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Original article

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Fluctuating sexual dimorphism and differential hibernation by sex in a primate, the gray mouse lemur (*Microcebus murinus*)

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Abstract The aim of this study was to investigate reproductive strategies and their consequences in gray mouse lemurs (*Microcebus murinus*), small solitary nocturnal primates endemic to Madagascar. Previous reports of sexual dimorphism in favor of males and females, respectively, a high potential for sperm competition and pheromonal suppression of mating activity among captive males, led us to investigate mechanisms of intrasexual competition in a wild population. Based on 3 years of mark-recapture data, we demonstrate that sexual dimorphism in this species fluctuated annually as a result of independent changes in male and female body mass. Male body mass increased significantly prior to the short annual mating season. Because their testes increased by 100% in the same period and because their canines are not larger than those of females, we suggest that large male size may be advantageous in searching for estrous females and in enabling them to sustain periods of short-term torpor. In contrast to reports from captive colonies, we found no evidence for two morphologically distinct classes of males. Finally, we also show that most adult males are active throughout the cool dry season that precedes the mating season, whereas most adult females hibernate for several months. This is in contrast to other solitary hibernating mammals, where males typically emerge 1–2 weeks before females. Thus, this first extended field study of *M. murinus* clarified previous conflicting reports on sexual dimorphism and male reproductive strategies in this primitive primate by showing that their apparent deviation from predictions of sexual selection theory is brought about by specific environmental conditions which result in sex-specific life history tactics not previously described for mammals. A general conclusion is that sexual selection can operate more strongly on males without resulting in sexual dimorphism because of independent selection on the same traits in females.

Key words Sexual dimorphism · Mating system · Hibernation · Life history · *Microcebus* · Lemurs

Introduction

According to sexual selection theory, male mammals are expected to compete among themselves for access to receptive females because the constraints associated with gestation and lactation predispose females towards slower potential reproductive rates (Clutton-Brock and Parker 1992). As a result, the vast majority of mammals has a polygynous mating system in which male reproductive competition via behavioral or physiological mechanisms may occur before, during, and after copulation (Clutton-Brock 1989; Parker 1984). Physiological mechanisms of competition include pheromonal or psychological suppression of rivals (Arnold and Dittami 1997; von Holst 1985), sperm competition (Møller and Birkhead 1989; Schwagmeyer and Parker 1990), and induced abortions (Schwagmeyer 1979), whereas established dominance relations and direct contests (Cowlishaw and Dunbar 1991; Creel et al. 1992; Haley et al. 1994) are the most important behavioral mechanisms mediating access to receptive females. Because superior size, strength, and endurance are often positively associated with male reproductive success irrespective of the mechanisms of competition, it is not surprising that sexual dimorphism in body size and weaponry are widespread among polygynous mammals (Alexander et al. 1979; Clutton-Brock 1991; Mitani et al. 1996; Packer 1983; Plavcan and van Schaik 1994).

Comparative studies of sexual dimorphism among primates, which are unusually comprehensive and detailed for mammals, confirmed and refined these fun-

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damental predictions of sexual selection theory: polygynous species are more sexually dimorphic than monogamous ones, and sexual dimorphism in body and canine size increase with increasing potential intensity of competition within polygynous species (Clutton-Brock 1985; Kappeler 1997a; Kay et al. 1988; Mitani et al. 1996; Plavcan and van Schaik 1992, 1997). Although a few apparent mismatches between current mating system and morphological correlates have been identified (Ford 1994; Milton 1985), no exception is as puzzling as that provided by the Lemuriformes, a monophyletic radiation of primates endemic to Madagascar. Polygynous lemurs are unusual in that sexual dimorphism in body and canine size are generally lacking despite widespread fierce male combat (Kappeler 1991, 1996; Richard 1992). This lack of sexual dimorphism is neither the result of unusually intense sperm competition (Kappeler 1997a), nor of non-adaptive constraints (Kappeler 1990). For polygynous group-living lemurs, it has been suggested that their lack of dimorphism may ultimately be due to evolutionary inertia resulting from a very recent shift from a nocturnal pair-living social organization, and thus presumably a monogamous mating system, to their current social system (van Schaik and Kappeler 1996). However, this hypothesis cannot account for sexual monomorphism in the many solitary lemurs because they are known or presumed to have polygynous mating systems (Kappeler 1997b,c; see also Dixson 1989; van Hooff 1995; Nash and Harcourt 1986; Rodman and Mitani 1987).

