

Impact of Intrasexual Selection on Sexual Dimorphism and Testes Size in the Mexican Howler Monkeys *Alouatta palliata* and *A. pigra*

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ABSTRACT One of the goals of physical anthropology and primatology is to understand how primate social systems influence the evolution of sexually selected traits. Howler monkeys provide a good model for studying sexual selection due to differences in social systems between related species. Here, we examine data from the sister howler monkey species *Alouatta palliata* and *A. pigra* inhabiting southeastern Mexico and northern Guatemala. We use a resampling approach to analyze differences in sexual dimorphism of body and canine size. In addition, we compare testes size as a way of gauging the intensity of sperm competition in both species. Morphometric data were collected from wild-caught individuals, including

body mass and length, and dental data were obtained from casts from wild individuals and from museum specimens. Although *A. pigra* individuals are larger than their *A. palliata* counterparts, we find that both species exhibit similar levels of sexual dimorphism for all of the variables considered. Testicular volume results indicate that *A. palliata* male testes are on average twice as large as those of *A. pigra* males, suggesting more intense sperm competition in the former species. Our study shows that *A. pigra* is not highly sexually dimorphic as was once thought, and testes size differences suggest the need for a clearer understanding of howler monkey social systems. *Am J Phys Anthropol* 146:179–187, 2011. ©2011 Wiley-Liss, Inc.

The theory of sexual selection was proposed to explain the presence of weaponry and/or ornamentation in males in addition to female discrimination of potential reproductive partners (Darwin, 1871). Sexual selection within the sexes, or intrasexual selection, favors traits that allow males to monopolize mating with receptive females, either by preventing rival males from gaining access to females or by maximizing their chances of fertilization (Kappeler and van Schaik, 2004). Larger body size and canine weaponry can confer a fitness advantage to primate males (e.g., mandrills, Leigh et al., 2008). One possible consequence of this advantage is the development of sexual dimorphism (or the difference in form between males and females of the same species). Sexual dimorphism in body mass and canine size is common in primate species (Plavcan and van Schaik, 1997). Presumably, the degree of sexual dimorphism would be greater in species in which males fight with each other for direct access to receptive females than in species that exhibit less male–male competition (Clutton-Brock et al., 1977; Alexander et al., 1979). However, the correlation of the level of sexual dimorphism with the intensity of sexual selection in primates is not always clear, partly due to difficulties in finding appropriate measures to estimate the intensity of sexual selection (Plavcan, 2004), which have included the socioeconomic sex ratio (Clutton-Brock et al., 1977), mating systems (Harvey et al., 1978; Leutenegger and Cheverud, 1985; Lindonfors, 2002), the operational sex ratio (Mitani et al., 1996), and competition levels (Kay et al., 1988; Plavcan and van Schaik, 1992; Ford, 1994). In addition, many comparative analyses suggest that multiple factors (such as mate choice, allometry, phylogenetic constraints, and natural selection

to name a few) can influence the expression of sexual dimorphism in primates (reviewed in Plavcan, 2001).

Intrasexual selection can also occur after mating via sperm competition, when multiple males copulate with the same female during a reproductive cycle (Birkhead and Kappeler, 2004). Therefore, male fitness depends not only on the ability to mate with females but also on successful fertilization. It has been demonstrated that in many primate species where females mate with more than one male, males have larger testes in relation to body size than in monogamous or polygynous species (Short, 1979; Harcourt et al., 1981; Harcourt, 1997). For example, in chimpanzees (*Pan troglodytes*), which live in multimale/multifemale groups, males have large testes on the order of approximately 120 g of combined weight, whereas the polygynous single-male gorillas (*Gorilla gorilla beringei*) have testes weighing 30 g (Dixson and

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Brancoft, 1998). Larger relative testes size accommodates greater sperm production and larger ejaculates (Setchell, 1978; as cited in Kenagy and Trombulak, 1986); hence, individuals with larger testes would in turn increase their chances of fertilization.

