

Proximate determinants of bite force capacity in the mouse lemur

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Abstract

Both mating system and diet are thought to drive inter-individual variation in bite force. Although previously published data suggest that bite force variation may be driven by variation in morphology (e.g. head morphology, body size, muscle size), age and physiology (e.g. fluctuating plasma testosterone levels) in some vertebrates, this remains untested in primates. Here, we explore the proximal determinants of bite force capacity in the grey mouse lemur *Microcebus murinus*. Our results show that in male grey mouse lemurs, bite force measurements are repeatable across a 1-month period. Yet, bite forces were independent of fluctuation plasma testosterone levels. Head dimensions and body mass were all positively correlated with bite force. Among these, head width was the best predictor of bite force as has been observed for other vertebrates. Unexpectedly, age was highly significantly and positively correlated with bite force. Whereas older animals generally bit harder, the oldest age group (5.5 years) showed a decline in bite force capacity. These results suggest that bite force in the grey mouse lemur is mostly determined by morphology and age, yet is independent of variation in testosterone. Future studies including a broader age range and animals of different sexes would be of interest to better understand the variation in bite force in this small lemur.

Introduction

Body size and dietary specialization have been suggested as the primary drivers of the evolution of cranial form and function in primates (e.g. Hylander, 1979; Ravosa, 1991; Daegling, 1992; Perry, Hartstone-Rose & Wall, 2011a). Whereas many studies have estimated bite forces in primates using anatomical estimates (e.g. Spencer, 1998; Perry, Hartstone-Rose & Logan, 2011b; Shi *et al.*, 2012), muscle stimulation (Dechow & Carlson, 1983, 1990) or indirectly through measures of the forces need to break food items (Lucas, Peters & Arrandale, 1994), surprisingly few studies have provided direct measures of bite force (but see Ross *et al.*, 2007). Yet, direct bite force measurements are of interest as they are non-invasive and can be used to test inter-individual correlations with morphology (Herrel *et al.*, 2008), behavior (Herrel *et al.*, 2009) and diet (Herrel *et al.*, 2006). For a given gape angle, bite force is determined by the force generation capacity of the jaw muscles and the lever system of the jaw. The force-generating capacity of the muscles is in turn determined by muscle cross-sectional area and fiber type (e.g. Herrel *et al.*, 2008). As individuals with bigger heads can harbor larger muscles, correlations between head dimensions and bite force generation capacity are often observed (Herrel *et al.*, 1999, 2005a,b), and head size is often used as a proxy for male fighting ability in species that bite

during territory defense or aggressive behaviors in general (Molina Borja, Padron Fumero & Alfonso-Martin, 1998).

However, physiological parameter such as fluctuating plasma testosterone levels may also affect bite force capacity. Indeed, testosterone is known to affect anatomical and physiological traits that contribute to variation in physical performance (Luine *et al.*, 1980; Tobin & Joubert, 1991; Girgenrath & Marsh, 2003; but see O'Connor *et al.*, 2011). However, evidence for testosterone affecting performance traits such as bite force is equivocal. Whereas in the lizard *Anolis carolinensis*, plasma testosterone levels are correlated with bite force capacity (Husak *et al.*, 2007), in another species of lizard *Gallotia galloti*, experimental elevation of testosterone levels increased the size of the jaw adductor muscles, but not bite force (Huyghe *et al.*, 2010). How general these results are, and whether other vertebrates also show correlations between fluctuating testosterone levels and bite force, remains, however, unknown.

Finally, bite force is known to be strongly influenced by growth and development (Herrel & Gibb, 2006). As animals grow, their heads and jaw muscles increase in size as well, thus affecting bite force (Herrel & O'Reilly, 2006). Moreover, these patterns are often allometric (i.e. different components growing at different rates), and larger animals often have disproportionately large bite forces for their size (Herrel & Gibb, 2006). Yet, most of these studies are based on

ectothermic vertebrates, which show continuous growth throughout their life (see Herrel & Gibb, 2006). However, whether growth and age independent of growth (i.e. after reaching adult size) affect bite force remains largely unknown. Yet, studies on skull development and bite force in carnivores suggest a developmental asynchrony between performance and growth with bite forces reaching maximal levels when animals have reached adulthood suggesting a relationship with hormonal changes (Binder & Van Valkenburgh, 2000; Tanner *et al.*, 2010; La Croix *et al.*, 2011). Whether such a pattern is characteristic of all mammals remains to be tested, however.

