VIVAMUS

Morphological Variation in Populations of *Eulemur albocollaris* and *E. fulvus rufus*

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Sexual dimorphism in body size and canine weaponry is commonly associated with high levels of male-male competition. When group living species do not rely heavily on male-male competition for access to females, sperm competition may represent a viable alternative strategy. Unlike most haplorhine primates, lemurs are typically monomorphic in body weight and canine height. We assessed variability of body mass dimorphism and canine size dimorphism in brown lemurs using morphometric data from 3 populations in southeastern Madagascar: Eulemur fulvus rufus, E. albocollaris, *and hybrids of the species. We found significant male-biased canine dimorphism in* E. albocollaris *in conjunction with body-size monomorphism. We observed similar patterns in the hybrids, but* E. fulvus rufus *exhibited significant female-biased size dimorphism and canine monomorphism. Testes volume was relatively high across study populations. Thus, sperm competition appears to be strong in brown lemurs.* E. albocollaris *males combine sperm competition with large canines, but not higher body mass, indicating a difference in sexual strategy from most lemurs. Patterns of body mass and canine size dimorphism are not uniform across brown lemur populations, indicating that future work on these populations*

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can explicitly test models that predict relationships between size dimorphism and various types of competition.

INTRODUCTION

Extensive research in primatology has focused on understanding the causes and socioecological implications of sexual dimorphism (e.g., Cheverud *et al.*, 1985; Clutton-Brock *et al.*, 1977; Crook, 1972; Kappeler, 1990, 1991; Kay *et al.*, 1988; Leigh, 1995; Leutenegger and Cheverud, 1982; Leutenegger and Kelly, 1977; Lindenfors and Tullberg, 1998; Martin *et al.*, 1994; Mitani *et al.*, 1996; Oxnard, 1987; Plavcan and van Schaik, 1992, 1994, 1997; Pochron and Wright, 2002). Morphological differences between males and females may take many forms, but sex differences in body mass and canine tooth height have been the central focus of theoretical and empirical research on primates (Plavcan, 1999, 2001).

The most common explanation for sexual dimorphism is sexual selection, particularly male-male competition (Crook, 1972; Kay *et al.*, 1988; Lindenfors and Tullberg, 1998; Mitani *et al.*, 1996; Plavcan and van Schaik, 1992, 1997). While female fitness is limited by food resources, male fitness is limited chiefly by the ability to gain access to females (e.g., Darwin, 1871; Emlen and Oring, 1977; Plavcan and van Schaik, 1994). Therefore, male-male competition for mates may lead to the development of larger body size and canines, and females may mate preferentially with such males. Sexual dimorphism should be particularly pronounced in species with polygynous mating systems, in which males can compete directly over estrous females (Harcourt *et al*., 1981; Lindenfors and Tullberg, 1998; Mitani *et al.*, 1996). General empirical support exists for this assertion (Crook, 1972; Plavcan, 2001), especially when operational sex ratios (Emlen and Oring, 1977; Mitani *et al.*, 1996) or more refined categories of competition levels are used (Kay *et al.*, 1988; Plavcan and van Schaik, 1992, 1997).

Male-male competition also occurs through sperm competition, indicated by variation in relative testes size across primate species (Harcourt, 1995; Harcourt and Gardiner, 1994; Harcourt *et al.*, 1981; Harvey and Harcourt, 1984; Møller, 1988; Short, 1979; Pochron and Wright, 2002; *cf.* Brown *et al.*, 1995). Under conditions in which females mate with several males, males should be under selection pressure to increase sperm output, with increased testes size as a corollary (Dixson, 1987, 1998; Fietz, 1999; Harcourt, 1994; Harcourt *et al.*, 1981; Kappeler, 1997; Møller, 1988). The mating system most conducive to sperm competition involves

multiple females, especially with promiscuous mating (Harcourt, 1991, 1994; Harcourt *et al.*, 1981; Jolly and Phillips-Conroy, 2003; Møller, 1988). Promiscuity may occur as a strategy against infanticide, as a result of highly dispersed females, or as a result of strong bonds among (often related) males, e.g., *Pan* (Harcourt *et al.*, 1995; Hrdy, 1977). In these situations, the inability to monopolize females may reduce direct male-male competition. Therefore, an inverse relationship between dimorphism and sperm competition can sometimes exist.

