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*griseus*.

## Morphometrics and testicle size of rain forest lemur species from southeastern Madagascar

Six species of prosimians inhabiting the montane rain forest of the Ranomafana National Park located in southeastern Madagascar were captured, weighed, and measured during the months of May or June of 1987, 1988, and 1989. There were no significant differences in body weights and measurements between male and female *Eulemur rubriventer* (red-bellied lemur) or *Eulemur fulvus rufus* (red-fronted lemur). Adult female *Propithecus diadema edwardsi* (Milne Edward's sifaka) were heavier than males but the difference was not significant. A few *Avahi laniger laniger* (woolly lemur), *Hapalemur aureus* (golden bamboo lemur) and *H. g. griseus* (gentle bamboo lemur) also were captured and measured. Body weights of the same individual adult *P. d. edwardsi* changed over the three years, suggesting variation in food availability. Although there was no difference in body weight among adult males of two groups of *P. d. edwardsi*, one male in each group had a testicular volume four times larger than that of other males, even though these measurements were taken five months after the breeding season. These data suggest that only one adult male mates in each group. Testicular size of the polygynous *E. f. rufus* males was significantly larger than that of the monogamous *E. rubriventer*.

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### Introduction

Behavioral studies of rain forest Madagascar lemurs are increasing in number (Ganzhorn, 1988; Ganzhorn *et al.*, 1985; Glander *et al.*, 1989; Meyers, 1988; Overdorff, 1988; Pollock, 1979, 1986; Wright *et al.*, 1987; Wright, 1986, 1987, 1988a,b,c), but detailed morphometrics for these rain forest prosimians have not been previously available. The only available morphometric data for prosimians is for lemurs living in dry forest habitats in southern Madagascar (Richard & Nicoll, 1987; Richard *et al.*, 1991).

In this paper we present detailed morphometric data for six lemur species from the southeastern rain forests of Madagascar. These individuals were captured, weighed, measured, uniquely marked, and released as part of an ongoing study of the behavioral ecology of the 12 species of lemurs living in these forests.

Marked populations of rain forest monkeys have yielded information on life history traits, transfers between groups, seasonal variation of body weights, and reproductive data including testicular development and changes, parity of females, weights and measurements of

infants and juveniles of known age (Glander, 1980; Goldizen, 1987; Goldizen *et al.*, 1988; MacKinnon & MacKinnon, 1980; Terborgh & Goldizen, 1985). In these studies, however, only one or two species were marked at each study site. At the Ranomafana site we hope to accumulate long term data on a majority of the 12 primate species in this community. Coupled with plant phenology and climate data, this comparative approach should produce important information on the complex dynamics of this primate community.

### Study area

All captured individuals were from within the limits of the Ranomafana National Park which is located in southeast Madagascar between 47 degrees 6'–47 degrees 42'E longitude and 21 degrees 0'–21 degrees 24'S latitude. The park is located approximately 90 km west of the Indian Ocean. The study site consists of a trail system 8 kilometers square located in disturbed rain forest. The site is traversed by swift-flowing streams with the white-water Namarona River as the northern border. Annual precipitation is approximately 2000 mm. Rainfall occurs throughout the year and is greatest from December to March. The terrain is steep and mountainous at 1100 m elevation.

There are 12 species of lemurs living in the Ranomafana rainforests: *Avahi laniger laniger*, *Cheirogaleus major*, *Daubentonia madagascariensis*, *Eulemur fulvus rufus*,\* *Eulemur rubriventer*, *Hapalemur aureus*, *Hapalemur griseus griseus*, *Hapalemur simus*, *Lepilemur mustelinus* or *microdon*, *Microcebus rufus*, *Propithecus diadema edwardsi*, and *Varecia variegata variegata*. All 12 species are found within the trail system at the study site.

The nocturnal lemur *A. l. laniger* has the highest density (80/km<sup>2</sup>) of the 12 species (Wright pers. obs.; Harcourt, pers. comm.). The population density is unknown for *D. madagascariensis* but it is certainly low. The medium-sized lemurs also occur at low densities, i.e., *E. rubriventer* population density is 30 per square kilometer, and *E. f. rufus* population density is 70 per square kilometer (Overdorff, 1991). The largest species, *P. d. edwardsi*, has a population density of 4 individuals per square kilometer (Wright *et al.*, 1987; Wright, 1988c) while the population density for *V. v. variegata* is only one individual per square kilometer (White, 1989). The population densities for the other species have not yet been determined.

There is a full complement of predators including the Madagascar harrier-hawk (*Polyboroides radiatus*) and several carnivores at the study site. The largest carnivore is the puma-sized fossa (*Cryptoprocta ferox*) which may eat lemurs (Jolly, 1980). Other viverrid carnivores are smaller (4–8 kg) and include the diurnal *Galidia elegans*, the nocturnal *Fossa fossana*, *Galidictis* and the rarely seen *Eupleres*.

### Methods

Capture of the animals was accomplished using the Pneu-dart<sup>®</sup> system. This system employs disposable non-barbed darts with a 9 mm needle delivered by a gun powered by carbon dioxide. In 1987 and 1988 the darts were loaded with Ketamine<sup>®</sup> (Ketamine hydrochloride, 100 mg/ml). The dosage was 30–35 mg/kg. In 1989 the capture drug was Telazol<sup>®</sup> (equal parts tiletamine hydrochloride and zolazepam hydrochloride; A. H. Robbins, Richmond, VA 23220). Dosage was 20 mg/kg. The switch to Telazol was made because it is more effective in preventing darted individuals from running away. Darted animals were also

\*Following the classification of Simons & Rumpler (1988) who place all species of *Lemur* other than *Lemur catta* in the genus *Eulemur*.

