

Rensch's Rule, Bergmann's Effect and Adult Sexual Dimorphism in Wild Monogamous Owl Monkeys (*Aotus azarai*) of Argentina

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ABSTRACT Some monogamous primates are characterized by biparental care, territoriality, and a reduced level of physical dimorphism. In others, the relationship between those behavioral patterns and dimorphism is less clear. I tested Bergmann's and Rensch's rules using *Aotus* spp. body mass data and I characterized the extent of sexual dimorphism in body mass, dental and physical measurements in a socially monogamous owl monkey population ($n = 91$ adults) from the Argentinean Gran Chaco. *A. azarai azarai* from the Argentinean Chaco is larger than the more tropical owl monkey species ($r = 0.7$, $N = 6$ species), but there is no apparent increase in sexual dimorphism with increased body mass. The body masses of adult

male and female *A. a. azarai* were remarkably similar (Mean = 1.26 kg); there were no marked sex differences in most skeletal measurements, but males had higher and wider upper and lower canines than did females. Body mass and neck circumference were positively and strongly related ($r = 0.533$, $n = 52$), and the body mass of adults was not a reliable indicator of their age ($r = 0.03$, $n = 10$). The data illustrate the complexities inherent in examining and summarizing within population variation in skeletal and nonskeletal measurements and contribute to a better understanding of the relationships between monogamous behavioral patterns and sexual dimorphism. *Am J Phys Anthropol* 000:000–000, 2011. ©2011 Wiley-Liss, Inc.

There are various primate taxa that live in small social groups (e.g., indris, avahis, owl monkeys, titi monkeys, gibbons). Some of those taxa usually display a suite of characteristics that includes paternal care of offspring, territoriality, and low frequencies of copulatory behavior involving a single partner (Fuentes, 2002; Kappeler and Van Schaik, 2002; Fernandez-Duque et al., 2009). Although a strong association between those characteristics and reduced dimorphism in body mass, canine size and skeletal dimensions has been shown for many primate taxa (Kay et al., 1988; Plavcan, 1993; Ford, 1994; Smith and Jungers, 1997), there are taxa in which the relationship is less clear (Milton, 1985; Kappeler, 1990; Lindenfors and Tullberg, 1998), has not been thoroughly examined (e.g., *Pithecia*), or has been evaluated relying on small collections of museum specimens or wild specimens of uncertain provenance and/or unknown sex and age (e.g., *Aotus*, *Callicebus*). Studies on larger sample sizes of sexually dimorphic free-ranging polygynous and polyandrous primates have illustrated some of the problems of assuming average population measurements from small samples of any particular location (Goldizen et al., 1988; Altmann et al., 1993; Jablonski and Ruliang, 1995; Turner et al., 1997; Schmid and Kappeler, 1998; Pochron and Wright, 2003; Johnson et al., 2005; Glander, 2006).

Behavioral reconstructions of early hominins are regularly based on the observed behavior and morphology of extant primates (Plavcan and Van Schaik, 1997; Lovejoy, 2009; Takai et al., 2009; Gettler, 2010) and the taxonomic classification of fossils is influenced by our understanding of between and within population variation in the extent of sexual dimorphism, as well as possible changes in body size and dimorphism with latitude

(Reno et al., 2003; Plavcan et al., 2005). In other words, our understanding of early hominin behavior and taxonomy will benefit from answering the following questions: What is the range of variation in sexually dimorphic physical traits of extant primates? How are physical and behavioral dimorphism correlated in extant primate species? The study presented here addresses those questions by focusing on the socially monogamous Azara's owl monkeys.

My first goal is to test Bergmann's and Rensch's rules examining interspecific differences in owl monkey body mass. Unlike other *Aotus* species, *A. azarai* of the South American Chaco has switched its activity pattern from strict nocturnality to one that includes regular diurnal activity (Wright, 1989; Fernandez-Duque et al., 2010). This change has occurred together with an increase in body mass (Fernandez-Duque, 2011). I first evaluate if

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there is a positive relationship between body mass and latitude for the genus *Aotus* (i.e., Bergman's Effect, Harcourt and Schreier, 2009). Second, I examine if the apparent increase in body mass is positively related to an increase in the degree of sexual dimorphism (i.e., Rensch's rule, Smith and Cheverud, 2002) or if, like suggested by recent analyses of micro and macroevolutionary processes underlying the evolution of scaling relationships, the socially monogamous owl monkeys show negative scaling like the polyandrous *Callitrichids* (Gordon, 2006a,b).

The second goal is to characterize the extent of sexual dimorphism in body mass, dental, and physical measurements among adults of a population of owl monkeys from the Argentinean Gran Chaco. Throughout the study, I present both standard body measurements regularly used by evolutionary morphologists and human biologists and nonstandard ones most frequently used by field primatologists (Antón et al., 2009; Stubblefield et al., 2010). I describe the relationship between the two and I evaluate which body measurements were the best predictors of body mass and age.

METHODS

Area of study, population, and capturing procedures

The owl monkey population found along the Pilagá and Guaycolec Rivers in the Province of Formosa (58° 11' W, 25° 58'S) has been regularly studied since 1997 (Fernandez-Duque et al., 2001,2002,). Since 1999, we have been capturing owl monkeys to mark and radio-collar them in order to facilitate behavioral and demographic data collection. We have captured adult individuals living in 34 different social groups or ranging solitarily on 142 occasions (48 females, 45 males). Most individuals (94%, $n = 81$) were captured within a core study area (~ 300 ha) of gallery forest along the Pilagá river (see Fig. 1), whereas the remainder (6%, $n = 12$) were sampled along the Riacho Pilagá between 3 and 10 km up or downstream from the core study area. One individual was sampled from the Monte Lindo River gallery forest another tributary of the Paraguay River located 25 km north of the field site.

