertility, 1984–1988

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ABSTRACT Eighty-five sifakas (*Propithecus verreauxi*) have been captured, marked, released, and monitored between September 1984 and August 1988 at the Beza Mahafaly Special Reserve in southwest Madagascar. Estimates are presented of the age and sex structure of this population and of age-specific fertility and survival. Using data from this and other studies, it is shown that sifaka tertiary sex ratios do not depart significantly from 50:50, but that they do differ significantly from those of haplorhine primates, which have strongly female-biased tertiary sex ratios. Two demographic mechanisms that could give rise to this distinction are considered: 1) intermittently male-biased birth cohorts among sifakas and 2) different patterns of survivorship in haplorhines and sifakas.

Knowledge of the demography of haplorhine primates has grown rapidly in the last 15 years (reviewed by Dunbar, 1986; Richard, 1985a; Dobson and Lyles, 1990). Basic parameters for several free-ranging populations have been estimated, including age at first reproduction, infant and juvenile mortality, inter-birth interval, neonatal and adult sex ratios, and the age and sex of migrants (Altmann, 1980; Altmann et al., 1977; Clarke and Glander, 1984; Glander, 1980; Koford, 1965, 1966; Southwick and Siddiqi, 1977; Struhsaker, 1973, 1976). Age-specific schedules of fertility and/or survival are available for some populations (e.g., Altmann, 1980; Altmann et al., 1981, 1985; Cheney et al., 1987; Dittus, 1975; Dunbar, 1980; Froelich et al., 1981; Goodall, 1983, 1986; Koyama et al., 1975; Masui et al., 1975; Sade et al., 1976; Strum and Western, 1982). By comparison, the demography of wild strepsirhines is poorly known (Tattersall, 1982), yet the little we do know suggests interesting contrasts with haplorhine primates.

In this paper we present results of a demographic study of a diurnal Malagasy lemur, the sifaka (*Propithecus verreauxi*), living in gallery and transitional forest at the Beza Mahafaly Special Reserve in southwest Madagascar (Fig. 1). The data come from 85 animals that were captured, marked, released, and monitored between September 1984 and August 1988.

At the outset of the study, demographic information about this species came primarily from a population in the private reserve of Berenty (Fig. 1, Table 1), which has been censused intermittently since 1963 (Jolly, 1966, 1972; Jolly et al., 1982; O'Connor, 1987; Richard, 1978). Although the lack of individually identified animals limited the kinds of data that could be collected,one striking result emerged from this work. In more than one-half of the censuses at Berenty, subadult and adult males outnumbered subadult and adult females. Comparable departures from a 50:50 sex ratio in favor of males have been reported in some, though not all, other sifaka populations censused (Table 1), and a male-biased tertiary sex ratio has also been reported in certain other lemur species (e.g., Petter, 1962). The ratios listed in Table 1 do not depart significantly from 0.5 (binomial test, $P = 0.304$; throughout this paper the tertiary sex ratio is expressed as a simple proportion, the fraction of subadults and adults who are female). What makes them unusual and distinctive, however, is the direction and magnitude of

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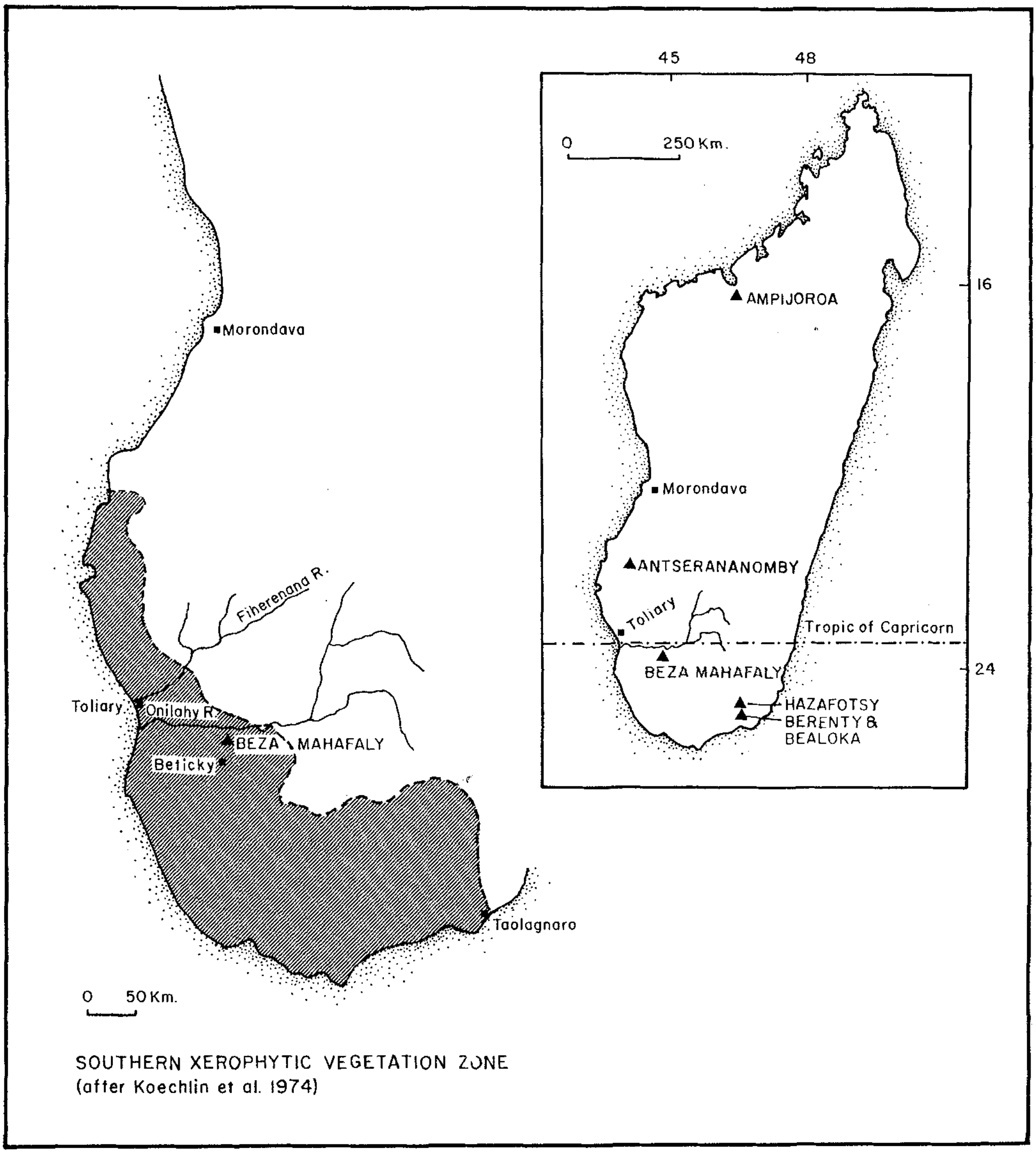