Mexican howler monkeys, *Alouatta palliata* (mantled howler monkey) and *A. pigra* (Central American black howler monkey), have marked differences in their social systems (Crockett and Eisenberg, 1987; Neville et al., 1988; Treves, 2001) and constitute a good model to explore the differences in sperm competition, as well as how the intensity of intrasexual selection affects sexual dimorphism in closely related species. Having diverged around 3 million years ago (Cortés-Ortiz et al., 2003), *A. palliata* and *A. pigra* are sister species that can be clearly distinguished on the basis of genetics (Cortés-Ortiz et al., 2003), cytogenetics (Steinberg et al., 2008), and morphology (Lawrence, 1933; Smith, 1970). Differences in social systems include that *A. pigra* groups usually range from 2 to 12 individuals, with groups averaging 4 to 8 individuals (Crockett and Eisenberg, 1987; Treves, 2001; Chapman and Pavelka, 2005; Van Belle and Estrada, 2006; Rosales-Meda et al., 2008). On the other hand, *A. palliata* typically have groups that are much larger than those of *A. pigra*, ranging from 2 to 45 individuals and averaging 8 to 23 individuals per group (Crockett and Eisenberg, 1987; Neville et al., 1988; Chapman and Balcomb, 1998; Treves, 2001; Pavelka and Chapman, 2006; Di Fiore and Campbell, 2007). The relative number of females per troop also differs between species: whereas *A. palliata* troops have a sex ratio between 1.37 and 4.11 females per male, the smaller *A. pigra* troops have a sex ratio between 1.2 and 2.1 females per male (Crockett and Eisenberg, 1987; Neville et al., 1988; Treves, 2001; Van Belle and Estrada, 2006). Females of both species are only receptive during 2–6 days of their approximately 16-day cycle (Glander, 1980; Van Belle et al., 2009), during which males must compete to gain reproductive access. In *A. pigra*, females copulate most often with the dominant male (Van Belle et al., 2009), whereas in *A. palliata* copulations with multiple males during a female's estrus cycle are common (Jones and Cortés-Ortiz, 1998; Wang and Milton, 2003).

In both species, males and females migrate from their natal groups and join other groups (Van Belle and Estrada, 2006; Clarke and Glander, 2008). In *A. palliata* male takeovers usually do not involve the ousting of resident males (Glander, 1980), but instead are a way to attain group membership by the invader male (Dias et al., 2010). Although nonalpha *A. palliata* males may face decreased possibilities of monopolizing a receptive female, they can still achieve reproduction through alternative strategies (Jones, 1985; Cortés-Ortiz, 1998; Jones and Cortés-Ortiz, 1998). Small, low-ranking males in these groups would still have an opportunity to reproduce by being able to sneak in copulations and pass on their characteristics to their offspring (i.e., not only large males will sire offspring). Furthermore, a larger number of females in the group implies a higher probability that two or more will be in estrus simultaneously, facilitating the access of multiple males to receptive females (Dunbar, 1988). In contrast, *A. pigra* males are often expelled from the group during a takeover (Brockett et al., 2000). As groups usually have one or two males, the invader male may actually be able to force out all resident males. However, it has been suggested that males in *A. pigra* groups are kin-related and cooperate in the defense of the group (Kitchen, 2004). Therefore, it would

be harder for an invader male to defeat a coalition of two or more related resident males. Only large males (and presumably those with large canines that can be useful during battle) would be able to successfully defeat a coalition of resident males, and so it would be expected that large body size and canines would be selected for by being preferentially passed on to the next generation.

In this study, we analyze sexual dimorphism and testes size for the two species of Mexican howler monkeys and explore the connection of these variables with male–male and sperm competition. While sexual dimorphism has been investigated via broad comparative analyses, a closer look at these two related species with different social systems can help to parse out some of the determinants of sexual dimorphism, at least in platyrrhines. Given the complexity of the social dynamics of these species (presented above), it is difficult to establish straightforward predictions in terms of the expression of sexual dimorphism for each species. The socionomic sex ratio alone suggests that *A. palliata* has more intense male–male competition and reproductive skew than *A. pigra*. This would imply that *A. palliata* should be more sexually dimorphic than *A. pigra*. Yet, since *A. palliata* groups are large and males may have difficulty monopolizing females, reproductive skew may be lower in this species than in *A. pigra*. Furthermore, although many *A. pigra* groups are unimale, the sex ratio is generally low, and the suggestion that group males are related could mean lower intragroup male–male competition. However, kinship of males in the group and the formation of coalitions may intensify intergroup male–male competition for group takeover. These issues, in addition to the role played by female choice and competition, complicate inferences that can be made about sexual dimorphism in body and canine size.