Gray mouse lemurs (*Microcebus murinus,* Miller 1777) provide the most remarkable and perplexing deviation from predictions of sexual selection theory among solitary lemurs because these small nocturnal animals represent the only primate species for which reversed sexual dimorphism in body mass has been demonstrated (in captivity) (Kappeler 1991). Female *M. murinus* also have longer skulls and canine teeth than males (Jenkins and Albrecht 1991; Kappeler 1996). These observations contrast with both the recent documentation of larger males during a brief field study (Fietz 1998) and theoretical expectations based on field reports of population nuclei in which dominant central males are able to exclude other, peripheral males from contact with females (Martin 1972). Furthermore, *M. murinus* has one of the relatively largest testes among lemurs (Kappeler 1997a), indicating a strong potential for sperm competition, and a urine-based pheromonal mechanism that allows captive dominant males to drastically suppress reproductive functions, as well as body and testes size, of rivals (Perret 1977, 1992; Schilling et al. 1984), indicating a potential to monopolize matings. Thus, it is not clear how male gray mouse lemurs compete for access to females, whether populations or males within populations follow different strategies in this respect, or whether some observations simply reflect artifacts of captive housing.

In order to resolve specific behavioral and genetic questions arising from these partly conflicting empirical observations and theoretical expectations, we initiated a long-term field study of a population of individually marked gray mouse lemurs. Here we summarize morphometric and mark-recapture data from the first 3 years of this study to examine patterns in sexual dimorphism and their proximate causes. We also use these data to examine the possibility that two morphologically distinct classes of males, with possibly different reproductive strategies, exist as a result of intrasexual competition.

Methods

M. murinus is found in the dry deciduous forests of southern and western Madagascar, where the animals spend the day alone or in groups in tree holes or nests and feed on fruits, small animals, gum, and insect secretions during their solitary nocturnal activity (Martin 1973). Males and females occupy home ranges that overlap with those of members of both sexes (Pagès-Feuillade 1988). Mouse lemurs are under intense predation pressure from owls and snakes (Goodman et al. 1993) and known for their ability to enter daily or seasonal torpor in response to low ambient temperatures (Petter-Rousseaux 1980; Schmid 1997, unpublished data). Reproductive activity is photoperiodically controlled and initiated by a brief estrus in October, followed by 2 months of gestation and the birth of one to three young, which are weaned about 2 months later (Perret 1996; Petter-Rousseaux 1980) (Fig. 1). In captivity, males and females begin reproducing within their first year of life (Glatston 1979).

This study took place in Kirindy forest, about 60 km northeast of Morondava, central western Madagascar. This area is characterized by pronounced seasonality; the rainy season between December and March is followed by 8–9 months with virtually no precipitation (Fig. 1). During the dry season, many trees drop their leaves and nightly temperatures regularly fall below 10 °C. Additional information on the phenology and history of this forest can be found in Ganzhorn and Sorg (1996).

