

Age- and size-related changes in hind limb muscles in two baboon species (*Papio anubis* and *P. papio*)

Anthony Herrel^{1,2,3,4}  | Jean-Christophe Theil^{1,5} | Léon Faure¹ | François Druelle^{3,6,7} | Gilles Berillon^{6,7}

¹Mécanismes Adaptatifs et Evolution, UMR 7179, Muséum national d'Histoire naturelle CNRS, Paris, France

²Department of Biology, Evolutionary Morphology of Vertebrates, Ghent University, Ghent, Belgium

³Functional Morphology Laboratory, Department of Biology, University of Antwerp, Antwerp, Belgium

⁴Naturhistorisches Museum Bern, Bern, Switzerland

⁵Ecole Nationale Vétérinaire Alfort, Maisons-Alfort, France

⁶UMR 7194 (Histoire Naturelle de l'Homme Préhistorique), CNRS-Muséum National d'Histoire Naturelle-UPVD, Paris, France

⁷UAR 846, Primatology Station-Celphedia, CNRS, Rousset, France

Correspondence

Anthony Herrel, Mécanismes Adaptatifs et Evolution, UMR 7179, Muséum national d'Histoire naturelle CNRS, Paris, France.
Email: anthony.herrel@mnhn.fr

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Abstract

Body size has an impact on all biological functions and analyzing how body size impacts functional traits such as locomotion is critical. Body size does not only vary across species but also during ontogeny. Indeed, juvenile animals are often at a competitive disadvantage due to their smaller absolute size. Consequently, understanding size- and age-related changes in the locomotor system is critical for our understanding of adult phenotypes. Here, we address this question by exploring growth of the hind limb muscles in two species of closely related baboons that differ in their ecology, the olive baboon, *Papio Anubis*, the Guinea baboon, and *Papio papio*. To do so, we dissected 40 *P. anubis* and 10 *P. papio* and measured the mass and physiological cross-sectional area (PCSA) of the hind limb muscles. Our results showed no sexual differences in size- or age-related growth patterns, but did show differences between species. Whereas the scaling of muscle mass and PCSA was largely isometric in *P. anubis*, allometric scaling was more common in *P. papio*. Despite these differences between species, the knee extensors and external rotators at the knee scaled with positive allometry in both species highlighting their important role during adult locomotion. Although life-history data for *P. papio* are scarce, we suggest that differences between species may be associated with differences in adult body size and age of locomotor independence between species.

KEYWORDS

Anatomy, function, locomotion, muscle architecture, primate

1 | INTRODUCTION

Body size is a critical feature of an organism that impacts its mechanics, physiology, behavior, ecology, and ultimately its evolution (Dick & Clemente, 2017; Hill, 1950; La Barbera, 1989; Schmidt-Nielsen, 1984). Consequently, understanding how size impacts the biology of an organism is an important endeavor and is often referred to as the analysis of scaling (Bishop et al., 2021; Schmidt-Nielsen, 1984).

Differences in body size and the consequences thereof on form and function have been studied extensively at an interspecific scale (e.g., Alexander et al., 1981; Biewener, 1989; Bishop et al., 2021; Cuff et al., 2016a, 2016b). However, also during ontogeny size is a critical determinant of an organism's form, function, physiology, behavior, and ecology (Carrier, 1996). Moreover, due to their small size, immature nervous system and lack of experience, juvenile forms are often at a competitive disadvantage compared to adults resulting in

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strong selection on performance and growth (Butcher et al., 2019; Carrier, 1996; Herrel & Gibb, 2006; Young & Shapiro, 2018).

The locomotor system is particularly impacted by the effect of size as survival, foraging, and finding sexual partners is in many organisms directly dependent on locomotor performance (Irschick & Garland Jr, 2001). However, as absolute locomotor performance is the trait under selection, juveniles of many species rapidly reach near-adult levels of performance. For example, in hares and rabbits, the contractile force and mechanical advantage of the ankle extensors increase with negative allometry (Carrier, 1983; Foster et al., 2019) allowing young animals to perform as well as adults. In addition to variation in the skeletal system impacting how forces are transmitted (i.e., lever arms), muscles are an equally important driver of variation in locomotor performance (James et al., 2007; Marsh, 1988), yet relatively few studies on intraspecific scaling of limb muscles and muscle architecture exist (e.g. Gand, 1977; Carrier, 1983; Eng et al., 2008; Martin et al., 2019; Butcher et al., 2019; Boettcher et al., 2020) and even fewer have focused on the hind limb, the dominant limb pair in generating propulsion in most quadrupeds (Demes et al., 1994; Hanna et al., 2006; Lee et al., 2004).

In the present study, we focus on two species of baboons, the olive baboon (*Papio anubis*) and the Guinea baboon (*Papio papio*). While baboons have long captured the interest of anthropologists for their ecology and social behavior (Washburn & DeVore, 1961), a recent study suggested they may provide an interesting model for studying the locomotor behaviors and ecology of early hominins (King, 2022). Due to their common use of terrestrial locomotor environments and the use of occasional bipedal locomotion, they represent a relevant model to study locomotion and the underlying anatomical design of the musculoskeletal system (Aerts et al., 2023; Druelle & Berillon, 2011; Druelle et al., 2022; King, 2022). The two species are of interest as they are sister taxa that are genetically similar (Rogers et al., 2019), yet show significant differences in their niches (Fuchs et al., 2017; Kunz & Linsenmair, 2008; Zinner et al., 2021). *Papio papio* show somewhat larger home range sizes compared to *P. anubis* (Zinner et al., 2021) and species also differ in their social organization (Boese, 1975; Melle & Lameed, 2018; Owens, 1975; Patzelt et al., 2011). Finally, over the past decade, a series of studies has been conducted aimed at understanding the ontogenetic changes in locomotion and morphology in *P. anubis* (Aerts et al., 2018; Aerts et al., 2023; Druelle & Berillon, 2011; Druelle et al., 2016, 2017, 2018, 2021, 2022; Cosnefroy et al., 2022) and in the yellow baboon, *P. cynocephalus* (Raichlen, 2005a, 2005b, 2006; Shapiro & Raichlen, 2006), providing an important baseline for the interpretation of the data presented here. These studies show that the center of mass of the hind limb in *P. anubis* and *P. cynocephalus* moves more proximal with age concomitant with a reduction in the length of the foot relative to overall hind limb and thigh length. These changes happen early on at the start of locomotor autonomy (1.1 years for females and 1.25 years for males), where quadrupedal locomotion becomes dominant and hip and thigh muscles are recruited (Druelle et al., 2017; Raichlen, 2005a, 2006).