**Table 1**      **Description of each measurement**


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*Tail-crown length* is measured from the tip of the tail to the most anterior point on the head with the head in normal position, i.e., chin near the chest.

*Tail length* is measured on the ventral side of the tail from the tip of the tail to the junction of the base of the tail with the perianal area. The tail is completely extended straight out behind the animal.

*Body length* is the tail-crown length minus the tail length.

*Hindlimb length* is measured from the groin to the end of the longest digit, excluding the nail.

*Hindfoot length* is measured from the heel to the end of the longest digit, excluding the nail.

*Big toe length* is measured 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 and the nail is excluded.

*Forelimb length* is measured from the axillary region to the tip of the longest digit, excluding the nail.

*Forefoot length* is measured from the proximal edge of the friction pad nearest the wrist to the tip of the longest digit, excluding the nail.

*Thumb length* is measured from the junction between the first and second digits to the tip of the thumb, excluding the nail.

*Testicle width and length* are measured with a vernier caliper.

*Testicular volume* is calculated by  $\frac{4}{3} \pi (0.5 L) (0.5 W)^2$  where  $L$  = length and  $W$  = width.

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more relaxed due to the tranquillizing property of zolazepam HCL and they recovered faster than with Ketamine.

Body weights and measurements were taken using portable spring scales (accurate to 10 g) and metal tape measure (accurate to 1 mm) (see Table 1 for a description of the body measurements). KEG estimated age from tooth wear. For future identification, adults were uniquely marked with different colored nylon or leather collars fastened with two rivets. A brightly colored circle of plastic was placed in the ears of juveniles and infants (see Glander *et al.*, in press, for description of capture and marking methods).

### Statistical analysis

Distributions were tested for normality, and they were found to be homoscedastic except for testicle size. Testicular volume was log-transformed. Means were compared using analysis of variance, ANOVA (Sokal & Rohlf, 1981). The level of significance was set at 0.05.

### Results

Table 2 presents the measurements and gives details of the number of individuals of each species that were captured in the different years. Table 3 presents the results of the statistical analyses for those species which had a large enough sample size.

#### *Avahi laniger laniger*

Body weight for adult females averaged 1316 grams while adult males averaged 1033 grams, but the sample size of four adult males and four adult females was too small to analyse statistically.

**Table 2 Morphometrics for the *Ranomafana* prosimians**

Species	Month	Year	Name	Sex	Group number	Weight	Body	Tail	Hind limb	Hind foot	Big toe	Fore limb	Fore foot	Thumb	Age	Right testicle (mm <sup>3</sup> )	Left testicle (mm <sup>3</sup> )	Both testicles (mm <sup>3</sup> )
Al	5	89	Yellow	f		900	252	314	345	99	56	202	74	30	Sub-adult			
Al	6	89	Green	f		1240	264	340	328	97	55	190	72	29	Adult			
Al	5	89	Blue	f		1225	285	259	351	102	58	207	75	28	Adult			
Al	5	88	Cinco	f		1600	271	352	345	95	57	214	76	32	Adult			
Al	5	87	Uno	f		1200	292	366	355	106	55	247	84	38	Adult			
Al	6	89	Red	m		1150	267	365	357	101	60	228	73	31	Adult	1227	2224	3451
Al	5	88	Quatro	m		900	251	324	321	80	48	184	70	27	Adult			
Al	5	87	Duo	m		1200	270	370	367	100	60	235	77	30	Adult	3285	2251	5536
Al	8	87	Tres	m		880	265	330	319	93	47	179	70	22	Adult	821	2619	3440
Ha	5	88	Red	f		1500	340	410	295	93	58	240	65	32	Adult			
Ha	5	88	Yellow	m		1540	330	405	303	97	60	212	68	33	Adult	3876	5920	9796
Ha	5	88	Blue	m		1640	347	417	310	105	60	203	64	32	Adult	8362	9052	17,414
Ha	10	88	Blue	m		1660									Adult	2750	3601	6351
Hg	5	88		m		770	240	370	252	85	50	171	55	24	Adult			
Lfr	6	89		f		1550	335	450	319	93	42	215	65	24	Juvenile			
Lfr	5	87		f		1600	312	473	334	97	45	245	65	25	Sub-adult			
Lfr	7	89	Buddah	f		2500	370	515	332	102	60	252	71	29	Adult			
Lfr	7	89	Rose	f		2250	405	535	360	102	50	282	75	30	Adult			
Lfr	7	89	Susan	f		2200	360	510	320	95	55	255	65	30	Adult			
Lfr	6	89		f		2650	389	540	346	107	58	238	79	32	Adult			
Lfr	2	89	Victoria	f		2200	378	471	304	101	56	231	74	27	Adult			
Lfr	5	89	Victoria	f		2000									Adult			
Lfr	6	89		f		2500	369	504	332	105	51	243	71	29	Adult			
Lfr	6	89	Agent Orange	f		2400	392	505	330	99	52	245	69	29	Adult			
Lfr	5	88		f		1810	350	498	319	100	51	239	70	28	Adult			
Lfr	5	88		f		2100	374	504	350	102	60	238	70	34	Adult			
Lfr	6	88		f		2300	378	546	358	106	55	252	73	34	Adult			
Lfr	5	88		f		2300	439	486	350	114	55	237	73	34	Adult			
Lfr	5	87		f		2100	360	484	337	105	53	238	67	29	Adult			
Lfr	5	87		f		2150	274	510	315	97		237	70	27	Adult			