These patterns in sexual dimorphism and levels of sperm competition are mostly consistent in haplorhines (Harcourt, 1994; Harcourt *et al.*, 1981, 1995; Plavcan and van Schaik, 1992, 1997) but not in strepsirhines (Godfrey *et al.*, 1993; Kappeler, 1996, 1997; Feitz, 1999, Wright, 1999; Pochron and Wright, 2002). For example, despite their diverse social systems, lemurs are generally monomorphic (Glander *et al.*, 1992; Kappeler, 1990, 1991, 1996; Plavcan and van Schaik, 1997; Pochron and Wright, 2002, 2003; van Schaik and Kappeler, 1996; Wright, 1999). Explanations for the deviation from haplorhine patterns include Madagascar's extreme seasonality, hypometabolism, female dominance, pair-bonding within multimale groups, activity patterns, narrow birth seasonality, developmental constraints, intraspecific variability in mating systems, or combinations thereof (Godfrey *et al.*, 1993; Leigh and Terranova, 1998; Pochron and Wright, 2003; Richard, 1992; van Schaik and Kappeler, 1993; Wright, 1999).

More in accord with haplorhine trends, lemurs generally demonstrate the expected relationships between sperm competition and mating systems (Glander *et al.*, 1992; Kappeler, 1997). Species with multimale/multifemale social groups often show evidence of sperm competition, with larger relative testes size compared to pair-living strepsirhines (Dixson, 1995; Kappeler, 1997). Thus, with constraints on dimorphism, sperm competition may be more prevalent in group-living lemurs (Fietz, 1999; Kappeler, 1997; Pochron and Wright, 2002).

We examined patterns of sexual dimorphism and relative testes size in populations of 2 forms of brown lemurs (*Eulemur fulvus rufus* and *E. albocollaris*). Brown lemurs possess many characteristics commonly associated with relatively strong male-male competition. Group structure is multimale/multifemale and breeding is highly seasonal (Gerson, 2000; Overdorff, 1998; Overdorff *et al.*, 1999; Sussman, 1974). Unlike many lemurs, brown lemurs are not female dominant (Gerson, 2000; Ostner and Kappeler, 1999; Overdorff, 1996, 1998; Pereira *et al.*, 1990). Researchers have noted some instances of significant canine dimorphism (favoring males) in northern populations of brown lemurs, including in *Eulemur fulvus albifrons* (Kappeler, 1996) and in *E. f. rufus* (Gerson, 1999, 2000).

Relatively little is known about the morphology of *Eulemur albocollaris*, a brown lemur group in southeastern Madagascar now considered a distinct species (Djlelati *et al.*, 1997; Wyner *et al.*, 1999). However, preliminary research indicated potential canine dimorphism in them (Bradley and Stumpf, 1997). Accordingly, we further investigated this relatively rare lemur trait by comparing *Eulemur albocollaris* to other closely related brown lemur populations. The comparative sample includes populations of *Eulemur fulvus rufus*, as well as *Eulemur albocollaris* × *Eulemur fulvus rufus* hybrids. The closely related set of populations has the particular advantage of controlling for phylogenetic effects that may impact dimorphism (Cheverud *et al.*, 1985).

The goal of our analysis is to compare levels of dimorphism and testes size among populations of brown lemurs from the southeast of Madagascar to understand better the interpopulation variability in these traits. Based on sexual selection theory, if sexual differences are found in canine height or body mass or both, we would predict the more dimorphic taxa to exhibit more direct competition, e.g., fighting over mates. If testes size is relatively large during the breeding season, we would predict less direct fighting, less dimorphism, and more promiscuous mating. This pattern may be associated with social systems in which estrous females are difficult to monopolize, e.g., more dispersed groups. Differences between populations in the expression of dimorphism and testes size may then reflect interpopulation differences in male-male competition.

