



## Losing grip: Senescent decline in physical strength in a small-bodied primate in captivity and in the wild



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### ABSTRACT

Muscle strength reflects physical functioning, declines at old age and predicts health and survival in humans and laboratory animals. Age-associated muscle deterioration causes loss of strength and may impair fitness of wild animals. However, the effects of age and life-history characteristics on muscle strength in wild animals are unknown. We investigated environment- and sex-specific patterns of physical functioning by measuring grip strength in wild and captive gray mouse lemurs. We expected more pronounced strength senescence in captivity due to condition-dependent, extrinsic mortality found in nature. Males were predicted to be stronger but potentially experience more severe senescence than females as predicted by life history theory. We found similar senescent declines in captive males and females as well as wild females, whereas wild males showed little decline, presumably due to their early mortality. Captive animals were generally weaker and showed earlier declines than wild animals. Unexpectedly, females tended to be stronger than males, especially in the reproductive season. Universal intrinsic mechanisms (e.g. sarcopenia) likely cause the similar patterns of strength loss across settings. The female advantage in muscle strength merits further study; it may follow higher reproductive investment by males, or be an adaptation associated with female social dominance.

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### 1. Introduction

As an organism reaches an advanced age, senescent changes at the molecular level cause functional declines (Monaghan et al., 2008; Nussey et al., 2013) that likely contribute to the frequently observed increasing mortality risk at old age (Gaillard, 1994; Ricklefs and Scheuerlein, 2001). Senescent declines in physical performance have been mainly studied in captive animals (Demontis et al., 2013; Guarente and Kenyon, 2000; Languille et al., 2012) and humans (Cruz-Jentoft et al., 2010), but recently, functional senescence has also been described in some natural populations (Nussey et al., 2008) despite condition-dependent survival that can mask senescence under natural conditions (Hämäläinen et al., 2014a; Nussey et al., 2011). The physical functioning of an organism depends largely on the quality and quantity of its skeletal muscle. Skeletal muscle mass and function decline at old age in humans and other organisms, a process termed sarcopenia (Cruz-Jentoft et al., 2010; Demontis et al., 2013). These declines are reflected in functional measures, such as reduced balance performance

(Laughton et al., 2003) and muscle strength (Cruz-Jentoft et al., 2010) and are associated with frailty and disability (Janssen et al., 2002; Rantanen et al., 1999) and all-cause mortality in aged humans (Cooper et al., 2010; Gale et al., 2007; Ling et al., 2010; Metter et al., 2002; Rantanen, 2003) as well as laboratory mice and rats (Carter et al., 2002; Fahlström et al., 2012; Ingram, 2000). Age-related declines in muscle mass and function have also been found in mammal and invertebrate species under laboratory conditions (Altun et al., 2007; Chazeau et al., 2013; Demontis et al., 2013; Piccirillo et al., 2014) and in some wild populations (Hindle et al., 2009a,b, 2010; Lailvaux et al., 2011). Muscle strength is a meaningful indicator of functional senescence since it directly influences the functioning of the individual, declines at a rate much higher than e.g. muscle mass (Goodpaster et al., 2006; Metter et al., 2002), and reliably predicts mortality at least in humans (Metter et al., 2002).

In wild animals, muscle atrophy would almost certainly lower the physical performance required for foraging, reproduction and predator avoidance and might directly impair survival or reproductive output of individuals in an inferior condition. However, physical strength has rarely been assessed in wild animals (bite force in birds: Herrel et al., 2005 and small mammals: Becerra et al., 2013; Becerra et al., 2011; Freeman and Lemen, 2008; Santana et al., 2010; bite force and grip performance in reptiles: Herrel et al., 2007; Herrel et al.,

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2013; McBrayer and Anderson, 2007; da Silva et al., 2014; Wikelski and Trillmich, 1994) and no studies have explored senescent changes in strength.

Muscle strength in adulthood and the rate of sarcopenia differ for the sexes in humans (Doherty, 2001, 2003; Gallagher et al., 1997; Janssen et al., 2002): sarcopenia is more prevalent in women (Janssen et al., 2000) but causes higher rates of disability in men (Baumgartner et al., 1998). Few studies have examined sex differences in strength in non-human species (Becerra et al., 2011, 2013; Herrel et al., 2007; McBrayer and Anderson, 2007; da Silva et al., 2014) and to our knowledge, none have addressed sex-specific rates of senescent decline in strength beyond human studies (Doherty, 2003).

The purpose of this study was to clarify the roles of intrinsic and ecological factors in shaping functional senescence. To this end, we examined the age trajectories of grip strength in male and female gray mouse lemurs (*Microcebus murinus*, Cheirogaleidae), a small-bodied (60 g) strepsirrhine primate under captive and natural conditions. The gray mouse lemur is emerging as a primate model of aging in captivity as it is relatively short-lived and matures early, at 6–8 months of age (Castanet et al., 2004; Némoz-Bertholet and Aujard, 2003), yet shows aging processes similar to humans (Languille et al., 2012). Data from captivity have revealed senescent declines in measures of functioning such as body mass and balance performance beginning around 4–5 years of age (Hämäläinen et al., 2014a; Languille et al., 2012; Némoz-Bertholet and Aujard, 2003), but no evidence of body mass senescence has been found in the wild (Hämäläinen et al., 2014a). Grip strength and hand dexterity are particularly important for the species due to its ecology: it is an omnivorous, arboreal primate that experiences high predation pressure. Food acquisition and manipulation (e.g. capturing flying insects), substrate use and predator avoidance all involve the use of hand grip, making grip strength an ecologically relevant measurement of muscle strength in the gray mouse lemur.

