

Sexual dimorphism in bite force in the grey mouse lemur

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Abstract

Sexual dimorphism is thought to be the result of sexual selection, food competition and/or niche differentiation, or simply the result of differential growth between the sexes. Despite the fact that sexual dimorphism is common among primates, lemurs are thought to be largely monomorphic. Yet, females of the species *Microcebus* are known to be larger than males. Here, we investigate if dimorphism in head dimensions is present in a colony of captive grey mouse lemurs *Microcebus murinus*. Moreover, we test whether any observed shape dimorphism is associated with differences in bite force between the sexes. Our results show that male and female grey mouse lemurs are indeed sexually dimorphic in head dimensions, with females having taller and wider heads than males. Moreover, we confirm previous observations that females are heavier than males. Bite force was principally determined by head dimensions and age in our dataset, and differed between sexes, with females biting harder than males. These data suggest a potential role for niche dimorphism in driving the observed shape and performance dimorphism as female reproductive output may depend upon the ability of animals to obtain resources that are difficult to ingest.

Introduction

Sexual dimorphism is common and widespread in the Animal Kingdom. The origins of differences between the sexes are often difficult to determine but can be roughly grouped into three phenomena: sexual selection (Darwin, 1871; Clutton-Brock & Harvey, 1977), natural selection leading to niche divergence (Hedrick & Temeles, 1989; Shine, 1989; Temeles, Miller & Rifkin, 2010), and differential growth or allometry (Leutenegger & Cheverud, 1982, 1985). In many ectothermic animals, females are generally larger than males, whereas the inverse is often true in endothermic animals (Liao *et al.*, 2013). Despite the strong male-biased sexual dimorphism that is common in primates (Clutton-Brock & Harvey, 1977), some lemur species are known to have a low degree of morphological dimorphism that is biased towards heavier females (Kappeler, 1990). For example, female grey mouse lemurs are known to be significantly heavier than males (Kappeler, 1991). Moreover, this species was one of the two species to show a difference in head length, with females having longer heads than males (Jenkins & Albrecht, 1991).

Males and females of a species often differ in their reproductive roles. Females typically allocate more energy to reproduction than males, which is often reflected in a large abdomen size or greater body mass in females compared with males. Selection for large body size that allows for an increase in reproductive output in females is often referred to as fecun-

dity selection (Hedrick & Temeles, 1989; Andersson, 1994). However, intrinsic differences in the energetic needs of males and females, irrespective of differences in overall size, may also result in a dimorphism between the sexes (Slatkin, 1984). If so, then selection should act on those structures that provide females with enhanced energy acquisition compared with males, such as feeding structures (Casselman & Schulte-Hostedde, 2004; Bulte, Irschick & Blouin-Demers, 2008). Although well-documented examples are rather rare, female northern map turtles bite harder than males, allowing them to consume larger snails and providing them access to resources not available to males. Moreover, reproductive output of females increased with relative head width and bite force, suggesting that bite force capacity is tightly linked to fitness in this species (Bulte *et al.*, 2008). Whereas bite force differences are often the direct result of differences in overall size between sexes, in some cases, specific head traits, such as head width or head depth, drive variation in bite force (e.g. Herrel *et al.*, 1999, 2001; Chazeau *et al.*, 2013). However, bite force is also determined by variation in the underlying muscle structure in many species (e.g. Herrel *et al.*, 2008).

Here, we explore the presence of sexual dimorphism in head dimensions and bite force in the grey mouse lemur *Microcebus murinus*. This species is of interest because females are heavier (Kappeler, 1990) and have longer heads than males (Jenkins & Albrecht, 1991). Differences in reproductive roles might explain the observed dimorphism as mouse lemurs

are omnivores that live in a highly seasonal environment (Radespiel *et al.*, 2006; Dammhahn & Kappeler, 2008; Thoren *et al.*, 2011). As such, individuals have to store fat when food is available and bite capacity could have an important role in allowing females to access food resources that may require higher bite forces. However, females are known to prefer males with greater fighting abilities (Gomez *et al.*, 2012), suggesting that male–male competition might alternatively drive the evolution of a male-biased dimorphism in bite force.

