

Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*)

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Abstract

A 16-year study of wild, unprovisioned sifaka *Propithecus verreauxi verreauxi* at Beza Mahafaly in south-west Madagascar provides estimates of age-specific fertility, mortality, and dispersal in a population of 426 marked animals, and longitudinal records of individual life histories. Sifaka females give birth for the first time later and live longer, for their size, than mammals in other orders; they also give birth later and continue reproducing longer, for their size, than other primates. Theory postulates that these features, commonly referred to as bet-hedging, evolve in unpredictable environments in association with widely varying infant survival and a trade-off between reproductive effort and adult survival. The climate of south-west Madagascar is highly unpredictable compared to almost all other regions in the tropics with similar average rainfall, and we argue that sifaka females are bet-hedgers *par excellence*. Male sifaka, in contrast, become reproductively active at an earlier age than females, and are less likely to have long lives than females. The atypical direction of this asymmetry between males and females reflects a 'slowing down' of female life histories rather than a 'speeding up' of male life histories. Two other unusual features of sifaka biology and behaviour may be linked to the unpredictability of Madagascar's climate: intense local competition between females, and a sex ratio at birth strongly biased in favour of males in most years. In drought years, reproductive females must cope with suddenly intensified resource constraints. This, in turn, may strongly limit the number of 'breeding slots' available over the long-term for females.

Key words: life history, demography, lemur, *Propithecus verreauxi verreauxi*, unpredictability, Madagascar

INTRODUCTION

In a review of ideas about the evolution of life-history patterns in plants and animals, Stearns (1976) emphasized the need for more comprehensive theory and also for experiments to test existing assumptions and predictions. Even descriptive studies were lacking for most mammals at that time, however, let alone the kinds of experiments called for by Stearns. The situation has improved since then, and the broadly based comparative analyses now possible have served both to advance ideas about life-history evolution and to sharpen the questions being asked (e.g. Promislow & Harvey, 1990; Stearns, 1992; Gage, 1998). Still, experimental studies remain rare and the data used in comparative analyses often contain several potential sources of error (Promislow & Harvey, 1990). Even today, there are relatively few longitudinal studies of wild populations of large-bodied mammals that track patterns of reproduction and mortality in cohorts of individuals over most or all

of their lives. Notable exceptions include long-term research on ungulates (e.g. Clutton-Brock, Illius *et al.*, 1997; and see review by Saether, 1997), a few large carnivore populations (e.g. Hanby & Bygott, 1979; Packer, Herbst *et al.*, 1988; Kelly *et al.*, 1998), and the elephant seal (Le Boeuf & Kaza, 1981; Le Boeuf & Reiter, 1988).

Data on primate population dynamics have grown steadily in recent years, even though with their long lifespans and low population densities, primates are difficult subjects for studies of this kind. With few exceptions, the most information still comes from provisioned, and often captive, populations of *Macaca mulatta* and *M. fuscata* (Masui *et al.*, 1975; Sade *et al.*, 1976; Southwick & Siddiqi, 1976, 1977; Fedigan, 1991; Fedigan & Zohar, 1997) and *Pan troglodytes* (Teleki, Hunt & Pfifferling, 1976; Goodall, 1983). Some data on age-specific fertility and mortality are available for wild, unprovisioned populations of *Lemur catta* (Sussman, 1991), *Papio cynocephalus* (Altmann, Hausfater &

Altmann, 1985; Alberts & Altmann, in press), *Pan troglodytes* (Sugiyama, 1994), *Theropithecus gelada* (Dunbar, 1980), *Macaca fuscata* (Takahata *et al.*, 1998), and *M. fascicularis* (van Noordwijk & van Schaik, 1999). In addition, model life tables have been developed for two macaque species (*Macaca mulatta*, *M. fuscata*), *Papio* spp., *Pan troglodytes*, and four New World primates (*Leontopithecus rosalia*, *Callithrix jacchus*, *Saguinus fuscicollis* and *S. oedipus*) (Dyke *et al.*, 1993; Gage, 1998). These tables are drawn primarily from captive breeding colonies, with a few data coming from provisioned or unprovisioned populations in the wild, and they do not distinguish between males and females. The substantial body of descriptive information on wild populations has been reviewed by Dunbar (1987).

Mammalian life histories fall along a continuum, from 'brief-and-fast' to 'long-and-slow'. To explain this variation, it has been postulated that life-history traits are shaped by body mass (Western & Ssemakula, 1982) brain mass (Martin, 1981; Harvey, Martin & Clutton-Brock, 1987), metabolic rate (McNab, 1980, 1986), or some combination of the three. The average relative brain size of primates exceeds the average value for most other orders of mammals (Martin, 1990), and so the idea that brain tissue is produced slowly and constrains overall growth rates (Sacher & Staffeld, 1974) fitted well with the general observation that primates live their lives 'in the slow lane'.

In 1993, Charnov & Berrigan (see also Charnov, 1991, 1993) emphasized anew the 'slowness' of primate life histories. But they pointed out that snakes and lizards have relatively small brains even though they too grow slowly and have lifespans (adjusted for body size) equal to or greater than primates. Read & Harvey (1989) examined life-history traits in 17 orders of mammals, and found considerable variability unaccounted for by body or brain mass or metabolic rate. Moreover, life-history factors covary along a fast-slow axis even after the effects of body mass, brain mass, and metabolic rate are held constant (Stearns, 1983; Harvey & Zammuto, 1985; Promislow & Harvey, 1990; Harvey, Pagel & Rees, 1991). These conclusions have fostered renewed attention to life-history traits as the primary targets of selection, and to earlier approaches linking them directly to environmental conditions (e.g. MacArthur & Wilson, 1967; Pianka, 1970; reviewed by Stearns, 1976, 1992). Understanding why life-history traits covary with one another requires an understanding of how selection works on them separately and together. Ross (1991, 1992) found a positive correlation between some forms of climatic variability and the maximum intrinsic rate of population increase (r_{\max}) in 72 primate populations, and suggested that unpredictable and/or open habitats favour the evolution of a high r_{\max} , whereas predictable and/or forested habitats select for a low r_{\max} . She noted the potential for error in her analysis, however, and emphasized the need for more data on primate mortality schedules to distinguish between competing models of the evolution of their life histories.

The importance of age-specific patterns of mortality in relation to ecological variation has been a central theme in many discussions of the evolution of life histories, regardless of the particular model advocated by the author. For example, even as they emphasize slow growth rates as the 'keystone' difference between the life histories of primates and other mammals, Charnov & Berrigan (1993: 193) implicate mortality as a crucial constraint: 'it takes primates so much longer to grow to a size of, for example, 10 kg, with their low production rates, that only with very low mortality (and very long life spans) will natural selection favor the delay in first breeding to enable a species to grow as large as 10 kg . . .'

In sum, perhaps the broadest consensus in the considerable body of empirical and theoretical work on life histories is that more, and more rigorous, data are needed from wild populations. There is also broad agreement that 'as mammal life histories go, primates are slow' (Charnov & Berrigan, 1993: 191), but still no clear understanding of the reasons for this. Among primates, it has been said that prosimians are the 'fastest' (Kappeler, 1996). We will show, however, that this is not true of all prosimians. Lacking longitudinal data from the wild, there has in fact been little systematic exploration of variability in life history among primates.

One further feature of these studies has been little remarked upon. With few exceptions (reviewed by Stearns, 1976, 1992), models have focused on the evolution of life histories in stable or cyclically fluctuating environments. Several studies of wild primates have recorded major perturbations in their environment (e.g. *Alouatta palliata*: Froelich, Thorington & Otis, 1981; Otis, Froelich & Thorington, 1981; *Macaca sinica*: Dittus, 1975; *Papio cynocephalus*: Altmann *et al.*, 1985; *Cercopithecus aethiops*: Struhsaker, 1973, 1976; *Lemur catta*: Gould, Sussman & Sauther, 1999), but there has been little discussion of the evolutionary implications of environmental unpredictability (c.f. Clutton-Brock, Illius *et al.*, 1997, for ungulates).

