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Mutual Mate Choice in a Female-Dominant and Sexually Monomorphic Primate

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ABSTRACT Sexual dimorphism is common in polygynous species, where intrasexual competition is often thought to drive the evolution of large male body size, and in turn, male behavioral dominance over females. In Madagascar, the entire lemur radiation, which embraces diverse mating systems, lacks sexual dimorphism and exhibits frequent female dominance over males. The evolution of such morphological and behavioral peculiarities, often referred to as "the lemur syndrome," has proven difficult to understand. Among other hypotheses, a potential role of intersexual selection has been repeatedly proposed but hardly ever tested. Here, we investigate whether female choice favors small and compliant males, and whether male choice favors large females in captive gray mouse lemurs (*Microcebus murinus*). Detailed analysis of a combination of behavioral observations and hormonal data available for both sexes shows that (1) females accept more matings from males with higher fighting abilities, (2) males adjust their investment in intrasexual competition to female fertility, and (3) both male and female strategies are weakly influenced by the body mass of potential partners, in directions contradicting our predictions. These results do not suggest a prominent role of intersexual selection in the evolution and maintenance of the lemur syndrome but rather point to alternative mechanisms relating to male–male competition, specifically highlighting an absence of relationship between male body mass and fighting ability. Finally, our findings add to the growing body of evidence suggesting flexible sex roles, by showing the expression of mutual mate choice in a female-dominant, sexually monomorphic and promiscuous primate. Am J Phys Anthropol 000:000–000, 2011. © 2011 Wiley Periodicals, Inc.

Vast evidence supports Darwin's original intuition that the evolution of sexual dimorphism results from reproductive variance among individuals of the same sex, generally males, due to mating competition (Andersson, 1994). Male-male competition can take various forms. In some species, it involves direct contests over females whereby male rivals aggressively exclude each other. In other species, competition can be indirect and rivals may not necessarily meet. This is the case in scrambles where rapid location of a mate is crucial for success or mate choice where the mate at stake influences which rival will win (Andersson, 1994). Polygynous mating systems—where some males mate with many females and others with none—contribute to increase the intensity of intrasexual competition, and typically favor male traits linked with fighting ability, such as sexual dimorphism in body size, weaponry, or aggressiveness (Crook, 1972; Clutton-Brock, 1991). Such physical and behavioral attributes often enable males to dominate females in intersexual conflict (Kummer, 1968; Archer, 1988).

The Malagasy primates (Lemuriformes) represent a striking exception to this general rule (Ralls, 1976). Here, an entire radiation, embracing a broad diversity of ecologies, life-histories, and sociosexual systems, is characterized by sexual size monomorphism (Kappeler, 1990, 1991; Godfrey et al., 1993) and female dominance over males (Richard and Nicoll, 1987; Kappeler, 1993). This original cortege of morphological and behavioral traits is not well explained neither by traditional theories of sex roles in relation to the mating system and parental care nor by other major hypotheses regarding the evolution of sexual dimorphism such as phylogeny or allometry (Kappeler, 1990). It has further been suggested that unusually high energetic maternal investment in lemur reproduction might select large females (Jolly, 1984; Richard and Nicoll, 1987; Young et al., 1990) or that male agility and speed are more advantageous than fighting abilities in mating systems, which may largely rely on scramble competition (Kappeler, 1990). Support from both comparative and field studies has proven elusive in the first case (Kappeler, 1996; Wright, 1999), while field observations of fierce male–male fights during the mating season suggest that contest competition drives mating success in male lemurs, at least to some extent (Jolly, 1967; Richard, 1992).

The possible role of intersexual selection in the evolution and maintenance of lemur monomorphism and female dominance has been recurrently evoked (Pereira

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et al., 1990; Pereira and Weiss, 1991; Richard, 1992; Jolly, 1998). Indeed, females might choose small and compliant males who would not challenge them or their offspring, for instance during conflicts over resources. Several studies suggest that lemur females might choose male traits that are independent of fighting abilities, such as body odor or sperm of genetically diverse or compatible partners (Schwensow et al., 2008; Charpentier et al., 2010), but it remains unknown whether females might specifically target traits that are disadvantageous in male mating competition.

Conversely, it is also possible that males prefer large females, for instance, if they are more fertile. Indeed, females are larger than males in many animals, and this has long been explained by fecundity advantages of large females (Darwin, 1871; Williams, 1966; Andersson, 1994). Mutual mate choice, where both sexes express mate choice (albeit the targets and intensity of mate choice might not be symmetrical), might also be widespread in nature, even in taxa where reproductive costs are unequally shared (Amundsen and Forsgren, 2001; Gowaty, 2004; Gowaty and Hubbell, 2005; Clutton-Brock, 2007). Yet, in species where female sexual receptivity is asynchronous, as in most lemurs (Wright, 1999), mating opportunities are sequential. In such cases, males might simply spend less mating effort on low-quality females (Engqvist and Sauer, 2001), rendering mechanisms of intersexual selection challenging to detect. Little is known regarding male choice in lemurs, but there is good evidence that mating is costly for males (Jolly 1967; Richard, 1992; Kraus et al., 2008; Huchard et al., in press), which might favor the evolution of choosiness (Kokko and Johnstone, 2002). In addition, choosing large females might increase male reproductive success, because gestation and lactation, the most energetically demanding stages of female reproduction, occur during periods of food scarcity in many lemurs (Wright, 1999).

