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RESEARCH ARTICLE

Morphometrics of Wild Black-and-White Ruffed Lemurs [*Varecia variegata*; Kerr, 1792]

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This study presents the first detailed morphometric measurements of wild caught black-and-white ruffed lemurs (*Varecia variegata*) from the eastern rainforests of Madagascar and aims to quantify the morphological variation present throughout their recognized range. One hundred and forty-four adult and juvenile individuals from 15 sites were sampled for 20 cranial, dental and postcranial morphometric and body mass measurements. Data were collected from an equal number of male and female individuals sampled across seasons over a 7-year period (1999–2002, 2004–2006). Results indicate that adult body mass and morphometric measurements varied between sexes across sites; however, the only significant intersexual difference found was that females possessed, on average, longer tails than males. Contrary to previous studies, significant seasonal variation could not be detected in either male or female body mass or testicular volume (i.e., breeding vs. nonbreeding, food-scarce vs. food-abundant seasons). Measurements did, however, vary significantly by site and subspecies, though clinal variation could not explain these differences. The introduced population from Nosy Mangabe exhibited significantly lower body mass and overall body length than all other populations; however, this distinction may not have been attributable to natural variation, and may have instead resulted from the ecologically restrictive habitat (e.g., unusually high lemur population densities, limited food resources, ecological isolation) of this introduced population. Finally, although fore-to-hindlimb, brachium-to-thigh and hindlimb indices were comparable to previous values, forelimb indices calculated here deviate significantly from previous reports, placing *V. variegata* within the upper range of lemurid taxa. It is currently unknown whether this is an artifact of sampling methods (i.e., live vs. skeletal specimens) or whether this is an avenue that warrants further investigation. Am. J. Primatol. 70:1–14, 2008.

Key words: *Varecia variegata*; morphometric variation; skeletal indices; body mass

INTRODUCTION

The black-and-white ruffed lemur (*Varecia variegata*) is a critically endangered primate species (IUCN Red List, CRA4cd) endemic only to the lowland and mid-altitude rainforests of eastern Madagascar [Mittermeier et al., 1994, 2006]. Within this range, *V. variegata* populations are patchily distributed and densities are often low [Mittermeier et al., 2006; Vasey, 2003]. Forest fragmentation and human encroachment threaten the taxon as degraded and damaged forests seem unable to support large-bodied frugivores such as *V. variegata* [e.g., Ratsimbazafy, 2002]. The species is further impacted by hunting pressures, given its reputation as one of the tastiest bush meat species [Golden, 2005]. Its patchy distribution makes it difficult to accurately estimate population densities [Irwin et al., 2005]; however, there are suggested to be fewer than 10,000 *V. variegata* individuals remaining in the wild [Mittermeier et al., 1994].

During the past 15 years, long-term field research has focused primarily on the behavioral ecology of *V. variegata* [e.g., Balko, 1998; Morland, 1991; Ratsimbazafy, 2002]. Although much effort has been dedicated to *in situ* studies aimed at understanding the behavioral plasticity of the

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species, there has been comparatively little effort made to quantify the morphological variation present both within and between these populations. Long-term projects have yielded important body mass data from studies of wild individuals [e.g., Balko, 1998; Morland, 1991; Ratsimbazafy, 2002], whereas additional body weights and limb proportions have been derived from captive specimens [e.g., Kappeler, 1990] and museum collections [e.g., Jungers, 1979, 1985; Tattersall, 1982]. However, despite these efforts, few morphometric data are currently available from wild *V. variegata* populations.

Here, we present the first detailed morphometric measurements of 144 free-ranging black-and-white ruffed lemurs from 15 regions throughout the known *V. variegata* range. The goal of this analysis is to compare body mass and cranial, dental and postcranial morphometric measurements among populations of black-and-white ruffed lemurs from eastern Madagascar to better understand both the intra- and interpopulation variability of these traits, as well as to assess the influences of geography, seasonality and endemicity on the variation expressed among these populations.

METHODS

Study Subjects and Sites

Morphometric measurements were collected on 144 wild black-and-white ruffed lemurs of both age (i.e., juvenile, adult) and sex classes (i.e., male, female) from 15 sites throughout the eastern rainforests of Madagascar (Table I; Fig. 1). Efforts were made to sample equally across subspecies (*V. v. subcincta, V. v. variegata*, *V. v. editorum*); however, a majority of samples comprise the subspecies *V. v. editorum* ($n = 10$ sites), which is currently thought to have the broadest range (Louis, personal communication). Captures were conducted year-round over a 7-year period (1999–2002, 2004–2006).

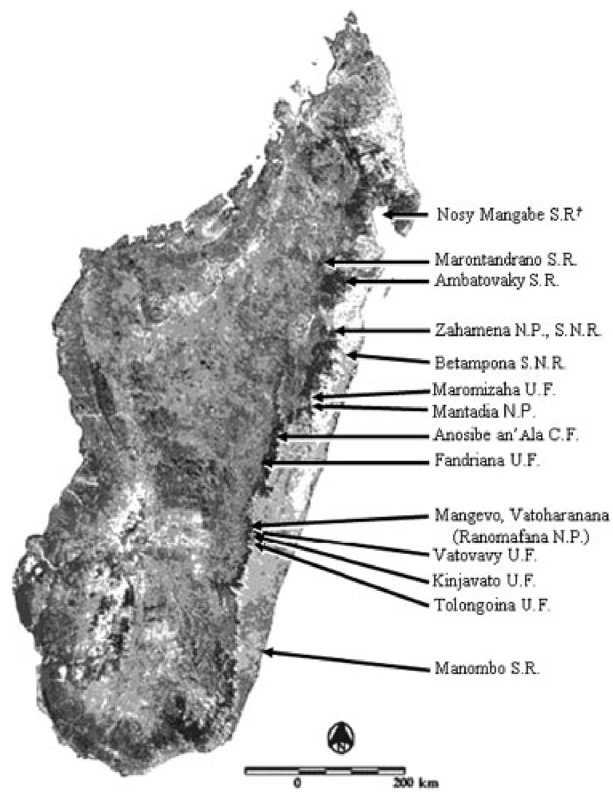

Fig. 1. Aerial map of Madagascar indicating *Varecia variegata* sampling locations ($n = 15$) throughout their range, i.e., the eastern rainforests of Madagascar. U.F., unclassified forest; C.F., classified forest; S.R., special reserve; S.N.R., strict nature reserve; N.P., national park; †, introduced population.

TABLE I. Sample Collection Sites, Locations, Number of Individuals and Subspecies Sampled From Each Site

Site name	Site code	GPS location		Sample name	*n*	Subspecies
Ambatovaky S.R.	A	S16°49′01.4″	E049°16′24.5″	VAK	6 (3)	*V. v. variegata*
Anosibe an'ala C.F.	B	S19°13′76.8″	E048°16′86.0″	ANOSIB	4 (2)	*V. v. editorum*
Betampona S.N.R.	C	S17°55′87.1″	E049°12′20.0″	BET	9 (4)	*V. v. variegata*
Fandriana U.F.	D	S20°23′40.2″	E047°38′09.8″	FAN	10 (9)	*V. v. editorum*
Kianjavato U.F.	E	S21°21′43.4″	E047°50′54.3″	KIAN	8 (7)	*V. v. editorum*
Mangevo (Ranomafana N.P.)	F	S21°22′22.8″	E047°26′59.1″	RANO	31 (22)	*V. v. editorum*
Manombo S.R.	G	S23°01′69.5″	E047°43′84.1″	L, M, MAB	8 (7)	*V. v. editorum*
Mantadia N.P.	H	S18°48′49.0″	E048°25′47.8″	TAD, VVE	11 (7)	*V. v. editorum*
Maromizaha U.F.	I	S18°58′30.2″	E048°27′43.5″	MIZA	2 (-)	*V. v. editorum*
Marotandrano S.R.	J	S16°16′82.5″	E048°49′08.3″	TANDRA, TAND	9 (6)	*V. v. subcincta*
Nosy Mangabe S.R.[a]	K	S15°30.11.7″	E049°45′30.5″	NOSY	5 (4)	*V. v. subcincta*
Tolongoina U.F.	L	S16°51′74.1″	E049°16′14.9″	TOL	5 (3)	*V. v. editorum*
Vatoharanana (Ranomafana N.P.)	M	S21°14′90.0″	E047°25′26.6″	RANO	18 (18)	*V. v. editorum*
Vatovavy U.F.	N	S21°24′20.0″	E047°56′26.0″	VVAT	7 (5)	*V. v. editorum*
Zahamena N.P., S.N.R.	O	S17°29′21.0″	E048°44′50.0″	ZAH, ZAHA	10 (6)	*V. v. variegata*
Total sample					144 (103)	

U.F., unclassified forest; C.F., classified forest; S.R., special reserve; S.N.R., strict nature reserve; N.P., national park. *n*, total sample including juveniles; ( ), number of adults.
[a]Introduced population.