A regular trail system consisting of small foot trails every 25 m in both north-south and east-west directions was established in a plot of secondary forest without logging activity in the last two decades (locally known as CS7) adjacent to the Kirindy river. Each intersection was marked with a plastic tag for orientation. An

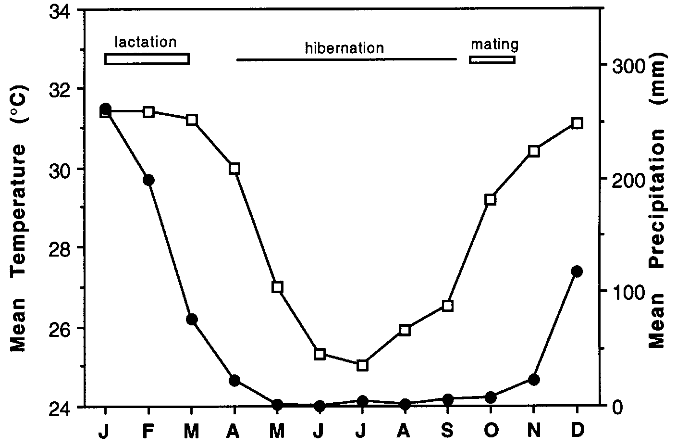

Fig. 1 Approximate timing of important life history events of gray mouse lemurs in relation to annual variation in mean temperature (*squares*) and precipitation (*circles*). Monthly means of meteorological data from Ganzhorn (1995)

approximately 250 × 375 m large section of this grid system with 145 intersections was chosen for intensive study after initial census walks. Beginning in March 1994, Sherman live traps were baited with pieces of banana and set near the intersections of the study grid system 1–3 m aboveground. Traps were opened and baited at dusk and checked and closed at dawn for 3 or 4 successive days. This procedure has since been repeated 31 times on 105 days for a total of 15,225 trap nights until December 1996.

Traps with *M. murinus* were collected and kept at a nearby research station during the day. Newly caught animals were briefly restrained and immobilized with a mixture of 0.05 ml Ketanest (100 mg/ml) and Rompun (2%). They were individually marked by implanting a unique transponder (Trovan) and by cutting a maximum of three small pieces of skin from defined positions on both ears. Each individual was also weighed, examined for injuries and reproductive state, and most were subject to a number of standard morphometric measurements, including canine height, head length, body length, and testis length and width (see Schmid and Kappeler 1994 for definitions). A total of 19 males and 18 females were fitted with 3-g radio tags (Biotrack, SS1 button cells) and regularly located and followed with a Televilt RX-8910 receiver. Animals already captured in the same month were only identified and immediately released at the capture site. Animals detained at the camp were released at their capture site on the same day in the late afternoon.

For the subsequent analyses of morphometric data, we only used the first datum of an individual in a given calendar month, excluding data obtained during the first 6 months of life, because body mass may be affected by spending several subsequent nights in a trap. Measurements of both testes were averaged and used to calculate the volume of a spherical ellipsoid. By dividing body mass by head length, we were able to index body condition because the linear measurement (head length) controls for size differences among individuals. For animals that were caught in the same calendar month in successive years, we used the most recent datum to ensure that animals were fully adult. Thus, for analyses of condition, body and testes size, only one datum per individual and calendar month was used.

For comparisons of mean body mass across months and between the sexes, we controlled for variation among repeated measurements of the same individuals by *z*-transformation of variates from individuals that contributed three or more data points to avoid using repeated-measures ANOVA with unequal sample size. Individuals contributing only one or two measurements were discarded for this analysis. Because of a highly significant interaction between sex and month ($F_{11,384}=3.83$, $P<0.0001$), comparisons among months were conducted for both sexes separately by ANOVA with unequal sample size, followed by all pairwise comparisons with the Tukey-Kramer method. These multiple tests employed an experimentwise error rate of 0.05 (Sokal and Rohlf 1981). Post hoc comparisons between the sexes were performed for each month with two-tailed *t*-tests on untransformed data.

For an analysis of mark-recapture data, we selected 18 males and 14 females which were adult and alive throughout 1995. For each of these individuals, we determined whether they were recaptured at least once in a given month in 1995. Using goodness-of-fit χ^2-tests, with adjusted alpha levels using the Bonferroni method, we tested whether the proportion of recaptured animals differed between the sexes in a given month.

