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Nicholas Heslep

*James Madison University*

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Locomotion and life history in a leaping primate: Mechanics and energetics of movement  
throughout the *Propithecus* lifespan

Nicholas Heslep

A thesis submitted to the Graduate Faculty of

JAMES MADISON UNIVERSITY

In

Partial Fulfillment of the Requirements

for the degree of

Master of Science

Department of Biology

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---

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Dr. Idelle Cooper

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## Chapter 1: Locomotor development in wild sifaka (*Propithecus verreauxi*)

### **Abstract**

Arboreal primates are typically altricial, exhibit long juvenile periods, and use dynamic locomotor behaviors that can be challenging and risky. Sifaka (*Propithecus verreauxi*) have particularly slow life histories for their size, with long juvenile periods, protracted reproductive careers, and long life spans. Slow somatic growth poses potential mechanical challenges for juvenile sifaka who use thigh-powered vertical clinging and leaping to follow group members during travel. I examined mechanical and energetic costs of movement in developing sifaka. I instrumented 8 wild sifaka (3 yearlings, 3 subadults, 2 adults) in 4 social groups with inertial sensors measuring tri-axial acceleration for 1.5-8 weeks and collected simultaneous continuous behaviors on focal pairs. I quantified overall dynamic body acceleration (ODBA), frequency and magnitude of peak accelerations, percentage active time, leap counts, and activity budgets across age classes. Yearling sifaka exhibit higher and more peak accelerations than adult sifaka ( $p < 0.05$ ), though yearlings spend similar energy and are active as often as adults. With absolutely shorter hindlimbs, yearling sifakas need to leap more often and produce higher and/or more accelerations to keep up with older individuals, though the subsequent energetic cost seems to be modulated by an exceptionally slow somatic growth rate. These results suggest that locomotor performance is an important component of the evolution of life history patterns.



## Introduction

Mammal life histories reflect the ecological and evolutionary constraints to which a population has been subjected over time. At each stage of the life cycle, mammals are under distinct neurological, physiological, and mechanical constraints, all of which have fitness consequences. One universal tradeoff is that of energy allocation, as energy spent on one physiological process cannot be used for another. At the broadest scale, energy must often be allocated toward either survival or reproduction, with many underlying traits contributing to one or the other (Stearns 1989, 1992; Husak & Lailvaux 2022).

While the energetic cost of reproduction is more obvious, examples of survival-related energetic costs include cellular maintenance, immune function, thermoregulation, and locomotion (Gray & Prince 1988; Lochmiller & Deerenberg 2000; Zera & Harshman 2001; Nilsson *et al.*, 2011; Husak *et al.* 2016). A primary tenet of life history theory states that these tradeoffs shape an organism's growth, reproductive timing and investment, and longevity, among other parameters (Stearns 1989, 1992).

Life histories can be described as a “fast-and-short” to “slow-and-long” continuum (Stearns 1992, 2000; Oli 2004). In mammals that evolved under highly unpredictable environmental conditions, life histories tend to fall on either extreme of the continuum. Mammals with a “fast-and-short” strategy fit an entire life cycle between disturbances, while mammals employing the “slow-and-long” strategy essentially bet-hedge by attempting reproduction on several separate occasions over an extended period of time (Stearns 2000). To better understand the evolution of a given life-history strategy, it is necessary to understand the physiological and mechanical constraints at each unique stage of the life cycle.

Locomotion is essential to overall fitness, as most animals must move to find mates, locate food and other resources, and avoid predation. The energetic cost of locomotion comprises a substantial portion of an animal's total daily energy expenditure (Kenagy & Hoyt 1989; Karasov 1992), and efficient budgeting of energy reserves is critical to performance and fitness (Leonard & Robertson 1997, Grémillet *et al.* 2018). Animals are tasked with ensuring sufficient energy intake from food to balance energy expenditure, and an imbalance in energy intake to expenditure often results in decreased performance or death. This suggests that maximizing energy efficiency with respect to locomotion confers a fitness benefit and is therefore acted upon by natural selection pressures.

#### *Ontogeny & life history*

Before animals are able to reproduce, they must grow and survive through juvenility, which comes with unique energetic challenges and selective pressures (Hurov 1991; Carrier 1996; Wunderlich *et al.* 2011). Although they must often navigate the same environment and evade the same predators as adults, developing animals are under several locomotor constraints, namely smaller body size and ongoing neuromuscular development (Carrier 1996; Doran 1997; Wells & Turnquist 2001; Main & Biewener 2006, 2007). Mechanisms which may mitigate this disadvantage include scaling musculature with positive allometry, modifying morphology of body parts used in locomotion, and adapting the locomotor behaviors themselves (Demes & Günther 1989).

The vast majority of locomotion research to date is focused on adult subjects, both because adults often make for more convenient subjects, and including developing subjects may introduce confounding variables (Hurov 1991; Carrier 1996; Lawler 2006;

Young & Shapiro 2018). Despite these challenges, measuring locomotor performance across the life cycle may elucidate constraints unique to certain life stages, and offers a more complete picture of the selective pressures associated with locomotor ontogeny and life history (Hurov 1991; Stearns 1992, 2000; Carrier 1996; Workman & Covert 2005; Wunderlich *et al.* 2011; Bezanson 2009, 2017; Young & Shapiro 2018).

Mammals display a wide range of locomotor abilities as neonates, from essentially physically mature, or precocial, to completely dependent, or altricial. Many species are capable of adult-like locomotion shortly after birth, though others depend on parental care for many months or years (Grand 1992; Muir 2000). Altricial young are born with a much smaller proportion of their eventual adult weight and muscle strength compared to precocial mammals (Grand 1992). This creates greater locomotor challenges for altricial juveniles, as they must cope with the challenges of being smaller and underdeveloped for an extended period of time (Hurov 1991; Grand 1992; Carrier 1996; Wells & Turnquist 2001). The precocial-altricial dichotomy can also be present within a single individual, with some structures highly precocial and others altricial in the same animal (Grand 1992).

#### *Propithecus verreauxi* life history

In order to better understand how locomotor performance varies during development, I investigated the strepsirrhine primate *Propithecus verreauxi*, commonly known as sifaka. Among primates, *Propithecus verreauxi* life history is one of the “slowest” in terms of life history because, when controlling for body size, it has a relatively late age at first reproduction and lives for a long time when compared to other wild primates (Richard *et*

*al.* 2002). Juveniles reach locomotor independence late compared to other strepsirrhines, making their first movements away from the mother around 6 weeks and reaching full independence as late as 6 months (Richard 1976; Eaglen & Boskoff 1978; Young & Shapiro 2018; Malalaharivony *et al.* 2021). While sexual maturity is reached around 3 to 6 years, *P. verreauxi* juveniles do not reach adult body mass until approximately 8 years, indicating a protracted period of somatic growth (Richard *et al.* 2002; Lawler 2006). Despite being altricial in general somatic growth and development, *P. verreauxi* are dentally precocious and born with most teeth fully erupted (Godfrey *et al.* 2004). For an animal roughly the size of a house cat (2.92 kg mean adult mass), individual *P. verreauxi* have been observed to live as long as 33 years in the wild (Bronikowski *et al.* 2016).

*P. verreauxi* life history characteristics have been attributed to the highly unpredictable environment that they inhabit (Wright 1999; Dewar & Richard 2007; Dunham *et al.* 2011). Madagascar experiences high inter- and intra-annual variation in rainfall patterns, which determines food availability for frugo-folivorous *P. verreauxi* (Jury *et al.* 1995; Dewar & Richard 2007). Stochastic food availability likely influenced the evolution of the long reproductive lives of *P. verreauxi*, which allow for several opportunities for successful reproduction inter-annually (Wright 1999; Richard *et al.* 2002; Lawler *et al.* 2009). The Malagasy climate consists of alternating wet and dry seasons, leading to seasonality in plant growth and flowering punctuated by stochastic inter- and intra-annual rainfall, resulting in stochastic droughts (Dewar & Richard 2007; Dunham *et al.* 2011). This in turn drives seasonal reproductive cycles, in which females store energetic “capital” during the wet season, give birth in the middle of the resource-limited dry

season, and wean infants during the next wet season (Wright 1999; Richard *et al.* 2000, 2002).

### *Propithecus verreauxi* locomotion

Indriids, including *P. verreauxi*, employ a highly specialized vertical clinging and leaping (VCL) style of locomotion. VCL is a locomotor strategy characterized by hindlimb-powered leaps between vertical supports, most often tree trunks (Napier & Walker 1967). Biomechanically, leaping sifaka can be modeled as projectiles using

$$d = \frac{v^2}{g} \sin(2\theta)$$

where  $d$  = distance,  $v$  = velocity,  $g$  = acceleration due to gravity ( $\sim 9.8 \text{ m/s}^2$ ), and  $\theta$  = takeoff/launch angle. Leap distance ( $d$ ) is proportional to the square of takeoff velocity ( $v$ ), and the takeoff velocity itself depends on initial speed and the acceleration generated from initiation of a leap to takeoff. Accelerating the body comes with an energetic cost, as energy is utilized to contract the muscle fibers required to move the necessary limb segments. To increase leap distance, sifaka must either apply more initial force (acceleration  $\times$  mass) and/or increase the time of pre-takeoff acceleration. In the case of *P. verreauxi*, leaps can be in excess of 10 meters between supports, which can increase the risk of injury/death from an imperfect or off-target leap (Napier & Walker 1967; Fleagle 1999). While the majority of *P. verreauxi* locomotor bouts consist of arboreal leaping, during terrestrial movement they “gallop” bipedally with the trunk turned approximately  $30^\circ$  to the direction of travel (Lawler 2006; Wunderlich & Schaum 2007).

Within specialized leapers, there are two main functional groups with distinct leaping mechanisms: the small-bodied leapers (i.e., tarsiers & galagos; adult body mass ~80g- <1kg), and the large-bodied leapers (*P. verreauxi* and other large-bodied indriids; adult body mass >2kg). One notable difference is in the method of propulsion when initiating leaps. Smaller leapers are not constrained by muscle mass relative to body size, and thus have the ability to produce large initial acceleration very quickly. They use “tarsal-powered” leaps, so named because of the elongated midfoot that increases the speed advantage (load arm/lever arm) of their leap (Demes & Günther 1989, Demes *et al.* 1996). Conversely, larger leapers are limited by their lower muscle cross-sectional area relative to their body mass. Larger species, however, have absolutely longer hindlimbs that allow for a greater period of acceleration from initiation to takeoff (Demes & Günther 1989, Demes *et al.* 1996). In contrast with the tarsal-powered leaps of smaller species, larger leapers depend on their thighs to produce the necessary force. In fact, larger species seem to rely very little, if at all, on the foot to power leaps (Demes *et al.* 1996). To summarize, small leapers accelerate primarily with the midfoot via high forces over a short time, while large leapers use the thighs, producing relatively lower instantaneous forces but over a longer period of time (Demes & Günther 1989).

*P. verreauxi* possess several morphological characters specialized for VCL locomotion, including relatively long hindlimbs for leaping and large hands and feet for grasping compared to non-leapers (Demes & Günther 1989). *P. verreauxi* have a low intermembral index, defined as the ratio of total forelimb length to total hindlimb length (Oxnard *et al.* 1981; Ravosa *et al.* 1993; Fleagle 1999). Elongated hindlimbs allow for greater angles at the hip & knee and a longer period of acceleration between initiating a

leap and takeoff, enabling individuals to reach the high takeoff velocities necessary to complete long-distance leaps (Demes *et al.* 1996; Demes & Günther 1989). In addition, *P. verreauxi* have large hands and feet (compared to non-leapers), with an elongated hallux which forms a deep cleft between it and the other digits (Gebo & Dagosto 1988; Lawler 2006). Enlarged hands and feet enhance grasping ability, a crucial trait when the primary mode of travel involves leaping among trees (Napier & Walker 1967; Gebo 1985). In developing *P. verreauxi*, the hindlimbs, hands, and feet grow with strong negative allometry as infants are born with disproportionately large extremities and “grow into” them (Lawler 2006; Wolf 2011). This allows for enhanced grasping ability in an arboreal environment from juvenility and likely aids the ability to cling to the mother during the period of locomotor dependence.

The challenges presented by arboreal VCL locomotion are exacerbated when considering them from an ontogenetic perspective. As social primates traveling in family groups, juvenile *P. verreauxi* are tasked with navigating the same physical environment as their adult counterparts, yet they have less-developed musculature and absolutely shorter hindlimbs (Ravosa *et al.* 1993; Godfrey *et al.* 2004; Lawler 2006). As a result, juveniles must either leap at a higher frequency than adults, using alternate supports, or exhibit higher instantaneous acceleration relative to adults to traverse the same distance. Coupled with an extended juvenile period during which young *P. verreauxi* are subjected to these constraints, it is apparent that *P. verreauxi* is an ideal species for the study of the mechanical constraints and energetic costs of locomotion associated with juvenility.

Conservation of energy is critical to fitness, costs of locomotion comprise a significant portion of animals’ energy budgets (Kenagy & Hoyt 1989; Karasov 1992), and specific

locomotor constraints differ across *P. verreauxi* life history. Measurement of energy expenditure and locomotor mechanics across the *P. verreauxi* life cycle may elucidate unique selection pressures and adaptive mechanisms acting at different points throughout ontogeny and is critical to understanding adaptation in strepsirrhine primates.

In this study, I compare the mechanics and energetics of locomotion among age classes in growing, wild *P. verreauxi*. Specifically, I hypothesize that:

**1) Juveniles experience greater biomechanical demand during locomotion**, via either a) producing greater acceleration to make similar leaps with absolutely shorter hindlimbs or b) performing more leaps to cover a similar distance, and **2) Juveniles expend similar energy compared to adults** despite these challenges, as a result of pressure to maximize conservation of energy with respect to locomotion during development.

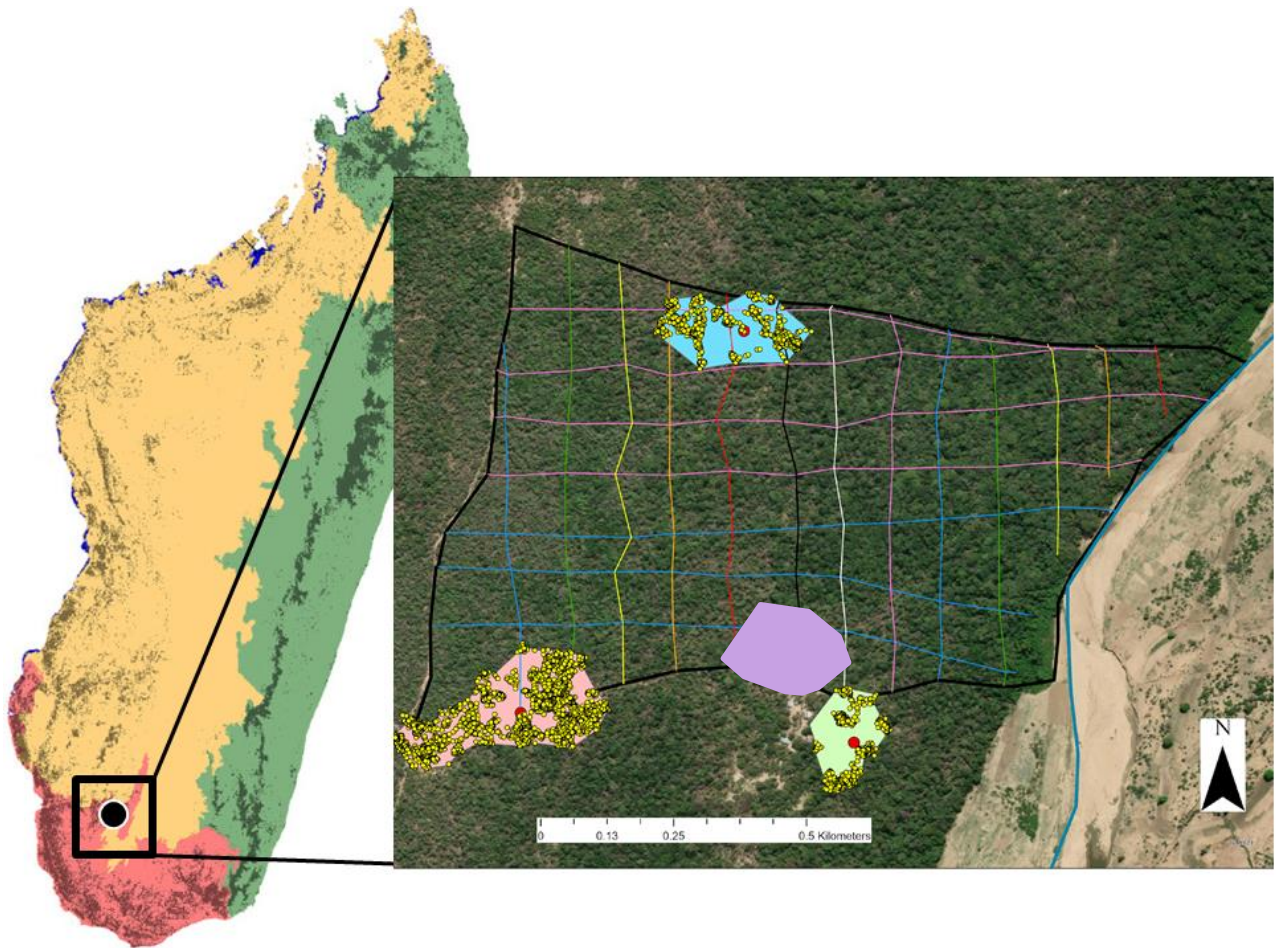
## Methods

### *Study site*

All data were collected at Beza Mahafaly Special Reserve (BMSR) in Southwest Madagascar (Figure 1.1). BMSR is a protected reserve consisting of an environmental gradient from dry spiny forest to riverine gallery forest, home to wild populations of several lemur species including *P. verreauxi* (Sussman *et al.* 2011). The site has been continuously operated as a research facility since 1977, and *P. verreauxi* population structure and demographics have been studied since 1985. Since 1985, an on-going research protocol has been in place in which yearling animals and new immigrants are



captured, measured, marked and released back into the wild. During this process numerous qualitative and quantitative morphometrics are taken from each animal. Animals are also fitted with a nylon collar and unique ID tag. For this study, the collar provided a convenient location for sensor attachment which would not inhibit behavior.



**Figure 1.1.** Location of BMSR (black dot), with map of the range boundaries inset. Colored polygons represent focal group home ranges, with individual GPS points in yellow and a spatial mean/center in red. Group Fety (purple) does not have GPS data due to lack of signal when collecting data in this home range, so this polygon is based on an existing BMSR dataset. Remaining groups are Perline (pink), Elyse (green), and Roshna (blue).