Fig. 1. Location of the study site, Beza Mahafaly, and other forests where populations of *P. verreauxi* have been censused.

their departure from those reported for haplorhine populations: In most haplorhines, like most mammals, the tertiary sex ratio favors females (Fig. 2, U = 0, $P < 0.001$; see also Caughley, 1977; Clutton-Brock and Harvey, 1977; Dunbar, 1986; Richard, 1985b).

Departures from parity in the tertiary sex ratio may be due to variations in the secondary sex ratio (i.e., the sex ratio at birth) working their way through the population (Dunbar, 1979), life history processes unfolding differently in males and females, or some combination of both. An uneven sex ratio at birth, usually involving an excess of males, is not uncommon among mammals (Clutton-Brock, 1982; Clutton-Brock and Iason, 1986; Hrdy, 1987). Imbalances may be population-

TABLE 1. Tertiary sex ratios of adult P. verreauxi *in five forests*[1]

Location	Year	Adults Males	Adults Females	Groups censused	Sex ratio[2] and standard error
Berenty	1963	20	14	9	0.411 ± .086
	1964	24	17	10	0.414 ± .078
	1970	14	13	6	0.481 ± .098
	1971	25	24	10	0.489 ± .072
	1974	34	40	17	0.540 ± .058
	1975	37	44	16	0.543 ± .055
	1980	15	11	6	0.423 ± .099
	1983	41	42	29	0.506 ± .055
	1984	58	59	35	0.504 ± .046
	1985	61	59	36	0.491 ± .046
Bealoka	1984	13	12	7	0.480 ± .102
	1985	17	13	9	0.433 ± .092
Ampijoroa	1970	15	19	7	0.558 ± .086
Hazafotsy	1970	8	11	5	0.578 ± .116
Antserananomby	1974	30	26	8	0.464 ± .067

[1] Sources: Berenty: 1963, 1964; Jolly (1966, Table II-6); 1970, 1980, Jolly et al. (1982, Table V); 1971, 1974, Richard (1978, Table 3-3); 1975, Jolly et al. (1982, Table III); 1983, 1984, 1985, O'Connor (1987, Table VI.4). Bealoka: 1984, 1985, O'Connor (1987, Table VI.3); Ampijoroa, Hazafotsy, Antserananomby, Richard (1978, Table 3.3).

[2] Sex ratio is expressed as the proportion of all adults censused that were female.

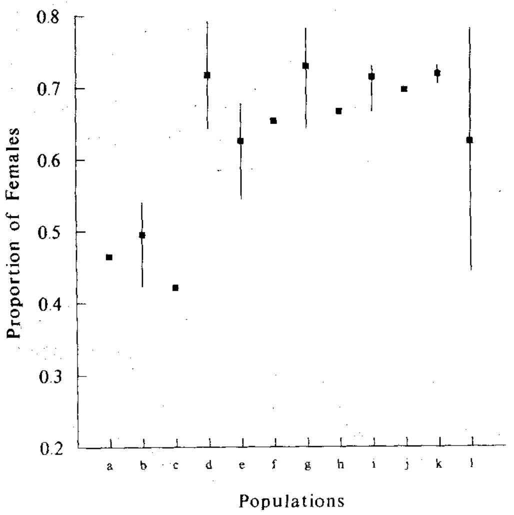

Fig. 2. Mean and range of tertiary sex ratios in *P. verreauxi* and selected haplorhine populations. a,b,c, *P. verreauxi;* d, *Alouatta palliata;* e, *Papio cynocephalus;* f,g,h, *Macaca mulatta;* i, *M. fuscata;* j, *M. sinica;* k, *Theropithecus gelada;* l, *Pan troglodytes.* Data for a–c are from Antserananomby, Berenty (Table 1) and this study; data for d–k are from sources cited in Richard (1985a, Table 7.1); data for l are from Goodall (1986).

wide or limited to births among a particular class of reproductive females, and they may be intermittent or persistent. Strongly skewed, population-wide secondary sex ratios are rare among primates, although there may be a slight preponderance of male births in some populations (van Schaik and van Noordwijk, 1983). Two exceptions stand out, however. One is *Galago crassicaudatus,* in which the secondary sex ratio strongly and consistently favors males (Clark, 1978; Dunbar, 1986). The other is *Ateles paniscus,* in which low-ranking females give birth almost exclusively to females while high-ranking females show a slight bias in favor of males, producing a strongly female-biased sex ratio at birth in the population as a whole (McFarland Symington, 1987). Differences in the sex ratio of infants born to high- and low-ranking females have been reported in *Papio cynocephalus* in the wild (Altmann, 1980) and in *Macaca radiata* and *Macaca mulatta* in captivity (Meikle et al., 1984; Silk, 1983; Simpson and Simpson, 1982; Small and Hrdy, 1986). Most of these studies report that high-ranking females produce a preponderance of daughters and low-ranking females a preponderance of sons, but in some instances the opposite bias has been found, and in others no bias at all has been found (e.g., Small and Smith, 1984). The proximate determinants of these variations are not well understood. Moreover, although several hypotheses concerning their adaptive significance have been put forward, there is still insufficient evidence to evaluate them conclusively (Clutton-Brock and Iason, 1986; Hrdy, 1987).