To investigate the possibility that there exist two distinct classes of adult males, we analyzed data collected around the 1995 breeding season. Frequency distributions of male condition and testes size obtained in August, September, and October, were subjected to a one-sample Kolmogorov-Smirnov test to examine deviations from normality. Furthermore, we calculated the skewness statistic g_1 for each frequency distribution and tested the (one-tailed) prediction that they are significantly skewed to the right. Finally, we calculated Pearson's product-moment correlation coefficient between condition and testes size. All tests were two-tailed (with one stated exception), follow Sokal and Rohlf (1981) and were performed with Statview 4.02.

Results

Between March 1994 and December 1996, we caught a total of 163 *M. murinus* (97 males and 66 females) 1405 times. We found that body mass of both male and female mouse lemurs was subject to significant seasonal variation ($F_{11,384}=8.35$, $P<0.0001$; Fig. 2). Overall, sexes did not differ ($F_{1,384}=1.13$, NS), but the interaction between sex and months was highly significant (see above). Comparisons between the sexes revealed that females were significantly heavier than males in February ($t=2.79$, $df=15$, $P=0.014$), March ($t=2.25$, $df=16$, $P=0.039$), April ($t=2.89$, $df=63$, $P=0.005$) and December ($t=2.95$, $df=31$, $P=0.006$), whereas males were heavier in September ($t=-1.95$, $df=54$, $P=0.055$) and October ($t=-2.07$, $df=85$, $P=0.041$). The resulting fluctuation in sexual dimorphism is depicted in Fig. 3. Both mean male ($F_{11,245}=5.95$,

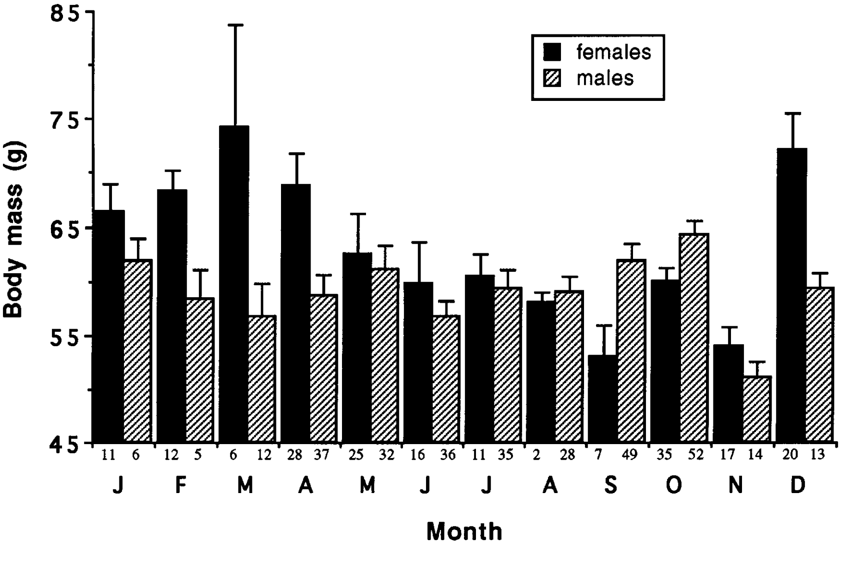

Fig. 2 Mean body mass (± SE) of male and female gray mouse lemurs across the year. *Numbers at the bottom of bars* denote sample size

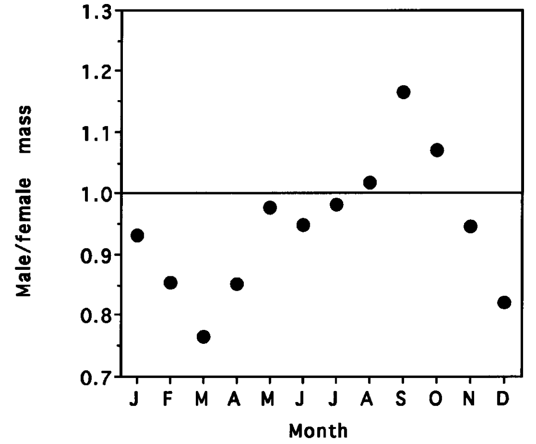

Fig. 3 Annual fluctuation in sexual size dimorphism in *Microcebus murinus*. The ratio of mean male and female body mass is depicted across the year

