

RESEARCH ARTICLE

Morphometrics and Pattern of Growth in Wild Sifakas (*Propithecus edwardsi*) at Ranomafana National Park, Madagascar

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We summarize morphometric data collected over a period of 22 years from a natural population of rainforest sifakas (*Propithecus edwardsi*) at Ranomafana National Park, Madagascar, and we use those data to document patterns of growth and development. Individually identified, known-age sifakas were successfully captured, measured, and released. We found that body segment lengths increased faster during growth than did body mass, with individuals attaining adult lengths earlier than adult mass. Females can begin reproducing before they are fully grown, but this may not be common. With the exception of hand length, we found no significant sex difference in any adult metric including body mass, chest, and limb circumferences, body segment lengths, and canine tooth height; however, body masses of individual females fluctuated more, independently of pregnancy, than did those of males. We found considerable interannual fluctuation in body mass with single individuals differing more within the same season in different years than from season to season in the same year. Such body mass fluctuation may be a consequence of eastern Madagascar's variable and unpredictable environment in which rainfall during any selected month varies from year to year. *Am. J. Primatol.* 73:155–172, 2011. © 2010 Wiley-Liss, Inc.

Key words: Ranomafana National Park; *Propithecus*; morphometrics; longitudinal; sexual dimorphism

INTRODUCTION

Although the number of long-term primate studies in the wild has increased over the past several decades, few have included a morphometric component [but see e.g., Altmann & Alberts, 1987; Johnson et al., 2005; Richard et al., 1993, 2000]. Therefore, researchers interested in growth and development have relied largely on cross-sectional data from wild-caught individuals [e.g., Baden et al., 2008; Bolter & Zihlman, 2003] or on data collected from captive individuals [e.g., Hamada et al., 2005; Leigh, 1992, 1994a; Leigh & Terranova, 1998]. Both wild cross-sectional and captive data are valuable, particularly in offering large samples. Captive studies frequently include known-age individuals and also can control for variable environmental conditions that may affect growth and development. Furthermore, captive and wild body masses are strongly correlated in anthropoid primates [Leigh,

1994b]. On the other hand, wild cross-sectional data from a single slice of time cannot capture interannual variation in body dimensions. Captive data may reflect the genetic potential for individual growth in a species or population; however, they may not reflect the extent to which animals realize that growth potential under natural conditions.

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Morphometric data from long-term studies of wild populations can complement wild cross-sectional and captive growth data by examining body size across both ontogenetic and calendar time, and by documenting the pattern of growth in a population in its natural social and ecological environments. Furthermore, like many captive studies, long-term studies of wild populations often have the benefit of including individuals of known or well-estimated age.

Here, we present a combination of longitudinal and cross-sectional morphometric data from identified individuals of known or well-estimated age, collected opportunistically as part of a long-term study of a natural population of the Milne–Edwards' sifaka, *Propithecus edwardsi*, at Ranomafana National Park (RNP), Madagascar [Glander et al., 1992; Karpanty & Wright, 2007; Pochron et al., 2004; Wright, 1995]. The island of Madagascar has diverse habitats with unusually unpredictable climates, conditions hypothesized to account for a suite of unusual life history and behavioral traits in lemurs and other animals [Dewar & Richard, 2007; Wright 1999, 2006]. It is important to assess lemur morphometric variation in addition to life history and behavioral trait variation in the context of Madagascar's unpredictable environmental conditions. The new data presented here are from different years and different seasons across the lifespans of many individuals, and complement a smaller, previously published data set from the same locality [Glander et al., 1992]. For the first time, we are able to analyze individual and age-related variation in morphometrics, including the pattern of growth in a rainforest sifaka.

METHODS

Treatment of live animals complied with the laws of the Republic of Madagascar; adhered to the American Society of Primatologists' Principles for

the Ethical Treatment of Nonhuman Primates; and was approved by IACUC, Stony Brook University.

Study Site

The data reported here derive from a 22-year study (1987–2008) of *P. edwardsi* in the submontane rainforest of RNP in southeastern Madagascar. Wright [1995] has previously described the site in detail. The park extends from 47°18' to 47°37' East longitude and from 21°02' to 21°25' South latitude. The elevation within RNP ranges from 600 to 1,487 m. Individuals included in our study were members of four social groups within the Talataky trail system (elevation 900–1,100 m), an area that was selectively logged between 1986 and 1989 [Arrigo-Nelson, 2006; Wright, 1997; Wright & Andriamihaja, 2002] and that is relatively homogeneous in habitat quality today.

On average, RNP receives approximately 3,000 mm of rain annually (RNP and Centre ValBio research station records). The climate varies seasonally with both rainfall and temperatures being higher during the months of December through March than during the remainder of the year (Table I) [Hemingway, 1996; Overdorff, 1993; Wright, 2006]. On the other hand, within this general seasonal pattern there is tremendous interannual variation, particularly in rainfall. From year to year, the monthly distribution of rain is unpredictable. For example, in January 1998 only 110 mm of rain fell, whereas in January 2007, 1,211 mm of rain fell—more than a ten-fold difference. Food availability can be similarly variable, being abundant 1 month but scarce in the same month of subsequent years [Lehman et al., 2005; Wright, 1999; Wright et al., 2005].

Study Subjects

The Milne–Edwards' sifaka has been described as an anatomical folivore [Hill, 1953] that includes a variety of leaves, fruits, and flowers in its diet

TABLE I. Mean Monthly Rainfall and Temperature at Ranomafana National Park, Madagascar, 1988–2007

Month	Mean rain (mm)	Rain CV (%)	Rain min–max (mm)	Mean temp min–max (°C)	Mean rain per month (mm)	Mean monthly temp min–max (°C)	Season
December	334	36.2	40–480	17.4–25.0	475	17.3–24.3	Wet
January	540	50.2	110–1211	17.7–24.0			
February	555	53.7	267–1200	17.5–24.4			
March	469	48.0	40–905	16.7–23.6			
April	219	63.5	35–549	15.9–22.7	184	13.3–19.3	Early Dry
May	157	65.0	15–394	14.2–19.7			
June	162	66.0	15–340	11.8–18.0			
July	197	68.0	21–510	11.3–16.7			
August	120	22.5	10–300	11.4–17.9	126	13.7–21.5	Late Dry
September	101	38.6	21–223	12.7–20.8			
October	127	84.3	11–488	14.4–22.8			
November	156	61.5	20–366	16.2–24.6			

[Arrigo-Nelson, 2006; Hemingway, 1996, 1998]. Over the course of this study, social groups ranged in size from two to nine individuals and typically included one or two breeding females [Morelli et al., 2009; Pochron & Wright, 2003, 1995]. Breeding was seasonal and occurred from late November through January and all but one of the births that we recorded (52/53) occurred during May, June, or July, with one birth occurring in September [Morelli, 2008; Morelli et al., 2009; Wright, 1995]. Gestation was approximately 6 months long [Wright, 1995]. Of the 53 births observed over the course of our study, three were known to be females' first births and occurred when mothers were 4 years old (3.5 years at conception). All other births were to females older than four years and none of those is known with certainty to have been a first birth. Four females followed from birth had not reproduced by 4 years and dispersed from the study area between 4 and 4.5 years, and their reproductive lives thereafter are unknown to us [Morelli, 2008; Morelli et al., 2009]. Females generally produced one offspring every 2 years (average = 1.7 years) [Morelli et al., 2009]. The population dynamics of these sifakas have been reported elsewhere [Karpanty & Wright, 2007; Pochron et al., 2004].

With veterinary supervision, we captured, measured, and released study animals on a nearly annual basis since 1987, using a well-established and successful protocol [Glander et al., 1992; Wright, 1995]. Adult and juvenile sifakas were darted with lightweight

9-mm darts. Darts delivered Telazol[®] (Pfizer Animal Health, Inc., NY, NY) intramuscularly at 10 mg/kg of body weight. Infants were not darted but were carried down with their mothers [Morelli, 2008]. The experienced capture team caught the animals with large nets and transported them to the research station for examination. We attached a combination of colored tags and collars to sedated animals older than 2 years to facilitate their future identification in the field, and replaced tags and collars yearly as needed. The season during which we conducted captures varied across the years. Table II presents the 22-year schedule of captures as well as the typical female reproductive seasons.