Owl monkeys were captured by anesthetizing them with Ketamine hydrochloride (25–50 mg/kg; Vetanarcol, König, Argentina) loaded on darts projected with a blow-pipe or rifle (Fernandez-Duque and Rotundo, 2003); procedures approved by the National Wildlife Directorate in Argentina, the Institutional Animal Care and Use Committee of the University of Pennsylvania and the Zoological Society of San Diego. Most individuals were fitted with a radio or bead collar depending on their age and the need to locate reliably that specific individual. The effects of capturing owl monkeys and fitting them with collars have been recently evaluated and found to have no obvious consequences for the welfare of the animals (Juárez et al., 2010).

Physical exam and body measurements

While the animals were anesthetized we conducted a physical exam. Until 2008 we used procedures that did not provide measures comparable to those regularly used by evolutionary morphologists and human biologists. More recently, we have implemented standardized protocols that, besides nonskeletal measures, include also

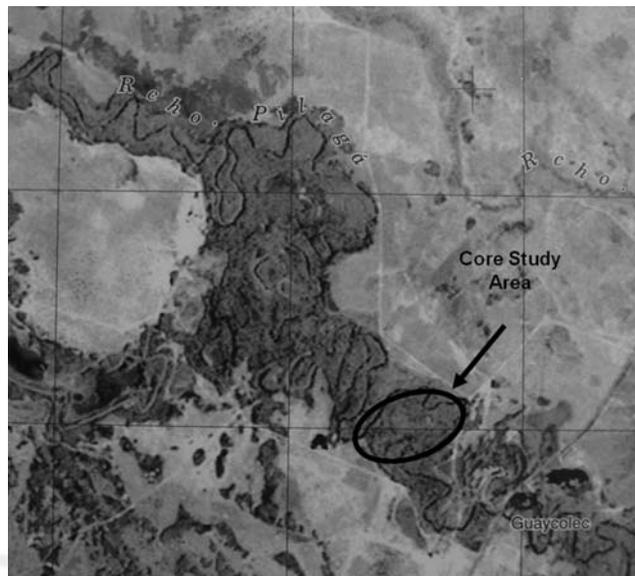


Fig. 1. Gallery forests (darker gray) along the Pilagá and Guaycolec rivers in the Province of Formosa, Argentina. Most individuals were sampled from the core study area indicated with a black circle.

some proxies for skeletal measures that can be approximated on both living and skeletal samples (Antón et al., 2009). All individuals were measured using the nonstandardized protocols and a small subset of those was also measured following the standardized protocols (three males, seven females). Results have different sample sizes because not all measurements were recorded for all individuals.

Body mass and nonstandardized skeletal body measurements

Body mass: We weighed each individual using a 2 kg spring scale with 10 g gradations (Pesola). Two people read the measurement on the scale and compared readings before recording the body mass to the nearest 10 g.

Body length (BL): the distance from the crown between the eyes to the beginning of the tail (i.e., not including the tail), when the animal was stretched and the spine was roughly linear.

Tail length (TL): with tail pulled straight, the distance from the dorsal base of the tail to the end of the bony portion of the tail.

Crown-heel length: the distance from the crown between the eyes to the base of the foot (posterior tip of calcaneus) when the animal was stretched and the spine roughly linear.

Heel-toe length: the distance from the base of the foot (posterior tip of calcaneus) to the tip of the longest digit, excluding the nail.

Left forelimb length: with the animal laying on its side and with the forelimb extended at the elbow, the distance from the top (round) part of the shoulder to the tip of the longest digit, excluding the nail.

Left hind limb length: with the animal laying on its side and with limb extended at the hip, the knee and the ankle, the distance from the lateral most bony point at the hip joint (greater trochanter) along the lateral side of the limb to the tip of longest digit, excluding the nail.

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Neck circumference: measured at roughly the middle of the neck.

Hand length: distance from base of hand to tip of the longest digit, excluding the nail.

Standardized skeletal measures

Proxies for measures of individual bone lengths are taken from standardized measurement protocols and illustrations (www.bonesandbehavior.org). While these proxies should approximate the lengths of individual elements, they are not identical to these measures because there is soft tissue cover. It would require a correction factor to make them equivalent.

Humerus length: with the animal laying on its side and with the forelimb extended at the elbow, the distance from the top (round) part of the shoulder to the most lateral bony protuberance on the elbow.

Ulna length: with the animal laying on its side and with the forelimb flexed at the elbow, the distance from the bony point on the elbow (olecranon process) to the most distal bony protrusion just above the wrist (styloid process of ulna).

Femur length: with the animal laying on its side and with lower limb extended at the hip and the knee, the distance from the lateral most bony point at the hip joint (greater trochanter) along the lateral side of the limb to the lateral most extension of the knee (i.e., lateral condyle of the femur), which should be at approximately the mid point of the kneecap (patella).

Tibia length: with the animal laying on its side and with lower limb extended at the hip and the knee, distance from the medial point used to take "tibial knee breadth" along the medial side of the leg to the inferior-most point on the malleolar medial bulge at the ankle.

Mandibular and maxillary canine height and width: height was measured as the distance from the tip of the tooth to the cementum-enamel junction on the buccal face, whereas the width ("mesiodistal length") was measured as the greatest dimension in the occlusal plane.

Measurements were recorded to the nearest 0.1 mm using dial calipers with needle points and averaged over the two canines of the mandible and maxilla, respectively.

Age estimates

Individuals were classified as of known (*K*) or estimated age (*E*) at the time of capture. Age was known for adults born after 1997 ($n = 8$) when the project began, and estimated for those born before 1997 ($n = 85$). We estimated birth years based on body size, tooth wear, and gland development relative to individuals of known age (Huck et al., in press). Two or more trained researchers estimated ages independently, and estimates were re-evaluated with every re-capture of an individual. It is unlikely that we regularly under or overestimated ages of adult individuals by more than one or two years. I report information from 93 individuals ($n = 48$ females, $n = 45$ males) classified as adults given their known date of birth (four females, four males), because their age was estimated to be older than 48 months (44 females, 41 males), or because they were reproductive adults based on their social status, relative size, and behavioral and reproductive patterns. One individual was discarded from all analyses because her data checksheet was lost (Atenas, ID109).