Lfr	7	89	Juv	m	3	1200	320	470	295	95	45	205	50	10	Juvenile	137,716	132,447	270,163
Lfr	6	89	Beethoven	m	V	2150	376	496	334	102	48	260	70	29	Adult	76,001	83,443	159,444
Lfr	5	89	M	m	V	2400	346	530	355	95	55	263	71	30	Adult	85,442	66,576	152,018
Lfr	5	89	DJ	m	V	2300	385	470	333	110	57	244	67	32	Adult	85,442	68,917	154,359
Lfr	5	89	Nemo	m	V	2650	411	526	373	118	60	250	67	33	Adult	10,175	45,547	90,431
Lfr	6	89		m	9	1900	370	470	321	103	50	236	68	30	Adult	44,884	91,524	176,062
Lfr	6	89	Star	m	V	2450	393	532	342	106	55	248	72	29	Adult	84,538	47,538	93,772
Lfr	5	89	J	m	V	2100	380	540	335	104	58	257	74	31	Adult	131,647	221,824	384,806
Lfr	5	89		m	V	2600	379	526	365	113	63	282	73	33	Adult	162,981	175,656	248,386
Lfr	5	88		m		2000	340	510	320	93	52	236	70	21	Adult	72,730	28,290	63,324
Lfr	5	88		m		2300	375	495	310	120	57	240	73	28	Adult	37,572	41,066	89,002
Lfr	5	87		m	1	2200	370	480	320	100	50	230	68	28	Adult	22,485	49,690	72,175
Lfr	5	87		m		2000	362	542	330	80	55	234	70	26	Adult	53,917	20,144	74,061
Lfr	5	87		m		2300	380	490	340	100	47	240	70	26	Adult	50,884	75,129	126,013
Lfr	8	89	Brown/red	m	1	2300	390	530	360	115	52	256	72	30	Adult	29,039	303	29,342
Lfr	7	89	Yel/blue	m	2	2100	386	484	300	105	50	228	70	28	Adult	43,850	54,215	98,064
Lfr	7	89	Yel	m	2	2000	480	390	320	92	42	205	69	24	Adult	25,644		
Lfr	7	89	Gr/blue	m	2	2000	352	490	305	105	51	205	63	27	Adult			
Lfr	7	89	Gr/orange	m	4	1750	360	460	312	102	50	222	71	28	Adult			
Lfr	7	89	Red/blue	m	4	2000	355	495	336	110	50	243	60	35	Adult			
Lfr	7	89	Blue/orange	m	5	2050	362	528	332	104	55	225	76	30	Adult			
Lr	7	89	Juv	f		1200	297	478	300	102	48	200	70	25	Sub-adult			
Lr	6	89		f		1100	301	429	298	95	49	204	65	27	Sub-adult			
Lr	5	89	Clara	f		1600	336	530	327	105	55	236	66	27	Sub-adult			
Lr	5	88		f		1440	320	500	307	104	53	214	72	21	Sub-adult			
Lr	2	89	Anna	f		2200	365	470	304	103	62	233	75	31	Adult			
Lr	5	89	Anna	f		2100									Adult			
Lr	2	89	Constanzie	f		1980	350	493	311	107	59	203	74	31	Adult			
Lr	6	89	Sky blue	f		1650	378	462	319	110	53	226	75	27	Adult			
Lr	6	89	Purple	f		1850	348	470	325	100	49	214	73	30	Adult			
Lr	5	89	Orange	f		2200	365	480	342	102	55	228	75	31	Adult			
Lr	5	88		f		2100	356	482	316	103	54	197	74	24	Adult			
Lr	5	88		f		1950	365	470	360	106	62	232	73	34	Adult			
Lr	5	87		f		1900	332	483	337	108	67	241	78	27	Adult			
Lr	7	89	Red/yel tri	f		2000	358	510	315	110	45	225	71	31	Adult			
Lr	7	89	Yel/Yel tri	f		1850	365	495	312	109	49	230	70	25	Adult			
Lr	7	89	Blue/yel	f		2050	348	532	335	99	58	195	80	28	Adult			
Lr	7	89	Violet/blue	f		1950	335	490	292	95	45	200	66	31	Adult			
Lr	8	89	Red/orange	f		1900	400	500	330	110	51	235	72	35	Adult			