Alouatta pigra has been reported to be more sexually dimorphic in body size than *A. palliata* (Jungers, 1985; Ford and Davis, 1992; Ford, 1994). However, previous analyses are based on a very small sample size (only two males) for *A. pigra*, so it remains unclear whether a larger sample size supports this difference. Canine data is available for both *A. palliata* and *A. pigra* (Swindler, 2002; Plavcan and Ruff, 2008) although not specifically for *A. palliata mexicana*. Testes size (only in terms of mass, not volume) has only been reported for *A. palliata* (Harcourt et al., 1981). With greater sampling of body mass data and newly acquired testicular volume and dental data from wild-caught individuals of both species, in this study we examine how body and canine size dimorphism and testicular volume vary between the two species, and discuss how the observed patterns may have been shaped by differences in social systems between *A. pigra* and *A. palliata*.

METHODS

Data collection

Between 1998 and 2008, we collected morphometric measurements, dental molds, and blood samples of howler monkeys from southeastern Mexico (*A. palliata* and *A. pigra*) and Northern Guatemala (*A. pigra*). We followed capturing procedures described in Rodríguez-Luna and Cortés-Ortiz (1994). Sample sizes for the collected data are shown in Table 1.

Although *A. pigra* and *A. palliata* are known to naturally hybridize in Mexico (Cortés-Ortiz et al., 2007), individuals in this study are all considered to be purebred. Both pure *A. palliata* and *A. pigra* individuals were col-

TABLE 1. Sample size (N), mean, standard deviation (SD), and ranges for *A. pigra* and *A. palliata* morphological variables for both sexes and results of testing for significance of the differences between the two species (*P* value)

	<i>A. pigra</i>				<i>A. palliata</i>				<i>P</i> value
	<i>N</i>	Mean	SD	Range	<i>N</i>	Mean	SD	Range	
Body mass (kg)									
Female	32	5.68	0.63	4.50–6.8	37	4.39	0.48	3.60–5.25	<0.001
Male	37	7.60	1.13	5.50–9.60	25	5.80	0.69	4.60–7.20	<0.001
Sitting height (cm)									
Female	32	43.5	2.9	34.5–49.0	36	38.8	2.4	33.0–43.7	<0.001
Male	37	48.5	3.2	42.6–58.0	26	41.0	2.3	37.0–45.4	<0.001
Testicular volume (cm ³)	36	11.33	3.79	5.06–18.95	24	22.66	10.89	11.39–61.22	<0.001
Canine height (mm)									
Female	18	8.88	1.39	7.12–11.63	23	8.14	1.06	6.65–10.06	0.083
Male	20	14.23	2.00	9.00–17.00	19	14.01	1.75	11.29–17.75	0.509
Canine mesiodistal length (mm)									
Female	9	6.72	0.43	6.06–7.35	15	6.15	0.49	5.12–7.18	0.006
Male	10	8.29	0.76	7.48–9.53	10	8.08	0.63	7.00–8.93	0.597
Canine labiolingual length (mm)									
Female	8	5.11	0.39	4.81–5.92	13	4.76	0.36	4.25–5.62	0.060
Male	9	6.57	0.75	5.64–7.62	10	6.81	0.97	5.44–8.65	0.744

lected outside the known hybrid zone in Tabasco (Cortés-Ortiz et al., 2007). We also included individuals from within the hybrid zone after confirming parental species status using 11 microsatellite markers, five of which are diagnostic of hybridization (Cortés-Ortiz et al., 2009). Procedures for capturing and handling primates were approved by the University Committee on Use and Care of Animals (UCUCA) at the University of Michigan.

