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Brief Communication: The Largest Relative Testis Size Among Primates and Aseasonal Reproduction in a Nocturnal Lemur, *Mirza zaza*

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KEY WORDS relative testis size; seasonal reproduction; strepsirrhines

ABSTRACT *OBJECTIVES:* Testis size is an indirect indicator of a species' mating system, along with sexual size and canine dimorphism, existence and usage of mating and advertisement calls as well as the spatial distribution of males and females ready to mate in solitary species. Upon its recent discovery, the northern giant mouse lemur *Mirza zaza* was suggested to have a polygynandrous mating system and to exhibit seasonal breeding. We tested these predictions in a field study in Sahamalaza National Park, NW Madagascar.
MATERIALS AND METHODS: We caught 12 *M. zaza*, before and during the suggested mating period and obtained standard field morphometric measurements, including testes size.
RESULTS: We show that *M. zaza* has the highest relative testis volume among primates, indicating strong sperm competition and polygynandrous mating. In addition, based on inferred age of captured animals, observed mating behavior, a female caught in met-estrus and data from captivity, we suggest *M. zaza* to be one of the few lemurs that breed aseasonally.
DISCUSSION: Future field work on this endangered species is required to illuminate the causes and consequences of intense promiscuity and aseasonal breeding despite strong habitat seasonality, which distinguish *M. zaza* from most other nocturnal lemurs. Am J Phys Anthropol 000:000–000, 2015.

INTRODUCTION

Sexual size and canine dimorphism, relative testis size, and spatial distribution of the sexes are often used as indirect indicators of primate mating systems (e.g., Leutenegger, 1978; Harcourt et al., 1981, 1995; Kappeler, 1997a). Monogamous species such as *Hylobates* spp. or *Aotus* spp. are morphologically characterized by a lack of sexual dimorphism and small testis size (Harcourt et al., 1981; Kenagy and Trombulak, 1986; Thorén et al., 2006). Polygynandrous or polygynous species with a predominant contest competition are physically competing about mates and thus show pronounced sexual dimorphism such as larger body size and large canines in males, but have relatively small testes, as seen in *Gorilla* spp. (Harcourt et al., 1981; Kenagy and Trombulak, 1986; Thorén et al., 2006). Species with a polygynandrous or polygynous mating system (Elgar et al., 2013) with scramble competition on the other side lack pronounced sexual dimorphism but have relatively large testes, and males may use copulatory plugs (Dixson and Anderson, 2002) such as *Brachyteles arachnoides* or *Lemur catta* (Milton, 1985; Kappeler, 1997b; Dixson and Anderson, 2002). Large testes and more sperm (Møller, 1989) are related to intensive sperm competition and mating with several females (Harcourt et al. 1981). Both types, scramble and contest competition may to some degree influence the mating system of a species, leading to a continuum of related traits. Male macaques *Macaca* spp. for instance are bigger than females, have larger canines but also large testes (Kenagy and Trombulak, 1986; O'Higgins and Collard, 2002; Thorén et al., 2006). Extra-pair matings exist in almost all mating systems (Isvaran and Clutton-Brock, 2007) but high extra-pair paternity does not necessarily lead to relatively large testes (Schülke et al., 2004). For species with a polygynandrous mating system, body mass and testis size may increase towards the onset of the mating season (Kappeler, 1997a; Schmid and Kappeler, 1998).

Most strepsirrhine primates do not show marked sexual dimorphism even though non-monogamous mating systems are common (Kappeler, 1990; Pochron and Wright, 2002). However, the harsh environment and seasonality of food availability in Madagascar constrain the length of most lemurs' mating seasons, so that males' ability to monopolize receptive females is limited (Harcourt et al., 1981; Young et al., 1990; Kappeler, 1991). Although Madagascar's many ecotones are indeed characterized by extreme seasonality, dietary specializations may allow some lemur taxa to evade seasonal breeding (Sterling, 1994).

