Size, Scaling, and Sexual Size Dimorphism in Wild South African Thick-Tailed Greater Galagos (*Otolemur crassicaudatus*)

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Abstract

The developmental bases of sexual size dimorphism vary across primates, with important implications for understanding the evolution of dimorphism. Here, we explore adult sexual size dimorphism and its developmental bases in *Otolemur crassicaudatus*. We aim to understand the anatomical pattern of adult sexual size dimorphisms and their developmental bases through allometric analyses of somatometrics. We caught and released wild subadult and adult animals annually at Lajuma Research Centre, South Africa from 2013 to 2023 (excepting 2020), and measured body mass and up to 23 body measurements. Among adults, males (mean body mass = 1242.89 g ± SD = 137.63 g, *n* = 91 observations of *n* = 52 individuals) are 1.21 times larger than females (mean body mass = 1027.55 g ± SD = 94.03 g, *n* = 85 observations of *n* = 44 individuals), possibly representing the highest body mass sexual dimorphism among extant strepsirrhines. The skeletal system shows limited sexual size dimorphism, suggesting decoupling of body mass size dimorphism and skeletal size dimorphism. Allometries lead to variation in adult sexual size dimorphism throughout the body, with high levels of dimorphism in circumferences, especially in the torso and proximal limb elements. Sexual selection, attributable to some level of intermale competition, probably accounts for sexual size dimorphism in this species. The conservatism of the skeletal system, combined with high body mass size dimorphism, may be related to generalized quadrupedalism and declining rates of leaping through ontogeny in the species. These findings complicate reconstructing and interpreting primate sexual size dimorphism in the fossil record.

Keywords: Primate sexual size dimorphism; Sexual selection; Ontogenetic allometry; Growth and development

Introduction

Studies of ontogeny (growth and development) have contributed substantially to our understanding of the evolution of primate sexual size dimorphism (SSD) (Leigh, 1992, 1995; Leigh & Shea, 1995; Li *et al*., 2023; Lumer & Schultz, 1941; Mariotto *et al*., 2024; O'Mara *et al*., 2012; Runestad Connour & Glander, 2020; Schaefer & Nash, 2007; Setchell *et al*., 2001; Shea, 1983, 1985a, b; Turcotte et al., 2022). By identifying growth processes that ultimately lead to adult size, ontogenetic perspectives on SSD provide opportunities to explore aspects of dimorphism inaccessible in analyses of terminal adult sizes. Growth and development ultimately produce size and shape differences both within and among species, and growth processes may vary substantially (Leigh, 1992, 1995, 2007; O'Mara et al., 2012). Sexual selection (Leigh et al., 2008, Mariotto et al., 2024; Runestad Connour and Glander, 20,209; Setchell et al., 2001) and life history factors (Leigh & Terranova, 1998; O'Mara et al., 2012) influence these processes, providing crucial insights into the evolution of SSD.

Ontogenetic data facilitate at least two approaches to SSD. These approaches include analyses of size-for-age or growth in time (Leigh & Shea, 1995; Leigh & Terranova, 1998; Mariotto *et al*., 2024; O'Mara *et al*., 2012; Runestad Connour & Glander, 2020) and analyses of allometric or relative growth (Jungers & Fleagle, 1980; Leigh, 2007; Lumer & Schultz, 1941; Mariotto *et al*., 2024; Runestad Connour & Glander, 2020; Shea, 1983, 1985a). Both kinds of analyses provide opportunities to link SSD to evolutionary processes ranging from life history variation to sexual selection (Leigh & Bernstein, 2006; Leigh *et al*., 2008; O'Mara *et al*., 2012). Of these approaches, allometric studies offer especially valuable insights regarding the attainment of SSD in size and shape in relation to functional changes as animals attain adult states (Boulinguez-Ambroise *et al*., 2021; Druelle *et al*., 2017a, b; Druelle *et al*., 2016, 2017a, b, 2018; Lawler, 2006; Schaefer & Nash, 2007; Shapiro & Raichlen, 2006; Young, 2005; Young *et al*., 2009; Young & Heard-Booth, 2016; Zeininger, *et al*., 2017). For example, young primates typically have relatively large distal limb elements, especially cheiridia (hands and feet), that change little in size after birth. This ensures infant grasping competence, whilst generating strong negative allometries during growth and development, typically producing small and nonsignificant allometric correlations (Jungers & Fleagle, 1980; Lawler, 2006; Lumer & Schultz, 1941; Ravosa *et al*., 1993; Runestad Connour & Glander, 2020; Turner *et al*., 1997; Turnquist & Wells, 1994; Young, 2005; Young & Heard-Booth, 2016). Negative allometries and low correlations result in low SSD for these variables. In contrast, positive allometries and high correlations with size may lead to high levels of SSD [e.g., facial growth in papionin primates (Leigh, 2007; Leigh & Cheverud, 1989, 1991)]. Allometric processes thus may be important drivers of a wide range of variation in adult SSD, with ontogenetic analyses directly revealing how various growth processes lead to adult SSD. In addition, interspecies studies of the allometry of size, shape, and SSD provide additional opportunities to understand evolutionary changes in size and shape (Feiner *et al*., 2021; Leigh, 1995, 2007; O'Mara *et al*., 2012; Shea, 1981, 1983, 1984, 1985a).

Developmental responses to evolutionary factors affecting dimorphism (e.g., sexual selection) may differ across anatomical elements, producing a variation in SSD. Differing patterns of SSD throughout the body suggest variation in both ontogenetic processes and evolutionary forces that impact these processes. Developmental analyses help identify the point which dimorphism emerges, which may indicate divergence of selective forces by sex (Leigh *et al*., 2008; Li *et al*., 2023; Setchell *et al*., 2001; Turcotte *et al*., 2022). Anatomical elements may be subject to competing evolutionary forces that impact development and limit responses to sexual selection, including biomechanical constraints. Several processes promote these outcomes, including differences in the length of the growth period (Jungers & Fleagle, 1980; Lawler, 2006; Schaefer & Nash, 2007), modularity in development (Leigh & Bernstein, 2006; Pereira & Leigh, 2003; Young & Heard-Booth, 2016), and functional considerations (Lewton & Patel, 2020). For example, differing degrees of size and SSD among dimensions may suggest that functional factors (Demes *et al*., 1995) play roles in either limiting or enhancing dimorphism. Finally, descriptions of SSD across numerous anatomical elements have important implications for reconstructing SSD in the fossil record. Individual dimensions may reliably predict levels of SSD in body mass, offering insights into SSD in fossils (e.g., Rehg & Leigh, 1999).

Several distinct ontogenetic allometric patterns have the potential to produce sexual size and shape dimorphism. Ontogenetic allometry is critical to exploring the causes and consequences of SSD, enabling investigation of a wide range of questions (Feiner *et al*., 2021; Jungers, 1985; Jungers & Fleagle, 1980; Leigh, 2007; Leigh & Shea, 1995; Shea, 1985a, b). First, female and male allometric trajectories may overlap entirely, with adult dimorphism produced simply by extending a shared or common trajectory to different body sizes between sexes. Allometry in this case produces shape changes throughout ontogeny, ultimately leading to different male and female terminal adult sizes and shapes. Second, allometric trajectories can diverge by sex, with females and males following distinct pathways to adult size. Shape differences between males and females can be expected in this case. Slope differences, intercept differences or some combination of slope and intercept differences in regressions may account for adult sex differences. Isometric growth, either with overlapping or parallel trajectories, preserves preadult shapes throughout growth and into different adult body mass or body length size ranges. In the presence of adult size differences, allometric (nonisometric) growth, adult shapes differ between females and males, indicating functional or life history distinctions between the sexes, especially if adult shapes differ substantially.