Measurements

Growth studies benefit from measurements that are taken regularly and frequently, ideally every month. However, to minimize potential stress to the sifakas, particularly in light of the endangered status of our study species (International Union for Conservation of Nature, www.iucnredlist.org), we collected morphometric data infrequently and only during yearly captures which were conducted primarily to monitor individuals' health. As a result, our data do not have the resolution of captive studies of growth and can address only some aspects of seasonal variation. Nonetheless, these data are unencumbered by other factors that make captive data less than ideal for understanding patterns of growth and development in natural habitats, and

TABLE II. Capture Schedule and Number of Individuals Captured

Capture date	Repro season	Female		Male		Total
		Adult	Juvenile	Adult	Juvenile	
May 20–22, 1987	Gest/birth	4	–	4	2	10
May 25–28, 1988	Gest/birth	4	1	4	1	10
May 21–25, 1989	Gest/birth	3	3	5	1	12
May 30–July 10, 1990	Gest/birth	–	2	–	1	3
March 12–22, 1991	Gest	2	2	4	1	9
January 6–7, 1993	Breeding	4	2	2	3	11
June 3–4, 1994	Birth	3	1	5	3	12
December 21–22, 1995	Breeding	3	1	6	2	12
July 2, 1996	Lactation	2	–	–	1	3
October 6, 1997	Lactation	1	1	1	–	3
November 14–18, 1998	Lactation	1	2	5	–	8
May 11–22, 2000	Gest/birth	–	–	6	2	8
November 18–29, 2000	Lactation	2	1	6	2	11
June 5–6, 2001	Birth	2	–	–	–	2
December 11–14, 2002	Breeding	5	3	4	5	17
May 24–June 3, 2003	Gest/birth	5	3	5	3	16
September 12–15, 2004	Lactation	5	6	5	4	20
June 23, 2005	Birth	1	–	1	–	2
October 29–November 4, 2005	Lactation	4	4	5	2	15
November 23–24, 2006	Lactation	5	2	7	2	16
June 7–8, 2007	Gest/birth	1	–	4	–	5
June 13–23, 2008	Birth	3	1	4	2	10
Total		60	35	83	37	215

they provide a unique opportunity to address the influence of natural variation in climate on body size and patterns of growth.

Trained technicians took measurements under controlled conditions in the Centre ValBio Annex laboratory at RNP while the animals were under sedation following capture in the field. We measured body masses of adults with a portable 10 kg spring scale and recorded them to the nearest 0.1 kg following the guidelines suggested by Smith and Jungers [1997]. We used a more sensitive 5 kg balance for individuals weighing less than 2 kg and recorded their body masses to the nearest 5 g. We recorded lengths and circumferences to the nearest 1.0 mm using a tape measure. On some occasions, we recorded only a subset of the measurements depending on the animal's level of sedation, but we recorded body mass in nearly every instance. Raw morphometric data are presented in the Appendix.

To be comparable to other studies, including earlier research on the same population, we employed the same measurements used by Glander et al. [1992] and Ravosa et al. [1993], as defined in Table III. In addition, we measured the height of the

right maxillary canine and the circumferences of the arm, chest, and thigh. For some metrics, we excluded individuals that had been injured in ways that affect measurements (e.g., terminal portion of tail missing, broken canine tooth). Some length measurements are defined by soft tissue landmarks that may be difficult to accurately locate even by trained researchers, and measurement errors were sometimes greater than would generally result from measurements taken on skeletal material. We favored measurements, such as tail-crown length, whose defining landmarks are terminal and thus easily located.

Age Determination

Because the birthdates of individuals born since the inception of this study were recorded, the ages of most of the individuals born after 1986 are known, usually to within 1 week. We estimated the ages of individuals born before the beginning of the study, and of those who immigrated from unmonitored groups during the course of the study, from mandibular molar wear as quantified from dental impressions taken during the capture seasons of 1993, 1994, 1995, 2002, 2003, and 2004 [King et al., 2005]. We took additional dental impressions in 2005, 2006, 2007, and 2008, some of which were used to document the schedule of early dental development.

Adult Size

Body mass is generally recognized as an important variable in many aspects of an animal's biology [Jungers, 1985]; therefore, we used individuals' body masses rather than linear measurements to identify those individuals that had attained adult size. We considered that adult values are those observed in nonpathological individuals who had stopped growing [Smith & Jungers, 1997]. We included very old animals in this group because we found that individuals exhibited no consistent decline in body mass as they aged. We determined adult size at the cessation of growth by examining Gompertz curves fit to growth data for each sex, and we controlled for the effects of pregnancy on adult female body mass.

Female reproductive adulthood is reached at an individual's first conception, minimally 3.5 years in our population. Male reproductive adulthood is more difficult to determine but males have been observed to mate when 3.5 years old.

Pregnancy

In calculating typical adult mass, we first excluded females known to be pregnant [Smith & Jungers, 1997]. However, some females who were weighed during December and January and included in our analysis may have been in the very earliest

TABLE III. Morphometric Variables

Tail-crown length	Tip of tail to the most anterior point on the head with the head in normal position, i.e., chin near the chest
Tail length	Measured on ventral side of fully extended tail, from tip of tail to junction of the base of the tail with the perianal area
Hindlimb length	From groin to the end of the longest digit, excluding the nail
Hindfoot length	From the heel to the end of the longest digit, excluding the nail
Big toe length	From the junction of skin and big toe to the tip of the big toe, with the big toe extended perpendicular to the other digits, excluding the nail
Forelimb length	From the axillary region to the tip of the longest digit, excluding the nail
Hand length	From the proximal edge of the friction pad nearest the wrist to the tip of the longest digit, excluding the nail
Thumb length	From the junction between the first and second digits to the tip of the thumb, excluding the nail
Arm circumference	Measured mid-arm
Chest circumference	Measured adjacent to axillae
Thigh circumference	Measured mid-thigh
Canine height	Right maxillary, measured buccally from gum to tip
Forelimb/ Hindlimb Index	$100 * (\text{Forelimb} - \text{Hand}) / (\text{Hindlimb} - \text{Hindfoot})$

After Glander et al. [1992].

stage of pregnancy when the contribution of pregnancy to the mother's body mass is trivial. Moreover, because sifaka neonates are generally very small (see below) and weigh much less in comparison to their mothers than do the neonates of similarly sized anthropoid species [Isler et al., 2008; Leutenegger, 1973; Wright, 1999], we separately calculated adult body mass without excluding the pregnant females.

Statistics

We report morphometric data collected from 57 different individuals of all ages and both sexes ($N = 29$ females, 28 males). Most individuals were sampled more than once across their lifespans for a total of 215 animal captures. Thus, our data include a combination of cross-sectional and longitudinal observations. In generating growth curves, the data were treated cross-sectionally for the population following Leigh [1992].

Because samples sizes were generally small and unequal, we used nonparametric Mann-Whitney U tests (two-tailed) to assess the significance of mean differences between females and males, with the significance level set at $\alpha = 0.05$. To eliminate potential bias introduced by the resampling of some, but not all, individuals in 2 or more capture years, we calculated each variable's mean value using the mean adult values for each resampled individual. Thus, each individual was included only once in the calculation of summary metrics. We addressed individual longitudinal variation obscured by such

averaging by finer scale analyses of individuals. We used SPSS 17.0 for all statistics and FindGraph software [UNIPHIZS Lab, Vancouver, BC] to fit Gompertz curves to growth data.

RESULTS

Pattern of Growth

Figure 1 illustrates the pattern of body mass growth for females and males between 1987 and 2008. The overall pattern of growth was very similar for both sexes. The Gompertz function for females ($r^2 = 0.92$) yields an asymptotic body mass of 5.68 kg while the curve for males ($r^2 = 0.90$) yields an asymptotic body mass of 5.49 kg. Both sexes gained weight rapidly during their first 2 years of life, after which growth rates began to decrease, decelerating rapidly by age 3 years. The body masses of both females and males reached their ultimate mean values at approximately 6 years of age (Fig. 1; vertical dashed line). Therefore, in calculating mean adult size for other metrics, we considered individuals older than 5.99 years to be adult in size. The shaded vertical bar in Figure 1 represents the timing of the onset of female reproductive maturation, with first female conception occurring minimally at 3.5 years and other first conceptions likely occurring at 4.5 years [Morelli, 2008; Morelli et al., 2009]. Arm, chest, and thigh circumferences reached their ultimate adult size in concert with body mass at approximately 6 years of age (not illustrated).

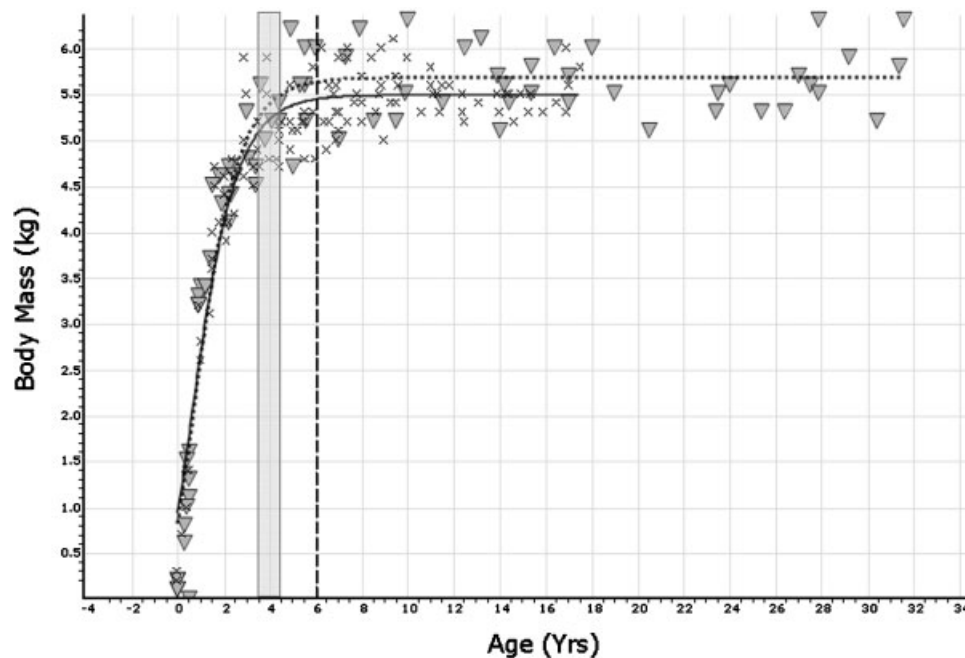


Fig. 1. Mixed longitudinal body mass values vs. age for males (\times) and females (∇). Growth curves (Gompertz): males, solid line; females, dotted line. Vertical dashed line indicates the completion of body mass growth at approximately 6 years. The shaded vertical bar represents the timing of female reproductive maturation.