This study investigates the role of intersexual selection in the evolution of morphological and behavioral lemur idiosyncrasies by examining the targets of precopulatory mate choice in both sexes in captive gray mouse lemurs (*Microcebus murinus*). Mouse lemurs are nocturnal solitary foragers widely distributed throughout Madagascar. A high degree of home-range overlap within and between the sexes, associated with the impressive enlargement of testes during the breeding season, have long suggested the importance of scramble competition among males, with low male monopolization potential and pronounced sperm competition (Fietz, 1999; Atsalis, 2000; Radespiel et al., 2001; Eberle and Kappeler, 2002). Later, direct field observations of mating behavior nevertheless revealed that male contest competition is far from negligible (Eberle and Kappeler, 2004b). The potential for female precopulatory mate choice is enhanced by the low synchrony of female sexual receptivity (limited to few hours per year: Perret, 1982; Eberle and Kappeler, 2004a), which increases the number of candidate mates for a given female (Eberle and Kappeler, 2002; 2004a). Although precopulatory choice has proven difficult to detect in the wild (Eberle and Kappeler, 2004a), behavioral experiments in captivity suggest that females might exhibit mating preferences for males who vocalize more (Craul et al., 2004). Finally, decreased male survival during the mating season probably reflects significant mating costs, in the form of injuries and energetic expenses spent in competing with other males, or increased predation risk when roaming (Kraus et al., 2008). The extent of such costs might select for male adjustment of reproductive investment to variations in female reproductive performance, provided that phenotypic cues accessible to males reliably indicate female performance. As large female size is typically associated with increased fecundity in small mammals (Ralls, 1976), male choice of large females is likely to be rewarded by direct (fertility) benefits in mouse lemurs.

Here, we first test whether female precopulatory choice targets male traits which are disadvantageous for fighting ability. Male fighting ability is rated by an index combining previous experience (age), together with morphological (body mass), behavioral (dominance rank and aggression levels) and hormonal (testosterone) traits. We then test whether males adjust their investment in intrasexual competition and intersexual selection to a range of female phenotypic traits including age, body mass, estradiol levels and scent marking activity. We finally assess whether female traits targeted by male preferences could reliably predict female fecundity, indexed by litter size at birth.

MATERIALS AND METHODS

Animals

All mouse lemurs used in this study (45 males and 15 females) were born in the breeding colony established at Brunoy (France, agreement A91.114.1) from a stock originally caught near the southern coast of Madagascar, in 1967–1972. Individuals included were sexually experienced (no primiparous female) and presented a restricted age range (2–4 years) to limit experience- and age-related effects on the variables examined. Captive conditions were maintained constant with respect to ambient temperature (24–26°C) and hygrometry (55–60%). Animals were fed *ad libitum* on a standardized diet, including fresh fruits, a homemade mixture and mealworms (Giroud et al., 2008). Except for the experiments, males and females were kept in single sex groups of two to four animals per cage. To ensure seasonal reproductive rhythms, animals were routinely exposed to an artificial photoperiodic cycle consisting of 22 weeks of summer-like photoperiod (14 h light day^{-1}) followed by 22 weeks of winter-like photoperiod (10 h light day^{-1}). The beginning of the breeding season was induced by the exposure to long days (Perret and Aujard, 2001). All animals studied were weighed the day before behavioral observations. Visual identification was made possible by individual shave rings on the tail.

Design

Two weeks after the photoperiodic shift triggering the hormonal start of the breeding season, 15 groups of three males were formed. Group members had no previous contact with one another. Each group was kept in a cage ($180 \times 150 \times 90$ cm^2) with wooden supports and two nest boxes. Approximately 2 weeks later, a female in estrus (indicated as the first day of vaginal opening) was introduced for 1 day into the cage of a male group. The male group was chosen so that the female was not closely related (first-order relatedness such as parentage or full sibship) with any of the males. A few days before and on the day of female–male encounter, individual behaviors within each group were video recorded during the first 6 h of nocturnal activity using an infrared camera (MediaZoomIR®, AXOS, France). When analyzing the videos, we recorded a set of behavioral items for each individual, be it male or female, and for each individual encounter (as in Andrès et al., 2001). For analysis, we used the total number of each behavioral item observed per individual per observation period. After the experiment, we recorded the number of offspring produced per female.

Behavioral traits

The male behavioral repertoire was characterized by three components (Andrès et al., 2001). The first two components were recorded for males in the absence and in the presence of the female:

1. Agonistic interactions included chases (a male forcing another male to flee to the ground or to enter a nest) or brief physical aggression. A chase or a fight immediately stopped when the chased animal entered a nestbox. Males engaged in a sustained fight only twice out of 883 interactions.
2. Scent-marking behaviors included urine-washing, ano-genital rubbing, and muzzle-wiping.
3. Sexual solicitations included sniffing or licking of female genitalia, sexual pursuits, mounting (the male climbs on the female and attempts to copulate), and copulation with ejaculation (the male performs deep pelvic movements and the completion of sexual behavior is followed by the male licking its penis). Effective copulations were confirmed by the presence of spermatozoa in vaginal smears.

For each male within a group, a dominance index was further calculated, based on the outcomes of aggressive interactions won (w) or lost (l) during the observation period using the formula: $(w - l)/(w + l)$. This dominance index varied from 1 for a male whose agonistic interactions were always successful, to –1 for a male who was systematically chased by other males (Perret, 1992). Male dominance rank represents an emergent property of aggressive interactions, but dominance rank and aggressiveness are not necessarily tightly correlated (a male can be dominant despite displaying little aggressiveness in a group characterized by low aggression levels). It can be envisaged that a female is attracted by dominant males independently of aggressiveness, or the reverse. As such, both indices might usefully contribute in achieving a fine-grained characterization of male competitive behavior.

Female behavior was characterized by two main components:

1. Scent-marking: as defined above.
2. Reaction (acceptance or refusal) to a sexual solicitation initiated by a male. A reaction was scored as an "acceptance" when a male sexual solicitation led to a copulation and a "refusal" otherwise.