Sampling sites were chosen based on a combination of their geographic location, lemur densities (from published survey results and local reports), presence of long-term research sites, and protection status as part of the larger Madagascar Biodiversity and Biogeography Project (MBP-HDZ). Efforts were made to sample equally among habitat types (e.g., low-land to mid-altitude; protected vs. unprotected forests) as well as throughout various geographical regions (e.g., northern vs. southern subspecies' boundaries).

Capture and Measurement Procedures

Capture Procedures

Subjects were immobilized via remote injection techniques following Glander and colleagues [Glander, 1993; Glander et al., 1992]. A CO_2-powered DANINJECT (Brrkop, Denmark) Model JM rifle was used to propel 9 mm (3/8″) Pneu-darts™ (Williamsport, PA) loaded with 10 mg/kg estimated body weight of Telazol® (Fort Dodge, IA). Location at the time of capture was recorded using a global positioning system, and animals were transported back to the base camp where complete morphometric data were collected. Home Again® (Home Again Pet Recovery Service, Eastern Syracuse, NY) microchips were placed subcutaneously between the scapulae of each lemur to field catalog all individuals for future identification. During sample collection, study subjects were monitored for heart rate, respiratory rate and body temperature and were given a subcutaneous balanced electrolyte solution (LRS, Lactate Ringer Solution). Animals were allowed to recover in breathable cloth bags (approximately 3 hr), and were subsequently released at the site of capture.

These protocols were approved by and are in compliance with Stony Brook University and Henry Doorly Zoo Institutional Animal Care and Use Committee (IACUC) standards (SBU IACUC 2006-1446). Furthermore, all protocols have been approved and research permits granted by the Tripartite Committee of the Malagasy government (ANGAP, DEF, ONE), as well as the US Fish and Wildlife Service. No animals were injured as a result of sampling procedures.

Data collection

All measurements were collected from the right side with the animal in left lateral recumbency. Morphometric data were collected to the nearest 1.0 mm with a tape measure following measurements described by Smith and Jungers [1997]; however, because measurements of living animals include overlying soft tissue, measurements are of body segments rather than of bones. All measurements were made between easily palpable bony landmarks, as described by Turnquist and Kessler [1989]. Body weights were measured by suspending animals in cloth bags from a 10 kg Pesola® scale and recording weight to the nearest 1.0 g. Testicular measurements and canine length were recorded to the nearest 0.01 mm with vernier calipers (see Appendix A for a description of measurements). To control for inter-observer reliability, all measurements were collected under similar field conditions by E. E. L. and two Malagasy doctoral students (John Zaonarivelo and Jean Freddy Ranaivoarisoa). Students were thoroughly trained by E. E. L. in data collection protocol before their involvement and all measurements were regularly checked for consistency amongst observers while in the field. Genetic and biomedical data were also collected during immobilizations and are presented elsewhere [e.g., Baden et al., 2006a,b; Junge & Louis, 2005; Louis et al., 2005].

Age assignment

In 106 of the 144 cases, age class was estimated at the time of capture ($n = 21$ juveniles; $n = 85$ adults) using previously established age indicators, including body mass, testicular development (i.e., descended or undescended testes) and dental characteristics (e.g., eruption patterns, staining and wear). In some cases, however, age assignments were unavailable (e.g., field notes indicate ''age uncertain''). Individuals not aged at the time of capture ($n = 38$) were assigned age-classes *post hoc*. First, unaged males with undescended testes were immediately assigned ''juvenile'' status ($n = 4$ cases) in *post hoc* analyses. Subsequently, all remaining individuals of undetermined age were considered ''adult'' if they fell within two standard deviations of the mean body mass for known adults of the same sex (calculated using a pooled data set across all sites and seasons), a criterion used to encompass 95% of the variation within a normally distributed population and at least 75% of the variation in any data set (Chebychev's inequality) [Sokal & Rohlf, 1995]. Following all *post hoc* analyses, an additional 20 juveniles and 18 adults were identified, resulting in an overall sample size of $n = 41$ juveniles and $n = 103$ adults. It should be noted that six of the 144 subjects (three adult females, two adult males and one juvenile female) were resampled during two consecutive years (2005, 2006). These measurements were collected during similar seasons (i.e., breeding season; food-scarce) and the morphometrics differed only marginally between years; thus, means were generated for each of these individuals before performing statistical analyses. All subsequent analyses are based on data from the 103 adult individuals.

Statistical Analysis

All distributions were tested for normality and nine of the 20 measurements collected were found to be heteroschedastic. Furthermore, it was often the case that unequal samples were available for each sex class within a given site and many sites were limited in their overall sample size. Therefore, nonparametric statistics including Kruskall–Wallis and Mann–Whitney *U* tests were used to test for significant differences within and between populations. For all statistical tests, significance levels were set a priori at 0.05.

It should be further noted that one introduced population was sampled during this study (Nosy Mangabe; Table I). Nosy Mangabe is a 520 ha area island located off the northeastern coast of Madagascar in the Bay of Antongil (Fig. 1). It is the smallest protected area in Madagascar and is the site of many faunal translocation projects [e.g., four of 11 mammal species are not endemic to the island; Morland, 1991]. Adult *V. variegata* individuals in this population were described in field notes as exhibiting poor body condition (i.e., unusually low body mass, high ectoparasite load and poor pelage condition), and fell outside the normal range of variation when compared with all other populations included in this study. Therefore, Nosy Mangabe individuals were excluded from descriptive statistics and were not used in comparative statistical analyses with the exception of comparisons between endemic and introduced populations.

RESULTS

The representative adult data set (Table I) included a total of 51 adult females and 52 adult males. Excluding the four adult individuals from the Nosy Mangabe site, summary adult morphometrics ($n = 99$; 48 females, 51 males) are presented in Table II, as well as significance values when applicable. Individual body mass and morphometric measurements for all individuals ($n = 144$) and testicular measurements for adult males ($n = 42$) sampled during this study can be found in Appendices A, B and C.

Adult body mass ranged from 2.5 to 4.8 kg, with adult females weighing slightly more on average than adult males, particularly during breeding and gestation seasons, though this difference was not significant ($z = -0.47$, $P = 0.64$). There were no significant differences between male and female morphometric measurements except that females had significantly longer tails ($z = -2.10$, $P = 0.04$).

Contrary to Morland's [1991] findings, morphological data presented here indicate little seasonal variation in body mass measurements in either males ($n = 51$; $z = -0.43$, $P = 0.67$) or females ($n = 48$; $z = -1.52$, $P = 0.13$). The female reproductive state (e.g., pregnant, lactating) was not explicitly noted at the time of capture; however, female body masses during estimated gestation and birth seasons (September–November) did not differ significantly from those observed during other times of the year ($z = -1.52$, $P = 0.13$). Testicular volume was bilaterally symmetrical among males ($z = -0.52$, $P = 0.60$) and there was no significant seasonal variation detected in male testes size during breeding (June–August) vs. nonbreeding seasons ($z = -1.07$, $P = 0.28$).