Female sifakas typically are reproductively mature before they attain their final adult body mass and circumferences. The same may be true for males; however, documenting the onset of male reproductive maturation is more difficult. Across the entire study period of 22 years, no males older than 19 years were found, whereas three females lived beyond 25 years and two of those were older than 30 years when they died.

As is the case for body mass, the pattern of growth of linear dimensions is similar in both sexes. Linear dimensions grow faster than do body mass and circumferences and they reach their ultimate size at a younger age. As an example typifying this pattern, Figure 2 illustrates the pattern of ontogenetic increase in the tail-crown length for females and males, with sex-specific Gompertz curves being nearly coincident. Asymptotic tail-crown lengths are 92.7 cm for females ($r^2 = 0.88$) and 91.9 cm for males ($r^2 = 0.76$). Both sexes reach their ultimate tail-crown lengths at approximately 2 years of age (vertical dashed line) vs. 6 years for body mass. This same growth pattern is typical of other linear dimensions (not illustrated), which also reach their maximum values well in advance of body mass and circumferences, and in advance of female reproductive maturation.

Body Mass and Age Categories

Because the age of each individual was known from recorded birth dates or estimated on the basis of dental wear, we were able to document the mean body mass for different age categories during early

ontogeny. Table IV presents these data for each sex separately and for both sexes pooled, until the age of 8 years.

Our smallest sifaka weighed 135 g when 3 days old. Five measured neonates (mean age = 5 ± 3 days) weighed 165 g on average, or approximately 3% of female adult mass. In the first 3 months of postnatal life, infant body mass increased almost four-fold to 700–800 g, and by 6 months of age infants weighed approximately 1.3 kg. During the subsequent 6 months, body mass more than doubled and yearlings weighed approximately 3.2 kg. These data confirm the pattern found by Wright [1999] whereby the rate of body mass growth increases almost two-fold after weaning.

Table IV reveals virtually no difference in the mean body masses of females and males at any age category despite the slight sex differences in growth trajectories after the age of 2 years (Fig. 1). The mean ratio of male to female mass across all age categories until age 8 years is 1.003.

Adult Body Mass and Circumferences

A summary of adult body masses and circumferences, calculated both with and without pregnant females, is presented in Table V. With data pooled from both sexes and all seasons, the overall mean adult body mass of *P. edwardsi* from 1987 to 2008 was $5.6 \pm \text{SD } 0.4$ kg. Nonpregnant adult females on average weighed slightly more than adult males (5.7 ± 0.4 kg vs. 5.5 ± 0.3 kg); however, the difference was not statistically significant (Mann-Whitney U : $P = 0.08$). When pregnant females were included,

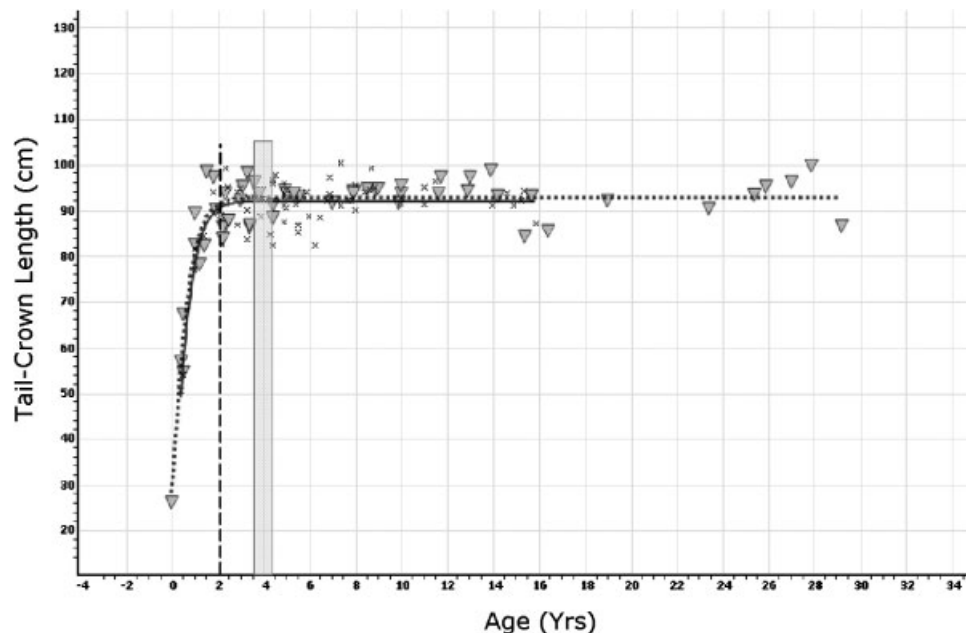


Fig. 2. Mixed longitudinal tail-crown length vs. age for males (\times) and females (∇). Growth curves (Gompertz): males, solid line; females dotted line. Vertical dashed line indicates the completion of tail-crown length growth at approximately 2 years. The shaded vertical bar represents the timing of female reproductive maturation.

TABLE IV. Body Masses of Specific Age Categories

Age category	Age interval (years)	Category mean age, years (<i>N</i>)			Mean body mass, kg (SD)			M/F ratio
		Sexes combination	Males	Females	Sexes combination	Males	Females	
Newborn	2–8 days	5 days (5)	4 days (2)	6 days (3)	0.165 (0.025)	0.178 (0.032)	0.156 (0.023)	1.14
3 months	0.25–0.28	0.27 (3)	0.25 (1)	0.28 (2)	0.695 (0.102)	0.730 (–)	0.678 (0.138)	1.08
6 months	0.39–0.74	0.45 (9)	0.43 (3)	0.46 (6)	1.28 (0.24)	1.26 (0.26)	1.29 (0.25)	0.98
1 year	0.75–1.24	0.95 (8)	0.96 (3)	0.95 (5)	3.1 (0.3)	2.9 (0.3)	3.2 (0.1)	0.91
1.5 years	1.25–1.74	1.42 (6)	1.47 (3)	1.37 (3)	3.7 (0.5)	3.5 (0.3)	3.8 (0.6)	0.92
2 years	1.75–2.24	2.03 (11)	1.99 (6)	2.08 (5)	4.3 (0.3)	4.2 (0.3)	4.4 (0.3)	0.95
2.5 years	2.25–2.74	2.43 (6)	2.49 (3)	2.36 (3)	4.5 (0.2)	4.5 (0.3)	4.5 (0.1)	1.00
3 years	2.75–3.24	2.95 (6)	2.92 (4)	3.01 (2)	5.2 (0.5)	5.3 (0.6)	5.1 (0.4)	1.04
3.5 years	3.25–3.74	3.40 (8)	3.40 (6)	3.40 (2)	4.7 (0.2)	4.7 (0.3)	4.6 (0.2)	1.02
4 years	3.75–4.24	3.97 (4)	3.94 (3)	4.05 (1)	5.3 (0.5)	5.4 (0.6)	5.2 (–)	1.04
4.5 years	4.25–4.74	4.39 (8)	4.39 (6)	4.40 (2)	5.1 (0.2)	5.0 (0.2)	5.3 (0.1)	0.94
5 years	4.75–5.24	4.96 (7)	4.95 (5)	4.99 (2)	5.2 (0.5)	5.1 (0.3)	5.4 (1.0)	0.94
5.5 years	5.25–5.74	5.44(9)	5.41 (5)	5.47 (4)	5.3 (0.4)	5.1 (0.2)	5.6 (0.3)	0.91
6 years	5.75–6.24	5.96 (4)	5.96 (3)	5.97 (1)	5.5 (0.5)	5.3 (0.3)	6.0 (–)	0.88
6.5 years	6.25–6.74	–	6.46 (3)	–	–	5.4 (0.5)	–	–
7 years	6.75–7.24	6.94 (8)	6.94 (7)	6.97 (1)	5.3 (0.3)	5.4 (0.3)	5.0 (–)	1.08
7.5 years	7.25–7.74	7.43 (6)	7.47 (5)	7.25 (1)	5.6 (0.4)	5.5 (0.4)	5.9 (–)	0.93
8 years	7.75–8.24	7.93 (5)	7.92 (4)	7.95 (1)	5.4 (0.2)	5.4 (0.2)	5.4 (–)	1.00

Mean M/F = 1.003.