Data analyses

Azara's owl monkeys body mass, Bergmann's effect and Rensch's rule. For computing the average body mass of adults, I considered both individuals of known and estimated age. Forty-seven individuals were weighed more than once as adults (six times, $n = 1$; 5 times, $n = 2$; 4 times, $n = 6$, 3 times, $n = 9$, twice, $n = 29$). For them, I first calculated an individual mean across repeated measurements, before computing the overall mean across subjects.

For testing Bergmann's effect, I obtained body mass data of male wild individuals from the published literature (Crile and Quiring, 1940; Hernández-Camacho and Defler, 1985; Aquino and Encarnación, 1986b; Smith and Jungers, 1997; Fernandez-Duque, 2011;) and estimated latitudinal mid-points of the different owl monkey taxa (*A. trivirgatus*, *A. lemurinus*, *A. zonalis*, *A. azarai azarai*, *A. azarai boliviensis*, *A. nancymae*) distribution range from published maps (IUCN Red List of Threatened Species). I evaluated the relationship with non-parametric Spearman correlation and two-tailed probability following Harcourt and Schreier (2009).

For testing Rensch's rule, I used a combination of published and original data and followed the methods of Smith and Cheverud (2002). They included data both from captive (*A. vociferans*) and wild animals (*A. nancymae*, *A. trivirgatus*, *A. lemurinus*). Their data on *A. lemurinus* were obtained from two sources; I considered their data from Crile and Quiring in Panamá (1940) as *A. zonalis* and data reported from Hernández-Camacho and Defler in Colombia (1985) as *A. lemurinus* following the taxonomy by Rylands (2001). To evaluate the relationship between sexual dimorphism and body mass, I regressed the natural logarithm of the male body mass\female body mass ratio on the natural logarithm of female body mass (Smith, 1999; Plavcan, 2003). To evaluate the relationship between canine size dimorphism and body mass I estimated the dimorphism of the mandibular and maxillary canines as the female\male ratio of the average maximum diameter of the canine at its base following Kay et al. (1988).

Sex differences in body mass, body measurements, and canines. I examined sexual dimorphism in body mass, body measurements and canines by calculating means and medians across each sex. I then compared the means of males and females using *t*-tests for independent samples after evaluating the kurtosis of each variable. I also computed effect sizes and confidence intervals of the mean given that they are more informative than inferential statistical tests alone (Nakagawa and Cuthill, 2007; McCloskey and Ziliak, 2008). This is particularly true in a sexually monomorphic species where relatively small effect sizes could still be biologically informative and meaningful (Taborsky, 2010). All analyses were conducted using SPSS 15.5. To evaluate sexual dimorphism of the intermembral index I computed the ratio of the forelimb length to the hind limb length $\times 100$.

For the analysis of canines, data on crown height had to be discarded for those animals that showed significant attrition in their canines because it is hard to estimate how the degree of wear affects the measurement of height (Leutenegger and Cheverud, 1982). Thus, for canine height I used only those individuals for whom the degree of attrition had been evaluated to be less than 1.4, since that indicates very little attrition given that it

TABLE 1. Male and female differences in body mass (kg) and body measurements (cm)

Measurement	Sex	n	Mean	SE	95% Lower Bound	95% Upper Bound	Median	Var	SD	Min	Max	t	p	ES
Body mass	Males	45	1.26	0.02	1.23	1.30	1.27	0.01	0.11	1.00	1.58	0.26	0.80	0
	Females	46	1.26	0.02	1.23	1.29	1.27	0.01	0.10	1.02	1.46			
Body length	Males	36	33.5	0.3	32.9	34.1	33.5	3.2	1.8	29.0	37.0	1.26	0.20	0.5
	Females	39	33.0	0.3	32.5	33.5	33.0	2.6	1.6	30.5	37.5			
Tail length	Males	38	39.1	0.7	37.6	40.5	40.0	18.4	4.3	26.0	44.5	-0.13	0.89	-0.1
	Females	40	39.2	0.5	38.2	40.2	40.0	9.8	3.1	30.0	43.0			
Neck	Males	28	11.8	0.3	11.1	12.4	11.3	2.8	1.7	10.0	17.8	0.3	0.7	0.1
	Females	24	11.6	0.2	11.1	12.1	11.5	1.5	1.2	10.0	14.5			
Crown-heel	Males	34	50.4	0.3	49.7	51.0	51.0	3.5	1.9	45.5	54.8	0.0	1.0	0.0
	Females	36	50.4	0.2	49.9	50.9	50.5	2.1	1.4	46.5	53.0			
Heel-toe	Males	35	10.1	0.0	10.0	10.2	10.0	0.1	0.3	9.5	10.7	1.4	0.2	0.1
	Females	36	10.0	0.0	9.9	10.1	10.0	0.1	0.3	9.0	10.5			
Forelimb	Males	37	23.7	0.4	23.0	24.4	23.0	4.6	2.2	20.5	29.0	0.2	0.8	0.1
	Females	39	23.6	0.3	23.0	24.2	24.0	3.3	1.8	20.0	28.5			
Hindlimb	Males	37	28.5	0.3	27.9	29.1	28.5	3.2	1.8	21.5	32.0	-0.9	0.4	-0.4
	Females	39	28.9	0.4	28.1	29.6	29.0	5.1	2.3	24.5	36.5			
Intermembral Index	Males	37	83.8	1.9	79.9	87.7	80.7	135.5	11.6	72.4	134.9	0.7	0.5	
	Females	39	82.2	1.4	79.5	85.0	83.1	73.6	8.6	67.1	116.3			