Three life history processes may contribute to differences in the representation of males and females in the adult population:

age-specific survival, maturation rate, and dispersal. These processes and their interactions with one another and with the secondary sex ratio have yet to be well studied in primates (however, see Dittus, 1980; Dunbar, 1979, 1980), but the evidence thus far suggests that sex differences in age-specific survival may be of primary importance. Haplorhines share the general mammalian pattern of initial low survival, followed by a higher survival during the juvenile period and a steady decline thereafter (Caughley, 1977; Dunbar, 1980, 1986). Within this pattern, lower survival among subadult and adult males has been reported in *Theropithecus gelada* (Dunbar, 1980), *Papio cynocephalus* (Altmann and Altmann, 1970), *Cercopithecus aethiops* (Cheney et al., 1987), *Macaca sinica,* and *Macaca fuscata* (Dittus, 1975; Sugiyama, 1976). Male and female infant and juvenile survival rates are often similar (Dunbar, 1986), although studies of macaques in captivity report higher mortality in male infants (Paul and Thommen, 1984; Wolfe, 1984; Small and Smith, 1986). In wild *M. sinica,* in contrast, Dittus (1980) reports lower survival among infant and juvenile females. The general point emerging from these studies, however, is that in haplorhines primates for which we have the most demographic data in the wild, sex-specific differences in survival commonly result in a disproportionate representation of females among subadults and adults, regardless of the sex ratio at birth or perinatal mortality.

Our goals in this paper are 1) to describe our methods of capture, censusing, and age estimation; 2) to characterize the age and sex structure of the study population; and 3) to present our findings with respect to age-specific fertility and survival. We then examine the hypothesis that the true tertiary sex ratio in sifaka populations is 50:50 and that reported male-biased sex ratios are attributable to sampling effects or mistaken sexing. Finally, we use data from this study to assess the plausibility of two demographic mechanisms that could give rise to the broad difference between sifaka and haplorhine tertiary sex ratios: 1) intermittent biases in favor of males among sifaka birth cohorts offset lower male survival after birth; 2) male and female sifakas are born in similar numbers, but their life histories have distinctively different trajectories from those of haplorhines, with unusually low survival among females, unusually high survival among males, or some combination of the two. We begin by briefly describing the field site and study population.

FIELD SITE AND STUDY POPULATION

The Beza Mahafaly Special Reserve is located in the driest region of Madagascar. The area around the reserve receives an average of only 720 mm of rain annually. Most of the rain falls during the austral summer between October and March, and in some winter months there may be no rain at all. Marked variations in rainfall occur from year to year (Fig. 3). Temperatures climb to 42°C during the day in the austral summer and sink to 21°C at night. Maximum temperatures in winter reach 36°C, and on clear, austral winter nights they may drop to 3°C.

The reserve consists of two small, protected areas within a much larger but unprotected forest. It harbors a diverse array of reptiles, birds, and mammals (Richard et al., 1987) and is the site of several on-going research projects, including a parallel study of the demography of *Lemur catta* (Sussman, 1991). For the past 12 years, the reserve and the area around it have been the focus of a collaborative effort to integrate conservation and development at the local level (Rakotomanga et al., 1987).

Our study is being conducted in Sector 1 of the reserve, which encompasses a gradient from xerophytic vegetation to a narrow strip of riverine forest on the west bank of the Sakamena River. About 100 ha in area, Sector 1 has been completely fenced since 1979. Like all such forests in south and west Madagascar, the riverine forest at Beza Mahafaly is dominated by *Tamarindus indica.* With increasing distance from the river, plant forms typical of the spiny forests of southern Madagascar, notably members of the Euphorbiaceae and Didiereaceae families, increase in abundance.

The study population comprises individuals from 28 social groups with home ranges partly or completely within the boundaries of Sector 1. These animals are part of a larger biological population, bounded 15 km to the north by a major river, the Onilahy, and about 20 km to the south by deforested land in the vicinity of Betioky. The geographical limits of the population in the east and west are unknown, but aerial photographs show extensive forests are present. The boundary of Sector 1 is delineated by a barbed wire fence and narrow trail across which animals move freely. Groups contain between 2 and

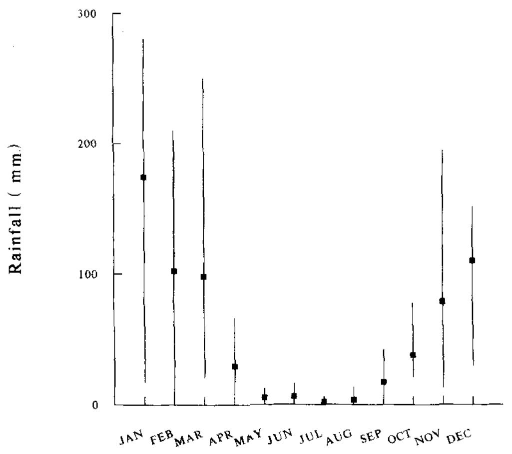

Fig. 3. Monthly means and ranges of variation in rainfall in the Beza Mahafaly area, 1951–1985. (Records from the Betioky-Sud Meteorological Station.)

13 animals and vary markedly in sexual composition (Richard et al., 1991a). Groups have home ranges of 4 to 6 ha, with considerable overlap between neighboring ranges. The sifakas' diet at Beza is composed primarily of young leaves, shoots, and seasonally available fruit.

METHODS

We began capturing animals in November and December 1984. In May, June, and July of 1985, 1986, and 1987, more animals were captured and marked, and previously marked individuals were censused. The size of all social groups encountered and, whenever possible, the sex of unmarked animals and any natural identifying marks were recorded. Data on group composition, births, and deaths were collected ad lib at other times by the head guard of the reserve, Monsieur Behaligno.

The analyses presented below are based primarily on information from 85 collared and tagged animals, for which we have biometric measures and age estimates. The analysis of inter-birth interval includes females identified by natural markings only.

Capture and individual identification

Animals were immobilized using an anesthetic agent delivered by a dart fired from a Telinject blowgun. Animals less than 1 year old were excluded as targets, and no darting was done in July to November, when females are still carrying their infants for all or part of the day. While it is possible that we captured males and females at different rates, we have no evidence of such a bias. Initially, ketamine was used alone as an anesthetic, but even at very high doses (0.5 ml/kg) it was sometimes ineffective. This was variously attributable to three causes: 1) failure to keep the ketamine cool enough to retain its potency; 2) delivery of an incomplete dose; and 3) apparent resistance to the drug of some animals, even when we were confident that a full, cool dose had been delivered. The subsequent addition of rompun (0.15 ml/kg) enabled us to reduce the volume of the dose and increased the frequency with which animals were immobilized as well as the likelihood that they would fall: When darted, most animals moved higher in the trees and were difficult to retrieve if they did not fall.