TABLE V. Adult Body Mass and Circumferences (Mean ± SD) and Comparison of Sex Differences (Mann–Whitney *U*)

Variable	Sexes combined		Females		Males		Sex differences	
	Mean	<i>N</i>	Mean	<i>N</i>	Mean	<i>N</i>	<i>z</i>	<i>P</i>
<i>Body mass (kg)</i>								
Pregnant females excluded	5.6 ± 0.4	26	5.7 ± 0.4	9	5.5 ± 0.3	17	–1.780	0.08
Pregnant females included	5.6 ± 0.4	28	5.8 ± 0.4	11	5.5 ± 0.3	17	–2.330	0.02
<i>Arm circumference (cm)</i>								
Pregnant females excluded	13.3 ± 1.6	20	12.7 ± 1.2	7	13.6 ± 1.7	13	–0.832	0.41
Pregnant females included	13.5 ± 1.4	22	13.2 ± 0.9	9	13.6 ± 1.7	13	–0.100	0.92
<i>Chest circumference (cm)</i>								
Pregnant females excluded	33.9 ± 1.9	21	34.3 ± 1.2	7	33.6 ± 2.1	14	–0.896	0.37
Pregnant females included	34.0 ± 2.0	23	34.7 ± 1.8	9	33.6 ± 2.1	14	–1.134	0.26
<i>Thigh circumference (cm)</i>								
Pregnant females excluded	20.4 ± 1.2	20	20.2 ± 0.8	7	20.5 ± 1.4	13	–0.357	0.72
Pregnant females included	20.7 ± 1.3	22	20.9 ± 1.3	9	20.5 ± 1.4	13	–0.635	0.53

Bold font indicates significant *P*-values.

there was a statistically significant sex difference in adult body mass ($5.8 \pm \text{SD } 0.4$ kg females vs. $5.5 \pm \text{SD } 0.3$ kg males, $P = 0.02$). Our two lightest adults, a 7 year old female and a 9 year old male, each weighed 5.0 kg which was 77% that of the heaviest individual, a 6.5 kg 26-year-old nonpregnant female. These individuals were weighed during the same season but in different years.

There were no statistically significant sex differences in arm, chest, or thigh circumferences (Table V).

We examined longitudinal data from identified individuals to uncover potential individual and sex differences in the extent to which body mass fluctuated across adulthood. Table VI summarizes

individual lifetime variation in the body masses of five nonpregnant females and nine males that were sampled on three or more occasions as adults. Individuals differed considerably in the extent to which their body mass fluctuated across adulthood. Among females, the adult body mass varied by 200 g across three observations in individual GS and by as much as 900 g across seven observations in individual BG. In males, the body masses of two individuals (YS, OR) varied by approximately 100 g across three observations each, whereas the body mass of Red varied by 800 g across seven observations

The mean body masses of these repeatedly sampled individual females and males did not differ

significantly by sex (5.7 ± 0.3 kg females vs. 5.5 ± 0.2 kg males, Mann–Whitney U : $P = 0.34$). However, despite the similar mean body masses of females and males, the masses of individual females fluctuated more across adulthood as indicated by their greater standard deviations (0.3 vs. 0.2, $P < 0.05$), larger range of body mass fluctuation (600 g vs. 300 g, $P = 0.11$ NS), and larger coefficients of variation (4.9 females vs. 3.0 males, $P < 0.05$).

Higher resolution analyses of single individuals sampled repeatedly across adulthood provided illustrative information on the pattern of adult body mass fluctuation. Tables VII and VIII present data on two individuals that show a pattern representative

TABLE VI. Longitudinal Body Mass Variation in Individual, Adult, Nonpregnant Females and Males Who Were Weighed on Three or More Occasions, and Comparison of Sex Differences (Mann–Whitney U)

Individual	Sex	N	Mean mass (kg)	SD	Range	CV%
BB	F	10	5.5	0.3	0.8	5.4
GG	F	4	6.2	0.4	0.8	6.5
GO	F	6	5.9	0.2	0.4	3.4
BG	F	7	5.4	0.3	0.9	5.6
GS	F	3	5.5	0.2	0.2	3.6
Red	M	7	5.6	0.3	0.8	5.4
RR	M	3	5.5	0.2	0.3	3.6
BR	M	3	5.4	0.2	0.3	3.7
YS	M	3	6.0	0.1	0.1	1.7
B(m)	M	9	5.4	0.1	0.3	1.9
P	M	9	5.5	0.1	0.5	1.8
BP	M	6	5.3	0.2	0.5	3.8
OB	M	4	5.2	0.1	0.2	2.0
OR	M	3	5.9	0.1	0.1	1.7
Mean	F	6.0	5.7	0.3	0.6	4.9
Mean	M	5.4	5.5	0.2	0.3	2.8
Sex difference	z		-0.949	-2.315	-1.620	-2.287
	P		0.34	0.02	0.11	0.02

n = Number of time weighed.

Bold font indicates significant P -values.

of that seen in other individuals of their sex. Table VII presents data for “Blue Blue Female,” whose nonpregnant adult mass was recorded on ten occasions between 1988 and 2006 and fluctuated by 800 g, from 5.1 kg in December 1995 to 5.9 kg in September 2004. There was little variation in her mean weight across seasons (wet, $5.4 \pm \text{SD } 0.4$ kg; early dry, 5.6 ± 0.1 kg; and late dry, 5.5 ± 0.3 kg). Perhaps surprisingly, two of her highest recorded weights (5.8 and 5.9 kg) were from the late dry season when food resources tend to be scarce, but in other years during that same season she weighed only 5.2 kg and 5.3 kg. Thus, across her long lifespan Blue Blue Female’s late dry season adult weight fluctuated year-to-year by approximately 700 g or 12%, depending on the year and irrespective of her reproductive status. Similarly, interannual fluctuation in her wet season mass was approximately 500 g.

Table VIII reports comparable data for “Blue Male” who was weighed on nine occasions across his adulthood. Overall, his body mass was much less variable (5.3–5.6 kg) than that of Blue Blue Female. Nonetheless, the body mass of this adult male also varied more within seasons in different years than across seasons. Data from both of these individuals suggest that season may not account for as much body mass variation as do year-to-year differences during the same season.

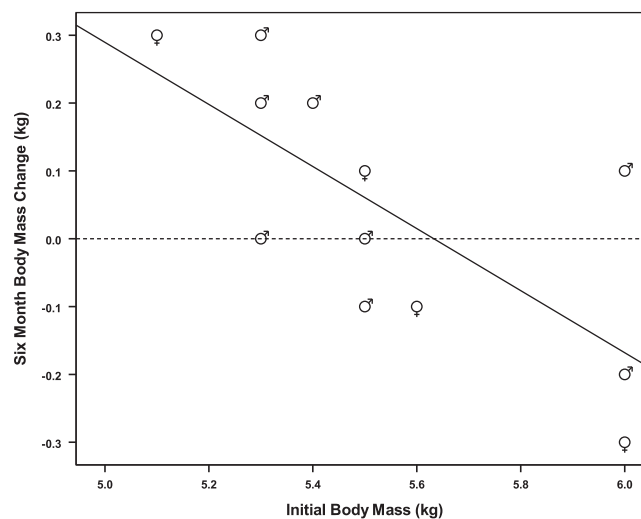
We further attempted to understand variation in adult body mass by closely examining particular individuals, females and males, who were weighed twice within approximately 6 months. There were 12 instances in which nonpregnant individuals were weighed in both May–June and in either the following or the previous October–December. Thus, we examined individuals’ weight changes between October and December and the following May–June, or between May and June and the following October–December. The mean duration between consecutive weighings was 5.9 months. Figure 3 plots individuals’ 6-month change in mass vs. their initial mass ($r^2 = 0.53$, $P < 0.01$). Some individuals

TABLE VII. Adult Body Mass Variation in “Blue Blue Female”

Season	Date	Reproductive status	Age (years)	Body mass (kg)	Mean (kg)	Within season range (kg)
Wet	December 21, 1995	Not pregnant	20.5	5.1	5.4	0.5
Wet	December 11, 2002	Lactating	27.5	5.6		
Early dry	May 21, 1989	Not pregnant	13.9	5.7		
Early dry	June 3, 1994	Not pregnant	19.0	5.5	5.6	0.2
Early dry	May 27, 2003	Not pregnant	27.9	5.5		
Late dry	November 18, 1998	Lactating	23.4	5.3	5.5	0.7
Late dry	November 29, 2000	Not pregnant	25.4	5.3		
Late dry	September 14, 2004	Not pregnant	29.2	5.9		
Late dry	November 4, 2005	Not pregnant	30.4	5.2		
Late dry	November 23, 2006	Lactating	31.4	5.8		

TABLE VIII. Adult Body Mass Variation in “Blue Male”

Season	Date	Age (years)	Body mass (kg)	Mean (kg)	Within season range (kg)
Wet	December 11, 2002	11.4	5.3	5.3	–
Early dry	May 23, 2000	8.8	5.5		
Early dry	May 28, 2003	11.8	5.6		
Early dry	June 7, 2007	15.9	5.3	5.4	0.3
Early dry	June 23, 2008	16.9	5.3		
Late dry	November 28, 2000	9.4	5.4	5.4	0.2
Late dry	September 12, 2004	13.1	5.4		
Late dry	October 31, 2005	14.3	5.5		
Late dry	November 24, 2006	15.3	5.3		

Fig. 3. Body mass change (positive or negative) in consecutive half-year weighings vs. initial body mass ($r^2 = 0.53$, $P < 0.01$).

gained weight (above the horizontal dashed lined) and others lost weight (below the line) in consecutive weighings. There was no correlation between season and either the direction (sign test, $P = 0.75$) or amount (Mann–Whitney U , $P = 0.75$) of weight gain or loss. Rather, we found that heavy individuals tended to lose weight in the subsequent half-year and lightweight individuals tended to gain weight in the subsequent half-year; however, this pattern was not universal and the sample is small. The mass of two individuals was unchanged, and one individual that was initially heavy (6.0 kg) gained weight slightly to 6.1 kg in the subsequent 6 months. This observed pattern suggests that these eastern sifakas may tend toward an ideal body mass.