When SSD results from common female and male allometric trajectories that terminate at different body size endpoints, males and females share shapes during ontogeny, at least until the larger sex attains terminal size and, possibly, a new shape. Sharing of shapes through development suggests a "conservative" path to adult dimorphism, implying comparable or identical functional capacities between sexes during growth. Such extensions are relatively common among primates for both craniometric and somatometric measures, leading to shape differences either by sex, interspecifically, or both by sex and interspecifically (Bonduriansky, 2007; Cheverud, 1982; Feiner *et al*., 2021; Gould, 1966; Klingenberg, 2007; Leigh & Cheverud, 1989; Ravosa, 1998; Ravosa *et al*., 1993; Shea & Bailey, 1996; Shea, 1983, 1985a). Distinct allometric trajectories suggest the potential for functional differences between sexes during growth and development. Departures from a shared scaling pattern could reveal adaptive or sexually-selected differences between sexes that emerge early in ontogeny.

Otolemur crassicaudatus (the thick-tailed greater galago) is among the most dimorphic of strepsirrhine primates, departing from an overall range of monomorphism to very low SSD across strepsirrhines more generally (Kappeler, 1990, 1991). However, the degree of body size SSD in *O. crassicaudatus* remains uncertain (Table I). In addition, only a few strepsirrhine species seem to reach a level of body mass SSD comparable to that of *O. crassicaudatus*. Moreover, both dentition (Kieser & Groeneveld, 1989) and cranial dimensions (Kieser, 1990) in *O. crassicaudatus* show low levels of SSD. Unfortunately, problems characterize strepsirrhine SSD data sets, including mixes of captive and noncaptive populations, small sample sizes, and discrepancies among published estimates of adult sizes and SSD. Consequently, the range of variation in strepsirrhine SSD remains uncertain, necessitating further investigation. Moreover, studies of the ontogeny of dimorphism in strepsirrhines mostly

Table I Estimates for strepsirrhine primates in which sexual size dimorphism (SSD, M/F) for at least one report measures SSD as equal to or greater than 1.20. Codes "c" and "nc" designate captive and noncaptive samples, respectively

Species and source, captive (c) or noncaptive (nc)	Female mean body mass (±SE, *n*)	Male mean body mass (±SE, *n*)	SSD (M/F)
Otolemur crassicaudatus (1, nc)	1110 g (*n*=35)	1190 g (*n*=66)	1.07
Otolemur crassicaudatus (2,3, c)	1241.5 g (±34.2 g, *n*=44)	1495.4 (±39.6 g (*n*=40)	1.20
Galago senegalensis (1, nc, estimate 1)	250 g (*n*=8)	315 g (*n*=9)	1.26
Galago senegalensis (1, nc, estimate 2)	199 g (*n*=67	227 g (*n*=80)	1.14
Nycticebus pygmaeus (2, c)	363.5 (±14.8 g, *n*=5)	440.8 (±16.5 g, *n*=7)	1.21
Nycticebus pygmaeus (3, c)	462 g (*n*=5)	376 g (*n*=7)	1.23
Cheirogaleus major (1, nc)	362 g (*n*=6)	438 g (*n*=6)	1.21
Cheirogaleus major (2,3 c)	443.3 (±35.8 g, *n*=3)	574.6 (±73.1 g, *n*=3)	1.30

Sources: 1, Smith & Jungers, 1997; 2, Kappeler, 1990; and 3, Kappeler, 1991 focus on body mass for captive samples (Leigh & Terranova, 1998; O'Mara *et al*., 2012). Very few studies of strepsirrhine body and limb development exist (Schaffer and Nash, 2007) and, with important exceptions (Lawler, 2006), concentrate on captive samples. These issues lead to considerable uncertainty about how growth dynamics produce size and shape variation within and among strepsirrhine species.

Otolemur crassicaudatus is widely distributed throughout sub-Saharan Africa spanning from the Atlantic Ocean to the Indian Ocean. A southern extension of the range runs along southeastern Africa into South Africa, including our study site at the Lajuma Research Centre (Penna & Pozzi, 2024: Fig. 1f). Like other galagids, the species is mostly solitary and nocturnal. *O. crassicaudatus* locomotion features frequent generalized quadrupedalism, in contrast to some other galagids, which often leap (Crompton, 1983, 1984). The diet includes fruits and gums (Fleagle, 2013; Harcourt, 1986), and they have morphological adaptations for gum feeding (Burrows & Nash, 2010). *O. crassicaudatus* is the largest galagid (Sauther *et al*., 2024, Fig. 1), with both male and female adults typically exceeding 1000 g (Kappeler, 1990, 1991; Sauther *et al*., 2024). Few other lorisids reach this size range, (Fleagle, 2013; Kappeler, 1990, 1991; Smith & Jungers, 1997). Therefore, analyzing *O. crassicaudatus* SSD helps establish the range of SSD in strepsirrhines, while revealing general factors involved in the evolution of variation in overall strepsirrhine size as well as SSD (Leigh & Terranova, 1998). These data also contribute to understanding the evolution of SSD across primates more generally.

To better understand the relations between growth, development, and adult SSD in *Otolemur crassicaudatus*, we analyze a large data set of measurements from individually known live, wild animals. We first aim to provide accurate measures of adult body mass SSD in *O. crassicaudatus*, as well as estimates of SSD in other body dimensions. We then investigate SSD in somatometrics, including body length, limb lengths, and body and limb circumferences. If body components have responded similarly to factors selecting for SSD, including sexual selection, then we predict that comparatively high overall body mass SSD in *O. crassicaudatus* accompanies comparable levels of SSD among body dimensions. Alternatively, if SSD is "localized," with different degrees of dimorphism among measures, as indicated by studies of skeletal dimorphism in catarrhine primates (Wood, 1976) and somatic growth in both *Alouatta palliata* (Runestad Connour & Glander, 2020) and *Alouatta guariba* (Mariotto et al., 2024), then we predict variation in dimorphism among anatomical units.

Our second aim is to characterize and understand relative growth (allometric) patterns that underlie SSD in different body measurements. We investigate the ontogenetic allometric bases of SSD by describing allometric trajectories that lead to terminal adult sizes. We investigate regressions of limb and body dimensions (lengths and circumferences) relative to two overall size measures (body mass and body length). If allometric processes produce adult size and shape differences between sexes, then we predict that SSD in *O. crassicaudatus* generally results from common female and male allometric trajectories that terminate at different body size endpoints. Alternatively, if SSD arises from distinct allometric trajectories between the two sexes, then we predict departures from a shared scaling pattern could reveal adaptive or sexually selected differences between sexes that emerge early in ontogeny.

