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Determinants of pull strength in captive grey mouse lemurs

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Abstract

Grasping is important for arboreal species as it allows them to hold on to branches. Although grasping has been studied previously in the context of primate origins and as an indicator of age-induced loss in overall performance, little is known about the proximate determinants of variation in strength. We measured hand pull strength in 62 adult captive individuals of grey mouse lemurs *Microcebus murinus* of known age. In addition, we measured the body mass and the length of the forearm in each individual. Our results showed that animals with a longer ulna, and animals that weighed more, and had a greater relative body mass had higher pull strength. However, despite the fact that females are bigger than males, differences in pull strength were not significantly different between the two sexes. Although comparative data for other species of vertebrates are scarce, our data suggest that mouse lemurs have relatively high pull strength for their size that may be interpreted as an adaptation to arboreal locomotion.

Introduction

The evolution of the hand is a topic of considerable interest in primatology. Indeed, the hand and its manipulative capacity have been considered important drivers of primate evolution (Wood Jones, 1916; Napier, 1956; Szalay, 1968; Bloch & Boyer, 2002; Reghem *et al*., 2011). Primates not only use their hands to capture food or grasp fruits but also use their hands and feet to hold onto arboreal substrates (Sustaita *et al*., 2013; Toussaint *et al*., 2013). The locomotor style of arboreal primates has been described as a 'grasp-leaping' locomotion (Le Gros Clark, 1959; Szalay & Dagosto, 1988; Bloch & Boyer, 2002). As such, the ability to grasp and hold onto substrates is likely a key component in the ecology of arboreal species. Grasping has been studied in a wide range of vertebrate models including frogs (Manzano, Abdala & Herrel, 2008), lizards (Herrel *et al*., 2013; da Silva *et al*., 2014), mice (Smith *et al*., 1995), non-human primates (Iwanami *et al*., 2005) and humans (Kivowitz *et al*., 1971; Doherty, 2003). However, whereas most studies on grip strength in humans have quantified the centripetally directed forces of the hands using a dynamometer (Kivowitz *et al*., 1971; Hamilton, Balnave & Adams, 1994; Doherty, 2003), most studies on animals actually quantify pull strength, that is, how well an animal can hold onto a substrate with the forelimbs, hind limbs or tail while being pulled off (Smith *et al*., 1995; Iwanami *et al*., 2005; Herrel *et al*., 2012, 2013; da Silva *et al*., 2014; but see Manzano *et al*., 2008).

Physical performance is generally determined by a variety of intrinsic factors, such as age, size, external morphology (Herrel *et al*., 2005; Chazeau *et al*., 2013) and muscle size and architecture (Herrel *et al*., 2008). Moreover, in males of many species performance is also affected by physiological parameter such as plasma testosterone levels (Husak *et al*., 2009; Huyghe *et al*., 2010). For example, in lizards bite force increases with increased levels of circulating testosterone (Husak *et al*., 2007). Moreover, pull strength was shown to decrease with age in both captive and wild individuals of the grey mouse lemur (Hämäläinen *et al*., 2015). Moreover, females of this species had higher performance during the dry season (Hämäläinen *et al*., 2015). Surprisingly, little is known, however, concerning the proximate determinants of pull strength. Whereas many studies in primates have focused on grasping precision during food manipulation tasks (Bloch & Boyer, 2002; Reghem *et al*., 2011), few have evaluated the factors that may affect pull or grip strength. In arboreal frogs, the hand musculature appears adapted for arboreal locomotion and was suggested to contribute significantly to both grip and pull strength (Manzano *et al*., 2008). Yet, whether this is also the case in other vertebrates remains largely unknown.

We here examine a set of possible determinants of pull strength in a population of captive mouse lemurs *Microcebus murinus*. The grey mouse lemur is a model of interest because it is a small and highly arboreal primate that has been used previously in studies of grasping and locomotion (Toussaint *et al*., 2013; Hämäläinen *et al*., 2015). Based on prior studies we predict that (1) pull strength should decline with age and (2) that females should be stronger than males. Based on data for other taxa (Manzano *et al*., 2008; Herrel *et al*., 2013), we further predict that pull strength should be closely related to the overall size of the animal as well as the size of their forearms and hands. We furthermore test whether pull strength is related to relative body mass in both sexes, and reproductive output in females as would be expected if this trait is fitness relevant.

