

Dynamics of testes size compensates for variation in male body size

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ABSTRACT

Lemurs demonstrate various mating systems but paradoxically lack sexual dimorphism. No convincing mechanism can explain the lack of large-bodied males. In mammals, testicle size correlates with body size; here, we examine how testicles vary relative to body weight within a population of Malagasy lemurs. We show that the significant positive relationship between body size and testicles in non-breeding seasons dissipates in breeding seasons because the testicles of lighter males grow more and match heavier males' testicles. Low and unpredictable plant productivity characterizes Madagascar's ecosystems, and natural selection may favour testicle–body size decoupling during challenging years, inhibiting the evolution of dimorphic males.

Keywords: intrasexual competition, lemurs, mating systems, sexual dimorphism, sperm competition.

INTRODUCTION

Heavier body weights and longer canine teeth generally allow primate males to dominate females in social and foraging contexts (Clutton-Brock *et al.*, 1977; Dunbar, 1988). Monogamous species demonstrate reduced sexual dimorphism relative to species with promiscuous females, indicating that sexual selection is a probable cause of dimorphism (Darwin, 1871; Trivers, 1976; Plavcan *et al.*, 1995). Lemurs do not conform to this pattern, providing one of the enigmas of primate biology (van Schaik and Kappeler, 1996; Wright, 1999; Kappeler, 2000). Lemurs demonstrate all social systems (Wright, 1999, Kappeler, 2000) and intense male–male aggression during breeding seasons (Sauther, 1991; Brockman *et al.*, 1998; Wright, 1999), yet no polygynous lemur demonstrates sexual dimorphism (Kappeler, 1991; Glander *et al.*, 1992; van Schaik and Kappeler, 1996; Plavcan and van Schaik, 1997; Wright, 1999). Even after 15 years of intensive lemur studies in the wild and in captivity, no convincing mechanism can explain the lack of large-bodied males. Here, we examine testicle size relative to body weight in the Milne-Edwards' sifaka (*Propithecus diadema edwardsi*) during breeding and non-breeding seasons to assess links between sperm competition and the lack of sexual dimorphism.

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Sperm competition (e.g. competition between sperm from different males to fertilize ova) is common among mammals (Harvey and Harcourt, 1984; Smith, 1984) and is thought to underlie relative differences in testes size among species (Short, 1977; Harcourt *et al.*, 1981). Classically, sperm competition in a species is detected by comparing the gonadosomatic index of the study species to that of other species with a linear regression, depicting male body weight on the independent axis and testicle size on the dependent axis (Harcourt *et al.*, 1981; Kappeler, 1997a; Fietz, 1999). Such allometric analyses provide a useful means for establishing both norms in animal design with respect to size and deviations from the norm arising from evolutionary modifications (Kenagy and Trombulak, 1986). Species with relatively large testicles per body weight (those above the regression line) are said to experience sperm competition, while species with a low gonadosomatic index are said to experience little or no sperm competition (Harcourt *et al.*, 1981; Harvey and Harcourt, 1984; Kappeler, 1997a; Fietz, 1999).

Wild sifakas provide a suitable candidate to investigate sperm competition and sexual dimorphism. Females sifakas are dominant to males and groups have been described as multi-male/multi-female (Wright, 1995). As in other lemurs, body and canine-tooth size dimorphism is not found in Milne-Edwards' sifaka (Glander *et al.*, 1992). In this paper, we hypothesize that sperm competition affects testicle growth during the breeding season. Specifically, we assess whether lighter males (with smaller non-breeding season testicles) increase their investment in testicular growth in the breeding season relative to heavier males (with larger non-breeding season testicles). If so, the ejaculates of lighter males may compete successfully against those of heavier males in a sperm-competition setting.

METHODS

Lemurs and study area

Between 1986 and 2000, we captured and measured male lemurs 30 times in the non-breeding season (May–July) and 19 times in the breeding season (November–January). All individuals came from Ranomafana National Park, Madagascar; well-studied groups reside in the Talatahely Trail System, while the other groups reside in the Vatoharanana area of the park. These areas adjoin each other. Continuous studies since 1986 provide the life history and demography of the well-studied groups (Wright, 1995, 1998). Descriptions of group compositions, sex differences in feeding behaviour and patterns of female dominance are available for the other groups, which were studied for 18 months (Hemingway, 1995).

Capture and measurement of individuals

Detailed capture methods have been described (Glander *et al.*, 1992). Briefly, all animals were darted with Ketamine ($30\text{--}35\text{ mg}\cdot\text{kg}^{-1}$) or Telazol ($20\text{ mg}\cdot\text{kg}^{-1}$). Body weight was measured to the nearest tenth of a kilogram using portable spring scales; testicles were measured to the nearest tenth of a millimetre with calipers. The date of capture was recorded.