Physiological traits

Females were weighed (±0.1 g) the day before their introduction in the male group. Male and female reproductive condition was also assessed using hormonal analyses. For males, a blood sample (ca. 100 μl) was drawn the day before the introduction of the female, 4 h before night. It was immediately centrifuged and stored at –20°C until assayed. For females, urine (1–3 ml) was collected from spontaneous urination during animal handling the day before vaginal opening, 4 h before night, and stored at –20°C until assayed. Plasmatic testosterone and urinary E_2 concentration were both measured in duplicate using an ELISA immunoenzymoassay (respectively DE1559 and RE52041, IBL, Hamburg, Germany). To take into account variations in urine concentration, the creatinine concentration (Cr, in mg ml^{-1}) was measured in each sample using a colorimetric test (Sigma Diagnostics, St Louis, Missouri, USA). Values of urinary E_2 were thus expressed in pg mg^{-1} Cr. Sampling methods, sample processing and assay characteristics are fully described for testosterone in Aujard and Perret (1998) and for E_2 in Perret (2005).

Ethical note

We have adhered to the Guidelines for the Treatment of Animals in Behavioral Research and Teaching (Animal Behaviour 2006, 71: 245-253) and the legal requirements of the country (France) in which the work was carried out. All the procedures were carried out in accordance with the European Communities Council Directive (86/609/EEC) and were done under personal licenses to experiment on mouse lemurs, delivered by the Ministry of Education and Science. Housing conditions enabled the animals to express their entire locomotion repertoire. Several nestboxes were provided so that animals could escape agonistic interactions. None of the animals tested in this study was injured and heterosexual groups were restricted in time to the day of female estrus.

Statistical analyses

We first quantified male and female phenotypic variations. Between-male phenotypic variation with respect to age, body mass, testosterone, dominance rank, agonistic behavior, marking behavior (the two latter variables were recorded in the presence of a female), and sexual solicitations was analyzed using a centered-scaled principal component analyses (PCA; $N = 45$ individuals). The same method was used to characterize between-female phenotypic variation with respect to age, body mass, urinary E_2 level, and marking behavior ($N = 15$ females). To evaluate if the ranking on the first principal component is indicative of female fertility, we correlated female phenotypic rank and litter size. For all PCAs, we retained the individual coordinates on the first two axes of the PCA as integrated individual indices of male phenotypic variation, quantified by multiple potentially collinear variables.

We then analyzed variations in the sexual behavior of each sex in relation to the phenotypic variation of the opposite sex ($N = 45$ observations corresponding to 45 male–female dyads). As this design involved repeated measures on the same females (each female encountering three males simultaneously), the outcome was analyzed with generalized linear mixed models (GLMMs), with female identity as a random effect.

First, we investigated female acceptance of male sexual solicitations in relation to male phenotypic variation. To do so, we analyzed the number of copulations accepted from each male (response variable, range: 0–4) weighted by the number of solicitations performed by each male (range: 1–36). The model was fitted with a

TABLE 1. Individual traits, and their variations, for male and female gray mouse lemurs used in mating experiments

Variable (unit)	Mean ± SD	RSD	PC1	PC2
Males				
Age (years)	2.82 ± 0.68	0.24	−0.01	−0.75
Body mass (g)	79.1 ± 9.9	0.13	0.24	−0.18
Testosterone (ng ml^{-1})	51.2 ± 11.5	0.23	0.26	−0.59
Dominance rank	−0.1 ± 0.8	8	0.49	−0.003
Agonistic interactions (Number/6 h)	17.0 ± 17.1	1.01	0.49	0.10
Scent-marking frequency (Number/6 h)	40.0 ± 24.7	0.62	0.45	0.19
Sexual solicitations (Number/6 h)	11.7 ± 9.9	0.85	0.44	0.13
Delta agonistic	14.02 ± 15.62	1.11	–	–
Delta marking	18.9 ± 22.15	1.17	–	–
Females				
Age (years)	3 ± 0.84	0.28	0.33	0.67
Body mass (g)	89.3 ± 7.0	0.08	0.41	0.52
Estradiol (pg mg^{-1} Cr)	301.1 ± 175.8	0.58	0.59	−0.41
Scent-marking frequency (Number/6 h)	34.2 ± 14.1	0.41	0.61	−0.33

The contribution of each variable to the first two axes of sex-specific principal component analyses (respectively labelled PC1 and PC2) are quantified by their loadings. Mean, standard deviations (SD), and relative standard deviation (RSD, absolute value of the ratio SD/mean) are presented for each variable. Missing values imply that the variable was not included in the PCA.

quasi-Poisson distribution, appropriate to the analysis of count data, and the two principal components retained from the PCA on male traits were included as fixed effects.

Second, we analyzed male behavior toward females ($N = 45$ observations) using a set of three GLMMs. We hypothesized that males quantitatively adjust their investment in intrasexual competition and intersexual selection to the phenotypic quality of the female introduced in their cage. Male behavioral adjustment was computed as the difference in the number of marking and agonistic behaviors expressed after versus before female introduction, and labeled Δ_{marking} and $\Delta_{\text{agonistic}}$, respectively. As sexual solicitations are not performed in the absence of a female, we used their number of occurrences in presence of the female only. Δ_{marking}, $\Delta_{\text{agonistic}}$ and number of sexual solicitations were the three response variables of our three models, which were all fitted with a quasi-Poisson distribution. In all cases, we tested as fixed effects the first two principal components retained from the PCA on female traits.

Throughout, we used a maximum likelihood approach, with minimization of the Akaike's Information Criteria (QAICc, i.e., after correction for small sample size and overdispersion), to select the statistical models that best described the data while maintaining the lowest number of explanatory variables (parsimony principle). Two models differing by less than two units of AIC were considered to receive equal statistical support (Burnham and Anderson, 1998). Coefficients and standard errors were estimated with the restricted maximum likelihood approach, and factor significance was tested using Wald z tests (Bolker et al., 2009). All statistical analyses were performed using R 2.11.1 (2008).

