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Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*

Accurate estimates of mass and size are important in a wide range of research questions in population and evolutionary biology, and yet such data are still rare for wild primates. This study presents detailed longitudinal data from a large population of wild indriids, and demonstrates links between fluctuations in body mass, environmental cycles, and reproduction. Understanding these links is a necessary step toward explaining the function and evolution of distinctive features of lemur biology and behavior.

During the first 12 years of an ongoing study of the sifaka, *Propithecus verreauxi verreauxi*, at Beza Mahafaly in southwest Madagascar, 320 animals were captured and weighed throughout the year. Adult males and females exhibit seasonal cycles of mass loss, with females losing significantly more mass than males. In 2 drought years this pattern was especially pronounced. Compared to lighter females, females who were heavier at the time of the mating season were more likely to give birth in the following birth season. By showing (1) seasonally greater mass loss in reproductive females compared to males, particularly in drought years, (2) a close link between female mass and fertility, and (3) an uncoupling of the periods of highest body mass and of gestation and lactation, these results suggest that energy acquisition and storage are critically important in the life history strategies of female sifaka, and that "capital breeding" may be a feature of sifaka reproductive strategies.

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Introduction

Issues of size and mass arise in most discussions of population and evolutionary biology. Body mass has long been recognized as an important determinant of the life history patterns, ecology, and social organization of mammals, including primates (e.g., Jarman, 1974; Clutton-Brock & Harvey, 1977; Gaulin, 1979; Western, 1979), and size and mass remain critical

elements in comparative studies today (e.g., Martin, 1990; Stearns, 1992; Garber & Leigh, 1997; Leigh, 1992). Fluctuations in body mass have also been used as indicators of change in the nutritional or socio-sexual status of individual animals (e.g., Martin, 1972; Altmann *et al.*, 1993; Fietz, 1998; Schmid & Kappeler, 1998).

The pressing need for accurate estimates of body mass led Smith & Jungers (1997) to examine the quality of existing estimates for

primate species, and to compile the “best available” primate body mass data. Common “operational” difficulties evident in the data include distinguishing between adult and nonadult body mass, between reproductive and nonreproductive females, and between estimates of body mass obtained in different seasons or different habitats.

Lemurs are not well represented in the data base assembled by [Smith & Jungers \(1997\)](#), and most of the sample sizes are small and derived from animals living in captivity. The results reported in this paper add significantly to the body mass records available for wild indriids, and also establish links between fluctuations in body mass, environmental cycles, and reproduction in the sifaka, *Propithecus verreauxi verreauxi*. Characterizing these links contributes to efforts to understand the evolution, distinctiveness and diversity of lemur biology and behavior.

All lemurs are sexually monomorphic with respect to body mass ([Kappeler, 1990](#)), many exhibit female social dominance ([Jolly, 1984](#)), and none exhibit systematic paternal care of young. Lemur species exhibit a wide range of mating patterns, including monogamy, polygyny, and polyandry, with all three reported at different times or in different social settings even within single populations of certain species ([Jolly, 1998](#); [Brockman, 1999](#)). The evolution and distribution of these variably clustered morphological and behavioral traits among lemurs is the subject of much debate and remains only partly understood ([Peirera et al., 1990](#); [Wright, 1990, 1993, 1999](#); [Kappeler, 1993, 1997a](#); [Pereira & McGlynn, 1997](#)).

Most attempts at explanation assume that the “lemur syndrome” represents an adaptive suite of traits, even though Madagascar’s ecosystems have been profoundly changed by the recent arrival of people, and some patterns of behavior may not be evolutionarily adapted to the environ-

ment today ([Richard & Dewar, 1991](#); [van Schaik & Kappeler, 1996](#)). Initially centered on the proposition that lemur physiology somehow burdens females with unusually high reproductive costs ([Jolly, 1984](#); [Richards & Nicoll, 1987](#); [Young et al., 1990](#); [Pereira, 1993](#)), debates about these costs and their source have shifted lately from endogenous to exogenous factors. In particular, a number of authors have argued that Madagascar’s markedly seasonal environments have favored the evolution of diverse strategies for acquiring or conserving energy in an unusually stressful environment ([Sauther, 1993](#); [Tilden & Oftedahl, 1995](#); [Pereira & McGlynn, 1997](#); [Overdorff et al., 1999](#); [Wright, 1999](#)). There are insufficient data on wild lemurs, however, to permit these arguments to be explored or tested.