Pde	5	88	Red-green	f	2	6000	457	478	575	187	107	415	140	60	Adult	890	603	1493
Pde	5	87	Red-green	f	2	6300	376	394	461	151	88	324	106	53	Adult	17,441	16,922	34,363
Pde	5	89	Yellow	f	1	5500	467	463	583	184	106	397	135	65	Adult	24,521	20,166	44,687
Pde	5	88	Yellow	f	1	6000	488	452	540	172	97	371	130	58	Adult	20,204	21,784	41,988
Pde	5	87	Yellow	f	1	6200	488	452	540	172	97	371	130	58	Adult	12,888	12,029	24,917
Pde	5	89	Bl/wh's son	m	1	155	150	110	140	60	30	102	41	21	2 days	2636	3722	6357
Pde	5	88	died	m	2	180	376	394	461	151	88	324	106	53	7 days	6157	7766	13,923
Pde	5	87	Year-10 mon	m	2	2600	423	444	555	175	100	377	132	52	Adult	10,229	9659	19,888
Pde	6	89	Grey	m	4	5700	467	463	583	184	106	397	135	65	Sub-adult	5206	3711	8917
Pde	5	89	Kevin	m	4	6000	486	434	530	163	108	365	130	56	Adult	21,256	19,464	40,720
Pde	5	89	Brown	m	3	6100	485	410	546	173	95	386	133	70	Adult	24,291	23,268	47,559
Pde	5	89	Orange	m	1	5600	518	460	560	184	97	411	135	66	Adult	23,268	31,278	54,546
Pde	5	87	Orange	m	2	4900	490	450	557	175	107	400	136	66	Adult	15,311	20,767	36,078
Pde	5	89	Yellow	m	2	5200	423	444	555	175	100	377	132	52	Adult	26,482	39,099	65,581
Pde	5	88	Yellow	m	2	4800	423	444	555	175	100	377	132	52	Adult	27,491	24,659	52,150
Pde	5	87	Yellow	m	2	5000	423	444	555	175	100	377	132	52	Adult	16,315	12,272	28,587
Pde	5	89	Red/red	m	2	5500	465	435	542	165	104	372	130	65	Adult	13,387	11,750	25,137
Pde	5	88	Red/red	m	2	5300	465	435	542	165	104	372	130	65	Adult	6148	8275	14,423
Pde	5	87	Red	m	1	5800	467	420	543	174	95	364	129	61	Adult			
Pde	5	88	Red	m	1	5600	467	420	543	174	95	364	129	61	Adult			
Pde	5	87	Red	m	1	5900	467	420	543	174	95	364	129	61	Adult			
Pde	5	89	Blue/red	m	2	5600	475	460	537	173	100	388	133	63	Adult			
Pde	5	88	Blue/red	m	2	5400	475	460	537	173	100	388	133	63	Adult			
Pde	5	87	Blue/red	m	2	5300	475	460	537	173	100	388	133	63	Adult			

Al = *Anahi laniger*; Ha = *Haplolepis aureus*; Hg = *H. griseus griseus*; Efr = *Eulemur fulvus rufus*; Er = *E. rubriter*; Pde = *Propithecus diadema edwardsi*. Linear measurements are not provided for recaptured individuals.

Table 3 Means and (SD) for *Eulemur fulvus rufus*, *Eulemur rubriventer* and *Propithecus diadema edwardsi*

	Sex	n	Weight (g)	Body (mm)	Tail (mm)	Hind limb (mm)	Hind foot (mm)	Big toe (mm)	Fore limb (mm)	Fore foot (mm)	Thumb (mm)
<i>Eulemur fulvus rufus</i>	m	20	2178 (233)	378 (30)	499 (36)	332 (20)	104 (9)	53 (5)	240 (19)	70 (3)	29 (3)
	f	13	2251 (228)	377 (38)	508 (21)	330 (15)	103 (5)	55 (3)	247 (13)	71 (4)	30 (2)
<i>Eulemur rubriventer</i>	m	9	2067 (195)	357 (25)	510 (21)	325 (31)	105 (6)	55 (4)	234 (17)	73 (5)	31 (3)
	f	13	1960 (140)	358 (18)	487 (20)*	324 (17)	105 (5)	54 (6)	220 (16)	73 (3)	30 (3)
<i>E. f. rufus</i>	m	20	2178 (233)	378 (30)	499 (36)	332 (20)	104 (9)	53 (5)	240 (19)	70 (4)	29 (3)
<i>E. rubriventer</i>	m	9	2067 (195)	357 (25)	510 (21)	326 (31)	105 (6)	55 (4)	234 (18)	73 (5)*	31 (3)
<i>E. f. rufus</i>	f	18	2251 (228)	374 (38)	509 (21)	338 (15)	103 (5)	54 (3)	247 (13)	71 (4)	30 (2)
	f	13	1960 (140)***	358 (18)	487 (20)*	324 (17)*	105 (5)	54 (6)	220 (16)***	73 (3)	30 (3)
<i>Propithecus diadema edwardsi</i>	m	8	5590 (373)	481 (8)	438 (20)	550 (16)	173 (7)	103 (6)	381 (14)	132 (3)	64 (4)
	f	6	5895 (373)	481 (15)	458 (19)	570 (18)*	178 (5)	103 (4)	395 (18)	135 (5)	61 (6)

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .Body weight for *P. d. edwardsi* is an average if there are more than one year's weight listed in Table 2.

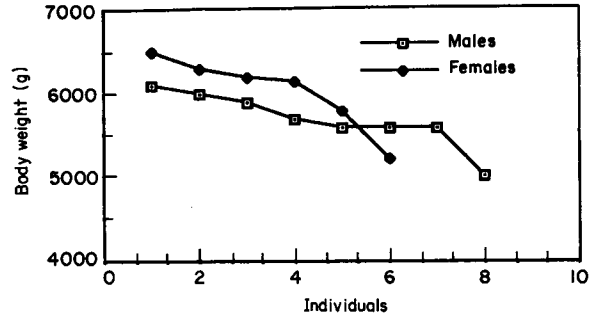


Figure 1. Comparison of *Propithecus diadema edwardsi* body weights. Individuals are arranged by decreasing body size.

