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Drivers of *in vivo* bite performance in wild brown mouse lemurs and a comparison with the grey mouse lemur

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Abstract

Physical performance is crucial for animal survival and fitness. In this context, greater bite forces can provide advantages and may allow an individual to gain access to reproductive partners and/or different food resources. Here, we explored the determinants of bite force in a wild population of the brown mouse lemur (*Microcebus rufus*). Our objectives were to elucidate (1) if sex, head width, heart rate (as an indicator of overall physical fitness) and body condition drive variation in bite force in this population of wild mouse lemurs; and (2) the relative importance of the ecological niche in determining bite force by comparing results from this wild population with previously published results on bite force, body mass and head width from a laboratory colony of the grey mouse lemur (*Microcebus murinus*). We captured 32 wild brown mouse lemurs at night in the Ranomafana National Park in Madagascar during the beginning of the rainy season from 1st to 31st October 2016. We measured bite force, heart rate, body mass and head width of all individuals, and assigned sex and body condition (estimated as the unstandardized residual of a regression of body mass against head size). Although maximum bite force was positively correlated with body mass, it was not correlated with body condition. Residual bite force was highly correlated with residual head width and heart rate. The mean bite force of wild brown mouse lemurs was much lower than that of grey mouse lemurs in captivity, but showed similar relationships to head dimension and body mass. Even when corrected by body condition, grey mouse lemurs bit significantly harder than brown mouse lemurs. The difference in bite force between species could be explained by differences in head size and niche divergence with brown mouse lemurs eating mostly soft fruits and grey mouse lemurs eating more hard insects.

Introduction

Physical performance is crucial for animal survival and fitness as natural selection acts directly on performance traits (Arnold, 1983). Physical strength, for example, is a performance trait that has been commonly investigated in evolutionary studies as it is likely relevant to fitness (Husak, Lappin & Van Den Bussche, 2009). Bite performance, for example, has been studied in a wide range of vertebrates through estimations based on cranial morphology and biomechanical models, or by direct *in vivo* measurements of bite force. These studies span a wide array of taxa including alligators (Erickson, Lappin & Vliet, 2003), turtles (Herrel, Petrochic & Draud, 2017), carnivores (Christiansen & Wroe, 2007; Sakamoto, Lloyd & Benton, 2010; Law, Young & Mehta, 2016), bats (Nogueira, Peracchi & Monteiro, 2009; Santana, Dumont & Davis, 2010), various other mammals (Thomason, 1991; Freeman & Lemen, 2008) and birds (van der Meij & Bout, 2004; Herrel *et al.*, 2005a,b). The importance of bite performance in feeding is well-illustrated by Darwin's finches of the Galapagos Islands, where individuals with large beaks, which have high bite forces (Herrel *et al.*, 2005b), are selected during drought episodes during which only large seeds are available (Boag & Grant, 1981). Superior bite forces can also provide advantages by allowing an individual to gain access to reproductive partners (Husak *et al.*, 2009). Finally, bite force has also been linked to reproductive output in female turtles (Bulté, Irschick & Blouin-Demers, 2008) and to dominance in male lizards (Lappin & Husak, 2005; Husak *et al.*, 2009).

Many studies have explored the determinants of physical strength and their relationships to fitness. In most species examined, bite force is determined by both body size and cranial morphology (Herrel *et al.*, 2005a, 2008; Thomas *et al.*, 2015b). This has been documented, for example, in Darwin's finches (Herrel *et al.*, 2005a), where the ability to crush seeds was found to be determined by bite force and head dimensions, suggesting that morphology and performance evolve together. Moreover, bite force is directly related to variation in the underlying jaw adductor muscles that generate the forces required for biting (Herrel *et al.*, 2007, 2008; Vincent & Herrel, 2007).

Since biting and chewing are essential during feeding (Herrel *et al.*, 2001; Vinyard, Yamashita & Tan, 2008) dietary specialization may lead to the evolution of high bite force. Bite force could therefore be important for niche divergence as it allows species to adapt their diet to the different prey available. This has been shown in lizards (Herrel *et al.*, 2001, 2006; Verwaijen, Van Damme & Herrel, 2002), for example, where prey size and hardness are related to bite performance. Similarly, in phyllostomid bats, which show a great diversity in trophic ecology, bite force is related to diet (Aguirre *et al.*, 2002, 2003; Nogueira *et al.*, 2009; Santana *et al.*, 2010), and in peccaries, species with different diets have different bite forces (Kiltie, 1982). However, there are few *in vivo* comparisons of bite force divergence between closely related species with divergent niches and it remains to be tested whether this could hold more generally.