Methods

Study Subjects

We investigate somatometrics (body measures) from a large and intensively studied sample of wild *O. crassicaudatus* from Lajuma Research Centre, South Africa. Most studies of SSD across primates investigate museum specimens in terms of body mass, dental, or skeletal materials (Gordon, 2006; Keiser, 1990; Keiser and Groeneveld, 1989; Plavcan, 2001, 2002, 2012; Shea, 1983, 1985a; Wood, 1976). Museum specimens obviously represent only a single time point in the life of animal (typically, time of death) and rarely include information about either body mass or body element dimensions. Museum data may also be influenced by collection biases, including a "trophy bias" (i.e., an emphasis on collecting large adult males Haraway, 1989; Zuckerman, 1926]). In contrast, data from wild-caught animals facilitate longitudinal analyses of somatometrics (Mariotto *et al*., 2024; Runestad Connour & Glander, 2020) in conjunction with information concerning behaviors, demography, ecology, phenology, range size, intergroup interactions, and other matters (Long *et al*., 2021; Phukuntsi *et al*., 2020).

The study population is from the Lajuma Research Centre, South Africa. MLS, FPC, ASWT, and IVW captured and measured individuals from 2013–2019 and then from 2021–2022, following IACUC-approved protocols. We endeavored to capture all individuals in the population yearly, capturing animals in large (26.67cm × 81.28 cm × 31.75 cm) Havahart® live animal traps (Woodstream Corporation, Lancaster, PA, USA) baited with bananas. We scanned individuals in the trap for a pre-existing microchip and, if they were a repeat capture from that same capture season, we released them immediately. If a new individual for that trapping season was caught, we allowed them to move on their own accord into a bag placed at the entrance of the cage and quickly placed them into a small pet carrier. Once at the field lab, we placed the animals in a quiet area in the field lab. They remained in the ventilated pet carrier until we sedated them for health and morphological measurements. We sedated most individuals using injected Telezol® based on the animal's body weight, and then administered anesthesia using inhaled Isoflurane™ in doses between 2–4% mixtures with air. We measured some individuals while sedated with Telezol® only. Most animals were anesthetized for 45 to 70 min, depending on which measurement sets we obtained, with all animals under veterinary supervision (ASWT, IVW). During recovery, we sequestered individuals in covered, portable pet kennels, then released them near the area of capture following recovery from the anesthesia. All animals were released before sundown on the day of capture.

Data Collection and Samples

The subjects available for analysis varied through time, given the annual vagaries of trapping and factors such as mortality and migration. Consequently, we collected a variety of measurement sets, with annual differences in the number of animals accessed and variation in the measurements obtained for each animal. In addition, we lack detailed chronological age data in this population sample. Our sample consisted of 219 observations across 122 individual animals. Many individuals provided only one set of measurements. Forty individuals presented multiple measurements, with three adult animals measured six times. We collected some multiple measures from the same year, with others from different years. We weighed all animals at capture and assigned them to age classes based on dental eruption, with completed dental eruption coded as "adults," while designating animals without full adult dentition as "subadult." A single investigator (MLS) collected a complete set of somatometrics from subadult animals, then obtained a complete set of measurements if that animal was captured later as an adult. For animals that were adults at first capture, we collected all somatometrics. If we caught that adult individual again, we collected only body mass, circumferences, testes, and vulva lengths to evaluate the animal's current reproductive and health condition. Some animals captured only once were represented by partial measurement sets, given constraints of field conditions. This collection protocol resulted in larger data sets of circumference than linear dimensions. Consequently, different analyses may use different sets of animals, with some animals contributing multiple data points.

Considering these complications, most of our analyses treat the data cross-sectionally, meaning that we treat each of the 219 observations as a statistically independent observation. Most repeated measures represent adult circumferences, with measures taken at least a year apart, so size variation is not attributable to fundamental growth. Aggregating these data, including using a mean measurement for repeated observations of an individual, would diminish both the total range of variation and variation across time. In addition to treating the full data set cross-sectionally, we did, however, estimate means for individual adults with repeated mass measurements. Thus, we report body mass SSD in two ways. First, we estimate adult masses and SSD based on the full cross-sectional sample, treating each adult observation as independent. Second, we calculate adult female and male means using the mean of measurements for adults measured repeatedly. For other analyses, we analyze all data cross sectionally.

Sex ratios in this sample vary between age groups. The full cross-sectional sample is closely balanced, with 111 observations from females and 108 observations from males. The adult female sample comprised 85 individuals and 26 subadults (30.5% subadult). The adult male samples included 91 observations from adults, and 17 subadults (18.6% subadult). Therefore, females provided the majority of subadult observations (26 females vs 17 males, ~ 60:40). The probability of observing 17 males in a sample of 43 individuals (assuming a 50:50 population sex ratio and using the binomial theorem) is only about 4.8%. Within the subadult category, underrepresentation of males may be even more pronounced for the smallest subadults. Specifically, of the 32 animals less than 700 g, only seven (22%) are males. Assuming a 50:50 population sex ratio, the probability of this result is only 0.07%. Differences in the abundance of data points by age may impact regression estimates. Given unbalanced sex ratios and growth dynamics, we refrain from comparing subadult means by sex.

Measurements

We measured body weight using a digital scale (taken to the gram) and use weight to approximate body mass or "mass" throughout our analyses. In addition to weight, we took 33 somatometric measurements (defined by standard anatomical landmarks and obtained with tape measure to the half-millimeter), representing anatomically defined lengths and circumferences, of which we analyze 23 lengths and circumferences describing the limbs and torso (Table II). We calculated measures of forelimb length and hindlimb length by summing three limb segments from proximal to distal (e.g., arm, forearm, hand lengths and thigh, leg, foot lengths). Cross-sectional data treatment results in allometric analysis that may differ both in sample composition and numbers of individuals.

