Convenience polyandry or convenience polygyny? Costly sex under female control in a promiscuous primate

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Classic sex roles depict females as choosy, but polyandry is widespread. Empirical attempts to understand the evolution of polyandry have often focused on its adaptive value to females, whereas ‘convenience polyandry’ might simply decrease the costs of sexual harassment. We tested whether constraint-free female strategies favour promiscuity over mating selectivity through an original experimental design. We investigated variation in mating behaviour in response to a reversible alteration of sexual dimorphism in body mass in the grey mouse lemur, a small primate where female brief sexual receptivity allows quantifying polyandry. We manipulated body condition in captive females, predicting that convenience polyandry would increase when females are weaker than males, thus less likely to resist their solicitations. Our results rather support the alternative hypothesis of ‘adaptive polyandry’: females in better condition are more polyandrous. Furthermore, we reveal that multiple mating incurs significant energetic costs, which are strikingly symmetrical between the sexes. Our study shows that mouse lemur females exert tight control over mating and actively seek multiple mates. The benefits of remating are nevertheless not offset by its costs in low-condition females, suggesting that polyandry is a flexible strategy yielding moderate fitness benefits in this small mammal.

Keywords: sexual selection; sexual conflict; coercion; polyandry; primates; Microcebus

1. INTRODUCTION

Bateman’s influential demonstration that a female’s reproductive success (in contrast to a male’s) cannot increase with her number of sexual partners [1] set up a founder paradigm in sexual selection: males compete to gain access to choosy females. Given that mating probably incurs costs associated with exposure to disease [2], predation [3] or physical harm from males [4], females are expected to select their mate carefully rather than mating with multiple partners. Yet promiscuous females, who accept, or even solicit, matings from more than one male (polyandry), are taxonomically widespread [5–7]. In the absence of direct benefits from mating (such as nuptial gifts or paternal investment), polyandry therefore remains an evolutionary puzzle.

Experimental attempts to understand the evolution of polyandry have often focused on its adaptive value to females. Promiscuous females might gain a variety of benefits such as fertilization insurance, improved offspring genetic diversity, or quality through sperm competition and selection in the female genital tract [8–11]. In contrast, fewer efforts have been dedicated to evaluate the extent and costs at which females can exercise control over their mating behaviour [12–14], and this is especially true in vertebrates [15–17].

Sexual coercion can take three forms [18]: (i) forced copulation, where a male physically restrains a female while he copulates; (ii) harassment, where repeated male attempts to copulate bear costs to females which induce them to mate; and (iii) intimidation, where males punish females that refuse to mate with them, thereby raising the chances that they will accept them as mates at some stage in the future. Identifying and estimating the costs faced by a female who refuses to mate represents an obvious initial step to elucidate the proximate and ultimate determinants of polyandry, but also wider aspects of inter-sexual relationships, such as sexual conflict and female mate choice.

Forced copulations are restricted to taxa where a single male cannot control mating access to one or more females effectively [19]. For example, in wild orangutans (Pongo pygmaeus), half or more copulations are estimated to occur coercively [20,21]. Sexual harassment is widespread and can have fatal consequences in its extreme forms, such as in elephant seals (Mirounga angustirostris), where about one in a thousand female dies from injuries inflicted by males following resistance to mating [22]. When the costs of resisting a male sexual attempt exceed the costs of mating, females may mate multiply to decrease the costs of sexual harassment [23]. Such
‘convenience polyandry’ has been demonstrated in several arthropod species [24–26], but similar experimental tests have never been conducted in vertebrates.

Intimidation, where the costs paid by resistant females are temporally decoupled from the mating itself, is most common in species living in mixed-sex groups. Many examples come from social primates, such as chimpanzees (*Pan troglodytes*), where males displaying most aggression towards sexually attractive females mate more often when they become sexually receptive [27,28]. Infanticide by males represents a dramatic case of intimidation, where killing a dependent infant might increase its mother’s probability of mating with the infanticidal male. Females often respond to this threat by mating promiscuously to confuse paternity [29,30]. Infanticide avoidance is currently considered to be the primary explanation underlying the evolution of polyandry in mammals [31,32]. Yet most mammals mate promiscuously, although vulnerability to infanticide by males is concentrated in a few orders [31], which leaves room for alternative or additional explanations.