We used only adults in this study. As we did not track these individuals from birth, we could not ascertain the exact age and had to rely on other proxies to determine adult status. For both species, we followed dental development and wear patterns of captured individuals according to the criteria developed in Pope (1966), and we assigned adult status for individuals with fully-erupted dentition and the third molar in functional occlusion, and at least slight wear found on some of the premolars and first molar. Howler monkeys are known to have reached sexual maturity at that stage (DeGusta and Milton, 1998), and although most craniometric studies only use the criterion that all teeth are erupted to determine adult status (Ravosa and Ross, 1994; Jones et al., 2000), we believe that our criteria is more stringent by including all sexually mature individuals.

Morphometrics. Once animals were captured, mass measurements were collected using a 20-kg Pesola® spring scale to the nearest 100 g. Body mass is commonly used as a marker of overall body size in living primates (e.g., Ford and Davis, 1992). Here we used body mass and a linear body length measurement to estimate sexual size dimorphism in the two species. Mass data for *A. palliata* from different sites throughout their geographic distribution have been reported extensively (17 studies and *N* >459 individuals: Ford and Davis, 1992; Glander, 2006), but data for *A. pigra* are scarce. Most studies that use body mass data for *A. pigra* relied on the data presented by Murie (1935) and Jungers (1985), with a sample size of two males and three females. Our larger *A. pigra* sample provides a more accurate representation of average *A. pigra* body mass (32 females and 37 males).

The body length measurement analyzed in this study is the sitting height (i.e., the length of the head and body excluding the tail, similar to the measurement

used by Schultz, 1929). This measurement was taken dorsally from the junction of the last lumbar and first caudal vertebrae to the occipital protuberance of the head using a metallic measuring tape to the nearest 0.1 cm. Body length measurements are sometimes favored over body mass measurements because they are less subject to variation caused by nutritional and health status (Alexander et al., 1979). We use both measurements in this study to account for possible biases due to such factors.

Dental casting. While the animal was anesthetized, negative dental impressions were made using vinyl polysiloxane material (Exaflex™ Putty, GC America, Alsip, IL). Casts were poured using polyester laminating resin thickened with talc and catalyzed with methyl-ethyl-ketone (Eastpointe Fiberglass Sales, Eastpointe, MI). A paired *t*-test was used to compare upper canine height measurements performed in the field with measurements taken from the casts of the same individuals (*N* = 50). Results of these tests revealed no significant differences (*t* = -0.491, *P* = 0.626), indicating that our casts were representative of live specimens. All measurements were made with Mitutoyo® Digital Calipers to the nearest 0.01 cm.

Canine measurement. We measured upper canine height, mesiodistal length, and labiolingual (also known as buccolingual) length from dental casts. Our own field observations suggest that upper canine height is highly susceptible to wear, and some wear was observed in the mesiodistal dimension as well. However, considering that wear is a continuous process and begins to occur prior to complete eruption of the tooth, we decided to include these data and consider this source of error in our analysis, excluding any teeth that were heavily worn. Our measurement of upper canine height is taken from the apex to the buccal-gingival margin, which is slightly above the cementum-enamel junction due to the presence of the gum in live-captured individuals. The mesiodistal and labiolingual dimensions are measured as described in Plavcan and van Schaik (1992) but are not exactly analogous to those measurements due to the presence of gum tissue in wild-captured individuals. We also included museum dental specimens housed at the University of Michigan Museum of Zoology mammal col-

lection ($N = 9$). Only Mexican *A. palliata* museum samples were included, and all *A. pigra* museum samples (which include those individuals analyzed by Murie, 1935) came from Petén, Guatemala. In the casts of live animals, measurements for upper canine base dimensions were made at the gum line. Museum specimens retained stains on the canines that indicate the location of the gum line when the animals were alive, making it possible to perform analogous measurements in live and museum specimens. We measured left maxillary canines, and in cases where the tooth was broken we used the right maxillary canine ($N = 2$).