Specifically, we test the following predictions: (1) No differences in size- or age-related patterns of growth will exist between sexes given the lack of sexual size dimorphism in hind limb features and overall proportions (Druelle et al., 2017; Morris et al., 2019); (2) differences in size- or age-related patterns of growth will exist between species; (3) muscle mass and muscle physiological cross-sectional area will scale with negative allometry overall, providing young animals with a relatively greater mechanical output of the hind limb that may impact locomotor performance and survival (Fellmann, 2011, 2012; Young, 2005); and (4) differences in allometry of proximal versus distal muscle groups will exist with proximal muscle groups showing positive allometry and distal muscle groups showing negative allometry. This would match the proximal displacement of the center of mass of the hind limb at the onset of locomotor autonomy (Druelle et al., 2017; Raichlen, 2005b, 2006).

2 | MATERIALS AND METHODS

2.1 | Material

Forty *Papio anubis* ranging from newborns to 26.8 years in age were dissected (six males ranging in age from 5 days to 17 years and 33 females ranging in age from newborns to 26.8 years in age and one specimen of unidentified sex that was 2 days old). An additional 10 *P. papio* ranging in age from 4 days to 22 years (six males ranging in age from 4 days to 17 years, three females ranging in age from 20 days to 22 years, and one individual of unknown sex of 7 days old) were also dissected for comparative purposes. All animals were housed at the primatology station of the CNRS (UAR 846) at Rousset-sur-Arc and died of natural causes. Animals are housed in groups and have access to large outdoor enriched enclosures with opportunities for climbing and scrambling.

Not all cadaver specimens could be used in all analyses as some the hind limbs were already separated from the body. In these specimens, the proximal hip muscles were largely destroyed and could not be included into the analyses. For others specimens, the body mass at time of death or age data were missing resulting in a subset of specimens that could be used for each analysis. The number of individuals used for each analysis is listed in Tables 1–4. All cadavers were transported frozen from the CNRS primatology station to the lab at the Muséum national d'histoire naturelle in Paris where they were stored, thawed, and subsequently dissected.

2.2 | Dissections

For each specimen, we dissected the different hind limb muscles (see Table S1). We weighed each muscle to the nearest 0.1 g on an electronic balance (Soehnle, model 9202), cut the muscle along its line of action and measured the muscle fascicle length (in cm) and the pennation angle directly on the muscle using a protractor when

TABLE 1 Allometry of hind limb muscle mass.

	N	Slope	Intercept	p	R ²	95% CI	Allometry
<i>Papio anubis</i>							
Hip extensors	33	1.19	-2.61	<0.001	0.86	1.02-1.37	+
Hip flexors	34	1.12	-2.87	<0.001	0.89	0.98-1.26	
Hip abductors	18	1.59	-4.99	<0.001	0.87	1.27-1.91	+
Hip adductors	30	1.03	-2.07	<0.001	0.81	0.84-1.22	
External rotators	21	1.37	-4.75	<0.001	0.89	1.14-1.60	+
Internal rotators	19	1.50	-4.48	<0.001	0.86	1.19-1.80	+
Knee extensors	34	1.14	-2.41	<0.001	0.91	1.01-1.27	+
Knee flexors	34	1.09	-2.06	<0.001	0.89	0.95-1.23	
Ankle extensors	34	1.04	-2.23	<0.001	0.90	0.92-1.16	
Ankle flexors	34	0.89	-2.29	<0.001	0.87	0.77-1.01	
External rotator knee	34	1.19	-2.84	<0.001	0.91	1.06-1.33	+
Internal rotator knee	28	1.14	-2.63	<0.001	0.93	1.02-1.27	+
Toe extensors	33	0.86	-2.38	<0.001	0.92	0.77-0.95	-
Toe flexors	29	0.92	-2.06	<0.001	0.97	0.85-0.98	-
Hallux abductor	33	0.93	-2.49	<0.001	0.94	0.84-1.02	
Hallux adductor	34	0.79	-2.98	<0.001	0.89	0.69-0.89	-
<i>Papio papio</i>							
Hip extensors	6	1.42	-3.35	<0.001	0.97	1.12-1.72	+
Hip flexors	6	1.23	-3.24	<0.001	0.98	1.04-1.43	+
Hip abductors	5	1.75	-5.00	<0.001	0.99	1.59-1.91	+
Hip adductors	5	1.36	-3.30	<0.001	0.99	1.15-1.57	+
External rotators	5	1.91	-6.07	<0.001	0.99	1.73-2.09	+
Internal rotators	5	1.71	-4.77	<0.001	0.99	1.52-1.90	+
Knee extensors	6	1.24	-2.82	<0.001	0.98	1.06-1.42	+
Knee flexors	6	1.29	-2.83	<0.001	0.98	1.09-1.49	+
Ankle extensors	6	1.20	-2.88	<0.001	0.98	0.99-1.40	
Ankle flexors	6	0.98	-2.70	<0.001	0.95	0.83-1.12	
External rotator knee	6	1.41	-3.66	<0.001	0.99	1.21-1.61	+
Internal rotator knee	6	1.20	-2.91	<0.001	0.98	1.00-1.41	
Toe extensors	6	0.95	-2.74	<0.001	0.96	0.72-1.17	
Toe flexors	6	1.03	-2.55	<0.001	0.97	0.82-1.24	
Hallux abductor	6	0.98	-2.75	<0.001	0.97	0.78-1.18	
Hallux adductor	6	1.06	-3.98	<0.001	0.96	0.81-1.31	