Testicle volume

The length (L) and width (W) of the right and left testicle were measured, and the volume of each testicle was calculated from the formula $4/3 \pi (L)(W^2)$. The volumes of the left and right testicles were then averaged.

Age

The ages of individuals born after 1985 are known; toothwear provides age estimates for those individuals born before 1986 or born in less studied groups (Wright, 1995). Only males aged 5 years or older contribute to this data set.

RESULTS

Non-breeding season gonadosomatic index

Glander *et al.* (1992) report that body weight explains 84.2% of the variance in log testes volume in the non-breeding season. We replicated their regression using their data and additional data collected since then. We found that, in the non-breeding season, log body weight explains a much lower 22.6% of the variance in log testicle volume. The relationship is significant ($n = 30$, $F = 8.2$, $P = 0.008$) (see Fig. 1).

Because the r^2 -values differed dramatically between this data set and that of Glander *et al.* (1992), we explored possible causes. After including all adult males but excluding sub-adult males, and correcting a minor error in the equation used to calculate testicle volume from length and width, the data set used by Glander *et al.* (1992) yields an r^2 -value of 27.8%, a value closer to our 22.6%.

Breeding season gonadosomatic index

In the breeding season, the relationship between log body weight and log testes volume is not significant ($n = 13$, $F = 0.33$, $P = 0.58$). As shown in Fig 1, testes volume cannot be predicted from body weight in the breeding season, since body weight explains only 2.9% of the variance in testicle volume.

Seasonal changes in testicle size

We hypothesized that if sperm competition affects Milne-Edwards' sifakas, lighter males would demonstrate a greater increase in testicle size with the onset of the breeding season than heavier males. To test this hypothesis, we used an analysis of covariance to examine the regression lines in both seasons (Fig. 1). The regression line in the breeding season is both significantly higher and shallower than that of the non-breeding season. The breeding-season intercept (0.118) significantly exceeds that of the non-breeding season (-1.33) ($t_1 = 29.75$, $P = 0.0001$), and the slopes (breeding = 1.75, non-breeding = 3.27) also differ significantly ($t_1 = -2.35$, $P = 0.02$). This implies that testes volume increases overall, and the testicles of lighter males grow more than those of heavier males.

Furthermore, changes in testicle sizes in all males measured in both seasons ($n = 7$) support the inference; testes volume increases overall, but the testicles of lighter males increase

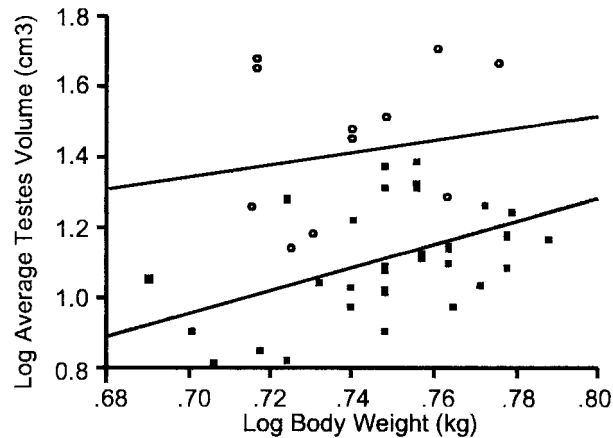


Fig. 1. The relationship between log body weight (kg) and log average testicle volume (cm^3) for both the breeding ($\circ$) and non-breeding ($\blacksquare$) season. Both the slopes and the intercepts of these regression lines differ significantly.

in size more than those of heavier males ($n = 7$, $F = 5.97$, $P = 0.06$). Therefore, heavier males appear to experience less growth in testicles as the breeding season approaches.

Relative testes size

The fact that heavier males grow less than lighter males in the breeding season requires attention, because the morphology of this primate indicates strong sperm competition. When we compare testes and body size of this sifaka to equivalent data from 18 captive strepsirrhines species (Kappeler, 1997a; Fietz, 1999), observed testes volume exceeds predicted testes volume by 206%.