Among the large variety of lemurs, mouse lemurs are small, nocturnal and generally sexually monomorphic primates that are widespread across Madagascar. The group comprises 24 different species (Setash *et al.*, 2017) that have been defined by morphological and molecular criteria (Hotaling *et al.*, 2016). They show a large diversity of ecologies, and can be found in seasonal dry deciduous forests (e.g. the grey mouse lemur, *Microcebus murinus*) and in rain forests (e.g. the brown mouse lemur, *Microcebus rufus*). These two particular species display small but marked differences in their feeding ecology: they are both fruit and insect eaters, but brown mouse lemurs are thought to be more frugivorous than grey mouse lemurs, which rely mostly on insect secretions, gum and arthropods (Atsalis, 1999; Dammhahn & Kappeler, 2008). More specifically, brown mouse lemurs live in the eastern rain forest of Madagascar and rely largely on mistletoe (*Bekarella*) fruit with a soft pulp, while grey mouse lemurs live in the western dry deciduous forest where a large part of its diet is composed of insects including beetles (Mittermeier & Nash, 2010). Differences in bite performance are expected in animals that eat different types of food because of evolutionary adaptations of the jaw muscles and the underlying bony structures (Perry, Hartstone-Rose & Logan, 2011; Ross, Iriarte-Diaz & Nunn, 2012; Marcé-Nogué, Püschel & Kaiser, 2017). For example, Vinyard *et al.* (2008) compared bite force in sympatric bamboo lemurs (*Hapalemur simus*, *H. aureus*, and *H. griseus*) to evaluate its relationship with adaptations in diet. They found that species that ate harder food (e.g. bamboo culm pith) had higher bite forces. Thus, in mouse lemurs, biting abilities could be of importance to access demanding food resources, such as beetles (Aguirre *et al.*, 2003), which are eaten by the grey mouse lemur. Grey and brown mouse lemurs also differ in size, with the grey mouse lemur weighing around 70 g and the brown mouse lemur around 50 g. Consequently, as size is a major determinant of physical performance (Chazeau *et al.*, 2013; Thomas *et al.*, 2015b), we expect further differences in biting capacity between brown and grey mouse lemurs.

Differences in biting abilities and diet can also occur between the sexes. In a previous study on captive grey mouse lemurs, Thomas *et al.* (2015b) explored the determinants of bite force and showed sexual dimorphism in biting capacity driven by dimorphism in head size and body mass. Indeed, females are slightly larger than males in this species, and individuals with taller heads had higher bite forces. In the brown mouse lemur, however, previous studies showed no difference in body weight between the sexes (Kappeler, 1990). Consequently, we predict no dimorphism in bite force in this species.

In this study, we investigate the proximal determinants of *in vivo* bite force in a species whose bite force has not been previously studied, and compare it with published data on another species of mouse lemur (*Microcebus murinus*) that differs in diet and body size. We addressed the two following questions: (1) what are the determinants of variation in *in vivo* bite force in a population of wild brown mouse lemurs; and (2) what is the relative importance of the ecological niche in determining bite force? To do so, we compare results collected for wild brown mouse lemurs with previously published results (bite force, body mass, head width) for a laboratory colony of the grey mouse lemurs (*Microcebus murinus*).

Materials and methods

Subjects

With the help of two field technicians, we captured brown mouse lemurs (*Microcebus rufus)* from the Centre Valbio Campsite area (Karanewsky & Wright, 2015) and the trails near the park entrance of Ranomafana National Park (21°16′S, 47°20′E; Wright *et al.*, 2012), at night from 1st to 31st October 2016. We used 20 to 70 Sherman live traps, baited with a small piece of banana. Traps were left open from 04:30 PM to 10:00 PM in the forest. One to ten individuals were captured each night, and measurements were made on 32 different individuals, 21 females and 11 males. The first time an individual was captured, it was tagged with a unique microchip identifier (Pro ID Mini chip). All measurements were made within 3 h following capture. Animals were released back into the forest at their capture site several hours later, between 01:00 and 02:00 AM the same night.