When an animal did fall or was retrieved by climbing, it was caught in a large sheet and then carried back to camp for processing. Once processing was completed, animals were taken back to the capture site and kept in holding cages and monitored until fully awake.

The major advantages of this capture system are that darts are delivered at low velocity, thereby minimizing the risk of injury, and that it is quiet and minimally disruptive to the group as a whole. One adult male died when the dart penetrated an artery, but there have been no other deaths or injuries associated with the capture program. Within 24 hours of being released after capture, habituated animals could be approached as closely as before, and habituated groups could be approached and followed even when one of their members was being held at camp. These animals did become "blowgun shy," however, moving up in the trees when they saw the blowgun again and making recapture more difficult. No changes in social relationships were observed in habituated groups after capture episodes. The major disadvantage of the capture system is that the blowgun is accurate only over a short distance, no more than 6 or 7 m, so that the rate at which we captured animals was low—only two to four individuals per day.

Three kinds of identification marks were used: 1) Each animal's I.D. number was tattooed on its thigh; although sifakas have black skin, the tattoo was nonetheless legible and still visible on two individuals recaptured a year later. 2) Each animal was given a 1/2 inch nylon collar with a numbered plastic tag. By permuting combinations of collar colors and tag shapes and colors, it was often possible to identify animals without reading the I.D. number on the tag. No collars have yet been lost, and no tags have been lost since we began using a metal S-hook to attach them. 3) Each animal was notched in one or more of three positions on each ear using a binary code that yields 63 distinct notch combinations. With animal 64 we started from 1 again, using a different collar color and tag color and shape to distinguish it from animal 1. Ear notching was initially done in case collars were lost, but, in practice, it was often easier to read notches than the tag.

Censusing

A grid of trails running north–south and east–west at 100 m intervals was walked slowly and systematically. If animals were located by sight or hearing away from the trail we tried to census them, because our goal was to count and, as far as possible, identify all animals. The presence of artificially marked or naturally recognizable individuals in all groups minimized the problem of inadvertently censusing the same group twice.

From October 1984 until July 1985, A.F.R. and P.R. were present at the study site almost continuously, and most groups were censused in most months. Since then, we have censused the population annually during a 1 month period between late May and July. The birth season extends into August, and females without infants at the end of the annual census were monitored in August by R.P. and Monsieur Behaligno, who also kept ad hoc records of demographic events throughout the year. If a female was not seen with an infant by the end of August, she was recorded as not having given birth that year. This is likely to underestimate the actual birth rate as not all groups were censused every day during the birth season. We may not have recorded some births of infants that died perinatally and thus mistakenly recorded their mothers as not having given birth that year.

Age estimates

Ages are known only for animals born during the study or 1 year prior to its beginning. The annual birth season lasts about 1 month and begins between mid-June and mid-July. Animals less than 1 year old are easy to recognize because they are small, but thereafter the age of immatures is less reliably inferred from size alone. Estimates of relative age were based on the toothwear detectable on cast replicas of the upper dentition of each animal captured. Eruption of the permanent dentition could not be used to estimate age, because that process was already complete in all individuals examined. Comparative studies in captivity suggest that eruption is complete by 12 to 14 months (Eaglen, 1985), which accords well with our findings: All animals were at least 15 months old at the time of capture. Notes were first made on the general condition of the teeth. Then the teeth were dried with pressurized air and an impression was taken using Xantoprin. Casts were made from a high precision epoxy (epo-tek) in the laboratory at Yale, using a vacuum chamber to prevent the formation of bubbles.

The casts, unidentified by sex, were sorted three times independently into five categories of wear (A to E). We assume these represent age categories. Although there was strong agreement over assignments to the categories of no wear (A) and maximum wear (E), discrepancies arose over the B–C and C–D boundaries, reflecting the difficulty of dividing up a wear continuum. It should also be noted that our method of assessing relative age assumes that wear proceeds at approximately the same rate in all animals. The number of years represented by each age/wear category will remain unknown until rates of wear are calibrated by recapturing animals, but our working assumption is that the A category spans about 3 years and categories B to E 4 or 5 years each. We base this "guesstimate" on the observation that all adult-sized animals showed some wear and on the assumptions that wear increases at an even rate and that maximum longevity is about 20 years. We know that the E category spans 4 years, because two of the eight animals assigned to it in mid-1985 were still alive in mid-1989. In the analysis below, however, animals have not been graduated from one age/wear category to the next because of our general uncertainty about the proportion that should graduate each year. The criteria defining each category are as follows: A, no wear on any teeth, all cusps sharp; B, some wear, especially on incisors, premolars not sharp; C, moderate wear on all teeth; D, heavy wear, dentine exposed, premolars rounded; and E, heavy wear, premolars and molars worn almost to gumline.

M.S. and an assistant, working independently, subsequently assigned animals in each age/wear category an ordinal rank according to degree of wear. Overall agreement between the independent assessments of wear was high, and major discrepancies occurred only when the cast was of poor quality. In these instances, the cast was re-examined and a "best estimate" was made.

RESULTS

Age and sex structure

The age and sex structure of the marked population alive in June 1985 and June 1987 is shown in the form of population pyramids in Figure 4. Differences between years are due to known or presumed deaths and emigration and to recruitment through new captures. In 1985, the age structure of the population resembles a barrel rather than a pyramid, with the fewest animals in the oldest and youngest age/wear categories. The 1987 pyramid, in contrast, exhibits a succession of cohorts of declining size.

Females were outnumbered by males in the capture population in both 1985 (0.424, n = 59) and 1987 (0.419, n = 74). The distributions of males and females between age/wear categories are statistically significantly different in both years (Kolmogorov-Smirnoff test, $P < 0.001$). The pattern of differences is hard to interpret with such small subdivided sample sizes, however, and to an unknown degree it may be an artifact of our analysis: As noted above, placement of the B–C and C–D age/wear boundaries was difficult, yet with such a small sample a minor change in the placement of these boundaries can produce a major difference in the representation of population structure. In other words, the precise shape of the pyramid may reflect decisions about the placement of boundaries rather than biologically meaningful distinctions between age/sex classes.