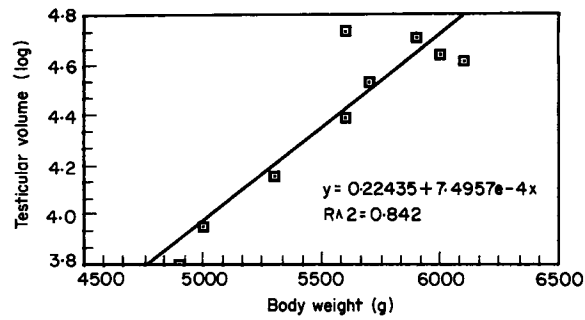


Figure 2. The relationship between body weight and testicle size for adult *Propithecus diadema edwardsi* males.

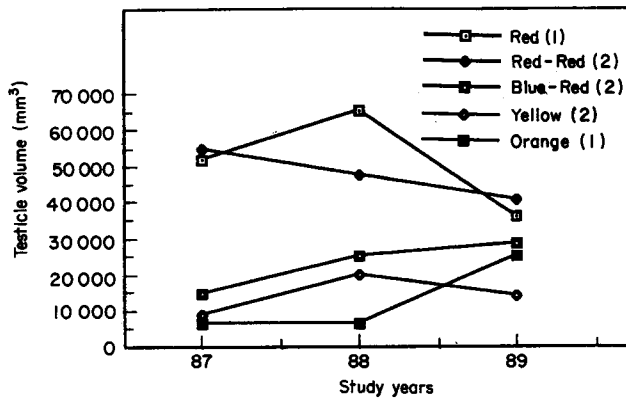


Figure 3. Changes in testicle size for individual *Propithecus diadema edwardsi* males during May (adults only).

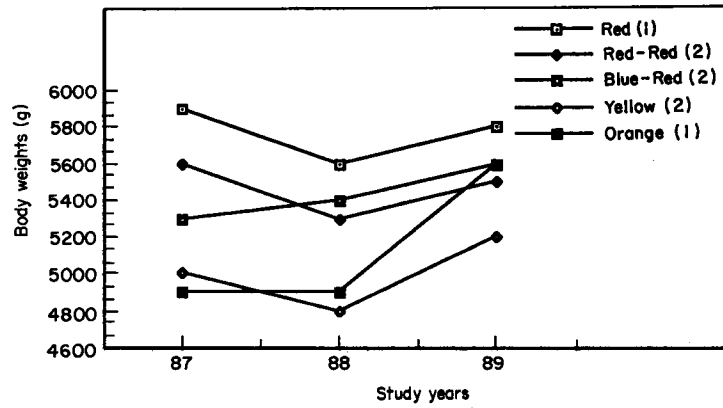


Figure 4. Changes in body weight for adult male *Propithecus diadema edwardsi* during the study.

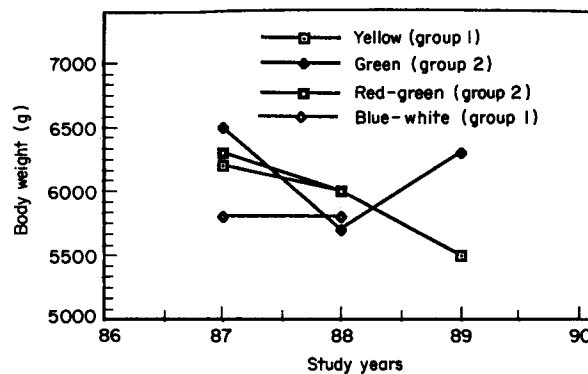


Figure 5. Changes in body weight for adult female *Propithecus diadema edwardsi* during the study.

#### *Eulemur fulvus rufus*

Capture occurred during the mating season. There were no significant differences between males and females in body weights or measurements. However, there was noticeable variation in testicle size as measured by volume. In the overall population some males had a testicular volume that was two to seven times that of others. Within the social groups, testicle size varied from all males having about the same sized testicles in Group 5 to Groups 2 and 4 where one male had testicles two to three times as big as the other male or males. There was no relationship between body weight and testicle size ( $R^2=0.158$ ;  $n=19$ ) nor was there any relationship between group size or group composition and testicle size (average group size was 7, range 6–12,  $n=9$ ; Overdorff, 1990, 1991).

#### *Eulemur rubriventer*

Capture occurred during the mating season. There were no significant differences between male and female weights and measurements except that males had significantly longer tails ( $F=8.8$ ,  $P=0.01$ ). There was no relationship between body weight and testicle size ( $R^2=0.02$ ;  $n=9$ ).

**Table 4** Intermembral indices for six wild *Ranomafana* prosimians with comparisons data from skeletal measurements by Jungers (1979). Jungers did not separate the sexes

Species	Sex	<i>n</i>	Mean	CV	<i>n</i>	Mean (Jungers, 1979, Table 6)	CV
<i>Avahi laniger</i>	m	4	60.3	6.97	10	57.7	2.4
	f	4	62.1	8.47			
<i>Eulemur fulvus rufus</i>	m	20	72.3	5.24	4	71.7	1.6
	f	14	73.3	5.11			
<i>Eulemur rubriventer</i>	m	9	72.3	11.50	2	68.2	-
	f	14	68.7	7.56			
<i>Haplemur aureus</i>	m	2	67.7	4.68			
	f	1	81.4	-			
<i>Haplemur griseus</i>	m	1	67.9	-	13	64.3	4.6
<i>Propithecus diadema edwardsi</i>	m	17	69.7	2.41	4	63.1	1.8
	f	12	69.7	2.98			

CV = coefficient of variation.