Note: Table entries are the regression slopes, the intercepts of the regressions, the *p*-value, the proportion of variation explained, the 95% confidence intervals and the direction of the allometry when present.

present. We then calculated the physiological cross-sectional area (PCSA) by dividing muscle volume by fiber length, assuming a muscle density of 1.06gcm⁻³ (Mendez & Keys, 1960) and correcting for pennation by multiplying this by the cosine of the pennation angle. Note that recent studies have shown that in rabbits, muscle density did change with age when comparing cohorts of rabbits of different ages (Leonard et al., 2021). However, the observed differences were minor (on average 0.01gcm⁻³). Moreover, as no data are available for other taxa, it remains to be seen whether these patterns apply to other taxa such as baboons.

Muscles were grouped into functional groups and a single muscle could be part of multiple functional groups. The functional groups were defined as follows (see also Table S1): the hip extensors (m. gluteus maximus, medius and minimus; m. adductor magnus; m. biceps femoris; m. semitendinosus; m. semimembranosus) and flexors (m. iliopsoas; m. sartorius; m. rectus femoris), the hip adductors (m. gracilis; mm. adductor longus, magnus and brevis; m. pectineus; m. obturator externus) and abductors (m. obturator internus; m. tensor fascia latae; m. piriformis; mm. gemellus superior and inferior; mm. gluteus medius and minimus),

TABLE 2 allometry of hind limb PCSA.

	N	Slope	Intercept	p	R ²	95% CI	Allometry
<i>Papio anubis</i>							
Hip extensors	30	0.89	-2.54	<0.001	0.80	0.72-1.07	+
Hip flexors	34	0.80	-2.35	<0.001	0.84	0.68-0.93	+
Hip abductors	17	1.24	-4.30	<0.001	0.81	0.92-1.56	+
Hip adductors	23	0.64	-1.44	<0.001	0.75	0.47-0.80	
External rotators	21	0.87	-3.37	<0.001	0.75	0.64-1.10	
Internal rotators	18	1.21	-4.00	<0.001	0.88	0.97-1.44	+
Knee extensors	34	0.77	-1.74	<0.001	0.86	0.66-0.88	
Knee flexors	33	0.78	-1.82	<0.001	0.84	0.66-0.90	
Ankle extensors	33	0.77	-1.86	<0.001	0.85	0.66-0.89	
Ankle flexors	34	0.64	-2.13	<0.001	0.76	0.52-0.76	
External rotator knee	33	0.88	-2.71	<0.001	0.85	0.75-1.01	+
Internal rotator knee	33	0.71	-2.05	<0.001	0.74	0.56-0.86	
Toe extensors	34	0.60	-1.97	<0.001	0.82	0.50-0.70	
Toe flexors	33	0.71	-1.78	<0.001	0.81	0.58-0.83	
Hallux abductor	34	0.75	-2.37	<0.001	0.88	0.65-0.85	
Hallux adductor	34	0.58	-2.59	<0.001	0.78	0.47-0.68	
<i>Papio papio</i>							
Hip extensors	6	1.08	-3.01	<0.001	0.91	0.70-1.47	+
Hip flexors	6	0.79	-2.20	<0.001	0.99	0.69-0.90	+
Hip abductors	5	1.42	-4.33	<0.001	0.99	1.19-1.65	+
Hip adductors	5	0.96	-2.69	<0.001	0.99	0.89-1.02	+
External rotators	5	1.55	-5.16	<0.001	0.98	1.27-1.83	+
Internal rotators	5	1.35	-4.04	<0.001	0.98	1.09-1.60	+
Knee extensors	6	0.79	-1.82	<0.001	0.96	0.61-0.97	
Knee flexors	6	0.90	-2.26	<0.001	0.98	0.75-1.05	+
Ankle extensors	6	0.86	-2.19	<0.001	0.97	0.70-1.02	+
Ankle flexors	6	0.69	-2.42	<0.001	0.97	0.54-0.84	
External rotator knee	6	1.00	-3.12	<0.001	0.98	0.84-1.15	+
Internal rotator knee	5	0.88	-2.64	<0.001	0.98	0.69-1.06	+
Toe extensors	6	0.66	-2.22	<0.001	0.96	0.51-0.82	
Toe flexors	6	0.85	-2.27	<0.001	0.97	0.69-1.02	+
Hallux abductor	6	0.80	-2.56	<0.001	0.97	0.65-0.95	
Hallux adductor	6	0.79	-3.36	<0.001	0.95	0.58-1.00	

Note: Table entries are the regression slopes, the intercepts of the regressions, the *p*-value, the proportion of variation explained, the 95% confidence intervals and the direction of the allometry when present.

the external (m. obturator externus; m. quadratus femoris; mm. gemellus superior and inferior; m. piriformis) and internal rotators (m. obturator internus; mm. gluteus maximus, medius and minimus; m. tensor fascia latae) of the thigh, the knee extensors (mm. vastus medialis, lateralis and intermedius; m. rectus femoris) and flexors (m. biceps femoris; m. semitendinosus; m. semimembranosus; m. gracilis; m. sartorius; m. gastrocnemius; m. popliteus), the ankle extensors or dorsiflexors (m. tibialis anterior; m. extensor digitorum longus; m. extensor hallucis longus) and plantar flexors (m. gastrocnemius; m. plantaris; m. soleus; m. tibialis posterior; m.

peroneus longus and brevis; m. flexor digitorum longus), the toe extensors (m. extensor digitorum brevis; m. extensor digitorum longus; m. extensor hallucis longus; m. extensor hallucis brevis; m. abductor digiti minimi) and flexors (m. flexor digitorum longus; m. flexor digitorum brevis; m. flexor hallucis longus; m. quadratus plantae), the hallux abductors (m. abductor hallucis; m. abductor hallucis caput accessorium; m. extensor hallucis brevis; m. abductor digiti minimi) and adductors (m. adductor hallucis; m. adductor hallucis caput transversus), and the external (m. biceps femoris) and internal rotators (m. popliteus; m. gracilis; m. sartorius; m.

semimembranosus; m. semitendinosus) of the shank. For muscle mass and PCSA we summed values for each contributing muscle.