TABLE II. Summary Morphometrics for Adult Individuals of *V. variegata* (Mean ± SD), and Results of Male–Female Comparison (Mann–Whitney *U*)

	n	Females	*n*	Males	*z*	*P*
Body mass (kg)	47	3.7 ± 0.5	51	3.6 ± 0.3	−0.47	0.64
Upper canine (mm)	46	11.2 ± 1.9	47	11.6 ± 1.4	−0.95	0.34
Lower second premolar (mm)	46	6.3 ± 1.1	46	6.4 ± 1.1	−0.82	0.41
Headcrown (cm)	43	12.2 ± 1.3	44	12.1 ± 1.0	−0.15	0.88
Body (cm)	43	44.8 ± 3.2	45	44.9 ± 3.6	−0.28	0.78
Tail (cm)	47	61.3 ± 3.8	50	59.7 ± 4.3	−2.10	0.04*
Brachium (cm)	44	11.0 ± 1.9	46	10.9 ± 1.6	−0.04	0.97
Antebrachium (cm)	47	12.5 ± 0.8	49	12.6 ± 1.0	−1.16	0.25
Hand (cm)	47	9.4 ± 1.0	51	9.5 ± 0.8	−0.46	0.65
Pollex (cm)	42	4.2 ± 0.9	44	4.3 ± 0.8	−0.47	0.64
Longest digit, hand (cm)	38	4.3 ± 0.5	41	4.6 ± 1.1	−0.42	0.68
Thigh (cm)	46	15.6 ± 1.4	49	15.7 ± 1.2	−0.18	0.86
Leg (cm)	47	14.3 ± 1.5	50	14.3 ± 1.5	−0.22	0.83
Foot (cm)	47	12.6 ± 0.9	49	12.6 ± 1.1	−0.30	0.77
Hallux (cm)	41	5.3 ± 1.3	44	5.4 ± 1.8	−0.09	0.93
Longest digit, foot (cm)	39	4.4 ± 1.5	41	4.4 ± 1.6	−0.66	0.51
Left testicle, length (mm)			43	22.1 ± 4.5		
Left testicle, width (mm)			43	13.7 ± 4.0		
Right testicle, length (mm)			43	21.4 ± 3.9		
Right testicle, width (mm)			43	13.3 ± 3.6		
Left testicular volume (mm^3)			43	33,551.2 ± 42,270.3		
Right testicular volume (mm^3)			43	27,526.0 ± 29,495.3		

*$P < 0.05$. See Appendix A for definitions.

TABLE III. Appendicular Postcranial Indices (Modified From Jungers, 1985)

	Fore-to-hindlimb Index[a]			Brachium-to-thigh Index[b]			Forelimb Index[c]			Hindlimb Index[d]		
Sex	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD
Males	44	78.8	6.93	46	69.90	10.93	45	118.4	13.87	49	91.7	9.64
Females	44	78.8	6.27	46	67.50	18.49	44	116.6	15.93	46	91.7	10.54
Both	88	78.8	6.57	92	68.70	15.15	89	117.5	14.87	95	91.7	10.03
Both[e]	17	72.2	2.44	17	70.60	1.90	17	96.9	1.80	17	92.4	1.80

[a]Modified from Intermembral Index; brachium+antebrachium/thigh+leg*100.
[b]Modified from Humerofemoral Index; brachium/thigh*100.
[c]Modified from Brachial Index; antebrachium/brachium*100.
[d]Modified from Crural Index; leg/thigh*100.
[e]Jungers (1985).

Seven of the 16 non-testicular measurements did, however, differ significantly across sites, though clinal variation could not be used to explain these differences (i.e., measurements did not vary predictably with geographic location). Measurements that differed significantly included body mass ($\chi^2 = 35.85$, $P < 0.001$), tail ($\chi^2 = 39.17$, $P < 0.001$), brachium ($\chi^2 = 28.65$, $P < 0.004$), pollex ($\chi^2 = 44.00$, $P < 0.001$), hallux ($\chi^2 = 42.62$, $P < 0.001$), longest digit on the hand ($\chi^2 = 31.73$, $P < 0.002$) and longest digit on the foot ($\chi^2 = 23.40$, $P = 0.03$). Four of these measurements also varied significantly between the three currently recognized subspecies (*V. v. subcincta, V. v. variegata, V. v. editorum*; body mass, $\chi^2 = 7.94$, $P = 0.02$; tail, $\chi^2 = 6.51$, $P = 0.04$; pollex, $\chi^2 = 13.47$, $P = 0.001$; longest digit on the hand, $\chi^2 = 6.98$, $P = 0.03$), though again, no pattern of clinal variation was evident. There was a north-to-south trend toward increasing body mass and tail length, though these differences were not significant.

Compared with endemic populations, the introduced population from Nosy Mangabe is significantly smaller than endemic populations in six of the 16 non-testicular measurements. The most notable of these are body mass ($z = -3.36$, $P = 0.001$) and body length ($z = -2.38$, $P = 0.01$), but significant differences were also found in the length of the thigh ($z = -2.83$, $P = 0.005$), longest digit on the hand ($z = -2.30$, $P = 0.02$), hand ($z = -3.05$, $P = 0.002$) and foot ($z = -2.22$, $P = 0.03$). Furthermore, when compared with the Marontandrano population, the only other *V. v. subcincta* population sampled in this study, the two populations differed significantly in 5 of the 16 nontesticular measurements, most notably in body mass ($z = -2.57$, $P = 0.01$), body length ($z = -2.56$, $P = 0.01$) and hand length ($z = -2.57$, $P = 0.01$).

Finally, although skeletal elements (e.g., those necessary for calculating standard skeletal indices) cannot be accurately measured in live animals because of overlying soft tissue, Kohn et al. [2000] have demonstrated that there is a significant correlation between body size in live specimens and their skeletal dimensions. Therefore, using morphometrics from this study, we generated "standard body indices" modified from Jungers [1985] and compared these with standard skeletal indices reported previously [Jungers, 1985]. Standard body indices are presented in Table III. Fore-to-hindlimb, brachium-to-thigh and hindlimb indices are comparable with previously reported values derived from smaller samples of museum specimens [Jungers 1979, 1985]. However, forelimb indices from this study ($n = 89$, mean: 117.5) were much higher than brachial indices previously described from this species [$n = 14$, mean: 90.3, Jungers, 1979; $n = 17$, mean: 96.9, Jungers, 1985].

DISCUSSION

Black-and-white ruffed lemurs are among the largest extant Malagasy primates [Fleagle, 1999; Mittermeier et al., 1994, 2006] and are the largest living members of the Lemuridae [Kappeler, 1990; Vasey, 2003]. However, detailed morphometric data are limited, especially from wild populations. Body mass data are available from very few long-term field studies [e.g., Balko, 1998; Morland, 1991; Ratsimbazafy, 2002], and morphometric measurements are even scarcer. Furthermore, measurements are limited in both their temporal and seasonal distribution. Small sample sizes across studies may have led to varied results regarding the morphological differences present within and between populations.

Balko [1998] provided field measurements for adult *V. variegata* from Ranomafana National Park (male, $n = 8$: mean body mass, 3.7 kg; range, 3.5–4.1 kg; mean body length, 493 mm; range, 436–565 mm; female, $n = 3$: mean body mass, 3.7 kg; range, 3.4–4.0 kg; mean body length, 516 mm; range, 469–570 mm). These body mass measurements are within the normal range of variation documented across populations in this study, but differ in that Balko [1998] characterizes males as consistently exhibiting heavier body mass than females. Although significant sexual dimorphism was not detected in the data presented here, there was a tendency for females to exhibit higher mean body mass than males, a result that runs counter to Balko's [1998] work. Instead, results from this study support Morland's [1991] observation that *V. variegata* is essentially a monomorphic species. In fact, the only significant intersexual difference found in this study was that females possessed, on average, longer tails than males, a finding that runs counter to other documented primate populations [males > females: Covert et al., 2008; males = females: Fooden, 1997; Fooden & Albrecht, 1999].

Unsurprisingly, wild adult *V. variegata* weighed less, on average, than captive animals, though these differences were not significant [Terranova & Coffman, 1997]. Body mass estimates ranged from 3.0 to 4.8 kg in captive and semi-free ranging adults [e.g., Pereira et al., 1987; Tattersall, 1982; Terranova & Coffman, 1997] and similar to wild *V. variegata*, captive animals showed no significant differences between mean female (3.5 kg, $n = 35$) and male (3.5 kg, $n = 45$) body masses [Kappeler, 1990]. Coupled with biomedical health assessments presented elsewhere [Junge & Louis, 2002, 2005], body mass measurements from wild populations can help to re-evaluate captive management and husbandry practices by contributing to the lemur reference database.

Though data presented here support that *V. variegata* are sexually monomorphic [e.g., Mittermeier et al., 2006; Vasey, 2003], data from this study are incongruent with previous claims of notable seasonal variation in body mass [e.g., Morland, 1991]. This study did not detect significant body weight seasonality among either sex (i.e., breeding vs. nonbreeding, food-scarce vs. food-abundant seasons); however, this may be, in part, because of assumptions of predictable breeding seasons. Although previous studies have described *V. variegata* breeding seasons as occurring during Madagascar's "cold, dry" period [e.g., Balko, 1998; Morland, 1991; Ratsimbazafy, 2002], seasonal shifts in mating have also been observed (Baden, unpublished data), a factor that may mask body weight seasonality when unaccounted for.