Materials and methods

Subjects

We conducted our study on captive individuals that were born and reared in Brunoy (at the UMR7179 CNRS/MNHN, France; European Institutions Agreement No. D-91-114-1) but descendant from a stock originally caught along the south-western coast of Madagascar. Animals are housed in cages with between one and seven individuals, sexes separated. The temperature is maintained around 25°C and the humidity around 30%; food and water are available *ad libitum*. All individuals are maintained under artificial light conditions that allow a control over the season and the period of the day by controlling the photoperiod. In total, we used 62 adult individuals: 28 males and 34 females. Individuals were aged between 1 and 7 years old (Table 1).

Morphometrics

Head dimensions (length, width and depth) were measured using digital calipers (Mitutoyo, Kanagawa, Japan). Head dimensions were measured across the greatest dimension as reported previously. In brief, head width and height were measured posterior to the eyes at the level of the zygomatic arch; head length was measured from the back of parietal to the tip of the snout (Chazeau *et al.*, 2013). Body mass was measured using a digital scale, and the measurements were carried out just after the reproductive season. The age of each individual at the time of bite force measurements was retrieved from the breeding records of the colony.

Bite force

We measured bite force from all individuals using a piezoelectric force transducer (Kistler, type 9203, range ± 500 N;

Kistler, Winterthur, Switzerland) attached to a handheld charge amplifier (Kistler, type 5995). The transducer was mounted between two bite plates, as described by Herrel *et al.* (1999) and Chazeau *et al.* (2013) for lemurs. The tips of both upper and lower bite plates were covered with a layer of cloth medical tape to provide a non-skid surface and to protect the teeth of the animals. The distance between the bite plates was adjusted to assure the same gape angle for each individual. Bite force was measured during unilateral molar biting, a posterior bite position where maximum bite forces have been recorded in mammals (Dumont & Herrel, 2003). Three recording sessions were conducted for each animal, during which several bites were recorded. Only the single highest bite force value was retained for further analysis.

Reproductive success

We extracted data on the reproductive success of each female in our dataset from the database for the colony at Brunoy. For each female, we noted the lifetime number of offspring produced until 2013. We corrected the number of offspring for the number of times a female was mated by regressing the total number of offspring on the number of times a female was mated and extracting the residuals as a measure of reproductive success. This was not possible for males as the sires are unknown.

Statistical analysis

Bite force and morphological measurements were \log_{10} -transformed in order to comply with the assumptions of normality and homoscedasticity required for parametric analyses. We first ran pairwise correlations between morphological data, age and bite force to explore the correlations among variables and did so both for the overall dataset as well as for males and females separately (Table 2). Next, we ran a stepwise multiple regression analysis to determine which variables were the best predictors of variation in bite force. We then tested for differences between the sexes in absolute head dimensions using a multivariate analysis of variance (MANOVA). We also tested for differences in absolute and relative bite force between the sexes using analysis of variance (ANOVA) and analysis of covariance (ANCOVA). In our ANCOVA, we used the single best morphological predictor of bite force (head depth) as our co-variable. We next ran a principal component analysis on the three head dimensions described previously and three limb dimensions (ulna length, tibia length and metatarsus length) and extracted the first principal component as an indicator of overall size. We then regressed body mass on size and extracted the unstandardized residuals as an indicator of body condition and regressed those against bite force. Finally, to explore whether reproductive success of females was related to morphological and performance traits, we tested for correlations of the relative number of offspring of each female with head morphology, bite force, body condition and body mass using Pearson's correlations.

Table 1 Summary table detailing differences between the sexes in morphology and bite force

	Females ($n = 34$)	Males ($n = 28$)
Head width (mm)	22.17 \pm 0.84	21.63 \pm 0.71
Head depth (mm)	16.26 \pm 0.71	15.72 \pm 0.84
Head length (mm)	35.70 \pm 1.82	35.12 \pm 1.41
Bite force (N)	35.61 \pm 6.41	31.36 \pm 6.05
Body mass (g)	99.00 \pm 15.47	81.18 \pm 11.00
Age (days)	1428.5 \pm 564.3	1190.2 \pm 540.5
No. of offspring	1.77 \pm 1.26	

Values are means \pm SD.