In this paper, we describe male and female life-history patterns and the dynamics of a wild, unprovisioned population of sifaka *Propithecus verreauxi verreauxi* (Grandidier), a Malagasy prosimian primate. These patterns are related to fluctuations in body mass, and to stochastic environmental events. Sifaka life histories are compared to those of other mammals, and the life histories of male and female sifaka to one another. Finally, we discuss how the extreme unpredictability of Madagascar's climate may have shaped the evolution of sifaka life-history patterns. We argue that a cogent explanatory framework is provided by the body of life-history theory referred to as 'bet-hedging', which predicts life-history traits in relation to patterns of fertility and mortality in fluctuating environments. Specifically, under conditions of fluctuating juvenile survival and a trade-off between adult survival and reproductive effort, species evolve longer lifespans and reproduce longer, and at a lower rate (Stearns, 1976).

The data on sifaka come from a continuing study of animals living in the forests of Beza Mahafaly, south-west Madagascar, initiated in 1984. Differences between the results presented here and those reported previously (Richard, Rakotomanga & Schwartz, 1991) are noted and discussed. Data for other mammals are drawn from the existing literature. The distinctiveness of south-west Madagascar's climate compared to larger tropical land-masses has been established by Dewar & Wallis (1999), and only a summary of those findings is given here.

MATERIALS AND METHODS

Study site and general methods

The present study at the Beza Mahafaly Special Reserve in south-west Madagascar began in 1984 as part of a collaborative programme of research and conservation with colleagues in Madagascar (Sussman & Richard, 1986; Rakotomanga, Richard & Sussman, 1987; Richard, Rakotomanga & Sussman, 1987). The ecology and behaviour of the 2 diurnal primates, *Propithecus verreauxi verreauxi* and *Lemur catta*, have been studied since the Reserve was created in 1977 (*P. v. verreauxi*: Richard, Rakotomanga & Schwartz, 1991, 1993; Ranarivelo, 1993; Brockman, 1994; Kubzdela, 1997; Ravelonjatovo, 1997; Brockman, Whitten, Richard & Scheider, 1998; Brockman & Whitten, 1999; *L. catta*: Ratsirarson, 1985; Sauther, 1989, 1991, 1992, 1993, 1998; Sussman, 1991; Sussman, 1992; Gould, 1996*a,b*, 1997*a,b*; Gould, Sussman & Sauther, 1999; Sauther, Sussman & Gould, 1999). The site and general methods of study are described in these publications (see also Sussman & Rakotozafy, 1994).

Located in the driest region of the island, the Beza Mahafaly Special Reserve protects 600 ha of riverine and xerophytic forest within a much larger, contiguous forested area. Sifaka occur throughout this area, which is bounded several km to the north by the intermittently shifting bed of the Onilahy River, and about 20 km to the south by deforested lands around the market town of Betioky. Continuous forest extends for many km to the east and west.

The capture of animals began in November 1984. Up to August 1999, 426 animals were captured. Of these, 99 were captured twice and 16 captured 3 times in order to gather longitudinal data from particular individuals. Each individual was given a coloured nylon collar with a plastic tag numbered on both sides, which varied in shape and colour. Several ways of attaching the tag to the collar were tried. The best method used a 2-inch length of multi-strand, stainless steel sailboat rigging wire, threaded through a small hole in the tag. The ends of the wire were then crimped together in a small lead sleeve using a swage, and the resulting ring suspended from the collar. No tags have been lost using this method since its initiation 3 years ago. As a back-up, the ears of each animal were notched using a binary system that yields a total of 63 distinct combinations

which can be 'read' using binoculars. Some animals alive today have identical notches because the binary system has necessarily been cycled through several times. For example, animals with tag numbers 1, 64, and 127, respectively, have a single notch in the same position.

There were 225 marked animals in the reserve in July 1999, together with an estimated 20 unmarked juveniles and adults, and 30 unmarked new-borns. All animals except a few males were assigned to 1 of about 54 social groups with ranges completely or partly in the reserve. The number of social groups fluctuated over the years. Although many groups have persisted within stable boundaries since 1984, new groups have formed and some existing ones have dissolved (Richard, Rakotomanga & Sussman, 1993). Groups contained 2–14 animals.

Animals were captured in every month except March. Animals < 1 year old were not darted, nor were mothers with dependent young, or females suspected to be gestating. Males and females were captured with equal success. The average body mass of adults was 2.8 kg, and there was no overall sexual dimorphism in this species. Long-bone growth is completed by the age of 5 years, but both males and females continue to gain mass for several years thereafter (Richard, Dewar *et al.*, 2000).

Animals were immobilized using an anaesthetic drug delivered by a dart fired from a Telinject blowgun. Initially, animals were sedated with Ketamine, but Telazol has been used since 1992 because it is more soluble than Ketamine and does not cause an excitatory phase. Telazol is a cocktail of tiletamine hydrochloride and benzodiazepines (minor tranquillizers of the valium class). The dart was loaded to deliver 25 mg/estimated kg in solution at a concentration of 500 mg telazol/3.3 ml sterile water. Sapolsky & Share (1998) discuss the problems of darting terrestrial primates in the wild, and almost all their observations match our experience with arboreal sifaka. There was, however, no difficulty darting upward at an animal in a tree because of the low stature of the forest at Beza Mahafaly and the exceptional skill of 2 local darters.

At the outset, animals were assigned to 1 of 5 age classes based primarily on toothwear analysis. Dental casts from recaptured animals were used to calibrate rates of wear (Richard, Rakotomanga & Schwartz, 1991). Births occurred during a 6- to 8-week period at about the same time each year, making it possible to identify size cohorts during the first 2 years of life. Animals older than this cannot be reliably aged by eye, because body mass ranges overlap between years in older cohorts. Today, most animals are known from birth and can be aged with certainty. Estimated ages were used only for adult immigrants and for the declining number of animals still alive that were mature when the study began.

Censuses were carried out annually from 1985 to 1991, and thereafter at least at monthly intervals by trained Beza Mahafaly Special Reserve local staff, and

by Malagasy and visiting researchers. The low, relatively open forest, together with the presence of north–south and east–west trails through the forest at 100-m intervals, facilitated the location and censusing of individuals and groups. The quality of data has improved since 1992, both because censusing has been more frequent and because most individuals in the population have been individually marked since then. Subsets of the complete data set were selected and are identified for each analysis presented here, with the aim of maximizing both the size and quality of the sample used. No outliers were removed.

The records used to estimate fertility are complete except for 1989, although some births may have been missed each year when neonates died perinatally. In 1989, the census was conducted early and births were not recorded systematically. Estimating mortality poses a greater problem. Deaths were occasionally observed during this study, and many intact collars with associated skeletal material were retrieved from the reserve. Sometimes, however, animals simply disappeared. Males leave their natal groups, usually in their third or fourth year (Richard, Rakotomanga & Sussman, 1993; Brockman, Whitten, Richard & Benander, in press). Most of these males transfer to a neighbouring group, and many transfer again several times thereafter. In 103 transfer episodes involving marked males since 1985, 89 were to a social group with an overlapping home range, 12 to a group no more than 1 home range away, and 2 to groups 3 or 4 home ranges away. Some nulliparous females also leave their natal groups and attempt to establish new groups (Richard, Rakotomanga & Sussman, 1993; Kubzdelá, 1997).