Similarly, testicular volumes presented here do not differ significantly between mating and nonmating seasons, a surprising result given the taxon's polygamous mating strategy and highly synchronous breeding season. As male–male aggression over receptive females has not been reported in *V. variegata* [see Morland, 1993; *V. rubra*: Vasey, 2007], one might predict that males have instead adopted indirect mating strategies by developing behavioral, morphological and/or physiological adaptations (e.g., developing large testes for the production of more sperm), as has been suggested in some *Eulemur* species [Johnson et al., 2005] and the New World muriquis [e.g., Strier, 1997]. Although results from this study do not suggest significant seasonal variation in testes size, testes volumes do fall within the range of other polygamous lemur taxa [Johnson et al., 2005; Kappeler, 1997], suggesting that sperm competition may still be among the primary *V. variegata* reproductive strategies. However, based on previous behavioral studies [Morland, 1993; Vasey, 2007] it seems likely that female choice may also play an important role in the mating strategies of this species, a possibility that warrants further investigation.

Aside from data presented here, only one other study has quantified the morphological variation expressed in the introduced population found in Nosy Mangabe. Morland [1991] reported adult body mass measurements (mean body mass, $n = 9$, 3.1 kg) and estimated a range of 2.6 and 3.7 kg from this site. Although the mean adult body mass provided by Morland [1991] was more than one standard deviation smaller than the overall species mean calculated across endemic populations in this study (Table II), it was consistent with our current findings from the Nosy Mangabe population. Furthermore, both studies are in agreement that females typically weigh more than males, although differences were not significant in either study. These morphological differences, particularly in body mass, are thought to be related to various ecological constraints associated with the island of Nosy Mangabe, including unusually high ruffed lemur population densities relative to other eastern rainforest sites [Nosy Mangabe: 29–43 ind/km^2, Morland, 1991; other sites: 0.4–23 ind/km^2; e.g., Baden et al., 2006a; Britt et al., 1999; Welch & Katz, 1992; but see Balko, 1992; Vasey, 1997], restricted emigration opportunities and, hence, heightened intra- and interspecific resource competition [with *Eulemur albifrons* and *Daubentonia madagascariensis*, Morland, 1991]. That the Nosy Mangabe population differs significantly even from its neighboring Marontandrano *V. v. subcincta* population, as demonstrated in this study, lends further support to the ecological constraint hypothesis, as Nosy Mangabe's population exhibits morphological dissimilarities such as smaller body size and body mass, both of which could be explained by their restricted ecologies.

When considering populations across the entire species' range, morphometric variation did not appear to be affected by geographical location (i.e., sampling site), despite the wide geographic sampling range. Although some morphometric parameters differed significantly across sites, they did not vary predictably with geographic location, suggesting that clinal variation in this taxon is unlikely. Morphologies did vary significantly between subspecies (*V. v. subcincta*, *V. v. variegata* and *V. v. editorum*) in four of the 16 non-testicular measurements collected during this study; however, subspecies status within *V. variegata* is currently debated (Mittermeier, personal communication), thus making claims of subspecific postcranial morphological variation speculative at best.

Finally, body indices generated here were compared with skeletal indices derived from previous morphological studies. Despite standard deviations that are three times (and in some cases as much as nine times) greater than those presented by Jungers [1985], fore-to-hindlimb, brachium-to-thigh and hindlimb indices are comparable to the equivalent skeletal indices. Forelimb indices, on the other hand, are much greater than the brachial indices previously described. It should be noted that past researchers have calculated such indices from isolated skeletal elements of museum specimens, whereas measurements presented here were collected from live individuals and include the soft tissue overlying the skeletal elements. Previous studies have found that morphometric discrepancies between live vs. skeletal specimens are particularly evident in the measurement of the antebrachium, as the skeletal index uses the radius, whereas live animal measurements are of the ulna as it is more reliably palpated (Turnquist, personal communication), a factor that may explain differences seen between measurements from this study and previously reported values.

In summary, sexual dimorphism is absent in *V. variegata*. Males and females shared similar mean body masses and overall morphometric body measurements. Females only differed significantly from males in that they had absolutely longer tails. Furthermore, unlike previous studies, seasonality (i.e., breeding vs. nonbreeding, food-scarce vs. food-abundant seasons) had little effect on body mass estimates of either males or females. Male testes size did not differ significantly between seasons.

Morphometric variation was not affected by geographical location (i.e., sampling site), despite the wide geographic sampling range. Although significant differences were present among some morphometric parameters, no consistent pattern could be found among sites (i.e., no clinal variation). Morphologies did, however, vary significantly among subspecies and there was a trend toward increasing body mass and lengthened tails from the northernmost to the southernmost subspecies (i.e., *V.v.s.* < *V.v.v.* < *V.v.e.*), although these differences were not significant. Animals from the introduced Nosy Mangabe site were significantly smaller (e.g., body mass, body length) than all other populations sampled. This is thought to be related to various ecological constraints, including unusually high population densities and heightened resource competition. Finally, morphological indices from this study were comparable with previous research; however, contrary to previous studies, forelimb indices calculated here place *V. variegata* within the upper range of lemurid taxa. It is currently unknown whether this is an artifact of sampling or whether this is an avenue that warrants further investigation.

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APPENDIX A

A description of morphometric measurements is given in Appendix A.

Body mass	Measured in kg of body weight
Upper canine height	Measured buccally on the midline of the tooth from the maxillary gumline to the tip of the canine crown
Lower second premolar height	Measured buccally on the midline of the tooth from the mandibular gumline to the tip of the second premolar crown
Headcrown length	Measured from the glabella to the midpoint of the superior nuchal line
Body length	Measured from the midpoint of the superior nuchal line to the base of the tail at the junction with the perianal region
Tail length	Measured dorsally from the base of the tail to the distal tip of the last caudal vertebra with tail extended straight out behind the animal
Brachium length	Measured laterally from the proximal tip of the greater tuberosity to the distal tip of the lateral humeral epicondyle
Antebrachium length	Measured laterally from the olecranon process to the tip of the ulnar styloid process
Hand length	Measured palmarly at the midline from the proximal edge of the friction pad nearest the wrist (at the radio-carpal joint) to the distal tip of the longest digit, excluding the nail
Pollex length	Measured palmarly from the first metacarpal–phalangeal joint to the distal tip of the thumb; includes proximal and distal phalanges, excluding the nail
Longest digit, hand (third digit) length	Measured palmarly from the third metacarpal–phalangeal joint to the distal tip of the third digit; includes proximal, middle and distal phalanges, excluding the nail
Thigh length	Measured laterally with the knee at a 90° angle from the tip of the greater trochanter to the most distal point on the lateral femoral condyle
Leg length	Measured laterally from the proximal edge of the lateral tibial condyle to the lateral fibular malleolus
Foot length	Measured plantarly from the proximal tip of the heel to the distal tip of the longest digit, excluding the nail
Hallux length	Measured plantarly with the hallux abducted at a 90° angle to the other digits from the first metatarsal–phalangeal joint to the distal tip of the toe; includes proximal and distal phalanges, excluding the nail
Longest digit, foot (third digit) length	Measured plantarly from the third metatarsal–phalangeal joint to the distal tip of the third digit; includes proximal, middle and distal phalanges, excluding the nail
Testicle width and length	Measured along the midline of the testes at the points of maximum width and length. Measurements collected separately for left and right testicles using vernier calipers
Testicular volume	Calculated by $4/3\ \pi\ (0.5L)(0.5W)^2$, where L = length and W = width

APPENDIX B

Cranial and postcranial morphometrics for all captured *V. variegata* individuals are given in Appendix B.