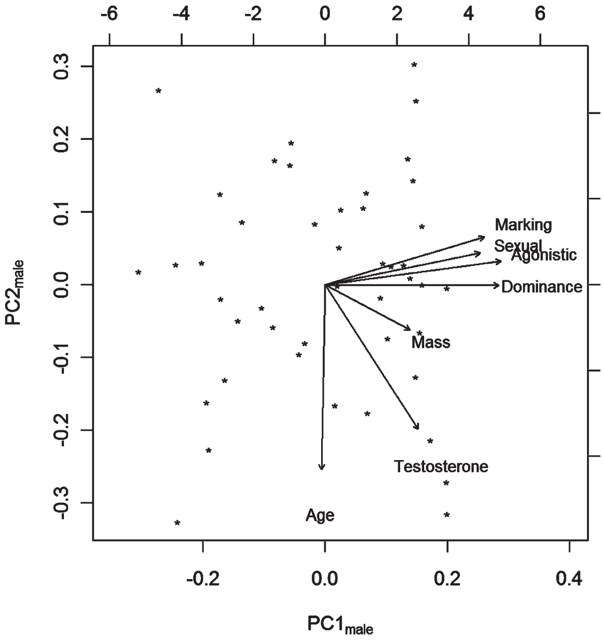

Fig. 1. Intermale variability in behavior and physiological status characterized by a Principal Components Analysis (PCA). Males are represented by their scores on PC1 (x-axis) and PC2 (y-axis). The top and right axes represent principal component loadings on PC1 and PC2 respectively, which correspond to the weights of each original variable (here, behavioral and physiological variables graphically represented by arrows) when calculating the principal components. Loading values are detailed in Table 1. Marking and agonistic behavior was recorded in presence of the female.

RESULTS

Between-male phenotypic variation

Males were more variable in behavior than in physiology, age, and body mass (Table 1). The first two principal components explained 65% of the total variation in male traits. The first axis (PC1_{male}) accounted for 49% of the variation and mainly received positive loadings from male agonistic, marking and sexual behaviors, as well as dominance rank (Table 1 and Fig. 1). PC1_{male} opposed relatively dominant and aggressive males, who were very active at soliciting the female, to relatively inactive males. The second axis (PC2_{male}) accounted for 16% of the variation and primarily received positive loadings from age and testosterone level. PC2_{male} opposed old males with high testosterone levels to young males with low testosterone levels (Table 1 and Fig. 1). Finally, both axes received weak and comparable loadings from body mass (accounting for less than 20% of the variation, Table 1 and Fig. 1).

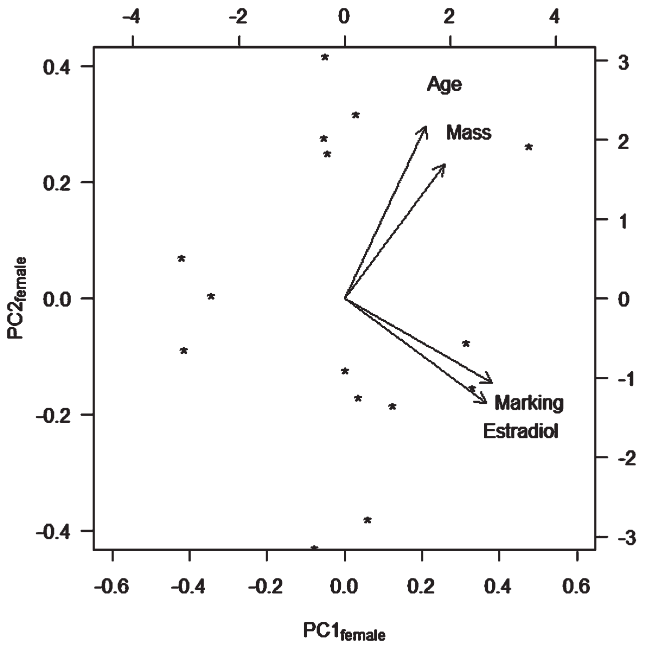

Fig. 2. Interfemale variability in behavior and physiological status characterized by a Principal Components Analysis (PCA). Females are represented by their scores on PC1 (*x*-axis) and PC2 (*y*-axis). The top and right axes represent principal component loadings on PC1 and PC2 respectively, which correspond to the weights of each original variable (here, behavioral and physiological variables graphically represented by arrows) when calculating the principal components. Loading values are detailed in Table 1.

Between-female phenotypic variation

Females were more variable in behavior and physiology than in body mass (Table 1). The first two principal components explained 81% of the total variation in female traits. The first component ($PC1_{female}$) accounted for 54% of the variation and received major loadings from estradiol rate and marking behavior (Table 1 and Fig. 2). The second component ($PC2_{female}$) accounted for 27% of the variation and received a major loading from age and body mass (Table 1 and Fig. 2). Female fertility estimated by litter size at birth was highly correlated to $PC1_{female}$ (Pearson's correlation: $N = 15$, $r = 0.81$, $P < 0.0001$; Fig. 3) but not to $PC2_{female}$ (Pearson's correlation: $N = 15$, $r = -0.29$, $P = 0.29$). The relationship between $PC1_{female}$ and litter size remained significant when excluding females that had not been fertilized (Pearson's correlation: $N = 10$, $r = 0.67$, $P = 0.03$), suggesting that it was not a simple consequence of increased fertilization chances in more attractive females. Consequently, $PC1_{female}$ can be interpreted as an indicator of "female reproductive quality," while $PC2_{female}$ mostly represented variability in age and body mass.