This viscosity of sifaka society makes it possible to distinguish with reasonable confidence between death and emigration in missing animals. The population was divided into 3 subsets for this purpose: (1) core social groups, at any given time consisting of 35–40 groups with home ranges completely or mostly in the reserve, that were censused every month and in which almost every adult animal was marked; (2) buffer zone groups, consisting of 15–20 groups with home ranges partly in the reserve, that were censused in most months and in which some adults were marked; (3) peripheral groups, with ranges outside the reserve that were checked at least once a year for the presence of marked emigrants from the reserve. Only males and females in core social groups were used to estimate age-specific mortality and fertility. A male was designated dead if he was not seen for 24 consecutive months in his group of origin, another core social group, a buffer zone group, or a peripheral group. Males not seen for shorter periods were assumed to be alive. This method overestimates male mortality if animals occasionally transfer over longer distances and move beyond the peripheral groups, or if they remain unobserved within the study area for several years. A female was designated dead if, during 12 successive monthly surveys, she was not observed in her natal social group, an adjacent group, or with other animals in an adjacent patch of forest.

RESULTS

Fertility, and patterns of reproduction

Fewer than half the females in the population gave birth for the first time by the age of 6 years, and fewer than half gave birth to a surviving offspring (i.e. an offspring that survives the first 12 months of life) at 7 years (Table 1). The sample included only marked females that were intensively observed in every birth season, starting with their third year of life. The youngest age at which females were observed with an infant was the end of their third year ($n=2$ of 50 3-year-olds observed in the birth season). These females both gave birth in 1990, the year with the highest overall fertility recorded throughout the study. Neither of their infants survived. Of the 12 births recorded to 5-year-old females, only one infant survived the first year. After the age of 6 years, reproductive success improved rapidly, and all females observed in every birth season since they were 3 years old have either died or given birth to a surviving offspring by the age of 11 years.

Fertility remained steady for about a decade after the sharp increase during the initial reproductive years (Fig. 1). From the age of 18 years, fertility begins to decline, but with high variability between cohorts. Only 15 females were estimated to be 20 years old or older, and so this variation may partly reflect small sample size. Still, it is notable that some females have very long and active reproductive lives, with 20- and 21-year-olds reproducing at about the same rate as 7-year-olds, and 22-year-olds exhibiting the highest birth rates of all. Among the very oldest females (>24 years, $n=4$), one gave birth at the age of 28.

The age-specific rate of giving birth to a surviving infant closely follows age-specific fertility, except for very young and very old mothers (Fig. 2). From 6 years of age to >20 years, mothers differed little in the proportions of their infants that survived. Only the very youngest and oldest mothers experienced markedly lower success in keeping their infants through the first 12 months.

Cross-cutting these population-wide patterns was the

Table 1. Onset of birth and successful reproduction (defined as infant survival for 12 months) for all captured female sifakas *Propithecus verreauxi verreauxi* in the Beza Mahafaly population

Age (years)	No. of females observed since age 3 years who gave birth at this age or younger	No. of females observed since age 3 years successfully reproducing at this age or younger
3	2 of 50	0 of 50
4	2 of 41	0 of 41
5	7 of 35	2 of 34
6	13 of 27	5 of 22
7	13 of 21	7 of 16
8	15 of 20	8 of 15
9	15 of 16	9 of 11

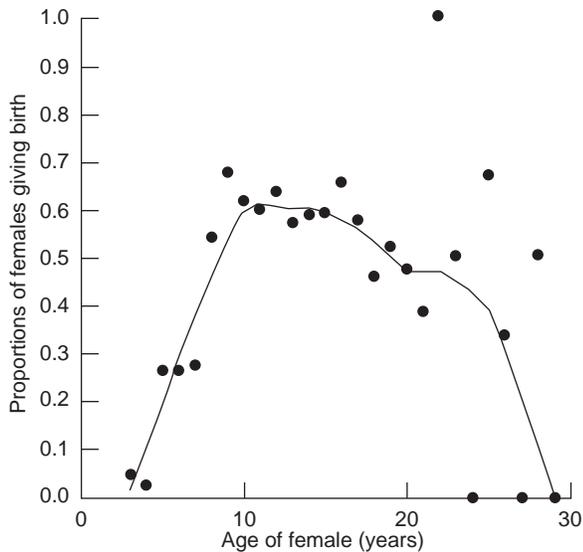


Fig. 1. Age specific fertility of marked female *Propithecus verreauxi verreauxi*, 1985–99. The smooth is LOWESS (locally weighted scatter plot smoothing; Cleveland, 1979) and was produced using Systat 9 (SPSS, 1999).

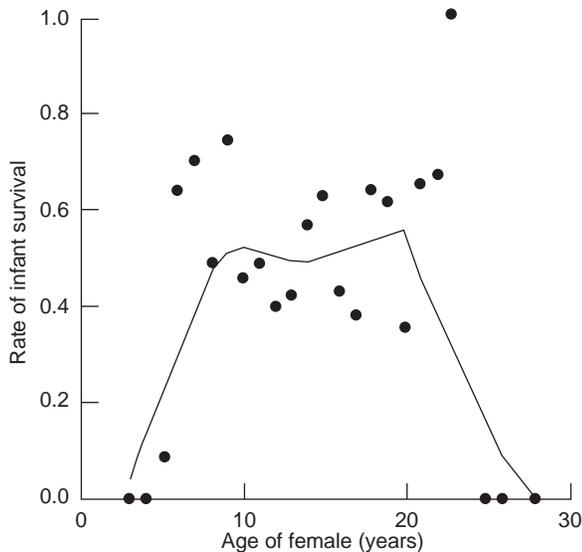


Fig. 2. The proportion of infant *Propithecus verreauxi verreauxi* surviving to 12 months as a function of maternal age. The smooth is LOWESS.

finding that both cumulative reproduction and the pattern of births varied widely between individual females (Fig. 3). Some females failed to give birth at all over many years, and others gave birth every year for as many as 9 years in a row. For the 14 females observed in at least 10 birth seasons, the proportion of years in which a female gave birth ranged from 23% to 77% (median 54.2%, quartiles 42.9% and 63.6%). For the same subset of females, the proportion of years that they gave birth to an infant that survived 12 months, ranged from 13% to 57% (median 30.3%, quartiles 18.8% and 38.5%).

Perhaps the most striking result is that ‘success

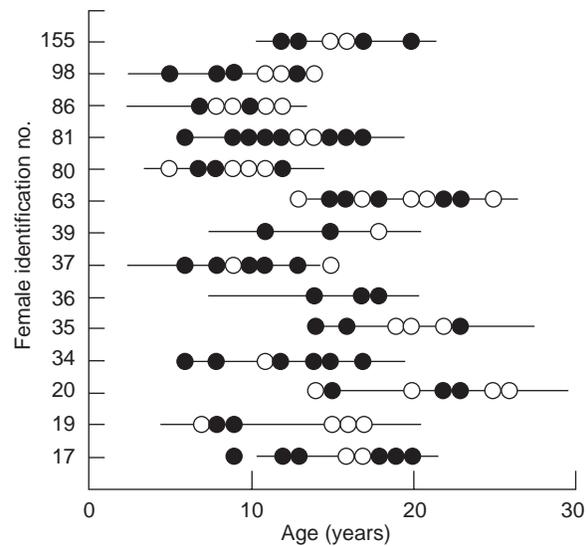


Fig. 3. Birth chronology of 14 female *Propithecus verreauxi verreauxi* monitored for at least 10 successive birth seasons. Births of infants surviving > 12 months are marked by filled circles, unsuccessful births by hollow circles, and years without births by a line. Missing cases are left blank.

begets success’ among sifaka females. At most ages, females who reproduced last year were as likely to give birth as females in the population as a whole (compare columns A and B in Table 2). For females with broadly similar fertility (8- to 21-year-olds), the average birth rate of those who had an infant the year before was slightly higher than the average birth rate for all females in this age range: 59.6% compared to 58.5% (Wilcoxon signed rank $Z = 0.105$, $P = 0.917$). Based on a large sample, this finding contrasts sharply with our previous suggestion, derived from fewer data, that 2 years is the typical inter-birth interval in this population (Richard, Rakotomanga & Schwartz, 1991). The newly documented variation was probably a consequence of both intrinsic differences among females and micro-demographic effects, particularly the number of females present in a group (Kubzdela, 1997; Brockman & Whitten, 1999).