P. v. verreauxi is among the longest and most intensively studied of wild lemurs, and the population of *P. v. verreauxi* at Beza Mahafaly in southwest Madagascar is the subject of this paper. Using data on seasonal and annual body mass changes, we will show that (1) females of reproductive age lose more mass than males during the annual dry season, when food availability is lowest ([Sauther, 1993](#)), and that this effect is particularly pronounced in drought years; (2) a female’s body mass at the outset of the mating season strongly influences the probability that she will give birth in the following birth season; (3) there is a body mass threshold below which females do not give birth, and (4) the period of maximum female body mass each year is temporally uncoupled from gestation and lactation, the time of greatest reproductive investment. These findings lead us to infer that in some years reproduction is particularly difficult for female sifaka in this population, and that strategies for energy acquisition, storage, and/or the minimization of energy expenditure play a crucial role in determining their long-term reproductive success.

Adult males and females in the Beza Mahafaly population are similar in average body mass. Studies of skeletal dimorphism in the sub-species as a whole have failed to reveal significant differences between males and females (Ravosa *et al.*, 1993), although females have slightly longer femora than males in the Beza Mahafaly population (see below). At all sites where they have been studied, adult females have priority over males in and outside the context of feeding (Jolly, 1966; Richard, 1978; Kubzdela, 1997). At Beza Mahafaly, monogamous, polygynous and polyandrous matings have been observed (Richard, 1974, 1992; Kubzdela, 1997; Brockman, 1999). Males sometimes mate in groups other than their own, and may transfer between groups several times during their lives. Males almost never contribute directly to the rearing of young.

Methods

We have been studying *P. v. verreauxi* at Beza Mahafaly Special Reserve in southwest Madagascar since 1984 (Figure 1). Mean annual rainfall in this driest region of Madagascar is about 600 mm, and is unequally distributed during the year (Figure 2). In this paper we divide the year into three periods: the wet season (November–February), the early dry season of declining rains (March–June), and the later dry season (July–October) when rainfall is rare or nonexistent. Within this general pattern, there is considerable inter-annual variation in the timing and amount of precipitation (Richard & Dewar, 1991). Droughts occur from time to time, evidenced by rainfall data and reports of severe nutritional stress and heightened mortality in the human population—1991 and 1992 were two such years (Figure 3).

The pattern of sifaka reproduction is highly seasonal. Most births occur between mid-June and mid-August, with minor vari-

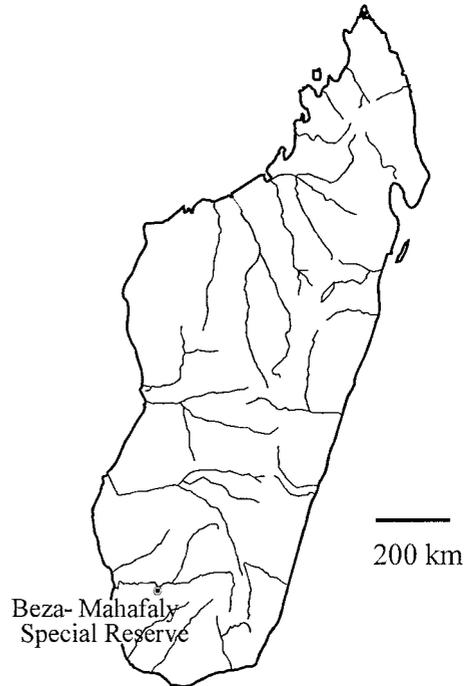


Figure 1. The location of Beza Mahafaly in Madagascar.

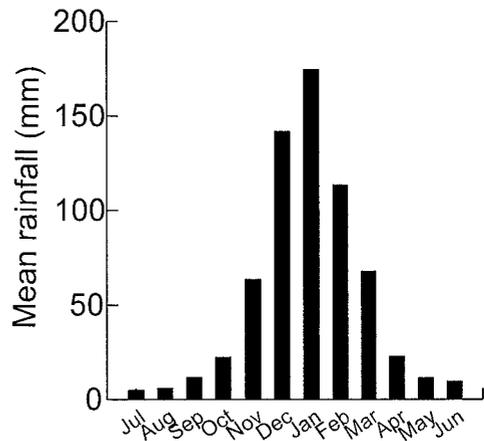


Figure 2. Mean monthly rainfall at Betsioky, southwest Madagascar, from 1945 until collection of rainfall data ceased in 1994 (source: Service Météorologique de Madagascar).

ations in timing from year to year. Infants are weaned during the following wet season, between January and March, although some