### *Data collection*

This study utilized collar-mounted logging sensors to characterize and compare acceleration peaks and estimated energy expenditure among yearling, three-year-old, and adult animals at BMSR. Collection of acceleration data allows for identification of leaps, peak acceleration (i.e., the highest acceleration an animal applies during a leap), and estimation of energy expenditure due to movement. I took advantage of the ongoing capture-collaring system at BMSR to add small TechnoSmart Axy 5 XS inertial sensors (TechnoSmart, Rome, Italy) to the collar of 3 yearling, 3 three-year-old, and 2 adult *P. verreauxi* in August-October 2022. All procedures were approved by Madagascar National Parks and the James Madison University Institutional Animal Care & Use Committee. Devices were attached to the collar using custom, in-house built mounts (entire configuration <3% average yearling body mass). A subset of collars were modified for automatic device drop-off to avoid unnecessary recapture. The length of continuous acceleration data collection ranged from 8-36 days per individual, with sensors configured to collect at 50-100hz depending on length of deployment. Two animals were instrumented per social group, with a total of four social groups spread across the reserve (Figure 1.1). During the capture process, morphometric measurements were taken on each individual, allowing body mass and thigh/leg length to be incorporated into analyses.

Locomotor behavior and GPS data were collected on a focal social group each day using the Behavve smartphone app (Fulton 2022). Table 1.1 provides definitions of locomotor variables. Additionally, video data were collected on a select focal group during daylight hours each day. Video collection allowed for behavior validation and the ongoing

training of a machine-learning algorithm with the goal of automating behavior classification from accelerometer data. Approximately 264 hours of behavior and 25 hours of video data were collected.

### *Accelerometry*

In order to measure how leaping mechanics (via peak accelerations) and energy expenditure due to locomotion vary throughout development and during different behaviors, it is necessary to collect data on a fine temporal scale in a natural environment, without significantly altering the subjects' behavior. Widely-used measures of energy expenditure are limited in at least one of these requirements, as doubly-labeled water yields data across a coarse temporal scale, making it impossible to measure fine-scale "bursts" of activity, while respirometry is only practical in non-field studies (Nagy 1983; Speakman 1998; Geissler *et al.* 1986; Westerterp *et al.* 1988). Ongoing development in sensor technology offers a promising alternative, as inertial sensors can collect and store high-frequency data and are small enough to deploy in a natural setting (Yoda *et al.* 2001). Inertial sensors can be mounted on wild animals to collect movement data, including acceleration, gyroscope, and magnetometer information remotely and non-invasively.

For the purpose of estimating locomotion-related energy expenditure, acceleration data is particularly useful. Wilson and colleagues (2006) provide a framework for estimating energy expenditure using overall dynamic body acceleration (ODBA), which has been validated by a growing body of work (e.g. Halsey *et al.* 2009, 2011; Gleiss *et al.* 2011; Qasem *et al.* 2012; Wilson *et al.* 2020). ODBA is derived from tri-axial accelerometer

data (which measures acceleration in three dimensions), and has demonstrated a strong relationship when compared with traditional measures of energy expenditure in a range of species (Wilson *et al.* 2006, 2020; Halsey *et al.* 2009, 2011). It is important to note that the specific nature of this relationship can vary between species, and comparisons using ODBA are strictly relative as there is no conversion from ODBA to a standard unit of energy without species-specific validation (Halsey *et al.* 2009; Wilson *et al.* 2020). Despite its limitations, when sensor placement and study species are consistent, ODBA is a validated predictor of relative locomotor energy expenditure.

**Table 1.1.** Ethogram for *P. verreauxi* behavioral observations

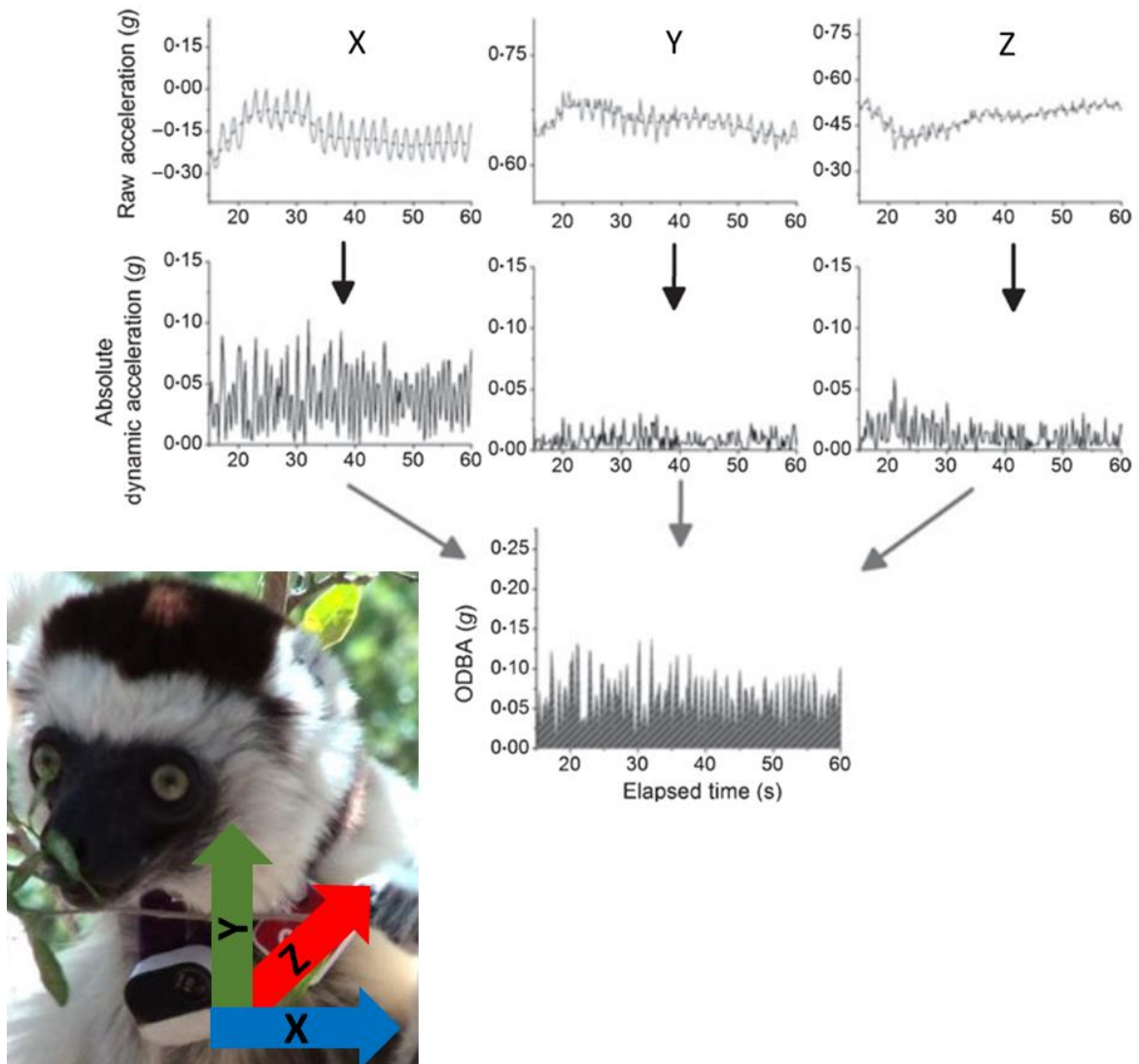
<b>Behavior</b>	<b>Definition</b>
Leap <sup>+</sup>	Cross gap using combined hindlimb propulsion with aerial phase
Hop up <sup>+</sup>	Ground to vertical substrate OR movement up vertical substrate, hindlimbs used together
Hop down <sup>+</sup>	Vertical substrate to ground OR movement down vertical substrate, hindlimbs used together
Bipedal gallop <sup>+</sup>	“Leap” on terrestrial substrate
Clamber <sup>+</sup>	Movement on multiple substrates (limbs in contact with at least 2 different substrates) in which at least one limb is in contact at all time
Climb up <sup>+</sup>	Movement up vertical substrate, separate movement of hindlimbs
Climb sideways <sup>+</sup>	Lateral movement, separate movement of hindlimbs
Climb down <sup>+</sup>	Movement down vertical substrate, separate movement of hindlimbs
Suspensory locomotion <sup>+</sup>	Locomotion while center of mass is below support
Crawl <sup>+</sup>	Movement on ground using four limbs, moving separately
Sit <sup>%</sup>	Rear down on substrate, forelimbs up
Hang <sup>%</sup>	Hanging by at least one limb
Lie <sup>%</sup>	Back flat against horizontal substrate
Crouch <sup>%</sup>	All four limbs on one horizontal substrate, rear lifted, no movement
Stand <sup>%</sup>	Upright posture with both hindlimbs extended
Cling <sup>%</sup>	All four limbs on one non-horizontal substrate, no movement

<sup>%</sup>Posture; <sup>+</sup>Locomotor behavior

## *Analyses*

Raw acceleration data were processed using custom-coded MATLAB/R programs designed to derive several metrics of interest: magnitude of acceleration peaks, frequency of acceleration peaks, estimated time spent active, and ODBA. A magnitude of 3g and minimum time-interval of 0.5s were used to define acceleration peaks, and the average magnitude & frequency per hour of these peaks were calculated. Activity was defined as acceleration >1g, and calculated as a percentage of total time. For ODBA, static (gravitational) acceleration is found by using a running mean on each orthogonal axis (X, Y, & Z) of the raw acceleration data. To find dynamic acceleration, or the acceleration due to the subject's movement, this static acceleration is subtracted from the raw value on each respective axis. Finally, the absolute value of the tri-axial dynamic accelerations are summed to derive ODBA, a proxy for energy expenditure (Figure 1.2).

In short,  $ODBA = |Acc_X| + |Acc_Y| + |Acc_Z|$ , where  $Acc_X$  represents the dynamic acceleration in the X direction, etc.. Lastly, GPS data were used to map home ranges of each focal group during the period of study. A machine-learning program is currently being developed by colleagues with the intent to label locomotor behaviors (i.e., leap, climb, gallop) automatically from raw acceleration data. This algorithm will be employed to identify specific behaviors as well as broad active vs resting contexts for analysis.



**Figure 1.2.** Graphical depiction of the derivation of ODBA, modified from Gleiss *et al.* (2011), and the standard device orientation when mounted (bottom left).

All statistical analyses were done in RStudio (RStudio, Boston MA). ANOVA or Kruskal-Wallis tests (depending on variable normality) were used to compare ODBA, rate & average magnitude of peaks, and activity time among the three age classes. In addition, mixed effects models were used to incorporate random effects such as

individual ID and social group in estimations of the effect of age class on ODBA and peak accelerations.

## Results

### *Morphometrics*

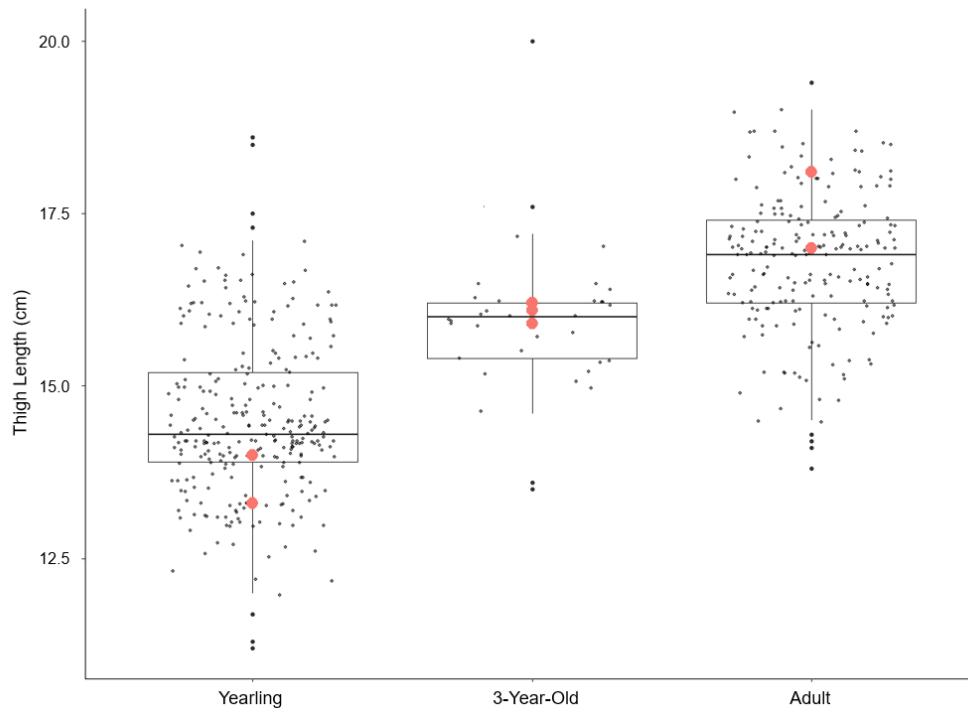
Due to the thigh-powered nature of *P. verreauxi* leaping, absolute thigh length (greater trochanter of femur to lateral condyle of tibia) was of particular interest in the analysis of morphometric data. I first compared the animals in my sample to data from the 1999-2022 capture seasons (n=522 animals). The thigh lengths from sampled animals are reasonably typical for the population, as none are outliers and the majority fall between the first and third quartiles for their age class (Figure 1.3). In this sample, absolute length of the thigh increased significantly with increasing age class (Figure 1.3;  $p < 0.01$ ), with average lengths of 13.5cm for yearlings, 16.1cm for 3-year-olds, and 17.6cm for adults. When relativized to body mass, thigh length ( $\text{cm}/\text{kg}^{(1/3)}$ ) yearlings have a larger thigh:mass ratio than adults (Figure 1.4).

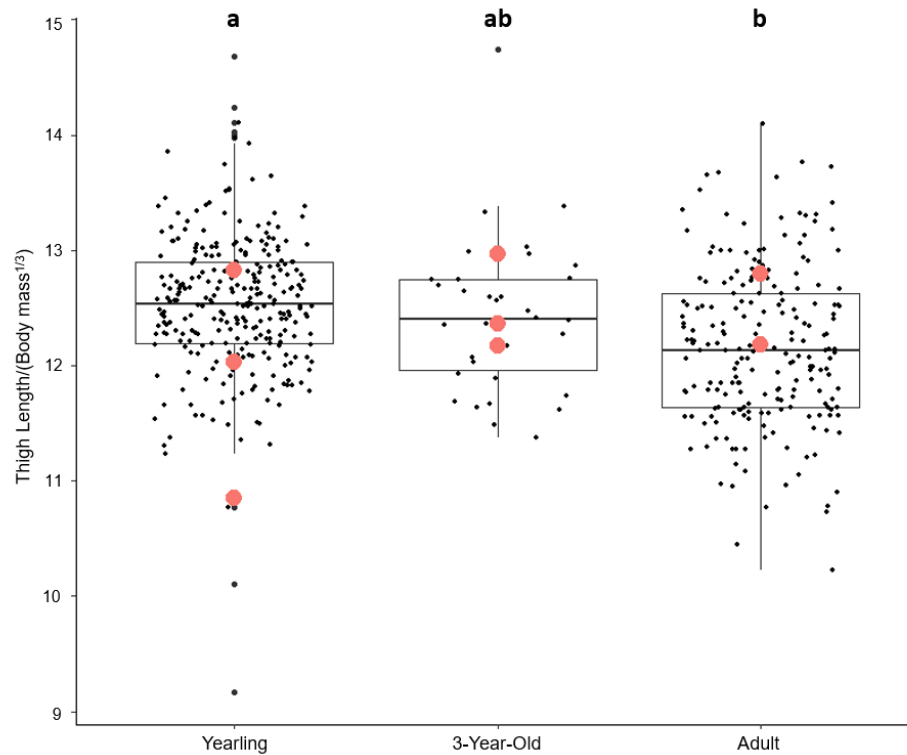


**Table 1.2.** Morphometric data for each subject in the sample.

Age	Group	Sex	Weight (kg)	Thigh Length <sup>1</sup> (cm)	Leg Length <sup>2</sup> (cm)	Foot Length <sup>3</sup> (cm)
1	Roshna	M	1.84	13.3	13.9	11.5
1	Fety	F	1.30	14.0	13.1	10.8
1	Perline	F	1.35	13.3	13.0	10.5
3	Elyse	F	1.95	16.2	15.4	12.1
3	Fety	M	2.23	15.9	16.0	12.1
3	Perline	F	2.21	16.4	16.4	12.8
Adult	Roshna	F	2.83	18.1	15.8	13.1
Adult	Elyse	M	2.72	17.0	15.3	12.1

<sup>1</sup>greater trochanter of femur to lateral condyle of tibia; <sup>2</sup>lateral condyle of tibia to lateral malleolus of fibula; <sup>3</sup>calcaneus to tip of longest digit

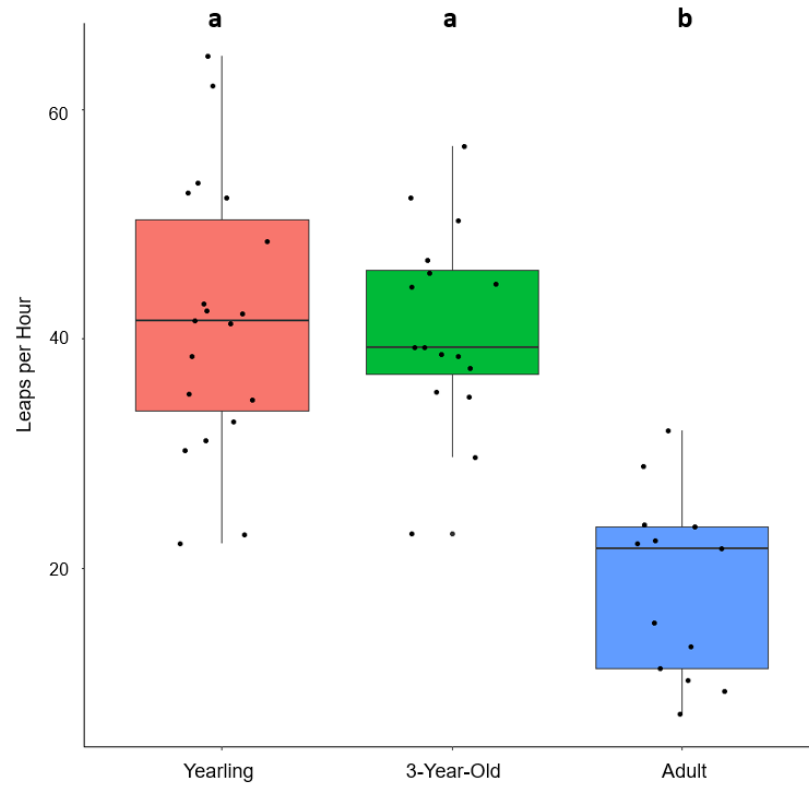
**Figure 1.3.** Thigh length among animals captured from 1999-2022. Points representing the 8 animals in my sample are highlighted red & enlarged.