Adult Linear Measurements

A summary of linear measurements is provided in Table IX. We found no statistically significant sex differences for any of the metrics except hand length, with females having slightly longer hands than males (13.4 ± 0.5 cm vs. 12.8 ± 0.7 cm, Mann–Whitney

U : $P = 0.03$). To minimize potential confounding effects of tooth wear, we summarized the length of right maxillary canines only in adults between the ages of 6 and 12 years (females $N = 5$, mean age = 9.6 years; males $N = 11$, mean age = 7.9 years) and found no statistically significant sex difference in canine height. With the exception of its variation in hand length, *P. edwardsi* is sexually monomorphic in linear dimensions.

Dental Development

We used tooth impressions taken from known-age individuals to document the schedule of early dental development in *P. edwardsi* (Table X). One individual (P \dot{Y} infant 2006; born in nearby Sakaroa, not Talatakely), born in September and examined approximately 2.5 months later, had its full complement of gingivally erupted deciduous teeth in the mandible. In two 3 month old infants, M_1 was erupting through the gum. By 4 months and 23 days, M_1 was fully erupted while M_2 and P_4 were in the process of erupting, but in a second individual 3 days

TABLE IX. Summary of Linear Metrics for Adult Individuals (Mean \pm SD) and Results of Male–Female Comparison (Mann–Whitney U)

Metric	Sexes combined	N	Females	N	Males	N	z	P
Canine height (mm)	8.8 \pm 0.7	16	8.7 \pm 0.7	5	8.9 \pm 0.8	11	–0.568	0.57
Tail–crown (cm)	92.9 \pm 3.2	21	93.2 \pm 2.7	9	92.7 \pm 3.6	12	–0.818	0.41
Tail (cm)	44.8 \pm 1.8	23	45.0 \pm 2.4	10	44.7 \pm 1.2	13	–1.117	0.26
Hindlimb (cm)	55.4 \pm 2.2	22	55.0 \pm 2.5	9	55.6 \pm 2.0	13	–0.768	0.44
Hindfoot (cm)	17.5 \pm 0.8	20	17.6 \pm 0.6	9	17.5 \pm 0.9	11	–0.114	0.91
Big toe (cm)	9.9 \pm 0.9	23	10.2 \pm 0.9	10	9.7 \pm 0.8	13	–1.458	0.15
Forelimb (cm)	37.4 \pm 2.4	21	38.5 \pm 2.3	8	36.7 \pm 2.3	13	–1.666	0.10
Hand (cm)	13.0 \pm 0.7	23	13.4 \pm 0.5	9	12.8 \pm 0.7	14	–2.209	0.03
Thumb (cm)	6.0 \pm 0.7	24	6.1 \pm 0.5	10	5.9 \pm 0.8	14	–0.234	0.84

Bold font indicates significant P -values.

TABLE X. Mandibular Postcanine Dental Development

Individual	Birth date	Capture date	Age	Dental development
PY infant 2006	September 15, 2006	November 27, 2006	< 3 months	Full deciduous
BG infant 2004	June 4, 2004	September 12, 2004	3 months, 8 days	Full deciduous, M_1 erupting
GS infant 2004	June 1, 2004	September 12, 2004	3 months, 11 days	Full deciduous, M_1 erupting
B infant 2006	July 1, 2006	November 23, 2006	4 months, 23 days	P_4 erupting, M_1 erupted, M_2 erupting
BS infant 2006	June 28, 2006	November 23, 2006	4 months, 26 days	dp_4 , M_1 erupted, M_2 not molded—no data
BG infant 2006	June 6, 2006	November 24, 2006	5 months, 18 days	P_4 erupting, M_1 erupted, M_2 erupted

older, P_4 was not yet erupting. In a 5.5 month old, P_4 was still erupting and the two anterior molars were fully erupted, but there was no evidence of M_3 above the gum line. By 1 year of age, the full complement of permanent mandibular molars had erupted.

DISCUSSION

Growth

Our morphometric data from identified, known-age individuals allowed us to construct growth curves for many traits. We found two general patterns. First, bone lengths, as reflected in the lengths of body segments, increased quickly. The elements we measured reached their adult lengths before 3 years of age, whereas long bone growth in the smaller-bodied *P. verreauxi* is reported to continue until 5 years of age [Richard et al., 2002]. These observations are consistent with the growth patterns reported by Ravosa et al. [1993] whereby the Milne–Edwards’ sifaka was found to attain its larger size relative to *P. verreauxi* via a faster rate of growth, but not an increased duration of growth. In fact, we found a shorter duration of growth in *P. edwardsi*. Second, individual *P. edwardsi* did not reach their ultimate body masses and circumferences until they were considerably older, at approximately 6 years of age. Thus, a young sifaka can, for example, have an adult-sized tail when it has only about 75% of its adult mass. This pattern, whereby body mass continues to accumulate after the cessation of long bone growth, is not uncommon in mammals [e.g.,

Childerhouse et al., 2010] including primates [Smith & Jungers, 1997; other sifakas, Richard et al., 2000, 2002].

In agreement with an earlier study of captive and wild-caught individuals [Godfrey et al., 2001], we found that dental development is extremely rapid in wild Milne–Edwards’ sifakas. Both limb segment and body mass growth lag behind dental development. From dental casts, we ascertained that the full complement of adult mandibular postcanine teeth erupted by 1 year of age. At this age, sifakas have, on average, grown to approximately 80% of their tail–crown length but only 55% of their adult body mass.

Female reproductive maturation in *P. edwardsi* sometimes occurs before females reach their ultimate adult body mass; however, it is unclear if this is the typical pattern. Females have been known to conceive when they are 3.5 years old, at which time their body mass averages approximately 4.6 kg or only 81% of the ultimate female mean value of 5.7 kg. Other females conceive for the first time when they are at least 4.5 years old when their body mass (mean \sim 5.3 kg) approximates 93% of the ultimate mean adult value. These observations will be enhanced in the years ahead as we gather more data on the age of first reproduction in known-age individual females who then live on to attain their ultimate body masses. Those data will allow us to determine the modal age and size at first female reproduction. Males, likewise, have been known to mate at 4 years [Morelli, 2008; Morelli et al., 2009]; however, it is likely that male first reproduction more commonly occurs at an older age and larger size.

Milne–Edwards' sifaka neonates, like those of other strepsirrhine species, are small in comparison to the neonates of anthropoids with similar adult body mass [Isler et al., 2008; Leutenegger, 1973; Wright, 1999]. For example, adult female *Macaca nemestrina* weigh 6.5 kg [Smith & Jungers, 1997] and their neonates weigh approximately 7% of that, or 463 g [Smith & Leigh, 1998]. Our study showed that, on average, the weight of sifaka neonates (165 g, $N = 5$) was less than 3% of their mother's weight (5.7 kg). Moreover, this mean value is likely to be exaggerated because the average neonatal age for our sample was 5 days by which time infants would already exceed their birth weights. Our youngest individual, a 3 day old baby, weighed 135 g, or approximately 2% of mean adult female mass. Given that the placenta and amniotic fluid also contribute mass, a neonatal mass of 135 g is consistent with the 300 g body mass difference between pregnant and nonpregnant females that we observed during the late gestation–birth period (May–July), when pregnant females average 6.0 kg and nonpregnant females average 5.7 kg (Mann–Whitney U : $P = 0.06$, NS).

Both dental precocity and low neonatal weight support the interpretation that female Milne–Edwards' sifakas have a reproductive strategy characterized by limited maternal investment with sustained fertility into old age [King et al., 2005; Wright et al., 2008]. Females produce small babies that are dentally well-endowed for early weaning. This pattern may allow mothers to invest more heavily in themselves to enhance their own future reproductive efforts in Madagascar's unpredictable environment [Dewar & Richard, 2007; Godfrey et al., 2004].

Sexual Dimorphism

Earlier researchers, using small samples or captive individuals, found *P. edwardsi* to be sexually dimorphic [Kappeler, 1990; Ravosa et al., 1993] with females being larger than males. However, when larger samples of wild-caught individuals were examined, sexual dimorphism was not found [Glander et al. 1992; Kappeler, 1991]. Our data support the absence of sexual dimorphism in Milne–Edwards' sifakas. Adult females, on average, were only marginally heavier than adult males ($5.7 \pm \text{SD } 0.4 \text{ kg}$ vs. $5.5 \pm \text{SD } 0.3 \text{ kg}$); however, this difference was not statistically significant ($P = 0.08$). Similarly, we found only trivial sex differences in body mass for each age category (Table IV), and even these differences sometimes indicated larger females and other times indicated larger males. Of all the lengths analyzed, the only sex difference that reached statistical significance was the length of the hand ($P = 0.03$); females have slightly longer hands than males. We did not find canine height to be a sexually dimorphic trait in *P. edwardsi*, contra Kappeler [1996]. The additional weight of pregnancy,

albeit small, did result in sex differences in body mass during the reproductive season with pregnant females being heavier than males ($5.8 \pm \text{SD } 0.4 \text{ kg}$ vs. $5.5 \pm \text{SD } 0.3 \text{ kg}$, $P = 0.02$), but this has no bearing on sexual dimorphism.