In this study, we aim at testing whether, and to what extent, polyandry is under female control by examining how mating behaviour varies in response to the manipulation of sexual dimorphism in body mass in captive grey mouse lemurs (*Microcebus murinus*). In this species, females are notoriously promiscuous in the wild [33], but not vulnerable to infanticide by males because of their extreme breeding seasonality, rapid maturation of offspring [34] and a spatial separation between mothers and dependent offspring [35]. Females routinely dominate males in contests over food [36]. Nevertheless, several aspects of their reproductive physiology and behaviour suggest that an evolutionary arms race among the sexes might have arisen from sexual coercion. First, the vagina of mouse lemurs is sealed year-round except for a few days around mating and parturition, and females are sexually receptive for only a few hours during one night per year [33]. These traits may well represent counter-adaptations to forced copulation. Second, sexual size monomorphism (or weak dimorphism), which is rare among polygonous mammals, could result from selection for large females in response to sexual harassment [19]. Third, mouse lemurs are solitary, and females’ brief receptivity window results in low breeding synchrony and an extremely male-biased operational sex ratio [37]. In the wild, up to 14 males can solicit an oestrus female, with sometimes 6 males simultaneously pursuing her [33]. One male can mate-guard a reluctant female during her full receptivity window, and oestrus females sometimes hide or flee when males approach [33].

In addition, mouse lemurs offer several practical advantages to test hypotheses about the evolution of polyandry experimentally. The brevity of female sexual receptivity allows obtaining a complete record of their mating activity [38]. Moreover, their small size, combined with a slight and seasonally fluctuating sexual dimorphism in body mass resulting from a sex differential use of energy savings during the winter period [39] offers the rare opportunity to conduct mating experiments and to manipulate sexual size dimorphism in a primate species.

If mating selectively is more costly than mating promiscuously, as proposed by the convenience polyandry hypothesis, we predict that (1a) females have more sexual partners and accept more matings when they are weaker than males, and (1b) energy spent by a female during a mating night is a negative function of her number of mates and matings. Conversely, if it is advantageous to have many sexual partners, as proposed by the benefit-driven hypotheses, we predict that (2a) females have more partners and accept more matings when they are in better condition than males, and (2b) energy spent by a female during a mating night is a positive function of her number of mates and matings. In contrast, energy spent by a male during a mating night is expected to be a positive function of his number of matings, independent of female strategies.

2. MATERIAL AND METHODS

(a) Animals

Animals were housed in unisexual groups at the laboratory breeding colony (Brunoy, Museum National d’Histoire Naturelle, France, European Institution Agreement no. 962773) under standard breeding conditions [40]. Seasonal variation of physiological functions is maintained by alternating a six-month period of long days (14 h of light and 10 h of dark), with a six-month period of short days (10 h of light and 14 h of dark) [41]. Animals were fed a standard homemade mixture with a caloric value of 4.8 \( \text{kJ g}^{-1} \) and the following macronutrient composition: 50 per cent carbohydrates, 20 per cent proteins and 30 per cent lipids [42]. Water was available ad libitum (AL).

(b) Experimental design

To manipulate female body condition experimentally, three replicates of 12 females (aged 2–4 years) were divided into two groups: control females were fed AL (\( n = 16 \)) while other females were exposed to an 80 per cent caloric restriction (CR; \( n = 20 \)); i.e. their daily food supply represented 20 per cent of the food mass offered to AL females). The CR started three weeks before the transition to long days, and was maintained until the first day of vaginal opening (indicating oestrus), lasting on average 33.3 ± 0.8 days. The first two replicates included six AL and six CR females, while the third one included four AL and eight CR females, to balance the number of mating nights filmed during the first two replicates between AL and CR females (missing the oestrous night of a female could occur when a female entered oestrus earlier than expected, or when more than two females mated synchronously while we only had two infrared cameras).

A detailed description and justification of the sample size used for each analysis is provided in electronic supplementary material, table S1.