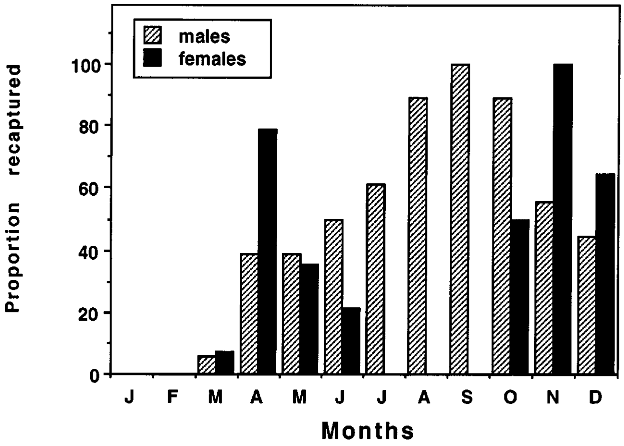

Fig. 4 Sex difference in recapture rates of male and female *M. murinus* across 1995. The number of recaptured males (total $n = 18$) and females (total $n = 14$) differed significantly from the expected number in July ($\chi^2 = 8.51$, 1 *df*, $P < 0.01$), August ($\chi^2 = 12.44$, 1 *df*, $P < 0.001$) and September ($\chi^2 = 14.08$, 1 *df*, $P < 0.001$) when more males were captured. Note that months are not directly comparable because capture effort varied (no captures in January and February, 4 nights in March, April, May, June and July, 8 nights in August and September, 7 nights in October and 4 nights in November and December)

$P < 0.0001$) and female ($F_{11,139} = 6.73$, $P < 0.0001$) body mass also varied significantly across months. Post hoc comparisons revealed that mean male mass was significantly lower in November than in all other months and that it increased significantly between June and October. Female mass was significantly lower in November than in the months between January and July. Furthermore, female mass in December was significantly higher than in the months between September and November. In contrast to the (seasonal) sex differences in body mass, the sex difference in the length of their maxillary canine teeth was statistically not significant ($t = -1.72$, $df = 50$, NS).

The sex difference in body mass in favor of males has two causes. First, male mass increased significantly just before and during the annual breeding season in October (see above). Second, males caught in August and September were compared with fewer females than in previous months, and these females were also in relatively poor condition (Schmid 1997). This observation prompted us to examine the recapture data for both sexes more closely, focusing on the well-sampled year 1995. We found that the proportion of recaptured adult females known to be alive throughout 1995 decreased steadily between April and July, whereas the proportion of recaptured adult males increased (Fig. 4). Furthermore, in July, August, and September, we recaptured no adult females, whereas the vast majority of adult males was caught more than once per month. Adult females began to appear again in October. Their average body mass was reduced by 29.1% (from 80.2 to 56.9 g; paired *t*-test, $t = 10.38$, $df = 12$, $P < 0.0001$) compared to the previous capture date. Controls of sleeping sites of radio-collared animals during the night confirmed that females were inactive for several months (mean 186 days, range 132–228), whereas only 3 adult males were not recaptured in 2 or more successive months (they “disappeared” for a mean of 106 days between April or May and July or August). The body mass of two of these males did not change during this period, whereas the mass of one male fell by 25.5%. Two males were first caught in June and 5 others in August, leaving open the possibility that they were also inactive for several weeks or months. Unfortunately, however, none of these males was radio-collared at the time. Nevertheless, our recapture data indicate that (1) only some males may hibernate, but (2) for at least 2 months less than adult females. This is, to our knowledge, the first evidence for such differential hibernation by sex in a mammal.