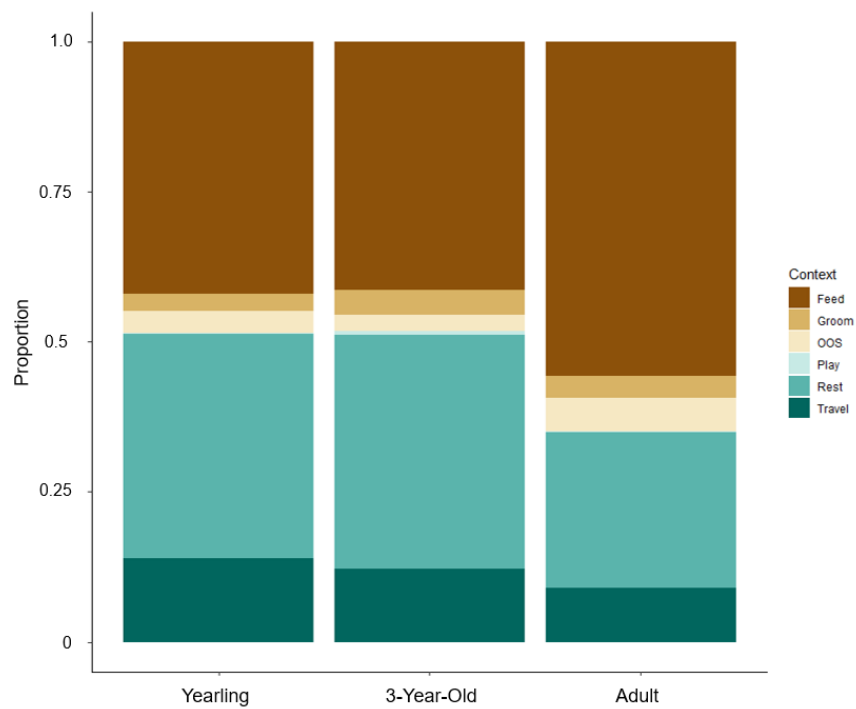
**Figure 1.4.** Thigh length relative to body mass ( $\text{cm/kg}^{(1/3)}$ ) for each age class. Enlarged red points represent the individuals in my sample. Yearlings and adults differ from each other at  $\alpha = 0.05$ .

### *Behavioral data*

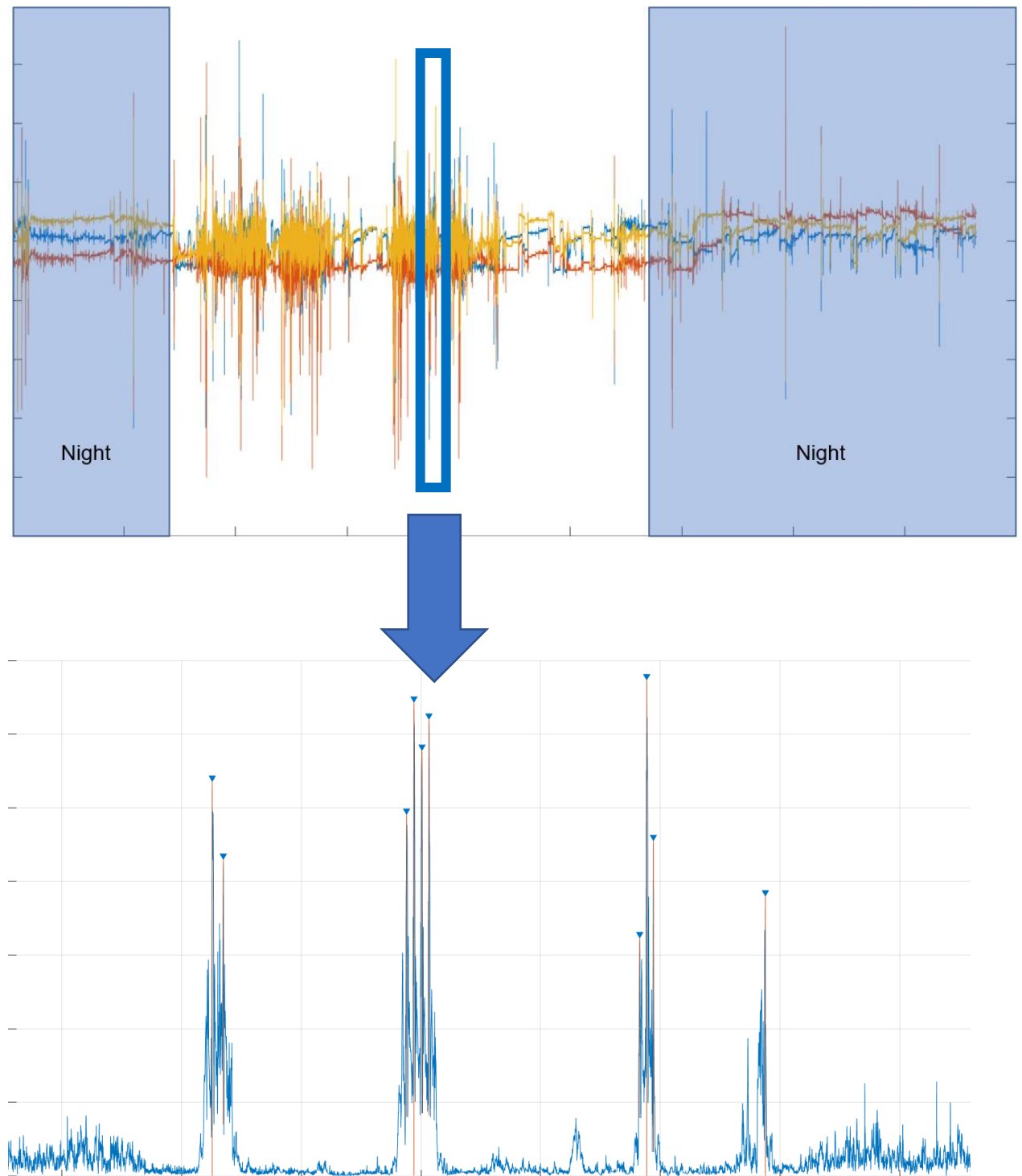
Leap frequency was calculated from behavioral data collected in the field by dividing leaps observed by the duration of observation on a given day. Leap frequency was lower in adults (Figure 1.5). In addition to leap frequencies, overall behavioral repertoire was calculated for five broad behavioral contexts – Travel, Rest, Feeding, Grooming, and Play (Figure 1.6). Travel and rest time seem to decline with age, while feeding time is increased in adult animals.



**Figure 1.5.** Leap frequency (observed leaps divided by total observation time on a given day) is significantly lower in adult *P. verreauxi* ( $p < 0.01$ ).



**Figure 1.6.** Proportion of total time spent in each behavioral context, by age class.

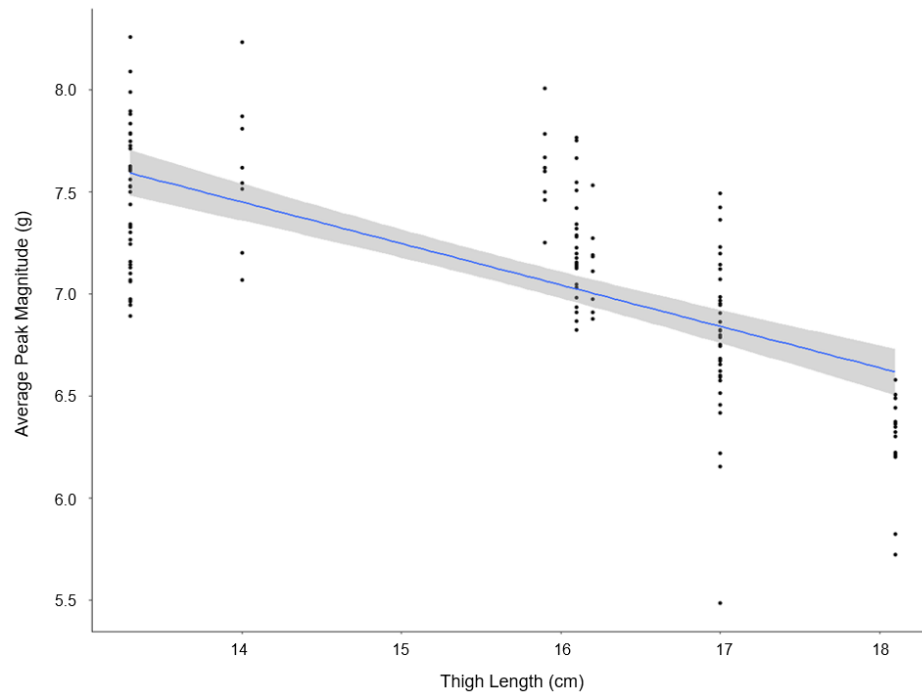
*Acceleration peaks*

**Figure 1.7.** Top panel: 24-hour tri-axial acceleration, with night hours shaded. Bottom panel: subsection of acceleration, converted to ODBA, with peaks marked (triangles).

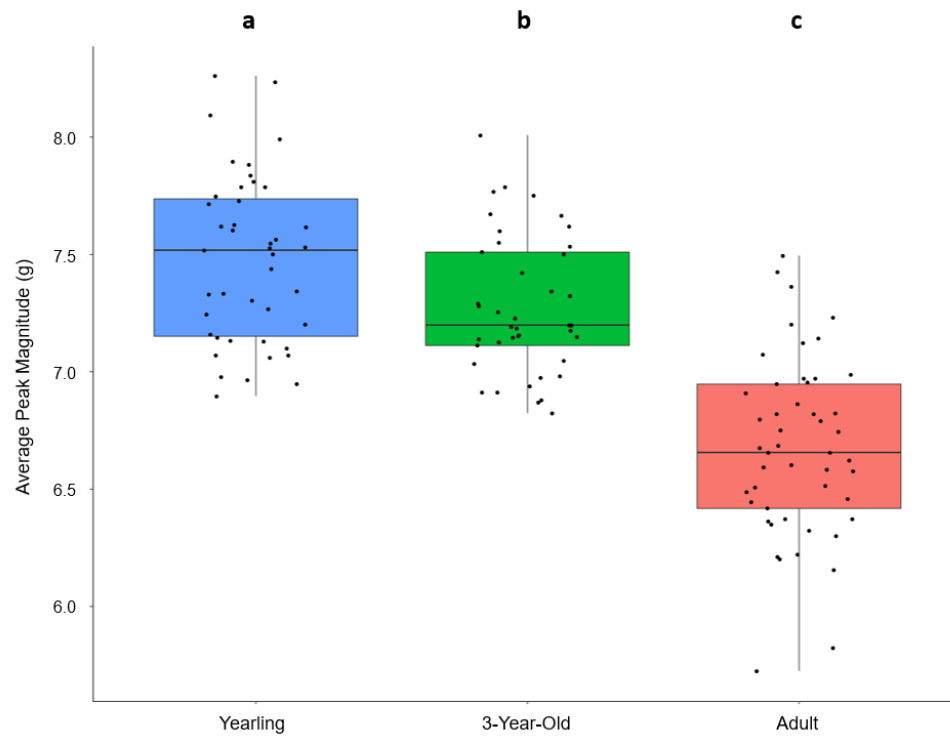
For the following analyses, acceleration peaks are defined as ODBA  $>3g$  with a minimum time interval of 0.5s, which represents high-intensity movement (Figure 1.7). As thigh length increases, the magnitude of peaks produced during locomotion decreases. Linear regression analysis indicated a significant, moderately strong negative relationship between length of thigh and average magnitude of peak accelerations (Figure 1.8;  $R^2=0.44$ ;  $p<0.01$ ).

When individuals within an age class are binned, the average magnitude of acceleration peaks decreases with increasing age class (Figure 1.9;  $p<0.05$ ). This is consistent with the previous observation that absolutely shorter thighs (in younger animals) are correlated with greater peak accelerations. There are, however, significant differences based on the social group in which the animal lives and an interaction effect between age class and social group in two-way ANOVA analysis (Figure 1.10).

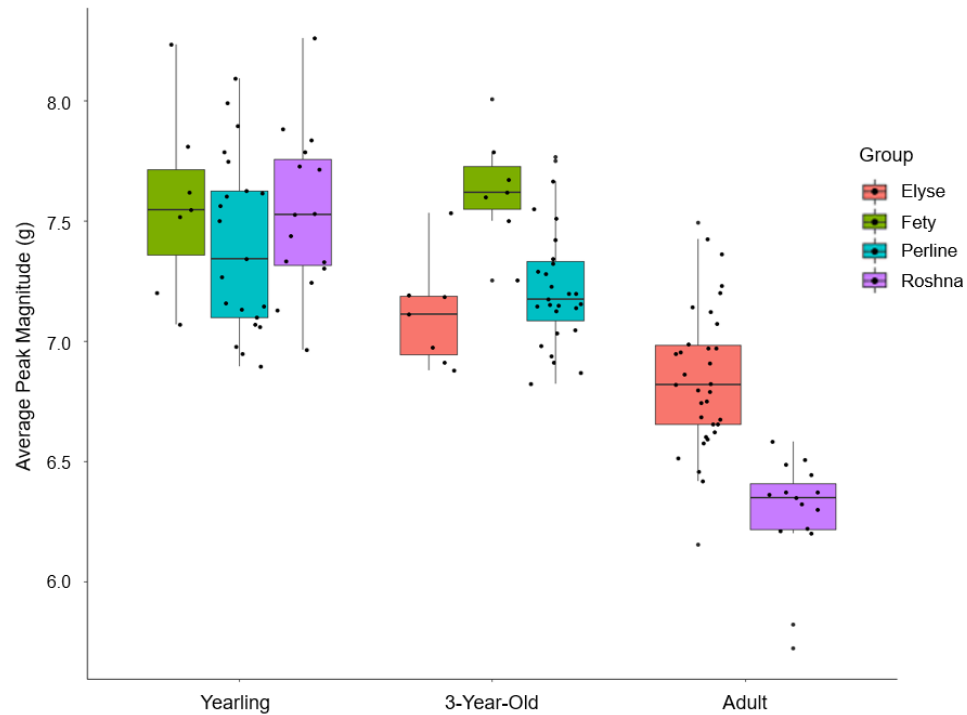
In addition to the magnitude, or intensity, of peak accelerations, the frequency (per hour) of peaks  $>3g$  was analyzed. While not a one-to-one predictor, the frequency of peaks is correlated with the frequency of leaps performed (Figure 1.11;  $R^2 = 0.63$ ;  $p<0.01$ ). Peak accelerations per hour are decreased in adult *P. verreauxi* compared to younger animals, with no significant difference between yearlings and 3-year-olds (Figure 1.12). This suggests that juvenile/subadult animals leap more frequently compared to adults. Again, there are differences depending on the animal's social group, but within social groups the younger individuals generally have a higher frequency of peak accelerations (Figure 1.13).



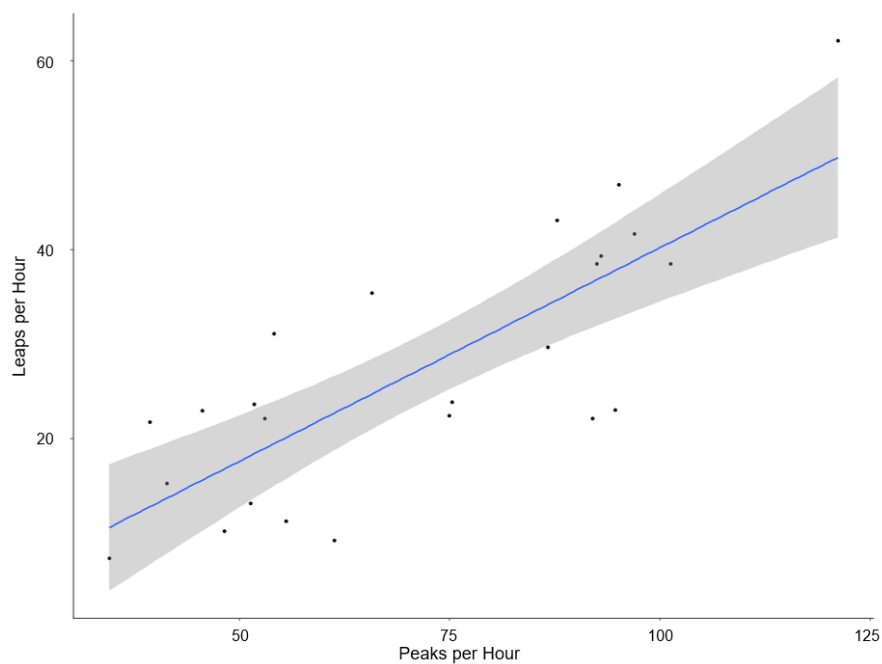
**Figure 1.8.** Linear regression of mean peak acceleration per day, displaying a significant, negative relationship ( $R^2=0.44$ ;  $p<0.01$ ; shaded area represents 95% confidence interval).



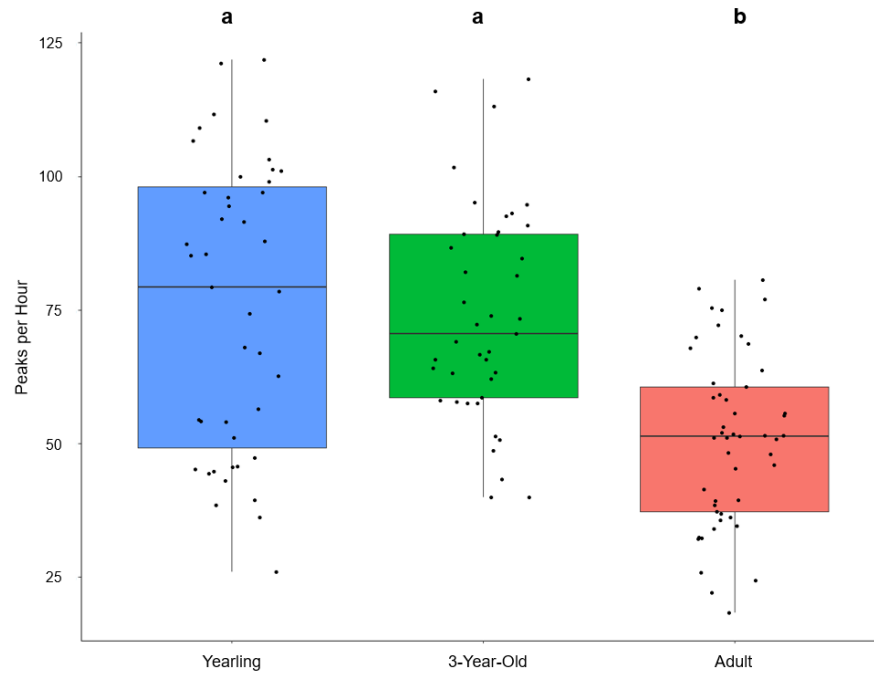
**Figure 1.9.** Mean magnitude of peak accelerations decreases with age (letters indicate significant differences at  $\alpha = 0.05$ ).