Mirza zaza is a squirrel-sized nocturnal member of the family Cheirogaleidae found in the dry deciduous forests

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TABLE 1. Summary of morphological and behavioral characteristics of Mirza zaza *providing hints about their mating system*

Characteristics of *M. zaza*	Reference	Inferred mating system	Similar species (reference)
No sexual dimorphism	Stanger et al., 1995	Monogamous, polyandrous	*Aotus* spp. (Kappeler, 1997c); *Other strepsirrhines (*Kappeler *1990*, 1991*)*
Estrous call	Stanger-Hall, unpublished data	Promiscuous	*Mirza, Microcebus* (Stanger, 1993); *Daubentonia* (Sterling, 1993; Stanger and Macedonia, 1994)
Relatively large testes	Stanger et al., 1995; Kappeler, 1997a	Promiscuous	*Microcebus berthae* (Schwab, 2000)*; Mirza coquereli* (Kappeler, 1997b)*; Microcebus murinus* (Fietz, 1999b)
Copulatory plug	Stanger et al., 1995	Promiscuous, polygynous with sperm competition	*Microcebus berthae* (Schwab, 2000)*; Microcebus murinus* (Eberle and Kappeler, 2004)

Examples of other species exhibiting the respective characteristics are given.

of northwestern Madagascar. The species was found to be genetically, morphologically and behaviorally different from its sister taxon *Mirza coquereli* that is found further to the south (Markolf et al., 2008). In contrast to *M. coquereli* (Kappeler, 1997a,b,c), *M. zaza* is smaller in all standard morphometric measurements, except testis volume, and was found to sleep gregariously in nests with up to eight individuals, including several related and unrelated adult males and females (Kappeler et al., 2005; Rode et al., 2013). Both taxa are sympatric with up to five other lemur species, at least three of which cope with the harsh climate of Madagascar's northwest coast by using hibernation or torpor. During the cool dry season, *Mirza* spp. frequently consume homopteran insect secretions (Pages, 1980), which may fuel their year-round activity. Due to large testes, loud estrous calls and the presence of copulatory plugs, *M. zaza* was suggested to have a polygynandrous mating system (Stanger et al., 1995; Kappeler et al., 2005). Mating in the wild was suggested to occur between July and August (Kappeler et al., 2005), whereas captive animals at the Duke Lemur Center (DLC) cycled throughout the year, reproducing aseasonally (Stanger et al., 1995; animals were reported as *M. coquereli* but according to their capture site were *M. zaza*).

We aimed to clarify patterns of reproduction of *M. zaza* during a field study conducted from May to July 2010. We expect *M. zaza* to exhibit polygynandrous mating, as suggested based on nesting behavior and relatedness between animals sharing a nest (Rode et al., 2013). A combination of large testes, estrous calls, copulatory plugs (Table 1), and low prevalence of wounds would indicate a mating system characterized by predominant scramble competition. Assuming that their mating season is restricted to July and August, testis size and body mass of males should increase between May and July. We expected to observe animals mating and to capture estrous females in July. Finally, we also expected to capture distinctly smaller members of a cohort of subadults born in October of the previous year.

METHODS

Study site

The study took place in the Ankarafa Forest, northwestern Madagascar, during the dry season from May until mid-July 2010. The Ankarafa Forest (S14°22'64.2", E47°45'31.5") is situated on the Sahamalaza Peninsula, Region Sofia, within the boundaries of the UN Biosphere Reserve and National Park Sahamalaza—Iles Radama. Sahamalaza is located in a transition zone between the Sambirano evergreen rainforest domain in the north and the western dry deciduous forest region in the south. The strict seasonal climate is represented by a dry and cool season from May to September and a rainy and hot season from October to April. In contrast to the western dry deciduous forests where all trees shed their leaves many trees at Sahamalaza keep their foliage. Mean annual rainfall is 1,600 mm, mean annual temperature 28.0°C, and monthly temperatures range from 20.6°C in August to 32.0°C in November (Schwitzer et al., 2007).