Following Kappeler (1997a) and Fietz (1999), we minimized statistical independence caused by phylogeny by limiting the data set to strepsirrhine primates (lemurs are strepsirrhine primates). We compared testes size and body mass of *Propithecus diadema edwardsi* with equivalent data from 18 species of captive species: *Cheirogaleus medius*, *Microcebus murinus*, *Mirza coquereli*, *Hapalemur griseus*, *Lemur catta*, *Eulemur coronatus*, *E. fulvus*, *E. macaco*, *E. mongoz*, *E. rubriventer*, *Varecia variegata*, *Galago moholi*, *Otolemur garnettii*, *O. crassicaudatus*, *Perodicticus potto*, *Loris tardigradus*, *Nycticebus coucang* and *N. pygmaeus* (Kappeler, 1997a). As with the captive species (Kappeler, 1997a), data from *P. diadema edwardsi* were taken during the breeding season. A simple regression using Kappeler's data set yields an equation describing the relationship between body mass (g) and testicle volume (mm^3): testicle volume = $1.66 (\text{body mass}) + 467.97$. The relationship is significant ($n = 18$, $F = 17.3$, $P = 0.0007$) and explains 51.9% of the variance. Fietz (1999) confirmed this relationship.

In the breeding season, the observed *P. diadema edwardsi* value for average testes volume ($n = 19$) was $29,860 \text{ mm}^3$. Using an average body weight of 5465.8 g ($n = 19$), the regression predicts a testicle volume of 9769 mm^3 for this species. The testis volume of wild *P. diadema edwardsi* is therefore 206% above the value predicted for strepsirrhine primates. However, although *P. diadema edwardsi* shows disproportionately large testicles, the exact magnitude

of the difference has to be treated with caution, because testes sizes and body weights measured in wild and captive lemur populations differ; sometimes body size is larger in captivity and other times it is larger in the wild. The same irregular pattern holds for testicle size (Kappeler, 1997b; Fietz, 1999).

DISCUSSION

Using several methods and techniques to detect sperm competition, we have shown that, by decoupling testicle volume from body weight, males compete equally in a sperm-competition arena, regardless of body weight. The positive, significant relationship between body weight and testes volume in the non-breeding season disappears in the breeding season, and the change seen between seasons indicates that, although all males increase their testes volume in the breeding season, lighter males increase their volume more. For the seven males captured in both seasons, the testicles of lighter males grew more and matched the testes volume of heavier males. Assuming that male fertility is positively correlated with testes volume via ejaculate size (Bercovitch and Nurnberg, 1996), in a sperm-competition setting, lighter and heavier sifaka males are equally likely to father offspring. Therefore, if our inferences are correct, heavier males might not have a correspondingly large share of paternity in this species. Lastly, the observed testes volume for wild *Propithecus diadema edwardsi* exceeds the expected testes volume for its body weight by 206%, suggesting the presence of considerable sperm competition.

Intrasexual competition

Sperm competition, as measured by relative testes size, is often linked with the mating system (Short, 1977; Harcourt *et al.*, 1981; Strier, 1992), canine tooth dimorphism (Dayan and Simberloff, 1994) and body size dimorphism (Harvey and Harcourt, 1984). The classic theory behind these associations is grounded in intrasexual competition. Intrasexual competition for mates favours increasing fighting ability among males, manifested as an increase in body size and canine size. These male features are seen and expected in polygynous species, but not in monogamous species (Table 1). In addition, polygynous species have single-male or multi-male breeding systems. In the former, sperm competition should be very low, since one male monopolizes all or nearly all of a group of females. The latter should experience intense sperm competition because more than one male has access to each oestrous female. As is evident from our study, *P. diadema edwardsi* exhibits a combination of polygynous and monogamous traits (Table 1). *P. diadema edwardsi* exhibits no dimorphism in either canine teeth or body size (Glander *et al.*, 1992); our additional unpublished data collected between 1986 and 2000 support this. Given the lack of dimorphism in either body size or canine teeth, we would expect sifakas to demonstrate a monogamous breeding system.

The breeding system of *P. diadema edwardsi*, however, has been difficult to categorize. The literature refers to this species as multi-male/multi-female (Hemingway, 1995; Wright, 1995, 1999). If one examines Wright's (1995) published data covering 22 breeding seasons, however, the operational sex ratios reflect harem (27%), pairs (18%), polyandrous (23%) and multi-male/multi-female (32%) systems. Similarly, Hemingway's (1995) data collected over nine seasons show operational sex ratios consistent with multi-male/multi-female (66%) and pairs (33%) systems. In the wild, other lemurs – *Propithecus tattersalli*,

Table 1. Patterns predicted by intrasexual selection theory^a

	Multi-male	Single-male	Monogamous	<i>P. d. edwardsi</i>
Sperm competition	High	Low	Low	High
Dimorphism	High	High	Low	Low

^a Intrasexual selection theory expects certain suites of traits. Multi-male groups (e.g. savannah baboons) are expected to experience high sperm competition, high body size dimorphism and high canine tooth dimorphism. Gorillas exemplify the single-male traits and gibbons exemplify the monogamous traits.