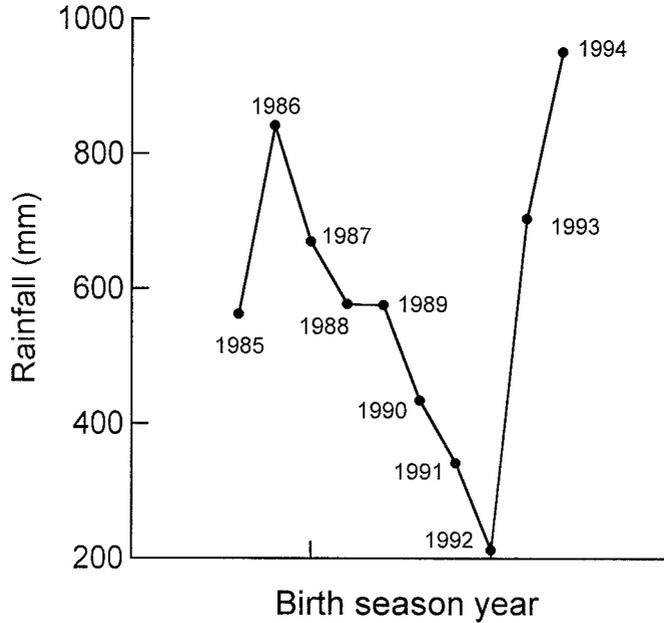


Figure 3. Annual rainfall at Betioky, July 1984 to June 1994. The totals presented are of July through June preceding the birth season (source: Service Météorologique de Madagascar).

offspring make unsuccessful attempts to nurse for several months thereafter.

Between 1984 and 1995, 320 animals were captured, marked and released; 38 of these individuals have been captured a second time, and nine others captured three times. Captures and recaptures have been spread over 10 months distributed throughout the year; only for March and October are there no records. Marked animals form part of a larger population living in or adjacent to the reserve (Richard *et al.*, 1993).

Animals were held in captivity for 4–8 h, and the mass of each animal was recorded, using a 5 kg pesola spring balance, as one of a series of procedures (Richard *et al.*, 1991). In order to avoid conflating the effects of growth and development with those of seasonal cycles, the analysis presented here distinguishes between animals known or estimated by dental wear to be 5 years and older, and younger animals. Morphometric data indicate that long-bone growth is com-

pleted by age 5 in both males and females. Figure 4 plots femur length against estimated age, with each animal arbitrarily assigned a birth date of 1 July. Separate LOWESS smoothes were applied for males and females. [We note in passing that most other measures show smaller differences by sex; the presence of slightly longer femora among females conforms to the pattern established by Ravosa *et al.* (1993) for the genus *Propithecus*.] Age estimates are accurate to within a few weeks, given the highly seasonal pattern of reproduction. Two females have been observed to give birth at the age of 3, but first reproduction for over half the females in the Beza Mahafaly population occurs at 6 years of age or more (Richard *et al.*, n.d.).

Like most other lemurs (Kappeler, 1990; Terranova & Coffman, 1997; but see Kappeler, 1997b; Fietz, 1998), *P. verreauxi* has been reported in a broad sense as sexually monomorphic. At Beza Mahafaly, averaging across our uncommonly large

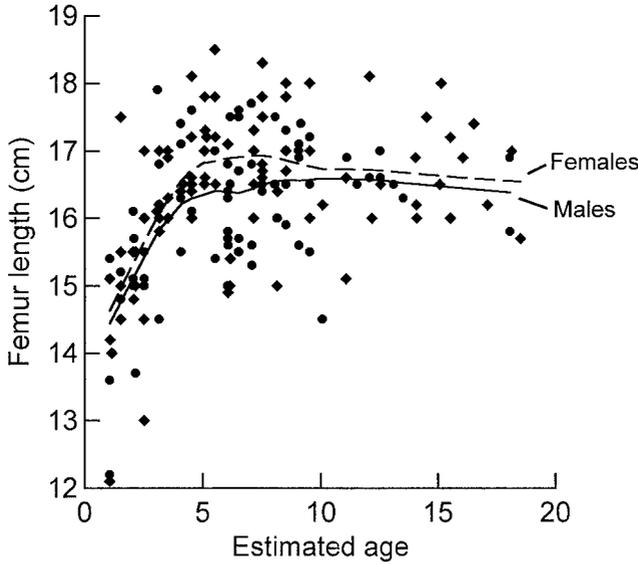


Figure 4. Changes in femur length plotted against estimated age, with separate LOWESS smoothes for females (diamonds) and males (circles).

dataset, male and female sifaka are not significantly different in body mass; adult females weigh 2.76 ± 0.36 kg ($n=105$) and males 2.84 ± 0.34 kg ($n=119$) ($t=1.76$, $df=222$, $P>0.05$). The comparison, thus, of absolute changes in body mass provides a good indicator of differential effects in adult males and females. Some females included in this sample were gestating at the time of capture, as ascertained by palpation and/or subsequent births, but no females with dependent young were captured.