2.3 | Statistical analyses

We Log_{10} -transformed all data before analyses to improve normality and homoscedasticity of the data. We first tested whether sexes differed in the mass or cross-sectional area of the functional groups using a multivariate analysis of covariance (MANCOVA) with either Log_{10} -transformed mass or age as our covariate. We did not include the hip adductors and hip abductors nor the internal or external rotators in this analysis due to too much missing data for these functional groups. As no sex differences were detected, subsequent analyses were run on the full data set including both males and females. We then regressed each Log_{10} -transformed variable (muscle mass and muscle cross-sectional area) by functional group on Log_{10} -transformed body mass using the entire sample and tested whether the slope of the regression deviated from predictions of geometric similarity. We considered that relationships were allometric when the predicted slope (1 for mass; 0.66 for cross-sectional area) fell outside the 95% confidence limits of the regression slope on the experimental data. Finally, we tested for differences between species using a MANCOVA with the muscle architecture values for each functional group as our dependent variables, species as a factor, and body mass or age as our covariables. The hip adductors, hip abductors, and the internal and external rotators were not included in this analysis due to the small sample size for these specific functional groups. To explore age-related changes in muscle anatomy, we tested the fit of different regression models using both raw and Log_{10} -transformed data. We tested the fit of a linear regressions, quadratic models, cubic models, Gompertz models, and modified Gompertz models. For both species and for all variables tested cubic models provided the best fit as determined by the R^2 value and were used throughout. Model parameters for the equation: Log_{10} muscle mass or PCSA = constant + b (Log_{10} age) + c (Log_{10} age)² + (Log_{10} age)³ are listed in Tables 3 and 4 and raw muscle data (mass and PCSA by functional group) are provided in the Tables S1 and S2. All analyses were performed using IBM SPSS V.29.

3 | RESULTS

Our results showed no differences in muscle mass between sexes when correcting for body mass (*P. anubis*: Wilks' lambda=0.57, $F_{12,12} = 0.75$, $p = 0.69$; *P. papio*: Wilks' lambda=0.66, $F_{10,23} = 1.20$, $p = 0.34$) or age (*P. anubis*: Wilks' lambda=0.68, $F_{10,26} = 1.25$, $p = 0.31$; *P. papio*: Wilks' lambda=0.51, $F_{4,1} = 0.24$, $p = 0.89$). Similarly, no differences in cross-sectional area were observed when correcting for body mass (*P. anubis*: Wilks' lambda=0.65, $F_{12,16} = 0.73$, $p = 0.70$; *P. papio*: Wilks' lambda=0.36, $F_{6,1} = 0.30$, $p = 0.88$) or age (*P. anubis*: Wilks' lambda=0.55, $F_{12,19} = 1.31$, $p = 0.29$; *P. papio*: Wilks' lambda=0.82, $F_{3,1} = 0.07$, $p = 0.97$).

3.1 | Scaling of muscle mass and cross-sectional area

Roughly half of the functional groups scaled with positive allometry in both *P. anubis* and *P. papio* (Table 1). Interestingly, these involved mostly muscles acting around the hip and knee in addition to the external rotators of the thigh. Thus, larger animals have disproportionately well-developed muscles acting around the hip and knee. In contrast, the toe extensors and flexors as well as the hallux adductors scaled with negative allometry in *P. anubis*, yet scaled isometrically in *P. papio* (Table 1). Finally, the knee and hip flexors as well as the hip abductors scaled with positive allometry in *P. papio* but scaled isometrically in *P. anubis* (Table 1). Differences between species were more striking for the scaling of the muscle PCSA (Table 2). Whereas more than half of the functional groups scaled isometrically in *P. anubis*, more than half of the muscles scaled with positive allometry in *P. papio* (Table 2). The hip flexors and extensors, the hip abductors, the internal rotators, and the external rotators scaled with positive allometry in both species. In *P. papio* only the knee extensors, ankle and toe flexors and the muscles attaching to the hallux scaled isometrically (Table 2).

The MANCOVA on the muscle mass data with body mass as a covariate detected significant differences between species (Wilks' lambda=0.36; $F_{12,19} = 2.77$; $p = 0.023$) with *P. anubis* generally having larger muscles for a given body mass. Subsequent univariate ANCOVAs detected differences in the knee extensors ($F_{1,30} = 4.50$; $p = 0.042$), the ankle flexors ($F_{1,30} = 9.87$; $p = 0.004$), and the hallux abductors ($F_{1,30} = 5.76$; $p = 0.023$). After correction for multiple testing only the difference in the ankle flexors remained significant. Similarly, the MANCOVA on the PCSA data with body mass as a co-variate was significant (Wilks' lambda=0.30; $F_{12,22} = 4.29$; $p = 0.002$), yet this time *P. papio* showed, on average, greater muscle cross-sectional areas for a given body size. Subsequent univariate ANCOVAs indicated differences only in the hip extensors ($F_{1,33} = 7.65$; $p = 0.009$) and hip flexors ($F_{1,33} = 7.76$; $p = 0.009$) which were no longer significant after correction for multiple testing (Figures 1 and 3).

3.2 | Age-related changes in muscle mass and PCSA

Of all the growth models tested the best fit (highest R^2) was always observed for the cubic model as it was the only model that accurately captured the slow initial increase in mass and PCSA as well as the decline in mass and cross-sectional area in the oldest individuals. Whereas the increase in mass and cross-sectional area was marked by a clear decline in the oldest individuals, this was not the case in *P. papio*. Moreover, muscle mass and cross-sectional area increased rapidly in *P. anubis* but was somewhat delayed in *P. papio* (Figures 3 and 4).