TABLE 2. Identification codes, sex and age of all individuals captured at the given dates in Ankarafa forest research station in May and July 2010

ID	Sex	Age	1. Capture	2. Capture
M1	Male	Adult	16/05/2010	11/07/2010
M2	Male	Adult	18/05/2010	09/07/2010
FS1	Female	Adult	19/05/2010	09/07/2010
M3	Male	Subadult	19/05/2010	10/07/2010
F2	Female	Adult	22/05/2010	11/07/2010
FJ3	Female	Juvenile		10/07/2010
M4	Male	Adult	27/05/2010	18/07/2010
M5	Male	Adult	28/05/2010	11/07/2010
FS4	Female	Subadult	29/05/2010	10/07/2010
M6	Male	Adult		10/07/2010
MS7	Male	Subadult		13/07/2010
F5	Female	Adult		17/07/2010

Data collection

We captured *M. zaza* using 30 live traps (Tomahawk Live Traps size 12) in May and July to collect data before and during the mating season. Traps were placed at locations where guides had previously observed *M. zaza*, on heights of approximately 1.5 m above the ground. We captured eight animals in May and fitted them with TW3 rubber-coated cable tie radio-collars (Biotrack Ltd., UK, 3–4 g) for radio-tracking. These animals, plus four additional ones, were recaptured in July (Table 2) and all radio-collars were removed. We followed animals and observed their behavior (instantaneous behavior sampling and ad libitum) for a larger study (see Rode-Margono et al., 2015).

We anesthetized animals with Ketamine (0.01 ml/100 g body mass, 100 mg/ml) (Lahann, 2008), and sexed and weighed them. Teats and appearance of the vagina (external monitoring) were investigated to determine reproductive status of females (Stanger et al., 1995). Morphometric measurements were taken of adult *M. zaza* with electronic calipers, including testis length and width (Schmid and Kappeler, 1994). Testis volume was

TABLE 3. Body mass, absolute and relative testis volume (testis volume divided by body mass) at the first and the second capture of five male individuals of Mirza zaza *in May and July*

ID	Body mass 1 (g)	Body mass 2 (g)	Testis volume 1 (mm^3)	Testis volume 2 (mm^3)	Rel. testis volume 1 (mm^3/g)	Rel. testis volume 2 (mm^3/g)
M1	294	318	495.29	1,714.48	1.68	5.39
M2	256	247	4,874.00	3,654.97	19.04	14.80
M3	295	280	1,357.48	4,655.26	4.60	16.63
M4	264	269	3,060.46	4,612.51	11.59	17.15
M5	299	287	3,237.85	4,716.90	10.83	16.44
Median	294	280	3,060.46	4,612.51	10.83	16.44
Mean	281.60	280.20	2,605.01	3,870.82	9.55	14.08
SD	20.01	25.99	1,714.90	1,282.35	6.75	4.94

calculated with the formula for a regular ellipsoid $V = 1/6 \times (\pi W^2 L)$ where W was the average width of both testes and L was the length of the longest testis (Kappeler, 1997b). Relative testis size was calculated as the mean testis volume divided by mean body mass (Schwab, 2000). Using the dataset of 18 strepsirrhines in Kappeler (1997b) we calculated the regression line $y = 1.7x + 80.5$, where y is testis volume (mm^3) and x is body mass (g). We used this equation to calculate the expected testis volume for *M. zaza*. Body mass, relative testis volume and the state of the vagina of adult animals were compared between May and July captures (Schwab, 2000). External injuries as a result of fighting were checked in males (Kappeler, 1997a). We used a one-way repeated measures ANOVA (Field, 2009) to compare body mass, absolute and relative testis volume between May and July after using a cosine transformation to ensure normality of our data. We used Shapiro-Wilk tests to check for normal distribution, and a Levene's test to check for homogeneity of variances. We used a one-way *t*-test to compare testis volume to expected testis volume. All tests were two-tailed with significance level set to $P = 0.05$. Statistical analyses were performed with SPSS 21. Our research adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-human Primates, and capture and handling protocols were approved by Madagascar Institute for the Conservation of Tropical Environments.

RESULTS

Although in most males relative testis volume was higher in July (Table 3), we found no significant differences in body mass (ANOVA, $df = 1.4$, $F = 3.29$, $P = 0.144$, $n = 5$), absolute testis volume (ANOVA, $df = 1.4$, $F = 0.202$, $P = 0.676$, $n = 5$), or relative testis volume (ANOVA, $df = 1.4$, $F = 1.982$, $P = 0.232$, $n = 5$) between the May and July captures. Testis volume varied between individuals. Mean relative testis volume of all male adults in July was 14.08 ± 4.94 mm^3/g ($n = 5$). Compared with the expected value of 987 mm^3 in strepsirrhines, average testis volume of adult *M. zaza* in July was significantly higher with 3870.82 ± 1282.35 mm^3 ($t(4) = 5.029$, $P = 0.007$) and almost four times larger than expected (Fig. 1).