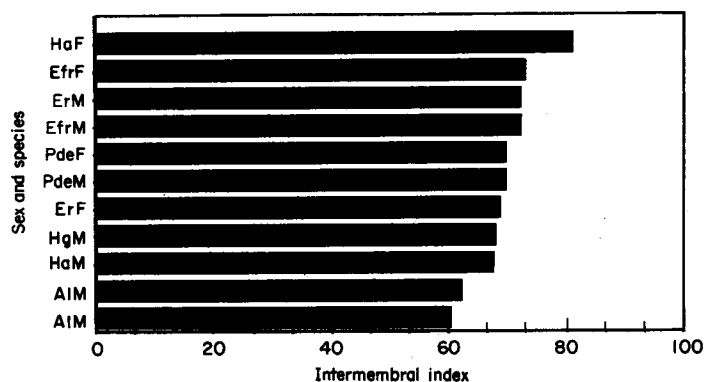


Figure 6. Comparison of intermembral indices for the *Ranomafana* prosimians.

Since *E. f. rufus* and *E. rubriventer* are closely related and occur sympatrically, their weights and measurements were compared. The males of these two species were the same size and had similar body dimensions, except that *E. rubriventer* males had significantly longer forefeet than *E. f. rufus* males ( $F = 4.0$ ,  $P < 0.05$ ). The testicles of *E. rubriventer* were significantly smaller than the testicles of *E. f. rufus* ( $F = 14.8$ ,  $P < 0.001$ ).

The females of these two species were significantly different in several measurements. Female *E. f. rufus* were heavier ( $F = 15.3$ ,  $P = 0.001$ ), had longer tails ( $F = 7.6$ ,  $P < 0.01$ ), longer hindlimbs ( $F = 5.2$ ,  $P = 0.03$ ) and longer forelimbs ( $F = 22.2$ ,  $P < 0.0001$ ) than *E. rubriventer* females.

#### *Haplemur aureus*

Only one female and two males were captured. The female (1500 g) was only slightly smaller than the males (average of 1590 g). One of the males (Blue) was captured in May and again

**Table 5** Statistical comparison of intermembral indices

	Sex	n	Mean	CV
<i>Avahi laniger laniger</i>	m & f	8	61.2***	4.5
<i>Propithecus diadema edwardsi</i>	m & f	29	69.8	2.3
Quadrupeds	m & f	62	71.6***	5.3
Vertical Clingers	m & f	34	67.8	4.7
<i>Eulemur fulvus rufus</i>	m & f	34	72.7	3.7
<i>Eulemur rubriventer</i>	m & f	23	70.1	6.7
<i>Eulemur fulvus rufus</i>	m	20	72.3*	3.8
<i>Eulemur rubriventer</i>	m	9	69.4	3.1
<i>Eulemur fulvus rufus</i>	f	14	73.3**	3.7
<i>Eulemur rubriventer</i>	f	14	68.7	5.2

CV = coefficient of variation; \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

in October 1988. His testicular volume in October was approximately one-third that exhibited in May (6351 mm<sup>3</sup> compared to 17 414 mm<sup>3</sup>).

#### *Haplemur griseus griseus*

Only one male was captured. This individual was less than one-half the weight of *H. aureus* (770 g compared to average of 1590 g for male *H. aureus*).

#### *Propithecus diadema edwardsi*

The average weight for infants at birth was 156 grams ( $n = 4$ ). Yearlings weighed about 2500 grams. Adult females were heavier than adult males but the difference is not significant (Table 3, Figure 1). None of the adult females were pregnant. Females did have significantly longer hindlimbs than males ( $F = 4.7$ ,  $P < 0.05$ ). Testicle size was related to body size (Figure 2), although the outliers suggest that there is also a social effect. The outlier above the regression line is the dominant and presumed breeding male in Group 2 (Red-Red), while the outlier below the line is a low ranking male in Group 4 (Figure 2).

Figure 3 compares changes in individual testicle size during the three years. The dominant male in Group 1 (Red) showed a sharp decrease from 1988 to 1989. Orange joined Group 1 in 1988, and while part of his increase in testicle size is due to maturation, his increased testicle size is mirrored by Red's decrease. A similar pattern is seen in Group 2 where Red-Red (dominant) showed a decrease, while the testicles of the other two males increased in size.

Changes in the males' yearly weights are shown in Figure 4. The dominant male in each group (Red in Group 1; Red-Red in Group 2) lost weight from 1987 to 1988 and regained about half of the lost weight by 1989. In contrast, the other males in each group gained weight from 1987 to 1989. Two of the males (Orange and Yellow) were subadults in 1987 and their weight gain was due to having matured by 1989.

All of the females except Blue-White weighed less in 1989 than they did in 1987 although Green did regain some of the 800 grams she lost between 1987 and 1988 (Figure 5). Yellow lost 700 grams from 1987 to 1989.

*Limb proportions*

The intermembral indexes are presented in Table 4 and graphed in Figure 6. There was no significant differences in sexual dimorphism for *Avahi laniger laniger*, *Eulemur fulvus rufus*, *E. rubriventer* or *Propithecus diadema edwardsi*. The *Hapalemur* sample size was too small to test statistically, but the female *Hapalemur aureus* had a much larger index than the two male *H. aureus* (Table 4). The *H. g. griseus* male's index was identical to that of the two *H. aureus* males.