The MANCOVA performed on the muscle mass data with age as a covariate detected significant differences between species (Wilks'

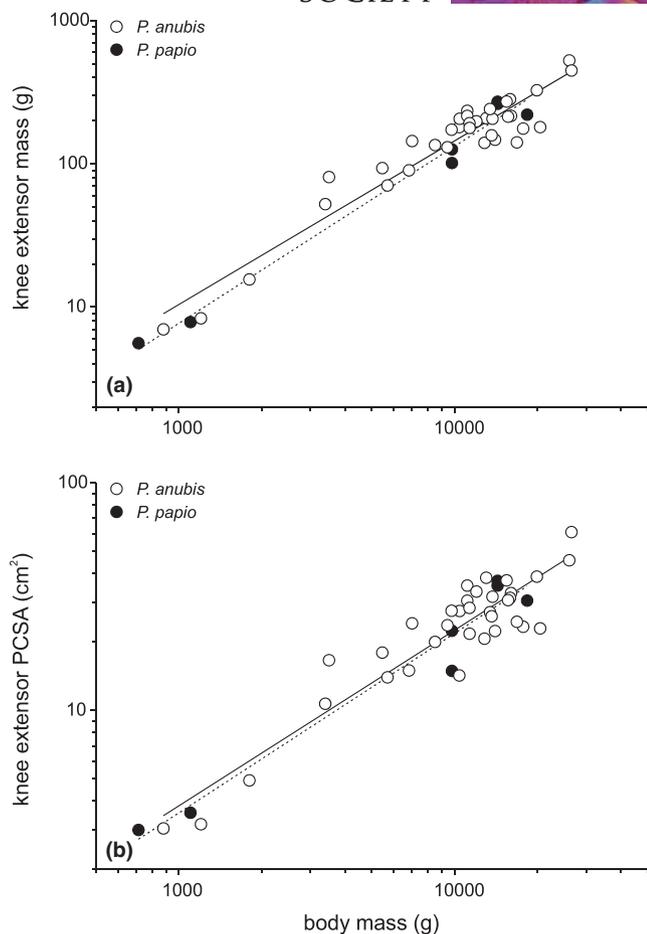


FIGURE 1 Scaling of the mass (a) and cross-sectional area (b) of the knee extensors. Open circles represent *P. anubis*; filled circles represent *P. papio*. The dotted line represents the linear regression for *P. papio*. Note the Log-scale on both axes.

lambda=0.46; $F_{12,26} = 2.57$; $p = 0.021$). The subsequent ANCOVAs showed differences for the knee extensors ($F_{1,37} = 7.36$; $p = 0.010$) and flexors ($F_{1,37} = 6.79$; $p = 0.013$), the ankle extensors ($F_{1,37} = 7.53$; $p = 0.009$) and flexors ($F_{1,37} = 11.37$; $p = 0.002$), the toe extensors ($F_{1,37} = 5.24$; $p = 0.028$) and flexors ($F_{1,37} = 5.90$; $p = 0.02$), the abductors of the hallux ($F_{1,37} = 8.08$; $p = 0.007$), and the internal rotators at the knee ($F_{1,37} = 7.93$; $p = 0.008$). However, after correction for multiple testing only the differences in the ankle flexors remained significant. The MANCOVA on the muscle cross-sectional areas with age as a covariate was also significant (Wilks' lambda=0.42; $F_{12,29} = 3.34$; $p = 0.004$). Subsequent univariate ANCOVAs showed significant differences for the knee extensors ($F_{1,40} = 7.74$; $p = 0.008$) and flexors ($F_{1,40} = 6.34$; $p = 0.016$), the ankle extensors ($F_{1,40} = 10.04$; $p = 0.003$), and flexors ($F_{1,40} = 9.62$; $p = 0.004$), the toe extensors ($F_{1,40} = 5.51$; $p = 0.024$) and the hallux abductors ($F_{1,40} = 9.04$; $p = 0.005$). After correction for multiple testing differences in the ankle extensors and flexors as well as the hallux abductors remained significant. Overall, *P. anubis* tended to have larger muscles with a greater cross-sectional area for a given age compared to *P. papio* (Tables 3 and 4; Figures 2 and 4).

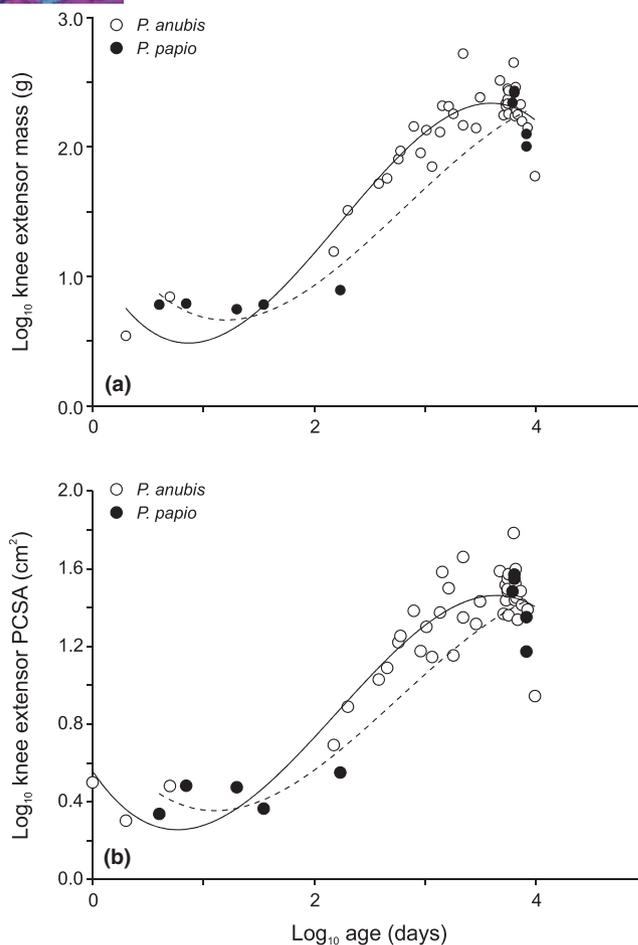


FIGURE 2 Age-related changes in knee extensor mass (a) and cross-sectional area (b). Open circles represent *P. anubis*; filled circles represent *P. papio*. The full line represents the cubic model fit for *P. anubis* and the dashed line represents the cubic model fit for *P. papio*.