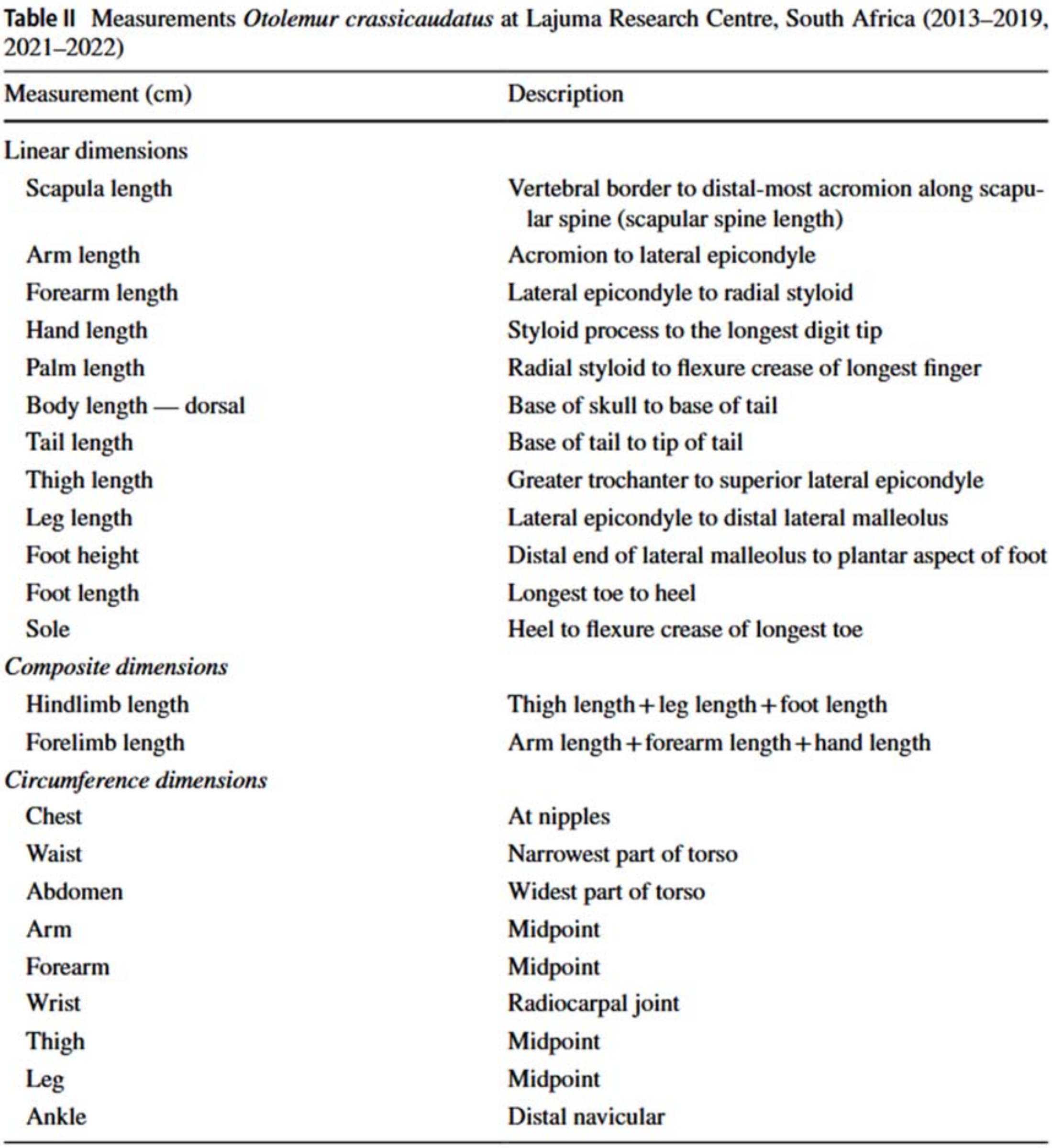

Table II Measurements *Otolemur crassicaudatus* at Lajuma Research Centre, South Africa (2013–2019, 2021–2022)

Measurement (cm)	Description
Linear dimensions	
Scapula length	Vertebral border to distal-most acromion along scapular spine (scapular spine length)
Arm length	Acromion to lateral epicondyle
Forearm length	Lateral epicondyle to radial styloid
Hand length	Styloid process to the longest digit tip
Palm length	Radial styloid to flexure crease of longest finger
Body length — dorsal	Base of skull to base of tail
Tail length	Base of tail to tip of tail
Thigh length	Greater trochanter to superior lateral epicondyle
Leg length	Lateral epicondyle to distal lateral malleolus
Foot height	Distal end of lateral malleolus to plantar aspect of foot
Foot length	Longest toe to heel
Sole	Heel to flexure crease of longest toe
Composite dimensions	
Hindlimb length	Thigh length + leg length + foot length
Forelimb length	Arm length + forearm length + hand length
Circumference dimensions	
Chest	At nipples
Waist	Narrowest part of torso
Abdomen	Widest part of torso
Arm	Midpoint
Forearm	Midpoint
Wrist	Radiocarpal joint
Thigh	Midpoint
Leg	Midpoint
Ankle	Distal navicular

Estimates of Adult Dimorphism

We measured adult SSD for somatometric measures by examining adult measurements by sex. We estimated SSD for 23 somatometric dimensions by dividing the mean male dimension by mean female dimension (M/F, untransformed measurements) and conducted *t*-tests to evaluate the significance of sex differences for body mass and body length. We also illustrated dimorphism with boxplots for mass and body length, presenting medians and confidence intervals on medians to summarize data distributions.

Allometric Analyses

We estimated bivariate allometric regressions to describe scaling patterns underlying terminal levels of adult dimorphism, using both body mass and body length as general size measures (x-variables). To simplify analyses, we used the cube root of body mass (mass [grams$^{1/3}$] and transform all measurements to base-10 logarithms. These transformations mean that the allometry coefficient for isometry of a linear dimension relative to body mass is 1.0 rather than 1/3 (Gould, 1966). Allometric approaches distinguish at least three different paths to SSD (Gould, 1966; Leigh, 2007; Shea, 1985a). First, females and males may follow a common (associated) allometric (or isometric) trajectory to differing endpoints (Leigh, 2007). Analytically, this would be represented by overlapping regression lines of dimensions against mass or body length by sex. In species with SSD, female and male regression lines typically reach different terminal sizes, with males extending beyond females. Second, trajectories (regression lines) may separate by sex as size increases, with regression lines diverging with increasing size, whether or not terminal adult size ranges overlap. Finally, regression lines may be parallel, indicating comparable levels of SSD throughout ontogeny. These possibilities correspond to theoretically significant differences in size and shape and can be described by heterochronic processes (Gould, 1977; Leigh, 2007). Regressions may be isometric (slope = 1, indicating no shape change with size), or allometric (slope < 1, negative allometry; slope > 1, positive allometry) (Gould, 1966).

We first present analyses of linear dimensions and then analyze circumference dimensions. We estimate bivariate allometries using both cube root of body mass and body length as measures of the overall or general size of the animal.

We conducted most analyses in R (R Core Team, 2022), and calculated Pearson product-moment correlations (pairwise estimation) in JMP 17 (SAS Institute, 2022). We estimated regression equations based on both ordinary least-squares (OLS) and reduced major axis (RMA) regression (Sokal & Rohlf, 1995) using the *lmodel2* package in R (R Core Team, 2022). Allometric studies usually prioritize RMA regression because this method accounts for measurement error in both independent and dependent variables (Sokal & Rohlf, 1995). OLS is optimal when the independent (x) variable is measured without error (e.g., when the independent variable is experimentally controlled). Both OLS and RMA yield identical results when the bivariate correlation is 1.0 (Sokal & Rohlf, 1995). Somatometric correlations are typically lower than those observed in osteological studies (Jungers & Fleagle, 1980; Lumer & Schultz, 1941). Low correlations for some variables can be biologically important, revealing dimensions that are near-adult size in small, young animals and thus altered minimally during ontogeny, even with substantial increases in body mass. In addition, while there are major changes in mass in this sample, the size range is small relative to more-frequently studied anthropoids, in which larger size ranges can drive increased correlations.