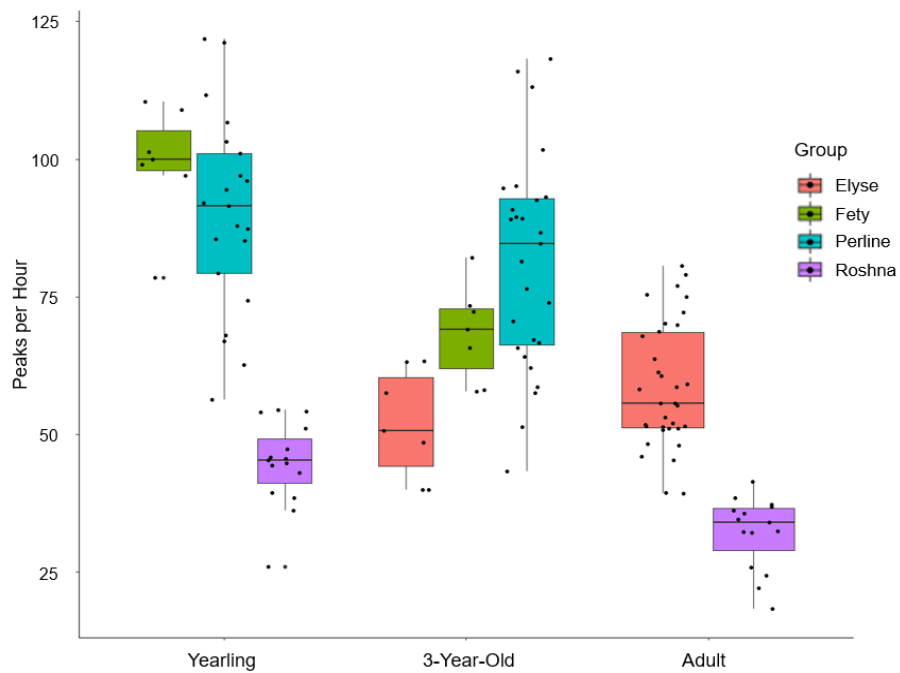
**Figure 1.10.** Mean peak magnitudes by age (x-axis) and social group (color). Effect of age class and social group, as well as the interaction term between the two, are significant ( $p < 0.01$ ).



**Figure 1.11.** Linear regression analysis indicates that the frequency of peak accelerations predicts the number of leaps performed ( $R^2 = 0.63$ ;  $p < 0.01$ ; shaded area represents 95% CI).



**Figure 1.12.** Number of peak accelerations (>3g) per hour, by age class. Letters indicate significance at  $\alpha = 0.05$

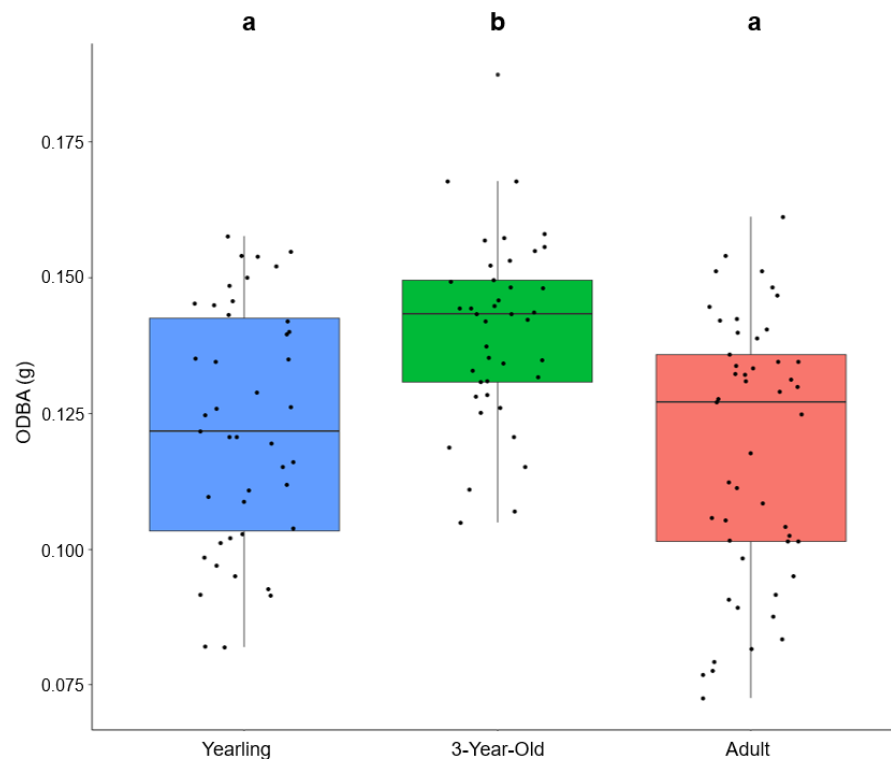


**Figure 1.13.** Frequency of peak accelerations by age class (x-axis) and social group (color). Significant differences due to age & group, as well as interaction between age and group, occur in two-way ANOVA.

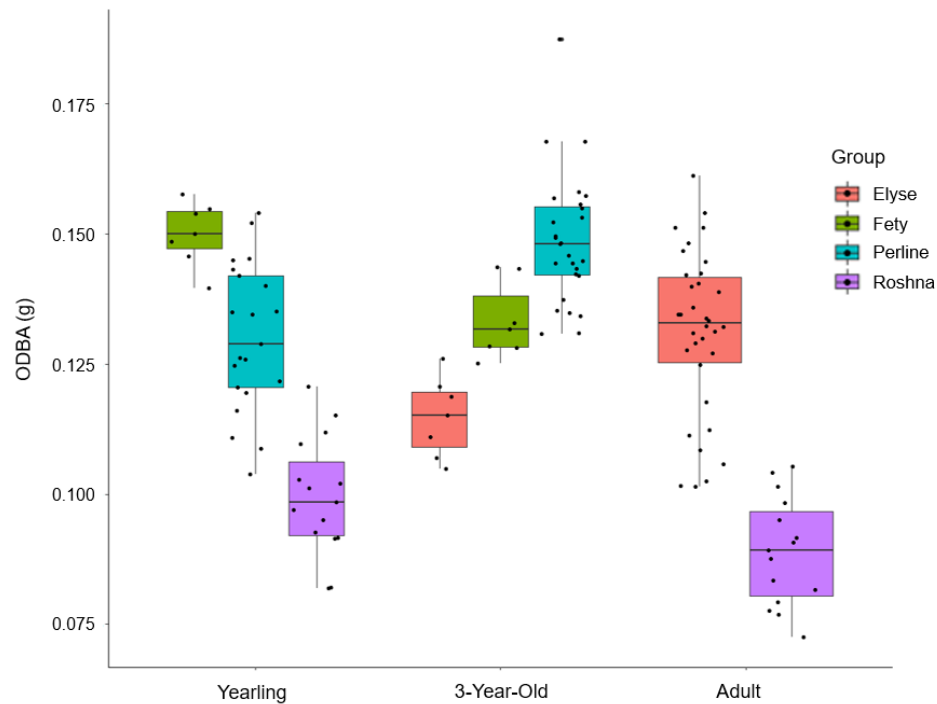


### *Energy expenditure & activity times*

While magnitude and frequency of peak accelerations are elevated in young animals compared to adults, daily average ODBA (a proxy for energy expenditure due to movement) was only elevated in 3-year-olds. Yearlings and adults were not statistically different, while ODBA in 3-year-olds was significantly greater than both (Figure 1.14). When including social group in the analysis, there are again differences by group but no clear pattern (i.e., younger animals of a group do not always have greater ODBA; Figure 1.15). It is evident, however, that some groups expended much less energy on locomotion during the time they were observed (e.g., group Roshna compared to Perline).

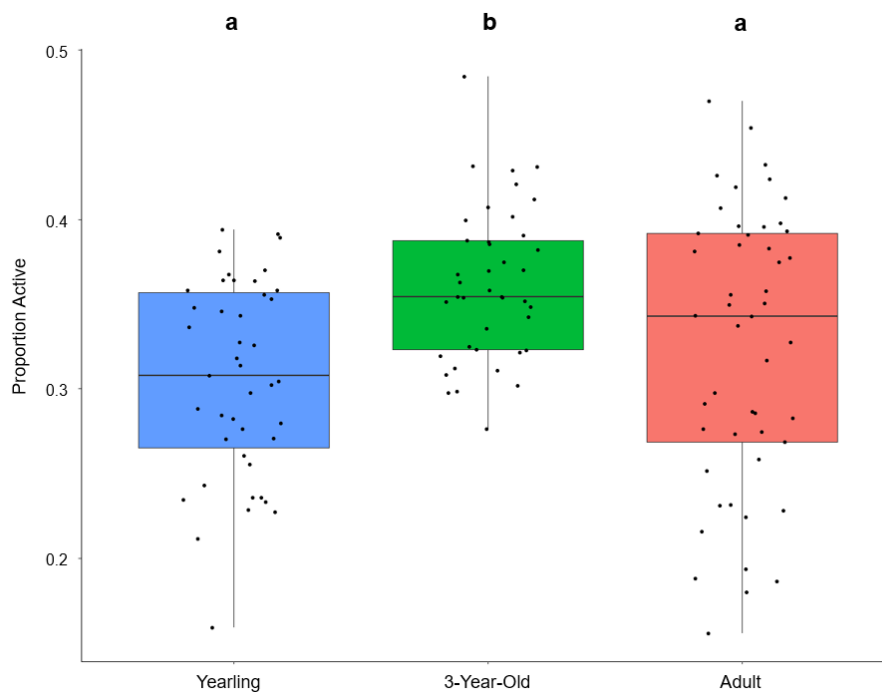


**Figure 1.14.** Estimated energy expenditure, as ODBA, is significantly greater in subadults (3 y/o) compared to yearlings and adults ( $p < 0.01$ ).

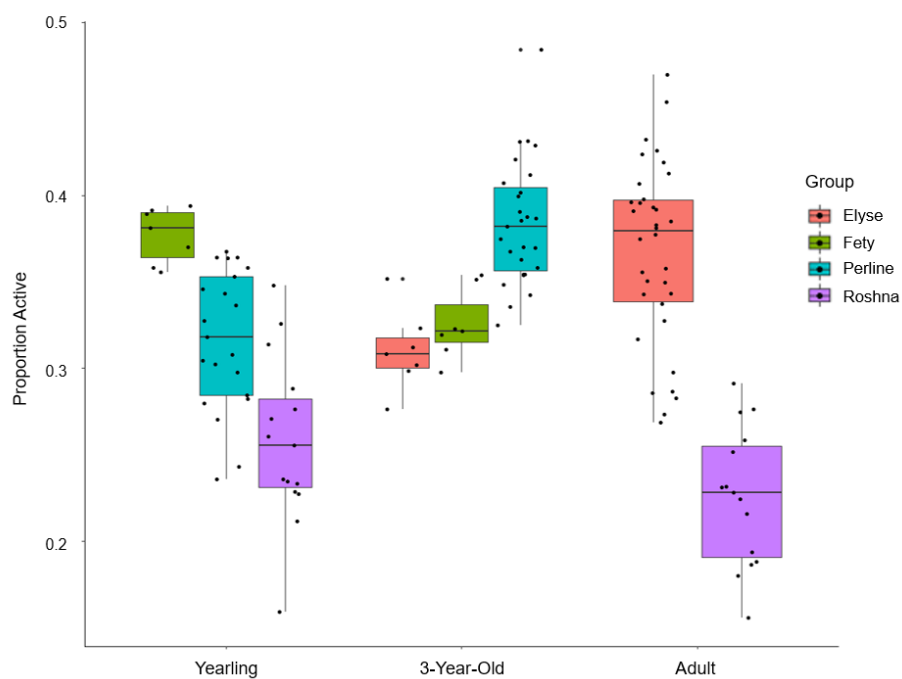


**Figure 1.15.** Overall Dynamic Body Acceleration (ODBA), a proxy for energy expenditure, by age class and social group.

Activity times, calculated as the proportion of time where ODBA > 1g, largely mirrored energy expenditure (as average ODBA), with 3-year-olds significantly higher than both yearlings and adults (Figure 1.16). Again, yearling and adult activity times were similar to each other. Mean activity percentages for each age class were 30.6% for yearlings, 36.1% for 3-year-olds, and 32.4% for adults. Similar to the results concerning energy expenditure, some social groups were much less active than others (Figure 1.17).



**Figure 1.16.** Proportion activity (amount of time where ODBA >1g) is elevated in 3-year-olds compared to yearlings and adults ( $p < 0.05$ ).



**Figure 1.17.** Proportion time spent active by age class and social group. Activity was heavily dependent on social group.

## Discussion

*P. verreauxi* life history is disproportionately slow for their body size, likely a reflection of their adaptation to highly seasonal and stochastic resource availability (Richard *et al.* 2002; Lawler *et al.* 2009). *P. verreauxi* achieve locomotor independence well before anatomical maturity, challenging juveniles traveling in mixed-age social groups (Richard *et al.* 2002; Lawler 2006; Wunderlich *et al.* 2011). *P. verreauxi* thighs, the primary driver of performance during vertical clinging-and-leaping locomotion (Demes & Günther 1989; Demes *et al.* 1996; Wolf 2011), are significantly shorter in juvenile sifaka compared to adults. Small juveniles with (absolutely) short legs may need to produce greater peak acceleration and/or leap more frequently to keep up with mature individuals in the group during locomotion. This may lead to increased mechanical costs of juvenility in *P. verreauxi*, although the subsequent energetic cost may be mitigated by selection for small and/or slow-growing body mass, growth rate, behavior, etc. in young animals (Wolf 2011).

Analyses indicated a negative relationship between thigh length and magnitude of peak accelerations. Because hindlimb length limits the time available to accelerate the body from leap initiation to takeoff, one- and three-year-old *P. verreauxi* must produce greater peak accelerations to reach the necessary takeoff velocity if they are required to leap similar distances as adults. In addition to the magnitude of peaks, the frequency of peak accelerations is again greater in juveniles compared to adults. I show that the frequency of peak accelerations is a reasonable predictor of the number of leaps performed by an animal, suggesting that adult *P. verreauxi* perform fewer leaps than yearlings or three-year-olds. This pattern was corroborated with observational behavior data. Higher leap

frequency in young individuals is likely due to the fact that juveniles perform a greater number of short-distance leaps, instead of covering a similar distance as adults (when the forest structure allows). When comparing age classes, the results concerning peak accelerations suggest that young *P. verreauxi* are both producing greater peak acceleration magnitudes (when necessary to cover long distances) and a higher peak frequency (when performing a greater number of short leaps) in order to cope with the limitations of a developing body while traveling in groups using highly-demanding leaping locomotion.

Although these data support the hypothesis that young *P. verreauxi* are under increased demand with respect to locomotion, the observed pattern with respect to energy expenditure differed from the prediction. While yearling and adult individuals had similar estimates of energy expenditure, three-year-olds exhibited increased energy expenditure and activity time compared to both yearlings and adults. There are several potential explanations for this pattern, although none can be directly supported by these data: 1) Three-year-olds are in a sociodemographic “middle ground” in which they are no longer given the preferential treatment of yearlings but have not yet reached dominant positions in the social hierarchy. Among other disadvantages, this forces three-year-old individuals to move more when feeding, as dominant animals maintain preferential access to feeding sites. 2) Increased activity in three-year-olds is driven by exploring dispersal options around the limits of their home range, as *P. verreauxi* generally start to disperse around age 3 (Richard *et al.* 1993). 3) Three-year-old *P. verreauxi* have longer hindlimbs relative to their body mass, allowing them to produce more force and “overshoot” leap distances leading to increased ODBA. I suggest that the most likely explanation is

sociodemographic, with 3-year-olds in a low-ranking social position forcing them to move more and expend more energy. Because two of the three-year-olds in this sample are female, dispersal is unlikely a strong factor as males are the primary dispersers in this species (Richard *et al.* 1993). Additionally, if the anatomy and biomechanics of the three-year-old body increased the likelihood of more/greater acceleration during locomotion than both yearlings and adults, one would expect to see the same pattern reflected in the aforementioned measures of the magnitude and frequency of peak accelerations.

It is also interesting that the pattern of increased biomechanical demand (as peak accelerations) among yearlings is not reflected in energy expenditure, which was similar to that of adults. Although yearlings produce greater magnitude of peaks and perform more leaps than adults, they exhibit ODBA similar to that of their adult counterparts. This suggests some means of compensating for their locomotor disadvantage, allowing young animals to travel with adults while incurring a similar energetic cost. Smaller body mass and higher hindlimb length:body mass ratios are likely a major factor, as young animals have less mass to move during travel. The ability to compensate for a biomechanical locomotor disadvantage may be another reflection of *P. verreauxi* life history evolution, as inter- and intra-annual stochasticity in resource availability leaves vulnerable juveniles with little energy to “spare” when fueling somatic growth in addition to typical cellular processes. These data suggest that, while growth continues long after locomotor independence is reached, yearling *P. verreauxi* do not necessarily incur an additional energetic cost when traveling compared to adults. In addition to ecological constraints on nutrient availability, the protracted juvenile period in *P. verreauxi* may be selected for because faster growth would increase body mass more rapidly than hindlimbs (which

must move the mass) can “keep up” with (Hurov 1991). Behavior and sociodemographic structure are once again likely factors, as traveling (the time during which the majority of peak accelerations are experienced) accounts for a relatively small proportion of overall daytime activity and time spent in other behavioral contexts is influencing differences (or lack thereof) in energy expenditure and activity time. It should be noted that ODBA exclusively estimates energy expenditure *due to movement* and does not account for other important aspects of metabolic expense such as cellular maintenance, immune function, digestion, etc.