As an alternative to "forcing" the data into discrete categories, we plotted males and females cumulatively according to their ordinal toothwear rank, which was assigned in a sex-blind analysis. Displayed in this way, the data reveal a broad pattern in both years (Fig. 5). Males and females are represented more or less equally in the segment of the population showing least tooth wear. Males begin clearly to outnumber females in the B category, the trend becomes more marked through the C category, and it levels off thereafter. Possible interpretations of this pattern are considered in the discussion.

Fertility

A female's lifetime fertility is determined by her age at first reproduction, inter-birth interval, and longevity. Her lifetime reproductive success is determined by these variables and by the survival of her infants to reproductive age. For the Beza Mahafaly population, we now have preliminary esti-

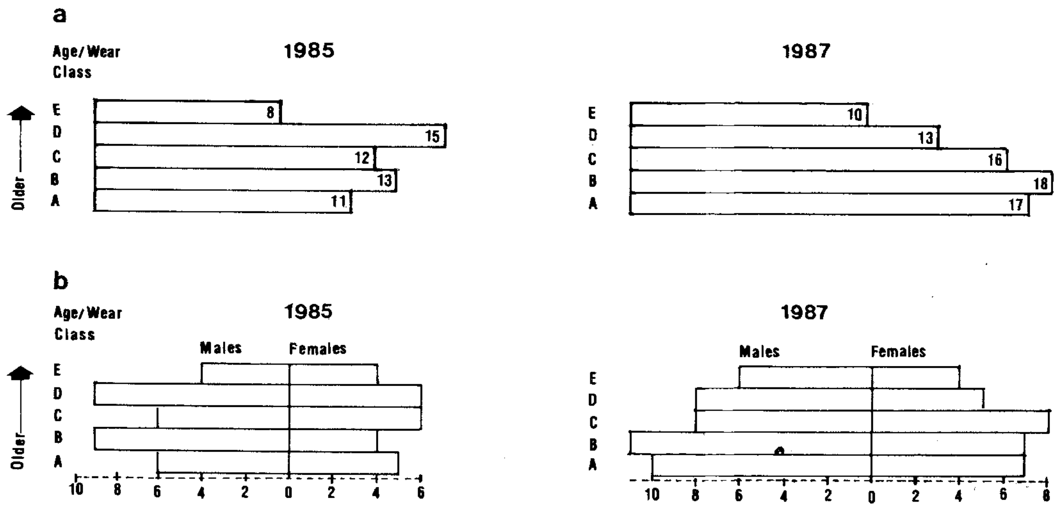

Fig. 4. Age (a) and age and sex (b) structures of marked population of *P. verreauxi* in June 1985 (n = 59) and June 1987 (n = 74).

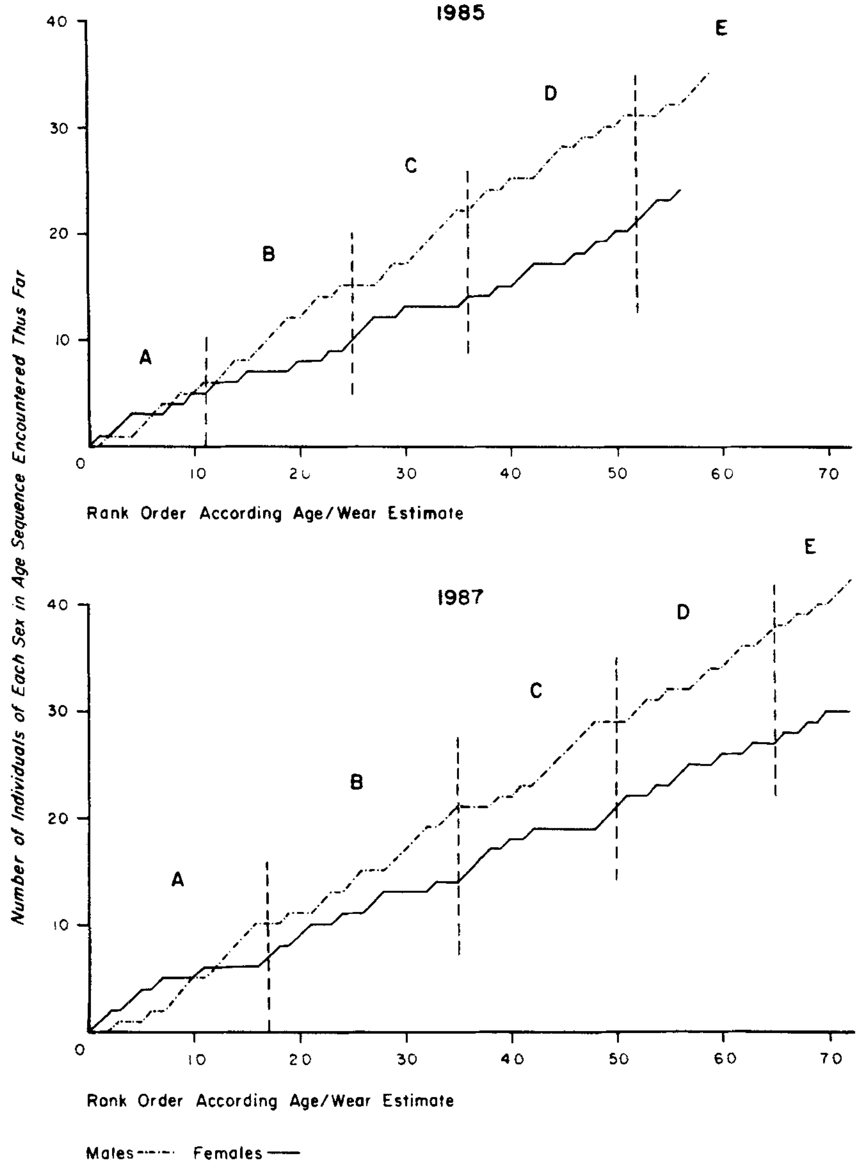

Fig. 5. Cumulative plot of male and female *P. verreauxi* rank-ordered by degree of toothwear, 1985 and 1987. Dashed line, males; solid line, females.

mates of age at first reproduction, age-specific fertility, inter-birth interval, and infant survival.