METHODS

Study Subjects and Sites

We collected morphometric data on brown lemur populations at 3 sites in southeastern Madagascar: Ranomafana National Park, Andringitra National Park, and Vevembe Forest (Fig. 1). At Ranomafana, we conducted red-fronted brown lemur (*Eulemur fulvus rufus*) captures and measurements from 1989 to 2000 ($n = 38$ adult individuals). At Vevembe, we sampled a white-collared lemur (*Eulemur albocollaris*) population from 1996 to 2000 ($n = 24$). Andringitra study subjects were *Eulemur albocollaris* × *Eulemur fulvus rufus* hybrids (Johnson and Wyner, 2000; Wyner *et al.*, 2002); we sampled this population from 1997 to 1999 ($n = 19$). We include the hybrids as a separate sample they have shown some important differences from parental groups, including genetics, population densities, behavior, and ecology (Johnson, 2002; Johnson and Wyner, 2000; Wyner *et al.*, 2002).
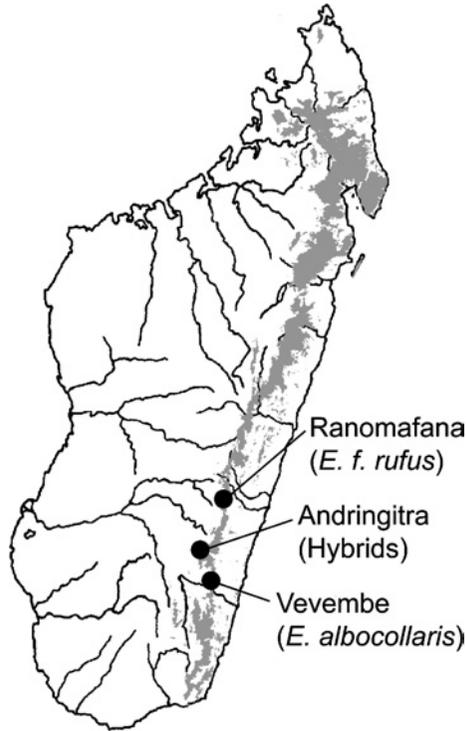
Fig. 1. Brown lemur sampling sites. Shaded regions indicate rain forest habitats of northern and eastern Madagascar.

Capture and Measurement Procedures

We followed the capture and morphometric procedures of Glander (1993) and colleagues (Glander *et al.*, 1992). During immobilization, we measured each individual via techniques modified from Glander *et al.* (1992). We measured body mass (kg), right maxillary canine height (mm), and testes length and width (mm). We included left canine measurements when right canines were broken. We did not record testicular skin fold thickness, which may have resulted in small measurement errors.

We converted testes length (L) and width (W) to volume (V) via the following formula:

$$V = \frac{4}{3}\pi \left(\frac{1}{2}L\right)\left(\frac{1}{2}W\right)^2 .$$

We then divided the mean volume (cm^3) for left and right testes by body mass (kg) to yield the gonadosomatic index (GI) (Glander *et al.*, 1992; Kappeler, 1997). To examine variation according to reproductive period, we sorted testes volume and GI measures into 2: mating season (April–June, centered on the short mid-May breeding season; Overdorff, 1998) and non-mating season (July–March). We used the mating season data for comparison with previous research on strepsirhine testes volume (Kappeler, 1997). We captured females at the same time of year to diminish the effect of seasonality and to provide reproductive-state synchrony.