While analysis of binned age classes is streamlined and allows for drawing simpler conclusions, the considerable differences among social groups should not be ignored. As an example, group Roshna (yearling male & adult female) in this sample had greatly reduced energy expenditure and activity time compared to others. Anecdotally, I noted that their home range had relatively dense and rich resources during my observation time compared to other groups that were followed. When observing group Roshna, the animals frequently remained feeding in a single large, leafy tree for several hours at a time. Other groups in the sample had less favorable microhabitat conditions, and had to constantly move to ensure group members had access to adequate forage. Some groups were also frequently involved in inter-group conflict associated with territory defense, which likely impacted their intensity and frequency of activity. The extent to which ecological and sociodemographic factors influence *P. verreauxi* movement cannot be fully determined with this dataset, and future work should incorporate both microhabitat condition (e.g., range size, resource availability, etc.) and sociodemographic factors (e.g., group size,

individual social rank, competition with neighboring social groups) to better address these questions.

In conclusion, this study demonstrates that yearling and three-year-old *P. verreauxi* experience a mechanical cost during locomotion, with increased magnitude and frequency of peak accelerations. This is not, however, reflected in measures of energy expenditure or time spent active, with no difference between yearlings and adults. Three-year-old animals had elevated energy expenditure and activity, but this is likely due to social behavior and demography as opposed to anatomical and/or biomechanical factors. Altogether, this suggests that juvenile *P. verreauxi* possess some mechanism to cope with their locomotor disadvantage which mitigates additional energetic cost in an exceptionally resource-stressed environment. Slow growth may provide a locomotor advantage (as well as helping to cope with limited resources), as maintaining a low body mass offsets the locomotor limitations associated with juvenility. Evolution of diverse life history patterns are driven by selective pressures acting across the life cycle. It is clear that an integrated understanding of ecology, behavior, demography, locomotion and biomechanics is critical to elucidating these pressures and how they act across the lifespan.



## Literature Cited

- Bezanson, M. (2009). Life history and locomotion in *Cebus capucinus* and *Alouatta palliata*. *American Journal of Physical Anthropology*, 140(3), 508–517. <https://doi.org/10.1002/ajpa.21099>
- Bezanson, M. (2017). Primate positional behavior development and evolution. *Annual Review of Anthropology*, 46, 279–298. <https://doi.org/10.1146/annurev-anthro-102116-041503>
- Bronikowski, A., Cords, M., Alberts, S., Altmann, J., Brockman, D., Fedigan, L., Pusey, A., Stoinski, T., Strier, K., & Morris, W. (2016). Female and male life tables for seven wild primate species. *Scientific Data*, 3, <https://doi.org/10.1038/sdata.2016.6>
- Carrier, D. R. (1996). Ontogenetic limits on locomotor performance. *Physiological and Biochemical Zoology*, 69(3), 467–488. <https://doi.org/10.1086/physzool.69.3.30164211>
- Demes, B., & Günther, M. (1989). Biomechanics and allometric scaling in primate locomotion and morphology. *Folia Primatologica*, 53, 125–141.
- Demes, B., Jungers, W. L., Fleagle, J. G., Wunderlich, R. E., Richmond, B. G., & Lemelin, P. (1996). Body size and leaping kinematics in Malagasy vertical clingers and leapers. *Journal of Human Evolution*, 31, 367–388.
- Dewar, R. E., & Richard, A. F. (2007). Evolution in the hypervariable environment of Madagascar. *Proceedings of the National Academy of Sciences of the United States of America*, 104(34), 13723–13727. <https://doi.org/10.1073/pnas.0704346104>
- Doran, D. M. (1997). Ontogeny of locomotion in mountain gorillas and chimpanzees. *Journal of Human Evolution*, 32(4), 323–344. <https://doi.org/10.1006/jhev.1996.0095>
- Dunham, A., Erhart, E., & Wright, P. (2011). Global climate cycles and cyclones: consequences for rainfall patterns and lemur reproduction in southeastern Madagascar. *Global Change Biology*, 17(1), 219–227. <https://doi.org/10.1111/j.1365-2486.2010.02205.x>
- Eaglen, R. H., & Boskoff, K. J. (1978). The birth and early development of a captive sifaka, *Propithecus verreauxi coquereli*. *Folia Primatologica*, 30(3), 206–219. <https://doi.org/10.1159/000155864>
- Fleagle, J. G. (1999). Primate evolution and adaptation. *Acad. Press San Diego CA*.
- Fulton, B. (2023). *Behayve* mobile app V3.1
- Gebo, D. L. (1985). The nature of the primate grasping foot. *American Journal of Physical Anthropology*, 67, 269–277.
- Gebo, D.L., & Dagosto, M. (1988). Foot anatomy, climbing, and the origin of the Indriidae. *Journal of Human Evolution*, 17(1), 135–154.
- Geissler, C.A., Dzumbira, T.M.O., & Noor, M.I. (1986). Validation of a field technique for the measurement of energy expenditure: Factorial method versus continuous respirometry. *American Journal of Clinical Nutrition*, 44(5), 596–602. <https://doi.org/10.1093/ajcn/44.5.596>
- Gleiss, A. C., Wilson, R. P., & Shepard, E. L. C. (2011). Making overall dynamic body acceleration work: On the theory of acceleration as a proxy for energy expenditure. *Methods in Ecology and Evolution*, 2(1), 23–33. <https://doi.org/10.1111/j.2041-210X.2010.00057.x>

- Godfrey, L. R., Samonds, K. E., Jungers, W. L., Sutherland, M. R., & Irwin, M. T. (2004). Ontogenetic correlates of diet in Malagasy lemurs. *American Journal of Physical Anthropology*, 123(3), 250–276. <https://doi.org/10.1002/ajpa.10315>
- Grand, T. I. (1992). Altricial and precocial mammals: A model of neural and muscular development. *Zoo Biology*, 11(1), 3–15. <https://doi.org/10.1002/zoo.1430110103>
- Gray, B. T., & Prince, H. H. (1988). Basal metabolism and energetic cost of thermoregulation in wild turkeys. *The Journal of Wildlife Management*, 52(1), 133–137. <https://doi.org/10.2307/3801073>
- Grémillet, D., Lescroël, A., Ballard, G., Dugger, K. M., Massaro, M., Porzig, E. L., & Ainley, D. G. (2018). Energetic fitness: Field metabolic rates assessed via 3D accelerometry complement conventional fitness metrics. *Functional Ecology*, 32(5), 1203–1213. <https://doi.org/10.1111/1365-2435.13074>
- Halsey, L. G., Shepard, E. L. C., Quintana, F., Gomez Laich, A., Green, J. A., & Wilson, R. P. (2009). The relationship between oxygen consumption and body acceleration in a range of species. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 152(2), 197–202. <https://doi.org/10.1016/J.CBPA.2008.09.021>
- Halsey, L. G., Shepard, E. L. C., & Wilson, R. P. (2011). Assessing the development and application of the accelerometry technique for estimating energy expenditure. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 158(3), 305–314. <https://doi.org/10.1016/J.CBPA.2010.09.002>
- Hurov, J. R. (1991). Rethinking primate locomotion: What can we learn from development? *Journal of Motor Behavior*, 23(3), 211–218. <https://doi.org/10.1080/00222895.1991.10118364>
- Husak, J. F., Ferguson, H. A., & Lovern, M. B. (2016). Trade-offs among locomotor performance, reproduction and immunity in lizards. *Functional Ecology*, 30, 1665–1674. <https://doi.org/10.1111/1365-2435.12653>
- Husak, J. F., & Lailvaux, J. P. (2022). Conserved and convergent mechanisms underlying performance – life-history trade-offs. *Journal of Experimental Biology*, 225. <https://doi.org/10.1242/jeb.243351>
- Jury, M. R., Parker, B. A., Raholijao, N., & Nasser, A. (1995). Variability of summer rainfall over Madagascar: Climatic determinants at interannual scales. *International Journal of Climatology*, 15 (12), 1323–1332, <https://doi.org/10.1002/joc.3370151203>
- Karasov, W. H. (1992). Daily energy expenditure and the cost of activity in mammals. *Integrative and Comparative Biology*, 32(2), 238–248. <https://doi.org/10.1093/icb/32.2.238>
- Kenagy, G. J., & Hoyt, D. F. (1989). Speed and time-energy budget for locomotion in golden-mantled ground squirrels. *Ecology*, 70(6), 1834–1839. <https://doi.org/10.2307/1938116>
- Lawler, R. R. (2006). Sifaka positional behavior: Ontogenetic and quantitative genetic approaches. *American Journal of Physical Anthropology*, 131, 261–271. <https://doi.org/10.1002/ajpa>
- Lawler, R. R., Caswell, H., Richard, A. F., Ratsirarson, J., Dewar, R. E., & Schwartz, M. (2009). Demography of Verreaux's sifaka in a stochastic rainfall environment. *Oecologia*, 161, 491–504. <https://doi.org/10.1007/s00442-009-1382-1>

- Leigh, S. R. (2004). Brain growth, life history, and cognition in primate and human evolution. *American Journal of Primatology*, 62(3), 139–164. <https://doi.org/10.1002/ajp.20012>
- Leonard, W. R., & Robertson, M. L. (1997). Comparative primate energetics and hominid evolution. *American Journal of Physical Anthropology*, 102(2), 265–281. [https://doi.org/10.1002/\(SICI\)1096-8644\(199702\)](https://doi.org/10.1002/(SICI)1096-8644(199702)102<265::AID-AJPA10202651003>3.0.CO;2-1)
- Lochmiller, R. L., & Deerenberg, C. (2000). Trade-offs in evolutionary immunology: just what is the cost of immunity? *Oikos*, 88(1), 87–98. <https://doi.org/10.1034/j.1600-0706.2000.880110.x>
- Main, R. P., & Biewener, A. A. (2006). In vivo bone strain and ontogenetic growth patterns in relation to life-history strategies and performance in two vertebrate taxa: Goats and Emu. *Physiological and Biochemical Zoology*, 79(1), 57–72. <https://doi.org/10.1086/498184>
- Main, R. P., & Biewener, A. A. (2007). Skeletal strain patterns and growth in the emu hindlimb during ontogeny. *Journal of Experimental Biology*, 210(15), 2676–2690. <https://doi.org/10.1242/jeb.004580>
- Malalaharivony, H.S., Kappeler, P.M. & Fichtel, C. (2021). Infant development and maternal care in wild Verreaux's Sifaka (*Propithecus verreauxi*). *International Journal of Primatology*, 42, 933–960. <https://doi.org/10.1007/s10764-021-00255-x>
- Muir, G. D. (2000). Early ontogeny of locomotor behavior: a comparison between altricial and precocial animals. *Brain Research Bulletin*, 53(5), 719–726. [https://doi.org/10.1016/S0361-9230\(00\)00404-4](https://doi.org/10.1016/S0361-9230(00)00404-4)
- Nagy, K.A. (1983). The doubly labeled water ( $\text{H}^3\text{H}^{18}\text{O}$ ) method: A guide to its use. *UCLA Publication*, 1–45.
- Napier, J. R., & Walker, A. C. (1967). Vertical clinging and leaping - A newly recognized category of locomotor behaviour of primates. *Folia Primatologica*, 6, 204–219. <https://doi.org/10.1159/000155079>
- Nilsson, A. L. K., Nilsson, J., & Alerstam, T. (2011) Basal metabolic rate and energetic cost of thermoregulation among migratory and resident blue tits. *Oikos*, 120, 1784–1789. <https://doi.org/10.1111/j.1600-0706.2011.19440.x>
- Oli, M. K. (2004). The fast-slow continuum and mammalian life-history patterns: an empirical evaluation. *Basic and Applied Ecology*, 5(5), 449–463. <https://doi.org/10.1016/j.baae.2004.06.002>
- Oxnard, C. E., German, R., Jouffroy, F. K., & Lessertisseur, J. (1981). A morphometric study of limb proportions in leaping prosimians. *American Journal of Physical Anthropology*, 54, 421–430.
- Qasem, L., Cardew, A., Wilson, A., Griffiths, I., Halsey, L. G., Shepard, E. L. C., Gleiss, A. C., & Wilson, R. (2012). Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? *PLoS ONE*, 7(2). <https://doi.org/10.1371/journal.pone.0031187>
- Ravosa, M. J., Meyers, D. M., & Glander, K. E. (1993). Relative growth of the limbs and trunk in sifakas: Heterochronic, ecological, and functional considerations. *American Journal of Physical Anthropology*, 92(4), 499–520. <https://doi.org/10.1002/ajpa.1330920408>

- Richard, A.F. (1976). Preliminary observations on the birth and development of *Propithecus verreauxi* to the age of six months. *Primates*, 17, 357-366. <https://doi.org/10.1007/BF02382791>
- Richard, A. F., Rakotomanga, P., Schwartz, M. (1993). Dispersal by *Propithecus verreauxi* at Beza Mahafaly, Madagascar:1984-1991. *American Journal of Primatology*, 30(1), 1-20. <https://doi.org/10.1002/ajp.1350300102>
- Richard, A.F., Dewar, R.E., Schwartz, M., & Ratsirarson, J. (2000). Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. *Journal of Human Evolution*, 39(4), 381-391. <https://doi.org/10.1006/jhev.2000.0427>
- Richard, A. F., Dewar, R. E., Schwartz, M., & Ratsirarson, J. (2002). Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). *Journal of Zoology*, 256(4), 421-436. <https://doi.org/10.1017/s0952836902000468>
- Speakman, J. R. (1998). The history and theory of the doubly labeled water technique. *American Journal of Clinical Nutrition*, 68(4), 932-938. <https://doi.org/10.1093/ajcn/68.4.932S>
- Stearns, S. (1989) Trade-offs in life-history evolution. *Functional Ecology*, 3(3), 259-268. <https://doi.org/10.2307/2389364>
- Stearns, S. (1992) *The Evolution of Life Histories*. Oxford University Press.
- Stearns, S. (2000) Life history evolution: successes, limitations, and prospects. *Naturwissenschaften*, 87(11), 476-486 <https://doi.org/10.1007/s001140050763>
- Sussman, R. W., Richard, A. F., Ratsirarson, J., Sauther, M. L., Brockman, D. K., Gould, L., Lawler, R. R., Cuzzo, F. P. (2011). In *Long-Term Field Studies of Primates* (pp. 45-66). Springer. [https://doi.org/10.1007/978-3-642-22514-7\\_3](https://doi.org/10.1007/978-3-642-22514-7_3)
- Wells, J. P., & Turnquist, J. E. (2001). Ontogeny of locomotion in rhesus macaques (*Macaca mulatta*): II Postural and locomotor behavior and habitat use in a free-ranging colony. *American Journal of Biological Anthropology*, 115(1), 80-94. <https://doi.org/10.1002/ajpa.1059>
- Westerterp, K. R., Brouns, F., Saris, W. H. M., & ten Hoor, F. (1988). Comparison of doubly labeled water with respirometry at low- and high-activity levels. *Journal of Applied Physiology*, 65(1), 53-56. <https://doi.org/10.1152/jappl.1988.65.1.53>
- Wilson, R. P., Börger, L., Holton, M. D., Scantlebury, D. M., Gómez-Laich, A., Quintana, F., Rosell, F., Graf, P. M., Williams, H., Gunner, R., Hopkins, L., Marks, N., Gerald, N. R., Duarte, C. M., Scott, R., Strano, M. S., Robotka, H., Eizaguirre, C., Fahlman, A., & Shepard, E. L. C. (2020). Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *Journal of Animal Ecology*, 89(1), 161-172. <https://doi.org/10.1111/1365-2656.13040>
- Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R., & Butler, P. J. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *Journal of Animal Ecology*, 75, 1081-1090. <https://doi.org/10.1111/j.1365-2656.2006.01127.x>
- Wolf, S. A. (2011). Ontogeny of postcranial morphology and locomotor behavior in *Propithecus verreauxi coquereli* and *Lemur catta*. Master's Thesis, James Madison University.

- Workman, C., & Covert, H. H. (2005). Learning the ropes: The ontogeny of locomotion in red-shanked douc (*Pygathrix nemaeus*), Delacour's (*Trachypithecus delacouri*), and Hatinh langurs (*Trachypithecus hatinhensis*) positional behavior. *American Journal of Physical Anthropology*, 128(2), 371–380. <https://doi.org/10.1002/ajpa.20205>
- Wright, P. C. (1999). Lemur traits and Madagascar ecology: Coping with an island environment. *American Journal of Physical Anthropology*, 110(S29), 31-72. [https://doi.org/10.1002/\(SICI\)1096-8644\(1999\)110:29+%3C31::AID-AJPA3%3E3.0.CO;2-0](https://doi.org/10.1002/(SICI)1096-8644(1999)110:29+%3C31::AID-AJPA3%3E3.0.CO;2-0)
- Wunderlich, R. E., & Schaum, J. C. (2007). Kinematics of bipedalism in *Propithecus verreauxi*. *Journal of Zoology*, 272(2), 165–175. <https://doi.org/10.1111/j.1469-7998.2006.00253.x>
- Wunderlich, R. E., Lawler, R. R., & Williams, A. E. (2011). Field and experimental approaches to the study of locomotor ontogeny in *Propithecus verreauxi*. In *Primate Locomotion* (pp.135–154). Springer. [https://doi.org/10.1007/978-1-4419-1420-0\\_8](https://doi.org/10.1007/978-1-4419-1420-0_8)
- Yoda, K., Naito, Y., Sato, K., Takahashi, A., Nishikawa, J., Ropert-Coudert, Y., Kurita, M., & le Maho, Y. (2001). A new technique for monitoring the behaviour of free-ranging Adélie penguins. *Journal of Experimental Biology*, 204(4), 685–690. <https://doi.org/10.1242/jeb.204.4.685>
- Young, J. W., & Shapiro, L. J. (2018). Developments in development: What have we learned from primate locomotor ontogeny? *American Journal of Biological Anthropology*, 165(S65), 37-71. <https://doi.org/10.1002/ajpa.23388>
- Zera, A. J., & Harshman, L. G. (2001). The physiology of life history trade-offs in animals. *Annual Review of Ecology and Systematics*, 32(1), 95-126. <https://doi.org/10.1146/annurev.ecolsys.32.081501.114006>

## Chapter 2: Physical aging in free-ranging captive sifaka (*Propithecus coquereli*)

### **Abstract**

*Propithecus* are particularly slow-developing strepsirrhine primates with long lifespans for their body size and little to no post-reproductive lifespan. Physical senescence, or age-related loss of locomotor performance, has been measured in humans and some primate species. Little is known about the degree to which this pattern of physical aging is conserved across primates or specific to certain species. *Propithecus* are highly arboreal, and vertical clinging and leaping comprise a large portion of their locomotor repertoire. Previous laboratory studies have suggested that sifaka exhibit few signs of physical senescence. In order to investigate further potential evidence for physical aging in *Propithecus*, I measured percent time active/resting, energy expenditure due to movement (as overall dynamic body acceleration, ODBA), and peak accelerations in 15 free-ranging captive *Propithecus coquereli*, aged 4–25 years, using lightweight inertial sensors. When free-ranging in natural habitat enclosures, the oldest age category (18+) *Propithecus* exhibited significantly lower active time, lower ODBA, and lower frequency of peak accelerations than adults. However, mean peak acceleration magnitude was not decreased in old animals. Contrary to previous studies finding only subtle gait changes during aging in *Propithecus*, these results indicate a pattern of age-related physical senescence in captive sifakas, especially in natural habitat environments, though old sifaka do not avoid/reduce peak musculoskeletal load. This suggests that old sifaka are under selective pressure to maintain peak locomotor performance, though old individuals move less frequently compared to younger adults.