Overall, 44% of females give birth each year on average, with considerable (though not statistically significant) variation from year to year (Table 2). The average birth rate rises to 54% if females in age/wear class A are excluded. Only two of the nine females assigned to the A age/wear category between 1984 and 1987 have given birth. We infer from biometric and behavioral data that

TABLE 2. Annual variations[1] in birth rate among female P. verreauxi *at Beza Mahafaly*[2]

Year	No. of females	Birth rate[3]	Adjusted birth rate[3]
1984	15	0.60	0.20
1985	13	0.77	0.62
1986	18	0.50	0.22
1987	23	0.43	0.35

[1] This variation is not statistically significant. ($X = 4.09, df = 3, P > 0.25$—birth rate; $X = 6.88$, df = 3, $P = 0.07$—adjusted birth rate).

[2] A age/wear class excluded.

[3] The birth rate is the proportion of females giving birth to infants; the adjusted birth rate is the proportion of females giving birth to infants that survived the first year.

both these females were born in 1983. One gave birth for the first time in August 1988 (and lost the infant shortly thereafter) and the other in August 1989. A third, A-class female assigned a 1983 birth date died in 1987 without having given birth. The six remaining A-class females, none of whom have given birth yet, are all known or presumed to have been born since 1983. Age at first reproduction in sifakas has previously been estimated to be 30 months (Tattersall, 1982), although there are no longitudinal data from the wild to support this estimate. However, it does seem unlikely that female sifakas at Beza Mahafaly, who weigh only 3 kg on average (unpublished data), always take 5 or 6 years to reproduce for the first time. Possible reasons for the long maturation time documented in this study are discussed below.

Birth rates are highest in the B and C age/wear categories, and there is some indication of a trend toward lower fertility in the older age/wear categories (Table 3). Successful reproduction (defined as the proportion of females giving birth to an offspring surviving through the first year) likewise appears to decline with increasing age. Table 4 shows that there is also considerable variation in cumulative reproductive success within age/wear classes in the small sample of females for which we have observations for at least three birth seasons. While the sample size is small, this result is consonant with mounting evidence of high variance in the lifetime reproductive success of haplorhine females (Fedigan et al., 1986).

Sifakas are known to be highly seasonal breeders, and the shortest observed interval between births at Beza was approximately 1 year. One year was also the most common inter-birth interval between 1984 and 1987 (Table 4, Fig. 6). In a majority of cases (6 of 10), a 12 month inter-birth interval occurred after the death of a neonate: The mother cycled and conceived again the following year. Of nine females observed in the birth season following the birth of a surviving infant, four gave birth again, but only two of these four successfully raised the second infant to the age of 1 year. The probability of giving birth to a second surviving infant *2* years after the birth of a first surviving infant was much higher, 0.67 compared with 0.22. The two females who reproduced successfully with a 1 year inter-birth interval were in the oldest age category, and both subsequently died without reproducing again. Excluding these two, however, the females who were most successful reproductively were those who gave birth at 24 month intervals (Table 4). Unfortunately, the sample size is too small to examine inter-individual differences while controlling for the effects of age, annual variations in temperature, rainfall, and the abundance of food.

Juvenile and adult survival

In our small sample, infant survival varied widely from year to year (Table 5). With respect to the pattern of age-specific survival in subadults and adults, there is a similar trend in both years among males and wide variation between years among females (Table 6). Kaplan-Meier product limit estimates show that female survival was slightly lower than male survival at all ages from 1985 to 1987 in the sample of 59 animals captured by June 1985 (Fig. 7), but the difference is not statistically significant (log-rank test, $P = 0.72$) (Steinberg and Colla, 1988; Namboodiri and Suchindran, 1987).

It should be emphasized that death was sometimes inferred from circumstantial evidence, thereby increasing the likelihood of error in our estimates of survival. Females typically remain in their natal group for life, and so we assume that a female is dead if she is not seen after repeated counts of her social group during an annual census. Males typically leave their natal group as they mature and may transfer between groups several times thereafter. Seventy-six percent of our marked males transferred at least once between 1984 and 1988. We assume that a male is dead, thus, only if he is not seen in one of the 28 social groups comprising the study population or in an adjacent social group in *two* successive annual censuses.

TABLE 3. Age-specific birth rates[1] *in* P. verreauxi *at Beza Mahafaly, June 1984 to June 1988*[2]

Age/wear category	No. of females	No. of census years	Birth rate[3]	Adjusted birth rate[3]
A	6	13	—	—
B	6	9	0.66	0.56
C	8	12	0.75	0.33
D	8	14	0.57	0.43
E	5	17	0.41	0.18

[1] Differences between age/wear classes are not statistically significant. (X = 3.67, df = 3, P = 0.299—birth rate; X = 4.36, df = 3, P = 0.227—adjusted birth rate).
[2] n = 81 female/birth seasons; 1988 birth season not included.
[3] The birth rate is the proportion of females giving birth on average. The adjusted birth rate is the proportion of females giving birth to infants that survived the first year.

TABLE 4. Birth sequences and cumulative reproductive success of female P. verreauxi *at Beza Mahafaly, 1984-1988*[1]

Female ID	Age/wear category	1984	1985	1986	1987[2]	Cumulative reproductive success[3]
34	B	—	b	no	b	0.67
41	C	b	(b)	(b)	b	0.50
58	C	—	b	(b)	no	0.33
20	D	(b)	b	no	no	0.25
35	D	—	b	no	b	0.67
13	E	no	no	(b)	no	0
18	E	(b)	b	b	no	0.50
36	E	no	no	no	no	0
54	E	b	b	no	no	0.50
101	E	no	b	no	(b)	0.25
19	?	no	no	(b)	b	0.25
105	?	(b)	(b)	no	no	0
107	?	no	b	no	b	0.50

[1] b, Birth of an infant surviving through the first year; (b), birth of an infant that died during the first year; no, female did not give birth; —, female was not seen during the birth season.
[2] Survival of infants born in 1987 was determined during the 1988 census.
[3] Average number of surviving offspring born per birth season.

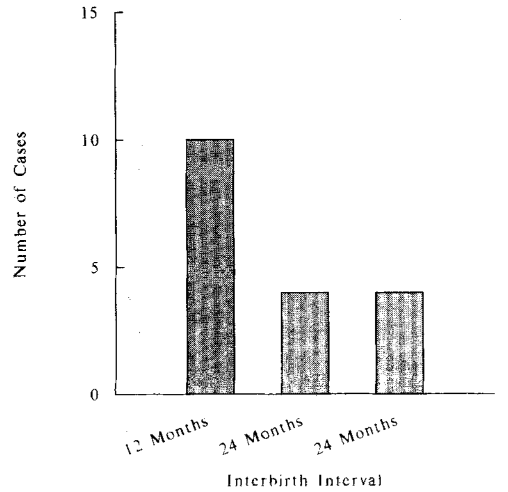

Fig. 6. Interbirth intervals in female *P. verreauxi* at Beza Mahafaly.