Statistical Techniques

For comparisons within and between populations, we used nonparametric statistics, including Kruskal-Wallis and Mann-Whitney U tests. To determine the relationship between body size and canine height, we calculated least-squares regressions using all samples. In addition, we analyzed differences in sexual dimorphism in body mass and maxillary canine height across populations, as well as significant departures from monomorphism. We conducted separate analyses for all individuals, for males only, and for females only. For these tests, we used a nonparametric bootstrapping technique coded with the R programming language (Ihaka and Gentleman, 1996). We calculated dimorphism ratios (expressed as mean male size divided by mean female size) for the observed sample and 4999-bootstrapped replications (sampled with replacement). We then determined 95% confidence limits for dimorphism ratios from this generated sample using the percentile method (Chernick, 1999). For all statistical tests, significance is $\alpha = .05$.

RESULTS

Body Mass

Body mass varied across sexes and populations (Table I; Fig. 2). There is no significant difference between the sexes in *Eulemur albocollaris* ($Z = -.420$; $p = .6743$) or the *Eulemur albocollaris* × *Eulemur fulvus rufus* hybrids ($Z = -.133$; $p = .8943$). However, there are significant differences between males and females in the population *Eulemur fulvus rufus* ($Z = -2.232$; $p = .0256$), with females outweighing males (Table I). Variation also existed in body mass in females ($H = 6.779$; $p = .0337$), but not in males ($H = 1.311$; $p = .5192$). Females of *Eulemur fulvus rufus* are significantly larger (2.29 kg) than those in either of the other

Table I. Mean body mass, canine height, and dimorphism ratios across populations

Species	Site	Sex	n^a	Body weight (kg)	Body weight dimorphism (M:F)	Body weight dimorphism 95% CI	Canine height (mm)	Canine dimorphism (M:F)	Canine dimorphism 95% CI[b]
Eulemur albocollaris	Vevembe	Males	15 (15)	2.19	1.02	0.942–1.09	10.9	1.21	1.10–1.31
		Females	9 (9)	2.14			9.1		
Hybrids	Andringitra	Males	13 (2)	2.07	0.989	0.879–1.11	10.6	1.33	—
		Females	6 (2)	2.09			8.2		
Eulemur f. rufus	Ranomafana	Males	23 (22)	2.13	0.937	0.888–0.988	8.7	1.02	0.928–1.12
		Females	15 (15)	2.29			8.5		

[a]Sample sizes for canine analyses are in parentheses.
[b]Confidence intervals are not calculated for canine dimorphism in the hybrids owing to small sample size.
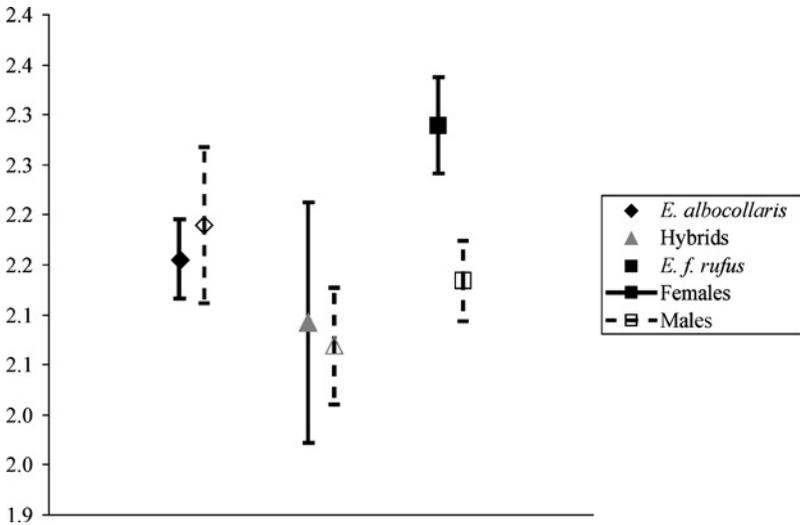
Fig. 2. *Eulemur* body mass (kg) across populations (±SE).

populations. Variation across sites remained significant ($H = 5.926$; $p = .05$), again with females of *Eulemur fulvus rufus* outweighing those at Andringitra and Vevembe.