This study was performed under the MNP Research Permit #220/16, allowing us to capture brown mouse lemurs in the field and to conduct phenotypic measurements in the laboratory of the field station. All measurements were approved by the animal care and use committee.

Morphometrics

We measured head dimensions with a digital caliper (±0.01 mm; Mitutoyo, Kanagawa, Japan). Head width (bizygomatic breadth) was measured posterior to the eyes at the level of the zygomatic arch, as commonly done in cheirogaleid species and mouse lemurs (Thomas *et al.*, 2015b). This measure is commonly used as an estimator of size in other studies on mouse lemurs (Vuarin, Dammhahn & Henry, 2013; Rakotoniaina *et al.*, 2016). Body mass was measured with a digital scale (AWS LB501 500 g ± 0.01 g).

Bite force measurement

Bite forces were measured with a piezoelectric force transducer (Kister, type 9203, range ±500N; Kistler, Winterthur, Switzerland; see Herrel *et al.*, 1999) attached to a charge amplifier (Kistler, type 5995) as described previously for captive mouse lemurs (Chazeau *et al.*, 2013; Thomas *et al.*, 2015b). Most animals were recaptured multiple times during the course of the study (1 to 5 times), and bite force was measured at each capture two to four times. We adjusted the distance between the plates to assure equivalent gape angles at around 30 degrees and measured unilateral molar biting in all individuals. The highest value obtained was used in the analysis; however, additional measurements were used in a repeatability test.

Heart rate measurements

We measured heart rate with a microphone (Tascam DR-05) placed on the chest of the animal that was held by the experimenter such that heart beats were detectable using ear phones. Audio files were analysed with the Audacity software (version 2.1.2) (Audacity Team, 2016). The number of heart beats in a 30 s interval was determined and the obtained value converted to beats per minute. One heart rate measurement was made during each capture event.

Statistical analysis

All statistical analyses were conducted using R (version 3.2.2) (R core Team, 2016). We $\log_{10}$-transformed bite force and morphological measurements to satisfy normality assumptions. To assess intra-individual variability and the repeatability of the measurements, we calculated Pearson correlation coefficients for the first and last measurements of bite force and heart rate for individuals that were captured at least twice. We used a one-way ANOVA to test for sexual dimorphism in bite force, head width, body weight and heart rate. Because we found no evidence of sexual dimorphism, the rest of the analyses were done on all individuals pooled. As all traits were correlated with overall body size (i.e. body mass), we calculated the residuals of a regression of bite force, head width, and heart rate on body mass and tested whether these traits were correlated independently of body mass. Finally, body mass was regressed against head width and we extracted the unstandardized residuals as an indicator of body condition (see Thomas *et al.*, 2015a,b) with higher (positive) residuals indicating animals that have a greater body mass for their size.

Comparison between brown and grey mouse lemurs

We used the data from a previously published study on bite force in captive grey mouse lemurs (Thomas *et al.*, 2015b) to compare with our data on wild brown mouse lemurs. To test for difference between species, we conducted linear regressions with bite force as the fixed variable and species and morphometric measures as predictor variables, using the lme4 package (Bates *et al.*, 2015) in R.

Results

Influence of sex, head width, heart rate and body condition on bite force in brown mouse lemurs

Bite force and heart rate measurements were repeatable within individuals across the first and the last capture as indicated by the Pearson correlations: $r = 0.57$ for bite force ($P = 0.02$); $r = 0.64$ for heart rates ($P < 0.01$).

There was no significant difference between the sexes in bite force in our sample of brown mouse lemurs (Table 1). There was also no significant sexual dimorphism in body mass, head dimension and heart rate between males and females (Table 1).

Bite force was positively correlated with head width, body mass and heart rate (Table 2, Figs. 1 and 2). Body condition was, however, not correlated with bite force in brown mouse lemurs ($r = 0.32$, $P = 0.07$). When applying a sequential Holm-Bonferroni correction for the eight Pearson correlations, the statistical significance of the correlation between heart rate and head width and body condition was lost, as the null hypothesis could not be rejected ($\alpha_6 = 0.05/(8-6+1) = 0.0167 < P_6 = 0.03$).

As bite force, head width and heart rate were correlated with body mass, we conducted linear regressions of these three variables against body mass and tested the correlations between the residuals in order to remove the possible effects of collinearity. The residuals of bite force, head width and heart rate were still inter-correlated suggesting that these effects are not due to an overall effect of size (Table 3).