This would still overestimate mortality if males commonly transferred over long distances, but they do not. Almost all transfers occur between neighboring groups, and none have been observed between groups separated by more than one intervening group (Richard et al., 1991a). To avoid the possibility of overestimating female mortality relative to male mortality (because our methods also have the effect of giving males twice as long to be declared dead), we have used data only through 1987, which have been corroborated for both sexes by two subsequent censuses (1988 and 1989).

No pattern has yet emerged with respect to seasonality of deaths. We have inferred the proximate cause of death in a few cases: Two animals have been found dying or dead on the ground, clutching dead branches in their hands and we assume they fell. One young adult male (age/wear class B) was

TABLE 5. Annual variations in survival (p_x) during the first year among P. verreauxi *at Beza Mahafaly*[1]

1984-85 (n = 9)	1985-86 (n = 10)	1986-87 (n = 9)	1987-88 (n = 10)
0.33	0.80	0.44	0.80

[1] Overall survival during the first year (p_{0-1}) = 0.61.

TABLE 6. Age-specific survival in male and female P. verreauxi *at Beza Mahafaly, 1985-86 (n = 59) and 1986-87 (n = 66)*

	Survival rate (p_x) by sex and age/wear class				
	A	B	C	D	E
Females					
1985-86	1.0	0.75	0.17	0.83	0.75
1986-87	0.86	1.0	1.0	1.0	1.0
Males					
1985-86	1.0	1.0	1.0	0.89	0.75
1986-87	1.0	0.91	1.0	1.0	0.80

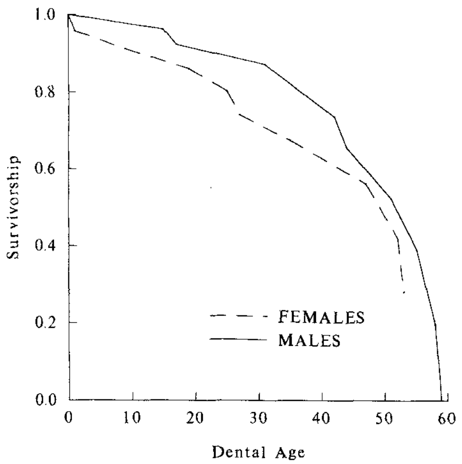

Fig. 7. Kaplan Meier product limit estimates of survival in male and female *P. verreauxi* at Beza Mahafaly, 1985–1987.

found eviscerated but otherwise intact; according to the forest guards, this signals predation by *Cryptoprocta ferox*, the largest of the Malagasy carnivores.

DISCUSSION AND CONCLUSIONS

At the outset of this paper, we proposed two possible mechanisms that could give rise to the distinctive difference between the tertiary sex ratios reported for sifakas and for haplorhine primates: 1) periodic pulses favoring males in the secondary sex ratio of sifakas and 2) differences in the life history trajectories of haplorhines and sifakas. Although our sample size is still small and few of our findings reach statistical significance, data from the Beza population enable us to make a preliminary assessment of the plausibility of these ideas. First, however, we consider two possible sources of error in the sifaka data, mistaken sexing and small sample effects.

Two factors make it unlikely that reported sifaka sex ratios are artifacts of mistaken sexing, although mistakes in sexing and censusing undoubtedly occur (O'Connor, 1987; Richard, 1978). First, it is likely that such mistakes would produce a bias in favor of females by wrongly counting as females young males with small or not yet descended testes. Second, an excess of males over females is present in the sample of animals captured at Beza Mahafaly, all of whom were sexed unequivocally; this imbalance was also found in the larger censused population, including uncaptured as well as captured animals, and we have no evidence that our capture techniques introduced a bias in favor of males.

Sampling problems have been repeatedly proposed but not fully evaluated as an explanation for reports of skewed ratios (Jolly et al., 1982; O'Connor, 1987; Richard, 1978). *P. verreauxi* live in groups of highly variable sexual composition (Richard, 1985b) so that sex ratio estimates derived from total censuses of a small number of groups are particularly susceptible to sampling error. Figure 8 shows the relationship between sample size (i.e., number of individuals censused) and estimated sex ratio, using data from Table 1. For each population we calculated a mean sex ratio with censuses weighted by sample size. The grand weighted mean for the six populations is 0.486, and all samples fall within the 95% confidence limits calculated from the binomial distribution assuming equal numbers of males and females. We cannot, thus, reject the hypothesis that departures from a 50:50 sex ratio are a consequence of sampling effects. However, we note that the most strongly male-biased sex ratio is found in the Beza population, which is the largest sample, the only one for which there is no possibility of error in the assignment of sex, and the only one in which a few individuals were sampled at random from a large number of groups (n = 28) rather than all the individuals from a few groups. As a result, it is more nearly a random sample of individuals from the population than a sample of groups from the total array of groups.

Our confidence that the sex ratios under consideration here are relatively accurate is further strengthened by the strong correlation between sex ratios estimated from censuses in consecutive years at Berenty between 1963 and 1985, even though the identity and number of censused groups was quite variable from year to year. Indeed, there is some indication of a long-term fluctuation in the Berenty sex ratio around a mean of about 0.5 (Fig. 9), although it is unclear what factors could drive a cycle of this periodicity. (We plotted the 1980 data point but did not fit the line to it because it is an outlier, the sample size is small, and Jolly et al. [1982] expressed doubts about the reliability of the 1980 census because social groups were uncharacteristically fragmented and difficult to count).