					Length (mm)		Length (cm)													
Site	Month	Year	Sample ID	Age/sex	Body mass (kg)	Upper canine	Lower *P*2	Headcrown	Body	Tail	Brachium	Antebrachium	Hand	Pollex	Longest digit, hand	Thigh	Leg	Foot	Hallux	Longest digit, foot
A	12	01	VAK15	Ad/F	3.5	10.3	4.8	12.8	39.2	57.8	11.5	13.7	9.6	4.2	4.5	16.0	15.8	12.8	6.0	4.1
A	12	01	VAK23	Ad/M	3.3	13.0	7.2	12.5	44.0	52.0	10.7	12.6	9.5	4.8	4.6	14.8	14.2	9.4	4.5	3.6
A	12	01	VAK5	Ad/M	3.2	13.2	7.3	11.3	43.0	57.0	10.5	12.8	10.0	5.3	4.5	14.7	14.0	13.0	6.0	3.5
A	12	01	VAK16	Juv/F	2.8	10.3	4.8	11.5	46.1	58.2	10.2	10.1	9.8	5.1	4.4	15.5	13.6	11.2	5.0	3.9
A	12	01	VAK22	Juv/M	2.9	7.0	3.0	11.5	39.0	11.5	7.1	12.2	9.0	4.0	4.5	14.1	13.9	9.4	5.0	3.5
A	12	01	VAK7	Juv/M	3.1	13.0	5.6	12.6	43.0	58.2	10.5	12.9	10.3	5.0	4.1	15.1	14.4	13.5	6.2	3.6
B	5	01	ANOSIB10	Ad/F	3.6	12.1	5.9	12.1	45.5	55.6	10.2	11.5	7.2	2.7	4.5	15.8	13.2	12.9	7.5	3.6
B	5	01	ANOSIB7	Ad/M	3.5	11.7	6.5	11.2	40.6	51.2	11.5	12.2	8.8	4.3	6.2	14.5	13.3	11.7	7.2	3.9
B	5	01	ANOSIB17	Juv/F	2.9	4.4	3.1	11.5	44.7	60.7	9.6	10.4	9.2	4.9	4.1	14.3	13.9	13.2	7.4	3.9
B	5	01	ANOSIB8	Juv/M	3.0	6.3	3.1	11.1	43.9	60.0	10.6	11.8	10.1	5.6	4.4	16.1	15.3	12.7	7.9	3.9
C	4	01	BET102	Ad/F	3.4	10.5	5.0	13.0	43.0	55.5	12.2	12.8	8.8	4.7	6.1	16.5	12.9	12.2	6.6	5.9
C	12	00	BET51	Ad/M	3.5	10.1	6.5	11.2	48.9	59.8	13.2	14.0	8.9	4.0	4.4	14.5	16.6	13.2	4.1	7.0
C	4	01	BET117	Ad/M	3.4	13.0	4.5	–	–	–	11.5	14.0	9.6	4.7	6.0	15.2	13.0	12.2	5.8	5.5
C	4	01	BET65	Ad/M	3.9	–	–	13.0	46.0	59.0	12.8	12.5	9.1	4.9	8.5	17.1	16.0	10.5	3.1	4.7
C	12	00	BET52	Juv/F	2.6	7.0	5.0	11.2	44.7	63.4	11.4	11.7	9.7	3.5	4.5	14.0	15.0	13.2	3.5	7.0
C	4	01	BET64	Juv/F	3.0	–	–	13.6	44.0	54.5	9.8	13.5	9.1	4.0	3.8	15.6	13.6	12.9	6.8	3.5
C	4	01	BET67	Juv/F	2.7	6.1	3.4	–	–	–	10.6	11.4	8.3	5.6	3.4	14.6	13.3	11.6	6.7	3.2
C	12	00	BET18	Juv/M	2.5	4.0	2.0	12.1	33.8	54.2	10.9	9.9	8.2	3.8	2.7	13.2	13.8	9.4	3.3	4.4
C	4	01	BET118	Juv/M	3.1	11.4	5.7	12.0	39.5	55.5	11.8	12.8	8.9	4.2	5.5	13.5	13.0	11.5	6.0	5.6
D	10	00	FAN21	Ad/F	3.3	12.7	7.0	13.8	40.0	64.6	10.4	11.9	10.6	4.2	5.3	16.3	15.2	13.9	4.1	7.2
D	10	00	FAN9	Ad/F	3.1	15.0	9.0	12.6	48.7	57.5	10.0	14.1	9.7	3.8	–	15.8	14.6	13.0	4.0	7.2
D	3	04	FAN4.10	Ad/F	3.4	9.3	6.4	11.5	49.2	63.1	11.8	14.1	9.7	5.1	4.2	15.8	13.5	13.3	5.5	3.7
D	3	04	FAN4.12	Ad/F	3.5	12.0	7.0	11.5	49.8	50.9	9.6	12.6	9.3	5.0	4.2	15.9	13.5	11.8	6.5	4.0
D	3	04	FAN4.18	Ad/F	3.4	13.4	5.5	11.5	47.5	60.6	10.5	12.6	9.2	4.5	4.2	15.2	13.5	12.4	6.2	3.7
D	6	02	FAN2.9	Ad/M	3.3	10.4	6.3	16.9	40.4	63.7	12.5	13.9	5.4	4.9	4.6	16.9	16.2	8.8	6.7	4.3
D	3	04	FAN4.15	Ad/M	4.0	14.0	7.6	11.4	47.8	61.6	10.2	11.6	9.2	4.6	4.4	16.1	13.2	13.5	6.0	4.2
D	3	04	FAN4.19	Ad/M	3.5	13.7	7.0	11.6	46.1	57.3	11.1	12.7	9.1	4.4	3.8	15.1	13.7	12.7	6.2	3.0
D	3	04	FAN4.9	Ad/M	3.2	10.6	6.2	11.5	43.8	57.1	11.6	13.2	9.3	4.6	4.2	15.2	13.3	12.7	6.6	4.1
D	3	04	FAN4.13	Juv/M	2.7	12.6	6.8	11.5	48.6	55.9	10.5	12.8	9.0	4.4	4.2	14.4	12.7	12.5	5.9	3.7
E	11	99	KIAN10	Ad/F	4.4	12.6	–	11.3	–	56.1	–	10.8	9.2	–	–	18.5	13.3	12.6	–	–
E	11	99	KIAN19	Ad/F	4.8	11.0	5.0	–	–	57.5	–	11.2	9.3	–	–	13.3	13.3	10.1	–	–
E	11	99	KIAN27	Ad/F	3.5	8.0	4.0	–	–	60.0	–	11.0	9.1	–	–	–	13.0	12.5	–	–
E	1	00	KIAN115	Ad/M	3.5	9.6	6.8	11.0	43.4	56.5	13.0	14.3	10.0	5.5	–	17.0	17.6	–	7.5	10.4
E	8	00	KIAN137	Ad/M	3.2	11.0	7.0	12.0	50.0	63.0	13.0	13.5	9.8	4.5	6.0	16.5	17.0	13.5	6.5	–
E	11	99	KIAN45	Ad/M	3.8	12.0	5.0	–	–	56.0	–	11.9	9.5	–	–	–	13.5	12.7	–	–
E	11	99	KIAN46	Ad/M	3.4	–	–	–	–	52.0	–	12.5	9.7	–	–	13.0	14.9	11.5	–	–
E	1	00	KIAN100	Juv/F	2.6	5.5	3.9	13.0	43.5	59.0	10.8	10.0	–	–	4.9	14.3	11.8	–	–	6.7
F	6	05	RANO5.11	Ad/F	3.7	11.3	6.0	12.0	48.0	63.0	11.3	13.7	10.2	3.2	4.4	14.4	15.2	13.2	3.7	4.0
F	6	05	RANO5.6	Ad/F	3.6	11.5	5.0	10.7	47.1	60.0	12.6	13.7	9.1	3.0	4.0	13.3	14.2	12.5	3.9	3.7