Body condition and testes size were positively correlated ($r = 0.554$, $n = 24$, $P < 0.01$; Fig. 5), but there was no evidence for two morphologically discrete classes of

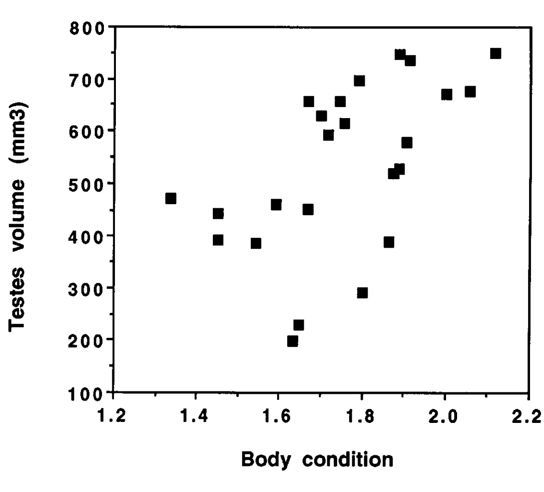

Fig. 5 Variation in male body condition and testes size during the breeding season (October 1995). Condition (mass/head length) is positively correlated with testes size for 24 males

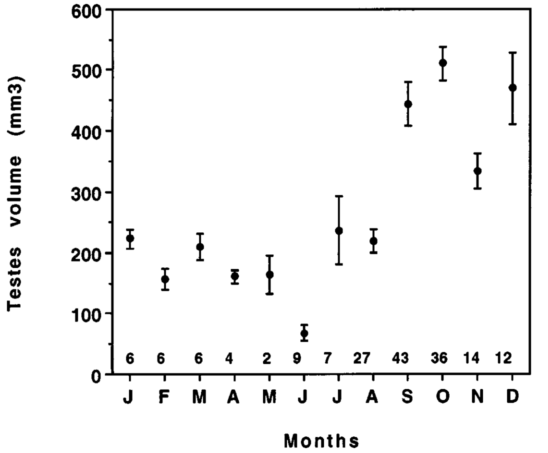

Fig. 6 Annual variation in testes size of gray mouse lemurs. Mean testes volume (±SE) is depicted for each month; *numbers at bottom* denote sample size

males. First, frequency distributions of male condition and testes size in August, September, and October did not deviate significantly from a normal distribution. Visual examination did not reveal any tendency for bimodality or a disjunct distribution. Second, only the frequency distribution of testes size in August was significantly skewed to the right ($g_1 = 0.790$, $n = 27$, $P < 0.05$), indicating that only a few males had large testes at that time, but there was no evidence for significant skew in condition and testes size at other times. Average testes size of all males showed marked annual variation with a 100% increase between August and October (Fig. 6).

Discussion

The results of this field study permitted us to reconcile previous conflicting reports of sexual dimorphism in gray mouse lemurs. We found that sexual dimorphism of body mass reversed twice a year, with females building up reserves prior to hibernation, whereas males gained mass prior to the mating season. When measurements were averaged across the year to one datum per individual, as was done in the captivity study (Kappeler 1991), females in our population were also significantly heavier. Previous reports of heavier males, on the other hand, were based on data obtained between August and October (Fietz 1998), when adult males gain mass and most adult females hibernate. Thus, both sexes exhibit independent variation in body mass across seasons that may reflect sex-specific adaptations, resulting in patterns of sexual dimorphism during the mating season that correspond to theoretical expectations. This observation indicates that sexual selection may operate more strongly on males without resulting in sexual dimorphism because of independent selection on these traits in females.