The vertical clinging species had significantly longer hindlimbs relative to forelimbs than the quadrupedal species ( $F = 12.06$ , d.f. = 95,  $P = 0.008$ ). In fact, *Avahi* (AlM and AlF) had the longest hindlimbs relative to forelimbs, while male *H. griseus* (HgM), *H. aureus* (HaM) and female *E. rubriventer* (ErF) had longer hindlimbs in relation to their forelimbs than did *P. d. edwardsi* (PdeM and PdeF) (Figure 6).

Even though they are both vertical clingers, there was a significant difference between the intermembral indices of *A. l. laniger* and *P. d. edwardsi*. The smaller *A. l. laniger* has relatively longer hindlimbs to forelimbs ( $F = 53.24$ , d.f. = 36,  $P < 0.0001$ ) (Table 5).

When males and females of each species are lumped together, there is no significant difference in the intermembral indices for *E. f. rufus* and *E. rubriventer* (Table 5). But, even though male *E. f. rufus* and male *E. rubriventer* are the same size, they have significantly different intermembral indices (Table 5). Male *E. rubriventer* have relatively longer hindlimbs. Female *E. f. rufus* and *E. rubriventer* are different in weight and also have significantly different intermembral indices. Female *E. rubriventer* have relatively longer hindlimbs (Table 5).

## Discussion

*Sexual dimorphism*

Sexual dimorphism has been linked to social structure (Kay *et al.*, 1988) and body size has been linked to social dominance (Richard, 1987; Smuts, 1987) in the sense that it is the larger sex which supplants the smaller from preferred resources (Young *et al.*, 1990). During feeding in most primates, the most common pattern is male dominance over females (Hrdy, 1981; Jolly, 1984). The only cases of female dominance over males in a feeding context occur in the Malagasy lemurs (Richard, 1987; Young *et al.*, 1990). Female feeding priority has been observed in wild and captive members of the genera *Eulemur*, *Indri*, *Microcebus*, *Phaner*, *Propithecus* and *Varecia* (Charles-Dominique, 1977; Hrdy, 1981; Jolly, 1984; Overdorff, 1988; Pollock, 1979; Richard, 1987; White, 1989; White *et al.*, 1989; Wright, 1987).

Dominance has also been linked to social structure with male dominance common in polygynous species (Hrdy, 1981; Jolly, 1984). It is not that simple at Ranomafana where individual males can be dominant in the polygynous *E. f. rufus*, but females are dominant in the monogamous *E. rubriventer* and the polygynous *P. d. edwardsi*. Nor can the fact of female dominance among the Malagasy primates be explained by size. For example, female *P. d. edwardsi* are heavier and have longer hindlimbs than the males, but *E. f. rufus* and *E. rubriventer* males and females are the same size in all measurements except that *E. rubriventer* males have longer tails than the females. In feeding situations, female *P. d. edwardsi* and *E. rubriventer* are dominant to males (Overdorff, 1988, 1991; Wright, 1988c), but *E. f. rufus* females can be subordinate to males (Pereira *et al.*, 1990).

Small sample size due to rarity of the species or difficulty in obtaining wild weights can have a dramatic impact on analysing the degree of sexual dimorphism. For example, in a preliminary report using the data collected in the first two years of our study (1987, 1988),

Kappeler (1990) listed *P. d. edwardsi*, as one of the 12 prosimian species where females are significantly larger than males. When he used the slightly larger sample size presented in this paper, Kappeler (in press) came to the same conclusion that we did, i.e., there is no sexual dimorphism in *P. d. edwardsi*.

#### *Limb proportions*

The differences in the intermembral indices for *A. l. laniger* and *P. d. edwardsi* (Table 4) was a surprise since both are classified as vertical clingers and leapers (Walker, 1979). This difference, however, can be explained by the difference in body size and forelimb length. Jungers (1979) showed that indriid forelimb length is positively allometric with body size. Forelimbs become relatively and absolutely longer in the size progression from *A. l. laniger* to *P. d. edwardsi* (Jungers, 1979).

All of the Lemuridae from Ranomafana are classified as quadrupedal by Walker (1974, 1979), although Overdorff (1988) reported that *E. rubriventer* uses clinging and leaping during 50% of its locomotor bouts. Tilden (1990) found that captive *E. rubriventer* used leaping during 58% of their locomotor bouts. Gebo (1987) found that captive *E. f. rufus* spent 34% of their locomotor time leaping and captive *H. g. griseus* leaped 56% of the time. Dagosto (1989) demonstrated that even the most quadrupedal of the lemurs (*V. v. variegata*) engaged in leaping 31% of the time.

Jungers (1979) showed that Lemuridae differ from indriids in that forelimb length is negatively allometric to body size in Lemuridae. He suggested that this relationship, in combination with the stronger negative allometry of the hindlimb, would permit the larger Lemuridae an increased ability to climb on vertical supports (Jungers, 1978).