APPENDIX B

Continued

Site	Month	Year	Sample ID	Age/sex	Length (mm)		Length (cm)													Longest digit, foot
					Body mass (kg)	Upper canine	Lower $P2$	Headcrown	Body	Tail	Brachium	Ante-brachium	Hand	Pollex	Longest digit, hand	Thigh	Leg	Foot	Hallux	
F	8	06	RANO6.16	Ad/F	4.1	12.1	5.9	12.5	43.8	63.5	9.0	11.8	8.1	3.7	3.3	16.1	13.1	12.3	4.4	3.7
F	8	06	RANO6.17	Ad/F	3.9	10.6	6.4	12.2	37.7	61.2	9.0	11.1	9.4	3.4	3.9	16.4	13.3	12.7	4.3	3.8
F	8	06	RANO6.20	Ad/F	4.3	11.2	7.3	12.2	41.5	63.7	9.5	12.3	9.6	3.8	4.5	15.5	13.0	12.4	4.4	3.9
F	8	06	RANO6.21	Ad/F	4.3	9.1	6.7	11.9	40.8	63.7	9.3	12.6	9.5	4.0	4.1	16.0	13.5	13.0	4.1	3.9
F	8	06	RANO6.22	Ad/F	3.8	11.7	7.0	12.1	41.8	65.7	10.0	12.1	9.7	3.8	4.2	16.6	13.7	12.8	4.5	3.9
F	8	06	RANO6.24	Ad/F	3.8	12.9	6.9	12.3	41.7	61.3	9.6	11.9	9.1	3.7	4.0	16.2	13.5	12.3	4.3	3.6
F	8	06	RANO6.26	Ad/F	3.5	12.1	6.7	12.2	43.2	60.3	9.2	11.5	9.2	3.6	4.0	15.3	12.6	12.4	4.3	3.6
F	[a]	[a]	RANO5.10[a]	Ad/F	3.7	10.9	6.8	12.1	45.8	64.8	10.8	12.9	9.8	3.7	4.3	15.5	14.3	13.0	4.5	4.0
F	[a]	[a]	RANO5.5[a]	Ad/F	3.6	9.3	6.1	11.5	44.4	66.2	11.8	11.7	10.2	4.7	4.9	15.7	14.5	13.4	4.9	4.9
F	[a]	[a]	RANO5.8[a]	Ad/F	3.7	12.2	8.0	11.8	46.4	62.0	11.6	12.8	9.1	4.3	5.0	14.4	14.3	13.3	4.6	4.8
F	6	05	RANO5.3	Ad/M	3.7	10.5	6.0	11.0	47.5	62.1	13.0	13.9	8.7	3.5	4.1	13.7	14.8	13.2	3.9	3.7
F	6	05	RANO5.9	Ad/M	3.5	12.0	6.0	11.4	48.3	61.8	11.8	13.4	9.0	3.2	4.2	13.2	14.4	13.2	4.1	4.0
F	8	06	RANO5.2	Ad/M	3.5	10.8	6.9	11.8	42.9	60.8	8.8	11.8	9.5	3.6	3.8	15.3	12.8	12.7	4.2	3.7
F	8	06	RANO6.15	Ad/M	3.7	10.4	6.5	12.5	43.3	55.5	9.6	12.3	9.8	3.4	4.0	16.4	13.2	13.1	4.6	4.0
F	8	06	RANO6.18	Ad/M	3.6	13.3	7.0	12.7	43.4	66.3	9.1	12.8	9.9	4.0	4.2	15.6	13.9	13.2	4.4	4.0
F	8	06	RANO6.19	Ad/M	3.4	12.1	6.5	11.9	41.4	62.2	8.6	12.1	9.9	3.8	4.4	16.2	13.1	12.8	4.7	4.0
F	8	06	RANO6.23	Ad/M	3.5	12.4	6.1	12.5	42.8	64.3	9.7	12.6	10.4	3.6	4.5	16.5	13.4	13.5	4.8	3.7
F	8	06	RANO6.25	Ad/M	3.8	11.6	7.1	11.9	42.2	62.9	8.8	11.9	9.2	3.5	4.1	15.3	12.8	12.5	4.4	3.8
F	[a]	[a]	RANO5.12[a]	Ad/M	3.6	10.8	6.2	12.2	45.3	62.6	10.5	12.8	9.4	3.4	4.1	15.2	14.1	12.9	4.1	4.0
F	[a]	[a]	RANO5.4[a]	Ad/M	3.7	12.0	5.9	11.9	47.3	64.4	12.0	12.8	9.7	4.0	4.7	15.8	13.8	13.2	4.7	4.8
F	6	05	RANO5.7	Juv/M	2.3	6.0	4.0	11.4	45.7	55.4	10.6	12.1	9.9	3.0	3.9	12.9	13.5	12.2	3.9	3.3
F	6	05	RANO5.13	Juv/M	3.0	10.0	6.0	11.3	41.9	62.4	11.8	13.2	9.2	2.9	4.0	14.2	14.4	13.3	3.7	4.1
F	6	05	RANO5.2	Juv/M	3.1	10.0	6.0	11.5	42.7	59.7	11.7	13.2	9.4	3.7	4.1	13.7	14.0	11.5	4.1	3.6
F	8	06	RANO6.14	Juv/M	2.9	8.3	6.2	12.4	43.5	62.4	10.5	11.7	8.9	4.5	5.2	16.9	12.3	11.6	5.4	5.3
F	8	06	RANO6.34	Juv/M	3.0	8.5	6.1	11.7	41.4	62.2	8.8	11.5	9.6	3.7	4.1	15.4	13.1	12.3	4.2	3.9
F	8	06	RANO6.30	Juv/M	3.1	7.6	6.5	11.4	40.6	64.4	9.4	12.2	9.3	3.7	3.9	14.7	13.4	12.2	4.6	3.9
F	8	06	RANO6.32	Juv/M	3.1	6.3	5.7	11.8	40.2	64.5	8.9	11.7	9.6	3.6	4.0	16.2	12.7	12.8	4.6	4.1
F	8	06	RANO6.35	Juv/M	3.1	9.1	6.2	11.8	42.2	59.9	8.7	11.2	9.8	4.1	4.0	15.8	13.1	12.9	4.6	3.8
F	8	06	RANO6.37	Juv/M	3.1	4.4	6.0	11.7	40.3	62.1	8.5	11.6	9.5	3.6	4.2	15.8	13.2	12.6	4.4	3.9
G	4	04	MAB4.2	Ad/F	3.1	5.3	5.0	11.5	48.6	59.1	9.7	12.6	9.1	5.0	4.2	14.2	12.3	12.7	6.4	4.2
G	4	04	MAB4.3	Ad/F	3.1	6.0	5.0	11.5	44.6	59.3	9.5	13.2	12.1	4.9	4.2	14.2	13.2	13.1	6.0	4.2
G	2	99	L3	Ad/F	2.5	–	9.8	–	–	52.5	10.5	12.0	10.2	–	–	15.4	13.5	11.5	–	–
G	11	00	M127	Ad/M	3.2	11.4	9.8	12.3	44.5	58.2	11.0	9.5	9.8	5.6	4.9	15.8	13.8	12.4	7.9	4.2
G	4	04	MAB4.1	Ad/M	4.0	13.0	6.0	11.5	46.5	65.7	10.5	13.1	10.1	5.2	4.3	16.2	13.7	12.8	6.2	4.3
G	2	99	L2	Ad/M	3.0	11.0	–	–	–	59.0	11.0	12.0	9.8	–	–	17.0	14.0	12.3	–	–
G	11	99	M92	Ad/M	3.7	11.5	7.0	–	–	57.0	–	10.2	8.1	–	–	16.5	15.7	11.6	–	–
G	2	99	L4	Juv/F	2.4	–	–	–	–	59.3	11.6	11.2	9.5	–	–	14.6	16.3	11.5	–	–
G	4	04	MAB4.4	Juv/M	2.9	5.4	4.7	10.8	40.6	59.2	9.3	13.1	9.5	5.2	4.6	15.1	13.6	13.2	6.0	4.3