Comparison between brown and grey mouse lemurs

Both male and female brown mouse lemurs bit less hard than grey mouse lemurs and were smaller and lighter (Table 4). When controlling for head width and body weight, there were no longer any differences in bite force between the two species. Body mass was the parameter that best explained bite

Table 1 Mean (± SD) bite force, head width, body mass and heart rate of male and female wild brown mouse lemurs along with the results of a one-way ANOVA analysis performed on the $\log_{10}$-transformed data

	Females (n = 21)	Males (n = 11)	$F_{1,30}$	P
Bite force (N)	18.5 ± 0.8	17.1 ± 1.3	1.05	0.31
Head width (mm)	20.2 ± 0.2	19.6 ± 0.4	1.83	0.19
Body mass (gm)	46.8 ± 1.31	44.7 ± 2.3	0.80	0.38
Heart rate (b/min)	226 ± 7	224 ± 12	0.09	0.76

Table 2 Pearson correlation coefficients (*R*) for correlations between bite force, head width, heart rate and body mass in wild brown mouse lemurs

	Body mass (g)	Head width (mm)	Body condition	Heart rate (b/min)
All individuals (N =)	32	32	32	32
R				
P-value				
Bite force (N)	**0.55**	**0.42**	0.32	−**0.48**
	0. 001	**0.01**	0.07	**0.005**
Heart rate (b/min)	−**0.52**	−0.37	−0.38	
	0.002	0.03	0.03	
Head width (mm)	**0.62**			
	0.0002			

Bolded values represent significant correlations among variables. Sequential Holm-Bonferroni correction: α_{rank} = 0.05/(8−rank number+1). (Holm (1979))

force (Table 5). When we compared species when controlling for the effect of body condition, we found that species differed in bite force with brown mouse lemurs having lower bite forces than grey mouse lemurs (Table 5, Fig. 3) suggesting that condition is not driving the observed differences between species.

Discussion

We found that bite force is a repeatable individual feature of wild brown mouse lemurs, as has been shown previously for captive grey mouse lemurs (Chazeau *et al.*, 2013), and that body mass is correlated with bite force, head width and heart rate. Larger animals and animals with larger heads thus generally had higher bite forces than smaller animals, as previously observed for the grey mouse lemur (Chazeau *et al.*, 2013; Thomas *et al.*, 2015b). As muscle volume scales with linear head dimensions to the third power, and muscle force to the second power, even small differences in head size may have a significant impact on bite force as illustrated by the strong correlations between residual head width and residual bite force as observed here (see also Herrel & O'Reilly, 2006). We found no significant differences in bite force between the sexes in the brown mouse lemur, although females showed a non-significant trend towards having higher bite forces. This absence of sexual dimorphism in this species agrees with previous reports on the morphology of this species (Harcourt, 1987; Kappeler, 1991).

Our results are, however, in agreement with the hypothesis of niche divergence which posits that species feeding on harder foods (grey mouse lemurs) should present higher bite forces than species relying more on soft foods (brown mouse lemurs) as demonstrated by our data. However, the effect of captivity may confound our results as captive grey mouse lemurs are fed with less challenging food items. Yet, if captivity has a significant effect on bite force due to a less challenging diet, bite force would be expected to be even lower in captivity and the difference between the two species should be reduced. Comparing wild grey mouse lemurs with wild brown mouse lemurs would clearly be the best option to confirm these results (Erickson *et al.*, 2004).

Body size, being an important driver of species differences in bite force, may be impacted by the seasonality of the environment, as seasonality is generally depicted as a factor for the evolution of large body size in mammals (Millar & Hickling, 1990). The grey mouse lemur faces a more seasonal climate, with one season of low food availability and one season of

