Determinants of pull strength in captive grey mouse lemurs

P. Thomas1,2, E. Pouydebat2, M. L. Brazidec2, F. Aujard2 & A. Herrel2,3

1 Département de Biologie, Master Biosciences, ENS de Lyon, Lyon, France
2 Département d’Ecologie et de Gestion de la Biodiversité, UMR 7179 CNRS/MNHN, Paris Cedex 5, France
3 Evolutionary Morphology of Vertebrates, Ghent University, Ghent, Belgium

Keywords
primate; locomotion; grip force; sexual dimorphism; morphology; grasping; pull strength.

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

<table>
<thead>
<tr>
<th></th>
<th>Females</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td>Metatarsus (mm)</td>
<td>19.33 ± 1.034</td>
<td>18.77 ± 1.11</td>
</tr>
<tr>
<td>Tibia (mm)</td>
<td>40.20 ± 1.37</td>
<td>39.71 ± 1.50</td>
</tr>
<tr>
<td>Ulna (mm)</td>
<td>29.49 ± 0.73</td>
<td>29.17 ± 0.93</td>
</tr>
<tr>
<td>Pull strength (N)</td>
<td>10.40 ± 1.53</td>
<td>9.96 ± 1.41</td>
</tr>
<tr>
<td>Body mass (g)</td>
<td>97.97 ± 16.71</td>
<td>82.54 ± 10.95</td>
</tr>
<tr>
<td>Age (days)</td>
<td>153 ± 567</td>
<td>1162 ± 568</td>
</tr>
</tbody>
</table>

Table entries are means ± standard deviations.

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

### Acknowledgements

We would like to thank Sandrine Gondor-Bazin and Lauriane Dezaire for their help with the care of the animals, and two anonymous reviewers were also thanked for their helpful and constructive comments that have helped improve our paper.

### References