Results

Pooled data on adults from 1984–1996 show that both males and females experience similar patterns of seasonal mass change, being heaviest in the early dry season, and lightest during the second half of the long dry season, but that mass loss is greater in females (Figure 5). *T*-tests reveal that males and females are monomorphic, except during the late dry season (July–September) when males are significantly heavier (Table 1). Analysis of variance of

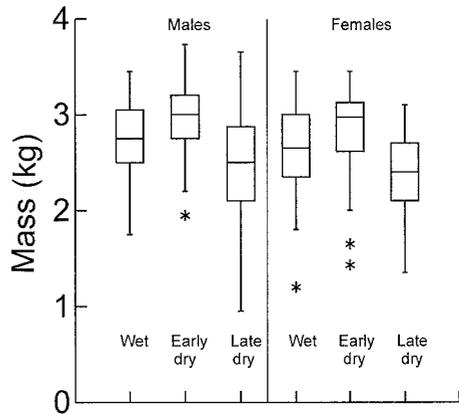


Figure 5. Box plots of body mass. The central box indicates the upper and lower quartiles, as well as the median. The lines indicate range of data points within 1.5 times the interquartile spread of the quartiles; asterisks mark individual outside values.

sifaka body masses by season and by sex reveal a significant effect for season ($F=29.5$, $P<0.0005$), no significant effect for sex ($F=0.469$, $P=0.494$), but a marginally significant interaction between sex and season ($F=3.086$, $P=0.048$): in short, both males and females have similar patterns of

Table 1 Male and female masses in this broadly monomorphic species vary seasonally

	Males	Females	<i>P</i>
Wet season (November–February)	2.92 ± 0.32 (<i>n</i> =40)	2.91 ± 0.29 (<i>n</i> =35)	n.s.
Early dry season (April–June)	2.99 ± 0.38 (<i>n</i> =23)	3.07 ± 0.25 (<i>n</i> =17)	n.s.
Late dry season (July–October)	2.73 ± 0.30 (<i>n</i> =43)	2.54 ± 0.30 (<i>n</i> =40)	<0.01

T-tests reveal that male and female masses are significantly different only in the late dry season.

Table 2 Mass changes between subsequent captures of the same sifaka adults

	First capture late dry next capture wet/early dry	First capture wet/early dry next capture late dry
Number of animals showing no change or mass gain	7	6
Number of animals showing mass loss	0	12

seasonal mass change, but the pattern is stronger for females.

This pattern of mass gain and loss among adults is confirmed in the patterns of mass changes of recaptured animals, which provide longitudinal evidence concordant with the seasonal trend exhibited by the pooled sample. Animals often showed significant changes in body mass when captured in different years and seasons, and usually late dry season masses are smaller than masses recorded for the same animal captured in the wet or early dry season. Table 2 presents these data for all pairs of recaptures that occurred in contrasting seasons. We contrast animals maintaining or increasing mass with those losing mass, and it is clear that late dry season mass loss, and mass rebound in the wet season is a common pattern and statistically significant (two-tailed Fisher's

exact test, $P=0.005$). The patterns are similar for males and females, although sample size limits the utility of statistical tests (Table 3). It is interesting to note that both males and females captured in similar seasons in different years were equally as likely to lose as to gain mass.

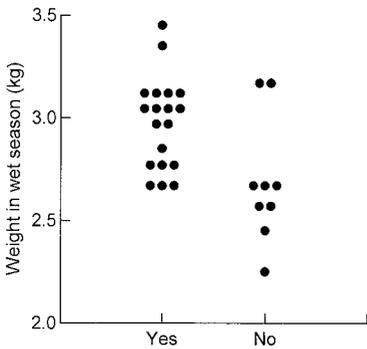
During the drought years of 1991 and 1992, the mean mass of adult females and males in the dry season were significantly lower than in other years. Females in the drought years' late dry seasons had an average mass of 2.43 ± 0.34 kg, compared to 2.66 ± 0.23 in other years ($t=2.98$, $df=51$, $P<0.01$). Males were also significantly lighter in the drought years' late dry seasons [2.64 ± 0.29 kg *vs.* 2.80 ± 0.29 [$t=2.05$, $df=55$, $P<0.05$]], although they suffered less loss than did females. Compared to average early dry season mass, females lost 21% of body mass whereas males lost only 12%. Animals less than 5 years old weighed less, on average, during the drought years, but there was no evidence of a differential effect by sex.