Male gray mouse lemurs increased in mass during the months preceding the brief mating season, suggesting that body size enhances male mating success. Specifically, this increase in male mass indicates that either strength in direct physical contests or endurance in a scramble competition situation that involves searching for receptive females are important determinants of male reproductive success. In addition, increased mass enables males to enter or extend torpor bouts (Schmid, unpublished data). In closely related and sympatric *Mirza coquereli*, male mass also increased before and during the mating season, concomitant with a more than fourfold increase in the size of their home ranges, which indicated intense scramble competition (Kappeler 1997b). On the other hand, group-living polygynous ring-tailed lemur (*Lemur catta*) males, which primarily compete by attacking and chasing rivals, also increased their body mass by about 10% in the 2 months preceding the mating season (Pereira 1993). In the same vein, experiments with captive mouse lemurs revealed that in newly formed groups, the heaviest male always became dominant over all the others and enjoyed the highest mating success (Perret 1977). However, the lack of canine dimorphism indicates that the potential for male combat is low. This notion is also supported by the observation from our study that males virtually lacked injuries during the mating season. Given the difficulties of direct observations of matings in these small nocturnal arboreal animals, ongoing analyses of male ranging behavior may help to further clarify mechanisms of competition.

Mating strategies of male mouse lemurs appear to be shaped by various factors. First, the fact that males were active in August and September, months characterized by relatively low food availability and high predation risk (Goodman et al. 1993) that females spend hibernating, suggests that these costs and risks are more than offset by reproductive pay-offs. Males may try to establish territories in areas of high female density, but radio-tracking during the pre-breeding season (Fietz 1998; Pagès-Feuillade 1988) revealed high range overlap among males. In other mammals where males emerge from hibernation before females, such as many ground squirrels (*Spermophilus* spp.), males also do not set up breeding territories (Michener 1983; Murie and Harris 1982). Instead, they move around in search of emerging females and suffer injuries in fights with rivals (Michener and McLean 1996). Simply being active before females may be sufficient in these taxa because the proportion of unmated females may decrease substantially within a few days after females begin emerging. The difference in mean emergence dates is, therefore, 1–2 weeks in most ground squirrels (Michener 1984). However, this potential advantage of early emergence does not explain the sex difference in mouse lemurs, which is either at least 2 months, or the qualitative difference of foregoing hibernation altogether.

Second, male testes volume showed marked annual variation with a 100% increase between August and September and a subsequent peak in October. The dramatic change in testes size, as well as their relative size at breeding (Kappeler 1997a), and the occurrence of vaginal plugs (Martin 1972) indicate that sperm competition constitutes an important mechanism of male reproductive competition in this species. Because the spatial distribution of female *M. murinus* does not appear to differ fundamentally from that of most other solitary primates, it is probably the temporal distribution of receptive females that favors the promiscuous mating (Fietz 1998) by both sexes. Highly synchronized estrous periods, possibly the result of photoperiodic changes around the spring equinox (Perret 1996), may make monopolization of several females by a single male difficult (Dunbar 1988). Females further enhance opportunities for multiple matings by emitting a unique estrous advertisement call to attract males (Stanger 1995). Matings by two adjacent females on the same night have been observed (Martin 1972), but exactly how synchronous female estruses are at the population level remains unknown, partly because they hide their newborn infants for several weeks in nests or tree holes, so that mating dates are difficult to reconstruct from birth dates.

Long-term grouping of several males in captivity always resulted in the formation of dominance hierarchies and the subsequent suppression of reproductive activity in subordinate males (Perret 1977, 1992). Intermale sexual inhibition is mediated by urinary pheromones that even affect naive males (Perret and Schilling 1987; Schilling et al. 1984). It has been suggested that this mechanism may be involved in generating so-called central and peripheral males in the wild, at least under high population density (Perret 1992). In the only extended previous field study in southeastern Madagascar, Martin (1972) found highly female biased sex ratios, and mating season sleeping groups consisting of heavy males and several females, which led him to suggest the existence of population nuclei, in which central males have priority of access to estrous females.