To control individual caloric intake, all females were housed individually in cages (50 × 50 × 50 cm) with branches and two nest-boxes. Following the transition to long days, female reproductive state and body mass (±0.1 g) was monitored daily. Female body size was estimated by measuring femur length using a digital calliper (±0.1 mm) [43,44], a measure for which the ratio of within-individual variance (across repeated measures) to between-individual variance was minimal (P.-Y. Henry & C. I. Canale 2008, unpublished data).

Females were transferred into bisexual groups (one female and three males) on the day of vaginal opening, following established breeding procedures in this colony. In each replicate, three groups of three males were formed two weeks before the transition to long days, and were presented to...
three or four oestrous females sequentially. Every male group was presented with both AL and CR females. In bisexual groups (including the mating nights), food was offered AL, and male body mass was monitored daily. Non-mated females \((n = 7)\) were removed when their vaginas started to reseal, after a maximal duration of 3 days spent in heterosexual groups. Mating success was determined every morning by checking for the presence of a vaginal plug and/or sperm in the vaginal tract following housing in bisexual groups [45,46]. To rate individual oestradiol variations sperm in the vaginal tract following housing in bisexual groups (including the mating nights), food was offered every morning from females in bisexual groups and stored at \(-80^\circ\text{C}\). Sampling methods, sample processing and assay characteristics are fully described in the electronic supplementary material. At the end of the experiments, all animals returned to their standard living conditions.

(c) Mating behaviour

Full-night recordings of sexual behaviour were conducted in the absence of human observers, using two cameras with a night shot option (Sony Handycam DCR-SR75E). To ensure visibility, bisexual groups were kept in a cage \((180 \times 150 \times 90 \text{ cm})\) with wooden supports and a Plexiglas door, as well as two nest-boxes transparent to infrared light (Viewpoint, Champagne au Mont d’Or, France). Individual identification was possible through a combination of shave rings on the tail and individual patterns of reflective tape on temporary collars. Full-night videos (lasting 12 h) were viewed to determine the number of copulations and mates per female. Copulations were identified as mountings involving thrusting and ejaculation (the male performs deep pelvic movements until ejaculation, followed by licking his penis) and typically last longer than one minute [45,46].

Behavioural events occurring during the first hour of the night, when mouse lemur sexual activity peaks [33], were analysed in more detail in order to record every occurrence of the following behavioural elements:

— Male sexual solicitations, defined as approaches to within 10 cm of a female prior to interacting with her, which may include sniffing or licking of female genitalia, sexual pursuit or mounting (the male climbs on top of the female from behind and attempts to copulate).

— Male–male aggression, defined as chasing (an individual forcing another one to flee to the ground or to enter a nest-box) or brief physical aggressions. A chase or a fight immediately stopped when the chased animal entered a nest-box.

(d) Ethical note

We have adhered to the Guidelines for the Treatment of Animals in Behavioral Research and Teaching [47] 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 by authorized experimenters (licenses nos 91-439 and 91-455 delivered by the departmental veterinary service). Housing conditions included branches and foliage, and enabled the animals to express their entire locomotor repertoire. Several nest-boxes were provided so that animals could escape agonistic interactions from conspecifics. Caloric restriction over a short period is physiologically sustainable and does not induce chronic stress (cortisol release) in the grey mouse lemur, which is adapted to drastic temporal changes in energy availability [42,48]. Nevertheless, the number of animals included in this experiment was kept to a minimum, and CR was interrupted when female body mass went below a predefined threshold of 60 g [42], to avoid difficulties of recovery to a standard body condition. This only occurred for 2 females out of 36. Standard mating conditions of captivity were used in the present experiment. The polyandrous mating system implies that females must have access to several males simultaneously, which implies that males engage in aggressive encounters when competing for access to a female. However, almost all agonistic interactions recorded in both sexes consisted of brief chases from which animals had the opportunity to escape by entering a nest-box. None of the animals tested in this study was injured, and heterosexual groups were limited in time to the few days surrounding female oestrus.