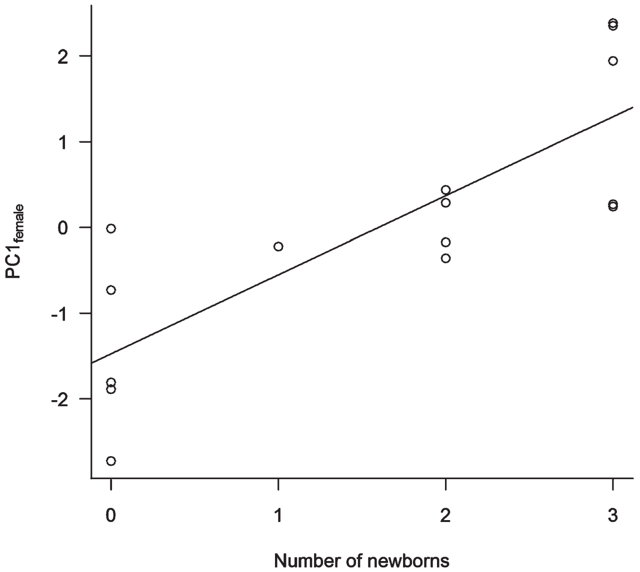

Fig. 3. Female phenotypic variation ($PC1_{female}$, receiving major loadings from estradiol levels and marking activity) in relation to female litter size at birth. Each circle represents one focal female. The line represents the values predicted by a linear model including only litter size as a predictor.

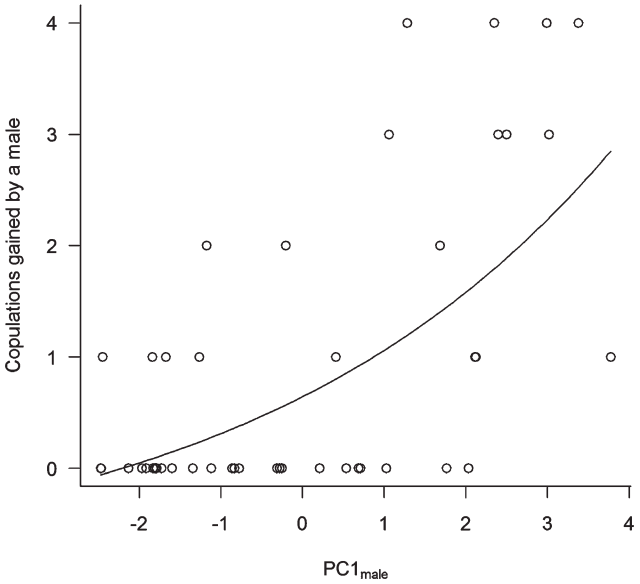

Fig. 4. Female sexual behavior (number of copulations accepted from a male) in relation to a synthetic index of male phenotypic variation ($PC1_{male}$, which receives positive loadings from male agonistic, marking and sexual behaviors, as well as dominance rank). Each circle represents one male–female dyad. The line represents the values predicted by the best model, including only the effects of $PC1_{male}$.

Female choice of male traits

The model that best explained the number of matings accepted by a female only retained $PC1_{male}$ (estimate 0.22 ± 0.02, $z = 10.73$, $P < 0.0001$; Fig. 4). This indicates that females were more likely to accept sexual solicitations from more dominant and aggressive males who performed more scent-markings and sexual solicitations. In contrast, $PC2_{male}$, which received primary loadings from age or testosterone levels, did not significantly influence the outcome of a sexual solicitation. Both $PC1_{male}$ and $PC2_{male}$ received weak loadings from body mass, which suggests that body mass effect on female choice is probably very weak. Regarding the direction of this effect, females would be more likely to accept sexual solicitations from larger than smaller males.