#### *Testicle size*

Testicle size between and within the species demonstrated some expected and unexpected patterns. The polygynous *E. f. rufus* have testicles which are significantly larger than the monogamous *E. rubriventer*. Testicle size in *E. f. rufus* groups did vary from a situation where all of the adult males in a group had about the same sized testicles (Group 5) to the situation where one male had much larger testicles than the other males (Groups 2, 4 and 9). In the second condition, the male with the larger testicles had testicles that were two to three times the size of the other males' testicles in the same group (Table 2). It appears as if suppression of testicle size is occurring in some but not all of the social groups. Testicle size may be suppressed in sons who stay in their natal groups. That would suggest that the four males in Group 5 are not related and are not in their natal group. Results from DNA fingerprinting may help solve this riddle by providing the relationship of these males.

The *H. aureus* male who was captured in May and then again in October had much smaller testicles in October (Table 2). Birth season for *H. aureus* is in December. The gestation length is unknown, but *H. g. griseus* has a gestation of 140 days (Wright, 1986). If *H. aureus* has a similar gestation period, their breeding season occurs in August. Apparently the testicles of this species change in size depending on whether or not it is the breeding season.

Testicle size in *P. d. edwardsi* males is linked to body size until maturity when social status apparently influences testicle size. Red (adult) was the only male in Group 1 in 1987, but Blue-red from Group 2 joined Group 1 in May, 1987. Blue-red then returned to Group 2 at the end of July (Wright, 1988) where he remained at least until December 10, 1987. Blue-red's testicles had increased in size as expected in a maturing individual (Figure 3). Red's testicles also had increased in size from 1987 to 1988, the time during which Blue-red

was visiting Group 1 (Figure 3). In 1987, Red-Red (adult) had testicles which were two to four times the size of the other three males in Group 2 (Blue-Red, Orange and Yellow). Orange's testicles increased dramatically after he switched from Group 2 to Group 1 in June 1988.

#### *Weight changes and diet*

The folivorous *P. d. edwardsi* females lost as much as 12% of their body weight from one year to another, while the frugivorous *E. f. rufus* females lost 9% and the frugivorous *E. rubriventer* females lost 5% of their body weight in a 3-month period (Table 2). This suggests that both fruit and leaf eaters are under similar ecological stresses. It should be noted that a male bamboo-eating lemur (*H. aureus*) who was captured in May 1988 and then again in October of the same year had not lost weight but had actually gained 20 grams (Table 2). Bamboo is cited as a low quality food (Schaller *et al.*, 1985) and contains large amounts of the toxin cyanide (Glander *et al.*, 1989). Despite eating this low quality diet, this male *H. aureus* did not lose weight as did those species eating the high quality foods. Granted this is only one case, but it does point out the danger of oversimplifications created by assuming that high quality food is better than low quality food and that the quality of the food affects individuals and populations. In this case it is likely that low quality bamboo was readily available while high quality fruit and leaves were scarce.

Diet quality and quantity is certainly affected by climatic factors, but it can also be altered by selective logging. And again, the change may not always be negative. In fact, selective logging (with minimal operational damage) may actually help some folivores, because it allows colonizing tree species an opportunity to grow. These regenerating forests provide better quality and greater quantities of food because the colonizing tree species are less well protected chemically and are higher in nutrients (Glander, 1979, 1981).

The forest at the study site has experienced selective logging for precious woods including *Dalbergia* spp., but the logs were extracted manually resulting in little loss of other trees due to operational damage. Selective logging may cause initial changes in group ranging and activity patterns as the primates avoid the logging sites and it may also cause high levels of infant mortality initially (Johns, 1983). It remains to be determined what the effects of selective logging will have in the long-term at Ranomafana, but *Varecia* does not occur in the logged areas (Wright & White, 1990).

These morphometric data will continue to be collected on a yearly basis in order to understand their dynamic nature and relationship. Similar data on the other six species at Ranomafana will provide new insights to the ecological and social data now accumulating.

### Summary

Female *Avahi laniger laniger* tend to be larger in body weight than males while there is no difference in size between male and female *Eulemur fulvus rufus* and *Eulemur rubriventer*. Male *Eulemur rubriventer* did have longer tails than females. There was no relationship between body size and testicle size for either *Eulemur fulvus rufus* or *Eulemur rubriventer*, but the polygynous *Eulemur fulvus rufus* had larger testicles than the monogamous *Eulemur rubriventer*. The males of *Eulemur fulvus rufus* and *Eulemur rubriventer* are the same size except that *Eulemur rubriventer* have larger forefeet. Female *Eulemur fulvus rufus* weighed more, had longer tails, longer hindlimbs and longer forelimbs than *Eulemur rubriventer* females.

Only one female and two male *Hapalemur aureus* and one male *Hapalemur griseus griseus* were captured, but *Hapalemur aureus* was twice the body weight of the *Hapalemur griseus griseus*. Male *Hapalemur aureus* apparently experience yearly changes in testicle size.

Infant *Propithecus diadema edwardsi* weighed 156 grams, yearlings weighed about 2500 grams. There was no significant sexual dimorphism in *P. d. edwardsi* but adult females did have significantly longer hindlimbs. Male testicle size is related to body size until adulthood is reached and then there is a social effect. Both male and females demonstrated a fluctuation of body weight from one year to the next which may be linked to fluctuation in available food.

Sexual dimorphism was not linked to social structure nor was body size linked to dominance in the species for which we have both behavioral and morphometric data, i.e., males can be dominant in the polygynous *Eulemur fulvus rufus* while females are dominant in the monogamous *Eulemur rubriventer* and neither species is sexually dimorphic. *Propithecus diadema edwardsi* are polygynous and sexually dimorphic with the females dominant to the males.

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