Canine Height

There are different patterns for maxillary canine height across populations (Table I; Fig. 3). Males of *Eulemur albocollaris* had larger canines than females ($Z = -3.046$; $p = .0023$). The hybrids at Andringitra followed this trend, but we excluded them from statistical tests because of sample size ($n = 4$ for the character). By contrast, *Eulemur fulvus rufus* showed no sex differences in canine height ($Z = -.636$; $p = .525$). Females of *Eulemur albocollaris* and *Eulemur fulvus rufus* do not differ in tooth height ($Z = -.483$; $p = .6292$). In males, there are significant differences between *Eulemur albocollaris* and *E. fulvus rufus* groups ($Z = -4.365$; $p < .0001$) because of the large canines of males of *Eulemur albocollaris* (mean = 10.9 mm) (Table I).

Sexual Dimorphism

Another means of examining the variation in mean dimorphism across groups is to compare dimorphism ratios (expressed as male means divided by female means). Figure 4 depicts sexual dimorphism for body mass and
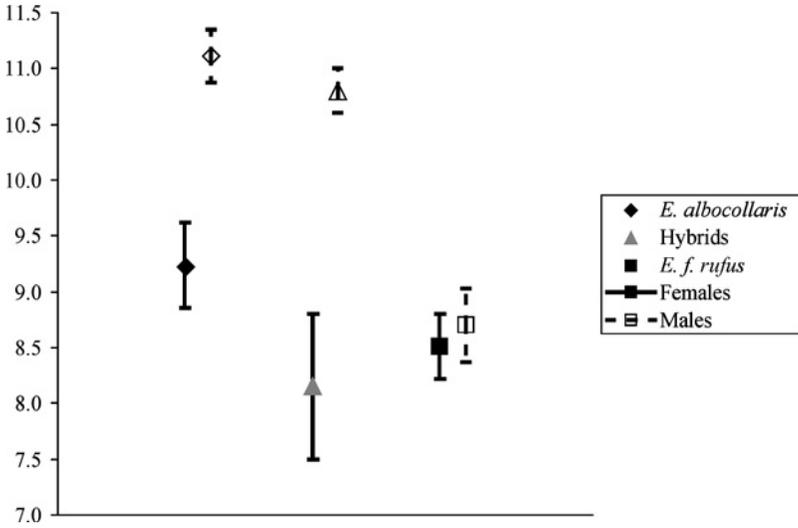
Fig. 3. Maxillary canine height (mm) across populations (±SE).
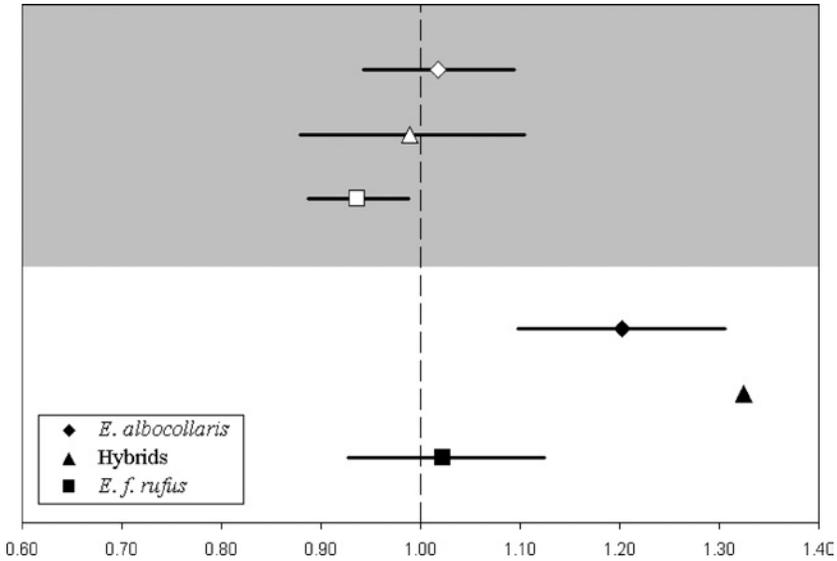

Fig. 4. Size dimorphism across populations. Open symbols represent body size dimorphism, closed symbols represent canine height dimorphism. Horizontal lines indicate 95% confidence limits. Hybrid limits for canine height dimorphism are excluded due to sample size ($n = 4$).