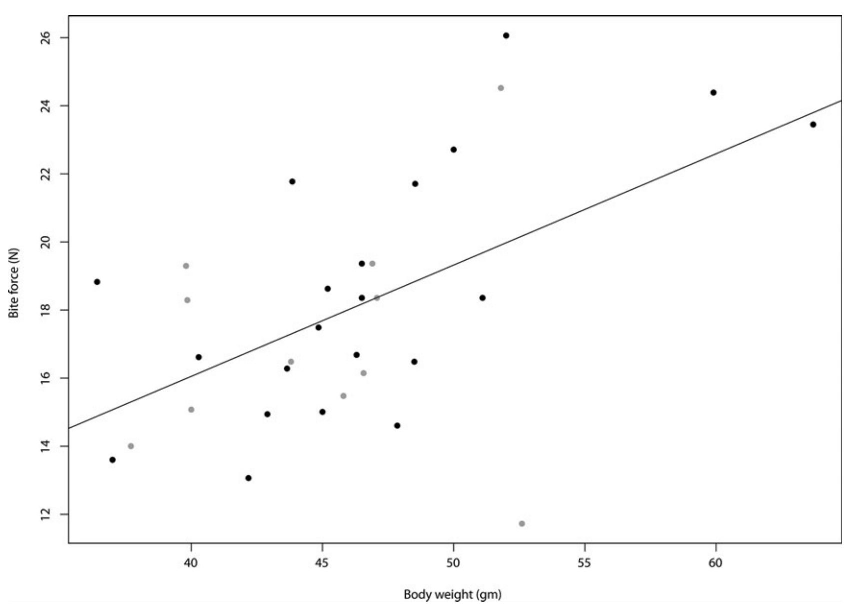

Figure 1 Scatterplots showing relationship between body weight and maximum measured bite force in wild brown mouse lemurs. *N* = 32 individuals: females (black dots), males (grey dots).

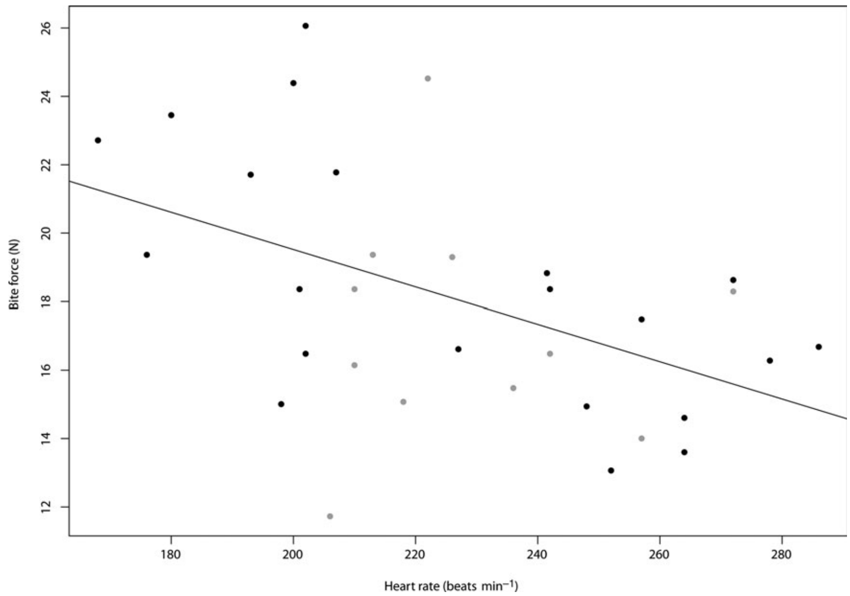

Figure 2 Scatterplots showing relationship between maximum measured bite force and mean heart rate measured during handling. $N = 32$ individuals: females (black dots), males (grey dots).

high food ability thus putting a premium on high bite forces that may allow access to a wider variety of food resources. In contrast, seasonality is less dramatic in the rain forest habitat of the brown mouse lemur with fruits being available year-round. These differences in seasonality may consequently contribute to the observed differences in body size and bite force**.**

We also found that in the brown mouse lemur, bite force was negatively correlated with heart rate. Individuals with lower heart rates were also in a better body condition. Finally, body mass had an important impact on heart rate as well. Even when correcting for body size, heart rate and bite force were still strongly correlated suggesting that wild mouse lemurs that are in a better overall physical condition (i.e. that have lower heart rates independent of variation in body size) and that have more energy reserves (slightly higher body condition, because they have more muscle mass or fat reserves) show higher bite forces (independent of variation in body size). Although we did not use a classic method (e.g. pulse oximetry) for measuring heart rate and did not measure the oxygen saturation of the blood, our measurements were repeatable suggesting that our measurements with the microphone are reliable and describe an individual attribute. However, we acknowledge that it would be of interest to evaluate overall physical fitness by estimating heart rate variability under different conditions (e.g. unrestrained, unstressed animals). Heart rate has been shown to be a good indicator of physical fitness in situations that require physical investment because it provides individuals with better aerobic capacity and could thus be an interesting variable to measure in future studies.