TABLE 2. Bergmann's effect

Taxon	N	Body mass (kg)	log10(kg)	Mean Latitude	Reference
<i>A. trivirgatus</i>	20	0.81	2.91	2.4	Smith and Jungers, 1997
<i>A. lemurinus</i>	7	0.92 ± 0.08	2.96	5.0	Hernandez-Camacho and Defler, 1985
<i>A. zonalis</i>	6	0.89	2.95	6.0	Crile and Quiring, 1940
<i>A. a. boliviensis</i>	4	1.18	3.07	12.0	Smith and Jungers, 1997
<i>A. nancymaae</i>	32	0.79	2.90	14.0	Aquino and Encarnacion, 1986
<i>A. a. azarai</i>	40	1.254 ± 0.11	3.10	25.0	Fernandez-Duque 2007 and this study

Average body mass (log10) and latitudinal mid-point of the geographic range of five owl monkey taxa.

corresponds to the average attrition score for subadults (Huck et al., in press). Measurements for the left and right canines were averaged after confirming that there were no marked differences between them. For the analysis of sexual dimorphism in canine size, the analyses was not limited to individuals 48 months or older (i.e., adults), but instead also included individuals who were between 36 and 48 months, since most individuals have fully developed canines then even if not considered adults by other criteria (Huck et al., in press).

To examine variation over a bigger area, I compared the data from the core study population with the data from other individuals captured up or downstream from the main area of study ($n = 12$). Because the body mass and morphometrics of those individuals fell well within the range of values for the core study population, all individuals were combined for analyses.

Standard and nonstandard measurements. To examine the relationship between the external dimensions of live animals and actual bone measurements, I obtained both nonstandardized and standardized skeletal measurements for 10 individuals (three males, seven females) captured since we implemented the new procedures. This comparison was done for males and females combined since samples were too small for evaluating sex differences. To evaluate whether body mass or age could be predicted by any of the skeletal measurements I performed least squares multiple regression. The variables were distributed normally, thus no transformations were necessary.

RESULTS

Azara's owl monkeys body mass, Bergmann's effect, and Rensch's rule

The average body mass of adults was 1.26 ± 0.10 kg ($n = 91$, median: 1.26, range: 0.58 kg, 25% percentile: 1.19, 75% percentile: 1.3 kg, Table 1). Five pregnant females had body masses higher than the population mean (1.30, 1.34, 1.35, 1.35, and 1.36 kg).

Owl monkey species show increased body mass with increased latitude. The Azara's owl monkeys (*A. azarai*) are the largest; whereas the more tropical species (*A. nancymaae*, *A. lemurinus*, *A. zonalis*, *A. trivirgatus*) tend to be smaller ($r = 0.695$, $N = 6$, $P = 0.125$; Table 2). *A. azarai* is also the owl monkey species with the widest latitudinal distribution ranging from Caviana Island in Brazil to the northeastern corner of the Province of Chaco in Argentina (Fernandez-Duque, 2011). An analysis of the three *A. azarai* subspecies showed a trend for an intraspecific positive relationship, the austral species (*A. a. azarai*; 1.26 kg, $n = 91$) being larger than the more tropical ones (*A. a. infulatus*, 1.19 kg, $n = 1$; *A. a. boliviensis*, 1.18 kg, $n = 4$).

Conversely, Rensch's rule did not hold for data on body mass for the six owl monkey taxa considered. The amount of sexual dimorphism in body mass was not positively related to body mass. Instead, there was a trend for negative scaling of sexual dimorphism against body mass ($r = -0.709$, slope = -0.715 , $P = 0.110$, Fig. 2).

Still, sexual dimorphism in canine size was more pronounced in the larger *A. azarai* than in other smaller owl monkey species. Dimorphism of the maximum diam-

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eter of the lower canine at its base was 1.10 in *A. a. azarai* (22 males, 20 females), whereas the ratios tended to be smaller in *A. trivirgatus griseimembra* (1.04; 2 males, 4 females), *A. trivirgatus lemurinus* (1.07, 13 males, 13 females), and *A. trivirgatus trivirgatus* (1.05, 10 males, 19 females, Kay et al., 1988). A similar pattern is apparent for the maximum diameter of the upper canines. There the ratio for *A. a. azarai* was 1.11 (20 males, 25 females), whereas the ratios for the other species were 0.97, 0.99, and 1.01 respectively. The small number of taxa for which data are available makes a quantitative estimation of the relationship uninformative and therefore unnecessary.

Sex differences in body mass, body measurements, and canines

The body mass of adult males and adult females was remarkably similar. Both sexes averaged 1.26 kg (1.26 ± 0.11 vs. 1.26 ± 0.10; Table 1). Sex differences in body length were also relatively small, but larger than differences in body mass. On average, the body length of males was 33.5 cm long, whereas the females' was 33.0 cm (Table 1).

There was a clear tendency for males to have a wider range of tail lengths than females (males, 26–44.5 cm; females, 30–43 cm, Table 1, Fig. 3). A few animals had tails that were distinctively shorter, to an extent that this characteristic was used for their identification. It seems most reasonable to assume that the shortness of their tails was not natural and that these animals had lost the distal portion of the tail as a result of an accident (e.g., a fight), disease or infection.

There were no clear sex differences in any of the other nonskeletal measurements. Table 1 provides descriptive and inferential statistics for the differences between

males and females in neck circumference, crown–heel, heel–toe, left forelimb, and left hind limb lengths. The length of the hind limb is the only measurement that shows a larger effect size. Females have hind limbs that are 0.4 cm longer than those of males. The mean population intermembral index was 83.0 (95% CI: 80.7–85.3) and females had a slight tendency to have a lower index than males (82.2 vs. 83.8) which is the consequence of longer hind limbs in females than males.