Most males had fully descended testes by the time they were 18 months old, and 4-, or possibly 3-year-old males, were observed mating (Richard, 1974, 1992; Brockman, Whitten, Richard & Schneider, 1998). Male reproductive success is the subject of ongoing research using microsatellite analysis (R. Lawler, pers. comm.).

Mortality, and the determinants of death

Mortality was high during the first year of life; 52% of infants survived the first 12 months on average, with wide variation from year to year (see below). It is not known whether male and female infants died at different rates, because animals can rarely be sexed reliably before being captured as yearlings.

Mortality rates were similar for immature males and

Table 1. Comparison of the age-specific proportions of female sifakas *Propithecus verreauxi verreauxi* giving birth (B), giving birth after having given birth the year before (C), giving birth to infants that survive 12 months (D), giving birth with a surviving yearling from the previous year (E), and giving birth to an infant that will survive 12 months with a surviving yearling from the previous year (F). Data 1984–99

A Age	B Birthrate (all ♀♀s)	C Gave birth last year with infant this year	D Birthrate of infants surviving > 12 months (all ♀♀s)	E ♀♀s giving birth, with surviving yearling	F ♀♀s giving birth to surviving infant with surviving yearling
3	0.07	0	0	0	0
4	0.03	0.5	0.02	0	0
5	0.21	1	0.03	0	0
6	0.21	0.5	0.13	0.5	0
7	0.36	0.75	0.21	0.75	0
8	0.59	0.88	0.35	0.78	0.14
9	0.78	0.67	0.56	0.75	0.43
10	0.63	0.65	0.36	0.8	0.75
11	0.63	0.93	0.26	0.88	0.33
12	0.76	0.58	0.34	0.5	0.4
13	0.45	0.57	0.23	0.35	0.33
14	0.65	0.5	0.46	0.4	0.17
15	0.59	0.64	0.38	0.56	0.38
16	0.64	0.58	0.38	0.5	0.44
17	0.5	0.63	0.29	0.5	0
18	0.5	0.29	0.23	0	1
19	0.5	0.50	0.57	0.57	0.16
20	0.47	0.25	0.13	0	1
21	0.5	0.67	0.15	1	0
22	0.67	0.75	0.43	0.67	0
23	0.75	1	0.75	0	0.67
24	0	0.5	0	0	0
25	0.33	0	0	0	0
26	0.5	0	0	0	0

females of > 1 year, and much lower than overall rates during the first year of life. Mortality remained low until animals reached the age of about 18 years (Fig. 4). On average, 9–10% of males and females 2 years old and older died each year (females, median 10.8%, quartiles 4.3% and 13.1%; males, median 8.0%, quartiles 6.3% and 14.3%), although there was wide variation from year to year (see below), and the age-specific pattern of mortality was different for males and females. Young adult females died at a higher rate than young adult males. From the age of about 12 years, the pattern reversed and females exhibited lower mortality than males thereafter.

Infant deaths were rarely witnessed, and the cause of death was almost never known. Mothers were twice observed repeatedly retrieving and finally abandoning new-borns that failed to cling. Several reasons for these deaths were possible, from lactational failure on the part of the mother to a birth defect in the infant itself. A recently transferred male was observed killing an infant (K. S. Kubzdela, pers. comm.), and there was indirect evidence pointing to infanticide on four other occasions. Infanticide did not seem to occur as frequently in *P. v. verreauxi* as has been reported for *P. diadema edwardsi* (Wright, 1995; Erhart & Overdorff, 1998).

Infanticidal behaviour in sifaka is puzzling, in that females who gave birth to a surviving infant (i.e. an infant that survives the first 12 months) the previous

year are as likely to give birth to an infant that will survive, as females in the population as a whole (compare columns D and F in Table 2). For mothers with broadly similar fertility (8- to 21-year-olds), there

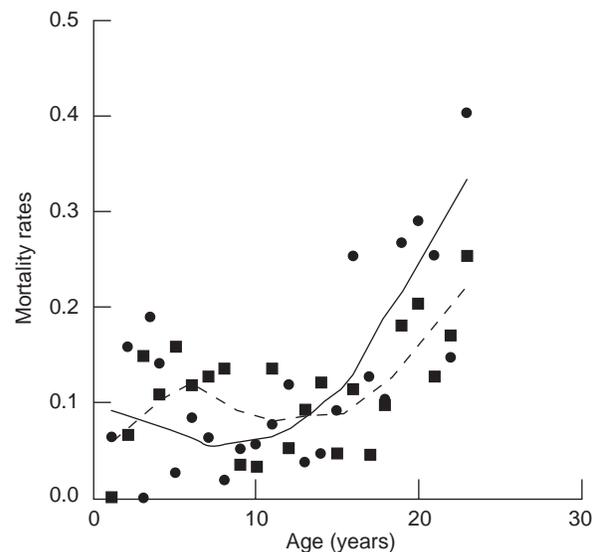


Fig. 4. Age-specific mortality of marked male (solid line) and female (dashed line) *Propithecus verreauxi verreauxi* from age 1 to age 23 years, 1985–99. The smooths are LOWESS.

Table 3. Season of death for *Propithecus verreauxi verreauxi*. (a) Infant sifakas recorded as dead in the first 12–14 months of life, 1955–98. (b) Months in which decomposing adult corpses were discovered, 1990–99. The rainy season months are shaded

(a) Infants	Month of death						
	Infant birth year	Jul–Aug	Sept–Oct	Nov–Dec	Jan–Feb	Mar–Apr	May–Jun
1995	?	2	4	2	2	0	2
1996	4			— 8 —			
1997	7	3	4	3	0	2	2
1998	5	1	3	4	1	2	?
(b) Adults							
Corpses found	18	0	2	2	0	6	

was no significant difference between these two groups: Wilcoxon signed rank $Z = -0.035$, $P = 0.972$. Moreover, an infant's chances of surviving the first 12 months were unaffected by the presence of a surviving sibling born the previous year. Of 87 surviving infants born between 1986 and 1997, 30 had older siblings (34.5%). Of 65 infants that died within the first year of life during this period, 22 had older siblings (33.9%).

Infant deaths occurred throughout the year, but our sample suggests that there may be two clusters: one shortly after birth, and another in the wet season (Table 3a). On days of heavy rainfall during the wet season, ambient temperatures dropped by as much as 10–15 °C. Animals fed little, and sat in the trees looking wet and cold. One may surmise that several such days in succession may lead to hypothermia and, perhaps, death. In the wet season, infants are also weaned and no longer carried by their mothers during the daily ranging activities of the group.

The determinants of juvenile and adult sifaka deaths were equally difficult to ascertain, and the effects of starvation, hypothermia, disease and predation probably interact with one another; 86% of decomposing corpses were found in the dry season (Table 3b). The sample size was small ($n = 28$) and may be biased because the dry season was also the time of most intensive observation in most years. None the less, the body mass of males and females was at its annual low-point at this time (see below), and elevated mortality is not unexpected.

Reproduction did not increase the likelihood that a female would die. Indeed, 57% of surviving females between the ages of 7 and 29 years, gave birth the previous year ($n = 376$), whereas only 27% of females who died gave birth the previous year ($n = 22$). Moreover, 59% of surviving females gave birth in two of the three previous years ($n = 274$), compared to only 38% of the females who died ($n = 21$).