Testicular volume. To determine testicular volume, we measured testicular breadth and length to the nearest millimeter using Mitutoyo® Digital Calipers, excluding scrotal skin folds. We used the following formula for calculating the volume of a prolate spheroid: $\pi LW^2/6$; where L is length and W is width (Harrison et al., 1977). We utilized total testicular volume (sum of left and right testes) to account for any variability that exists between the left and right testes and to have data that are comparable to results presented in the literature. Comparison of testes size across species often involves relating absolute testicular volume with body mass (Short, 1979; Harcourt et al., 1981); here we only present absolute testicular volume, but using relative volume did not affect our results.

Statistical analyses

We used the Shapiro–Wilk test of normality and found that of 22 sample groups, all were normally-distributed except for 4: *A. palliata* male sitting height and *A. pigra* female body mass, sitting height, and canine labiolingual length. For that reason and since some sample sizes are small, we used the Mann–Whitney nonparametric test to determine whether there were significant differences between the sexes (except for testicular volume) and between the species.

To quantify sexual dimorphism, we used the intuitive ratio of average male to female values, which is widely used since the larger sex is preferred in the numerator (Smith, 1999). Because sample sizes and variances are unequal and because some of the variables are not normally distributed, we utilized a resampling method to avoid making assumptions about how the data were distributed (Lee, 1999). We pooled males of the two species in one group and females in the other. We randomly selected and averaged a group of males based on the male sample size of one species and divided that value by the average of a randomly selected group of females based on the female sample size of the same species to obtain a value of sexual dimorphism. We repeated this procedure to obtain a random value of sexual dimorphism for the second species, and then subtracted the dimorphism values of the two species from one another. This process was repeated 10,000 times to generate a distribution of randomly sampled sexual dimorphism differences. Then, we tested the null hypothesis that our test statistic, which is the difference between the actual sexual dimorphism values of *A. palliata* and *A. pigra*, fell within the 95% confidence interval (alpha value of 0.025 for a two-tailed test). Statistical analyses were done using SPSS 16.0 and the Resampling Statistics Excel macro.

TABLE 2. Dimorphism values (mean male/mean female) for *A. pigra* and *A. palliata*, and results of testing for significance of differences in dimorphism using resampling

	<i>A. pigra</i>	<i>A. palliata</i>	<i>P</i> value ^a
Body mass dimorphism	1.34	1.31	0.431
Sitting height dimorphism	1.12	1.06	0.053
Canine height	1.60	1.72	0.127
Canine mesiodistal length	1.23	1.31	0.113
Canine labiolingual length	1.29	1.43	0.059

^a *P* value represents the significance value generated using resampling statistics.

RESULTS

Table 1 shows the descriptive statistics for body mass, sitting height, canine dimensions, and testicular volume for both species. Table 1 also shows results for significance testing of all variables for differences between the species for each sex. Males are significantly larger than females for all variables ($P < 0.001$). Both male and female *A. pigra* individuals are heavier in body mass and larger in sitting height than their *A. palliata* counterparts. Interestingly, male upper canine dimensions are not significantly different between the two species but female canine mesiodistal length is, and other female dimensions approach significance.

Although *A. pigra* males are the larger of the two, *A. palliata* males have testes that are twice as large as their *A. pigra* counterparts. The difference in absolute testicular volume is great enough that correcting for the effects of body size has no bearing on our results and only serves to increase the difference in the relative testicular volume between the two species.

Table 2 shows the sexual dimorphism values for body mass, sitting height, and upper canine dimensions, and the significance values from the resampling test. Upper canines exhibit greater dimorphism than body mass (while canine dimensions are linear, body mass is volumetric, so taking the cube root gives values of 1.10 and 1.09 for *A. pigra* and *A. palliata* respectively). Nevertheless, neither body mass, sitting height, nor canine dimensions showed any significant differences in sexual dimorphism between the species.