4 | DISCUSSION

As predicted, no differences between the two sexes were observed in size- or age-related growth patterns, even though males and females are highly dimorphic in both species. This suggests that constraints on the hind limb are similar in both sexes. The hind limb in primates differs from that in other mammals in that it is the primary weight-bearing limb (Demes et al., 1994; Larsen & Stern Jr, 2009; Raichlen et al., 2009; Schmitt, 2003; Schmitt & Hanna, 2004). However, baboons deviate from this general pattern and show an equal distribution of mass between fore and hind limbs (Demes et al., 1994). Consequently, when correcting for size, differences between males and females are no longer observed. However, this does not explain the absence of age-related differences in muscle mass or PCSA. Indeed, whereas females reach their growth asymptote around 6 years of age, males continue to increase rapidly in body size until the age of 10 years (Druelle et al., 2017; Leigh et al., 2009; Strum, 1991). Yet, both males and females show similar patterns in the changes of the center of mass with age (Druelle et al., 2017). Possibly the limited number

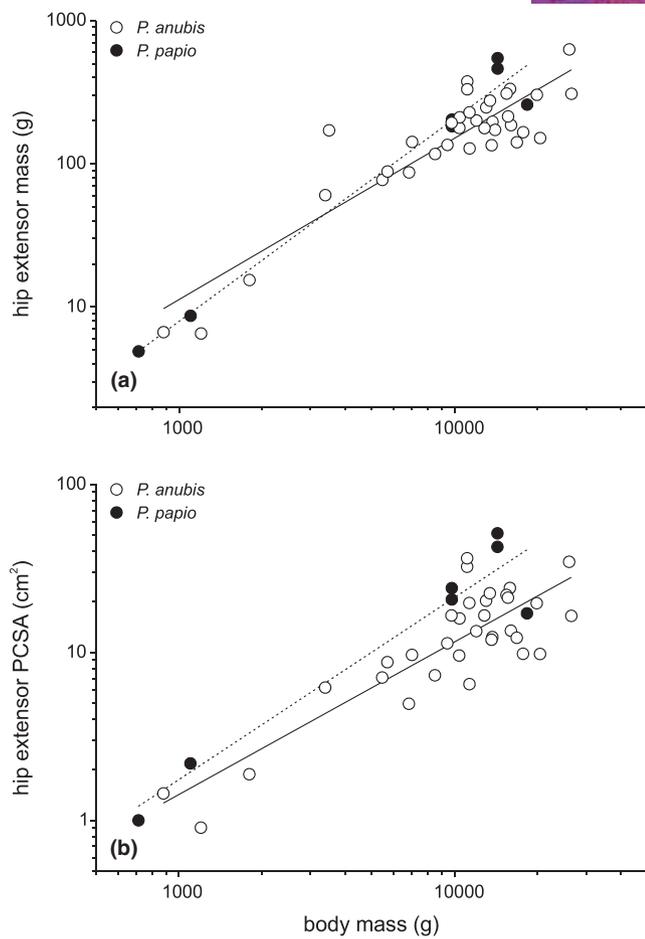


FIGURE 3 Scaling of the mass (a) and cross-sectional area (b) of the hip extensors. Open circles represent *P. anubis*; filled circles represent *P. papio*. The dotted line represents the linear regression for *P. papio*. Note the Log-scale on both axes.

of males included in our study for *P. anubis* and the overall small data set for *P. papio* prevented us from detecting sex-specific age-related growth patterns. Additionally, females tend to carry their infants (Anvari et al., 2014), which may increase the demands imposed on the limbs for weight bearing and may render patterns similar in both sexes.

Positive allometry in the mass and cross-sectional area of muscles acting around the hip and knee was observed in both species. Consequently, adults had larger hip and knee muscles with a greater force-generating capacity, in line with our predictions. This may be due to growth-related changes in body mass causing the disproportional scaling of mass relative to force in larger animals. Thus, the scaling patterns observed here ensure functional similarity across ontogeny. Moreover, the onset of locomotor autonomy and the dominance of a quadrupedal locomotor repertoire in adults places specific demands on the limbs (Cosnefroy et al., 2022; Druelle et al., 2016, 2021) which may be reflected in the scaling patterns observed here. These results are also in accordance with the shift in segmental masses documented in *Papio* spp. with proximal segments becoming heavier (Druelle et al., 2016, 2017; Raichlen, 2005a, 2005) similar to results for other primates (Baker et al., 2011; Grand, 1977;