Despite the overall similarity in male and female mean body masses, there was a tendency for mass to fluctuate more across adulthood in females than in males (Table VI) [Arrigo-Nelson, 2006]. The coefficient of variation in body mass of nonpregnant females exceeds that for males (4.9 vs. 2.8, $P < 0.05$). The CV in tail–crown length, by contrast, was very similar in males and females (2.37 vs. 2.61, NS). This is to be expected because, in the absence of pathology or trauma, lengths will not vary across adulthood.

Seasonal and Interannual Variation

The climatic (Table I) and concomitant variation of food resources [Lehman et al., 2005; Wright, 1999; Wright et al., 2005] experienced by the lemurs of RNP are well established. Body mass and circumferences, but not linear measurements, may be expected to vary in adults as environmental conditions change, sometimes dramatically. Our data support this expectation. We found that body mass can fluctuate considerably from year to year across adulthood independently of season (i.e., interannual variation in the same month may exceed variation from season to season in the same year), as illustrated by our in-depth look at particular individuals who were sampled on multiple occasions across their adulthoods (Tables VI–VIII). For example, the mass of our most frequently measured individual, Blue Blue Female, fluctuated by 800 g across her long adulthood. And, in a single season (late dry) but in different years, her weight varied by 700 g, with pregnancy playing no role in this fluctuation. In an earlier but shorter study of this same population, Glander et al. [1992] found that the mass of single individuals changed across years during the same season, specifically during May and June, 1987–1989. They suggested that such interannual body mass fluctuation might be attributable to variation in food availability.

Although our data lack sufficient density to fully explore seasonal body size variation, our evidence does suggest that the systematic and strong seasonal body mass fluctuation seen in western sifakas [Richard et al., 2002] is absent or weaker in the eastern Milne–Edwards' sifaka. This east–west difference in the degree of seasonal body mass fluctuation may be related to the greater annual climatic variation in western Madagascar, described by Dewar and Richard [2007]. These same authors also found that the *patterns* of climatic variation differ. They characterized western Malagasy sites as having predictably similar amounts of rain in each month across years (high “contingency”) but greater variation from month-to-month in the same year

(low “constancy”), with some months having no rain at all. Eastern sites, by contrast, exhibit at least some rain in every month (high “constancy”) but extreme rainfall variation in the same month from year-to-year (low “contingency”). In essence, western sifakas predictably experience high rainfall seasonality, whereas those in the east experience less pronounced but poorly predictable rainfall seasonality. As additional data become available, we will be able to more thoroughly evaluate sifaka body mass variation in the context of these east–west climatic differences.

Mean adult body mass in 1987 was 5.7 kg, but had decreased to 5.3 kg by 2008. It is unclear at this time whether this represents a secular trend or is simply the result of unpredictable interannual variation. It is perhaps noteworthy that across the same years both the mean group size and the total population have also decreased [Wright, unpublished data].

Dental Development, Somatic Growth, and Reproductive Maturation

Our data demonstrate that the teeth develop rapidly in *P. edwardsi*, with our youngest individual having its full complement of deciduous teeth before it was 3 months old. This finding is consistent with those of Godfrey et al. [2001, 2004] and Schwartz et al. [2002] who found rapid dental development, both absolutely and relative to somatic growth and reproductive maturation, in indriids including *P. edwardsi*, *P. tattersalli*, and *P. verreauxi*. Godfrey et al. [2004] demonstrated that diet can affect the pace of dental development independently of body size, with primate folivores (including sifakas) typically having more accelerated dental development than similarly sized frugivores. In addition, these authors found that dental development has a phylogenetic component, with closely related taxa sharing similar dental schedules independent of diet. That dental development among sifaka species is rapid relative to both growth and reproductive maturation demonstrates that fast dental schedules are not necessarily indicative of fast life histories. Indeed, Godfrey et al. [2001, 2004] found that sifakas tend to grow more slowly than like-sized lemurids, and their sexual maturation may be delayed.

P. edwardsi shares a rapid pace of dental development, relatively early weaning, and delayed first reproduction with its congeners [Godfrey et al. 2001; Appendix I], but attains a larger adult size via faster, but not longer, growth [Ravosa et al., 1993]. Although the rate of dental development may be phylogenetically constrained among sifakas, various authors have related body size differences to ecological factors, including annual rainfall, resource quality, resource availability, seasonality, and lemur density [Albrecht et al., 1990; Godfrey et al., 1990; Lehman, 2007; Lehman et al., 2005; Ravosa et al., 1993, 1995; Wright, 1999].

SUMMARY

The postcranial linear dimensions of Milne–Edwards’ sifakas at RNP attained their adult values before both adult body mass and reproductive maturation. Females can conceive before they reach adult body mass; however, they more typically reproduced when they approached adult weight. We found no strong evidence of sexual dimorphism in this species in either body mass or in the lengths of body and limb segments except the hand, which is slightly longer in females. From 1987 to 2008, the average adult nonpregnant body mass at RNP was 5.6 ± 0.4 kg. Females weighed slightly more than males on average but this difference was not statistically significant. Neonates weighed between 100 and 200 g, or 3% of mother’s weight. The small body size of neonates was consistent with our finding that pregnancy contributes very little to female adult body mass, especially in comparison to like-sized anthropoid species. We lack strong evidence of consistent seasonal body mass differences; however, it is apparent that Milne–Edwards’ sifakas lack exposure to the consistently strong seasonality observed in the west. This east–west difference may relate to differences in the degree and pattern of rainfall unpredictability. Our analysis of weight loss or gain in consecutive half-year periods suggests that sifakas may tend toward an ideal body mass. Heavy individuals tended to lose weight and lighter individuals tended to gain weight in the subsequent half-year period.