DISCUSSION

Our results show that overall *A. pigra* males and females are bigger than their *A. palliata* counterparts, but have similar upper canine size, and that both species exhibit sexual dimorphism in body mass, sitting height, and upper canine size. Our data for *A. palliata mexicana* fall within the ranges in mass reported by other authors for *A. palliata palliata* inhabiting Costa Rica (Ford and Davis, 1992; Glander, 2006), but not for *A. palliata aequatorialis* in Barro Colorado Island, Panama (Scott et al., 1977; Glander, 2006). On the other hand, *A. pigra* average male body mass has been overestimated (11.352 kg; Ford and Davis, 1992), probably because most studies for *A. pigra* relied on the data presented by Murie (1935) and Jungers (1985) using males on the largest end of their size range. Because of the overestimation in male size in previous studies, *A. pigra* has been found to be highly sexually dimorphic (1.764; Ford and Davis, 1992). However, in our study the degree of sexual dimorphism for all three variables does not differ between *A. palliata* and *A. pigra*. On the other hand, the evidence

that *A. palliata* testes are much larger than those of *A. pigra* supports the argument that there is more intense post-copulatory competition in *A. palliata*.

Sexual dimorphism

In most anthropoid primates, males are larger than females (Plavcan, 2001). Although platyrrhines on the whole have been characterized by lesser degrees of body mass dimorphism, some authors claim that *A. pigra* is the exception, with body mass dimorphism comparable to cercopithecoid species (Ford, 1994). Our new data do not support that view, and instead place *A. pigra* within similar body mass and length dimorphism ranges as other New World primates with high levels of male–male competition (e.g., *Saimiri* and *Cebus* species), and more specifically, similar to some other howler monkey species (Alexander et al., 1979; Kay et al., 1988; Ford, 1994; Plavcan and Ruff, 2008).

Like in body mass and length, we found that both species exhibit sexual dimorphism in upper canine size. When used as a weapon, a canine is most effective with respect to its height (Greenfield and Washburn, 1992; Plavcan, 1993). While some argue that, in addition to canine height, the basal dimensions are also good indicators of competition (Lucas et al., 1986), others have found them to be weakly correlated with behavioral measures (Plavcan, 2000). While we present upper canine data for *A. palliata mexicana*, and although our measurements on teeth of live-captured animals are not necessarily comparable to measurements normally conducted on museum specimens (see methods), all dimensions seem to be similar to other *A. palliata* reported values (Swindler, 2002; Plavcan and Ruff, 2008). Our sexual dimorphism values are slightly higher for *A. palliata* labiolingual length primarily because we observed larger male measurements. Our *A. pigra* values are higher than those reported by Swindler (2002; summarized in Plavcan and Ruff, 2008) of 1.1 for canine mesiodistal length, 1.12 for canine height, and 1.11 for canine labiolingual length, but are in agreement with values reported in Plavcan and van Schaik (listed as *A. villosa*, 1992). All these values fall within the range of canine sexual dimorphism values for many New World monkeys such as *Ateles*, *Lagothrix*, and other *Alouatta* species, but are not as high as those of many Old World monkeys like *Macaca* or *Papio* (Plavcan, 2001; Thorén et al., 2006).

Sexual size dimorphism in anthropoids is generally associated with male reproductive skew depending primarily on precopulatory competition, in which selection leads to increased male weaponry (e.g., large canines: Plavcan and Kay, 1988; Kay et al., 1988; Plavcan, 2001) and competitive ability (e.g., large body size: Ford, 1994; Mitani et al., 1996; Plavcan and van Schaik, 1997; Plavcan, 2001). The fact that both *A. palliata* and *A. pigra* are dimorphic in both upper canine teeth and body size fits well with the concept that sexual selection has favored these traits because of the advantages they confer in winning fights (Plavcan, 2001). Indeed, there is evidence in both species for aggressive encounters among males that lead to fights, injuries and death (DeGusta and Milton, 1998; Cristóbal-Azkarate et al., 2004; Van Belle et al., 2008; Dias et al., 2010). Body mass dimorphism for these two species appears to be similar to those reported for other howler monkeys (see Ford and Davis, 1992; Plavcan and Ruff, 2008). However,

upper canine dimorphism data is more variable across the genus (Plavcan and Ruff, 2008), although given methodological differences with other studies and without significance testing, the apparent differences in dimorphism values may not reflect real differences among all the species.