Measurement error may be a problem with somatometrics obtained from live animals, either in laboratory or field contexts (Lumer & Schultz, 1941), with important implications for choice of regression approach (OLS or RMA). Somatometric landmarks are more difficult to locate than landmarks on dry bones. Moreover, factors such as age and body condition, including fat levels, fur density, and animal hygiene affect the ability to locate landmarks. Furthermore, animals usually move during measurement sessions, even though sedated. The depth of sedation and resultant immobilization varies both by individual and time since sedation. The imperative to minimize sedation duration means that multiple measures to calibrate observer error are rarely feasible. Substantial size ranges typical of ontogenetic samples may also complicate measurement. For example, in some cases, small animals can be measured with more precision and accuracy than large animals. These factors mean that somatometric correlations may be reduced relative to skeletal correlations, affecting the choice of regression model, particularly model II regressions. To interpret results cautiously, we provide allometric interpretations only for variables in which the regression R^2 accounts for about 50% of the total variation, corresponding to a Pearson correlation coefficient of about 0.70. Regressions with correlations at or above this level can likely be reliably interpreted in allometric terms, with comparable results for both RMA and OLS regression. In addition, we present selected regression results for correlations near this threshold. We use a significance level of $p < 0.05$ to designate significant results, recognizing that our analyses involve many correlations and regressions, so a more restrictive level of assessing significance may be valid. Because many correlations are somewhat weak, especially for distal limb elements, we primarily used OLS regression so as not to generate unrealistically positively allometric coefficients (which RMA may do). We tested for isometric slopes (slope = 1.0) by sex. We tested for sex differences in regression lines through analyses of covariance (ANCOVA) based on OLS regressions, using Fisher's exact test to evaluate the significance of intercept differences when slopes differed significantly (Runestad Connour & Glander, 2020). Finally, we limited this study to univariate and bivariate approaches because of the relatively high frequency of missing and "unevenness" of the data. While multivariate allometric analyses provide excellent approaches to somatometric data, the complexities of this data set restricted opportunities for these analyses.

Ethical Note

This research had ethical clearance to conduct research as described herein from the Research and Ethical Sciences Committee at the South African National Biodiversity Institutes' (SANBI) National Zoological Gardens (NZG; Project 18/26), the Animal Ethics Committee off the University of Pretoria (Project V037-17, REC078-20), and Animal Protocol Approval Assurance D16-00388 from the IACUC office of the University of Colorado, which reviewed our research protocols.

Results

Patterns of Adult Sexual Size Dimorphism: Body Mass and Body Length

Body mass during ontogeny in this sample ranges from 456 g (a subadult female) to 1551 g (an adult male), a 3.5-fold difference. The total size range observed here is limited in relation to the total postnatal size range for the species from birth to adulthood [van Schaik and Isler (2011) report neonatal mass at 43.2 g]. For the full, cross-sectional sample, mean adult male body mass was 1242.89 ± SD = 137.63 g, about 1.21 times larger than females (1027.55 ± SD = 94.03 g) (Fig. 1). Accounting for repeated measures by taking the mean body mass of each adult animal measured more than once changed these means only slightly [male = 1237.96 g, (− 5 g from cross-sectional estimate), female = 1013.98 g, (− 14 g from cross-sectional estimate) for an SSD estimate of 1.22]. Sex differences in mean body mass for the cross-sectional sample were statistically significant ($t = 12.19$, $p = 0.0001$). Female masses never exceeded the male mean of about 1240 g (female median = 1034, lower 95% CI = 986, upper 95% CI = 1166 g, $n = 84$; male median = 1260, lower 95% CI = 1201, upper 95% CI = 1294 g, $n = 93$ in Fig. 1). However, estimates for about half of the males at the low end of the distribution overlapped with nearly the full range of female data points.

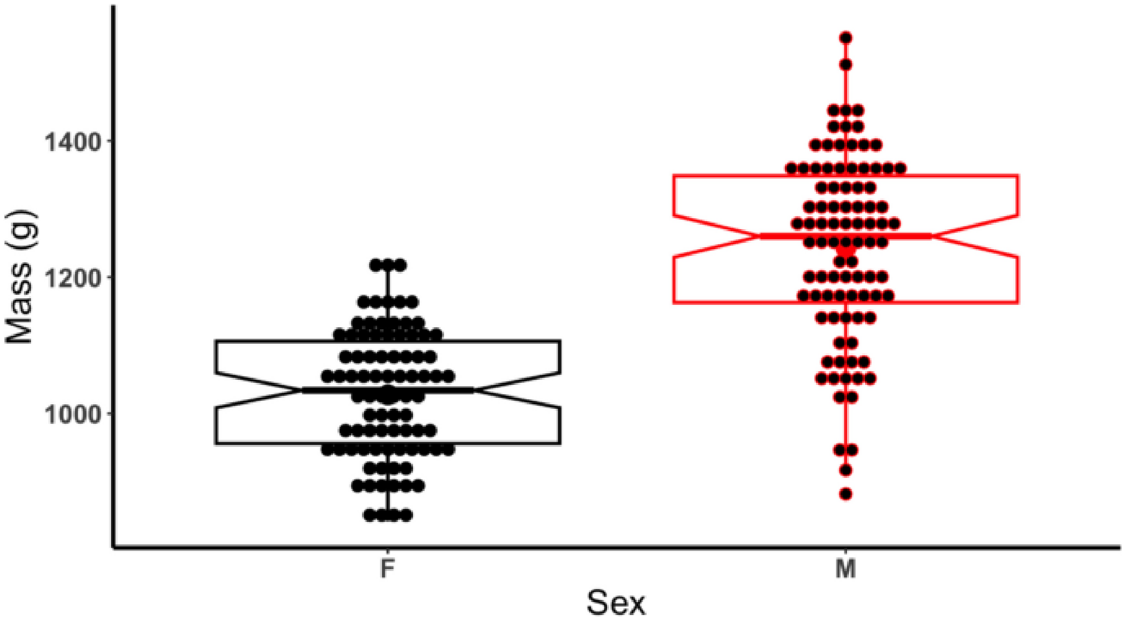

Figure 1. Female (*left, black*, *n* = 84) and male (*right, red/black*, *n* = 93) body mass for adult *Otolemur crassicaudatus* from Lajuma Research Centre, South Africa (2013–2019, 2021–2022). *Notched boxes* represent 95% confidence intervals around the median, the *large data point* is the sample mean, and *horizontal lines away from the median* represent the 75th and 25th percentiles. *End points of vertical lines* represent maximum or minimum values, with *points beyond lines* representing likely outliers.

In contrast to body mass dimorphism, adult body length SSD is low, with the male mean of 24.15 ± SD = 1.50 cm (*n* = 42), only 1.037 times larger than female mean of 23.28 ± SD = 1.48 cm (*n* = 56). Only the four longest male observations exceed the female size distribution, and only the shortest two females extend below the range of the male distribution (female median = 23.35, lower 95% CI = 23 cm, upper 95% CI = 24 cm, male median = 24.35, lower 95% = 23.8, CI = upper 95% CI = 25.00 cm in Fig. 2). Mean length differences are statistically significant (*t* = 2.87, *p* = 0.005).