Table 2 Correlation matrices summarizing correlations between morphological variables, age and bite force

	Age (days)	Body mass (g)	Head length (mm)	Head width (mm)	Head depth (mm)
All individuals					
<i>n</i>	62	62	62	62	62
Mass (g)	0.373 0.003				
Head length (mm)	0.235 0.066	0.406 0.001			
Head width (mm)	0.272 0.032	0.661 <0.001	0.558 <0.001		
Head depth (mm)	0.345 0.006	0.465 <0.001	0.382 0.002	0.393 0.002	
Bite force (<i>n</i>)	0.422	0.408	0.269	0.271	0.509
<i>n</i> = 51	0.002	0.003	0.056	0.055	<0.001
Males					
<i>n</i>	28	28	28	28	28
Mass (g)	0.452 0.016				
Head length (mm)	0.279 0.151	0.466 0.012			
Head width (mm)	0.207 0.290	0.632 <0.001	0.565 0.002		
Head depth (mm)	0.269 0.166	0.283 0.144	0.273 0.160	0.271 0.163	
Bite force (<i>n</i>)	0.400	0.316	0.259	0.105	0.342
<i>n</i> = 23	0.059	0.142	0.234	0.634	0.110
Females					
<i>n</i>	34	34	34	34	34
Mass (g)	0.248 0.157				
Head length (mm)	0.169 0.339	0.333 0.054			
Head width (mm)	0.228 0.194	0.503 0.002	0.541 0.001		
Head depth (mm)	0.347 0.044	0.423 0.013	0.424 0.013	0.301 0.083	
Bite force (<i>n</i>)	0.355	0.279	0.223	0.199	0.653
<i>n</i> = 28	0.064	0.150	0.255	0.310	<0.001

Bolded values represent significant correlations among variables.

Results

Determinants of bite force

Bite force was positively correlated with age, body mass and head depth (Table 2; Figs 1 and 2). Head dimensions were strongly intercorrelated and were generally correlated with body mass. Age and body mass were also correlated in the overall dataset and in males (Table 2). A multiple stepwise regression analysis performed for all individuals combined extracted a single model with head depth ($\beta = 0.41$) and age ($\beta = 0.28$) as the only two predictors of bite force ($R^2 = 0.337$; $P < 0.001$). Thus, animals that have taller heads and that are older can bite harder. Body condition was not correlated to bite force ($R^2 = 0.02$; $P = 0.32$).

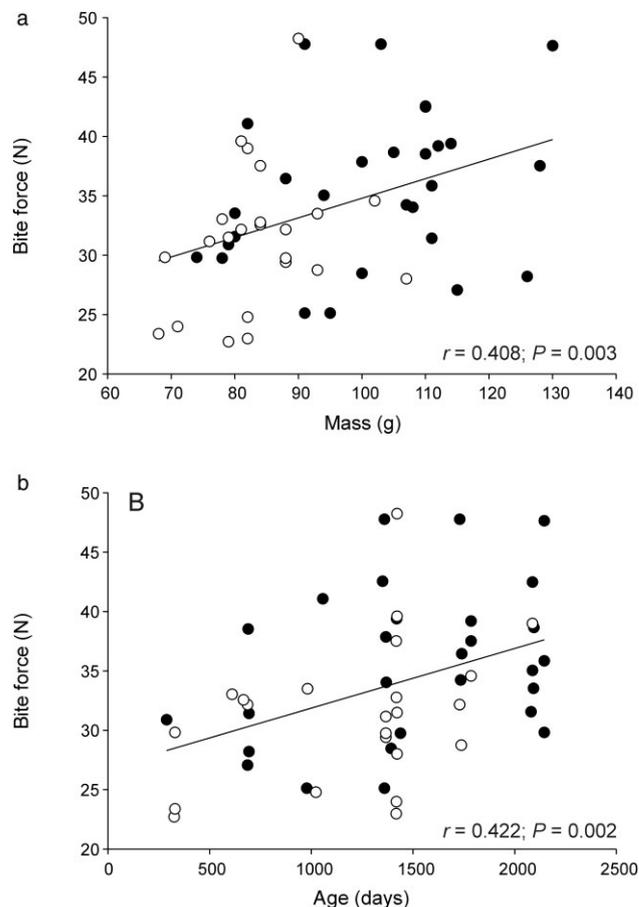


Figure 1 (a) Scatterplot illustrating relationships between body mass and bite force. (b) Scatterplot illustrating relationships between age and bite force. Note that body mass axis is plotted on a \log_{10} scale. Filled circles represent females and open circles represent males.