For all of the measures of sexual dimorphism considered in this study, we found no statistically significant differences between the two species, despite the differences between the species in the availability of receptive females over space and time and the differences in male and female mating strategies. Females of *A. palliata* will not only mate with the dominant, and presumably largest, male but may also mate with smaller males, when the dominant male is unable to monopolize access to all receptive females (Cortés-Ortiz, 1998). However, *A. palliata* sexual dimorphism is not reduced in comparison with *A. pigra* despite that whenever females copulate with more than one male, sexual dimorphism is typically reduced (Harvey and Harcourt, 1984; Dunbar and Cowlishaw, 1992; Plavcan, 2001). Perhaps greater sexual dimorphism that is otherwise expected in *A. pigra* (since one male is more likely to monopolize reproduction) is tempered by his relatedness to the other group males. While the lack of differences in sexual dimorphism between *A. palliata* and *A. pigra* may result from a similarity in the intensity of male–male competition in the two species, other determinants could also affect male and female body and canine size independently. Phylogenetic factors, especially considering the similarities in body mass sexual dimorphism of the species considered in this study with other howler monkeys (possibly with the exception of *A. caraya*), could restrict changes in sexual dimorphism (Cheverud et al., 1985; Plavcan, 2001). Female–female competition and female choice are also likely to contribute to sexual dimorphism in these howler monkeys.

Female–female competition may increase female body and canine size, leading to smaller differences between males and females (Plavcan and van Schaik, 1992). Howler monkey females may compete against one another not only for resources, but also to avoid infanticide risk (Ostro et al., 2001). Large groups with many females are good candidates for male takeover (Crockett, 2003), so it would be in a female's interest to keep group size down by evicting other females (Pope, 2000). This would limit the selection on males for larger body and canine size, and would also result in selection on females for those traits (Plavcan, 2001), as the ability of natal females to compete against immigrating females and expelling nonrelated females from their group may also depend on the development of weaponry and larger body size. In *A. pigra*, where extra-group male takeovers are common and sometimes result in infanticide (Brockett et al., 1999; Horwich et al., 2001), females may choose to limit group size by engaging in aggressive encounters, much like in red howler monkeys (Crockett, 1984). Male takeover, infanticide, and female emigration also occur in *A. palliata* (Clarke and Glander, 1984; Crockett and Eisenberg, 1987; Glander, 1992). However, when many males exist in a large group, one male is unable to monopolize all females, and females may develop less costly strategies to confound paternity and lower risk for infanticide (Crockett and Janson, 2000, see female choice below). The *A. pigra* female canine mesiodistal length is significantly larger than that of *A. palliata* females. Relative canine size of males and females, and not only sex-

ual dimorphism, can be informative on the levels of intrasexual competition (Plavcan, 2004). Therefore, whereas the similarity in sexual size dimorphism between the two species could mean that both have the same intensity of precopulatory male–male competition, the facts that both male and female *A. pigra* individuals are larger in body size than their *A. palliata* counterparts, and females have larger canines, suggest the alternative possibility that for both sexes, competition is greater in *A. pigra* than it is in *A. palliata*.

Female choice may also play a role in shaping sexual dimorphism (Plavcan, 2004). On the one hand, females may choose to confound paternity by mating with multiple males as a strategy to counteract infanticide (Plavcan, 2001). *A. palliata* females are known to copulate with several males in their group (Cortés-Ortiz, 1998; Jones and Cortés-Ortiz, 1998; Wang and Milton, 2003) and *A. pigra* females sometimes cross the boundaries of their own group and mate with extragroup males (Horwich, 1983, 2000; Van Belle et al., 2009). On the other hand, females may choose to associate with specific males that they select to sire their offspring and protect them (Plavcan, 2001). Van Belle et al. (2009) present evidence that *A. pigra* females direct many of their sexual solicitations specifically towards dominant males. Therefore, female choice is likely to be an important factor in the evolution of sexual dimorphism in howler monkeys.

Additional studies of howler monkey social behavior and genetic data on paternity are needed to further elucidate the correlates of sexual dimorphism in these species. Nevertheless, our knowledge of these howler monkeys' social systems suggests that both male and female reproductive strategies can influence the degree of sexual dimorphism in *A. palliata* and *A. pigra*, and that sexual dimorphism is not necessarily a unique function of male–male competition. Furthermore, these results highlight the complexity of primate social dynamics and the difficulty of drawing simple predictions about the levels of sexual dimorphism based on behavior, warning those researchers that make inferences about behavior from sexual dimorphism data of fossil taxa.