(e) Analyses

First, variation in female body mass and body size in relation to calorie restriction was tested using two linear models, with experimental replicate included as a control variable. Replicate identity was systematically used as a covariable in further analyses to control for potential heterogeneity among the three experimental replicates. In addition, replicate identity was initially fitted in interaction with food treatment in each model, in order to control for the consistency of the food treatment effect across replicates. As the interaction was never found to be significant, it was omitted in order to estimate the simple effects and test their significance. Sexual dimorphism in body mass was calculated on the oestrous day as the ratio between female body mass at oestrus and the average body mass of her three potential mates. Variations in sexual dimorphism in body mass were analysed in relation to calorie treatment using a linear model.

Variation in the probability that females mated (coded as a binary variable: mated or not) in relation to calorie restriction was tested using a generalized linear mixed model (GLMM) fitted with a binomial distribution. Male group was used as a random factor to control for a potential non-independence of observations made within the same male group. Variations in the probability that females mated polyandrously (coded as a binary variable: polyandry or monandry) in relation to caloric restriction was tested similarly. A similar structure of fixed and random effects was used to model the influence of calorie restriction on the number of matings per female, which was fitted using a Poisson distribution, particularly adapted to the analysis of count data.

Body mass loss per night was calculated as the difference in body mass measured before and after the mating night (animals were weighed every morning at 09.00). For females, variations in body mass lost during oestrous night in relation to their number of mates (coded as a binary variable: polyandry versus monandry) and matings were tested using linear mixed models (LMMs), including male group as a random factor. For males, variations in body mass lost during a mating night in relation to their number of matings were tested using a similar model, except that the random factor fitted here was female identity (to control for the non-independence of observations among males fighting for the same female).

Finally, variations in female E2 levels at oestrus (after log-transformation) in relation to food treatment were tested using a linear model. The effect of female food treatment
(along with replicate identity) was further tested on three components of male sexual behaviour: (i) the rate of solicitations towards females, (ii) the probability of occurrence of solicitations towards females and (iii) the probability of occurrence of male–male agonistic interactions. The first variable excluded the observations for which no solicitations had been recorded (to deal with a 0-inflated distribution) and was analysed using a GLMM fitted with a Poisson distribution accounting for overdispersion [49], while the last variable was coded as a binary variable (instead of counts) and analysed using binomial GLMMs owing to low variance in the number of recorded items. All three models included female identity (to account for the non-independence of observations made among males competing for the same female) crossed with male identity (to account for the repeated appearances of males in the dataset).

The significance of the fixed variables was always tested using the full model (i.e. inferences were drawn with all predictors present, but without interaction term) to avoid the potential problems associated with stepwise model-selection procedures [50,51]. The significance of the fixed effects was evaluated according to the principle of marginality (testing after accounting for the potential effect of all others, i.e. comparing two nested models differing in one fixed effect only) [52]. We used likelihood-ratio tests to evaluate the significance of variables in GLMMs fitted with binomial or Poisson distributions, whereas $F$-tests were used in LMMs and quasi-Poisson GLMMs. All statistical analyses were run using R v. 2.10.0 software [53].

3. RESULTS

Behavioural observations yielded strong indications for sexual harassment, as sexually receptive females were chased up to 109 times per hour (median = 12), whereas they never chased males. The food restriction treatment effectively modified female body mass at oestrus, generating two groups of low (CR) and high (AL) body mass ($n = 20$ CR females: mean $\pm$ s.d. = 74.8 $\pm$ 12.1 g; $n = 16$ AL females: mean $\pm$ s.d. = 113.6 $\pm$ 28.3 g; $F_{1,32} = 29.48$, $p < 10^{-3}$). Body mass also differed among replicates ($F_{2,32} = 5.90$, $p < 10^{-2}$). In contrast, female body size was homogeneous across food treatments ($F_{1,32} = 0.95$, $p = 0.33$) and replicates ($F_{1,32} = 1.28$, $p = 0.29$). Sexual dimorphism in body mass between females and their potential mates (measured on the day of oestrus) was modified by calorie restriction ($n = 17$ CR females with 51 candidate mates: mean $\pm$ s.d. = 0.81 $\pm$ 0.22; $n = 16$ AL females with 48 candidate mates: mean $\pm$ s.d. = 1.25 $\pm$ 0.38; $F_{1,29} = 19.72$, $p < 10^{-3}$; see also figure 1a, which excludes non-mated females) and differed among replicates ($F_{2,29} = 16.64$, $p < 10^{-3}$).