Two demographic mechanisms were proposed that might give rise to the significant difference between sifaka tertiary sex ratios and the strongly female-biased tertiary sex ratios of haplorhines. Observations from this study suggest that it would be premature to rule out the first of these, namely, that the sifaka secondary sex ratio is intermittently or persistently skewed in favor of males and that this bias persists into adulthood. First, conventional representation of the population's age and sex structure shows an excess of males in the youngest age/wear class in 1985 and 1987 (Fig. 4b). Second, in the most recent field season (August 1989), all yearlings present in seven groups were captured and sexed unequivocally (n = 9). All were male. Nine births were recorded in these seven groups in the 1988 birth season, indicating that there were no infant deaths and that the strongly biased sex ratio in the yearling cohort, at least in this small sample, represented the sex ratio at birth. The probability of this sex ratio occurring by chance is low ($P = 0.007$). (Captured males were assigned to the yearling class based on weight, size, absence of toothwear, and small or incompletely descended testicles).

The second mechanism we proposed to account for differences between sifaka and haplorhine tertiary sex ratios invokes factors acting differently on males and females after birth. Once again, we cannot exclude this possibility. The cumulative plot of age-ranked males and females (Fig. 5) gives some support to the idea that the shift toward a male-biased sex ratio occurs after birth and perhaps after animals reach adulthood. In the introduction, we identified three demographic or life history variables that may act differently upon sifaka males and females: sex differences in age-specific mortality, maturation, and migration in and out of the

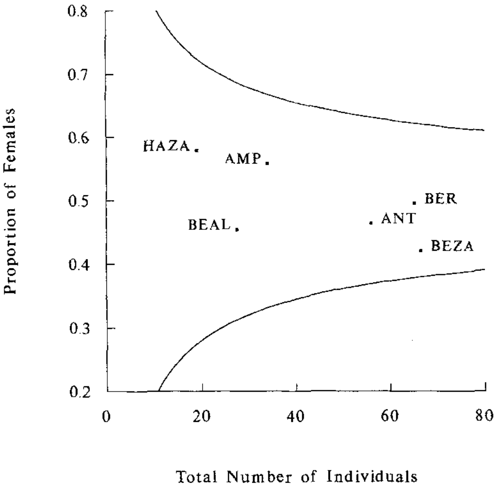

Fig. 8. Mean sex ratio and sample size in six populations of *P. verreauxi;* Amp, Ampijoroa; Ant, Antseranamomby; Beal, Bealoka; Ber, Berenty; Beza, Beza Mahafaly; Haza, Hazafotsy; for data sources, see Table 1.

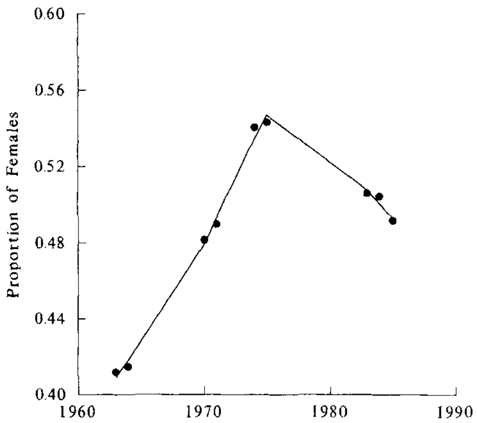

Fig. 9. Sex ratio of *P. verreauxi* censused at Berenty, 1963–1985; the line was fitted to all points except the 1980 census by locally weighted scatterplot smoothing (Wilkinson, 1988).

study area. With regard to the last, there is no obvious reason, such as deforestation or major habitat disturbance, to suspect differential immigration of males into the reserve (c.f. Richard, 1978). With regard to maturation, there is no evidence of major differences in growth rate in this sexually monomorphic species (Haring, 1988; Richard et al., 1991b), and both males and females older than 1 year were captured and included in the study population.

Of the three variables potentially acting on the tertiary sex ratio, the one most plausibly important in differentiating sifaka sex ratios from haplorhines is sex-specific survival. As an alternative or complement to the skewed secondary sex ratio hypothesis, we suggest that the distinctive tertiary sex ratio in sifakas compared with haplorhines is generated by irregular pulses of mortality among females of reproductive age. This suggestion receives preliminary support from the cumulative plot of age-ranked males and females, the generally lower survival of females indicated by the Kaplan-Meier product limit estimate, and wide variance in female mortality between years. There is mounting evidence from several primate species that reproduction is energetically costly, entailing risks for the mother as well as her infant, and increased mortality associated with motherhood has been reported among baboons and macaques (Altmann, 1980; Silk, 1988). A constellation of behavioral and physiological features, including female social dominance, a low basal metabolic rate, and high prenatal maternal investment rate suggest that reproduction may be particularly stressful for female *P. verreauxi* (Jolly, 1984; Richard, 1987; Richard and Nicoll, 1987; Young et al., 1990). Even in the absence of unusual physiological traits, intermittently high mortality among reproductively active females would not be an unexpected pattern in a population living in the highly seasonal and from year-to-year unpredictable environment of southwest Madagascar (Fig. 2). Possible evidence of stress in the Beza population is provided by the advanced age of females (>5 years) at first reproduction. In contrast, in 1985 A.F.R. watched a male copulate, with ejaculation, when he was less than 3 years old (inferred from his size, weight, and toothwear).

Despite the possibility that female mortality associated with reproduction may be high in sifakas in general and in the Beza population in particular, we were nonetheless puzzled by the finding that male survival was as high as or higher than that of females. Bloody, even deadly, fights between males have been observed during the mating season (Jolly, 1966; Richard, 1974, 1987), and males spend time outside groups, thereby increasing their vulnerability to predators. With these observations and the survival patterns of other primates in mind, we expected to find high mortality among young and prime adult male *P. verreauxi*. Instead, in over 250 male-years of observation, mortality has been overwhelming concentrated in the oldest age/wear class. This result may be due to sampling error. Alternatively, dramatic as such events are, severe injury and death among males during the mating season may be much rarer than we once thought, and predation pressure on lone adults may be negligible.

The study of demographic patterns, processes, and their determinants is important. It is an essential component of research on many aspects of mammalian biology and behavior, including life history patterns (e.g., Stearns, 1976, 1977), social systems (Altmann and Altmann, 1979; Dittus, 1988; Hausfater et al., 1982), population genetics (Melnick and Kidd, 1983; Rogers, 1989), and community ecology (Wiens, 1977; Richard, 1985a). It can also contribute to the development of management plans (Fowler and Smith, 1981). In Madagascar, where the rate of habitat destruction is increasing and primate populations are declining (Jolly, 1980; Richard and Sussman, 1988), this is a particularly urgent concern and one to which we hope our work will make a contribution.

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