In July, individual F2 showed a swollen, pink, and wrinkled vagina, characteristic for met-estrus. All other females were assessed to be in di-estrus (vagina white, not swollen, closed).

We observed *M. zaza* mating three times in mid-June (11th, 15th, and 18th June), always between the individuals M5 and FS4. Two times mating took place in the first half of the night, one time in the early morning (5:45 am) a few meters from the shared nest. While due to the dense foliage not many details could be observed, mating always involved sniffing, following, and quiet "hn" vocalizations.

Fig. 1. Testes of *Mirza zaza*.

The average mass of subadult females FS1 and FS4 were 207.5 ± 7.78 g ($n = 2$) and 214 ± 8.49 g ($n = 2$) while the subadult MS7 weighed 231 g and the juvenile FJ3 weighed 144 g. F2 and FJ3 shared a nest and were probably mother and daughter. Although FJ3 roamed independently from the mother, enlarged teats of F2 suggested ongoing lactation. Compared with data from DLC the female subadults should be aged between 165

TABLE 4. Summary of suspected birth and mating season of Mirza zaza

Birth	Mating	Method	Source
September	Early June	Pregnancy of wild-captured female	Stanger et al., 1995
March, September	December, June	Observations of captive animals under Madagascar time	Stanger et al., 1995
September	June	Observation of mating	This study
October	July	Capture of female in met-estrus	This study
November/December and April	August/September and January	Estimated from weights of subadults (n = 3) and a juvenile (n = 1)	This study[a]

If only birth or only mating time was known, the missing variable was calculated using the gestation time of approximately 3 months. Methods are mentioned to clarify how conclusions about mating season were drawn. Individuals studied by Stanger et al. (1995) were reported as *M. coquereli* but were *M. zaza* according to the capture site.
[a] Body mass data from captivity for comparison in this study stem from only two sets of twins. Although twins might be lighter than singletons, food supply in captivity might be better and primates are often overweight (Schwitzer and Kaumanns, 2003). Accordingly, estimated birth months should be treated with caution.

to 179 days (FS1) and 186 to 221 days (FS4) old at their capture in May. M7 should be around 242 days old in July. We estimated that births of these animals occurred between mid-November and late December 2009. FS4 should have been around 80 days old at her capture and thus born in April. Even though the juvenile FJ3 was small and the mother was still lactating, it foraged independently. The mother was observed alone and in company of the juvenile during the night.

DISCUSSION

In order to prepare for high activity and sperm competition during the short mating season, strepsirrhine species with a polygynandrous mating system like *Microcebus murinus* (Schmid and Kappeler, 1998), *M. coquereli* (Kappeler, 1997c), or *Galago moholi* (Pullen et al., 2000) show an increase of male body mass and testis volume. In *M. zaza* no significant increase in mass, relative or absolute testis volume could be found towards the onset of the mating season. Most lemurs show a strict reproductive seasonality with a narrow birth season and a birth peak due to Madagascar's highly seasonal environment (Ridley, 1986; Tecot, 2010). There are only two known lemur species with relaxed breeding, *Daubentonia madagascariensis* (Sterling, 1994) and *Eulemur rubriventer* (Tecot, 2010). Mirza zaza seems to represent another exception, as a combination of data available from the literature and this study suggest that mating is not restricted to a discrete season but can take place year-round (Table 4). Body mass of immature animals in the wild (this study), mating behavior, pregnancies, and cycling of wild or wild-caught animals indicate that there is no strict mating and birth season but aseasonal reproduction. The geographic situation of Sahamalaza between the dry western forests and more humid Sambirano region, resulting in fewer trees shedding leaves, might allow a more flexible timing of reproduction in *M. zaza*.

Large testis volume found in this study, as well as estrous calls and copulatory plugs reported for *M. zaza* by Stanger et al. (1995; unpublished data), indicate a polygynandrous mating system. Other species with the same mating system show the same traits (see Table 1). The lack of sexual dimorphism may point to either a monogamous or a polygynandrous mating system. However, strepsirrhines generally do not show marked sexual dimorphism (Pochron and Wright, 2002). Kappeler (1990) suggested that the lemurs of Madagascar might be more selected for speed and agility, aiding in their ability to roam widely for finding mates (scramble competition) instead of strength and body size (contest competition). Compared with *M. coquereli*, where injuries are more common in males compared with females in the mating season (Kappeler, 1997a; Schwab, 2000), copulatory plugs, estrous calls, and lack of injuries in *M. zaza* emphasize a higher importance of sperm competition and a higher importance of scramble competition instead of contest competition.