Experimental manipulation of female body condition did not affect the probability that females mated (electronic supplementary material, table S2), but decreased their probability of mating with multiple males (table 1 and figure 1b) as well as their overall number of copulations (table 1 and figure 1c). Moreover, polyandrous females lost more weight than monogamous ones (table 2 and figure 2a), and multiple mating appeared to be energetically costly for both sexes: during the oestrous night, individual loss of body mass declined linearly with the number of matings for both males and females (table 2 and figure 2b).

Finally, differences in female mating behaviour did not arise from decreased sexual attractiveness of calorie-restricted females. Indeed, there was no effect of female food treatment on female oestradiol level at oestrus (electronic supplementary material, table S3). In addition, male sexual behaviour towards females (measured by the probability and rate of sexual solicitations) and male–male competition (measured by the probability of fighting) remained unaffected by female food treatment (electronic supplementary material, table S4).

4. DISCUSSION

This study revealed that manipulation of female body condition profoundly affected mating behaviour, but not in the direction predicted by the ‘convenience polyandry hypothesis’: females in good condition were more promiscuous than calorie-restricted ones, and such differences in mating behaviour were not caused by lower sexual attractiveness of the calorie-restricted females. We further found that multiple mating incurred energetic costs, which were symmetrically shared among the sexes. Here, we briefly discuss some strengths and limitations of our design before considering the implications of our study for understanding the proximate and ultimate determinants of polyandry in this species.

(a) Ethical and methodological considerations

Although our results illustrate the power of experimental manipulation of sexual dimorphism in body mass to disentangle the respective influence of each sex over mating outcomes, this approach could be questioned on ethical grounds. However, our study species exhibits an unusual life history, where weak dimorphism in body mass naturally fluctuates throughout the annual cycle owing to a seasonal sex bias in activity [39]. In captivity, average female body mass fluctuates between 80 g in summer and 120 g in winter, which is of the same magnitude as the body mass variations observed in the present experiment [54]. In western Madagascar, females mate shortly after their emergence from three to four months of inactivity, at a time when food is still scarce and when their body mass is at an annual low. Our

Table 1. Condition dependence of polyandry and multiple mating. Polyandry is coded as a binary variable. Mated females with a known mating history are included (n = 10 AL and 7 CR females). One out of seven CR females was polyandrous, versus seven out of AL females. Parameters and tests were computed using GLMMs with male group as a random factor. β, slope estimate; s.e., standard error.

<table>
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* Intercept: replicate A.

Figure 2. Effect of the number of (a) mates and (b) matings on body mass lost during oestrous night. (a) The raw data are shown and the error bars depict the standard deviation of the mean. Seventeen mated females with known mating history are included. M, monandry; P, polyandry. (b) Grey dots represent female points while black circles represent male points (raw values). Seventeen mated females and seven non-mated females are included, as well as 42 males. The grey line represents the predicted values of the female model, and the black dotted line of the male model.

Experimental treatment similarly decreased food availability for females in the month preceding oestrus. As such, we believe that our study system provides an ethically acceptable opportunity to test current hypotheses of sexual selection by manipulating female body mass—and in turn sexual dimorphism—within its biological range. However, similar designs may be more problematic in species that do not have the physiological ability for females to easily compensate for the energetic costs of additional matings.

(b) Female control over mating

Previous work in the same population suggested that females accept more matings from males who solicit them more and perform better in male–male competition [45,46], which could result either from female preference for dominant males or from sexual harassment. Our results show that mouse lemur females keep tight control over their mating activity: low-condition females had no difficulty in rejecting sexual attempts from heavier males, despite a biased operational sex ratio and intersexual interactions suggestive of sexual harassment. As such, our findings suggest that mouse lemur females can easily afford the energetic costs supposed to be associated with filtering potential candidates [55], and that female pre-copulatory strategies are primarily aimed at increasing, rather than restricting, the set of candidate mates.