H	1	04	TAD4.54	Ad/F	3.4	12.3	6.5	11.2	43.1	58.6	10.8	13.1	9.5	5.1	4.2	15.3	14.4	13.1	6.5	4.2
H	1	06	VVE6.1	Ad/F	3.3	12.1	6.9	12.3	40.5	62.0	9.9	11.2	9.7	3.4	4.0	16.2	14.9	12.6	4.4	3.7
H	7	01	TAD26	Ad/M	4.1	11.0	4.0	13.0	44.1	60.6	10.5	13.5	9.8	4.7	4.5	14.0	12.2	12.6	3.7	3.8
H	7	01	TAD27	Ad/M	3.7	11.0	4.0	12.2	43.3	61.9	8.8	12.8	9.5	4.2	4.5	15.4	15.5	11.2	2.2	3.8
H	1	04	TAD4.50	Ad/M	3.3	12.6	6.5	11.2	51.6	51.8	12.2	12.8	10.5	5.0	3.6	15.2	13.2	12.9	5.5	4.4
H	1	06	VVE6.2	Ad/M	3.4	12.4	6.8	11.6	44.7	63.3	9.4	12.5	9.2	3.3	4.0	15.4	13.5	12.1	4.7	3.5
H	1	06	VVE6.3	Ad/M	3.2	12.1	6.0	12.2	42.0	56.9	9.0	12.1	9.1	3.6	3.7	14.7	12.5	12.4	4.1	3.7
H	3	04	TAD4.57	Juv/F	2.5	5.3	3.6	11.3	39.2	53.8	8.7	11.3	8.4	3.3	3.9	14.4	12.3	12.1	6.4	3.7
H	1	06	VVE6.4	Juv/F	2.7	11.0	6.0	11.5	48.5	55.8	8.2	11.2	8.5	3.7	3.6	15.0	12.2	12.1	4.5	3.5
H	1	04	TAD4.49	Juv/M	2.6	6.6	3.6	11.5	36.3	59.8	10.4	12.8	9.3	4.6	4.5	15.3	13.0	13.0	6.1	4.1
H	1	04	TAD4.53	Juv/M	2.7	6.0	3.0	11.8	34.5	54.7	10.3	13.6	9.4	4.1	3.7	14.8	13.4	12.6	6.2	3.7
I	12	04	MIZA4.2	Juv/F	2.5	9.0	7.4	11.3	42.8	57.4	9.8	12.2	9.0	4.7	4.3	15.2	12.6	12.1	5.0	4.3
I	12	04	MIZA4.1	Juv/M	3.0	9.6	6.7	11.5	44.2	53.9	11.0	14.1	8.9	4.3	3.5	14.5	13.3	12.3	5.0	4.2
J	10	00	TAND27	Ad/F	3.6	11.6	5.3	15.5	42.9	62.4	12.5	12.6	10.3	6.4	4.5	17.3	16.7	13.8	4.4	8.0
J	9	04	TANDRA4.12	Ad/F	3.5	13.0	7.0	11.5	47.8	61.1	10.3	12.5	9.7	4.9	4.5	15.9	13.6	13.3	6.0	4.4
J	9	04	TANDRA4.14	Ad/F	3.3	12.2	6.7	11.2	47.2	59.7	10.3	12.4	9.5	4.8	3.9	14.6	13.6	11.9	4.5	3.6
J	9	04	TANDRA4.4	Ad/F	3.2	15.0	7.4	11.0	42.8	53.3	7.9	11.9	9.5	4.1	4.1	14.1	13.2	12.5	4.5	3.7
J	10	00	TAND39	Ad/M	3.6	13.0	6.0	12.0	53.0	60.0	14.0	14.5	10.0	5.2	4.0	19.0	18.0	13.0	8.5	4.5
J	9	04	TANDRA4.13	Ad/M	3.4	11.0	5.0	11.5	43.5	55.0	9.9	12.4	10.1	5.1	4.5	16.0	13.2	13.2	5.5	4.4
J	9	04	TANDRA4.11	Juv/F	2.6	8.6	6.6	11.0	44.8	52.5	10.2	12.8	9.2	4.4	4.4	15.3	12.6	12.8	5.5	3.8
J	10	00	TAND9	Juv/M	3.0	11.0	5.0	13.8	47.3	21.7	11.0	10.8	9.1	5.0	4.1	17.3	15.4	9.9	4.2	3.2
J	9	04	TANDRA4.5	Juv/M	3.0	13.2	6.0	11.2	43.8	55.5	9.8	12.3	8.9	4.2	4.2	15.2	13.2	12.8	5.7	4.2
K[b]	10	04	NOSY16	Ad/F	2.2	7.5	5.0	11.1	38.2	61.0	10.6	11.4	6.9	3.0	3.9	13.2	13.6	12.1	3.9	3.5
K[b]	10	04	NOSY17	Ad/F	2.8	12.0	6.0	11.9	42.6	63.6	12.4	12.4	8.6	3.7	3.6	14.7	14.9	12.4	4.5	4.0
K[b]	10	04	NOSY18	Ad/F	2.6	12.0	5.0	12.5	42.4	58.1	12.2	12.8	8.5	3.9	3.7	12.2	13.9	11.7	4.7	3.5
K[b]	10	04	NOSY60	Ad/M	2.3	10.1	6.0	12.2	40.3	58.1	10.6	12.6	8.5	3.4	4.2	13.2	11.6	12.0	4.1	4.0
K[b]	[a]	[a]	NOSY40[a]	Juv/F	1.6	6.0	2.0	11.2	40.5	58.7	10.6	11.4	8.8	3.8	3.5	11.5	13.1	10.4	4.6	8.5
L	2	01	TOL7	Ad/F	4.1	12.0	6.0	16.5	44.0	64.9	14.3	13.5	10.5	6.0	–	16.1	17.7	13.7	8.3	11.0
L	3	01	TOL9	Ad/F	4.3	11.0	5.0	15.5	48.0	61.9	14.9	12.5	6.1	4.6	4.2	15.7	16.5	9.7	7.3	3.5
L	2	01	TOL1	Ad/M	4.0	16.0	6.0	14.5	45.1	65.0	13.6	14.2	10.8	4.7	8.6	16.6	17.2	14.0	7.2	11.3
L	2	01	TOL6	Juv/M	3.4	7.0	5.0	15.3	46.2	62.1	13.2	12.8	10.2	5.1	9.8	14.6	17.6	12.7	7.5	10.1
L	2	01	TOL3	Juv/M	3.6	7.0	4.0	15.5	46.7	64.4	10.3	13.5	10.0	5.5	9.7	15.8	16.8	14.0	7.3	10.2
M	1	00	RANO322B	Ad/F	4.2	–	–	–	–	64.5	–	–	9.5	5.0	–	–	–	–	7.2	–
M	2	02	RANO2.39	Ad/F	3.4	11.0	5.5	10.3	47.2	63.9	10.8	13.9	9.3	3.3	4.0	13.8	14.8	12.5	4.0	3.8
M	2	02	RANO2.40	Ad/F	3.3	11.0	5.5	11.2	45.9	64.8	10.9	12.2	10.2	3.0	4.0	12.1	13.5	12.4	4.2	3.3
M	2	02	RANO2.42	Ad/F	3.6	12.0	7.0	11.2	46.0	63.0	11.8	12.5	8.9	2.5	3.8	12.7	15.6	12.7	4.5	3.8
M	8	06	RANO6.29	Ad/F	4.6	12.1	6.9	12.7	42.3	62.7	9.4	12.7	9.5	3.7	4.0	16.5	13.7	13.3	4.5	4.1
M	8	06	RANO6.38	Ad/F	4.6	12.2	6.5	12.1	44.4	60.8	9.9	12.3	9.8	3.8	4.1	16.5	13.1	12.9	4.5	3.8
M	8	06	RANO6.41	Ad/F	3.1	8.6	6.1	12.2	41.2	62.9	9.1	12.0	9.4	3.6	4.0	16.1	13.6	12.4	4.6	4.0
M	12	99	RANO313	Ad/F	–	11.0	6.0	12.6	49.5	63.9	17.9	12.6	9.6	–	–	18.0	19.5	12.3	–	–
M	1	00	RANO321B	Ad/M	4.4	–	–	–	–	59.5	–	–	9.6	6.0	–	–	–	12.3	–	–
M	2	02	RANO2.43	Ad/M	3.8	10.0	5.0	11.1	46.1	56.5	11.8	13.2	9.1	2.8	4.0	12.8	13.7	13.4	3.3	3.6
M	8	06	RANO6.27	Ad/M	3.6	10.9	7.3	12.2	44.1	64.4	9.8	12.7	9.9	3.6	4.3	16.6	14.0	13.1	4.4	4.1
M	8	06	RANO6.28	Ad/M	3.7	12.1	6.5	12.2	40.7	65.3	9.1	12.3	9.7	4.2	4.4	16.2	13.3	13.8	4.5	4.2
M	8	06	RANO6.31	Ad/M	3.6	12.0	6.3	11.8	40.9	63.3	9.1	12.4	9.7	3.7	4.0	16.2	13.4	12.5	4.1	3.9
M	8	06	RANO6.33	Ad/M	3.3	10.1	7.0	11.9	41.7	60.6	9.2	11.1	9.3	3.9	4.0	15.5	13.4	12.9	4.3	4.1
M	8	06	RANO6.36	Ad/M	3.8	11.0	6.6	12.2	41.1	61.7	9.5	12.8	9.6	3.9	4.2	16.1	13.7	12.9	4.2	3.8
M	8	06	RANO6.39	Ad/M	3.3	12.2	6.6	12.0	41.7	61.2	13.1	–	9.8	3.7	4.0	15.8	13.2	12.6	4.5	3.8
M	8	06	RANO6.40	Ad/M	3.5	10.5	6.0	12.0	42.2	62.0	9.2	12.1	9.5	4.1	4.0	16.1	12.8	12.7	4.2	3.8