Based on our morphometric data, we found no evidence for the existence of two morphologically distinct classes of males, however. At least two explanations for this discrepancy are possible. First, there may be regional differences in social organization as a result of variation in the availability and distribution of important mouse lemur resources. This idea is supported by the results of a brief radio-tracking study in a northwestern forest (Barre et al. 1988; Pagès-Feuillade 1988), which failed to find evidence for population nuclei and two classes of males. Regional differences also predict a stronger contest component in competition, and thus more pronounced sexual dimorphism and relatively smaller testes in the southeastern population studied by Martin (1972). Second, mouse lemur males may pursue different reproductive tactics despite a lack of morphological differences, as has been documented for other small mammals, such as gray squirrels (*Sciurus carolinensis*, Koprowski 1993), common shrews (*Sorex araneus*, Stockley et al. 1994) and alpine marmots (*Marmota marmota*, Arnold and Dittami 1997), for example. Ongoing paternity analyses, in conjunction with analyses of ranging and nesting behavior, will contribute to further clarification of this unresolved question.

As a result of the increase in male size, gray mouse lemurs exhibited the theoretically expected sexual dimorphism, albeit only during the mating season. Such seasonal sexual dimorphism, which has previously been described for seasonally breeding squirrel monkeys (*Saimiri sciureus,* Boinski 1987), has also been found in other lemurs (*M. coquereli*: Kappeler 1997b; *L. catta*: Pereira 1993). In squirrel monkeys, males increase body weight by more than 20% beginning 2 months prior to the mating season, possibly because females prefer large males. Proximately, this increase in male mass is not associated with increased food consumption, but has been linked to the anabolic effects of high steroid levels. In mouse lemurs, testosterone levels are also extremely high at this time of year (Perret 1985), but much of the weight gain before the mating season may be attributable to the proliferation of testicular tissue. This hypothesis is based on the observation that the size and mass of only one testis obtained from a male that was sacrificed after being attacked and dropped by a raptor exceeded the size and mass of his entire brain! Future opportunistic studies of fat depots (Pereira and Pond 1995), i.e., of dead animals that may become available, may help to identify causes of the seasonal increase in body mass. Irrespective of the possible proximate causes, such seasonal adjustments in male body size, which appear to be under narrow photoperiodic control (Pereira 1993), may only be adaptive when seasonally sharply reduced food supplies impose strong costs on large size. However, controlled experiments with *L. catta* revealed that these annual cycles are maintained independent of feeding regimes and after generations in captivity (Pereira 1993), indicating limited flexibility for situation-dependent adjustments.

Female gray mouse lemurs exhibited seasonal patterns of size variation that contrasted with those of males. After changes in body mass associated with gestation and parturition in December and January, females put on weight again during lactation and weaning seasons. By mid-April, many females had accumulated enough reserves to initiate months of hibernation. This behavioral and physiological response to months of reduced food availability and low overnight temperatures (<5 °C in June and July) may ultimately improve female survival, and thus fitness, by avoiding feeding competition and by reducing exposure to predators. In addition, studies of physiological mechanisms involved in entering and maintaining daily torpor revealed daily energy savings of around 40% through this strategy (Schmid 1996, 1997). To enjoy these benefits maximally, however, females need to reach a critical minimum mass at the beginning of the dry season, which juveniles and females in poor condition may fail to do. The latter may initiate hibernation later or forego it altogether in favor of sporadic activity and daily torpor.

Finally, patterns of annual changes in body mass and activity documented here for male and female *M. murinus* contrast sharply with those of sympatric members of the same family (Cheirogaleidae). In *Cheirogaleus medius*, both males and females hibernate between May and October, whereas in *M. coquereli* and *Phaner furcifer* both sexes remain active throughout the year (Kappeler 1997c). *Microcebus myoxinus*, which can also enter at least daily torpor, has not yet been studied in this respect. In the eastern Malagasy rain forest, *C. major*, *Microcebus rufus*, and *Allocebus trichotis* also become seasonally inactive (Wright and Martin 1995). Because the closely-related *M. rufus* may show a similar sex-specific pattern of activity as their dry-forest congeners (Harcourt 1987; S. Atsalis, personal communication), the sex difference in hibernation in *M. murinus* is probably not caused by a single species-specific ecological factor. Because such extended periods of inactivity are not known from other primates, illumination of relevant causes and mechanisms have to await detailed field studies of the other cheirogaleid primates.

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