Here we use the grey mouse lemur *Microcebus murinus* as a model to explore the proximal determinants of bite force in primates. This small lemur is of interest as it has a promiscuous mating system where female choice is strong and males will fight over access to females in captivity (Andres, Solignac & Perret, 2003; Gomez *et al.*, 2012). Moreover, recent studies (Gomez *et al.*, 2012) have demonstrated that females preferred males with high fighting abilities, independent of body mass. Finally, during mating, males move across the back of a female while facing the same direction. Next, they wrap their arms around the abdomen of the female and in some cases maintain the female's neck by biting suggesting an additional role for bite force during mating (Eberle, Perret & Kappeler, 2007). In the wild, a high degree of home-range overlap within and between the sexes has been observed and interpreted as suggesting that the mating system of the mouse lemur is based on scramble competition among males with pronounced sperm competition (Radespiel, Ehresmann & Zimmermann, 2001; Eberle & Kappeler, 2002, 2004a). However, direct field observations of mating behavior revealed that males are able to temporarily guard receptive females. During guarding episodes, the males aggressively engage in fights with other males and try to deter the females from escaping (Eberle & Kappeler, 2004b). Aggressive behavior among wild males is thus non-negligible during the period when females are in estrus. Moreover, the decreased survival observed during the mating season may reflect the energetic costs (or injuries) from sexual competition (Kraus, Eberle & Kappeler, 2008).

As such, it can be expected that seasonal variation in circulating androgen levels may be correlated to aggression and also bite force through its effects on muscle growth (Huyghe *et al.*, 2010). Male mass in *M. murinus* also increases just before, and during, the annual breeding season in October. This increase in male mass indicates that either strength in direct physical contests or endurance in a scramble competition situation involving searching for receptive females are important determinants of male reproductive success. This increase in male mass is not associated with increased food consumption, but has been linked to the anabolic effects of high steroid levels (Schmid & Kappeler, 1998), which may increase muscle mass to cope with the physical demands of competition for females. As the grey mouse lemur is an omnivore consuming a variety of prey ranging from gum to fruits to arthropods (Radespiel *et al.*, 2006; Dammhahn & Kappeler, 2008; Thoren *et al.*, 2011), seasonal variation in bite force capacity could affect individual quality and survivorship. For

example, harder insects such as beetles may be only accessible to males with sufficient high bite forces and as such bite force may be an important structuring agent at the intraspecific level.

Materials and methods

Animals and morphometrics

The mouse lemurs *M. murinus* used in this study were born in the laboratory breeding colony of Brunoy (UMR7179 CNRS/MNHN, France; European Institutions Agreement # D-91-114-1) from a stock originally caught along the south-western coast of Madagascar 40 years ago. In the colony, seasonal Malagasy rhythms were reproduced by alternating 6-month periods of long days (light : dark 14:10) and short days (light : dark 10:14). A total of 28 male individuals were measured and tested for bite force. Animals were housed in groups of males only without access to females. Four individuals refused to bite and were eliminated from the analysis. Moreover, we were unable to extract enough blood for the analysis of testosterone for eight individuals. Head dimensions (length, width and depth) were measured using digital calipers (Mitutoyo, Kanagawa Japan; see Fig. 1). Head dimensions were measured across the greatest dimension and may thus include the bulging of the jaw muscles in case of width and height, which were measured posterior to the eyes at the level of the zygomatic arch. Calipers were closed until they touched the head, but without exerting pressure. All measurements were repeatable within days and across measurement periods (all correlations > 0.5). Body mass was measured using a digital scale. 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 Aguirre *et al.* (2002). 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 constant gape. Bite force was measured during unilateral molar biting, a posterior bite position where maximum bite forces have been recorded in mammals (Dumont & Herrel, 2003). At least five trials were conducted for each animal during each recording session. Two recording sessions were conducted, one in April and one in May 2011.