There are great differences in individual fertility rates among *P. verreauxi* females, and our data indicate that this variation is strongly related to differences in mass. Among females observed for ten or more birth seasons, the proportion of years in which a given female was observed to have an infant ranged from 23% to 77% ($n=14$, $mean=51\%$). Twenty-eight females were captured between November and February, before or during the mating season, and were then observed at the end of the subsequent birth season. The 19 who were observed with an infant had weighed 2.99 ± 0.23 kg in the previous season; the nine without infants had weighed 2.69 ± 0.31 kg (Figure 6); this difference in mean body mass is significant ($U=134.5$, $P<0.02$). The average age of the two classes of females did not differ significantly, and none were gestating or lactating at the time of capture.

Table 3 Changes in body mass between subsequent captures by sex and season

	First capture Jul.–Sept., then captured Nov.–Jun.	First capture Nov.–Jun., then captured Jul.–Sept.	Both captures in similar season
Males			
Gained mass	1	0	3
No change	1	3	0
Lost mass	0	5	3
Females			
Gained mass	3	1	2
No change	2	1	1
Lost mass	0	7	2

In all cases animals were known or estimated to be at least 5 years of age at the time of the first capture.



Was the female observed with an infant in the next dry season?

Figure 6. Symmetrical dot plot of the wet season weight of females observed with and without infants in the following late dry season.

One further, puzzling result warrants mention. [Smith & Jungers \(1997\)](#) examined the variability of body mass in primates, and offered a least squares equation to predict coefficient of variation from mean body mass. The coefficients of variation for Beza Mahafaly sifaka are close to their predicted values: the CV of male mass is 11.97, while the predicted CV is 12.51 and the CV of female mass is 13.04 while the predicted CV is 12.48. Although the male CV is less than predicted and the female CV greater, neither is significantly so. The CV for sifakas at Beza Mahafaly is the sum of variation due to (1) seasonal effects, (2) effects of drought, and (3) unknown effects and random variation, the first two of which we have demonstrated.

The conformity of our results to the average for other primates is not easily explained, given the extreme environmental fluctuations experienced by the Beza Mahafaly population. It may simply be an artefact of different sampling regimes between our study and those compiled by [Smith & Jungers \(1997\)](#). We note the alternative possibility that strong stabilizing selection may dampen genetically-based mass variation in lemurs.

Discussion

Mass data yield a kind of “running commentary” on the lives of wild primates, providing evidence about individuals’ health status, and the nature and timing of events that shape their behavior. Mass data also offer broad insight into the evolution of species-wide reproductive strategies. We discuss our results in the context of both these temporal scales.

Several proximate causes of body mass change have been reported or proposed in lemurs. They include (1) environmental cycles in resource availability (e.g., [Overdorff et al., 1999](#)) or photoperiod (e.g., [Pereira, 1993](#)); (2) shifting social and socio-sexual contexts at the level of the population or social group (e.g., [Martin, 1972](#); [Kappeler, 1997b](#); [Feitz, 1998](#); [Schmid & Kappeler, 1998](#)); and (3) physiological

changes originating in the individual, particularly gestation and lactation. It is often difficult to separate these effects in the field, and we are sensitive to this challenge with our own results.

It is not surprising that lemurs living in seasonal environments exhibit fluctuations in body mass in response to variations in resource availability, for this has been generally reported in several primate species. However, the extent and patterning of these fluctuations are still poorly documented or understood. Goldizen *et al.* (1988) have shown dry season mass losses averaging 5.8% in three adult males and five juvenile and subadult *Saguinus fuscicollis* in the Manu National Park. At Ranomafana National Park in Madagascar, Glander *et al.* (1992) report female mass losses at 12% over the course of a year for the folivorous *P. diademata*, and of 9% and 5%, respectively, for the more frugivorous *Eulemur fulvus rufus* and *E. rubriventer* within a three month period. Variations in resource availability are not clearly marked or easily determined at this rain forest study site, but the authors comment that mass changes of this magnitude suggest that both fruit and leaf eaters are under similar ecological stresses.