The importance of predators at Beza Mahafaly is unknown. The fossa *Cryptoprocta ferox*, attacked adult as well as juvenile and infant *P. d. edwardsi* at Ranomafana in the eastern rain forest (Wright, Heckscher & Dunham, 1997). Fossa are rare at Beza Mahafaly, however, and there was only one probable episode of predation by fossa, as evidenced by an eviscerated corpse which is the signature of a fossa attack (Albignac, 1971, 1973). Karpanty & Goodman (1999)

report the first direct observations of predation on *Propithecus verreauxi* by the Madagascar harrier-hawk *Polyboroides radiatus*. The remains of two adult and three juvenile *P. verreauxi* were found at two nests during a 5-month study at Berenty and Behaloka, in the extreme south-east of the island. The Madagascar harrier-hawk is present at Beza-Mahafaly, but no attacks were witnessed.

Two dead or dying animals were found clutching dead branches, suggesting that they had fallen. Certainly, animals were observed falling considerable distances from time to time.

Sex ratio

The sex ratio of the Beza population reached 50:50 in only 1 year since the study began, and in most years females make up 45–48% of marked animals in the core groups (Fig. 5). Richard, Rakotomanga & Schwartz (1991) proposed that the male-biased sex ratio of the Beza population between 1984 and 1988 was generated by a sex ratio at birth biased in favour of males and subsequently magnified by higher survival among young adult males. Additional data allowed this proposition to be confirmed and amplified.

First, previously recorded differences in the age-specific survival of adult males and females persisted, even when the analysis was limited to the core groups (Fig. 4). Second, complete records since 1995 of the sex of all infants in the core population that survived the first year of life showed that females were under-represented in most yearling cohorts (35%, 41%, and 29% in 1995, 1996, and 1997, respectively). 1998 saw a striking swing toward females, however, with daughters making up 75% of the marked yearling cohort in 1999 ($n = 8$). A larger sample drawn from the entire marked population confirmed this result ($n = 13$, of which 77% were female). The 1999 birth cohort has not yet been sexed. If male and female infants die at similar rates, as older immatures do, the sex ratios of these yearling cohorts confirm a ratio at birth strongly favouring males in 3 out of 4 years.

Differential migration into the reserve by males did not contribute significantly to the composition of the population. Males left and entered the core population at similar rates. Complete records on migration by

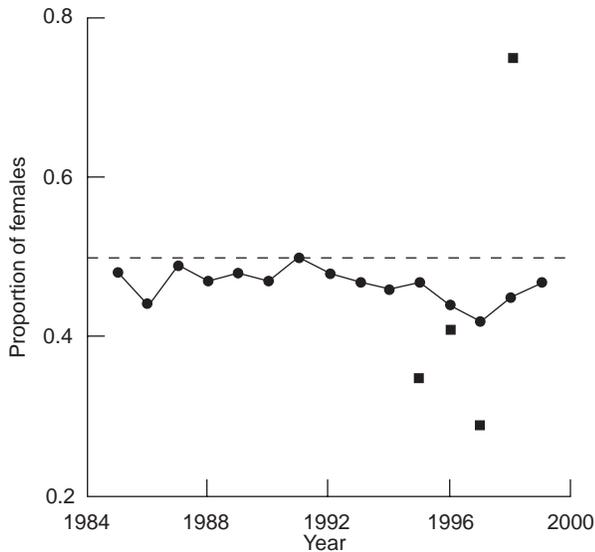


Fig. 5. Sex ratio, by year, of juvenile and adult *Propithecus verreauxi verreauxi* in core groups (circles) and infant sex ratios in core groups (squares).

males into and out of the core population between 1995 and 1999 show that 12 unmarked males immigrated and nine marked males left and were observed in groups outside the reserve.

Impact of the 1992 drought

The age structure and sexual composition of marked animals in the core groups in 1994 and 1999 are shown in Fig. 6a, b. Yearlings and 2-year-olds were excluded from this figure because fewer were marked at these particular 'slices through time' compared to older animals, and so their cohort sizes were not comparable. The structure of the population exhibited broad similarities in the 2 years. First, younger animals outnumbered older animals in both years, but in neither did the age structure of the population have the pyramid-like shape characteristic of a stable age distribution. Second, although males outnumbered females overall, as they have done in almost every year of the study, the ratio changed with age: in younger age cohorts, males generally outnumbered females whereas most older age cohorts contained a higher proportion of females.

The population's ragged age structure indicates that it has experienced dynamic changes since the study began in 1984, making it inappropriate to use a life table to estimate the growth rate of the population. Comparison of total population size in 1994 and 1999 yielded an annual growth rate of 3.5% in recent years.

Large differences between age cohorts in their size and composition suggest that environmental events have an important impact on this population. All lemurs except aye-ayes exhibit highly seasonal reproduction in Madagascar, for reasons not yet fully explained (Martin, 1990). Some plants produce leaves, flowers and fruit intermittently during the long dry season in

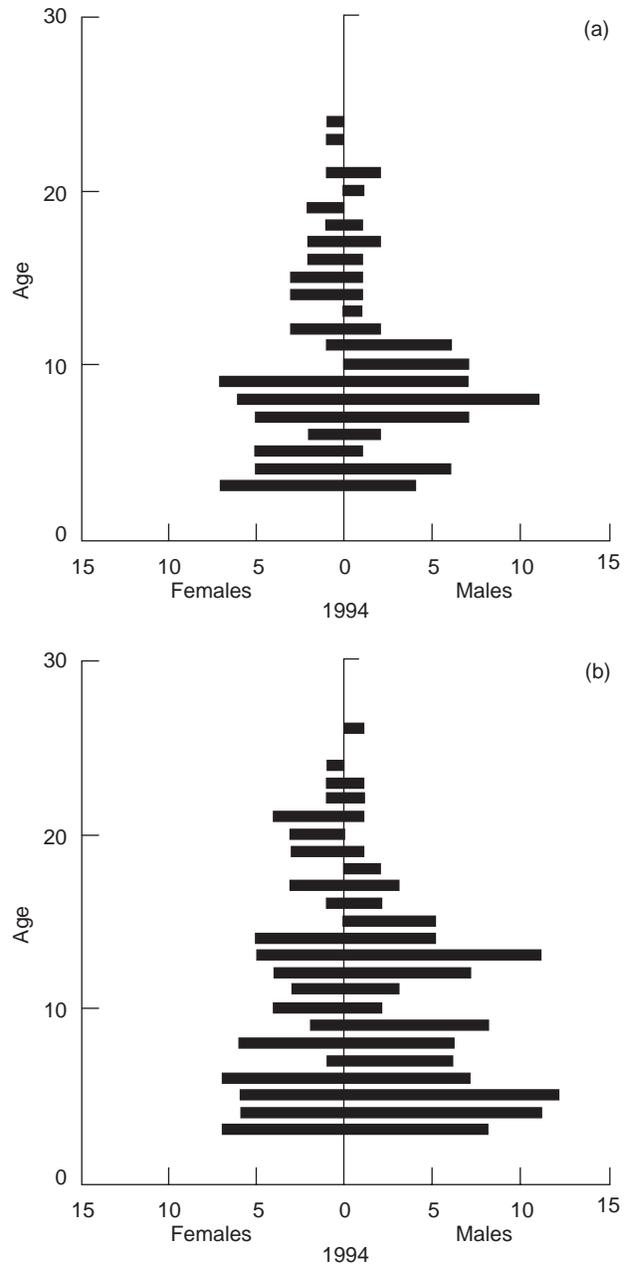


Fig. 6. Age structure and sexual composition of the marked population of *Propithecus verreauxi verreauxi* at Beza Mahafaly: (a) 1994; (b) 1999.

southern Madagascar, but in normal years the onset of the short wet season (November–February) triggers a burst of leaf and flower production (Richard, 1978; Sauter, 1998). Sifaka mated toward the end of the wet season, and females gave birth in the middle of the dry season and weaned their young during the next wet season.