Table II. Gonadosomatic index (GI) and testes volume across populations

					Mating season		Non-mating season	
	Site	n		GI	Testes volume (mm^3)		GI	Testes volume (mm^3)
Eulemur albocollaris	Vevembe	15	Mean	2.70	12,378		2.16	8,426
			Min	1.24	4,824		1.07	4,070
			Max	4.28	18,394		3.86	14,673
Hybrids	Andringitra	13	Mean	2.43	9,948		1.58	6,782
			Min	1.98	8,252		0.76	2,566
			Max	3.01	13,258		3.17	15,237
E. f. rufus	Ranomafana	23	Mean	2.18	9,313		1.47	6,256
			Min	1.27	6,238		0.27	1,095
			Max	3.49	15,006		2.99	13,746

canine height, including 95% confidence limits generated by bootstrapping techniques. Two populations in the analysis were monomorphic for body size (Table I, Fig. 4). However, *Eulemur fulvus rufus* demonstrated significant body size dimorphism favoring females (Fig. 4).

Canine-height dimorphism also varied across groups (Table I, Fig. 4). *Eulemur albocollaris* showed significant dimorphism favoring males (with hybrids following this trend), while *Eulemur fulvus rufus* had monomorphic canines (Fig. 4).

Testes Volume

Populations varied in testes volume, represented by the gonadosomatic index (GI) (Table II; Fig. 5). Testes volume is significantly larger during the breeding season in male *Eulemur fulvus rufus* ($Z = -2.030$; $p = .0423$). Seasonal variation fell short of significance in hybrids ($Z = -1.757$; $p = .0790$) and *Eulemur albocollaris* ($Z = -1.135$; $p = .2566$). *Eulemur albocollaris* had the largest overall relative and absolute testes size (Table II).

DISCUSSION

Despite the close taxonomic affinities among the brown lemur groups, there was notable variation in body size, canine height, and the extent of sexual differences. *Eulemur albocollaris* (and likely the hybrids as well) demonstrated canine size dimorphism favoring males, a rare trait in the Lemuriformes (Kappeler, 1996; Wright, 1999). In contrast, *Eulemur fulvus rufus* exhibited female-biased body size dimorphism. The differences in both sexes across populations show that sexual dimorphism is often the
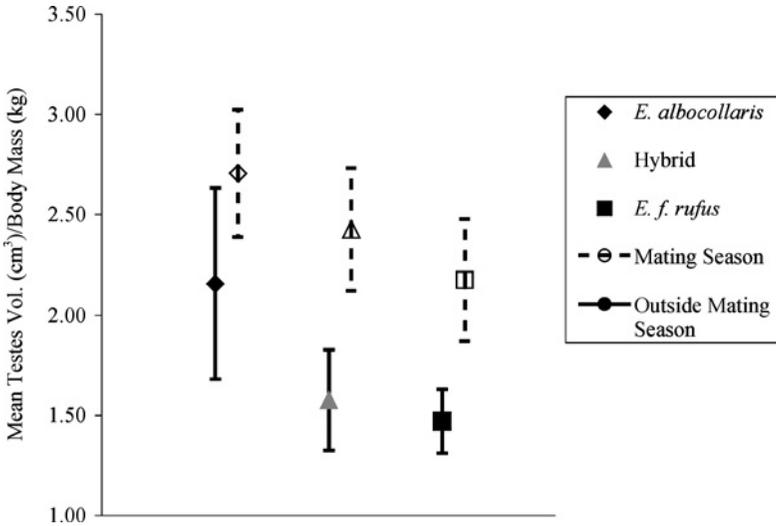
Fig. 5. Gonadosomatic index (GI) across populations and seasons (± SE). Mating season category includes individuals captured April–June.

result of variability in both males and females (Leigh, 1995; Masterson, 2003; Plavcan, 2001; Plavcan *et al.*, 1995). There is also variation in testes volume among the brown lemur groups—but all populations exhibited large testes size compared to other lemurs (Kappeler, 1997).