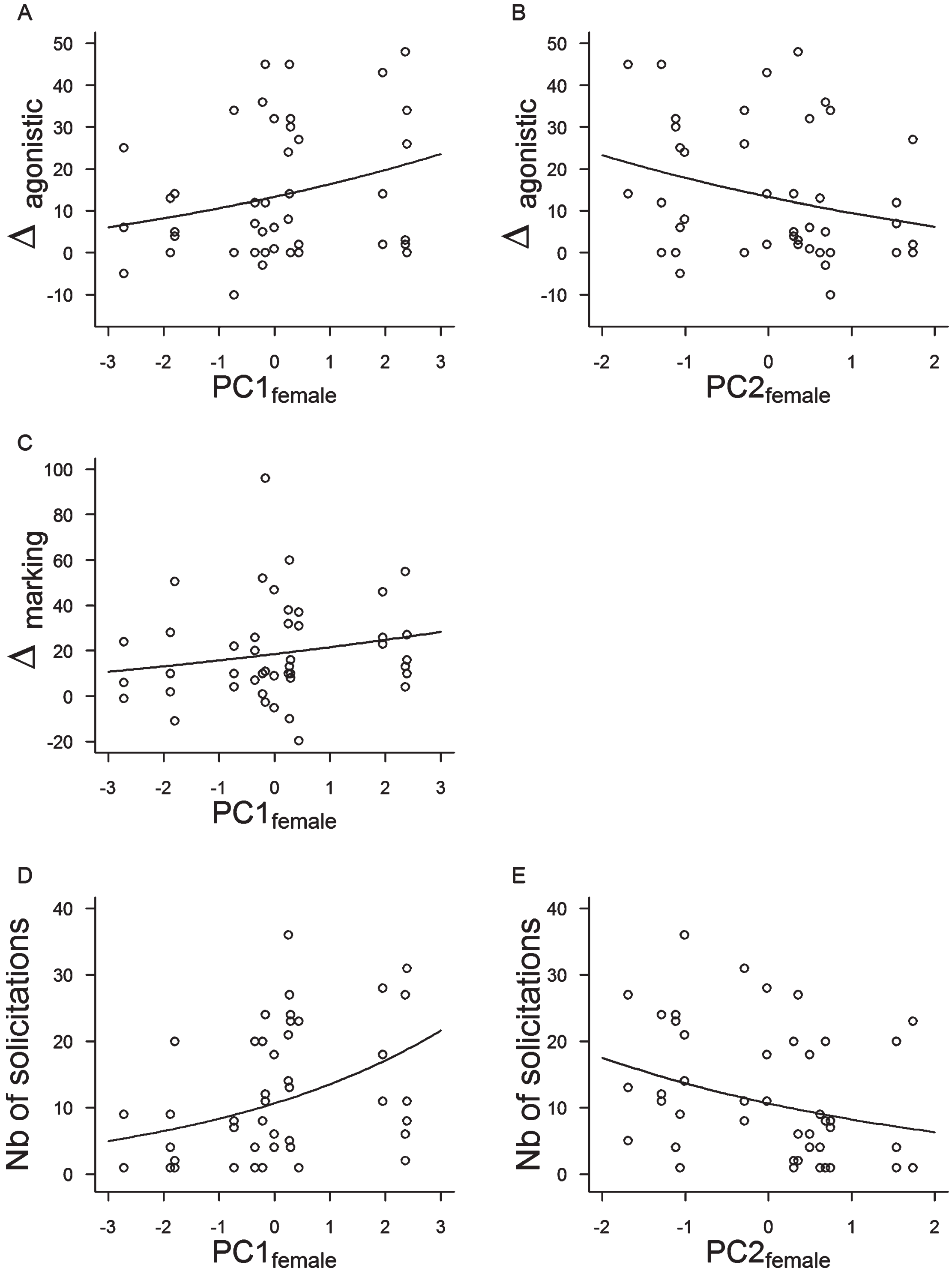

Fig. 5. Male sexual behavior in relation to female phenotypic variation, here indexed by $\mathrm{PC1}_{\mathrm{female}}$ (receiving major loadings from estradiol levels and marking activity) and $\mathrm{PC2}_{\mathrm{female}}$ (receiving major loadings from age and body mass). (**A**) Male–male agonistic behavior in relation to $\mathrm{PC1}_{\mathrm{female}}$, (**B**) Male–male agonistic behavior in relation to $\mathrm{PC2}_{\mathrm{female}}$, (**C**) Marking behavior in relation to $\mathrm{PC1}_{\mathrm{female}}$, (**D**) Sexual solicitations in relation to $\mathrm{PC1}_{\mathrm{female}}$, and (**E**) Sexual solicitations in relation to $\mathrm{PC2}_{\mathrm{female}}$. Male behavioral adjustments to the female presence, measured as the difference between the number of occurrences of agonistic and marking behavior expressed in the presence *versus* in the absence of this female, are respectively noted $\Delta_{\mathrm{agonistic}}$ and $\Delta_{\mathrm{marking}}$. Each circle represents one male–female dyad. The line represents the values predicted by the best model, systematically including the effects of $\mathrm{PC1}_{\mathrm{female}}$, in addition to the effects of $\mathrm{PC2}_{\mathrm{female}}$ for male agonistic behavior and sexual solicitations.

Male choice of female traits

Females of higher reproductive quality (i.e., high score on the $\mathrm{PC1}_{\mathrm{female}}$) induced males to display more agonistic interactions ($\Delta_{\mathrm{agonistic}}$: estimate 0.12 ± 0.02, $z = 22.84$, $P < 0.0001$, Fig. 5A), more marking behaviors ($\Delta_{\mathrm{marking}}$: estimate 0.08 ± 0.03, $z = 22.66$, $P < 0.001$, Fig. 5C) and more sexual solicitations (estimate 0.22 ± 0.05, $z = 4.88$, $P < 0.0001$, Fig. 5D). In addition, males displayed more agonistic interactions and sexual solicitations towards younger and lighter females ($\mathrm{PC2}_{\mathrm{female}}$: $\Delta_{\mathrm{agonistic}}$: estimate 20.17 ± 0.03, $z = 7.48$, $P < 0.0001$, Fig. 5B; sexual solicitations: 20.24 ± 0.06, $z = 23.70$, $P < 0.0001$, Fig. 5E).

DISCUSSION

This study investigated a potential role of intersexual selection in the evolution and maintenance of female dominance and monomorphism in lemurs, by asking if females might choose small and compliant males possessing traits that are disadvantageous for fighting abilities, or if males might choose large females. We found no support for such hypotheses. Instead, females accepted more solicitations from more competitive males, while male choice primarily targeted fertile females. Finally, both male and female strategies were weakly influenced by the body mass of potential partners, in a direction contradicting our predictions: female choice, if anything, favored large males, whereas small females were preferred by males.

Female choice for aggressive males

According to our results, females preferentially accept copulations from dominant and aggressive males. Previous studies in captive gray mouse lemurs, mainly based on genetic analyses of paternity, provided mixed evidence with this respect, suggesting that female choice might either strengthen (Andrès et al., 2001) or weaken (Radespiel et al., 2002) the relationship between male dominance and mating success. Differences in sample sizes and group composition (specifically with respect to age and sex-ratio) might have contributed to generate such discrepancies. Our study, which provides an integrated analysis relying on extended behavioral and endocrine data available for both sexes, supports the first conclusion. At the proximate level, our data suggest that female mating strategies might combine direct mate choice, which comprises active mate discrimination through selective acceptance of matings, with indirect mate choice, where behavioral and physiological manifestations of estrus enhance male–male competition, thereby increasing the chances of mating with a successful competitor (Wiley and Poston, 1996). We cannot exclude that female higher acceptation rates of competitive males reflect sexual harassment rather than mate choice, especially in a captive context where escaping male mating attempts might prove more difficult than in natural conditions. However, recent experimental work suggests that females can easily resist male sexual assaults, and that female sexual strategies favor polyandry (by trying to escape male monopoly) over mate selectivity (Huchard et al., in press). Mating with several males does not exclude choosing them by influencing the distribution of matings across potential partners, and these findings in combination suggest that females exert control over both the number and identity of their mates.