Sexual dimorphism was more conspicuous in the size of the canines (Table 3). The differences in the upper canines were particularly pronounced. The average male upper canine was 1.1 mm higher (5.2 vs. 4.1 mm) and 0.3 mm wider (3.1 vs. 2.8 mm) than the average female one. On the other hand, the average male lower canine was only 0.4 mm higher (3.7 vs. 3.4 mm) and 0.2 mm wider (2.1 vs. 2.0 mm) than the average female one.

Relationships between skeletal and nonskeletal measurements

Body mass was strongly related to neck circumference and body length (Table 4). Heavy individuals tended to have thicker necks; body mass and neck circumference were positively and strongly related ($r = 0.533, n = 52, P = 0.0001$). Body mass was also strongly related to body length (i.e., trunk), whereas it showed no strong relationship to the lengths of the limbs. Although the

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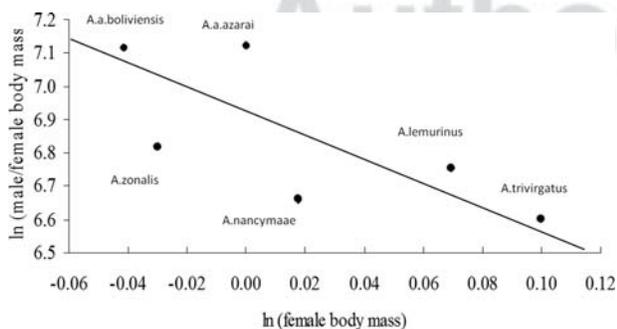


Fig. 2. Rensch's rule. Relationship between the natural logarithm of the male body mass/female body mass ratio on the natural logarithm of female body mass.

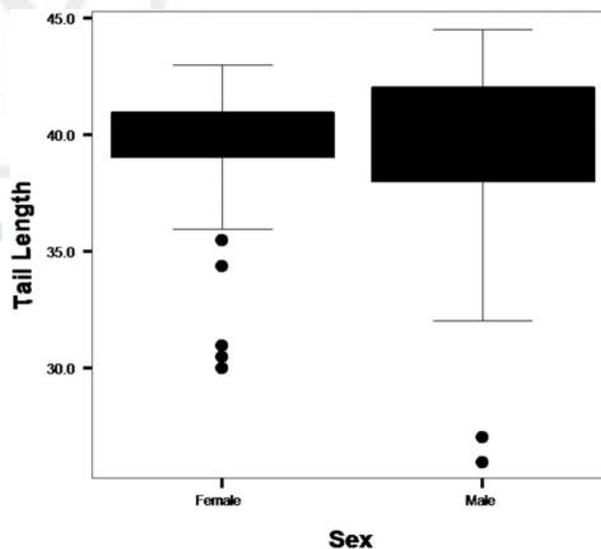


Fig. 3. Sex differences in tail length. Black dots indicate outliers that had unusually short tails most likely the result of losing the distal portion during a fight.

TABLE 3. Height and width (mm) and descriptive statistics of maxillar and mandibular canines of adult male and female owl monkeys

		n	Mean	SE	Lower Bound	Upper Bound	Median	Var	SD	Min	Max	Z	U	P	ES
Mandibular Canine Height	M	22	3.7	0.1	3.6	3.9	3.7	0.1	0.4	3.1	4.4	-2.6	97	0	0.4
	F	19	3.4	0.1	3.1	3.6	3.3	0.4	0.6	1.9	4.9				
Maxillar Canine Height	M	22	5.2	0.2	4.9	5.6	5.3	0.6	0.8	3.6	6.2	-3.9	54	0	1.1
	F	19	4.1	0.2	3.7	4.5	4.2	0.6	0.7	2.1	4.8				
Mandibular Canine Width	M	28	2.1	0.0	2.1	2.2	2.2	0.0	0.2	1.6	2.6	-2.9	180	0	0.2
	F	24	2.0	0.0	1.9	2.0	2.0	0.0	0.2	1.5	2.5				
Maxillar Canine Width	M	27	3.1	0.1	3.0	3.2	3.1	0.1	0.4	2.0	3.9	-3.1	192	0	0.3
	F	28	2.8	0.1	2.7	2.9	2.9	0.1	0.3	2.1	3.4				

TABLE 4. Relationships (Pearson correlations, P-values and sample sizes) between body mass and body measurements

	Body length	Hindlimb	Forelimb	Heel-toe	Neck Circumference	Femur	Tibia	Humerus	Ulna
Body mass (kg)	0.39	-0.13	-0.02	0.20	0.53	0.74	-0.30	0.37	0.10
P-value	0.00	0.26	0.89	0.09	0.00	0.02	0.40	0.30	0.79
N	74	75	75	70	52	10	10	10	10
Body Length		-0.14	0.05	0.21	0.19	0.47	0.08	0.03	-0.12
P-value		0.24	0.66	0.08	0.18	0.17	0.82	0.93	0.74
N		74	74	70	51	10	10	10	10

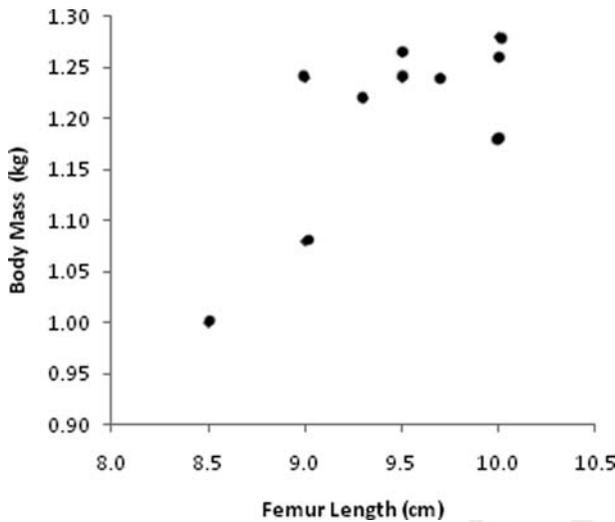


Fig. 4. Relationship between femur length and body mass.