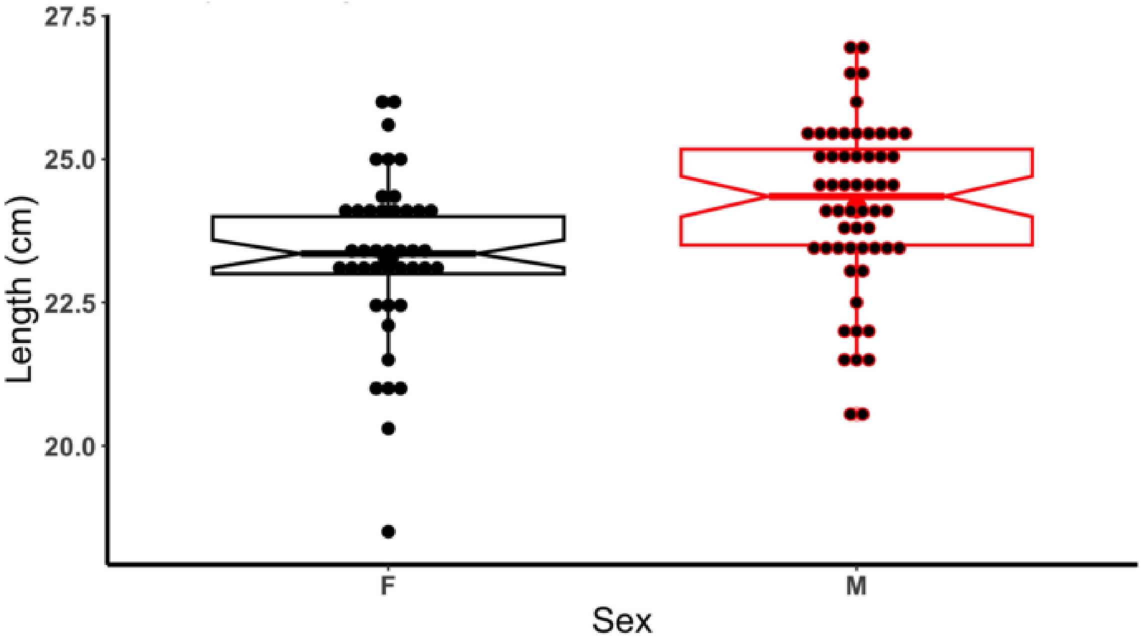

Fig. 2. Female (*left, black*, *n* = 42) and male (*right, red/black*, *n* = 56) body lengths for adult *Otolemur crassicaudatus* from Lajuma Research Centre, South Africa from 2013–2023 (excepting 2020). *Notched boxes* represent 95% confidence intervals around the median, the *large data point* is the sample mean, and *horizontal lines away from the median* represent the 75th and 25th percentiles. *End points of vertical lines* represent maximum or minimum values, with *points beyond lines* representing likely outliers.

Patterns of Adult Sexual Size Dimorphism: Linear Dimensions

Lengths: other linear dimensions roughly match total mean body length in returning modest levels of SSD (Table III). Specifically, SSD among linear dimensions spans a narrow range, with a maximum male/female ratio of 1.08 in arm length to a minimum of 0.88 for foot height. Other foot dimensions lack SSD entirely. The mean of dimorphism for linear dimensions is 1.05, slightly exceeding mean body length dimorphism, and comparable to skull measures (Keiser, 1990). Mean forelimb lengths show higher SSD (1.07), while mean hindlimb dimensions are minimally dimorphic (1.03).

Circumferences: measures of circumferences for the torso and limbs fill the gap between body mass SSD and linear dimensions (Table II). Specifically, mean SSD in the torso (chest, abdomen, waist) is 1.06, while the forelimb circumference dimorphism mean is 1.13 and the hindlimb circumference mean SSD is 1.08. Forearm circumference is the most dimorphic measure, with only a few females exceeding the male mean.

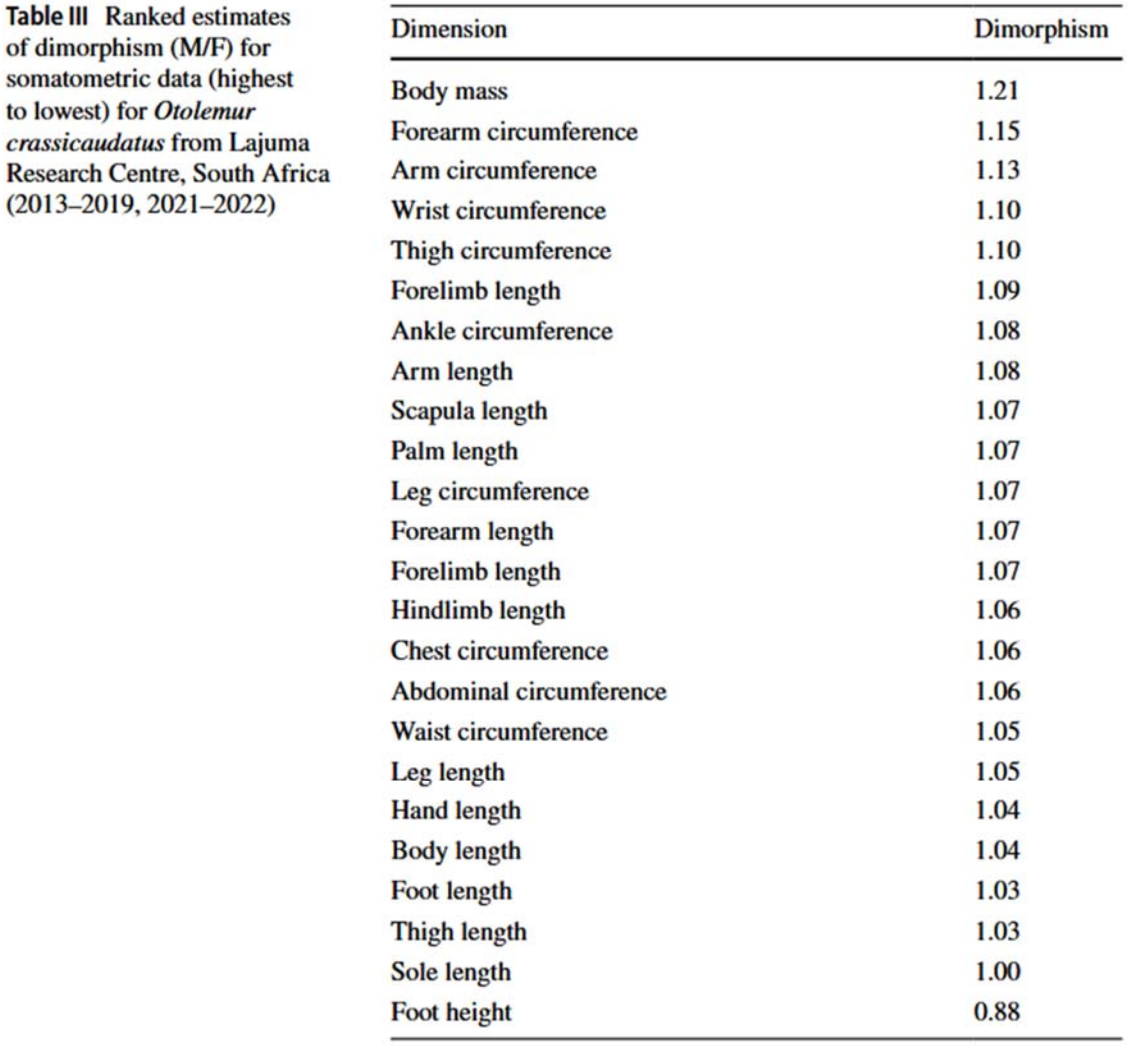

Table III Ranked estimates of dimorphism (M/F) for somatometric data (highest to lowest) for *Otolemur crassicaudatus* from Lajuma Research Centre, South Africa (2013–2019, 2021–2022)