APPENDIX B

Continued

Site	Month	Year	Sample ID	Age/sex	Body mass (kg)	Length (mm) Upper canine	Length (mm) Lower *P*2	Length (cm) Headcrown	Body	Tail	Brachium	Ante-brachium	Hand	Pollex	Longest digit, hand	Thigh	Leg	Foot	Hallux	Longest digit, foot
M	12	99	RANO317	Ad/M	4.0	11.0	10.0	–	42.2	59.8	12.1	12.6	10.0	–	–	15.5	17.7	9.3	–	–
N	1	00	VVAT44	Ad/F	4.1	9.0	6.4	11.2	46.2	69.5	13.2	11.9	10.2	–	–	17.9	17.4	11.2	–	–
N	1	00	VVAT58	Ad/F	4.6	12.1	7.0	11.7	50.5	–	11.9	12.8	–	5.9	–	16.7	15.8	13.4	–	–
N	5	02	VVAT2.10	Ad/F	4.4	10.9	6.0	–	43.3	64.5	13.0	13.5	6.0	5.5	5.1	18.0	16.7	10.5	8.0	5.0
N	1	00	VVAT1	Ad/M	4.1	7.0	6.4	11.4	53.7	45.4	–	12.8	10.2	–	–	16.7	15.1	–	12.9	–
N	1	00	VVAT35	Ad/M	3.9	11.8	6.6	12.1	55.4	63.5	14.1	13.7	10.8	–	–	17.3	15.9	13.9	–	–
N	1	00	VVAT57	Juv/M	2.5	5.4	3.3	11.0	37.5	51.0	9.6	9.8	–	–	8.6	12.3	12.7	–	–	11.4
N	1	00	VVAT64	Juv/M	2.5	6.2	4.2	9.7	37.4	55.2	9.4	8.8	–	–	8.7	12.3	12.1	–	–	4.8
O	3	00	ZAH267	Ad/F	3.3	11.0	5.0	15.3	48.1	58.6	13.9	12.2	9.8	5.6	–	16.4	13.3	13.1	8.3	–
O	8	04	ZAHA4.2	Ad/F	3.1	10.8	5.9	11.3	41.5	64.0	10.5	12.6	10.2	4.3	4.2	15.3	13.3	12.6	4.2	3.5
O	8	04	ZAHA4.4	Ad/F	3.4	9.3	5.3	11.6	45.6	66.5	11.2	12.7	10.4	3.8	4.3	16.2	13.1	13.7	5.7	4.3
O	3	00	ZAH112	Ad/M	3.4	–	–	13.3	48.5	61.2	10.9	11.1	9.4	5.9	–	16.9	15.2	13.3	7.6	–
O	10	00	ZAH280	Ad/M	3.3	11.4	5.8	13.0	43.5	58.0	11.2	12.9	9.4	5.7	3.8	15.8	15.1	12.9	7.8	4.0
O	9	04	ZAHA4.8	Ad/M	3.4	12.4	6.9	11.1	41.8	58.8	10.2	11.6	10.2	4.7	5.2	15.4	14.3	13.3	5.4	4.5
O	10	00	ZAH291	Juv/F	2.4	6.0	8.3	13.5	44.0	56.1	10.3	12.5	8.9	4.7	4.1	18.3	14.4	12.5	4.3	7.3
O	10	00	ZAH293	Juv/F	2.6	9.6	6.0	13.3	52.0	62.5	12.3	12.7	9.7	5.2	4.4	15.2	15.4	13.1	4.0	7.2
O	8	04	ZAHA4.3	Juv/F	2.7	7.8	5.2	11.4	41.9	68.0	10.9	12.6	10.3	4.3	4.5	16.0	14.4	13.7	5.9	4.9
O	9	04	ZAHA4.13	Juv/F	2.9	6.6	5.1	12.1	39.8	57.9	10.2	12.7	9.6	5.4	4.4	16.3	13.3	12.8	6.1	4.7

See Table I for site abbreviations.
[a]Mean calculated from 10/2005 and 10/2006.
[b]Introduced population.

APPENDIX C

The size of adult male testes is given in Appendix C.

Site	Month	Year	Sample ID	Testicular dimensions (mm)				Testicular volume (mm^3)		
				Left length	Left width	Right length	Right width	Left	Right	Total
A	12	01	VAK23	16.0	10.0	18.0	9.0	6,702	6,871	13,573
A	12	01	VAK5	16.8	8.8	18.9	11.4	5,722	12,154	17,876
B	5	01	ANOSIB7	18.6	12.6	19.1	12.2	14,379	14,215	28,594
C	4	01	BET117	22.5	15.0	21.5	15.0	29,821	27,229	57,049
C	12	00	BET51	19.5	12.5	18.0	10.1	15,555	8,567	24,122
D	6	02	FAN2.9	32.9	27.4	29.4	27.5	212,746	171,131	383,877
D	3	04	FAN4.15	29.0	19.4	30.0	17.0	82,864	68,094	150,958
D	3	04	FAN4.19	29.0	18.0	27.0	15.0	71,336	42,942	114,278
D	3	04	FAN4.9	20.0	11.0	19.0	12.0	12,671	13,609	26,280
E	1	00	KIAN115	21.3	11.4	19.0	11.2	15,532	11,900	27,432
E	8	00	KIAN137	27.0	16.0	28.0	17.0	48,858	59,317	108,176
E	11	99	KIAN45	32.0	26.0	24.0	21.0	181,224	66,501	247,725
E	11	99	KIAN46	19.5	13.0	19.5	12.0	16,824	14,335	31,159
F	[a]	[a]	RANO5.12[a]	20.5	12.1	20.4	12.0	15,898	15,597	31,494
F	8	06	RANO5.2	18.0	10.0	17.9	10.5	8,482	9,248	17,730
F	6	05	RANO5.3	14.0	10.0	14.0	7.0	5,131	2,514	7,646
F	[a]	[a]	RANO5.4[a]	19.3	13.5	19.3	14.2	17,773	19,663	37,436
F	6	05	RANO5.9	19.5	12.2	19.0	11.0	14,817	11,436	26,253
F	8	06	RANO6.15	25.8	15.0	24.1	15.2	39,209	35,131	74,340
F	8	06	RANO6.18	25.6	13.2	23.1	15.0	29,895	31,432	61,327
F	8	06	RANO6.19	21.8	11.8	22.0	12.8	17,324	20,760	38,084
F	8	06	RANO6.23	24.5	15.2	23.3	15.1	36,307	32,407	68,713
F	8	06	RANO6.25	19.0	12.9	18.1	12.8	15,727	14,052	29,780
G	11	00	M127	26.7	14.3	22.8	14.8	38,165	29,810	67,975
G	11	99	M92	22.0	14.0	23.0	15.0	24,835	31,161	55,996
G	4	04	MAB4.1	28.0	18.6	26.5	15.3	71,009	43,037	114,046
H	7	01	TAD26	27.0	19.0	30.0	19.0	68,897	85,059	153,956
H	1	04	TAD4.50	22.0	13.0	20.5	12.0	21,414	15,843	37,257
H	1	06	VVE6.3	15.2	9.2	16.1	9.0	5,120	5,497	10,616
J	10	00	TAND39	24.0	12.0	22.0	12.0	21,715	18,246	39,961
J	9	04	TANDRA4.13	17.0	9.0	15.5	10.0	6,128	6,290	12,418
K[b]	10	04	NOSY60	23.0	13.7	24.0	15.1	25,994	34,383	60,377
L	2	01	TOL1	20.0	12.0	23.0	9.0	15,080	11,218	26,297
M	2	02	RANO2.43	22.5	12.5	22.0	13.0	20,709	21,414	42,123
M	8	06	RANO6.27	24.0	15.5	23.1	14.8	36,229	30,600	66,828
M	8	06	RANO6.28	24.5	15.2	24.0	14.4	36,307	31,269	67,576
M	8	06	RANO6.31	21.8	13.1	20.9	13.2	21,351	19,925	41,277
M	8	06	RANO6.36	22.1	13.1	22.4	12.8	21,943	21,522	43,465
M	8	06	RANO6.39	18.9	11.7	18.2	10.9	12,802	10,303	23,105
M	8	06	RANO6.40	21.5	10.7	22.1	11.8	13,855	17,804	31,659
O	10	00	ZAH280	15.0	8.5	15.5	8.4	4,256	4,438	8,694
O	9	04	ZAHA4.8	19.8	14.3	17.3	14.3	20,988	16,023	37,011

See Table I for site abbreviations.
[a]Mean calculated from 10/2005 and 10/2006.
[b]Introduced population.

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