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APPENDIX

Individual	ID#	Sex	Group	Capture date	Age (years)	Body mass (kg)	Tail-crown (cm)	Tail (cm)	Hind-limb (cm)	Hind-foot (cm)	Big toe (cm)	Fore-limb (cm)	Hand (cm)	Thumb (cm)	Arm circumference (cm)	Chest circumference (cm)	Thigh circumference (cm)
Yellow	1	f	Tala I	20-May-1987	7.9	6.2	94.0	45.2	54.0	17.2	9.7	37.1	13.0	5.8	12.6	35.0	21.0
Yellow	1	f	Tala I	25-May-1988	8.9	6.0	94.1	45.0	51.9	17.1	8.7	37.1	12.9	5.9	15.1	39.7	21.6
Yellow	1	f	Tala I	23-May-1989	9.9	5.5	91.5	45.5	53.1	16.9	10.4	38.4	13.0	6.3	12.5	34.0	21.5
Yellow	1	f	Tala I	13-Mar-1991	11.7	5.8	97.0	45.5	56.0	16.5		37.0	13.5	5.5	33.5	20.0	
Red	2	m	Tala I	20-May-1987	3.9	5.9	88.7	42.0	54.3	17.4	9.9	36.4	12.9	6.1	13.2	33.7	21.7
Red	2	m	Tala I	25-May-1988	4.9	5.6	93.5	41.3	54.0	17.7	9.4	31.5	12.7	6.5	13.6	34.0	23.7
Red	2	m	Tala I	21-May-1989	5.9	5.8	94.0	44.5	54.5	16.1		41.6	13.0	5.7	14.1	33.6	22.8
Red	2	m	Tala I	13-Mar-1991	7.7	5.4	92.0	44.5	54.0	17.9		35.5	13.0	5.7	31.0	31.0	21.0
Red	2	m	Tala I	03-Jun-1994	11.0	5.8	91.2	42.5	54.3	17.5	9.5	38.2	13.3	6.1	15.0	35.4	22.4
Red	2	m	Tala I	21-Dec-1995	12.5	5.2											
Red	2	m	Tala I	14-Nov-1998	15.4	5.5	94.1	48.0	57.0	19.7		32.4		6.8	16.2	44.0	24.5
Red	2	m	Tala I	22-May-2000	16.9	6.0											
Red	2	m	Tala I	27-Nov-2000	17.5	5.8											
Blue Blue	3	f	Tala I	25-May-1988	12.9	5.8	94.0	46.0	56.7	17.5	11.0	37.3	13.3	6.5	14.4	35.0	21.0
Blue Blue	3	f	Tala I	21-May-1989	13.9	5.7	98.5	45.4	57.3	17.5		38.5	13.1	5.1	14.8	35.5	21.2
Blue Blue	3	f	Tala I	13-Mar-1991	15.7	5.6	93.0	46.0	56.5	17.8		38.1	13.4	6.0	34.5		22.0
Blue Blue	3	f	Tala I	06-Jan-1993	17.6												
Blue Blue	3	f	Tala I	03-Jun-1994	19.0	5.5	92.0	45.0	54.0	17.1	10.7	39.3	12.6	6.4	15.0	32.9	20.4
Blue Blue	3	f	Tala I	21-Dec-1995	20.5	5.1											
Blue Blue	3	f	Tala III	18-Nov-1998	23.4	5.3	90.1	39.2	53.4	17.1	10.0	38.1	12.2	6.2	12.0	33.3	21.2
Blue Blue	3	f	Tala III	29-Nov-2000	25.4	5.3	93.3		55.5	17.9	10.8	37.3	13.5	6.4	11.7	30.6	19.1
Blue Blue	3	f	Tala III	11-Dec-2002	27.5	5.6											
Blue Blue	3	f	Tala III	27-May-2003	27.9	5.5											
Blue Blue	3	f	Tala III	14-Sep-2004	29.2	5.9	86.3		57.1	16.6	9.0	42.3		4.4	12.9	46.6	20.5
Blue Blue	3	f	Tala III	04-Nov-2005	30.4	5.2											
Blue Blue	3	f	Tala III	23-Nov-2006	31.4	5.8											
Green Green	5	f	Tala II	20-May-1987	25.9	6.5	95.0	46.2	59.3	18.2	10.1	43.2	14.2	7.0	14.6	33.0	21.0
Green Green	5	f	Tala II	28-May-1988	27.0	5.7	96.0	46.0	58.5	18.1	10.9	41.1	14.0	6.7	12.9	33.3	20.2
Green Green	5	f	Tala II	25-May-1989	27.9	6.3	99.5	47.0	60.3	19.2	10.8	43.0	13.8	6.6	13.5	33.0	21.0
Green Green	5	f	Tala II	06-Jan-1993	31.6	6.3											
Inf GG86	12	m	Tala II	22-May-1987	1.0	2.6	77.0	39.4	46.1	15.1	8.8	32.4	10.6	5.3	10.0	26.5	15.2
Red Red	6	m	Tala II	28-May-1988	14.0	5.3	90.8	43.0	55.7	16.2	10.5	37.3	12.9	5.8	13.2	31.7	22.0
Red Red	6	m	Tala II	25-May-1989	14.9	5.5	91.0	43.2	51.9	16.9	10.3	37.3	12.4	6.6	13.3	31.0	21.1
Red Green	7	f	Tala II	21-May-1987	7.9	6.3	93.5	47.8	57.5	18.7	10.7	39.5	14.0	6.0	14.0	41.0	22.0
Red Green	7	f	Tala II	28-May-1988	9.0	6.0	94.5	47.0	57.2	18.0	11.0	42.4	13.7	6.2	13.2	35.3	25.7
Inf RG88	85	f	Tala II	28-May-1988	0.0	0.2	26.0	11.0	14.0	6.0	3.0	10.2	4.1	2.1			
Yellow Green	8	f	Tala II	20-May-1987	4.9	6.2	94.3	47.5	56.1	17.7	10.0	38.6	13.6	6.3	14.2	38.8	23.1
Blue Red	9	m	Tala II	21-May-1987	6.9	5.3	93.5	46.0	53.7	17.3	10.0	34.2	13.3	6.3	15.3	38.9	23.1
Blue Red	9	m	Tala II	28-May-1988	8.0	5.4	95.5	46.0	56.8	17.5	10.0	40.0	13.0	6.5	12.5	32.5	20.0
Blue Red	9	m	Tala II	25-May-1989	8.9	5.6	95.0	47.5	56.0	17.5	11.0	40.3	13.3	6.4	14.8	36.9	23.5
Orange	10	m	Tala II	21-May-1987	4.9	4.9	95.8	46.8	55.7	17.5	10.7	41.6	13.6	6.6	13.5	35.0	19.4
Orange	10	m	Tala I	23-May-1989	6.9	5.6	97.0	45.0	56.0	18.4	9.7	41.1	13.5	6.6	16.1	33.5	21.5

Pink	26	m	Tala II	06-Oct-1997	11.3	5.5	83.2	52.5	33.2	12.7	6.9	12.5	36.8	19.0
Pink	26	m	Tala II	14-Nov-1998	12.4	5.3	55.4	55.4		13.1	6.3	13.3	34.2	20.2
Pink	26	m	Tala II	22-May-2000	13.9	5.5								
Pink	26	m	Tala II	19-Nov-2000	14.4	5.5								
Pink	26	m	Tala II	12-Dec-2002	16.5	5.4								
Pink	26	m	Tala II	03-Jun-2003	17.0	5.6								
Yellow male	27	m	Tala II	22-Mar-1991	7.8	5.5	92.0	56.0	18.2	35.0	6.2	16.0	34.0	18.0
Yellow male	27	m	Tala II	06-Jan-1993	9.6	5.6								
Yellow male	27	m	Tala II	04-Jun-1994	11.0	5.6	95.0	53.0	18.1	38.0	5.0	14.2	34.8	20.5
Blue Purple	29	m	Tala III	03-Jun-1994	2.1	3.9	88.9	44.0	13.6	35.0	5.5	12.2	25.0	17.5
Blue Purple	29	m	Tala III	22-Dec-1995	3.6	4.7	93.0	43.0	55.5	38.0	5.0	13.5	25.4	
Blue Purple	29	m	Tala III	18-Nov-1998	6.5	4.9	88.3	43.1				13.0	38.2	20.0
Blue Purple	29	m	Tala III	29-Nov-2000	8.6	5.3	94.4	43.9	18.3	33.4	6.6	14.1	29.3	18.3
Blue Purple	29	m	Tala III	11-Dec-2002	10.6	5.3								
Blue Purple	29	m	Tala III	27-May-2003	11.1	5.5								
Blue Purple	29	m	Tala III	14-Sep-2004	12.4	5.5								
Blue Purple	29	m	Tala III	23-Nov-2006	14.6	5.2	93.6	41.4	58.0	36.0	4.0	12.2		20.5
Brown	31	m	Tala I	22-Dec-1995	2.5	4.6	95.0	47.0	8.5					
Brown	31	m	Tala I	14-Nov-1998	5.4	5.2	91.1	44.0	10.2	35.2	6.3		31.1	20.3
Brown	31	m	Tala I	11-May-2000	6.9	5.0								
Purple Green	35	f	Tala II	21-Dec-1995	0.5	1.3	67.0	32.7	39.0	24.6	3.8	10.3	16.5	11.2
Purple Green	35	f	Tala II	06-Oct-1997	2.3	4.4	93.5	44.5	13.6	32.2	5.1	10.3	31.3	18.1
Purple Green	35	f	Tala II	14-Nov-1998	3.4	4.7	86.0	45.2	52.2	34.3	5.1	12.4	31.2	
Green Orange	36	f	Tala III	22-Dec-1995	5.5	5.6	92.8	43.8	17.4	35.2	7.0	15.2	31.1	17.5
Green Orange	36	f	Tala I	12-Dec-2002	12.5	6.0								
Green Orange	36	f	Tala I	27-May-2003	12.9	6.5								
Green Orange	36	f	Tala I	13-Sep-2004	14.2	5.6	93.0	43.0	17.0	39.0	5.5	11.0		21.5
Green Orange	36	f	Tala I	29-Oct-2005	15.4	5.8								
Green Orange	36	f	Tala I	23-Nov-2006	16.4	6.0	85.4	41.3	18.0	39.0	5.9	12.7	35.0	20.8
Green Orange	36	f	Tala I	08-Jun-2007	17.0	5.7	39.7	52.3	9.1	38.7	5.2	11.5	30.0	20.0
Green Orange	36	f	Tala I	13-Jun-2008	18.0	6.0	38.4		9.4		5.9		38.5	
Green Silver	41	f	Tala IV	14-Dec-2002	23.5	5.5	48.0		10.6		6.9			
Green Silver	41	f	Tala IV	28-May-2003	24.0	5.6								
Green Silver	41	f	Tala IV	12-Sep-2004	25.2									
Green Silver	41	f	Tala IV	31-Oct-2005	26.4									
Rose Blue	92	f	Tala IV	02-Jul-1996	10.0	6.3	95.1	45.6	18.2	11.4	6.7	13.9	35.5	19.6
Blue Green	42	f	Tala IV	02-Jul-1996	5.0	4.7	93.5	39.3	17.4	36.2		13.3	26.6	17.5
Blue Green	42	f	Tala IV	28-Nov-2000	9.5	5.2								
Blue Green	42	f	Tala IV	05-Jun-2001	10.0	5.7	93.4	42.4	17.5	36.8		12.9	32.1	20.9
Blue Green	42	f	Tala IV	14-Dec-2002	11.5	5.4	41.9							
Blue Green	42	f	Tala IV	28-May-2003	12.0									
Blue Green	42	f	Tala IV	12-Sep-2004	13.2	6.1								
Blue Green	42	f	Tala IV	23-Jun-2005	14.0	5.1								
Blue Green	42	f	Tala IV	31-Oct-2005	14.4	5.4								
Blue Green	42	f	Tala IV	24-Nov-2006	15.4	5.5	84.0	39.5	17.0	37.2	4.8	10.5	29.1	19.2
Blue Green	42	f	Tala IV	14-Jun-2008	17.0	5.4	40.9		9.2	32.4	5.7	14.6	35.6	18.2
Pink II	43	m	Tala IV	02-Jul-1996	5.0		90.5	45.2	17.7	9.8	7.1			
Pink II	43	m	Tala IV	23-May-2000	8.9									
Pink II	43	m	Tala IV	28-Nov-2000	9.5									
Purple male	45	m	Tala IV	23-May-2000	2.9									