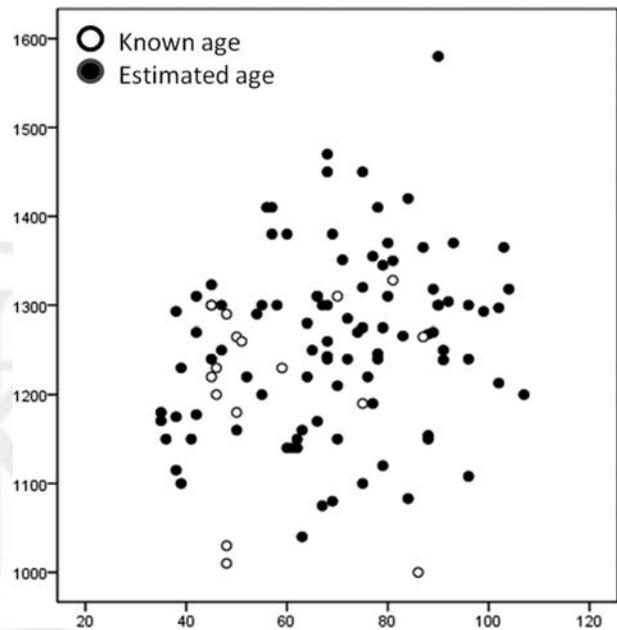


Fig. 5. Relationship between body mass and estimated or known age of adults.

total length of the limbs was not a good predictor of body mass, there was a stronger relationship between the length of the foot (i.e., heel-toe) and body mass ($r = 0.203$, $n = 70$, $P = 0.092$, Table 4). The analysis of the small set of individuals on which standardized measurements were taken, showed that the femur was the individual element that best predicted body mass ($r = 0.74$, $n = 10$, $P = 0.02$) and body length ($r = 0.47$, $n = 10$, $P = 0.17$, Table 4 and Fig. 4.). In fact, of all measurements, the length of the femur showed the strongest relationship with body mass.

The body mass of adults was not a reliable indicator of their age. A linear regression of body mass on age, for adults with known age of birth measured on more than one occasion, showed an extremely weak relationship between the two variables ($r = 0.030$, $P = 0.93$, Fig. 5).

Finally, the preliminary comparison of standardized and nonstandardized measurements showed a relationship in the expected direction. The mean forelimb measured as a single segment was 0.3 cm shorter (22.5 cm) than the estimate obtained from adding the lengths of the humerus, ulna, and hand (22.8 cm, Table 5). This is expected since part of the elbow joint is measured twice when measuring individual elements, but only once when measuring forelimb length. On the other hand, the mean hind limb measured as a single segment was 0.3 cm longer (28.6 cm) than the estimate from adding the lengths of the femur, tibia, and foot (28.3 cm, Table 5). Similarly, we expect the hind limb length to be longer than the two segments individually because we exclude some parts in the individual lengths that are measured in the total length.

DISCUSSION

Azara's owl monkeys body mass, Bergmann's effect, and Rensch's rule

The Azara's owl monkeys of the South American Gran Chaco are almost 50% larger than other owl monkey tropical species (Fernandez-Duque, 2011). The findings agree with recent analyses of Bergmann's effect on primates (Harcourt and Schreier, 2009); the effect being largest among taxa with the greatest latitudinal distribution.

It seems plausible that the increase in body mass is an adaptation to the harsher climate characteristic of the Gran Chaco, an environment quite different from the tropical forests where other owl monkey species are found. The Gran Chaco is highly seasonal, characterized by significant fluctuations in rainfall, temperature, and photoperiod (Fernandez-Duque, 2003). Extreme low (below 10°C) and high temperatures (above 35°C) occur regularly in winter and summer; even below freezing temperatures are a yearly occurrence (Fernandez-Duque, 2009).

There are additional lines of evidence indicating evolutionary adaptations associated to changes in climate. First, contrary to other owl monkeys species that are strictly nocturnal, *A. a. azarai* has become cathemeral, most likely as a metabolic adjustment to the extreme

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TABLE 5. Comparison of standardized and no-standardized measurements of the extremities of owl monkeys (cm)

	Forelimb	Humerus		Ulna	Hand	Hindlimb	Femur		Tibia	Foot
		+Ulna	+Hand				+Tibia	+Foot		
Mean	22.5	22.8	8.3	8.0	6.5	28.6	28.3	9.4	10.3	8.6
SE Mean	0.4	0.3	0.2	0.1	0.1	0.3	0.3	0.2	0.2	0.2
Lower Bound	21.5	22.1	7.8	7.7	6.3	27.9	27.7	9.0	9.9	8.2
Upper Bound	23.4	23.5	8.8	8.3	6.6	29.3	29.0	9.8	10.8	9.0
Median	22.0	23.0	8.5	8.0	6.5	28.6	28.5	9.4	10.2	8.5
Variance	2.1	1.0	0.6	0.2	0.1	0.9	0.8	0.3	0.4	0.3
s. d.	1.4	1.0	0.8	0.5	0.2	1.0	0.9	0.5	0.6	0.6
Minimum	20.0	21.0	7.0	7.0	6.0	27.4	27.0	8.5	9.3	8.0
Maximum	25.5	24.5	9.5	8.5	7.0	30.7	29.5	10.0	11.5	9.5

cold and warm temperature of this latitude (Wright, 1989; Fernandez-Duque and Erkert, 2006; Fernandez-Duque et al., 2010); a response that has also been proposed to explain cathemerality in lemurs (Kappeler and Erkert, 2003; Curtiss and Rasmussen, 2006; Tarnaud, 2006; Donati et al., 2009). Second, the concentration of births during October-December may also be an adaptation to a seasonal habitat (Di Bitetti and Janson, 2000; Fernandez-Duque et al., 2002). Finally, an increase in body mass may also be the reason why Azara's owl monkeys sleep in vine tangles or open branches, but never use tree holes for sleeping as other species do (Aquino and Encarnación, 1986a; García and Braza, 1993; Pueras et al., 1995).