The dimorphism trends among the southern brown lemur taxa are similar to closely related populations from western Madagascar. At Anjamena, Gerson (1999, 2000) found that both male (1.78 kg) and female (1.84 kg) *Eulemur fulvus rufus* were smaller than their eastern counterparts. The larger body masses for eastern brown lemurs (Table I) corroborate these findings. Previous studies on ecogeographic variation in Madagascar have also demonstrated that eastern rain forest lemurs are larger than those from drier habitats in western Madagascar (Albrecht *et al.*, 1990; Godfrey *et al.*, 1990). Gerson (1999, 2000) also found significantly larger canines in males, while body size dimorphism was absent. These trends mirror those in *Eulemur albocollaris* and the hybrids in the present study but not those in eastern *Eulemur fulvus rufus*. Thus, dimorphism patterns in brown lemurs do not appear to be closely linked to allometric scaling (because similar levels of dimorphism are present in large- and small-bodied populations) or phylogeny (as greater similarities are found in more distantly related groups). Instead, the similarities in dimorphism between less closely related populations may reflect similar forms of intrasexual competition.

Body mass dimorphism favoring females (as observed in eastern *Eulemur fulvus rufus*) exists in *Microcebus murinus* (Kappeler, 1991), and nonsignificant tendencies for larger females occur in *Propithecus diadema* (Glander *et al.*, 1992; Kappeler, 1991), *Indri indri* (Powzyk, 1997), and in a slightly smaller (yet overlapping) sample of *Eulemur fulvus rufus* from Ranomafana (Glander *et al.*, 1992). With the exception of *Eulemur fulvus rufus*, the taxa are female dominant and/or have female feeding priority (Hemingway, 1995; Pollock, 1979; Radespiel and Zimmerman, 2001; Wright, 1993, 1995). By contrast, neither sex is dominant in *Eulemur fulvus* (Peirera *et al.*, 1990) though females lead group movements (Erhart and Overdorff, 1999). What then explains the relatively larger females in *Eulemur fulvus rufus* compared to other brown lemurs? We speculate that female-female competition may play a role (Plavcan, 1999, 2001; Sterck *et al.*, 1997). As feeding resources are likely more important for females, they may evolve a higher body mass as a result of a high incidence of conflict among females (Pereira and Weiss, 1991; Wright, 1999). Indeed, rates of aggression during intergroup encounters—frequently in feeding contexts—are twice as high in *Eulemur fulvus rufus* at Ranomafana as those in *Eulemur albocollaris* at Vevembe or among hybrid groups at Andringitra (Overdorff, unpublished data; Johnson, 2002).

Different yet complementary patterns exist in canine height across brown lemur populations. Both *Eulemur albocollaris* and the hybrids demonstrate dimorphism favoring males. Although the pattern is rare in lemurs (Kappeler, 1996), canine dimorphism also occurs in *Eulemur fulvus albifrons*, *E. mongoz*, *Lemur catta* (Kappeler, 1996), and western *Eulemur fulvus rufus* (Gerson, 1999, 2000).

Dental measures are particularly vulnerable to error because of biases in age structure (with pronounced wear in older individuals) (Godfrey *et al.*, 2002). Yet, there was no indication of age bias according to sex in these populations. The observations of sexual dimorphism in canines may have important implications for the behavioral ecology of the populations, suggesting strong direct male competition relative to other lemurs. The multimale/multifemale social structure in brown lemurs is generally an important precondition for more intense intrasexual conflict (Crook, 1972; Emlen and Oring, 1977; Mitani *et al.*, 1996). Moreover, unlike many lemur species, brown lemurs do not have female dominance (Overdorff and Johnson, 2003; Pereira *et al.*, 1990), which can mitigate the effects of male competition. Sufficient behavioral observations during the breeding season are at present lacking to test predictions regarding male fighting and mate access in these populations showing larger canines.