Dimension	Dimorphism
Body mass	1.21
Forearm circumference	1.15
Arm circumference	1.13
Wrist circumference	1.10
Thigh circumference	1.10
Forelimb length	1.09
Ankle circumference	1.08
Arm length	1.08
Scapula length	1.07
Palm length	1.07
Leg circumference	1.07
Forearm length	1.07
Forelimb length	1.07
Hindlimb length	1.06
Chest circumference	1.06
Abdominal circumference	1.06
Waist circumference	1.05
Leg length	1.05
Hand length	1.04
Body length	1.04
Foot length	1.03
Thigh length	1.03
Sole length	1.00
Foot height	0.88

Somatometric Correlations

Pearson product–moment correlations for linear dimensions and body mass range from $r = 0.91$ (arm circumference *vs*. mass in males) to $r = -0.21$ (foot length *vs*. body mass in males) (see Online Resource). The mean correlation of linear dimensions with body mass is $r = 0.65$ for females and $r = 0.56$ for males. Low correlations for tail length reflect numerous very short lengths among larger animals, probably indicating traumatic loss of tail segments. Given a strong correlation between body mass and body length ($r_{\text{female}} = 0.87$, $r_{\text{male}} = 0.86$), patterns of correlations between linear dimensions and body length parallel correlations with body mass.

Mean Pearson product–moment correlations for circumferences and body mass between sexes ($r_{\text{female}} = 0.74$ and $r_{\text{male}} = 0.81$) exceed correlations between body mass and linear dimensions. Mean Pearson product–moment correlations between circumferences and body mass exceed correlations between circumferences and body length (mean $r_{\text{female-}} = 0.67$, mean $r_{\text{male}} = 0.69$), comparable to mean correlations between lengths of body segments and circumferences ($r_{\text{female}} = 0.63$, $r_{\text{male}} = 0.68$).

Allometry of Linear Dimensions With Body Mass

Positive correlations between various dimensions and the cube root of body mass (Table IV) suggest that body dimensions and body mass change in concert through ontogeny. Seven correlations for females and four for males are near or above 0.70 ($R^2 \sim 0.49$) (Table IV). Regressions of linear dimensions against the cube root of body mass results in overlapping female and male regression lines, although female regression slopes are nominally higher in most cases (Fig. 3). Overall, larger adult body mass indicates that males simply extend established allometric relations to larger mass size ranges. Bivariate regressions of linear dimensions against body mass show positive allometry, isometry, and negative allometry, a typical range of relationships.

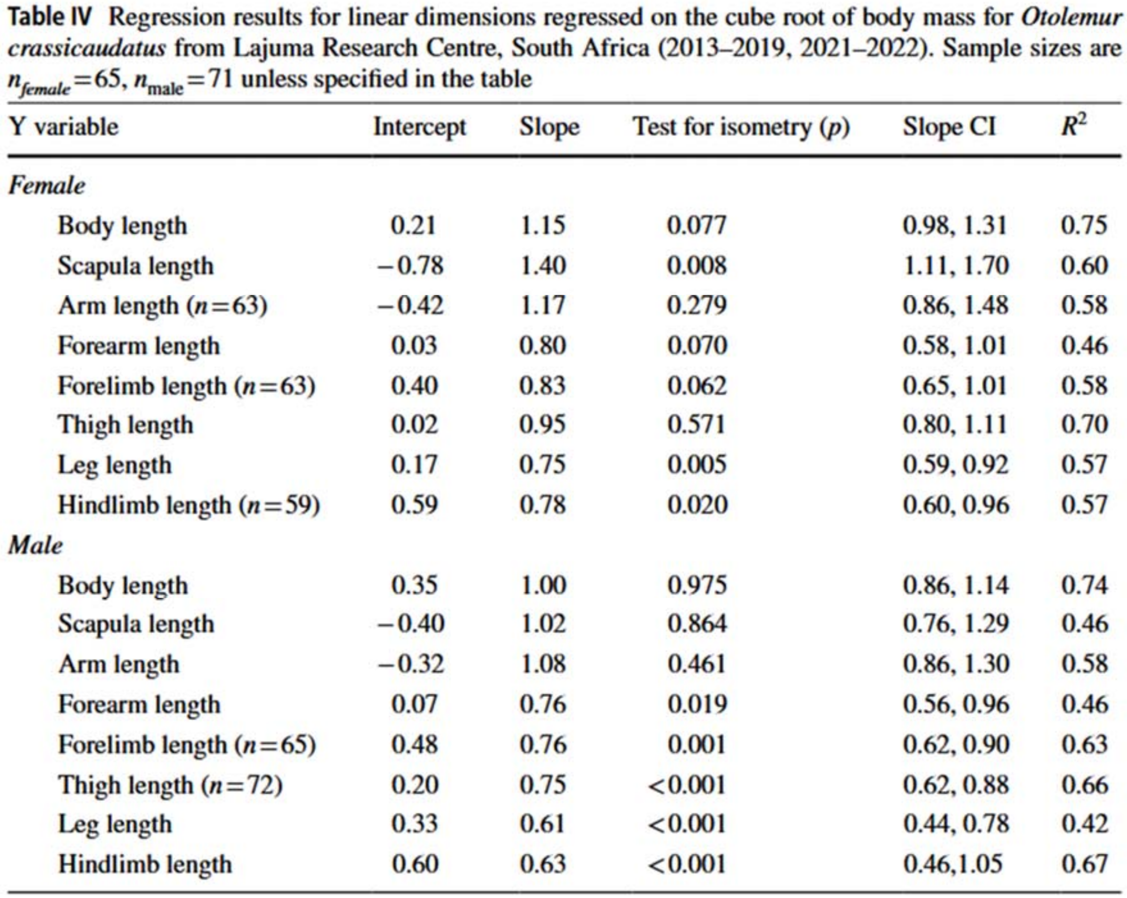

Table IV Regression results for linear dimensions regressed on the cube root of body mass for *Otolemur crassicaudatus* from Lajuma Research Centre, South Africa (2013–2019, 2021–2022). Sample sizes are $n_{female}=65$, $n_{male}=71$ unless specified in the table

Y variable	Intercept	Slope	Test for isometry (*p*)	Slope CI	R^2
Female					
Body length	0.21	1.15	0.077	0.98, 1.31	0.75
Scapula length	−0.78	1.40	0.008	1.11, 1.70	0.60
Arm length ($n=63$)	−0.42	1.17	0.279	0.86, 1.48	0.58
Forearm length	0.03	0.80	0.070	0.58, 1.01	0.46
Forelimb length ($n=63$)	0.40	0.83	0.062	0.65, 1.01	0.58
Thigh length	0.02	0.95	0.571	0.80, 1.11	0.70
Leg length	0.17	0.75	0.005	0.59, 0.92	0.57
Hindlimb length ($n=59$)	0.59	0.78	0.020	0.60, 0.96	0.57
Male					
Body length	0.35	1.00	0.975	0.86, 1.14	0.74
Scapula length	−0.40	1.02	0.864	0.76, 1.29	0.46
Arm length	−0.32	1.08	0.461	0.86, 1.30	0.58
Forearm length	0.07	0.76	0.019	0.56, 0.96	0.46
Forelimb length ($n=65$)	0.48	0.76	0.001	0.62, 0.90	0.63
Thigh length ($n=72$)	0.20	0.75	<0.001	0.62, 0.88	0.66
Leg length	0.33	0.61	<0.001	0.44, 0.78	0.42
Hindlimb length	0.60	0.63	<0.001	0.46,1.05	0.67