The relationship between latitude and body mass among the three *A. azarai* subspecies should be considered with more caution. Although the analysis indicated a positive relationship, sample sizes are small and the unclear *Aotus* taxonomy warrants additional analyses in the future. The taxonomy of *Aotus* spp. is far from resolved (Rylands, 2001; Deffer and Bueno, 2007) and although *A. azarai* shows the widest latitudinal distribution ranging from the equator to outside the tropics (0–26°S), more information is needed to determine whether the three taxa should be distinguished at the subspecies or species level.

The owl monkey body mass data did not support Rensch's rule; if anything, body mass and sexual dimorphism were negatively associated. The extensive literature evaluating the relationship in a wide range of taxa including primates shows variation in the strength of the relationship in different groups (Ford, 1994; Abouheif and Fairbairn, 1997; Fairbairn, 1997; Webb and Freckleton, 2007). For example, there is no relationship between sexual size dimorphism and size in the Strepsirhini (Kappeler, 1990), but positive scaling within Haplorhini as a whole, as well as within the Platyrrhini, Cercopithecoidea, Colobinae, and Hominoidea (Gordon, 2006b).

For some of the groups it is necessary to evaluate if the observed patterns are real or the artifacts of sampling methods (Lindenfors and Tullberg, 2006). A solid evaluation of the rule requires body mass values of high confidence from free-ranging populations, generally lacking for most primate species (Smith and Cheverud, 2002). The precision of body mass data is even more important when conducting within genus tests. Then it is important to have, for the same taxon, multiple populations that are relatively close in space and time and to sample, for each of the populations, a large number of adult males and females to reduce potential problems associated with sampling error. In one of the most systematic evaluations of the rule for primate groups, Gordon (2006a) tested the relationship within four different

taxa and found that the scaling of body mass and SSD was positive for baboons (*Papio anubis*), but negative for tamarins (*Saguinus mystax*) and vervets (*Cercopithecus aethiops pygerythrus*).

The apparent support of Rensch's rule with regards to canine dimorphism is worth considering, its preliminary nature notwithstanding. I consider it preliminary for at least two reasons: (1) sample sizes are small for some of the smaller species and, (2) there are most likely profound differences in the reliability of measurements across taxa. The data on smaller species come from museum specimens, whereas the data on *A. azarai* were collected from anesthetized individuals measured in the forest. In view of studies suggesting that, in haplorhines, the effects of sexual selection on canine size are stronger than those on body size (Plavcan and Van Schaik, 1997; Thoren et al., 2006) it will be important to confirm the validity of this preliminary finding.

What are possible mechanisms, evolutionary and/or proximate responsible for a positive or negative scaling relationship? Although Rensch's rule has been found to be applicable to a wide range of nonprimate taxa (Abouheif and Fairbairn, 1997; Fairbairn, 1997; Weckerly, 1998; Webb and Freckleton, 2007), the mechanisms explaining the relationship are still debated (Blanckenhorn, 2005; Dale et al., 2007). The hypothesis that allometry evolves because of correlational selection between the sexes appears most promising as a general model (Plavcan, 1998), still it remains difficult to test. The testing of predictions has been particularly difficult for primate taxa because there is a general lack of knowledge about the selective forces that may be operating on each taxon (Gordon, 2006a).

Gordon recently proposed a new model to predict the relationships between sex-specific size and relatively variability (2006a) under a range of situations including different intensity and direction of selection in males and females. His evaluation of four different populations of moustached tamarins (*Saguinus mystax*) is particularly relevant. Moustached tamarins live in social groups that include a small number of adult males (1–4) and females (1–4). Usually one female monopolizes most of the breeding and mates with more than one male (Huck et al., 2005). The observed negative scaling of size and SDD in both sexes of tamarins suggests that selection may have acted primarily on the females; a reasonable proposition given that in polyandrous groups there may be competition among females for securing the participation of males in the care of offspring. Owl monkeys live in socially monogamous groups and show intense paternal care of the infant (Fernandez-Duque et al., 2009). There is evidence to suggest that competition for reproductive positions between resident females and solitary females

is intense and as frequent as between males. Thus, it seems possible that selection may have operated primarily on increasing female size in owl monkeys.

Sex differences in body mass, body measurements, and canines

Adult male and adult female owl monkeys look very much alike. Still, the average male body length was 1.5% (0.5 cm) longer than the average female body length. And females had hind limbs that were 1.4% (0.4 cm) longer than those of males. On the other hand, sex differences in canine size were more pronounced. Males had upper canines that were 25% higher (1.1 mm) and 10% wider (0.3 mm) than those of females. Although there have been reports indicating larger canines in male than female owl monkeys (Swindler, 1976; Kay et al., 1988), the reported sex differences are not as marked, in particular with regard to the height of the upper canines.

Among many primate taxa, sexual dimorphism has frequently been explained as evolving primarily in response to selective forces acting on male size rather than female size given the assumed bigger advantages of larger body size in males than females (Gordon, 2006a; Kappeler, 1990; Ford, 1994; Lindenfors, 2002). Studies indicate that sexual size dimorphism in primates is primarily caused by intrasexual selection on male size, whereas female size may also increase due to genetic correlation between the sexes. This hypothesis has received good support, at least partially because much of the discussion about the relationship between sexual dimorphism, mating systems and levels of competition in primates has centered around the clear and robust contrast between polygynous and monogamous taxa (Leutenegger and Kelly, 1977; Plavcan and van Schaik, 1992; Leigh, 1995; Plavcan et al., 1995; Mitani et al., 1996; Plavcan, 2001; Thoren et al., 2006). The general conclusion is that polygynous species are more sexually dimorphic than monogamous ones, and that within polygynous species sexual dimorphism in body and canine size also increases with increased competition. Although the relationship may hold at the interclade level or in a comparison of polygynous and monogamous taxa, our understanding of the causal relationships among those factors is somewhat limited.