The study reported here, the first systematic comparison of both seasonal and year-to-year mass changes in a large sample of male and female primates, demonstrates a strong link between body mass and environmental changes, as indicated by rainfall fluctuations. Of particular significance, the impact on body mass of dry seasons and drought years documented for the population as a whole is strongest among females of reproductive age. Immature animals were also affected by the drought years, but there is no evidence of differences between young males and females. The data also show that variation in mass is important for reproduction: heavier females are more likely to give birth than lighter ones.

What are the evolutionary implications of this pattern? A positive correlation between body mass and reproductive activity is common but not universal within mammalian species. It is helpful to recognize a conceptual distinction between species in this regard, even though in practice there is more likely to be a continuum of variation among species than categorical differences between them. Species that store resources needed for reproduction have been called "capital breeders" (Stearns, 1989, 1992; Jonsson, 1997). Such species contrast with "income breeders", which have a very short-term "physiological memory" (Stearns, 1989:263) and increase their food intake concurrently with gestation and lactation. Income breeders do not depend heavily on energy reserves and cannot decouple feeding and reproduction spatially or temporally as capital breeders may do.

An implied feature of these contrasting reproductive strategies is that there should be difference in the scheduling of resource conflicts in capital and income breeders. Income breeders compete to turn current resources into reproductive investments, and may be expected to compete most fiercely during gestation and lactation, and to align these reproductive states with periods of greatest resource availability. Capital breeders, in contrast, may compete at any time, whether for storage or immediate use.

We suggest that *P. v. verreauxi* is a capital breeder, albeit not in the pronounced form seen in certain other animals, notably the emperor penguin and some pinnipeds (Jonsson, 1997). Capital breeding may indeed be widespread among lemurs, for the reproductive schedules of all lemurs, except the aye-aye, seem to align the period of greatest resource availability with weaning, and not with the period of highest maternal energetic effort (Martin, 1972; Wright, 1999). Capital breeding may also occur in some of the seasonally breeding haplorhine

primates. At least one population of langurs (*Presbytis entellus*), for example, seems to exhibit features characteristic of capital breeding (Koenig *et al.*, 1997).

If *P. v. verreauxi*, and perhaps other lemurs, are capital breeders, interfemale feeding competition may be expected to be most intense when the returns are highest. This is concordant with reports of increased levels of resource-related aggression in *P. v. verreauxi* during the wet season (Richard, 1978), when females are neither lactating nor gestating. The level of aggression and, indeed, of all activity is lower in the dry season, when females give birth and nurse their young. Capital breeding may help explain Hemingway's (1999) failure to find behavioral compensation for increased costs during the reproductive season in *P. diademata edwardsii*. More generally, it may be a contributing element in the "puzzle" of year-round social dominance by females over males in many lemur species.

The proposition that *P. v. verreauxi* is a capital breeder carries with it the implication that particular caution should be exercised before inferring that mass loss is necessarily evidence of energetic stress. "[I]n a capital breeder mass loss during breeding is part of an employed breeding tactic" (Jonsson, 1997:59). We have shown that females with low body mass are less likely to reproduce, and we assume that males as well as females that lose significant body mass are at higher risk of mortality. Our point here, simply, is that body mass cycles cannot be easily interpreted as indicators of cycles of physiological stress.

Past claims about the distinctiveness or uniqueness of "all lemurs", and by implication the island of Madagascar, have tended to underestimate the variability as well as the complexity of lemur biology and behavior (Pereira *et al.*, 1990). Today, one might even ask whether there are any distinctive features requiring special explanation. Like van Schaik & Kappeler (1996),

we continue to answer this question with a strong affirmative. Like Tilden & Oftedal (1995), we believe that unusual fluctuations in resource availability may be crucially important in explaining the evolution and adaptive significance of the "lemur syndrome". Wright (1999) has recently expanded this idea into an "energy frugality hypothesis". She suggests that the harsh, unpredictable island environment of Madagascar has favored the evolution of traits in lemurs that are either adaptations to conserve energy or to maximize the use of scarce resources.

Our results are certainly consonant with Wright's hypothesis. By demonstrating the significance and sex-specific impact of fluctuations in rainfall and resource availability on mass and fertility in *P. v. verreauxi*, we provide direct evidence for the first time of biologically important links between environmental events and a crucial feature of lemur life history. By showing that the time of highest body mass and of greatest maternal investment are temporally uncoupled, our data suggest that storing energy harvested in "good times" may be an important feature of female reproductive strategies and, perhaps, a key to other features of sifaka behavior.