Materials and methods

Animals

We conducted our study on captive individuals that were born and raised in Brunoy, France (at the UMR7179 CNRS/MNHN; European Institutions Agreement # D-91–114-1) but descendant from a stock originally caught along the south-western coast of Madagascar. All measurements were approved by the ethics committee at the Muséum National d'Histoire Naturelle. Animals are maintained in cages housing between one and seven individuals. 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, thus allowing a controlled photoperiod mimicking natural seasons. In total, we used 62 adult individuals: 28 males and 34 females. Individuals were between 1 and 7 years old.

Morphometrics

The length of the ulna, tibia and metatarsus was measured using a digital calliper (±; 0.01 mm; Mitutoyo, Kanagawa, Japan; Table 1). Body mass was measured using a digital scale (Ohaus Scout Pro; Ohaus, Nänikon, Switzerland). All measurements were taken just after the reproductive season. The age of each individual at the time of grip force measurements was retrieved from the breeding records of the colony.

Pull strength

We measured pull strength from all individuals using small iron bar that was mounted on a piezo-electric force platform (Kistler squirrel force plate, ±0.1 N; Winterthur, Switzerland). The force platform was positioned on a custom-designed metal base (Fig. 1) and connected to a charge amplifier (Kistler charge amplifier type 9865). Forces (N) were recorded during a 60-s recording session and recorded at 1 kHz. During that interval, animals were allowed to repeatedly grip a dowel with their hands and then pulled away horizontally from the dowel (see Herrel *et al*., 2013). As animals were pulled from the dowel in the horizontal direction, we extracted peak forces in the X direction only using the Bioware software (Kistler). The single highest force obtained was kept for further analysis. Repeatability was tested by comparing forces recorded during two different trials and was found to be high (intra-class correlation coefficient: $n = 79$, $r = 0.91$ $P < 0.001$). This high repeatability suggests that maximal pull strength was indeed obtained for each individual. Note that what we describe as pull strength is often referred to as grip strength in the literature (e.g. da Silva *et al*., 2014; Hämäläinen *et al*., 2015). All measurements were approved by the institutional animal care and use committee at the Muséum in Paris.

Table 1 Summary table detailing differences between the sexes in morphology and pull strength

	Females	Males
Metatarsus (mm)	19.33 ± 1.034	18.77 ± 1.11
Tibia (mm)	40.20 ± 1.37	39.71 ± 1.50
Ulna (mm)	29.49 ± 0.73	29.17 ± 0.93
Pull strength (N)	10.40 ± 1.53	9.96 ± 1.41
Body mass (g)	97.97 ± 16.71	82.54 ± 10.95
Age (days)	1532 ± 567	1162 ± 568

Table entries are means ± standard deviations.

Statistical analysis

Grip force and morphological measurements were $\log_{10}$ transformed in order to comply with the assumptions of normality and homoscedasticity. We first ran a principal component analysis on the 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 relative body mass. We first ran pair-wise correlations between morphological data, relative body mass, age and pull strength to explore the correlations among variables. We also ran similar correlations for males and females separately where relative body mass was calculated based on data 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 pull strength in the

Figure 1 Picture of an individual performing a pull strength test.