Three successive years of diminishing rainfall culminated in a major drought in south-west Madagascar in 1991–92 (Fig. 7). This event was associated with the lowest fertility recorded in this 15-year-study. Only 27% of females aged 3 years and older gave birth compared to an overall average of 48% (Fig. 8). Only a third of the

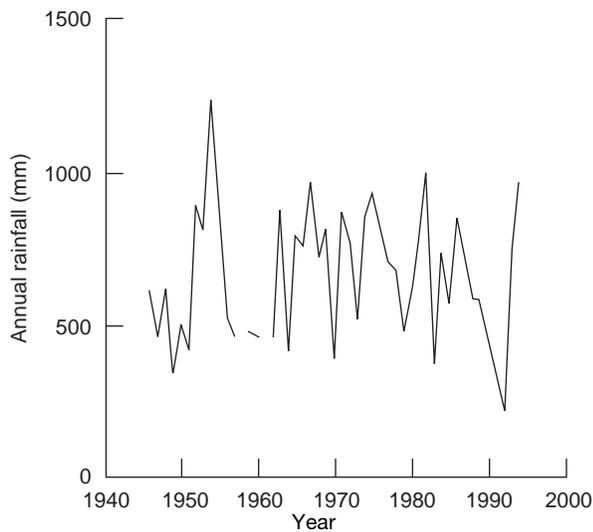


Fig. 7. Rainfall at Betioky, 1945–93. Rainfall year is July–June, and the labelled year is that of January–June. Data missing, 1958, 1961.

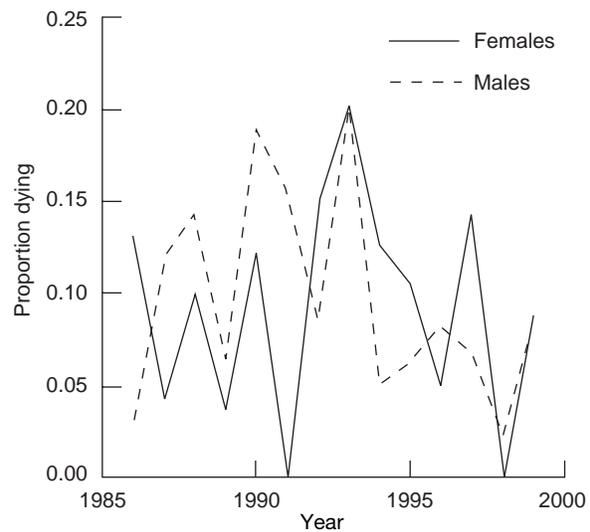


Fig. 9. Proportion of sifakas *Propithecus verreauxi verreauxi* aged 2 years or more dying in core groups, 1986–99.

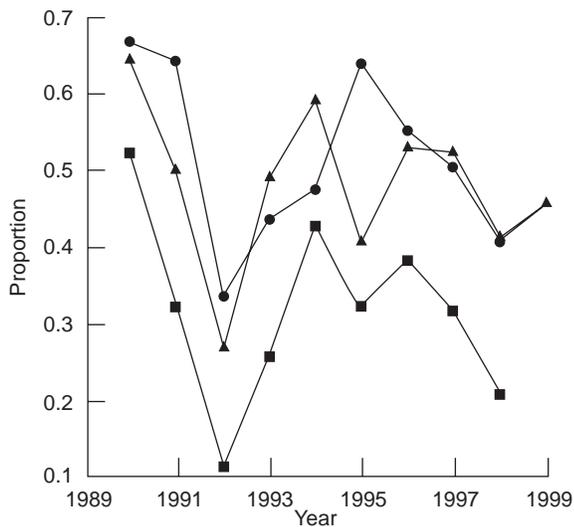


Fig. 8. Triangles, fertility by year for female *Propithecus verreauxi verreauxi* in core groups, 1990–99; circles, proportion of infants surviving in core groups, 1990–99; squares, proportion of females in core groups with a surviving infant, 1990–99.

few infants born survived, compared to an average of 52% (Fig. 8). The proportion of females 6 years old or older giving birth to a surviving infant that year fell to 11% (mean = 30%, range = 11–52%) (Fig. 8). In addition, mortality rates among males and females 2 years old and older peaked in 1992–93, with the death of about 20% of the marked population (Fig. 9). Almost all these deaths occurred in the late dry season of 1992, after the rains had failed earlier in the year, and were recorded in the July 1993 census. We note that survival among all age classes of *Lemur catta* was even more severely reduced during these drought years (Gould *et al.*, 1999).

Overall, year-to-year mortality in males and females was not strongly correlated (Pearson's $r = 0.242$, $n = 12$ years, $P > 0.40$) nor significantly correlated with rainfall history overall. This lack of correlation may reflect differences in the determinants of male and female mortality, or 'noise' in the data due to our inability to pinpoint the time of most male deaths. The impact of the drought was evidently sufficient to overwhelm either or both these effects. Echoes of the drought on fertility and survival may be evident in the 'ragged' age structure of the population in subsequent years; for example, the particularly small cohort of 7-year-olds in 1999 was born at the height of the drought in 1992.

Body mass, fertility and survival

Our data on fluctuations in body mass reflect the stresses that precipitated the plunging fertility and heightened mortality in 1992 (see also Richard, Dewar *et al.*, 2000). In normal years, sifaka body mass begins to increase shortly after the onset of the wet season. Adults achieve maximum body mass about 6 months later, in the early dry season (March–June), and then experience significant loss in the late dry season. The pattern of seasonal loss of mass was significantly stronger in adult females than in adult males, but did not differ by sex in animals < 5 years old. Compared to lighter females, females who were heavier at the time of mating were significantly more likely to give birth in the following birth season (Richard, Dewar *et al.*, 2000).

Like most lemurs, the reproductive schedule of *P. verreauxi* aligns the season of greatest resource availability with weaning, and not with the period of greatest maternal energy expenditure (Martin, 1972). Successful reproduction depends upon the storage of resources, and in this sense, this species is a 'capital breeder' rather than an 'income breeder' (Stearns, 1989; Jönsson, 1997).

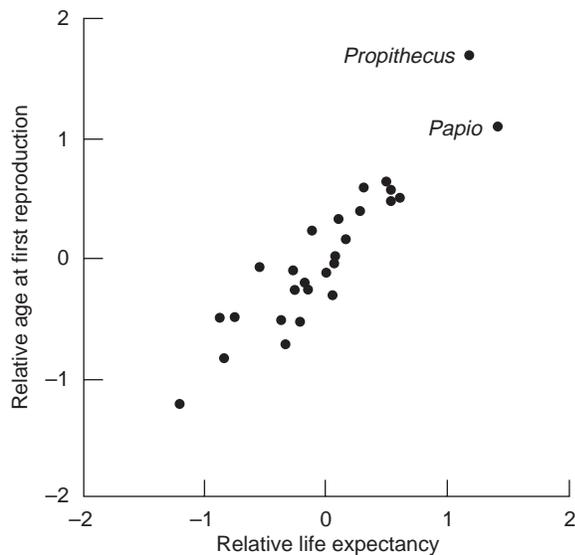


Fig. 10. Relative age at first reproduction and longevity, controlling for the effects of body mass with regressions of log-transformed values, in 27 species of mammals (after Zammuto & Harvey, 1985, with additional data from this paper; Altmann *et al.*, 1985; Alberts & Altmann, in press).