Sexual dimorphism

A MANOVA indicated significant sexual dimorphism (Wilks' lambda = 0.66; $F_{5,56} = 5.88$; $P < 0.001$). Subsequent univariate *F*-tests indicated that sex differences were significant for head width ($F_{1,60} = 15.86$; $P < 0.001$), head depth ($F_{1,60} = 7.90$; $P = 0.007$) and body mass ($F_{1,60} = 25.53$; $P < 0.001$). Average age and head length were not significantly different between the sexes ($P > 0.05$). Inspection of the means showed that females have wider and taller heads and are heavier than males (Table 1). An ANOVA performed on the bite force data indicated significant differences between the sexes ($F_{1,49} = 5.96$; $P = 0.018$), with females biting harder than males. When taking into account differences in head height, however, differences in bite force were no longer significant ($F_{1,48} = 2.21$; $P = 0.14$).

Reproductive success

The mean reproductive output for females was 1.77 ± 1.26 offspring (Table 1). However, values ranged from zero to

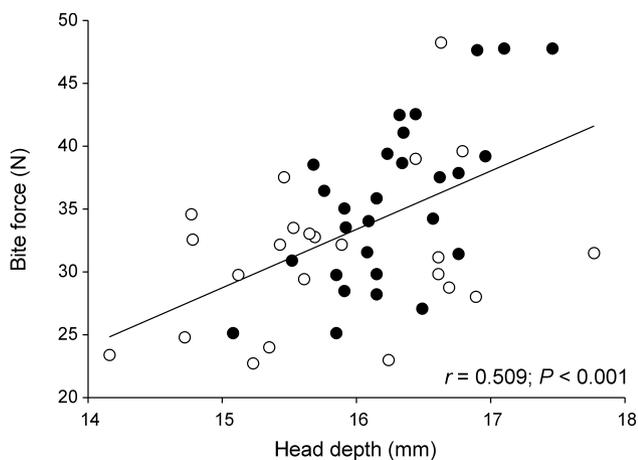


Figure 2 Scatterplot illustrating relationships between head depth and bite force. Filled circles represent females and open circles represent males.

four. Relative reproductive output (number of offspring relative to the number of times an animal was mated) ranged from zero to three, suggesting important differences between females in reproductive output independent of mating opportunities. Correlations were significant for head width ($r = 0.36$, $P = 0.036$, $n = 34$), body mass ($r = 0.442$, $P = 0.009$, $n = 34$) and body condition ($r = 0.391$, $P = 0.027$, $n = 32$). Thus, females that are heavier, that are in better body condition and that have wider heads have a higher reproductive success.

Discussion

As expected, we observed sexual dimorphism in body mass and head dimensions in our captive mouse lemurs. Females were heavier in accordance with previous studies (Kappeler, 1990, 1991; Jenkins & Albrecht, 1991) and had taller and wider heads. In contrast to earlier findings (Jenkins & Albrecht, 1991), we did not find dimorphism in head length. However, given that we measured live animals in contrast to Jenkins & Albrecht (1991), who measured dry skulls from the British Museum and from the Duke University Primate Center, this is not entirely surprising. Measuring head dimensions, such as length in live animals, is prone to greater error relative to measures of head width or head depth, which are more easily measured in a live animal (see Table 1). In addition, females in our dataset had higher bite forces than males. However, after controlling for variation in head dimensions between males and females, sexual differences in bite force disappeared. This means that females bite harder because of their larger heads and suggests an intimate relationship between trophic morphology and performance. Larger heads should result in higher bite forces as they allow for a larger muscle volume. Moreover, taller heads may allow for a different orientation of the jaw adductors, providing them with a greater moment arm during biting. Yet, this remains to be tested based upon dissections of the jaw muscles in male and female mouse lemurs.