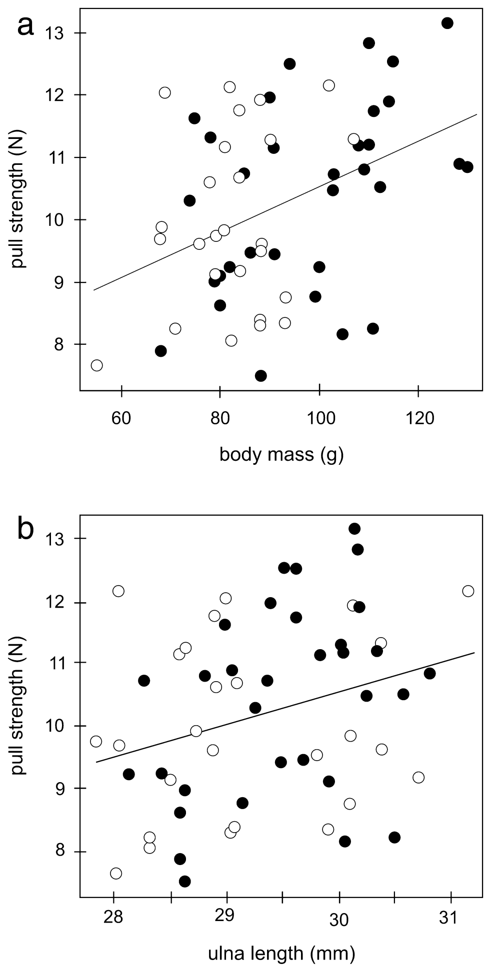

Figure 2 (a) Scatter plot illustrating relationships between body mass and pull strength; (b) scatter plot illustrating relationships between ulna length and pull strength. Filled circles represent females and open circles represent males.

overall dataset as well as for males and females separately. We then tested for differences between sexes in morphology and pull strength using a multivariate analysis of variance (MANOVA) coupled to subsequent univariate analyses of variance (ANOVAs). Next, we tested for relative differences in morphology and pull strength between sexes using a multivariate analysis of covariance with body mass as our covariable. Finally, we retrieved the number of offspring for each female from the records of the breeding colony and tested whether this was correlated to grip strength.

Results

Determinants of pull strength

Pull strength was positively correlated with body mass, ulna length and relative body mass in the overall dataset as well as in females (Table 2). Moreover, in females pull strength was also positively correlated to the number of offspring ($r = 0.39$; $P = 0.014$; Table 2; Fig. 2). In males, pull strength was correlated only with body mass with heavier animals being stronger. Stepwise multiple regressions extracted a significant model ($R^2 = 0.27$; $P < 0.001$) with body mass and age as only predictors of pull strength for the overall dataset. Whereas body mass contributed positively ($\beta = 0.53$), age contributed negatively ($\beta = -0.25$) to the overall variation in pull strength. For males, however, a significant model with body mass as only predictor of strength was found ($R^2 = 0.17$; $P = 0.035$). In females, a significant model with ulna length and age was found ($R^2 = 0.30$; P = 0.004), with ulna length contributing positively ($\beta = 0.47$) and age negatively ($\beta = -0.31$) to variation in pull strength (Fig. 2).

Sexual dimorphism

The MANOVA showed significant differences between males and females (Wilks' lambda = 0.72; $F_{5,54} = 4.17$; $P = 0.003$). Subsequent univariate ANOVAs showed that this difference was due to differences in body mass ($F_{1,58} = 18.64$; $P < 0.001$) and relative body mass ($F_{1,58} = 12.87$; $P = 0.001$), with females being heavier in both absolute and relative terms than males at the end of the reproductive season. Differences in ulna length were marginally non-significant between sexes ($F_{1,58} = 4.02$; $P = 0.05$), with females showing a tendency towards having longer forearms. The ANOVA on grip strength showed no significant differences between sexes ($F_{1,58} = 2.77$; $P = 0.10$). When correcting for differences in body mass, the overall difference in morphology between sexes was no longer significant (Wilks' lambda = 0.95; $F_{4,54} = 0.66$; $P = 0.62$).

Discussion

Our data show that morphology and pull strength are correlated, with larger animals and animals with longer forearms being stronger. The longer forearms likely allow for an increased attachment surface for finger and hand flexors, and such may allow a stronger grip. Although this seems intuitive, this should be tested in future studies using *in vivo* magnetic resonance imaging or dissections of animals with known pull strength (Fig. 2). Moreover, we found that age negatively impacts pull strength, especially in females. Moreover, in females but not males, pull strength was related to relative body mass. A significant correlation between the number of offspring reared and pull strength was also observed. Our data support previous findings on captive and wild mouse lemurs (Hämäläinen *et al.*, 2015) where significant effects of size and age on pull strength were demonstrated. However, in our dataset no differences in pull strength were observed between two sexes although females showed a tendency to have a higher pull strength.