## Introduction

Senescence, or age-related physical deterioration, can be measured at many biological scales, from cellular to population-level (Finch 1990; Rose 1991). Proximate physiological mechanisms of aging, such as accumulated molecular damage, oxidative stress, or telomeric shortening, are often measured at smaller scales (Partridge & Gems 2002; Kenyon 2005). On the contrary, broad evolutionary theories concerning senescence are often developed from demographic studies measuring age-related change in mortality rates or reproductive success in a population (e.g., Rose 1991; Austad 1993). It is generally thought that age-related deterioration arises evolutionarily because selective pressure favoring somatic maintenance and repair, as well as negative selection against deleterious alleles, is greatest through early adulthood and “relaxes” after individuals have reproduced (Williams 1957; Hamilton 1966).

Though most mammals are reproductively active until death, there is evidence of physical senescence in the form of age-related declines in reproductive success and increased age-specific mortality (Hamilton 1966; Pavelka & Fedigan 1991; Austad 1993; Nussey *et al.* 2013). Individual reproductive success tends to follow a plateau-shaped curve, with an increase in offspring survival through early adulthood leveling off in a period of relatively high success (“prime” reproductive age), followed by a decline in advanced age (Dugdale *et al.* 2011; Hayward *et al.* 2013; Campos *et al.* 2022). Though declining reproductive success is a standard measure of physical senescence, the underlying causes or mechanisms leading to a reduction in fertility, as well as how these differ among species, are not as well-understood (Moorad & Nussey 2016; Campos *et al.* 2022).

One important aspect of physical aging is the loss of locomotor performance associated in part with a decline in muscle mass and strength, known as sarcopenia and dynapenia, respectively (Mitchell *et al.* 2012; McGregor *et al.* 2014). Locomotion is essential to foraging, reproduction, and avoiding predation in wild animals, thus loss of locomotor function likely increases mortality risk. Age-related decline in locomotor performance has been studied extensively in humans (e.g., Odding *et al.* 2001; Kulmala *et al.* 2014; Bohm *et al.* 2015), though there is growing interest in this phenomenon in other species (Ingram 2000; Nussey *et al.* 2013; Marck *et al.* 2017). In humans, locomotor aging manifests as reductions in walking speed, range of motion, peak ground reaction forces, stride length, and overall activity, as well as an increased risk of falling (Murray *et al.* 1969; Gabel & Nayak 1984; Yamada *et al.* 1988). Marck and colleagues (2017), measuring locomotor velocity and activity levels, demonstrated similar patterns of locomotor senescence in species spanning orders of magnitude in body size and longevity, from *C. elegans* to humans and horses. This suggests that, despite generally lacking post-reproductive lifespans, some non-human animals do experience physical senescence which can be measured as a decline in locomotor performance with age.

### *Senescence in primates*

Among mammals, primates generally have extended lifespans and reproductive “careers” (relative to body size) compared to other clades, though there is considerable interspecific variation (Charnov & Berrigan 1993; Alberts *et al.* 2013; Campos *et al.* 2022). The slow life history of primates, especially their abnormally long lifespan relative to body mass, makes them interesting subjects for the study of senescence both in wild populations and under laboratory conditions. Some non-human primate species are used as aging models



due to their phylogenetic proximity and physiological similarity to humans (Black & Lane 2002; Colman *et al.* 2005; Ruff *et al.* 2020), sharing many age-related diseases with our species such as arthritis (Carlson *et al.* 1996; Rothschild *et al.* 1997), neurodegenerative disease (Bons *et al.* 2006), and cardiovascular disease (Brady *et al.* 2003). While useful for modeling human aging, only a few species, e.g., macaques (*Macaca* sp.) and more recently the gray mouse lemur (*Microcebus murinus*), are widely used as primate models in the study of senescence (Fischer & Austad 2011; Didier *et al.* 2016; Colman 2018).

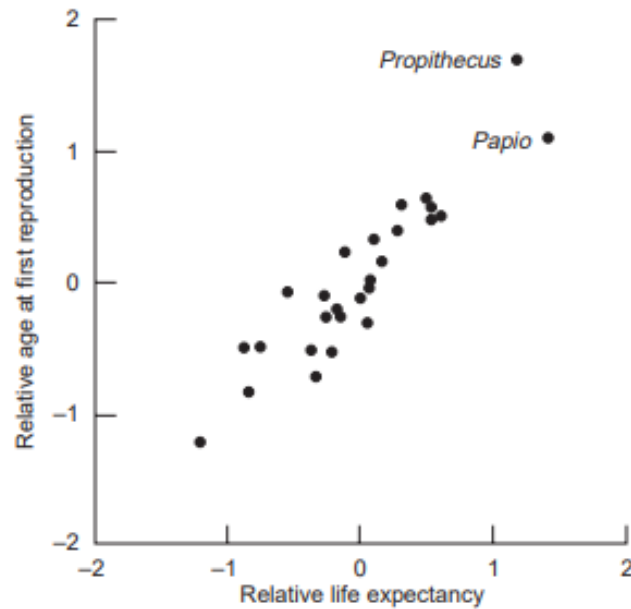
Because the vast majority of primates are not a focus of aging research, the degree to which patterns of senescence are conserved among the diverse primate order is relatively poorly understood (Campos *et al.* 2022). For example, non-human hominids are thought to undergo relatively little osteoarthritis, though bonobos exhibit increased rates compared to other representatives (chimpanzees, gorillas, orangutans; Lovell 1990; Jurmain 2000). Additionally, prevalence of osteoarthritis in cercopithecine monkeys seems to be much higher than in hominids, though these data are likely biased as there is an effect of captivity on osteoarthritis rate (Rothschild & Woods 1992, Rothschild 1993). Additionally, nearly every study of age-related sarcopenia in primates is done on captive rhesus macaques (e.g., Colman *et al.* 2005, 2008; McKiernan *et al.* 2009; Pugh *et al.* 2013).

Study and comparison of physical aging among non-human primates, including age-related changes in locomotor performance, may elucidate the evolutionary history and associated selective pressures which shape their remarkable life histories (Fischer & Austad 2011; Madimenos 2015; Ruff *et al.* 2020). Whether a trait is widely conserved or

unique to more specific clades could potentially shed light on when or how that trait evolved. While broad comparative studies may be very powerful, investigations of this nature require large amounts of baseline information across a wide range of species, much of which remains undiscovered (Ruff *et al.* 2020; Campos *et al.* 2022). Before thorough comparisons of physical senescence can be drawn among primates, we must obtain information on patterns of aging from a diversity of primate species.

### *Propithecus* life history

Among mammals, *Propithecus* life history is exceptionally slow for their body size (Figure 2.1; Richard *et al.* 2002). Individual longevity has been recorded up to 33 years in the wild, and a separate study found that *Propithecus verreauxi* females were reproductively active until nearly 30, though infant survival begins to decrease around age 20 (Richard *et al.* 2002; Bronikowski *et al.* 2016). In captivity, female *P. coquereli* have lived up to 25 years, and are reproductively active until age 22 (Zehr *et al.* 2014). This suggests a general lack of post-reproductive lifespans in *Propithecus*. When controlling for body mass, *Propithecus* females have a later median age at first and last reproduction compared to several other primate populations including representatives of the apes and neo- and paleotropical monkeys (Richard *et al.* 2002). Age-specific mortality in *Propithecus* is slightly sexually dimorphic, with young adult females (age 1-10) experiencing greater mortality than males, and older males (age 12+) experiencing greater mortality than females (Richard *et al.* 2002). In both sexes, there is a general increase in mortality beginning at approximately 18 years (Richard *et al.* 2002).



**Figure 2.1** Relative life expectancy & age at first reproduction in select mammals. Effect of body mass is controlled for using regression of log-transformed values. From Richard *et al.* 2002.

*Propithecus* (and all lemur species) are endemic to Madagascar, which undergoes oscillating wet and dry seasons, with highly variable year-to-year rainfall (Jury *et al.* 1995). The “slow” life history of *Propithecus* may be attributed to the highly stochastic intra- and inter-annual food availability that results from this climatic variability (Wright 1999; Dewar & Richard 2007; Dunham *et al.* 2011). The differential inter-annual likelihood of successfully reproducing leads to a tradeoff sacrificing investment in single reproductive events in favor of a greater number of total reproductive attempts, described as “bet-hedging” (Stearns 1992; Richard *et al.* 2002). *Propithecus* reproductive success in a given year is not particularly likely, which may lead to positive selection for an extended lifespan and reproductive career (Wright 1999; Richard *et al.* 2002; Lawler *et al.* 2009).

*Physical senescence in Propithecus coquereli*

With respect to senescence, *Propithecus* is relatively understudied and the information that does exist pertains to population-based demographic parameters such as reproductive success and mortality rates (e.g., Richard *et al.* 2002; Lawler *et al.* 2009). Data on physical senescence is nearly absent in this species (but see Snyder & Schmitt 2018). In addition to the need for these data for comparative primate studies and evolutionary analysis, it can be argued that *Propithecus* are candidate species for modeling human locomotor aging. *Propithecus* is one of very few primates to utilize a bipedal gait with sequenced footfall when moving terrestrially (“bipedal galloping”; Wunderlich & Schaum 2007; Snyder & Schmitt 2018). In a controlled (i.e., non-free-ranging) study analyzing gait, velocity, and ground reaction force during *P. coquereli* bipedal locomotion, Snyder & Schmitt (2018) found no reduction in peak ground reaction force and only slight reductions in velocity in old individuals. These findings indicate that *P. coquereli* may experience very little physical senescence leading to decline in locomotor performance. The fact that *Propithecus* (and most mammals) lack a significant post-reproductive lifespan may account for the weak evidence for physical senescence in *P. coquereli* compared to humans, as senescence is thought to result from waning selective pressure (Pavelka & Fedigan 1991; Richard *et al.* 2002; Snyder & Schmitt 2018).

Laboratory-based study of locomotor senescence may fail to account for naturalistic behavior and the “bigger picture” of physical aging in *Propithecus*. While the terrestrial bipedalism of *Propithecus* may be a useful model, the majority of travel bouts in their natural environment consist of vertical clinging-and-leaping, and they spend considerable time clambering and leaping during feeding (Napier & Walker 1967; Lawler 2006). Free-

ranging data may better elucidate the physical changes (or lack thereof) associated with aging in non-human primates. Naturalistic data also better lends itself to comparative studies among wild populations, which may lead to a better understanding of primate physical senescence and life history evolution. In this cross-sectional study, I aim to describe and compare metrics of locomotor mechanics and energetics typically associated with physical senescence, such as the magnitude and frequency of acceleration peaks produced, time spent active, and energy expenditure, between adult and aging individuals in a population of free-ranging *Propithecus coquereli*.

Because *Propithecus* lacks a significant post-reproductive lifespan, I hypothesize that **free-ranging *P. coquereli* will not exhibit significant age-related declines in locomotor performance**. This follows life history and evolutionary senescence theories, as well as a previous experimental study, which suggest that *Propithecus* has been under selection to maintain locomotor performance throughout the lifespan.

## Methods

### *Data collection*

All data were collected at the Duke Lemur Center, Durham NC, by researchers from James Madison and Duke Universities between 2017 and 2022. All procedures were approved by the Duke Institutional Animal Care & Use committee and the Duke Lemur Center research committee. 15 captive *P. coquereli* aged 4-25 years were instrumented while free-ranging in forested “natural habitat enclosures” (Table 2.1). These enclosures range in size from 0.65-5.79 hectares and allow for naturalistic locomotor behavior.

Detailed facility records allowed for exact aging of each subject. Accelerometer models used for data collection were Humotion accelerometers (Münster, Germany) from 2017-2018, Mbient MetaMotionS (San Francisco, USA) and ActivPAL 4 (Glasgow, UK) from 2020-2021, and TechnoSmart Axy 5 XS (Rome, Italy) in 2022. Sensors were configured to collect at 20-100hz dependent upon the model. 92 individual accelerometry sessions spanning 573.25 hours of reliable acceleration data were collected in total (Table 2.1).

### *Data processing*

Duration of individual data collection sessions ranged from ~15 minutes to 8 hours, but sessions less than one hour (generally a result of sensor error) were omitted from the dataset. Data were trimmed to the hours of 08:00-16:00 each day (the time during which the Duke Lemur Center is open for research activity). All measurements were converted from the sensor's native units to g's ( $1g = 9.8m/s^2$ ) for comparison. The metrics of interest derived from each accelerometry session were average magnitude of acceleration peaks, representing the highest acceleration applied during movement; frequency of acceleration peaks (greater than 3g's) per hour, approximately representing the frequency of leaps performed (see Figure 1.12); estimated time spent active; and average overall dynamic body acceleration (ODBA), a proxy for energy expenditure due to movement. The theory supporting the use of accelerometry and the methodology used in data processing is discussed in detail in Chapter 1.

**Table 2.1.** Age, sex, and duration of data collection per animal sampled.

<b>Age<sup>1</sup></b>	<b>ID</b>	<b>Sex</b>	<b>Age Class</b>	<b>Data Duration (hr)</b>	<b>Sensor Type</b>
4.17	Magdalena	F	Adult	54.25	ActivPAL
4.53	Furia	F	Adult	3.5	Mbient
5.79-6.44	Lupi	F	Adult	33.75	Mbient/ActivPAL
7.41	Gertrude	F	Adult	62.25	ActivPAL
7.86	Beatrice	F	Adult	44.75	ActivPAL
8.39	Ferdinand	M	Adult	71.25	ActivPAL
9.39	Remus	M	Adult	53	ActivPAL
9.56	Martin	M	Adult	3.75	Humotion
9.69	Thrax	M	Adult	4.75	Mbient
10.03-14.85	Rodelinda	F	Adult	37.75	Humotion/TechnoSmart
10.39	Bertha	F	Adult	77.75	ActivPAL
13.45	Pompeia	F	Adult	45	TechnoSmart
16.67	Marcus	M	Adult	3.5	ActivPAL
24.36-24.47	Julian	M	Old Adult	7	Humotion
25.53	Gordian	M	Old Adult	71	ActivPAL

<sup>1</sup>A range of ages is given if data were collected at multiple timepoints on the same individual

### *Data analysis*

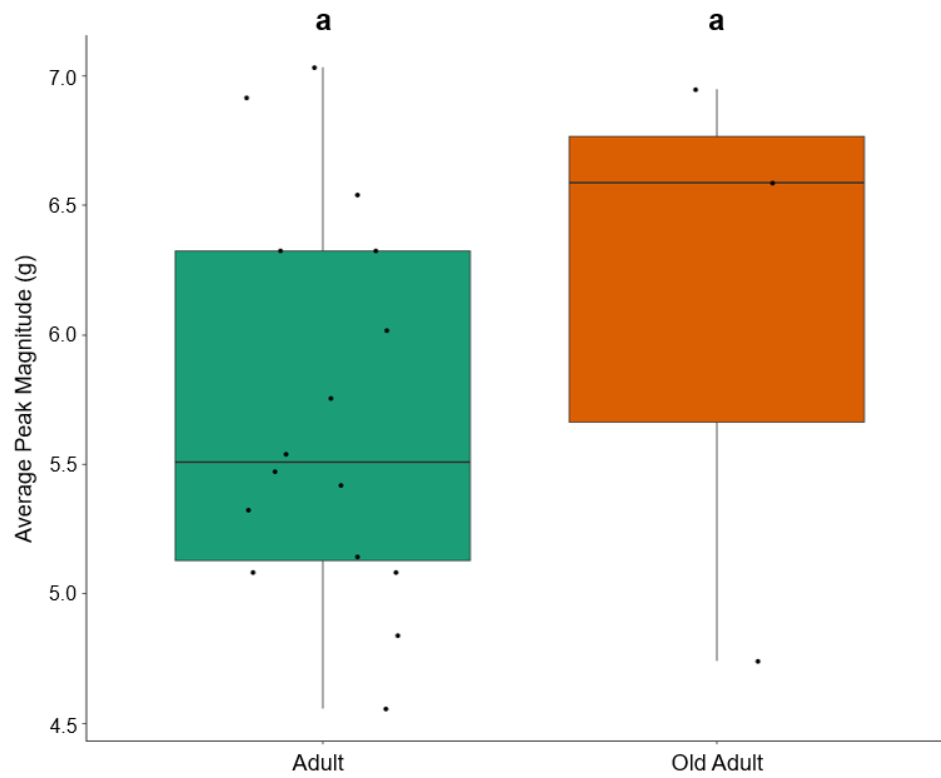
For a subset of analyses, animals were binned in the following age classes: Adult – age 4-17; Old Adult – age 18+. The Adult delineation was made because 4 is approximately the onset of sexual maturity in *Propithecus* (Richard *et al.* 2002; Lawler 2006). The Adult - Old Adult delineation was made due to the increase in age-specific mortality at age 18 (Richard *et al.* 2002) and follows the methodology of Snyder & Schmitt (2018). All statistical analyses were done in RStudio (RStudio, Boston MA). Linear regression was used to compare locomotor metrics across continuous age, while ANOVA or Kruskal-Wallis tests (dependent upon variable normality) were used to compare among binned age classes.