The species is overall sexually monomorphic, hence size dimorphism should not cause significant differences in strength between the sexes, but sex-specific behaviors (female-biased torpor use: Schmid and Kappeler, 1998; male roaming in the mating season: Eberle and Kappeler, 2004a) cause seasonal fluctuation in body mass sex dimorphism (Hämäläinen et al., 2014a; Schmid and Kappeler, 1998) and, possibly, body composition. There is also a known male bias in mortality in the wild that escalates during the mating season (Kraus et al., 2008). Due to these life-history differences, we were particularly interested in addressing potential sex differences in physical functioning.

We established age trajectories of forelimb grip strength in a captive population that experiences no extrinsic mortality and should therefore reflect intrinsic functional deterioration in a manner comparable with studies on other captive model species. To test whether the oldest surviving animals in the wild also experience functional senescence, we examined grip strength in the natural environment. While senescent decline in grip strength in the wild animals might be absent or modest due to high rates of extrinsic mortality in the natural population that rapidly eliminates individuals with declining condition (Hämäläinen et al., 2014a), captive animals were expected to show senescent declines in grip strength, since conditions in captivity are standardized, extrinsic mortality is absent and muscle-preserving exercise is limited. Because the seasonally varying resource availability, fluctuating energetic demands and the use of existing tissue (fat and muscle) for energy might have important consequences for physical strength, we measured strength in the dry and rainy season in the wild. Based on sex differences found in other species we expected males to have higher muscle strength than females throughout life (Crabbe et al., 2003; Doherty, 2001; Van Damme et al., 2008), but possibly lose strength at a more rapid rate towards old age (as found in humans, reviewed in Doherty, 2003).

## 2. Methods

### 2.1. Study populations

For the captive part of the study, we used adult individuals from an ad libitum fed breeding colony in Brunoy, France (see Némoz-Bertholet and Aujard, 2003; Perret, 1997 for details). All grip strength measurements were made within one week in February 2012. The animals were housed in 7 different rooms, and each room was in a slightly different stage of the annual photoperiodic schedule (enforced to trigger seasonal behaviors in captivity, Perret, 1997; Perret and Aujard, 2001) in transition from long day to short day length conditions. This stage marks the onset of fattening, i.e. is roughly comparable to early rainy season in the wild.

The wild population (locally known as the “N5” population) has been monitored since year 2002 in a 25 ha study site of dry deciduous forest in Kirindy/CNFEREF, central Western Madagascar by researchers of the German Primate Center (DPZ). The area experiences pronounced seasonal variation with a distinct dry season (~May–November), and a rainy season (~November–April), with consequent variation in food availability (Dammhahn and Kappeler, 2008), leading to substantial seasonal, sex-specific body mass fluctuation in the gray mouse lemurs (Hämäläinen et al., 2014a; Schmid and Kappeler, 1998). The brief mating season takes place at the end of the dry season (mid-October to November) and offspring are weaned by the end of the rainy season (March–April) (Eberle and Kappeler, 2004b). For long term data collection, trapping has been conducted at minimum 6 times per year (monthly in March–May and September–November) with Sherman live catch traps baited with small pieces of banana. All captured animals are equipped with an individual subcutaneous transponder (Trovan EURO ID, Germany) at first capture. The animals were almost exclusively first captured as juveniles (<1 year of age), and the age estimates were confirmed by morphometrics. The capture and handling protocols have been detailed elsewhere (Dammhahn and Kappeler, 2008; Eberle and Kappeler, 2004b; Hämäläinen et al., 2014b).

### 2.2. Quantifying grip strength

Grip strength was measured with a method adapted from rodent studies (e.g. Ingram, 1983; Justice et al., 2013; Smith et al., 1995), where it has become a standard measure of muscle dexterity and has been shown to reliably predict overall motor function (Justice et al., 2013). A force gauge (Chatillon LG Series Mechanical Force Gauge 50 N,  $5 \pm 0.025$  kg) was mounted horizontally on a stand and attached to a metal grid. The gauge was set to record the maximum strength of a pull. The test subject was held by the rump and lifted so that their front paws were in reach of the metal grid, which usually induced the animal to grasp the bar closest to them (Fig. 1). Once the animal was holding firmly with both hands, it was steadily but rapidly pulled horizontally away from the gauge until it released both hands from the bar. The procedure was repeated three times per individual in rapid succession, only recording grips where both hands of the animal were on the same bar of the grid. If the individual refused to grasp the grid, the testing was discontinued (<5% of sessions). The maximum force was recorded for each grip attempt and the highest of the measurements within the testing session was considered as the maximum grip strength of the animal at that time (e.g. Gale et al., 2007; Herrel et al., 2013; Kallman et al., 1990).

In captivity, 118 individuals (aged 2–11 years) were tested once each. In the wild, a total of 351 measurements from 142 individuals (aged 2–10 years) were collected over two late dry seasons (September–November,  $N = 151/75$  (measurements/individuals)) and two late rainy seasons (March–May,  $N = 200/112$ ) in the years 2010–2012. All measurements were made by the same person (AH). The body mass (precision  $\pm 1$  g) of each individual was recorded within three days of the grip strength measurement with an electronic scale (captivity) or a Pesola spring scale (wild).

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