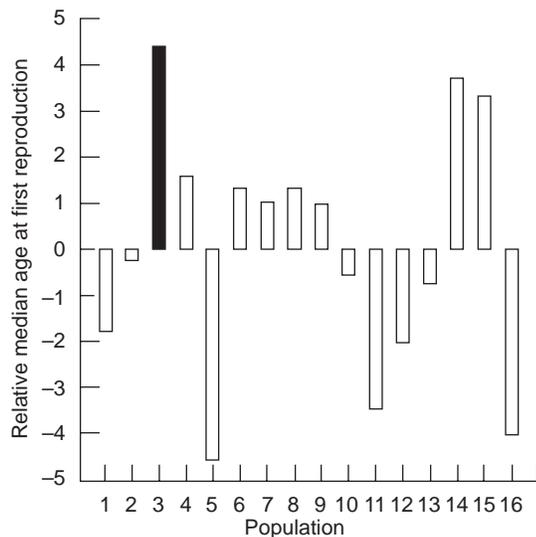


Fig. 11. Median age at first reproduction, controlling for body mass, in 16 wild, unprovisioned primate populations: 1, *Microcebus murinus*; 2, *Eulemur fulvus rufus*; 3, *P. verreauxi*; 4, *Cebus capuchinus*; 5, *Alouatta palliata*; 6, *Ateles geoffroyi*; 7, *Cercopithecus aethiops*; 8, *Macaca fascicularis*; 9, *M. fuscata fuscata*; 10, *M. f. yakui*; 11, *M. sylvanus*; 12, *Papio cynocephalus*; 13, *P. anubis*; 14, *Pan paniscus*; 15, *P. troglodytes*; 16, *Gorilla gorilla beringei*. Body mass data: Smith & Jungers (1997); reproductive data: 1, Martin (1972); 2, Overdorff *et al.* (1999); 3, this study; 4–6, Fedigan & Rose (1995); 7, Cheney *et al.* (1988); 8, van Noordwijk & van Schaik (1999); 9–10, Takahata *et al.* (1998); 11, Ménard & Vallet (1996); 12, Altmann, Hausfater & Altmann (1988); 13, Packer *et al.* (1995); 14, Kuroda (1989); 15, Nishida, Takasaki & Takahata (1990); Pusey (1990); 16, Watts (1991).

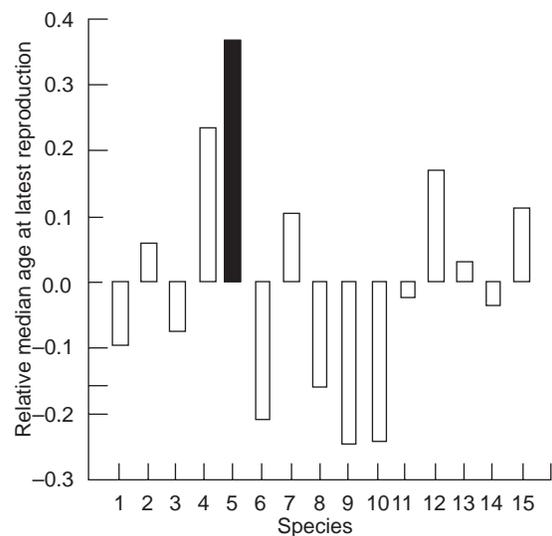


Fig. 12. Age at last reported reproduction, controlling for body mass, for 15 primate populations: 1, *Callithrix jacchus*; 2, *Saguinus fuscicollis*; 3, *Leontopithecus rosalia*; 4, *Saimiri sciureus*; 5, *Propithecus verreauxi verreauxi*; 6, *Cercopithecus aethiops*; 7, *Macaca fascicularis*; 8, *M. radiata*; 9, *M. mulatta*; 10, *M. nemestrina*; 11, *M. fuscata*; 12, *Presbytis entellus*; 13, *Pongo pygmaeus*; 14, *Pan troglodytes*; 15, *Homo sapiens*. Body mass data: Smith & Jungers (1997); reproductive data: 1–4, 6, 8–10, 13–15, Caro *et al.* (1995); 5, this study; 7, van Noordwijk & van Schaik (1999); 11, Koyama *et al.* (1992); 12, Borries, Sommer & Srivastava (1991).

Income breeders transform resource pulses into immediate reproductive efforts, while capital breeders store resources for later reproduction. If *P. verreauxi* females compete with one another for storable resources, then it is understandable that female–female feeding competition is most marked during the season of greatest resource availability (Richard, Dewar *et al.*, 2000).

Superimposed upon the annual cycle of body mass gain and loss, are the effects of changing climatic conditions between years. In 1992, the mean mass of adult females and males in the dry season was significantly lower than in other years, although males suffered less loss than females. Compared to average mass early in the dry season, females lost 21% of body mass, and males 12%. Animals <5 years old also weighed less, on average, during the drought years, with no evidence of a differential effect by sex.

Snails among tortoises?

Using data from 25 species of mammals, none of them primates, Harvey & Zammuto (1985) showed that mammals that start reproducing late, for their body mass, live longer than those that start reproducing earlier. Extending their analysis to include the two wild primate populations for which data are available confirms the widely held view that primates are particularly ‘slow’ compared to other mammals (Fig. 10).

In order to explore further the possibility that sifaka females have an unusually long and drawn out life-history pattern, even among primates, median age at first reproduction was compared in 16 wild and unprovisioned primate populations. The effect of female body mass was removed through a regression of log-transformed values (Fig. 11). Sifaka females from Beza Mahafaly stood out in this analysis not only because they took relatively longer than any other primate to begin reproducing, but also because they were the only primates with specializations for folivory in our sample to start reproducing later, not earlier, than average.

Data on the duration of reproduction in the wild are very rare and, as in this study, ages of the oldest females are uncertain. Comparing information from captive populations with the few estimates from the wild adds further uncertainty, but Fig. 12 none the less carries a striking suggestion. Estimates of age of latest recorded birth were compared, with the effect of female body mass removed with a regression of log-transformed values. Wild sifaka extended their reproductive lives to greater ages, for their mass, than any other primate in this sample.

DISCUSSION

Madagascar: an unpredictable environment

South-west Madagascar is one of a few regions in the tropics characterized by extremely high unpredictability of annual rainfall totals (Dewar & Wallis, 1999), and it is much more variable than other areas in which primates have been studied. This conclusion is based on an analysis of precipitation over a 40-year period at 1492 weather stations in the tropics. Compared to other regions with similar average annual rainfall, south-west Madagascar is more likely to experience a major drought in 1 or more years over the course of a given decade. Such droughts occur frequently, but unpredictably, and seem to be distantly linked to El Niño episodes in the Pacific (Ropelewski & Halpert, 1987).

In the eastern rain forests of the island, climatic unpredictability takes a different form. Although the total rainfall is quite stable from year to year, the months in which rain falls vary greatly from year to year (R. E. Dewar & A. F. Richard, pers. obs.). Ganzhorn (1995) has called attention to the high frequency of cyclones that strike Madagascar, arguing that they may have played a role in shaping the island's flora. Presumably, cyclones also have direct as well as indirect effects on the fauna of Madagascar.

A major role in shaping the phenology of tropical woody plants has been claimed for abiotic factors, particularly irradiance and water stress (van Schaik, Terborgh & Wright, 1993). Based on the unusual prevalence of folivory among Malagasy primates, Terborgh & van Schaik (1987) speculated that phenological cycles might be distinctively different in Madagascar. Efforts to explore this possibility and,

more broadly, the impact of climatic unpredictability on fluctuations in resource availability are hampered by the absence of multi-year phenological records. A growing number of shorter studies covering 1–4 years, however, suggest that the unpredictability of precipitation is indeed reflected in cycles of leaf, flower and fruit production.