Especially striking is the enormous testis volume of *M. zaza*. Using the width of both testes at their broadest point to calculate volume, mean testis volume for this study of 15.48 cm^3 was similar to testis volume of 13.63 cm^3 in captivity (Stanger et al., 1995). This corresponds to eight times the volume normally expected for strepsirrhines (Kappeler, 1997a). Compared from available data for other primate species (Kappeler, 1997b; Harcourt et al., 1981; Kenagy and Trombulak, 1986; Schwab, 2000), *M. zaza* has the largest relative testis size among primates.

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LITERATURE CITED

Dixson AL, Anderson MJ. 2002. Sexual selection, seminal coagulation and copulatory plug formation in primates. Folia Primatol 73:63–69.

Eberle M, Kappeler PM. 2004. Sex in the dark: determinants and consequences of mixed male mating tactics in *Microcebus murinus*, a small solitary nocturnal primate. Behav Ecol Sociobiol 57:77–90.

Elgar MA, Jones TM. McNamara KB. 2013. Promiscuous words. Front Zool 10:66.

Field A. 2009. Discovering statistics using SPSS. London: Sage Publications.

Harcourt AH, Harvey PH, Larson SG, Short RV. 1981. Testis weight, body weight and breeding system in primates. Nature 293:55–57.

Harcourt AH, Purvis A, Liles L. 1995. Sperm competition: mating system, not breeding season, affects testes size of primates. Funct Ecol 9:468–476.

Isvaran K, Clutton-Brock T. 2007. Ecological correlates of extra-group paternity in mammals. Proc R Soc B Biol Sci 274:219–224.

Kappeler PM. 1990. The evolution of sexual size dimorphism in prosimian primates. Am J Primatol 21:201–214.

Kappeler PM. 1991. Patterns of sexual dimorphism in body weight among prosimian primates. Folia Primatol 57:132–146.

Kappeler PM. 1997a. Determinants of primate social organization: comparative evidence and new insights from Malagasy lemurs. Biol Rev 72:111–151.

Kappeler PM. 1997b. Intrasexual selection and testis size in strepsirhine primates. Behav Ecol 8:10.

Kappeler PM. 1997c. Intrasexual selection in *Mirza coquereli*: evidence for scramble competition polygyny in a solitary primate. Behav Ecol Sociobiol 41:115–127.

Kappeler PM, Rasoloarison RM, Razafimanantsoa L, Walter L, Roos C. 2005. Morphology, behavior and molecular evolution of giant mouse lemurs (*Mirza* spp.) GRAY, 1870, with description of a new species. Primate Rep 71:3–26.

Kenagy GJ, Trombulak SC. 1986. Size and function of mammalian testes in relation to body size. J mammal 67:1–22.

Lahann P. 2008. Habitat utilization of three sympatric cheirogaleid lemur species in a littoral rain forest of southeastern Madagascar. Int J Primatol 29:117–134.

Leutenegger W. 1978. Scaling of sexual dimorphism in body size and breeding system in primates. Nature 272:610–611.

Markolf M, Roos C, Kappeler PM. 2008. Genetic and demographic consequences of a rapid reduction in population size in a solitary lemur (*Mirza coquereli*). The Open Conservation Biology Journal 2:21–29.

Milton K. 1985. Mating patterns of woolly spider monkeys, *Brachyteles arachnoides*: implications for female choice. Behav Ecol Sociobiol 17:53–59.

Møller AP. 1989. Ejaculate quality, testes size and sperm production in mammals. Funct Ecol 3:91–96.

O'Higgins P, Collard M. 2002. Sexual dimorphism and facial growth in papionin monkeys. J Zool 257:255–272.

Pages E. 1980. Ethoecology of Microcebus coquereli during the dry season. In: Charles-Dominique P, Cooper HM, Hladik A, Hladik CM, Pages E, Pariente GF, Petter-Rousseaux A, Petter JJ, Schilling A, editors. Nocturnal Malagasy primates: ecology physiology and behavior. New York: Academic Press. p 97–106.