Purple male	45	m	Tala IV	28-Nov-2000	3.5	4.9	41.4	17.5	9.9	37.1	6.7	10.7	17.3
Purple male	45	m	Tala IV	11-Dec-2002	5.5	5.2	42.3				5.8		
Purple male	45	m	Tala IV	28-May-2003	5.9	5.3							
Teal Silver	48	f	Tala I	06-Oct-1997	5.3	5.6	43.2	47.6		34.2	5.4	11.8	21.1
Teal Silver	50	f	Tala II	06-Jun-2001	9.0	4.6							
Turquoise	50	m	Tala II	22-May-2000	2.0	4.6							
Turquoise	50	m	Tala II	18-Nov-2000	2.4	4.8	99.0	53.5	18.2	11.1	6.4	12.9	18.8
inf BB98	51	f	Tala III	18-Nov-1998	0.5	1.1	54.2	30.5	12.3	8.0	4.4	6.0	11.0
inf GB99	52	f	Tala III	29-Nov-2000	1.5	4.5	98.3	55.5	17.8	10.1	5.8	11.6	16.5
Purple Silver	55	m	Tala I	12-Dec-2002	2.5	4.2	43.2				5.9		
Radio Silver	57	f	Tala II	12-Dec-2002	5.5	6.0	44.5				6.7		
Radio Silver	57	f	Tala II	03-Jun-2003	6.0	6.0							
Radio Silver	57	f	Tala II	15-Sep-2004	7.3	5.9							
Yellow Red	59	m	Tala IV	11-Dec-2002	1.5	3.7	41.9		8.9	8.9	6.1		
Yellow Red	59	m	Tala IV	28-May-2003	2.0	4.4	44.3		11.9	8.6	6.4		
Yellow Red	59	m	Tala IV	12-Sep-2004	3.3	4.7	83.5	59.0	16.0	9.0	4.5		
Yellow Red	59	m	Tala IV	31-Oct-2005	4.4	5.1							
Yellow Red	59	m	Tala IV	24-Nov-2006	5.5	5.3	85.0	60.5	15.8	8.4	4.7	10.6	20.2
Yellow Red	59	m	Tala IV	14-Jun-2008	7.0	5.1	44.1		8.9	8.9	6.7	31.0	31.8
Red Purple	60	m	Tala IV	11-Dec-2002	1.5	3.6	42.1		9.5	9.5	5.4		
Red Purple	60	m	Tala IV	28-May-2003	2.0	4.1	42.0		10.7	8.5	5.8		
Red Purple	60	m	Tala IV	12-Sep-2004	3.3	4.5	90.0	50.0	14.5	9.0	5.5	10.0	19.5
Red Purple	60	m	Tala IV	31-Oct-2005	4.4	4.7	96.5	56.0	16.5	6.8	4.5	12.5	15.2
Red Purple	60	m	Tala IV	24-Nov-2006	5.5	4.8	86.6	41.6	15.8	8.1	4.9	10.6	18.0
Red Purple	60	m	Tala IV	07-Jun-2007	6.0	4.8	88.7	43.1	15.6	7.0	4.9	11.4	20.5
Red Purple	60	m	Tala IV	14-Jun-2008	7.0	5.3	45.6		9.8	9.8	6.9		
inf GO02	61	f	Tala I	29-Oct-2005	2.3	4.7	86.4	41.9	16.5	8.0	4.1	10.5	18.8
Orange Blue	62	m	Tala I	12-Dec-2002	3.5	5.2	43.8		8.7		6.1		
Orange Blue	62	m	Tala I	27-May-2003	3.9	5.5							
Orange Blue	62	m	Tala I	13-Sep-2004	5.2	5.1							
Orange Blue	62	m	Tala I	29-Oct-2005	6.4	5.2							
Orange Blue	62	m	Tala I	23-Nov-2006	7.4	5.2	90.9	55.0	16.8		6.0	11.8	19.2
Orange Blue	62	m	Tala I	08-Jun-2007	8.0	5.2	89.9	59.5	16.9	8.9	4.4	11.0	18.5
Orange Blue	62	m	Tala I	13-Jun-2008	9.0	5.0	43.4		10.7	10.7	6.0	37.4	
Blue Silver	63	f	Tala II	12-Dec-2002	0.5	1.6	33.5		7.1	7.1	4.4		
Blue Silver	63	f	Tala II	03-Jun-2003	0.9	3.2	42.7		8.3	8.3	5.8		
Blue Silver	63	f	Tala II	15-Sep-2004	2.2	4.4							
Blue Silver	63	f	Tala II	23-Nov-2006	4.4	5.4	88.1	54.0	18.5	8.6	3.7	10.9	19.8
Red Green	64	f	Tala III	11-Dec-2002	0.4	1.5	33.0		7.0	7.0	5.4		
Red Green	64	f	Tala III	24-May-2003	0.9	3.3	45.0		11.2	8.1	6.0		
Red Green	64	f	Tala III	14-Sep-2004	2.2	4.7	86.0	55.1	15.4	7.9	5.2	11.1	18.5
Red Green	64	f	Tala III	04-Nov-2005	3.3	4.7	97.9	46.4	14.6	6.6	4.5	10.5	19.8
Red Green	64	f	Tala III	23-Nov-2006	4.4	5.2	90.8	61.0		6.9	4.2	10.5	19.5
Pink Orange	65	f	Tala IV	14-Dec-2002	0.5	1.3	31.7		7.9	7.9	5.4		
Pink Orange	65	f	Tala IV	28-May-2003	0.9	3.2	44.5		11.0		5.1		
Pink Orange	65	f	Tala IV	12-Sep-2004	2.2	4.1	83.5	53.0	16.0	7.5	5.0	13.0	17.0
Pink Orange	65	f	Tala IV	31-Oct-2005	3.4	4.5	86.7	42.5	16.2	8.5	4.8	11.1	16.8
Purple Purple	66	m	Tala IV	14-Dec-2002	0.4	1.4	33.0		7.8	7.8	4.6		
Purple Purple	66	m	Tala IV	28-May-2003	0.9	3.2	40.1		10.6	7.9	5.6		
Purple Purple	66	m	Tala IV	12-Sep-2004	2.2	4.1	82.5	41.0	15.0	7.0	5.0	9.5	18.0

Purple Purple	66	m	Tala IV	31-Oct-2005	3.3	4.5	82.2	42.1	54.9	17.4	8.1	37.1	10.4	4.1	10.5	29.9	18.5
Purple Purple	66	m	Tala IV	24-Nov-2006	4.4	5.0	87.3	44.1	54.4	15.2	7.4	34.0	13.0	4.4	11.9	29.0	18.5
Purple Purple	66	m	Tala IV	07-Jun-2007	4.9	4.9	78.0	39.0	52.0	15.0	8.0	37.0	11.5	4.5	9.0	29.0	17.0
Br-NT	69	f	Tala I	13-Sep-2004	1.2	3.4	82.3	43.9	60.0	17.8	8.3	35.5	11.2	3.7	13.2	36.5	22.5
Orange Red	71	m	Tala II	15-Sep-2004	6.3	6.0											
Orange Red	71	m	Tala II	23-Jun-2005	7.0	5.9											
Orange Red	71	m	Tala II	29-Oct-2005	7.4	5.9											
Orange Red	71	m	Tala II	23-Nov-2006	8.4	5.9	94.0	45.0				32.5		4.2			
Purple Orange	72	m	Tala II	15-Sep-2004	4.3	4.8	84.5	41.0	57.6	17.1	8.1	40.7	11.7	5.8	12.9	30.8	20.0
inf BB04	73	m	Tala III	14-Sep-2004	0.2	0.7											
inf BB04	73	m	Tala III	04-Nov-2005	1.4	3.1	84.3	40.8	51.2	16.2	7.0	38.2	11.1	4.5	9.1	29.5	15.8
inf GS04	74	f	Tala IV	12-Sep-2004	0.3	0.6											
Tan Red	75	f	Tala IV	12-Sep-2004	0.3	0.8											
Tan Red	75	f	Tala IV	31-Oct-2005	1.4	3.7	82.0	41.5	52.5	15.4	6.5	36.7	11.9	4.4	9.7	30.5	17.5
Tan Red	75	f	Tala IV	24-Nov-2006	2.5	4.6	87.5	42.5	55.1	15.5	7.4	40.4	13.5	4.8	9.9	31.6	17.5
Tan Red	75	f	Tala IV	23-Jun-2008	4.1	5.2	44.8	44.8			10.7			6.4		29.8	
inf BS06	77	m	Tala II	23-Nov-2006	0.4	1.0	50.6	24.2	41.9	10.5	5.5	23.8	8.2	3.0	6.0	17.0	9.2
inf BB06	78	f	Tala III	23-Nov-2006	0.4	1.0	56.5	27.8	41.0	12.9	6.2	26.2	9.0	4.2	6.8	19.2	9.9
Inf BG06	80	m	Tala IV	24-Nov-2006	0.5	1.4	53.8	27.8	39.1	13.7	6.2	26.2	8.2	3.1	6.5	18.2	12.7
infGG08	116	m	Tala I	13-Jun-2008	0.0	0.2											
infBG08	117	m	Tala IV	14-Jun-2008	0.0	0.3											
infTR08	118	f	Tala IV	23-Jun-2008	0.0	0.1											

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