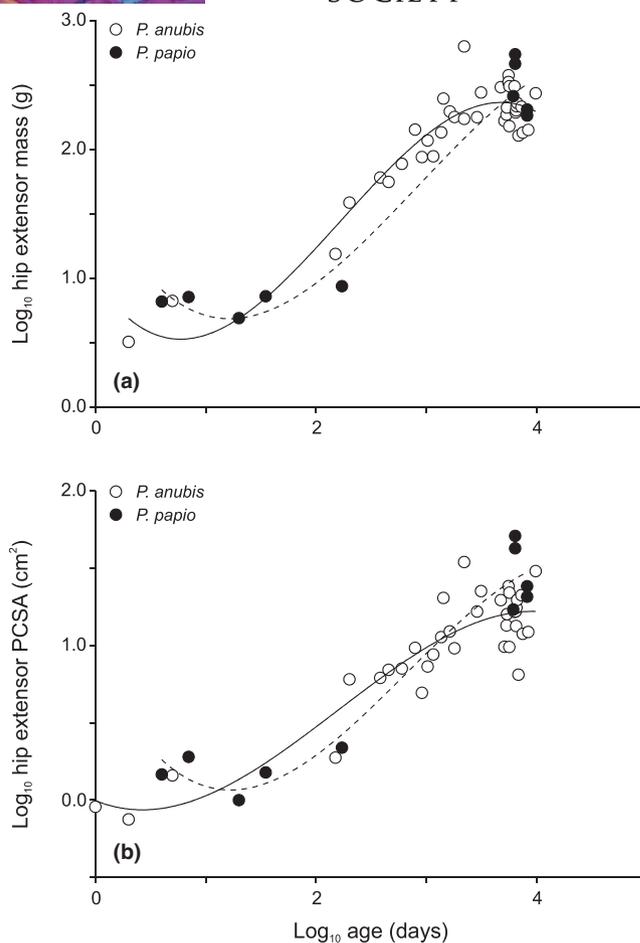


FIGURE 4 Age-related changes in hip extensor mass (a) and cross-sectional area (b). Open circles represent *P. anubis*; filled circles represent *P. papio*. The full line represents the cubic model fit for *P. anubis* and the dashed line represents the cubic model fit for *P. papio*.

Schoonaert et al., 2007; Turnquist & Wells, 1994). This is likely due to the greater investment in proximal locomotor muscles important for quadrupedal locomotion. Interestingly, distal muscles showed negative allometry in *P. anubis* suggesting that juveniles had relatively large and forceful distal muscles. This again accords well with the importance of grasping and climbing in juvenile primates as documented previously in olive baboons (Druelle et al., 2016, 2018) and other primate species (Jungers & Fleagle, 1980; Turnquist & Wells, 1994; Young & Heard-Booth, 2016). Overall, both species showed a rapid development of the proximal hind limb muscles allowing them to become independent at quadrupedal locomotion at an early age.

Despite these similarities in scaling patterns differences between species were significant in both muscle mass and PCSA. Interestingly, whereas muscle mass for a given body size was generally greater for *P. anubis*, the opposite was true for muscle cross-sectional area. Thus, whereas olive baboons have relatively heavier muscles, Guinea baboons have muscles with a greater force-generating capacity. Although some muscles were specifically impacted, our analyses showed that this was an overall

TABLE 3 Age-dependent growth of hind limb muscle mass.

	N	Constant	b	c	d	p	R ²
<i>Papio anubis</i>							
Hip extensors	37	0.99	-1.28	1.00	-0.15	<0.001	0.88
Hip flexors	38	0.79	-1.82	1.23	-0.18	<0.001	0.87
Hip abductors	22	-0.25	-0.56	0.63	-0.092	<0.001	0.73
Hip adductors	34	0.63	-0.56	0.65	-0.10	<0.001	0.89
External rotators	24	-1.00	0.43	0.12	-0.026	<0.001	0.76
Internal rotators	23	0.15	-0.79	0.75	-0.11	<0.001	0.75
Knee extensors	38	1.16	-1.70	1.22	-0.18	<0.001	0.87
Knee flexors	38	1.23	-1.40	1.06	-0.16	<0.001	0.89
Ankle extensors	38	0.81	-1.08	0.86	-0.13	<0.001	0.89
Ankle flexors	38	0.13	-0.58	0.58	-0.09	<0.001	0.86
External rotator knee	38	0.87	-1.74	1.26	-0.19	<0.001	0.85
External rotator knee	32	0.80	-1.12	0.89	-0.13	<0.001	0.90
Toe extensors	37	0.21	-0.83	0.64	-0.092	<0.001	0.86
Toe flexors	33	0.63	-0.88	0.70	-0.10	<0.001	0.90
Hallux abductor	37	0.15	-0.73	0.64	-0.095	<0.001	0.89
Hallux adductor	38	-0.65	-0.88	0.68	-0.10	<0.001	0.84
<i>Papio papio</i>							
Hip extensors	9	1.66	-1.75	0.91	-0.10	<0.001	0.96
Hip flexors	9	0.83	-1.11	0.95	-0.061	<0.001	0.97
Hip abductors	8	1.09	-2.33	1.25	-0.15	<0.001	0.96
Hip adductors	8	1.33	-1.42	0.76	-0.086	<0.001	0.95
External rotators	8	-0.60	-0.53	0.39	-0.026	<0.001	0.95
Internal rotators	8	1.31	-2.20	1.16	-0.14	<0.001	0.96
Knee extensors	9	1.57	-1.66	0.88	-0.10	<0.001	0.95
Knee flexors	9	1.72	-1.58	0.82	-0.092	<0.001	0.95
Ankle extensors	9	1.25	-1.26	.65	-0.069	<0.001	0.94
Ankle flexors	9	0.71	-1.07	0.55	-0.059	<0.001	0.94
External rotator knee	9	1.17	-1.47	0.77	-0.083	<0.001	0.95
External rotator knee	9	1.46	-1.68	0.86	-0.10	<0.001	0.95
Toe extensors	9	0.48	-0.77	0.38	-0.034	<0.001	0.91
Toe flexors	9	1.24	-1.51	0.81	-0.10	<0.001	0.91
Hallux abductor	9	0.56	-0.87	0.45	-0.045	<0.001	0.92
Hallux adductor	9	-0.52	-0.61	0.28	-0.016	<0.001	0.91

Note: Table entries are the cubic growth model parameters (constant, *b*, *c*, *d*), the *p*-value and the proportion of variance explained by the model (*R*²).

pattern. What the drivers of this pattern are remains unclear. Possibly, the fact that our sample size is unbalanced in the two species (more females in *P. anubis* vs. more males in *P. papio*) may be driving some of these differences. Too few data on morphology, locomotor patterns, and ecology are available for Guinea baboons that could help us understand the observed patterns. However, our data suggest interesting differences in the investment of the locomotor system in these closely related species. Possibly, the slightly greater home ranges and daily movements observed in Guinea baboons (Zinner et al., 2021) may put a premium on lighter, but more forceful muscles, yet this remains to be tested.