In some primate clades, the relationships among mating system, male–male competition, and sexual dimorphism are less clear or have not been thoroughly examined. Among Malagasy lemurs there are well known mismatches between mating system, social organization and morphological traits where allometric and traditional sexual selection models cannot account for low size dimorphism (Godfrey et al., 1993; Schmid and Kappeler, 1998). Malagasy lemurs cover a wide range of body sizes (60 g–10 kg) and mating systems (Kappeler, 1997), but do not exhibit any significant sexual dimorphism in body mass or tooth characteristics. Thus, it has been suggested that traditional mating system categories may be inadequate indicators of the nature and intensity of intrasexual competition in this primate group (Richard, 1992). After examining possible hypotheses for explaining the lack of dimorphism in extinct lemurs, Godfrey (1993) proposed that hypometabolism and intersexual resource competition during a critical period in the reproductive cycle of females may have constrained the evolution of sexual size dimorphism in Malagasy lemurs.

To evaluate the hypothesis that sexual dimorphism evolves through the operation of sexual selection, we need solid data on the extent of male and female intrasexual competition. Lawler looked for possible signals of sexual selection on morphological traits and considered alternative socioecological mechanisms that may influence those relationships among Verreaux's sifakas (*Propithecus verreauxi verreauxi*) (2009). He found that directional selection does not seem to operate on body mass or canine size, but instead on traits like leg shape suggesting that behaviors related to locomotion may be more relevant to the reproductive success of males than those related to fighting. Stabilizing selection may be a mechanism contributing to reduced sexual dimorphism through its operation on male body size since males with intermediate body mass show the most reproductive success, with reduced fitness among the larger but less agile males and the smaller but less competitive ones. A second mechanism he proposed to explain the lack of sexual dimorphism in sifakas is reproduction outside the group. If monogamy is the prevailing mating system, but some males obtain extra-pair copulations and fertilizations there will be increased opportunities for intrasexual selection (Webster et al., 1995). Given the significant difference in canine size between males and females and the infrequent, but intense, competition observed between resident adults and solitaries and between neighboring groups it seems entirely plausible that owl monkey males are competing outside their socially monogamous groups for access to females.

The relationship between sexual dimorphism, mating strategies and intrasexual competition in other owl monkeys species and other socially monogamous neotropical primates (i.e., *Callicebus*, *Pithecia*) will require more information than is currently available. It is primarily group size information that has been used to infer a monogamous mating system in *Callicebus*, *Pithecia*, and *Aotus* (Fernandez-Duque, 2011; Norconk, 2011). Although the findings are robust for titis and owl monkeys, the situation is less clear for sakis, given reports of larger groups (Aquino et al., 2009; Norconk, 2011). Although owl monkeys, titi monkeys and saki monkeys are regularly considered to display “low frequency, low intensity” competition, the behavioral and demographic data from identified individuals that can support those classifications is, at best, limited. Assuming competition levels based on the observed level of sexual dimorphism in museum specimens is problematic, since it leads to circular reasoning when concluding that their competition level matches the predicted extent of dimorphism.

Extant and fossil primates: behavior and morphology

The behavior and morphology of extant primates will continue to be a valuable source of information for the reconstruction of early hominin morphology and behavior (Plavcan, 2000). The extent of dimorphism in skeletal material and canines is consistently used to infer aspects of the social behavior and mating patterns of early hominins and fossil primates. “Sexual dimorphism is the primary morphological evidence for social behavior in early hominins” (p. 318 Plavcan et al., 2005), although paleontologists also claim that “skeletal dimorphism in itself is a poor predictor of reproductive strategy in hominoids” (p. 9409, Reno et al., 2005). Two recent studies illustrate adequately the use of published literature on owl mon-

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keys and other socially monogamous taxa for inferring the behavior of fossil hominins. A recent evaluation of the evolution of male care in *Homo erectus* was heavily informed by patterns of care in extant primates (Gettler, 2010) and a reexamination of human origins in light of *Ardipithecus ramidus*, was based on a rather selective use of data on socially monogamous primates (Lovejoy, 2009).

Behaviorally, data on owl monkeys have also been used to reconstruct the behavior of fossil owl monkeys. A new specimen of *Aotus dindensis* consisting of cranial fragments and isolated teeth of the upper and lower jaws led the authors to propose that the specimen could have been a male individual of a sexually dimorphic monkey in a nonmonogamous social system (Takai et al., 2009). However, the suggestion seems premature given that our *Aotus azarai* population shows strict social monogamy together with some conspicuous sexual dimorphism of the canines. Second, the authors suggested that the large upper canines of the specimen may be indicative of diurnal activity pattern (Takai et al., 2009) because it is during the day that the visual display of large canines would be more adaptive. Our data do not support the hypothesis that the increased sexual dimorphism in the canine size of *Aotus azarai* could be associated to its partially diurnal activity patterns. Although male and female owl monkeys regularly fight, threat displays where the canines are visually displayed are not regularly observed.

The owl monkey data I presented makes only a small contribution to our understanding of the relationships among mating systems, intra and intersexual competition and sexual dimorphism. The study highlights, once again, the need to acknowledge the limitations of the available data and the potential complexity of the relationship between monogamous behavioral patterns and dimorphism (Plavcan, 2001; Lawler, 2009). It is necessary that the limitations of our understanding of socially monogamous nonhuman primate species be properly acknowledged when used to infer hominin behavior.

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