Living with uncertainty: the evolution of sifaka life-history strategies

The impact of habitat on life history has been discussed (e.g. Dobzhansky, 1950) for many years within the theoretical framework of *K* and *r* selection (e.g. Pianka, 1970). Recently, it has been argued that a relationship ignored by that body of theory, namely that between habitat and age-specific fertility and mortality, is crucial to understanding broader patterns (Charnov & Berri-gan, 1990; Promislow & Harvey, 1990; Stearns, 1992).

Stearns (1976) identified a cluster of life-history traits which he called 'bet-hedging', and linked them to regimes of fertility and mortality in fluctuating environments. 'If there is variation among reproductive events in the probability that offspring will survive to breed, and if reproductive effort and adult survival trade-off, then it pays to reduce reproductive effort in order to live longer and reproduce more times, sampling a larger number of reproductive conditions and increasing the number of offspring born into good conditions' (Stearns, 1992: 168).

We contend that sifaka females are bet-hedgers *par excellence*, and that the life histories of male sifaka are best interpreted in the context of this distinctive female attribute. Sifaka females give birth for the first time later and live longer, for their size, than mammals in other orders; they also give birth later and continue reproducing longer, for their size, than other primates for which there are data. The late onset of reproduction cannot be attributed to the failure of young females to raise infants successfully. Although infant survival was low for the youngest mothers (3- to 5-year-olds), there was no subsequent age-related effect until the very oldest age cohorts (24–28 years old) (Fig. 2).

If bet-hedging is a central element of sifaka female life history strategy as the above features suggest, Stearns' model predicts that females should also display other life-history traits, namely high variation in infant survival and a trade-off between reproductive effort and adult survival. Birth rate and infant survival varied widely between years in the Beza Mahafaly sifaka, conforming to predictions of the bet-hedging model. Conversely, reproductive effort was positively correlated with survival among adult females, in conflict with the model. This may be because females in poor condition are simply less likely to survive, let alone give birth. Certainly, females with low body mass at the onset of the mating season were less likely than heavier females to give birth in the following birth season. Unfortunately, we do not have sufficiently finely calibrated data

to explore the relationship between body mass fluctuations and mortality.

Born in much larger numbers than females, males are far from being the 'fragile sex' (van Schaik & Devisser, 1990). They survived their juvenile years at the same rate as females and fared much better than females as young adults, even though during these years males left their natal groups. Males' testes were fully descended by the age of 18 months, and males were sexually active from at least the age of 4 years although their reproductive success has yet to be ascertained. From about the age of 12 years, the fortunes of males take a turn for the worse and far fewer males than females lived long lives. In short, relative to females, male sifaka were 'early bloomers'.

In most mammalian species, males and females mature at different ages and experience different age-specific mortality (e.g. Dunbar, 1987). It is not surprising, therefore, to find differences between male and female sifaka. Typically, however, male mammals take longer to mature than females, a difference attributed to breeding structure and other factors such as the growth trajectories associated with differing adult size (Clutton-Brock, Guinness & Albon, 1983; Stearns, 1992: 129). We postulate that the inversion of time to maturation seen in sifaka occurs because sifaka female life histories are 'slowed down', not because male life histories are 'speeded up'. If the breeding structure is one in which younger (smaller) males mate with older (larger) females, this may help explain the importance of female mate choice in this species (Brockman & Whitten, 1999).

Two other features of sifaka biology and behaviour warrant discussion here, namely intense local competition between females and the strongly male-biased sex ratio at birth present in most years. We infer that these features are linked to each other and, like sifaka life histories, are an evolutionary response to climatic unpredictability.

Female sifaka at Beza Mahafaly competed intensely, if discreetly, in several contexts. Feeding efficiency was lower in large groups than in small ones, and females in large groups had lower overall fertility with younger, lower ranking, females giving birth to fewer infants than older, higher ranking females (Kubzdela, 1997). Nulliparous young adult females in large groups dispersed from their natal group, but those living in small groups did not. Dispersing females typically tried to establish new groups in the interstices between home ranges of existing groups, but they were often unsuccessful (Richard, Rakotomanga & Sussman, 1993; Kubzdela, 1997). Competition between females was also evident during the mating season. Females exhibited age- and rank-related asynchronous receptivity, with heightened aggression and harassment of copulation by females when synchronous receptivity occurs (Brockman & Whitten, 1999).

Females exhibit social dominance over males in many gregarious lemur species, including sifaka. This is

generally presumed to be a female strategy for energy conservation, but energy conservation by males too is evident in species-wide traits of many Malagasy primates. These traits include hypometabolism, seasonal torpor, sun bathing and group huddling. Their presence has led several authors to argue that lemurs must have special needs with respect to the acquisition or conservation of energy (Jolly, 1984; Morland, 1993; Tilden & Oftedahl, 1995; Pereira & McGlynn, 1998; Overdorff *et al.*, 1999; Wright, 1999). Especially in drought years, these needs are probably most acute for reproductive females, whose success as capital breeders depends upon their capacity to accumulate reserves in advance of gestation and lactation. This, in turn, may limit the number of 'breeding slots' available for females.

In most years, sifaka males were born in far larger numbers than females. Deviations from an equal sex ratio at birth are quite common in mammal populations, although their direction is highly variable. Explanatory models produce conflicting predictions, all of which can be supported by the wide range of data available (Clutton-Brock & Iason, 1986). Seeking to resolve these conflicts, Kruuk *et al.* (1999) point out that several mechanisms are likely to determine the sex ratio at birth, and that their action depends on environmental conditions. We concur with the view that complex interacting effects are involved in the determination of natal sex ratios, but discussion of this issue is beyond the scope of our paper. We note, however, that our results are broadly congruent with Clark's (1978) proposition that females will give birth to more sons than daughters, if competition between females for limited resources is intense. One mechanism whereby females may influence the sex of their offspring is suggested by Perret's (1996) report of facultative changes in the sex ratio at birth of captive mouse lemurs, induced by manipulating the intensity of interaction experienced by reproductive females. At Beza Mahafaly, the shift toward a female-biased sex ratio at birth in 1998 came 1 year after the proportion of females in the population as a whole fell to its lowest recorded level (Fig. 5). It is tempting to infer a feedback mechanism between the abundance of females in the population and the sex of offspring, but a longer time series will be required to document this.

CONCLUSION

The case for bet-hedging among sifaka females is good, and environmental conditions that favour the evolution of this suite of life-history traits have been demonstrated for south-west Madagascar. The case will be strengthened by a better understanding of the nature of the trade-off between reproduction and survival. The idea of comparatively 'early blooming' males requires confirming evidence from paternity analyses of reproductive activity by young males.

If selection for bet-hedging traits has been stronger

for females than for males, with a concomitant slowing-down of female lives compared to males, and if the intensity of competition between females is particularly acute, then other anomalous features of sifaka biology and behaviour become more comprehensible. These include, in particular, the salience of female mate choice, female social dominance, and the heavily male-skewed sex ratio at birth reported not only for sifaka but for several other species of Malagasy primates (Petter, 1962; Jolly, 1984, 1998; Kappeler, 1997).

Climatic unpredictability and its diverse ecological manifestations are key to understanding the evolution of Madagascar's flora and fauna, we conclude, and other species native to the island should also display distinguishing features when compared to related species in other parts of the world. Bet-hedging is not the only possible evolutionary response to unpredictability (Stearns, 1976; and see Gould *et al.*, 1999 for an empirical illustration from Beza Mahafaly). The important point is that there should *be* a response.

Some of the anomalies long known to characterize Madagascar's unique flora and fauna undoubtedly derive from the island's ancient isolation. We predict, however, that others will be more powerfully interpreted as distinctive evolutionary responses to a world in which it is particularly difficult to know what next month, or next year, will bring. The results of this study provide a point of departure for further exploration of this prediction.

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