P. verreauxi, *Eulemur mongoz*, *E. fulvus* and *E. coronatus* – demonstrate similar variability (Kappeler, 2000, Richard *et al.*, 2000). Regardless, the operational sex ratios in the Milne-Edwards' sifaka do not reflect the dedicated monogamous breeding system typically associated with monomorphism.

Furthermore, female sifakas have been observed to mate promiscuously (Richard, 1992; Brockman *et al.*, 1998; Brockman, 1999; Richard *et al.*, 2000). In the Milne-Edwards' sifaka, we have observed matings to be of short duration (30–90 s), which may further facilitate opportunities for promiscuous matings. All this evidence indicates that sifakas exhibit a more polygamous than monogamous breeding system.

Despite the lack of sexual dimorphism, *Propithecus* spp. demonstrate intense male–male aggression – typical of polygynous breeding systems – during the breeding season, often resulting in long canine gashes and severe injuries (Wright, 1995, 1999; Altmann *et al.*, 1996). Therefore, the suite of characteristics exhibited by *P. diadema edwardsi* (no size dimorphism, no tooth dimorphism and high sperm competition) does not match any intrasexual selection predictions shown in Table 1.

Decoupling of sperm competition and body size

In a mating system with female promiscuity, heavier males (with larger testicles) generally mate more often during female fertile periods and father more offspring than lighter males, who have smaller testicles (Bercovitch, 1995; Altmann *et al.*, 1996). All else being equal, this creates directional selection leading towards sexual dimorphism in body size. In lemurs, however, we have shown that body size and testes size are decoupled during the breeding season. This implies that lemurs have evolved physiological mechanisms that sidestep directional selection. The compensated ejaculates of lighter males compete on a level playing field with heavier males.

This decoupling of testicle size and body size requires an explanation. Madagascar's harsh and unpredictable environment, characterized by low plant productivity and cyclones that decimate food resources (Ganzhorn *et al.*, 1999; Wright, 1999), has been implicated in limiting both male and female body size (Pollock, 1979; Overdorff *et al.*, 1999; Wright, 1999; Richard *et al.*, 2000), selecting for body weights near the ecological minimum. In some years, reproduction in *Propithecus verreauxi* has been shown to be particularly difficult for females, and strategies for energy acquisition, storage and the minimization of energy expenditure play a crucial role in determining long-term reproductive success (Richard *et al.*, 2000). Furthermore, male access to preferred foods is limited by female feeding dominance (Pollock, 1979; Jolly, 1984; Sautther, 1991). In the context of female dominance, Richard's (1992) 'wimpy male' hypothesis suggests that female preference for compliant mates may

drive monomorphism. Our new data on testicles suggest that decoupling body weight and testes volume reduces the need for directional selection by females on male body size. Male lemurs, who face intense male–male competition in the context of scarce and unpredictable food resources, may have evolved mechanisms to retain a body size equal to that of females, which primatologists have deemed the ‘ecological sex’, since females are theorized to have the smallest possible body size to minimize metabolic requirements relative to the requirements of gestation and lactation (Gaulin and Sailer, 1985; Jolly, 1998; Gould *et al.*, 1999).

CONCLUSIONS

To determine whether sperm competition occurs in a monomorphic but polygynous species (the Milne-Edwards’ sifaka), we examined seasonal changes in testicle sizes of adult males, hypothesizing that if sperm competition exists, lighter males would increase testicle size more than heavier males. By testing for the existence of sperm competition in this species, we have found a possible explanation for the question posed in Table 1: why do Malagasy primates show no sexual dimorphism, despite demonstrating testes-size dynamics consistent with sperm competition? Females provide a resource for which males compete (Wright, 1995, 1999), yet male body size does not exceed female body size (Glander *et al.*, 1992).

In the breeding season, body weight cannot predict testicle size; therefore, males of all body weights enter a level playing field when it comes to paternity. Sexual dimorphism will result if the ejaculates of heavier males (with larger testicles) outcompete the ejaculates of lighter males (with smaller testicles). However, when ejaculate size becomes independent of male body size, sperm competition cannot easily lead to dimorphic males. This reduces selection for heavy males and still allows females to select for male traits (Small, 1988), such as genetic health, parasite resistance or histocompatibility. By decoupling the two – body size and testicular volume – males escape from selection for larger body size, which would pose a risk for survival in Madagascar’s unusually challenging ecology.

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