Such female control over mating behaviour might not appear surprising in lemurs, which are characterized by female dominance over males [56,57] and a lack of consistently male-biased sexual size dimorphism [58–60]. As emphasized before, these traits are nevertheless not incompatible with sexual harassment, as female mouse lemurs might have evolved several adaptations to counter sexual coercion, including a short sexual receptivity window and sealed vulva. It is possible that female control over mating directly results from such adaptations, for instance if the costs of female mating resistance can only be afforded over short periods. It has even been proposed that selection for large female size might have evolved in response to sexual harassment in morphologically and polygynous primates [19]. Our results do not support this hypothesis, as females had no difficulties in resisting mating attempts under male-biased sexual dimorphism.

(c) The costs and benefits of polyandry

We found that multiple mating is condition-dependent in mouse lemurs, which has also been reported in some (but not all) arthropods, where food-deprived females resist remating for longer than satiated females [26,61]. This was interpreted as the result of a trade-off between foraging and mating opportunities, despite the existence of nuptial gifts in these species, which apparently cannot compensate for the energetic costs of additional matings. The same interpretation might not apply here, where females were rarely observed feeding during mating nights, and rather spent large amounts of time sheltered in nest-boxes, probably because foraging would increase...
Overall, our results indicate that polyandry is not always a by-product of sexual conflict in mammals, so that alternative hypotheses deserve more attention in the future.

(d) The metabolic costs of mating in both sexes
Finally, our results revealed that body mass loss during a mating night can represent 5 to 10 per cent of body mass, which is likely to be significant on such a short timescale, especially for a small-sized mammal. Body mass lost under intense physical exercise probably included a mix of water, stored carbohydrates and lipid metabolites, in proportions that are impossible to establish in the absence of metabolic measurements [69]. Small tropical mammals inhabiting dry tropical forests, such as mouse lemurs, obtain water and energy from food. Since the mating season often occurs at the end of a long dry season [33], when food is rare, this combined loss of stored energy and water is likely to be costly under natural conditions.

The metabolic cost of mating was strikingly symmetrical in both sexes. This is difficult to reconcile with the fact that males presumably derive more benefits from remating than females. Such costs, which are symmetrically shared among the sexes in absolute value, might nevertheless be more significant for males in a female-dominated species, where they might face more difficulties to regain the lost weight. In addition, energetic costs are presumably not the only mating costs, and probably not the most significant ones from an evolutionary perspective. Males probably pay extra costs compared with females (for instance, in the form of search costs or injuries during male–male fights), and they pay such costs on repeated occasions, which ultimately translate into a pronounced male–male fights), and they pay such costs on repeated occasions, which ultimately translate into a pronounced male-biased mortality during the mating season in the wild [70]. Overall, these results add to the increasing body of evidence suggesting that the costs of reproduction are more balanced among the sexes than previously thought, which might be particularly true in weakly dimorphic species with scramble competition mating systems [71].

5. CONCLUSIONS
Our study revealed that mouse lemur females exert tight control over mating while they actively seek multiple
mates, suggesting that polyandry might constitute a more rewarding strategy than pre-copulatory mate choice in this species. The fitness benefits of remating are nevertheless moderate as they are not offset by its energetic costs in low-condition females. As such, our findings suggest that polyandry can evolve in response to moderate fitness benefits, most probably in the form of indirect genetic benefits. Our results further indicate that polyandry is not always explained by sexual conflict in mammals, and parallel findings in arthropods suggest that this notion might apply to a wide range of species.

We have adhered to the Guidelines for the Treatment of Animals in Behavioral Research and Teaching (2006) 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 licences to experiment on mouse lemmings, delivered by the Ministry of Education and Science. Financial support was obtained from UMR 7179 CNRS MNHN, and a PEP 2009 grant attributed to P.Y.H. by INEE-CNRS. E.H. was in accordance with the European Communities Council, and parallel findings in arthropods suggest that this notion might apply to a wide range of species.

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