Age-related differences between species in muscle mass and PCSA area were also prominent with *P. anubis* generally having larger and more forceful muscles for a given age compared to *P. papio*. These differences were especially striking in subadults ages and suggest that olive baboons show rapid growth of their muscles after birth compared to Guinea baboons. Neonate weight is lower in Guinea baboons (Lindfors, 2002) which may be at least partly driving the observed patterns. Moreover, the maximal recorded age and the interbirth interval are lower in *P. papio* (Lindfors, 2002) suggesting this species has a slower pace of life compared to *P. anubis*. These life-history traits may at least partly explain the rapid growth of the hind limb muscles allowing

TABLE 4 Age dependent growth of hind limb muscle cross-sectional area.

	N	Constant	b	c	d	p	R ²
<i>P. anubis</i>							
Hip extensors	35	-0.002	-0.29	0.38	-0.058	<0.001	0.82
Hip flexors	39	0.11	-1.01	0.73	-0.11	<0.001	0.81
Hip abductors	22	-0.67	-0.15	0.34	-0.051	<0.001	0.72
Hip adductors	28	-0.28	0.011	0.28	-0.047	<0.001	0.88
External rotators	25	-1.06	0.21	0.15	-0.028	<0.001	0.75
Internal rotators	23	-0.57	0.21	0.17	-0.029	<0.001	0.81
Knee extensors	39	0.56	-0.85	0.67	-0.10	<0.001	0.82
Knee flexors	38	0.42	-0.66	0.58	-0.088	<0.001	0.88
Ankle extensors	38	0.34	-0.55	0.49	-0.073	<0.001	0.90
Ankle flexors	39	-0.28	-0.78	0.62	-0.095	<0.001	0.80
External rotator knee	38	-0.15	-0.72	0.63	-0.097	<0.001	0.79
External rotator knee	38	-0.014	-0.75	0.62	-0.095	<0.001	0.83
Toe extensors	39	-0.22	-0.49	0.39	-0.056	<0.001	0.85
Toe flexors	37	0.32	-0.71	0.54	-0.078	<0.001	0.84
Hallux abductor	39	-0.20	-0.66	0.54	-0.078	<0.001	0.89
Hallux adductor	39	-0.87	-0.60	0.44	-0.062	<0.001	0.80
<i>P. papio</i>							
Hip extensors	9	0.91	-1.51	0.79	-0.093	<0.001	0.94
Hip flexors	9	0.27	-0.84	0.53	-0.069	<0.001	0.97
Hip abductors	8	1.07	-2.89	1.57	-0.21	<0.001	0.95
Hip adductors	8	0.45	-0.84	0.46	-0.049	<0.001	0.97
External rotators	8	-1.08	-0.02	0.16	-0.001	<0.001	0.93
Internal rotators	8	1.16	-2.67	1.44	-0.19	<0.001	0.96
Knee extensors	9	0.83	-0.93	0.53	-0.064	<0.001	0.93
Knee flexors	9	0.84	-0.99	0.52	-0.058	<0.001	0.95
Ankle extensors	9	0.68	-0.83	0.44	-0.047	<0.001	0.94
Ankle flexors	9	0.22	-1.25	0.67	-0.087	<0.001	0.93
External rotator knee	9	0.35	-1.10	0.57	-0.06	<0.001	0.94
External rotator knee	8	0.32	-0.81	0.40	-0.038	<0.001	0.97
Toe extensors	9	-0.096	-0.51	0.32	-0.037	<0.001	0.92
Toe flexors	9	1.16	-1.95	1.06	-0.14	<0.001	0.94
Hallux abductor	9	0.027	-0.59	0.32	-0.031	<0.001	0.94
Hallux adductor	9	-1.01	-0.001	-0.046	0.027	<0.001	0.93

Note: Table entries are the cubic growth model parameters (constant, *b*, *c*, *d*), the *p*-value and the proportion of variance explained by the model (*R*²).

animals to become independent early-on in life. Unfortunately, no data on the age of weaning or the age at which *P. papio* juveniles show locomotor independence are available. Future studies would benefit from a greater understanding of these life-history traits to explain species-specific growth patterns in baboons. The species differences in size- and age-related growth patterns observed here are likely not due to differences in environmental parameters as both species were maintained and raised at the same primatology station in similar enclosures and with similar food sources. As such, the observed patterns likely reflect intrinsic species-specific differences in growth. However, as captivity is known to

impact growth and development of the musculoskeletal system (Hartstone-Rose et al., 2014; O'Regan & Kitchener, 2005) including the morphology of the hind limb (Harbers et al., 2020), care must be taken when extrapolating these results to wild animals.

5 | CONCLUSION

In conclusion, our data highlighted no differences in sex-related growth patterns in baboons. In both species the knee extensors and external rotators scaled with positive allometry possibly

reflecting the importance of these muscles in weight support and locomotion from the moment they acquire locomotor autonomy. However, species-specific patterns were noted with the Guinea baboon (*Papio papio*) showing more rapid growth in muscle mass and muscle cross-sectional area compared to the olive baboon (*P. anubis*). Consequently, scaling pattern differed between species with *P. papio* having smaller muscles for a given age and showing more positive allometry in the growth of the hind limb muscles. Overall, this may lead to an earlier age of locomotor independence in the latter species, yet empirical data remain scarce.

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DATA AVAILABILITY STATEMENT

Data for the functional groups by individual are available in the [Tables S1](#) and [S2](#).

ORCID

Anthony Herrel  <https://orcid.org/0000-0003-0991-4434>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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