Testicular volume

Consistent with the prediction that testes size is larger in species with multimale groups, *A. palliata* males have larger testes than *A. pigra* males. In fact, the volume of *A. palliata* testes was twice as large as those of *A. pigra*. As these howler monkey species are nonseasonal breeders (Neville et al., 1988), we can assume that there is no seasonal variation in testicular volume (Muehlenbein et al., 2002) and that differences in testes size reflect differences in the intensity of sperm competition (Birkhead and Kappeler, 2004). Thus, sperm competition appears to be more intense in *A. palliata*.

Compared with other anthropoids, the *A. palliata* gonadosomatic index (testicular volume relative to body size) fits within the ranges documented for large group multimale/multifemale breeding systems, such as savanna baboons (Bercovitch, 1989), though it is not as large as many macaque species, which are known to have the highest levels of sperm competition (Harcourt et al., 1981). The gonadosomatic index of *A. pigra*, on the other hand, is slightly higher than those single male/polygynous species such as gorillas, orangutans, colobus monkeys or hamadrayas baboons (Harcourt et al., 1981). Another howler monkey species, *A. caraya*, exhibits a

combined testicular volume of approximately 16 cm³ (Moreland et al., 2001) and lives in groups that typically have 5–15 individuals (i.e., slightly larger than in *A. pigra*), which can be both unimale and multimale (Juárez et al., 2005). Compared with our measurements of 11 cm³ and 22 cm³ for *A. pigra* and *A. palliata*, respectively, these differences suggest more sperm competition in *A. caraya* than in *A. pigra*, but perhaps not as much as in *A. palliata*.

Early studies characterized *A. palliata* as predominantly polygynous with one dominant male monopolizing breeding opportunities with all the females in the troop (Clarke, 1983), and subordinate males copulating with females outside of the peak of the estrus cycle (Jones, 1985). However, the difference in testicular volume suggests that subordinate *A. palliata* males are sometimes successful at fertilizing receptive females. As noted earlier, *A. palliata* groups are large, and there can be up to six males and nine females in a group (Treves, 2001). In larger groups, it is statistically reasonable to assume that many females will be in reproductive synchrony (Dunbar, 1988), and a male must guard all of them against solicitations from other males. Thus, it may not be possible for one male to control access to all females in estrus. Observations from Mexico (Cortés-Ortiz, 1998; Jones and Cortés-Ortiz, 1998), Costa Rica (Jones, 1978) and Panama (Wang and Milton, 2003) indicate that *A. palliata* females may repeatedly copulate with different males during the same estrus cycle. As opposed to engaging in aggressive combat with the dominant male, subordinate males may instead benefit by sneaking in copulations (Harcourt, 1996). Sneaking males may copulate with a receptive female while the guarding male is momentarily away from the female, eating or chasing away other males (Cortés-Ortiz, 1998). Therefore, the high levels of sperm competition and the strong selection for larger testes observed in our data for *A. palliata* are consistent with our expectations based on what is known about the sociosexual behavior of this species.

As we mentioned earlier for *A. pigra*, females copulating with males of neighboring groups have been recorded (Horwich, 1983; 2000) but selection for larger testes would be weak if the dominant male succeeds at fertilizing most receptive females, as suggested by recent studies (Van Belle et al., 2009). In the red howler monkey, *A. seniculus*, where subordinate males may copulate with receptive females (Sekulic, 1983), paternity analysis showed that in nine different troops, only the dominant male sired all the offspring (Pope, 1990). To determine the extent of reproductive success and skew among *A. pigra* and *A. palliata* males, it is imperative to conduct long-term behavioral and genetic studies.

The results presented in this study provide strong evidence that corrects the misconception that *A. pigra* is more dimorphic than any other New World primate and sets up new hypotheses to be tested to understand the social systems of howler monkeys.

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