In a previous study (Chazeau *et al.*, 2013), bite force capacity in males was principally determined by head dimensions and was not influenced by season, even if males exhibited seasonal variability in plasma testosterone because of a variation in testes size (Aujard & Perret, 1998; Schmid & Kappeler, 1998). Moreover, bite force was also affected by age, with older animals biting harder. In males in the present study, correlations of bite force with age were only marginally non-significant (Table 2), suggesting similar overall patterns. Yet, correlations of bite force with head width were not observed in males in the present study. Why this is the case remains unclear at this point. However, each head dimension will affect bite force differently. Whereas head width likely mainly reflects variation in overall muscle volume, a greater head depth may allow for changes in the orientation of the jaw adductors relative to the jaw joint, providing an individual with a greater moment arm of the temporalis muscle (Herrel *et al.*, 2008). However, irrespective of the specific dimensions influencing bite force, both studies indicate that head dimensions and age are the principal determinants of bite force. How differences in head dimensions may result in larger or heavier muscles, or differences in muscle orientation remains to be tested for *M. murinus*, however.

Three hypotheses can be put forward to explain the evolution of sexual dimorphism in trophic structures: (1) sexual selection; (2) growth differences; (3) niche differentiation (Shine, 1989; Kappeler, 1990). Sexual dimorphism in body size is thought to be the result of an increase in female body size as the result of selection on female fecundity, in addition to a decrease in male size as a selection on male agility (Kappeler, 1990). However, Gomez *et al.* (2012) found that mate choice in captive mouse lemurs does not favour the selection of small compliant males and larger females through sexual selection. In contrast, heavier males had a better chance to reproduce in captivity (Perret, 1977). However, no relationship between body mass and fighting ability was detected in males. Although this suggests that other traits, such as bite force, might be important, this is unlikely as the dimorphism in bite force is clearly female-biased. Thus, our results provide little support for sexual selection on male biting capacity. In cheirogaleids, morphological disparity between genera associated with diet has been suggested (Viguié 2004). However, whether differences in diet exist between males and females remains largely unknown (Radespiel *et al.*, 2006; Dammhahn & Kappeler, 2008). If females were to exploit harder prey or resources that are difficult to extract or to chew, then this might explain the observed sexual dimorphism in bite force capacity. As such, our data do support some of the basic premises of the niche divergence hypothesis.

Our data on reproductive success show that females with wider heads have relatively more offspring. Although bite force was not directly related to reproductive output, the correlation between head dimensions and reproductive output suggests that the reproductive role hypothesis may at least partly explain the origin of the observed dimorphism in head dimensions (Bulte *et al.*, 2008). Moreover, body condition and body mass were the two other variables that were significantly related to reproductive success. Although food intake and the

trophic apparatus appear to play a key role in female fitness, this remains to be tested in wild populations. Finally, behavioural differences between the sexes may also play a role and could potentially drive some of the observed differences between males and females. In general, females of the colony at Brunoy appear to be much more aggressive than males, and as such, might be inclined to bite harder. Indeed, correlations between personality and functional traits (such as exploration behaviour and maximal sprint speed in lizards; Le Galliard *et al.*, 2013) have been demonstrated in other taxa. Such correlations are typically explained by the pace-of-life syndrome, which predicts that behavioural, metabolic, immune and hormonal traits could have evolved together under specific ecological conditions (Réale *et al.*, 2007, 2010). As such, this more aggressive behaviour combined with a higher bite performance could be due to the differences in niches between male and females that may be related to the different costs of reproduction in the two sexes.

Conclusion

In summary, this study provides the first evidence for sexual differences in head dimensions and bite force in a small prosimian (*M. murinus*). Although the ultimate drivers of this dimorphism remain unknown, the fact that females bite harder than males suggests a role for niche divergence and/or reproductive roles in driving the observed dimorphism. However, both niche divergence and reproductive roles may act in concert and the importance of one versus the other factor may be difficult to tease apart. Clearly, field studies are needed to better understand the selective pressures on trophic morphology in this species.

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