Testosterone concentrations

Blood samples were taken from the saphenous vein of the hind limb in non-sedated animals using sterile needles and heparinized capillary tubes on the same day bite forces were

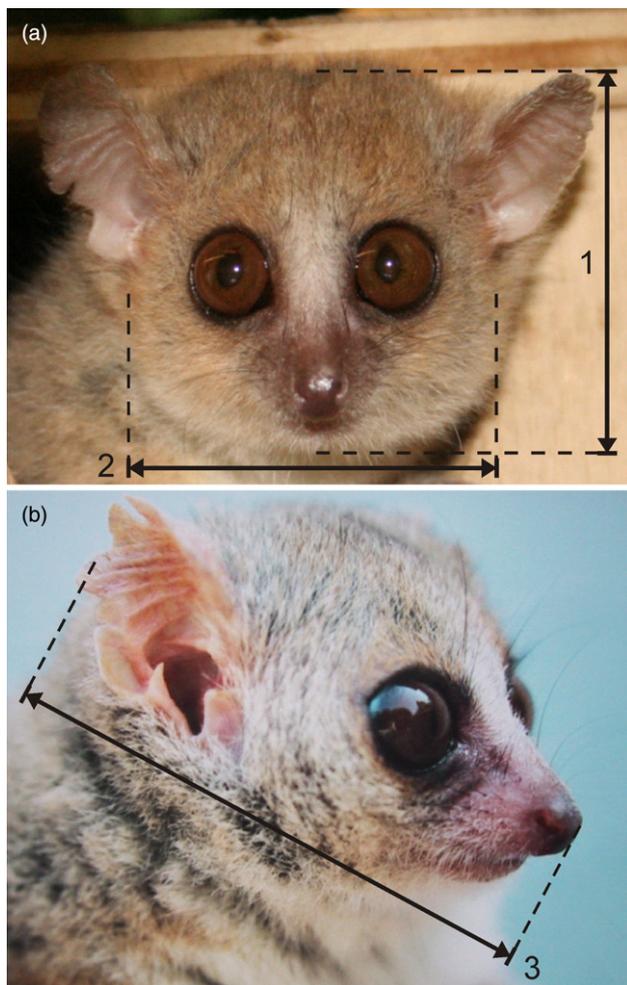


Figure 1 Pictures illustrating the measurements taken on the animals. (a) frontal view illustrating head width and head depth measures; (b) lateral view illustrating how head length was measured.

measured. Blood was collected in capillary tubes containing ethylenediaminetetraacetic acid (EDTA) and immediately centrifuged (7000 rpm at 4°C for 30 minutes) after collection. Plasma was recovered, transferred to an Eppendorf (Hamburg, Germany) and stored -20°C. Given known daily variation in testosterone levels in *M. murinus* (Perret, 1985), we only took blood samples between 11:00 AM and noon. Blood samples were always collected at the same time after the onset of daylight whatever the photoperiod. This ensures that samples were taken at an equivalent phase of the circadian rhythm. The period sampled corresponds to medium levels with the peak testosterone level occurring 1–2 hours before the onset of night (Perret, 1985). Plasma testosterone concentration was measured in duplicate on two aliquots of 25 µL of plasma using an enzyme linked immunosorbent assay immunoassay (ELISA) (DE1559, Demeditec, Kiel, Germany). Percentages of cross-reactivity were: testosterone 100%, 5 α -dihydro-testosterone 27.4%, 5 β -dihydro-testosterone 18.9%, andros-

tenedione 3.7%, other steroids tested < 0.5%. The mean intra-assay coefficient of variation was 4.9%, the mean inter-assay coefficient of variation was 3.7%. The minimum detectable level in plasma was 6 pg mL⁻¹. Plasma testosterone concentrations were measured twice, once in April when animals were kept under short daylight conditions (10 hours per day) and once in May when animals were maintained under a long daylight regime (14 hours per day). Blood samples were always collected at the same time after the onset of daylight whatever the photoperiod. This ensures that samples were taken at an equivalent phase of the circadian rhythm. The period sampled corresponds to medium levels with the peak testosterone level occurring 1–2 hours before the onset of night (Perret, 1985).