Table 3 Pearson correlations between the residuals of bite force, head width and heart rate

Residual against body mass:	Head width	Heart rate
Bite force	**r = 0.76** **P < 0.001**	**r = 0.81** **P < 0.01**
Heart rate	**r = 0.72** **P < 0.01**	

Bolded values represent significant correlations among variables.
Residuals were calculated based on the regression of each variable against body mass.

Conclusion

In wild brown mouse lemurs, bite force was correlated with body weight and head width. Moreover, this performance trait

Table 4 Bite force, head width and body mass of brown mouse lemurs and grey mouse lemurs extracted from Thomas *et al.* (2015b)

	Brown mouse lemurs		Grey mouse lemurs (Thomas *et al.* (2015b))	
	Females	Males	Females	Males
N	21	11	34	28
Bite force (N)	18.5 ± 0.8	17.1 ± 1.3	35.6 ± 6.4	31.4 ± 6.1
Head width (mm)	20.2 ± 0.2	19.6 ± 0.4	22.2 ± 0.8	21.6 ± 0.7
Body mass (g)	46.8 ± 1.31	44.7 ± 2.3	99.0 ± 15.5	81.2 ± 11.0

Table 5 Linear regression models of species and morphological dimensions on $\log_{10}$-transformed bite force

Response variable	Predictor variable	Estimate ± SE	*P*
Bite force	**Species (*Brown mouse lemur*)**	**−0.39 ± 0.07**	**< 0.001**
	Head width	**1.72 ± 0.53**	**0.0016**
Bite force	Species (*Brown mouse lemur*)	−0.15 ± 0.11	0.19
	Head width	0.7633 ± 0.62	0.22
	Body mass	**0.47 ± 0.17**	**0.007**
Bite force	Species (*Brown mouse lemur*)	**−0.95 ± 1.5**	**0.53**
	Body mass	**0.56 ± 0.16**	**<0.001**
	Species*Body mass	**0.21 ± 0.39**	**0.57**
Bite force	**Species (*Brown mouse lemur*)**	**−0.52 ± 0.07**	**<0.001**
	Body condition	0.013 ± 0.15	0.93

Bolded values represent significant predictor variables.

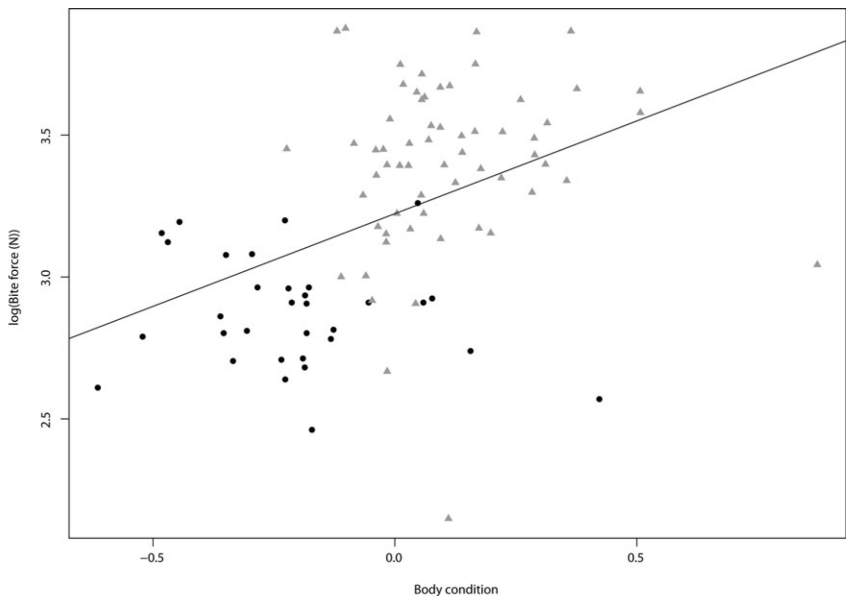

Figure 3 Scatterplots showing relationship between body condition and maximum measured bite force in wild brown mouse lemurs (black dots) and grey mouse lemurs (grey triangles).

was negatively correlated with heart rate suggesting that animals in better overall physical fitness (low heart rate for a given size) are also able to generate higher bite forces. Captive animals of another mouse lemur species that eats harder prey in the wild had a better biting performance, principally due to their higher body mass and larger heads.

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