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References

- Altmann, J., Schoeller, D., Altmann, S. A., Muruthi, P. & Sapolsky, R. M. (1993). Body size and fatness of free-living baboons reflect food availability and activity levels. *Am. J. Primatol.* **30**, 149–161.
- Brockman, D. K. (1999). Reproductive behavior of female *Propithecus verreauxi* at Beza Mahafaly, Madagascar. *Int. J. Primatol.* **20**, 375–398.
- Clutton-Brock, T. H. & Harvey, P. H. (1977). Primate ecology and social organization. *J. Zool. Lond.* **183**, 1–39.
- Fietz, J. (1998). Body mass in wild *Microcebus murinus* over the dry season. *Folia primatol.* **69** (Suppl. I), 183–190.
- Garber, P. A. & Leigh, S. R. (1997). Ontogenetic variation in small-bodied New World primates: implications for patterns of reproduction and infant care. *Folia primatol.* **68**, 1–22.
- Gaulin, S. J. C. (1979). A Jarman–Bell model of primate feeding niches. *Hum. Ecol.* **7**, 1–20.
- Glander, K. E., Wright, P. C., Daniels, P. S. & Merenlender, A. M. (1992). Morphometrics and testicle size of rain forest lemur species from southeastern Madagascar. *J. hum. Evol.* **22**, 1–17.
- Goldizen, A. W., Terborgh, J., Cornejo, F., Porras, D. T. & Evans, R. (1988). Seasonal food shortage, weight loss and the timing of births in saddle-back tamarins (*Saguinus fuscicollis*). *J. Anim. Ecol.* **57**, 893–901.
- Hemingway, C. A. (1999). Time budgets and foraging in a Malagasy primate: do sex differences reflect reproductive condition and female dominance? *Behav. Ecol. Sociobiol.* **45**, 311–322.
- Jarman, P. J. (1974). Social organization of antelope in relation to their ecology. *Behaviour* **48**, 215–267.
- Jolly, A. (1966). *Lemur Behavior*. Chicago: University of Chicago Press.
- Jolly, A. (1984). The puzzle of female feeding priority. In (M. F. Small, Ed.) *Female Primates: Studies by Female Primatologists*, pp. 197–215. New York: Alan R. Liss.
- Jolly, A. (1998). Pair-bonding, female aggression and the evolution of lemur societies. *Folia primatol.* **69** (Suppl. I), 1–13.
- Jonsson, K. I. (1997). Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* **78**, 57–66.
- Kappeler, P. M. (1990). The evolution of sexual size dimorphism in prosimian primates. *Am. J. Primatol.* **22**, 201–214.
- Kappeler, P. M. (1993). Female dominance in primates and other mammals. In (P. P. G. Bateson, P. H. Klopfer & N. S. Thompson, Eds) *Perspectives in Ethology*, Vol. 10, pp. 143–158. New York: Plenum.
- Kappeler, P. M. (1997a). Determinants of primate social organization: comparative evidence and new insights from Malagasy lemurs. *Biol. Rev. Camb. Phil. Soc.* **72**, 111–151.
- Kappeler, P. M. (1997b). Intrasexual selection in *Mirza coquereli*: evidence for scramble competition polygyny in a solitary primate. *Behav. Ecol. Sociobiol.* **45**, 115–127.
- Koenig, A., Borries, C., Chalise, M. K. & Winkler, P. (1997). Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). *J. Zool. Lond.* **243**, 215–235.
- Kubzda, K. S. (1997). Sociodemography in diurnal primates: The effects of group size and female dominance rank on intra-group spatial distribution, feeding competition, female reproductive success, and female dispersal patterns in white sifaka, *Propithecus verreauxi verreauxi*. Ph.D. Dissertation, University of Chicago.
- Leigh, S. R. (1992). Patterns of variation in the ontogeny of primate body size dimorphism. *J. hum. Evol.* **23**, 27–50.
- Martin, R. D. (1972). Review Lecture: Adaptive radiation and behaviour of the Malagasy lemurs. *Phil. Trans. Roy. Soc., Lond., B* **264**, 295–352.
- Martin, R. D. (1990). *Primate Origins and Evolution: A Phylogenetic Reconstruction*. Princeton: Princeton University Press.
- Overdorff, D. J., Merenlender, A. M., Talata, P., Telo, A. & Forward, Z. A. (1999). Life history of *Eulemur fulvus rufus* from 1988–1998 in southeastern Madagascar. *Am. J. phys. Anthrop.* **108**, 295–310.
- Pereira, M. E. (1993). Seasonal adjustment of growth rate and adult body weight in ringtailed lemurs. In (P. M. Kappeler & J. U. Ganzhorn, Eds) *Lemur Social Systems and their Ecological Basis*, pp. 205–222. New York: Plenum.
- Pereira, M. E. & McGloyn, C. A. (1997). Special relationships instead of female dominance for red-fronted lemurs, *Eulemur fulvus rufus*. *Am. J. Primatol.* **44**, 85–88.
- Pereira, M. E., Kaufman, R., Kappeler, P. M. & Overdorff, D. J. (1990). Female dominance does not characterize all of the Lemuridae. *Folia primatol.* **55**, 96–103.
- Ravosa, M. J., Meyers, D. M. & Glander, K. E. (1993). Relative growth of the limbs and trunk in Sifakas: Heterochronic, ecological and functional considerations. *Am. J. phys. Anthrop.* **92**, 499–520.
- Richard, A. F. (1974). Patterns of mating in *Propithecus verreauxi*. In (R. D. Martin, A. C. Walker & G.