Analyses

All data were Log₁₀-transformed before analysis. First, we tested whether bite force data were repeatable over time using Pearson correlations. Next, the single highest bite force for each individual was extracted and used as input for a stepwise regression model with the maximal bite force as dependent variable and head dimensions and body mass as independents. We also regressed all head dimensions against body mass. Next, we tested whether age was correlated with bite force capacity using a Pearson correlation. Repeatability of testosterone measures across time and correlations between bite force and testosterone were tested using Pearson correlations. Finally, we regressed bite force against head width and extracted the unstandardized residuals and tested for correlations between residual bite force and age. All analyses were conducted in IBM Statistical Package for the Social Sciences statistics v.20 (SPSS Inc., Chicago, IL, USA).

Results

Bite force

Bite force measurements were repeatable over time ($r = 0.77$; $P < 0.001$). All head dimensions as well as body mass were significantly correlated with bite force (head length: $r = 0.50$ $P = 0.01$; head width: $r = 0.64$, $P = 0.001$; head depth: $r = 0.54$, $P = 0.008$; body mass: $r = 0.46$, $P = 0.027$). Yet, a stepwise regression extracted a significant model with head width only ($R^2 = 0.42$; $P < 0.001$), indicating that animals with wider heads have higher bite forces (Fig. 2a; Table 1). Bite force was highly correlated with the age of the animal ($R^2 = 0.71$; $P < 0.001$) with older animals having higher bite forces. A visual inspection of the data (Fig. 2b) shows, however, a distinct decrease in the bite force of the oldest animals. Consequently, a cubic function fitted the data slightly better ($R^2 = 0.73$). A correlation of residual bite force with age was highly significant ($r = 0.67$; $P < 0.001$), suggesting that the increase of bite force with age is not solely due to growth (Table 1). The plot of residual head width against age (Fig. 2c) shows no decrease in residual bite force in the oldest animals, suggesting that the decrease may be caused by a decrease in muscle mass.