From an evolutionary perspective, female control over reproductive strategies can be favored by several aspects of lemur natural history. First, behavioral dominance over males (Radespiel and Zimmermann, 2001) might help females to impose their mating strategies. Second, female mouse lemurs might have evolved adaptations to counter sexual coercion, including a short sexual receptivity window and a sealed vulva (which only opens around ovulation and parturition). Such adaptations might increase female control over mating, for instance if the energetic costs of female mating resistance can only be afforded over short periods (Huchard et al., in press). Finally, their extreme breeding seasonality, combined with a major uncertainty of reaching the next mating season (Kraus et al., 2008), might also increase the selective pressure for maximizing the current reproductive output by choosing the best possible partners.

Yet, precopulatory mate choice has rarely been reported in mouse lemurs or in other lemurs, although female dominance and seasonal breeding are shared by most lemurs. Female preferences for particular traits have sometimes been detected using two-way choice tests outside male presence (body odor: Cooper and Hosey, 2003; vocalizations: Craul et al., 2004; Charpentier et al., 2010), but evidence for female mate choice in more realistic situations where females have to cope with male strategies remains elusive (Pereira and Weiss, 1991; Brockman, 1999; Eberle and Kappeler, 2004a). This lack of evidence might result from the difficulty of disentangling male from female strategies if they converge in selecting competitive males. In such context, detecting female choice requires direct observations of mating behavior (because indirect evidence relying on paternity data would not allow disentangling male and female strategies), which are particularly challenging to gather in species such as mouse lemurs where females are receptive only few hours per year. More generally, our results highlight the necessity of observing sexual behavior to decrypt the mating system of a species, whereas sexual selection studies increasingly often rely on indirect inferences based on molecular markers of paternity.

Taken together, our results clearly show that female mating strategies do not favor the evolution of male traits that are disadvantageous in contest competition. As such, the "compliant male" hypothesis does not seem to explain the evolution of lemur morphological or behavioral idiosyncrasies.

Male behavioral adjustments to female phenotypic traits

We further found that males increase mating efforts towards fertile females, and, independently and to a lesser extent, toward young and small females. This constitutes the first evidence of male choice in mouse lemurs, and one of the first case described in lemurs (see also Parga, 2006). From a proximate perspective, our data suggest, as mentioned above, that male sexual behavior is stimulated by, thereby adjusted to, a suite of behavioral (such as scent-marking) and/or endocrine (such as estradiol levels) cues produced by estrus females. From an evolutionary perspective, our study further identifies the benefits of such behavior. Whereas previous work in a long-lived lemur, the ring-tailed lemur, suggested that males might invest more efforts into females from the age class in which fecundity and infant survival is highest (Parga, 2006), we show that in the short-lived gray mouse lemur, male preferential investment into females displaying higher estradiol levels and sexual motivation translates into higher reproductive success, indexed by litter size at birth (although it is impossible to establish the causality of the relationship linking female attractiveness to her litter size).

In contrast, male preferential mating investment in young and small females is harder to understand. Indeed, our initial predictions stated that males should choose larger females, who might be more successful at weaning offspring (but not necessarily more fertile). In addition, our analyses show that female age and body mass (indexed by $PC2_{female}$) do not predict litter size at birth. One interpretation could be that younger, smaller females are easier to monopolize, because they are less able to impose their own sexual strategies (Huchard et al., in press), which might increase male chances of siring (more) offspring.

At first sight, the existence of male choice is unexpected in lemurs for several reasons. Firstly, male choice is classically predicted to evolve in species providing costly paternal care (Trivers, 1972; Andersson, 1994), which is rare or absent in the lemurs (Kappeler, 1996, 1997). In addition, the evolution of male choice seems surprising in a female-dominant species where male sexual strategies might be constrained by female behavior. Yet, male preferences are here expressed as an increased investment in intrasexual competition and might only translate into actual choices if they converge with, rather than contradict, female strategies; it is the case here, because the number of matings gained is a positive function of the number of matings solicited.

Second, recent theoretical work suggests that the evolution of male choice is impeded when mating encounters are sequential and mate availability is rare: rejecting a current mating opportunity in the hope of better future opportunities is then not easily selected for (Barry and Kokko, 2010). Although mate encounters are sequential in mouse lemurs, due to low female cycling synchrony (Eberle and Kappeler, 2002), mating encounters cannot be considered rare in this seasonal breeding species. In contrast, males probably face the challenge of maintaining their competitive performance throughout a short and intense mating season. In addition, our study does not report a binary decision, where males “accept” or “reject” a mating opportunity, but a more subtle process where males would adjust their allocation to mating effort as a function of partner quality. Such fine-tuning is difficult to detect, which might contribute to explaining why the importance of male choice has long been under-appreciated (Engqvist and Sauer, 2001; Clutton-Brock, 2007; Gowaty and Hubbell, 2009). In this context, comparing individual investment in male–male competition in the absence versus in the presence of a potential mate represents an interesting approach. Indeed, it allows detecting subtle variations in male motivation, by controlling for baseline individual differences (for instance affecting personalities or physical capacities) that are independent of female quality (and thus also expressed in the absence of female).