- Doyle, Eds) *Prosimian Biology*, pp. 49–74. London: Duckworth.
- Richard, A. F. (1978). *Behavioral Variation: Case Study of a Malagasy Lemur*. Lewisburg: Bucknell University Press.
- Richard, A. F. (1992). Aggressive competition between males, female-controlled polygyny and sexual monomorphism in a Malagasy primate. *J. hum. Evol.* **22**, 395–406.
- Richard, A. F. & Dewar, R. E. (1991). Lemur ecology. *Ann. Rev. Syst. Ecol.* **22**, 145–175.
- Richard, A. F. & Nicoll, M. E. (1987). Female social dominance and basal metabolism in a Malagasy primate, *Propithecus verreauxi*. *Am. J. Primatol.* **12**, 309–314.
- Richard, A. F., Rakotomanga, P. & Schwartz, M. (1991). Demography of *Propithecus verreauxi* at Beza Mahafaly: sex ratio, survival and fertility, 1984–1988. *Am. J. phys. Anthropol.* **84**, 307–322.
- Richard, A. F., Rakotomanga, P. & Schwartz, M. (1993). Dispersal by *Propithecus verreauxi* at Beza Mahafaly, Madagascar: 1984–1991. *Am. J. Primatol.* **30**, 1–20.
- Richard, A. F., Dewar, R., Schwartz, M. & Ratsirarson, J. (n.d.). Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). (In preparation.)
- Sauther, M. L. (1993). Resource competition in wild populations of ringtailed lemurs (*Lemur catta*): implications for female dominance. In (P. M. Kappeler & J. U. Ganzhorn, Eds) *Lemur Social Systems and their Ecological Basis*, pp. 135–152. New York: Plenum Press.
- Schmid, J. & Kappeler, P. M. (1998). Fluctuating sexual dimorphism and differential hibernation by sex in a primate, the gray mouse lemur, *Microcebus murinus*. *Behav. Ecol. Sociobiol.* **43**, 125–132.
- Smith, R. J. & Jungers, W. L. (1997). Body mass in comparative primatology. *J. hum. Evol.* **32**, 523–559.
- Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecol.* **3**, 259–268.
- Stearns, S. C. (1992). *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Terranova, C. J. & Coffman, B. S. (1997). Body weights of wild and captive lemurs. *Zoo Biol.* **16**, 17–30.
- Tilden, C. C. & Oftedal, O. T. (1995). The bioenergetics of reproduction in prosimian primates: is it related to female dominance? In (L. Alterman, G. A. Doyle & M. K. Izard, Eds) *Creatures of the Dark: The Nocturnal Primates*, pp. 119–131. New York: Plenum.
- van Schaik, C. P. & Kappeler, P. M. (1996). The social systems of gregarious lemurs: lack of convergence with anthropoids due to evolutionary disequilibrium? *Ethology* **102**, 915–941.
- Western, D. (1979). Size, life-history and ecology in mammals. *Afr. J. Ecol.* **17**, 185–204.
- Wright, P. C. (1990). Patterns of paternal care in primates. *Int. J. Primatol.* **11**, 89–102.
- Wright, P. C. (1993). Variations in male–female dominance and offspring care in non-human primates. In (B. D. Miller, Ed.) *Sex and Gender Hierarchies*, pp. 127–145. Cambridge: Cambridge University Press.
- Wright, P. C. (1999). Lemur traits and Madagascar ecology: coping with an island environment. *Yearb. phys. Anthropol.* **42**, 31–72.
- Young, A. L., Richard, A. F. & Aiello, L. C. (1990). Female dominance and maternal investment in strepsirrhine primates. *Am. Nat.* **135**, 473–488.