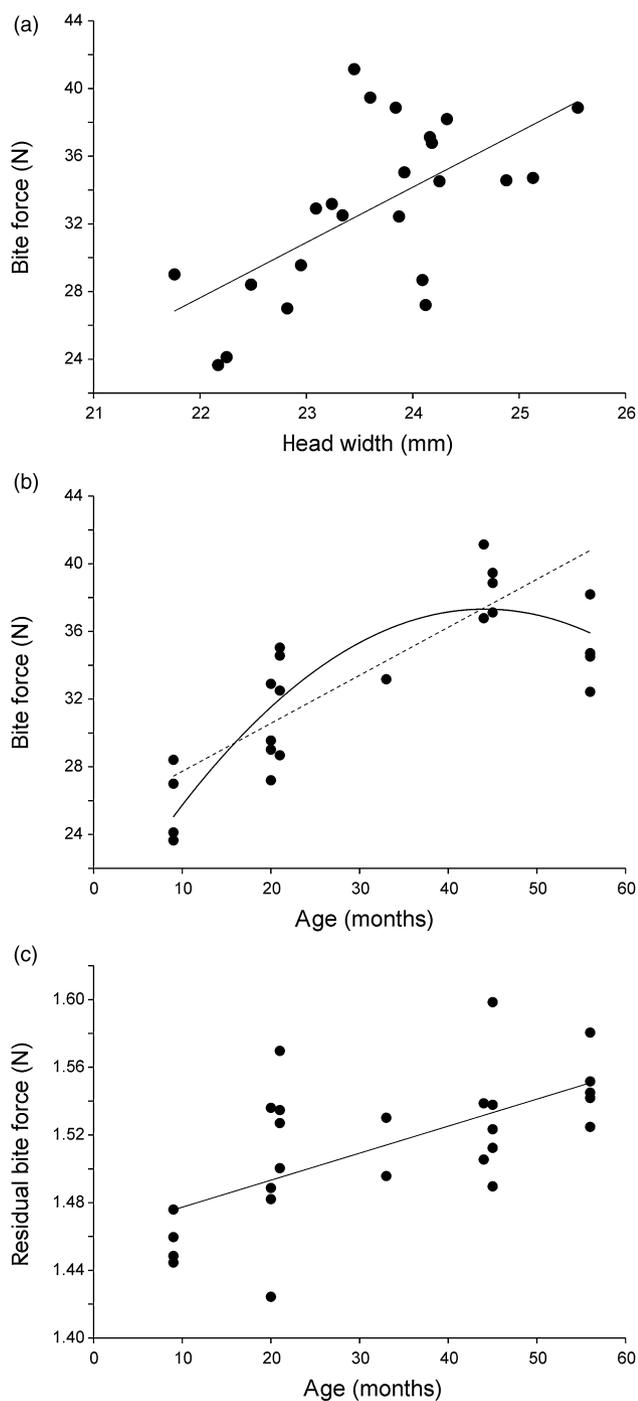


Figure 2 Scatter plot illustrating the correlations between (a) head width and bite force and (b) age and bite force. In (b) both a linear regression and cubic fit are plotted. Note the distinct drop in bite force in the oldest animals. The scatter plot in (c) represents the relationship between age and residual bite force. Note how the drop in bite force is no longer present.

Table 1 Summary of regression analyses

Variable	Intercept	Slope	R^2	P
Independent = mass (g)				
Head length (mm)	1.35	0.095	0.24	0.008
Head width (mm)	1.04	0.16	0.40	<0.001
Head height (mm)	0.85	0.20	0.43	<0.001
Bite force (n)	0.58	0.45	0.21	0.027
Independent = age (months)				
Mass (g)	1.90	0.12	0.19	0.028
Head length (mm)			0.11	0.10
Head width (mm)	1.31	0.04	0.45	<0.001
Head height (mm)	1.20	0.043	0.28	0.006
Bite force (mm)	1.22	0.21	0.71	<0.001
Residual bite force (n)	1.36	0.10	0.45	<0.001
Independent = bite force (n)				
Head length (mm)	1.38	0.11	0.25	0.014
Head width (mm)	1.12	0.17	0.41	0.001
Head height (mm)	1.00	0.17	0.29	0.008

All variables were Log_{10} -transformed before analyses. Blank cells indicate non-significant relationships for which no slope and intercept can be calculated.

Testosterone

Measures of plasma testosterone varied between 0.68 and 98.5 ng mL^{-1} , but were not repeatable across sampling periods ($r = -0.15$; $P = 0.52$) with testosterone levels increasing from April to May for about half of the individuals tested. Other individuals maintained low levels or slightly decreased in plasma testosterone concentrations. Neither measure of testosterone is correlated to bite force in either of the two periods (April: $r = -0.11$, $P = 0.58$; May: $r = -0.25$, $P = 0.29$).

Discussion

Our data show that bite force is highly repeatable across seasons in the mouse lemur suggesting that it is a reliable measure of individual performance capacity. Bite forces have been shown to be repeatable in a wide variety of taxa (e.g. Herrel *et al.*, 2005b; Anderson, McBrayer & Herrel, 2008), but is variable across season in some species of lizards (Irschick *et al.*, 2006). The seasonal changes in bite force and head width observed in some lizards have been suggested to be related to seasonal fluctuations in circulating plasma testosterone levels (Irschick *et al.*, 2006; Husak *et al.*, 2007; Huyghe *et al.*, 2010). In the mouse lemurs studied here, however, circulating plasma testosterone levels were not correlated to variation in bite force capacity. Plasma testosterone levels did change being higher in the active season when daylight is longer (Petter-Rousseaux & Picon, 1981; Perret & Aujard, 2001). Interestingly, circulating plasma testosterone increased for about half of the individuals only. However, when investigating correlations between circulating plasma testosterone levels only for those animals showing an increase ($r = -0.02$, $P = 0.98$) or those not showing an increase ($r = -0.46$, $P = 0.13$), correlations remained non-significant. Thus, our data demonstrate that in male *M. murinus*, testosterone does

not affect bite force generation, in contrast to what has been observed for some lizards (Husak *et al.*, 2007). Whether this is an intrinsic difference between species or rather a general feature of mammals compared with ectotherms such as lizards remains to be investigated.