## **Results**

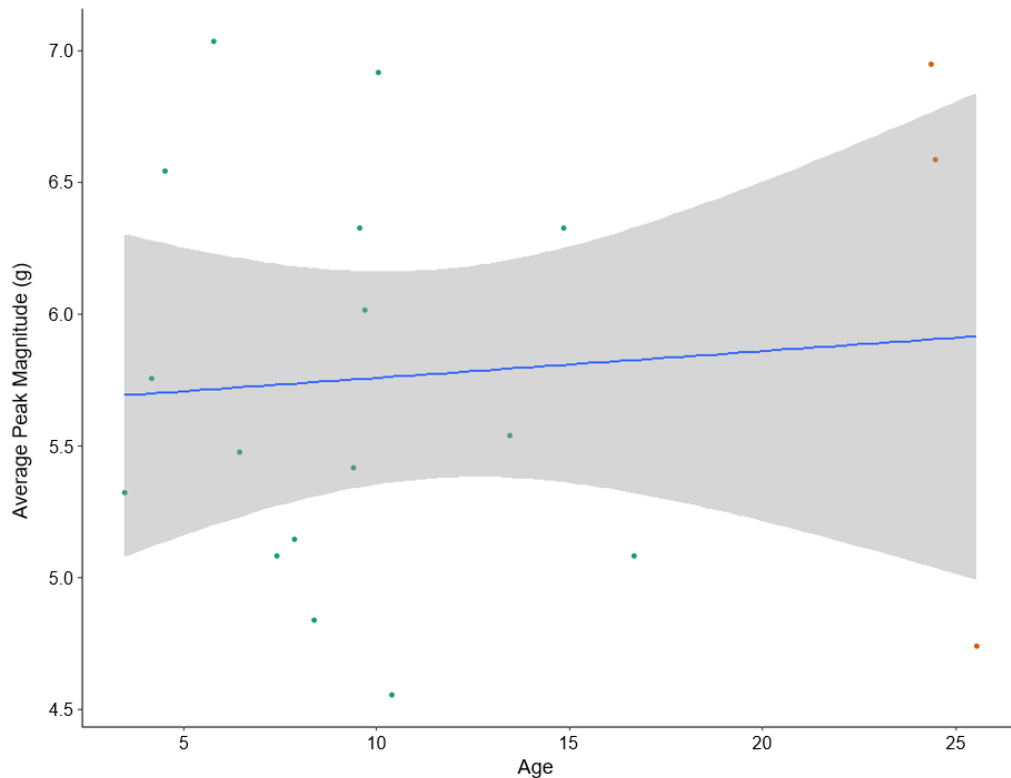
### *Acceleration peaks*

The magnitude of acceleration peaks, representing the highest acceleration produced during a bout of locomotion, seem to decrease slightly with increasing age. When comparing binned age classes, old adult peak magnitudes were not significantly different from adults ( $p=0.64$ ; Figure 2.2). Linear regression analysis using continuous age did not indicate a significant relationship with average peak magnitudes ( $p=0.72$ ;  $R^2 = -0.05$ ; Figure 2.3).



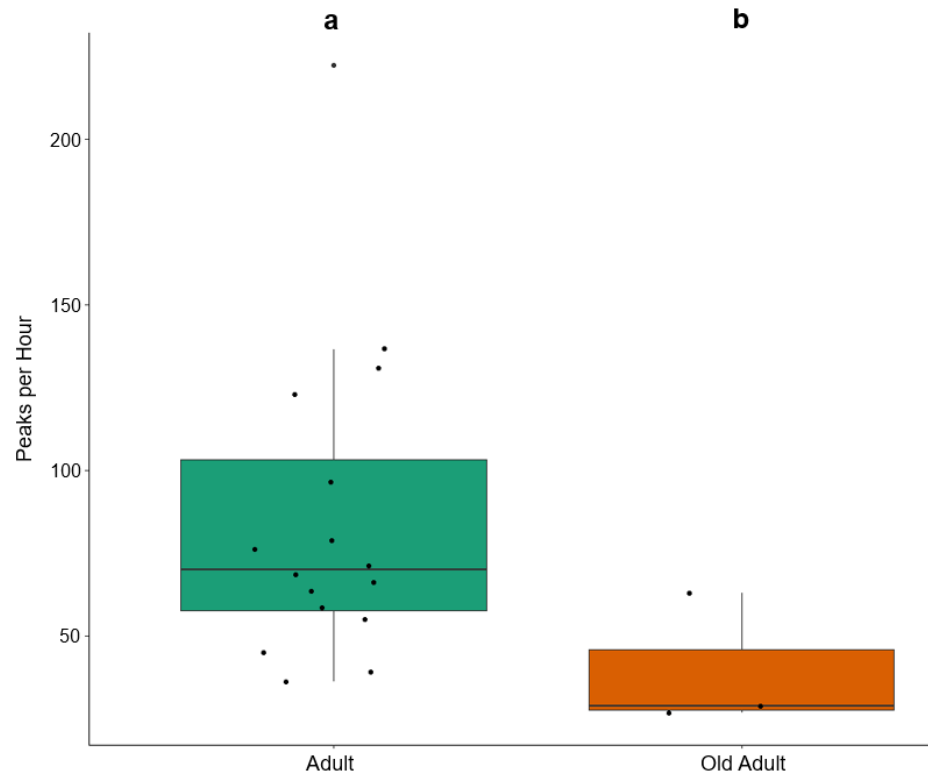


**Figure 2.2.** Average magnitude of acceleration peaks  $>3g$ , representing the highest acceleration an animal produces, does not significantly decrease with age ( $p=0.64$ ). Individual points represent the average magnitude for each individual. Lowercase letters indicate significance at  $\alpha = 0.05$ .

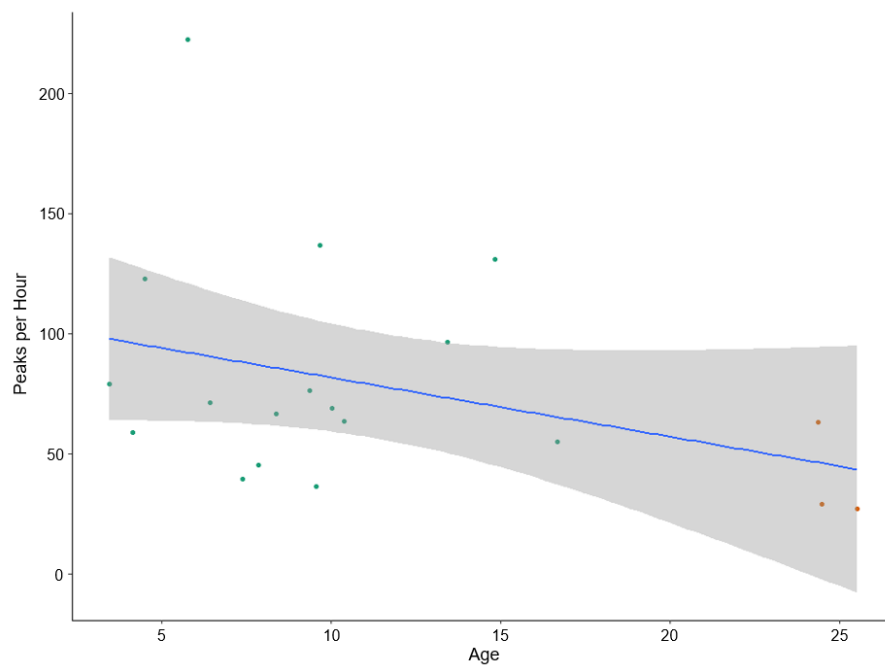


**Figure 2.3.** Regression analysis indicates no significant negative relationship between average magnitude of acceleration peaks and age ( $p=0.72$ ;  $R^2=-0.05$ ). Shaded region indicates a 95% confidence interval. Individual points represent peak magnitudes averaged per individual.

The frequency of acceleration peaks per hour, a predictor of the number of leaps performed, was lower in old adult animals compared to adults ( $p=0.03$ ; Figure 2.4). There was, however, no significant relationship between age and peak frequency in linear regression analysis ( $p=0.13$ ;  $R^2=0.08$ ; Figure 2.5).



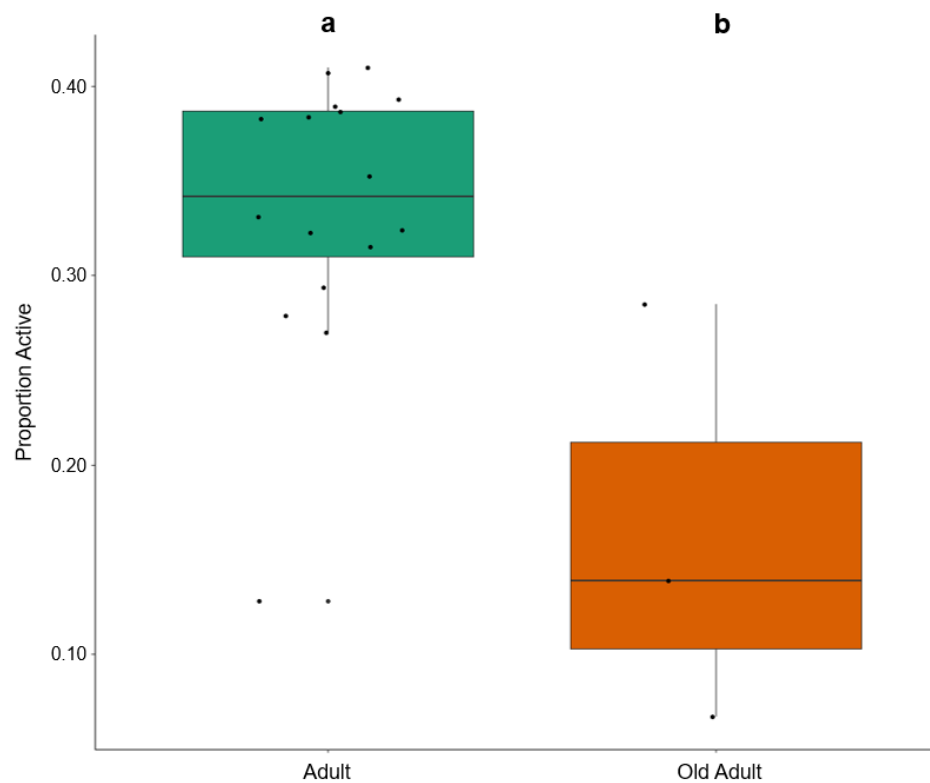
**Figure 2.4.** Peak frequency is significantly lower in *P. coquereli* individuals >18 years old. Letters indicate significance at  $\alpha = 0.05$ .



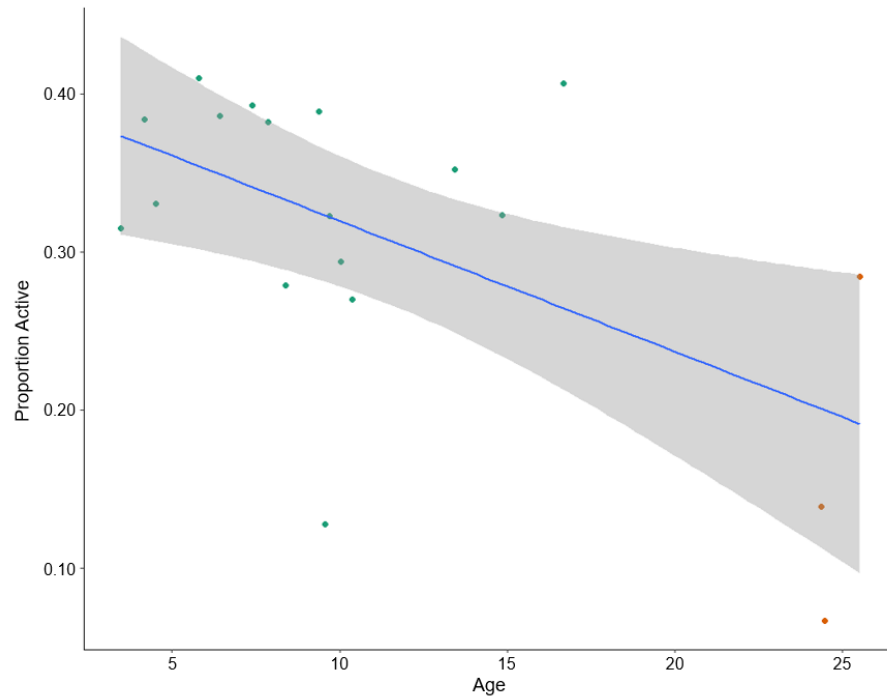
**Figure 2.5.** Frequency of acceleration peaks did not have a significant relationship with age ( $p=0.13$ ;  $R^2=0.08$ ). Shaded region represents 95% CI.

### *Activity & energy expenditure*

Activity time and energy expenditure showed very similar patterns to one another, though not identical. Activity times were decreased in the old adult age class compared to adults ( $p=0.02$ ; Figure 2.6). Linear regression again indicated a significant, somewhat weak negative relationship between age and time spent active ( $p=0.01$ ;  $R^2=0.29$ ; Figure 2.7).

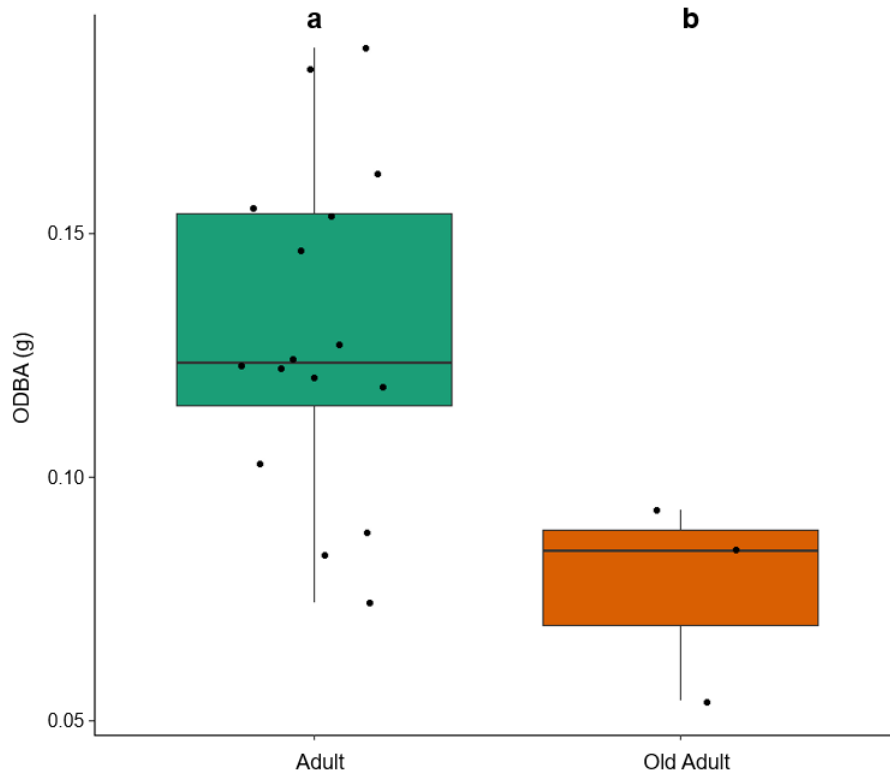


**Figure 2.6.** Time spent active is lower in old adults compared to adults ( $p=0.02$ ).

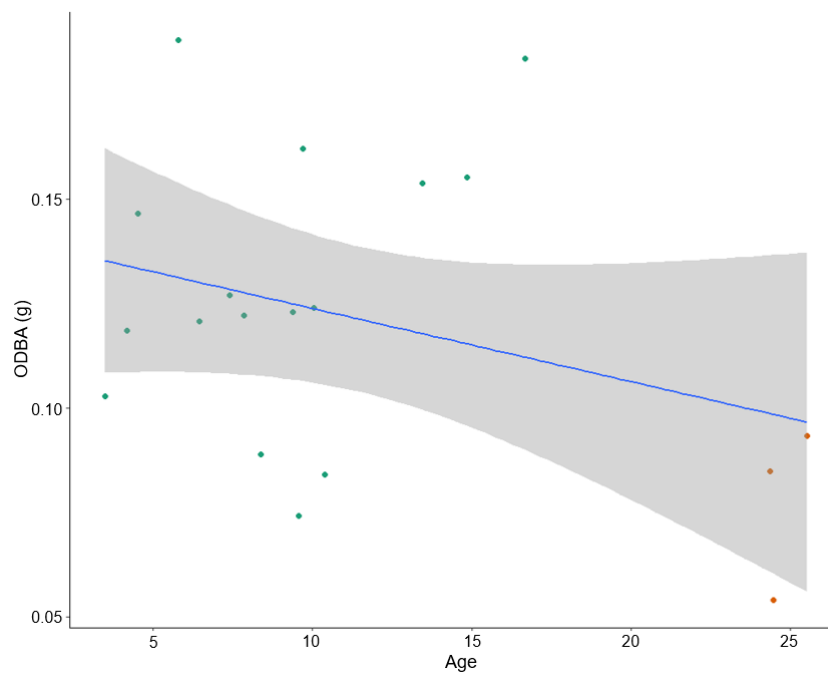


**Figure 2.7.** Increasing age is significantly related to a decline in time spent active ( $p=0.01$ ;  $R^2=0.29$ ). Shaded region represents 95% CI.

Energy expenditure due to movement, as average overall dynamic body acceleration (ODBA), was again significantly lower in the old adult age class compared to adults ( $p=0.02$ ; Figure 2.8). When analyzed using a continuous age variable, energy expenditure differs from activity time in that there is no significant relationship between age and energy expenditure ( $p=0.173$ ;  $R^2=0.054$ ; Figure 2.9).



**Figure 2.8.** Energy expenditure, as ODBA, is decreased in old adults ( $p=0.02$ ).



**Figure 2.9.** Linear regression analysis indicates no relationship between increasing age and energy expenditure due to movement ( $p=0.173$ ;  $R^2=0.054$ ). Shaded region represents 95% CI.

## Discussion

*Propithecus coquereli* have disproportionately long lifespans and reproductive careers for their body size (Richard *et al.* 2002). This species exhibits some degree of reproductive senescence, but despite reproductive success decreasing with age, females are sexually active nearly until death (Richard *et al.* 2002; Bronikowski *et al.* 2016). Reproducing throughout the lifespan may lead to selective pressure favoring the maintenance of locomotor performance, thus suppressing the manifestation of significant age-related declines in locomotor ability (Hamilton 1966; Pavelka & Fedigan 1991; Snyder & Schmitt 2018). The limited research to date concerning physical senescence in *P. coquereli* indicated very slight, if any, age-related decreases in locomotor performance, evidenced by a lack of reduction in peak ground reaction force and only slight reduction in velocity (Snyder & Schmitt 2018).

Analysis of biomechanical and energetic metrics of locomotor performance, collected in a naturalistic free-ranging environment, provided mixed results and altogether weak but significant evidence for physical aging in *P. coquereli*. Average magnitude of acceleration peaks, which represents the maximum acceleration applied during locomotion, did not significantly decrease with age both in analysis of binned age class and regression over continuous age. These results corroborate laboratory-based findings (Snyder & Schmitt 2018), suggesting that data from a controlled study may in some cases be applied to free-ranging animals. This may indicate a lack of (or very slight) muscular senescence in older individuals that would cause a decrease in the peak acceleration they are capable of producing *during locomotion*. Human locomotor aging is characterized by a reduction of peak ground reaction forces, reducing impact on the musculoskeletal

system (Yamada *et al.* 1988). Because *P. coquereli* peak accelerations occur at both takeoff and landing during leaps, this also suggests that old sifaka are not avoiding impacts (when landing) on their musculoskeletal system. However, the frequency of peaks, which has been validated to predict number of leaps performed, was significantly lower in older individuals. While this could indicate a decrease in overall locomotor ability, it could also reflect a behavioral down-regulation in old animals which may or may not relate directly to physical performance. When using continuous age as opposed to binning age classes, frequency of acceleration peaks did not significantly decrease with age. This may indicate a more threshold-based relationship as opposed to a continuous decline with age. It seems that if physical senescence affecting *P. coquereli* locomotor biomechanics is occurring, it is to a limited degree.