Our results suggest an important role of relative body mass on pull strength, especially in female mouse lemurs. The first explanation of this effect on pull strength could

Table 2 Table summarizing correlations between morphological variables, age and pull strength

	Age (days)	Body mass (g)	Ulna (mm)	Relative body mass	# Offspring
All individuals					
Pull strength (N)	r = 0.008	**r = 0.52**	**r = 0.44**	**r = 0.40**	
n = 65	P = 0.95	**P < 0.001**	**P = 0.001**	**P = 0.002**	
			n = 60	n = 60	
Males					
Pull strength (N)	r = −0.03	**r = 0.41**	r = 0.36	r = 0.38	
n = 27	P = 0.90	**P = 0.035**	P = 0.06	P = 0.051	
Females					
Pull strength (N)	r = −0.004	**r = 0.57**	**r = 0.45**	**r = 0.35**	**r = 0.39**
n = 38	P = 0.98	**P < 0.001**	**P = 0.008**	**P = 0.045**	**P = 0.014**
			n = 33	n = 33	

Bold values represent significant correlations among variables.

simply be the fact that relatively heavier individuals have more muscle mass. A second explanation is that individuals with higher level of fat reserves perform better, and that our relative body mass is thus an indicator of body condition. Clearly, both explanations are possible and not mutually exclusive. The second explanation is also supported by the fact that fattening and energy saving is correlated with the general health of the individuals (Vuarin, Dammhahn & Henry, 2013) and with sex (Schmid, 1999). Moreover, in females we found a significant correlation between pull strength and the number of offspring, which is likely an overall body condition effect reflecting greater energy stores. We also found that age significantly and negatively affected performance as previously shown for both pull strength (Hämäläinen *et al.*, 2015) and bite force (Chazeau *et al.*, 2013; Thomas *et al.*, 2015). Interestingly, the effect was significant for females only, in accordance with the data of Hämäläinen and co-authors which showed that pull strength decreased more rapidly with age in females than in males. Given the absence of very old individuals in our dataset (the oldest ones were 7 years), the effect of age on strength in males may simply have been too weak to be detected.

Mouse lemurs have a promiscuous mating system where several females mate several males. During copulation males have to hold on to the females using their arms (Eberle & Kappeler, 2004) and their mouths (Eberle, Perret & Kappeler, 2007), which suggests that high forces could be selected in males. However, we found that pull strength was not significantly different between sexes even if females have slightly longer forelimbs and are significantly heavier than males. The differences in morphology are in accordance with previous studies showing that female mouse lemurs are generally bigger (Kappeler, 1991) and dominant over males (Génin, 2003). Interestingly, Hämäläinen *et al.* (2015) found that females in the wild were also stronger than males during the summer reproductive season. The differences in pull strength between sexes are, however, most likely due to overall size differences rather than sex-specific selection on females.

Pull strength is of crucial importance in the everyday life of mouse lemurs as it is used to hold on to branches and to grasp food items (Toussaint *et al.*, 2013). From a comparative perspective, mouse lemurs are exceptionally strong. For example, a rat can pull only 7% of its body weight (40 g; Clark *et al.*, 2004), and a mouse 22.5% of its body weight (4–4.5 g; Personius *et al.*, 2010; Wu *et al.*, 2013). In contrast, a mouse lemur is capable of pulling over 100 times its own body weight on average (1 kg of force for an average body weight of 91 g; this study), indicating strong selection towards high pull strength in arboreal animals like mouse lemurs. These values are similar to values for other specialized narrow branch walkers such as chameleons that can also pull over 100 times their own body weight (Herrel *et al.*, 2013). Further comparative studies would be of interest to better understand whether mouse lemurs are exceptional among primates or not.

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