Our results show that head and body dimensions are correlated to bite force capacity in the grey mouse lemur with heavier and larger-headed males biting harder. Among the morphological traits studied, head width was the best predictor of bite force. This is similar to what has been observed in other animals (e.g. Herrel *et al.*, 2005a,b). The observed correlation is logical as individuals with wider heads have more space available for the jaw adductors and thus likely also larger jaw adductors and consequently a higher bite force. However, only 42% of the variation in bite force was explained by variation in head width suggesting that other factors play an important role. For example, muscle architecture is known to have an effect on bite force capacity with animals with more pinnate muscles having a greater cross-sectional area and thus greater force-generating capacity (Herrel *et al.*, 2008; Taylor *et al.*, 2009). Moreover, it has been demonstrated in bats that the principal determinant of bite force is the temporalis muscle. As this muscle originates on the postero-dorsal aspect of the skull variation in its size is not captured by measures like head width, which principally reflect the space available for the masseter and pterygoid muscles.

One unexpected result from our analysis is the strong correlation between age and bite force generation capacity. Indeed, the correlation between age and bite force is stronger than the one between any of the head dimensions and bite force (Fig. 2). Although this could be partly due to age-related changes in morphology, correlations of bite force corrected for head size were highly significant (Fig. 2c). The animals in this study varied in age between 9 and 56 months of age and were thus all sexually mature (Lutermann *et al.*, 2006), yet, showing a wide range of age variation. Studies on skull development and bite force in carnivores have demonstrated a developmental asynchrony between performance and growth with bite forces reaching maximal levels when animals have reached sexual maturity (Binder & Van Valkenburgh, 2000; Tanner *et al.*, 2010; La Croix *et al.*, 2011). Our data for *M. murinus* suggest a similar continued increase of performance well after animals have reached adulthood. Although the proximate causes for this difference remain unclear at this point in time, continued muscle development, age-related changes in fiber type expression, training effects or late maturation of the neuro-muscular system could underlie the observed pattern.

One noticeable trend in our data consisted of a distinct drop in bite force for the oldest animals in our sample. These animals were just under 5 years of age and this age correlates with the termination of growth in this species (Castanet *et al.*, 2004). Interestingly this drop in bite force is not present in the plot of residual bite force against age suggesting that this may be due to a decrease in head width (presumably due to muscle atrophy) in the oldest animals. Although individuals of *M. murinus* can live up to 12–14 years (Aujard & Perret, 1998), animals over 5 years are considered to be elderly (Bons *et al.*,

2006). In the captive colony from which the animals were derived, the median survival time is estimated at about 5 years (Languille *et al.*, 2012). The observed decline in bite force may potentially be caused by aging-related processes such as muscle atrophy as suggested by the differences between correlations of bite force versus residual bite force with age. However, as our oldest animals are only just entering the aged population, this seems unlikely and needs to be tested using *in vivo* imaging methods such as magnetic resonance imaging. Further studies including older animals are needed to better understand the observed pattern of changes in bite force with age.

Although our data are based on captive animals, they may have implications for animals in the wild. For example, mouse lemurs feed on fruit, but also on tough food items such as insects, small animals or gum (especially during the dry season; Génin, 2004; Corbin & Schmid, 1995). As such, high bite forces in older individuals, but younger than 5 years, would give them an advantage in broadening their dietary spectrum. Moreover, field observations of mating behavior showed that males temporarily guard receptive females. During guarding episodes, the males aggressively engage in fights with other males and try to deter the females from escaping (Eberle & Kappeler, 2004b). As such, high bite force would be advantageous to males in guarding females. Yet measurements for wild-caught animals are needed to test the validity of our observations on captive animals.

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