Overall, our results suggest that male modulation of competitive efforts might be common where female quality is variable, where encounter rates are locally high, and where male–male competition bears considerable fitness costs, reflected in mouse lemurs by male excess mortality during the short mating season in the wild (Kraus et al., 2008). Yet, here again, our results show that male choice does not play any role in the evolution of lemur monomorphism.

Mate choice targets and covariance among traits in both sexes

In females, the PCA analyzing covariation among traits displayed colinearity between estradiol levels and frequency of scent marking behavior, which reliably predicted female litter size at birth. Mechanistically, such relationship might underline the estrogen-dependence of scent marking and fertilization probability. Note that it was not a simple consequence of increased fertilization chances for attractive females since the relationship remained significant after excluding unfertilized females. In contrast, the quasi-orthogonality observed between female body mass (captured by $PC2_{female}$) and fertility indicators was less expected, since female size is associated with fecundity in most animals (Darwin, 1871; Williams, 1966), especially in small species (Ralls, 1976; Peters, 1983). Similarly, body mass was a weak predictor of male performance in intrasexual contest competition, which is unusual in mammals (Ralls, 1976; Clutton-Brock, 1991). Although we cannot exclude that such patterns arise from captivity conditions and abundant food provisioning, the lack of dependence of female fertility or of male competitive performance on body mass cannot be explained by a lack of interindividual variation in body mass in captive animals. Actually, the variance in body mass was far greater in captive than in wild gray mouse lemurs (after controlling for dependence on age, sex and reproductive state; Huchard et al., in press).

Examining these results in light of mouse lemur life history might draw an alternative functional interpretation. In Madagascar, females typically come into estrus at the end of the dry season, immediately after the winter period of inactivity where females stop feeding for 3–4 months (Eberle and Kappeler, 2002; Eberle and Kappeler, 2004a). In contrast with most larger diurnal lemurs (Wright, 1999), the most energetically demanding phases of their reproduction (namely late gestation and lactation) temporally match the early rains, when the availability of resources (especially insects) increases. As female reproductive investment in mouse lemurs is thought to rely more on current energetic intake (income breeders; Jönsson, 1997) than on energetic reserves (capital breeders; Brockman and van Schaik, 2005), female body mass at estrus might be independent of her reproductive output in any given year. In this context, our findings suggest that it is more advantageous for males to choose females with high estradiol levels, which are also more active at scent-marking, than large ones.

The covariance among male traits also revealed interesting patterns. First, we found a weak relationship between testosterone and behavioral traits connected with male–male mating competition (agonistic and marking behavior, initiation of sexual solicitations). Such lack of correlation is unlikely to represent an artifact of captivity and *ad libitum* feeding, as long-term caloric restriction does not affect male testosterone levels (Dal-Pan et al., 2011), suggesting that food supply has a moderate effect on testosterone fluctuations. Wingfield et al. (1990) underline that the relationship between testosterone and aggressiveness is expected to be labile in species with no paternal care, which is the case of most lemurs including our study species (Kappeler, 1996, 1997). More generally, this result adds to existing evidence that individual testosterone levels do not always reliably reflect aggressiveness and competitive abilities (e.g., Ostner et al., 2011).

Second, our results do not support patterns reported in wild gray mouse lemurs, whereby heavier males win more contests over females and sire more offspring, as revealed by genetic paternity analyses (Eberle and Kappeler, 2004b). However, age might have represented a confounding factor in such analyses. Indeed this field study also reported that first-year—sexually inexperienced—males were lighter and lost more frequently than older males in contests, but did not control for heterogeneity in male age when analyzing body mass effects on fighting or reproductive success (Eberle and Kappeler, 2004b). In addition, the same study failed to detect an effect of male body mass on mating success based on behavioral observations. In this context, it is possible that the weak relationship between adult male body mass and mating success observed in our study is widespread in the lemurs.

From an ultimate perspective, it has been proposed that large body size provides little competitive advantages in a mating system which may rely largely on scramble competition (Kappeler, 1990). Although fierce fights among lemur males are regularly witnessed and suggest some importance of contest competition in lemur mating systems (Jolly, 1967; Richard, 1992), the relationship between male body mass and competitive ability in contests has rarely been tested in the wild. Reduced size increases agility and might thus be selected by intrasexual contest competition in three-dimensional habitats with no firm substrate to take support (Andersson and Norberg, 1981). In line with this, comparative analyses suggest that sexual dimorphism is more pronounced in terrestrial than in arboreal primates (Clutton-Brock and Harvey, 1977). In arboreal lemurs (*Propithecus verreauxi*), existing evidence suggests that morphological traits relating to locomotor performance are more important than those relating to fighting ability (body mass, canine size) during intrasexual contests (Lawler et al., 2005). Our findings support this conclusion: although captivity artificially inflates the importance of contest relatively to scramble competition, our design still hardly detects any advantage of male body mass for fighting abilities or mating success, in line with previous studies in the same species and conditions (Andrès et al., 2001; 2003; Radespiel et al., 2002). Overall, contest competition might determine male mating success to a large extent in the lemurs, but might not generate a strong selective pressure for large-sized individuals, which might help to understand the general independence between sexual size dimorphism and mating systems in the lemurs.

CONCLUSIONS

Our findings do not support the existence of female choice for small or compliant males, neither of male choice for large females in mouse lemurs. This is congruent with a minor role of intersexual selection in the evolution of female dominance and the maintenance of a lack of sexual size dimorphism in the lemurs. Our results rather point to alternative mechanisms, specifically highlighting the weakness of the relationship linking male body mass to fighting ability or mating success. Finally, our study shows that males adjust their sexual behavior to female quality, thereby expressing mate choice in spite of female-dominance and sexual size monomorphism. This adds an interesting data point to the accumulating evidence suggesting that sex roles are flexible (Clutton-Brock, 2007; Gowaty and Hubbell, 2005; 2009).

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