In analysis of binned adult vs old age classes, time spent active was lower in old animals. Activity time is used in other species as a measure of physical senescence, and though decreased activity may be due to a slight decline in locomotor ability, it could also be attributed to non-physiological behavior in which old animals simply move less often than younger animals. One potential explanation unrelated to physiology is that old animals are likely at the top of their group's social hierarchy, needing to move less often when feeding or finding a resting location. This effect, however, is likely weakened or absent in captivity. The relationship between age and activity was again significant but somewhat weak, leading to the conclusion that other factors aside from age alone may impact activity levels. Energy expenditure due to movement, measured by proxy as ODBA, showed a similar pattern to activity time when binning age classes. Old individuals spent less energy during movement than adults, which may indicate some



degree of physical aging. Energy expenditure differed from activity time in that linear regression indicated the lack of a significant relationship between age and ODBA.

Energy expenditure, like activity, is influenced by many physical and non-physical factors, making straightforward interpretation of these results difficult.

Some notable limitations of this study are that the sample structure is considerably unbalanced, and data were collected over a wide time span on different models of accelerometer. Much of the data collected are concentrated on adult animals from 4-17 years old. This is largely a matter of convenience, as the majority of animals at the Duke Lemur Center fall within the adult age range, and older animals sometimes have limitations on when they can be handled for instrumentation and/or free-ranged. There is also a concentration of sampling intensity on a few of the individuals within this sample, with several individuals accounting for ~3-8 hours of data each and others surpassing 50 or up to 80 hours in the most extreme example. Additionally, while care was taken to make acceleration data from various sensor models as standardized as possible, there is likely still some inherent variation due to hardware differences specific to each model.

Future work would benefit from a direct focus on evenly sampling across ages and standardizing the duration and mode of data collection as much as possible. Sampling each age category with similar intensity would better determine whether differences are due to inter-individual variability or truly a reflection of physical senescence. Similarly, standardizing the duration of collection (e.g., over one 8-hour day) would make for better comparisons as each session represents a similar temporal span. In addition, thorough and consistent behavioral data may help to better distinguish the effects of physiology, behavior, or social group dynamics.

Despite its limitations, this study is among the first to provide evidence of physical senescence in *Propithecus coquereli*, though weak in many cases. Previous laboratory-based work (Snyder & Schmitt 2018), as well as the present study, suggest that peak force/accelerations do not decrease with age. This is likely due to the need to produce sufficient locomotor force and sustain the subsequent impacts involved in performing the leaps necessary for VCL locomotion. With respect to the number and frequency of locomotor impacts and overall activity, it appears that there is some degree of “slowing down” among older individuals. It cannot, however, be ruled out that this is (at least in part) due to non-physiological factors. Aging *P. coquereli* individuals, though reproductively active for the entire lifespan, may be subjected to somewhat weakened selective pressure to maintain locomotor function in advanced age. This may lead to slight declines in performance, which is supported by the fact that reproduction is attempted but with considerably reduced success when individuals surpass age ~20 (Richard *et al.* 2002). Contrary to the prediction that *P. coquereli* does not undergo detectable physical aging, the results presented herein suggest that *P. coquereli* does experience locomotor senescence, though to a relatively small degree. This work provides a baseline for further aging research within *Propithecus*, as well as a preliminary dataset for comparison among other primate species.

## Literature Cited

- Alberts, S. C., Altmann, J., Brockman, D., & Bronikowski, A. (2013). Reproductive aging patterns in primates reveal that humans are distinct. *Proceedings of the National Academy of Sciences*, 110 (33), 13440-13445, <https://doi.org/10.1073/pnas.1311857110>
- Austad, S. N. (1993). Retarded senescence in an insular population of Virginia opossums (*Didelphis virginiana*). *Journal of Zoology*, 229 (4), 695-708, <https://doi.org/10.1111/j.1469-7998.1993.tb02665.x>
- Black, A. & Lane, M. A. (2002). Nonhuman primate models of skeletal and reproductive aging. *Gerontology*, 48, 72-80, <https://doi.org/10.1159/000048930>
- Bohm, S., Mademli, L., Mersmann, F., & Arampatzis, A. (2015). Predictive and reactive locomotor adaptability in healthy elderly: A systematic review and meta-analysis. *Sports Medicine*, 45, 1759-1777, <https://doi.org/10.1007/s40279-015-0413-9>
- Bons, N., Rieger, F., Prudhomme, D., Fisher, A., & Krause, K. H. (2006). *Microcebus murinus*: a useful primate model for human cerebral aging and Alzheimer's disease? *Genes, Brain, and Behavior*, 5 (2), 120-130, <https://doi.org/10.1111/j.1601-183X.2005.00149.x>
- Brady, A. G., Watford, J. W., Massey, C. V., Rodning, K. J., Gibson, S. V., Williams, L. E., & Abee, C. R. (2003). Studies of heart disease and failure in aged female squirrel monkeys (*Saimiri* sp.). *Comparative Medicine*, 53 (6), 657-662.
- Bronikowski, A., Cords, M., Alberts, S., Altmann, J., Brockman, D., Fedigan, L., Pusey, A., Stoinski, T., Strier, K., & Morris, W. (2016). Female and male life tables for seven wild primate species. *Scientific Data*, 3, <https://doi.org/10.1038/sdata.2016.6>
- Campos, F. A., Altmann, J., Cords, M., & Alberts, S. C. (2022). Female reproductive aging in seven primate species: Patterns and consequences. *Proceedings of the National Academy of Sciences*, 119 (20), e2117669119, <https://doi.org/10.1073/pnas.2117669119>
- Carlson, C. S., Loeser, R. F., Purser, C. B., Gardin, J. F., & Jerome, C. P. (1996). Osteoarthritis in cynomolgus macaques III: Effects of age, gender, and subchondral bone thickness on the severity of disease. *Journal of Bone and Mineral Research*, 11 (9), 1209-1217, <https://doi.org/10.1002/jbmr.5650110904>
- Charnov, E. L. & Berrigan, D. (1993). Why do female primates have such long lifespans and so few babies? or Life in the slow lane. *Evolutionary Anthropology*, 1 (6), 191-194, <https://doi.org/10.1002/evan.1360010604>
- Colman, R. J., McKiernan, S. H., Aiken, J. M., & Weindruch, R. (2005). Muscle mass loss in Rhesus monkeys: Age of onset. *Experimental Gerontology*, 40 (7), 573-581, <https://doi.org/10.1016/j.exger.2005.05.001>
- Colman, R. J., Beasley, T. M., Allison, D. B., & Weindruch, R. (2008). Attenuation of sarcopenia by dietary restriction in Rhesus monkeys. *The Journals of Gerontology: Series A*, 63 (6), 556-559, <https://doi.org/10.1093/gerona/63.6.556>
- Colman, R. J. (2018). Non-human primates as a model for aging. *Biochimica et Biophysica Acta (BBA) – Molecular Basis of Disease*, 1864 (9), 2733-2741, <https://doi.org/10.1016/j.bbadis.2017.07.008>

- Dewar, R. E., & Richard, A. F. (2007). Evolution in the hypervariable environment of Madagascar. *Proceedings of the National Academy of Sciences of the United States of America*, 104(34), 13723-13727. <https://doi.org/10.1073/pnas.0704346104>
- Didier, E. S., MacLean, A. G., Mohan, M., Didier, P. J., Lackner, A. A., & Kuroda, M. J. (2016). Contributions of nonhuman primates to research on aging. *Veterinary Pathology*, 53 (2), 277-290, DOI:10.1177/0300985815622974
- Dugdale, H. L., Pope, L. C., Newman, C., Macdonald, D. W., & Burke, T. (2011) Age-specific breeding success in a wild mammalian population: selection, constraint, restraint, and senescence. *Molecular Ecology*, 20 (15), 3261-3274, <https://doi.org/10.1111/j.1365-294X.2011.05167.x>
- Dunham, A., Erhart, E., & Wright, P. (2011). Global climate cycles and cyclones: consequences for rainfall patterns and lemur reproduction in southeastern Madagascar. *Global Change Biology*, 17(1), 219-227. <https://doi.org/10.1111/j.1365-2486.2010.02205.x>
- Finch, C. E. (1990). *Longevity, senescence, and the genome*. University of Chicago Press
- Fischer, K. E. & Austad, S. N. (2011). The development of small primate models for aging research. *ILAR Journal*, 52 (1), 78-88, <https://doi.org/10.1093/ilar.52.1.78>
- Gabell, A. & Nayak, U. S. L. (1984). The effect of age on variability in gait. *Journal of Gerontology*, 39 (6), 662-666, <https://doi.org/10.1093/geronj/39.6.662>
- Hamilton, W. D. (1966). The moulding of senescence by natural selection. *Journal of Theoretical Biology*, 12 (1), 12-45, [https://doi.org/10.1016/0022-5193\(66\)90184-6](https://doi.org/10.1016/0022-5193(66)90184-6)
- Hayward, A. D., Wilson, A. J., Pilkington, J. G., Clutton-Brock, T. H., Pemberton, J. M., & Kruuk, L. E. B. (2013). Reproductive senescence in female Soay sheep: variation across traits and contributions of individual ageing and selective disappearance. *Functional Ecology*, 27 (1), 184-195, <https://doi.org/10.1111/1365-2435.12029>
- Ingram, D. K. (2000). Age-related decline in physical activity: generalization to nonhumans. *Medicine and Science in Sports and Exercise*, 32 (9), 1623-1629, DOI: [10.1097/00005768-200009000-00016](https://doi.org/10.1097/00005768-200009000-00016)
- Jurmain, R. (2000). Degenerative joint disease in African great apes: an evolutionary perspective. *Journal of Human Evolution*, 39 (2), 185-203, <https://doi.org/10.1006/jhev.2000.0413>
- Jury, M. R., Parker, B. A., Raholijao, N., & Nassor, A. (1995). Variability of summer rainfall over Madagascar: Climatic determinants at interannual scales. *International Journal of Climatology*, 15 (12), 1323-1332, <https://doi.org/10.1002/joc.3370151203>
- Kenyon, C. (2005). The plasticity of aging: Insights from long-lived mutants. *Cell*, 120 (4), 449-460, <https://doi.org/10.1016/j.cell.2005.02.002>
- Kulmala, J., Korhonen, M. T., Kuitunen, S., Suominen, H., Heinonen, A., Mikkola, A., & Avela, J. (2014). Which muscles compromise human locomotor performance with age? *Interface*, 11 (100), 20140858, <https://doi.org/10.1098/rsif.2014.0858>
- Lawler, R. R. (2006). Sifaka positional behavior: Ontogenetic and quantitative genetic approaches. *American Journal of Physical Anthropology*, 131, 261-271, <https://doi.org/10.1002/ajpa>

- Lawler, R. R., Caswell, H., Richard, A. F., Ratsirarson, J., Dewar, R. E., & Schwartz, M. (2009). Demography of Verreaux's sifaka in a stochastic rainfall environment. *Oecologia*, 161, 491-504, <https://doi.org/10.1007/s00442-009-1382-1>
- Lovell, N. C. (1990). Skeletal and dental pathology of free-ranging mountain gorillas. *American Journal of Physical Anthropology*, 81 (3), 399-412, <https://doi.org/10.1002/ajpa.1330810309>
- Madimenos, F. C. (2015). An evolutionary and life-history perspective on osteoporosis. *Annual Review of Anthropology*, 44, 189-206, <https://doi.org/10.1146/annurev-anthro-102214-013954>
- Marck, A., Berthelot, G., Foulonneau, V., Marc, A., Antero-Jacquemin, J., Noirez, P., Bronikowski, A. M., Morgan, T. J., Garland Jr., T., Carter, P. A., Hersen, P., Di Meglio, J., & Toussaint, J. (2017). Age-related changes in locomotor performance reveal a similar pattern for *Caenorhabditis elegans*, *Mus domesticus*, *Canis familiaris*, *Equus caballus*, and *Homo sapiens*. *The Journals of Gerontology: Series A*, 72 (4), 455-463, <https://doi.org/10.1093/gerona/glw136>
- McGregor, R. A., Cameron-Smith, D., & Poppitt, S. D. (2014). It is not just muscle mass: a review of muscle quality, composition, and metabolism during ageing as determinants of muscle function and mobility later in life. *Longevity & Healthspan*, 3, 9, <https://doi.org/10.1186/2046-2395-3-9>
- McKiernan, S. H., Colman, R., Lopez, M., Beasley, T. M., Weindruch, R., & Aiken, J. M. (2009). Longitudinal analysis of early stage sarcopenia in rhesus monkeys. *Experimental Gerontology*, 44 (3), 170-176, <https://doi.org/10.1016/j.exger.2008.09.014>
- Mitchell, W. K., Williams, J., Atherton, P., Larvin, M., Lund, J., & Narici, M. (2012). Sarcopenia, dynapenia, and the impact of advancing age on human skeletal muscle size and strength; a quantitative review. *Frontiers in Physiology*, 3, 260, <https://doi.org/10.3389/fphys.2012.00260>
- Moorad, J. A. & Nussey, D. H. (2016). Evolution of maternal effect senescence. *Proceedings of the National Academy of Sciences*, 113 (2), 362-367, <https://doi.org/10.1073/pnas.1520494113>
- Murray, M. P., Kory, R. C., & Clarkson, B. H. (1969). Walking patterns in healthy old men. *Journal of Gerontology*, 24 (2), 169-178, <https://doi.org/10.1093/geronj/24.2.169>
- Napier, J. R., & Walker, A. C. (1967). Vertical clinging and leaping - A newly recognized category of locomotor behaviour of primates. *Folia Primatologica*, 6, 204-219, <https://doi.org/10.1159/000155079>
- Nussey, D. H., Froy, H., Lemaitre, J., Gaillard, J., & Austad, S. N. (2013). Senescence in natural populations of animals: Widespread evidence and its implications for bio-gerontology. *Ageing Research Reviews*, 12 (1), 214-225, <https://doi.org/10.1016/j.arr.2012.07.004>
- Odding, E., Valkenburg, H. A., Stam, H. J., & Hofman, A. (2001). Determinants of locomotor disability in people aged 55 years and over: The Rotterdam study. *European Journal of Epidemiology*, 17, 1033-1041, <https://doi.org/10.1023/A:1020006909285>
- Partridge, L. & Gems, D. (2002). Mechanisms of aging: public or private? *Nature Reviews Genetics*, 3, 165-175, <https://doi.org/10.1038/nrg753>
- Pavelka, M. S. M. & Fedigan, L. M. (1991). Menopause: A comparative life history perspective. *American Journal of Physical Anthropology*, 34 (S13), 13-38, <https://doi.org/10.1002/ajpa.1330340604>

- Pugh, T. D., Conklin, M. W., Evans, T. D., Polewski, M. A., Barbian, H. J., Pass, R., Anderson, B. D., Colman, R. J., Eliceiri, K. W., Keely, P. J., Weindruch, R., Beasley, T. M., & Anderson R. M. (2013). A shift in energy metabolism anticipates the onset of sarcopenia in rhesus monkeys. *Aging Cell*, 12 (4), 672-681, <https://doi.org/10.1111/ace.12091>
- Richard, A. F., Dewar, R. E., Schwartz, M., & Ratsirarson, J. (2002). Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). *Journal of Zoology*, 256 (4), 421-436, <https://doi.org/10.1017/s0952836902000468>
- Rose, M. R. (1991). *Evolutionary Biology of aging*. Oxford University Press.
- Rothschild, B. M. & Woods, R. J. (1992). Osteoarthritis, calcium pyrophosphate deposition disease, and osseous infection in old world primates. *American Journal of Physical Anthropology*, 87 (3), 341-347, <https://doi.org/10.1002/ajpa.1330870308>
- Rothschild, B. M. (1993). Skeletal paleopathology of rheumatic diseases: the sub-*Homo* connection. In *Arthritis and Allied Conditions*, pp. 3-7. Lea & Febiger.
- Rothschild, B. M., Hong, N., & Turnquist, J. E. (1997). Naturally occurring inflammatory arthritis of the spondyloarthropathy variety in Cayo Santiago rhesus macaques (*Macaca mulatta*). *Clinical and Experimental Rheumatology*, 15 (1), 45-51.
- Ruff, C. B., Junno, J., Eckhardt, W., Gilardi, K., Mudakikwa, A., & McFarlin, S. C. (2020). Skeletal ageing in Virunga mountain gorillas. *Philosophical Transactions of the Royal Society B*, 375 (1811), 20190606, <http://dx.doi.org/10.1098/rstb.2019.0606>
- Snyder, M. L. & Schmitt, D. (2018). Effects of aging on the biomechanics of Coquerel's sifaka (*Propithecus coquereli*): Evidence of robustness to senescence. *Experimental Gerontology*, 111, 235-240, <https://doi.org/10.1016/j.exger.2018.07.019>
- Stearns, S. (1992) *The Evolution of Life Histories*. Oxford University Press.
- Williams, G. C. (1957). Pleiotropy, natural selection, and the evolution of senescence. *Evolution*, 11, 398-411, <https://doi.org/10.1126/sageke.2001.1.cp13>
- Wright, P. C. (1999). Lemur traits and Madagascar ecology: Coping with an island environment. *American Journal of Physical Anthropology*, 110(S29), 31-72, [https://doi.org/10.1002/\(SICI\)1096-8644\(1999\)110:29+%3C31::AID-AJPA3%3E3.0.CO;2-0](https://doi.org/10.1002/(SICI)1096-8644(1999)110:29+%3C31::AID-AJPA3%3E3.0.CO;2-0)
- Wunderlich, R. E., & Schaum, J. C. (2007). Kinematics of bipedalism in *Propithecus verreauxi*. *Journal of Zoology*, 272(2), 165-175, <https://doi.org/10.1111/j.1469-7998.2006.00253.x>
- Yamada, T., Maye, K., & Kondo, S. (1988). The characteristics of walking in old men analysed from the ground reaction force. *Journal of the Anthropological Society of Nippon*, 96 (1), 7-15, <https://doi.org/10.1537/ase1911.96.7>
- Zehr, S. M., Roach, R. G., Haring, D., Taylor, J., Cameron, F. H., & Yoder, A. D. (2014). Life history profiles for 27 strepsirrhine primate taxa generated using captive data from the Duke Lemur Center. *Scientific Data*, 1, 140019, doi: 10.1038/sdata.2014.19