There is also evidence of relatively large testes size, including increases during the breeding season, across populations. Figure 6 demonstrates
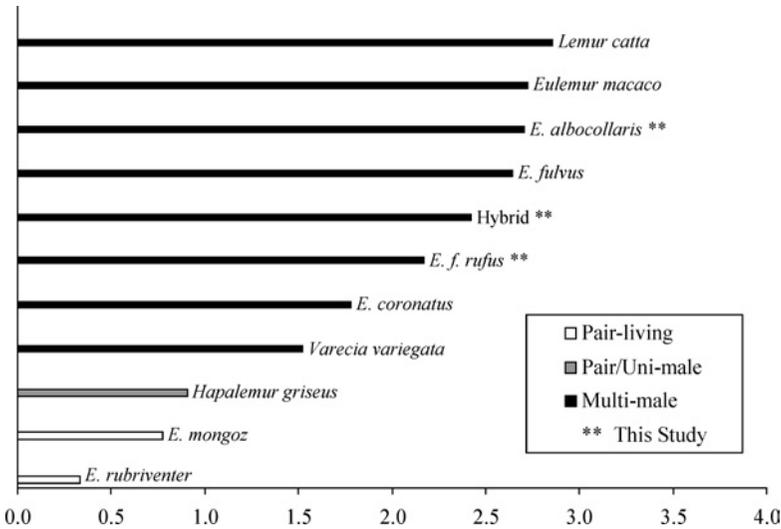
Fig. 6. Gonadosomatic index (GI) in the Lemurids. Data are from mating seasons only. Data are adapted from Kappeler (1997) or the present study (**).

gonadosomatic indices in lemurids, calculated from Kappeler (1997). Our subjects have high GI scores, falling in with other multimale/multifemale species in which sperm competition is expected to be stronger (Harcourt *et al.*, 1981; Kappeler, 1997; Møller, 1988). The species with the largest relative testes size are promiscuous breeders (*Lemur catta*: Sauther, 1991; Sussman, 1992) and taxa that maintain dispersed, fission-fusion social structure (*Eulemur macaco*: Colquhoun, 1997; *Varecia variegata*: Morland, 1991; Vasey, 2000) wherein access to females may be difficult for males to control directly. While most brown lemurs maintain cohesive social groups, *Eulemur albocollaris* is regularly fission-fusion (Johnson, 2002; Overdorff and Johnson, 2003). As predicted, the taxon also has the highest absolute and relative testes size among the study populations.

Brown lemur populations vary in the expression of canine and body mass dimorphism. We predicted that if sex differences exist in canine height or body mass or both, the populations with larger weapons and body mass may exhibit more direct intrasexual competition. Male *Eulemur albocollaris* (and likely the hybrids) have proportionally larger canines. Further behavioral studies of the species are needed to confirm or to reject the prediction of increased male-male aggression in the population. However, as evidenced by the large testes size, the species exhibits morphological traits associated with both direct and indirect forms of

male-male competition, which is contrary to predictions that reduced dimorphism may occur in populations with larger testes size. In contrast, female *Eulemur fulvus rufus* in our sample have proportionally larger body mass than other female brown lemurs, suggesting increased female-female competition. Variability in dimorphic patterns is highlighted in the taxon, in which 2 populations of the same subspecies appear to be responding to different sets of selective forces (this study: male and female canines nonsignificantly different, female mass significantly larger than males; Gerson, 1999, 2000: male canines significantly larger than females, male and female mass nonsignificantly different). Future work on behavioral and ecological differences between these populations can explicitly test predictions regarding the influence of competition on dimorphism within the brown lemur group.

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