Pochron ST, Wright PC. 2002. Dynamics of testes size compensates for variation in male body size. Evol Ecol Res 4:577–585.

Pullen SL, Bearder SK, Dixson AF. 2000. Preliminary observations on sexual behavior and the mating system in free ranging lesser galagos (*Galago moholi*). Am J Primatol 51:79–88.

Ridley M. 1986. The number of males in a primate troop. Anim Behav 34:1848–1858.

Rode EJ, Nekaris KAI, Markolf M, Schliehe-Diecks S, Seiler M, Radespiel U, Schwitzer C. 2013. Social organisation of the northern giant mouse lemur *Mirza zaza* in Sahamalaza, north western Madagascar, inferred from nest group composition and genetic relatedness. Contrib Zool 82:71–83.

Rode-Margono EJ, Schwitzer C, Nekaris KAI. 2015. Morphology, behavior, ranging patterns and habitat use of the northern giant mouse lemur *Mirza zaza* in Sahamalaza, northwestern Madagascar. In: Lehman S, Radespiel U, Zimmermann E, editors. Dwarf and mouse lemurs of madagascar: biology, behavior and conservation biogeography of the Cheirogaleidae. Cambridge, UK: Cambridge University Press.

Schmid J, Kappeler PM. 1994. Sympatric mouse lemurs (*Microcebus* spp.) in Western Madagascar. Folia Primatol 63:162–170.

Schmid J, Kappeler PM. 1998. Fluctuating sexual dimorphism and differential hibernation by sex in a primate, the gray mouse lemur (*Microcebus murinus*). Behav Ecol Sociobiol 43: 125–132.

Schülke O, Kappeler PM, Zischler H. 2004. Small testes size despite high extra-pair paternity in the pair-living nocturnal primate *Phaner furcifer*. Behav Ecol Sociobiol 55:293–301.

Schwab D. 2000. A preliminary study of spatial distribution and mating system of pygmy mouse lemurs (*Microcebus cf myoxinus*). Am J Primatol 51:41–60.

Schwitzer C, Kaumanns W. 2003.Foraging patterns of free-ranging and captive primates–implications for captive feeding regimes. In: Fidgett A, Clauss M, Ganslosser U, Hatt JM, Nijboer J, editors. Zoo animal nutrition, Vol.II. Fuerth: Filander Verlag. p 247–265.

Schwitzer N, Randriatahina GH, Kaumanns W, Hoffmeister D, Schwitzer C. 2007. Habitat utilization of blue-eyed black lemurs, *Eulemur macaco flavifrons* (Gray, 1867), in primary and altered forest fragments. Primate Conserv 22:79–87.

Stanger KF. 1993. Structure and function of the vocalizations of nocturnal prosimians (Cheirogaleidae). PhD Thesis. Tuebingen: Tuebingen University.

Stanger KF, Coffman BS, Izard MK. 1995.Reproduction in Coquerel's dwarf lemur (*Mirza coquereli*). Am J Primatol 36: 223–237.

Stanger KF, Macedonia JM. 1994. Vocalizations of aye-ayes (*Daubentonia madagascariensis*) in captivity. Folia Primatol 62:160–169.

Sterling EJ. 1993. Patterns of range use and social organization in aye-ayes (*Daubentonia madagascariensis*) on Nosy Mangabe. In: Kappeler PM, Ganzhorn JU, editors. Lemur social systems and their ecological basis. New York: Plenum Press.

Sterling EJ. 1994. Evidence for non-seasonal reproduction in aye-ayes (*Daubentonia madagascariensis*) in the wild. Folia Primatol 62:46–53.

Tecot SR. 2010. It's all in the timing: birth seasonality and infant survival in *Eulemur rubriventer*. Int J Primatol 31: 715–735.

Thorén S, Lindenfors P, Kappeler PM. 2006. Phylogenetic analyses of dimorphism in primates: evidence for stronger selection on canine size than on body size. Am J Phys Anthropol 130:50–59.

Young AL, Richard AF, Aiello LC. 1990. Female dominance and maternal investment in strepsirhine primates. Am Nat 135: 473–488.