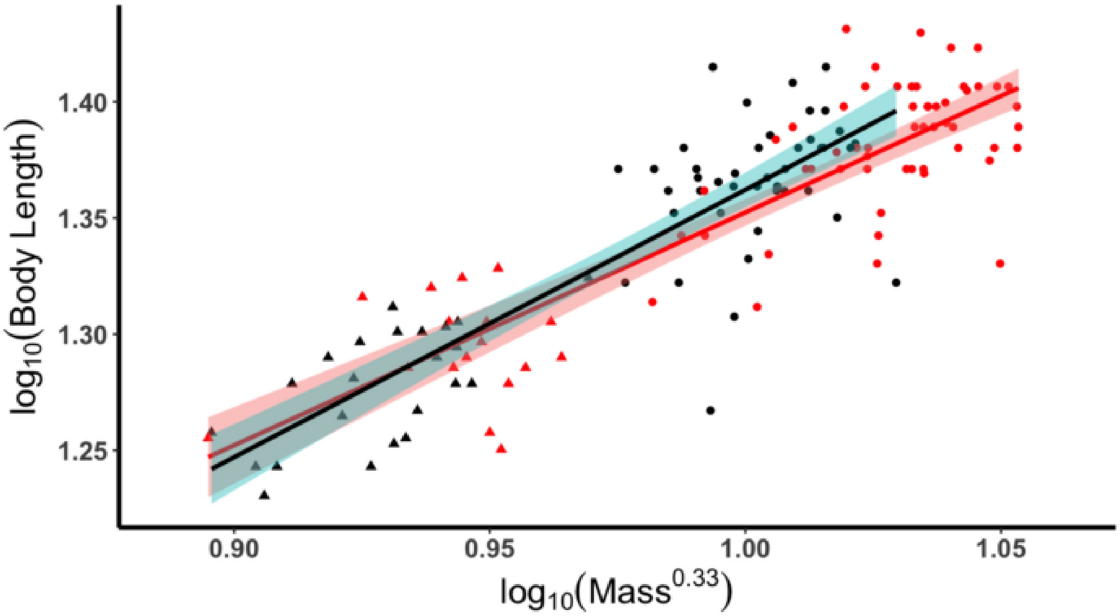

Figure 3. Body length [$\log_{10}$(cm)] plotted against the logged cube root of body mass for *Otolemur crassicaudatus* from Lajuma Research Centre, South Africa (2013–2019, 2021–2022). *Female data points are black* and *male data points are red*. *Triangles* illustrate subadults, while *circles* represent adults. OLS regression (*blue for females*, *red for males*) estimators are bounded by 95% confidence intervals on the slope (*blue for females*, *red for males*).

In females, scapula length, leg length, and hindlimb length can be distinguished from isometry, with significant positive allometry for scapula length and negative allometry for other allometric variables (Table IV). The correlation between forearm length and body mass falls just short of the $r = 0.70$ threshold and probably scales isometrically with body mass.

In males, five linear variables show correlations at or above $r = 0.70$, although three additional correlations are close to the correlation threshold. Most dimensions are probably allometric, while body, scapula, and arm lengths cannot be distinguished from isometry relative to mass (Table IV). Modestly correlated variables, including leg, forelimb, forearm, and leg lengths are negatively allometric, while scapula length is isometric. As with females, variables with limited correlations with mass show only small changes in size in concert with body mass, and early establishment of adult sizes.

Despite the difficulty of interpreting allometric relations between linear dimensions and mass, female regression coefficients usually exceed male coefficients (slopes match for arm and forearm lengths, Table IV). Given prevalence of negative allometries in males, steeper female slopes suggest that females experience somewhat less shape change per unit size than males. However, the lines rarely diverge by much, so females and males generally share ontogenetic regression lines for dimensions scaled against body mass. Specifically, confidence intervals for regressions overlap uniformly.

ANCOVAs for linear dimensions regressed against body mass show no significant sex differences in either slope or intercept, except for hindlimb length, with a higher female slope (Table V).

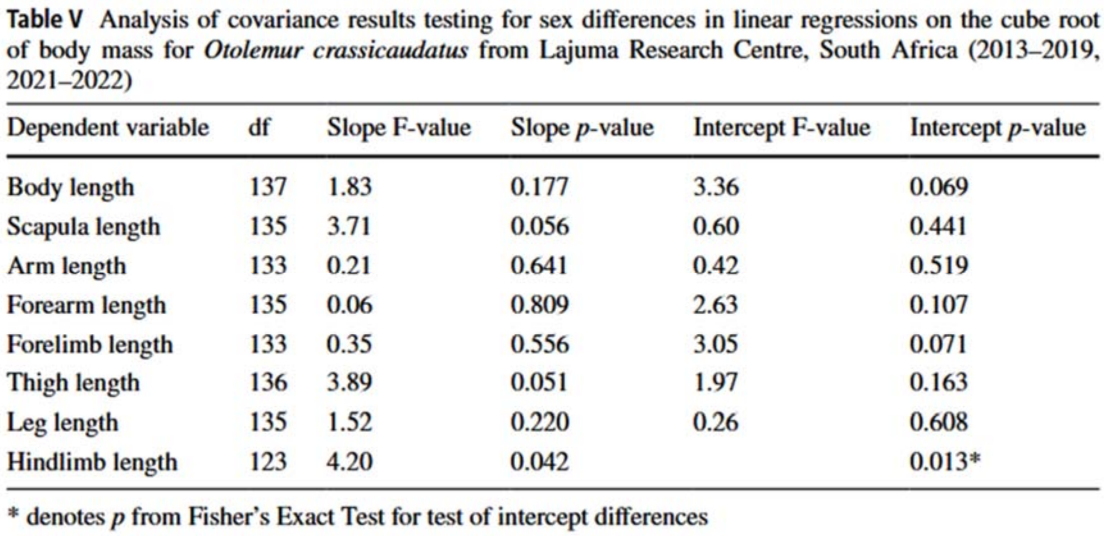

Table V Analysis of covariance results testing for sex differences in linear regressions on the cube root of body mass for *Otolemur crassicaudatus* from Lajuma Research Centre, South Africa (2013–2019, 2021–2022)

Dependent variable	df	Slope F-value	Slope *p*-value	Intercept F-value	Intercept *p*-value
Body length	137	1.83	0.177	3.36	0.069
Scapula length	135	3.71	0.056	0.60	0.441
Arm length	133	0.21	0.641	0.42	0.519
Forearm length	135	0.06	0.809	2.63	0.107
Forelimb length	133	0.35	0.556	3.05	0.071
Thigh length	136	3.89	0.051	1.97	0.163
Leg length	135	1.52	0.220	0.26	0.608
Hindlimb length	123	4.20	0.042		0.013*

* denotes *p* from Fisher's Exact Test for test of intercept differences

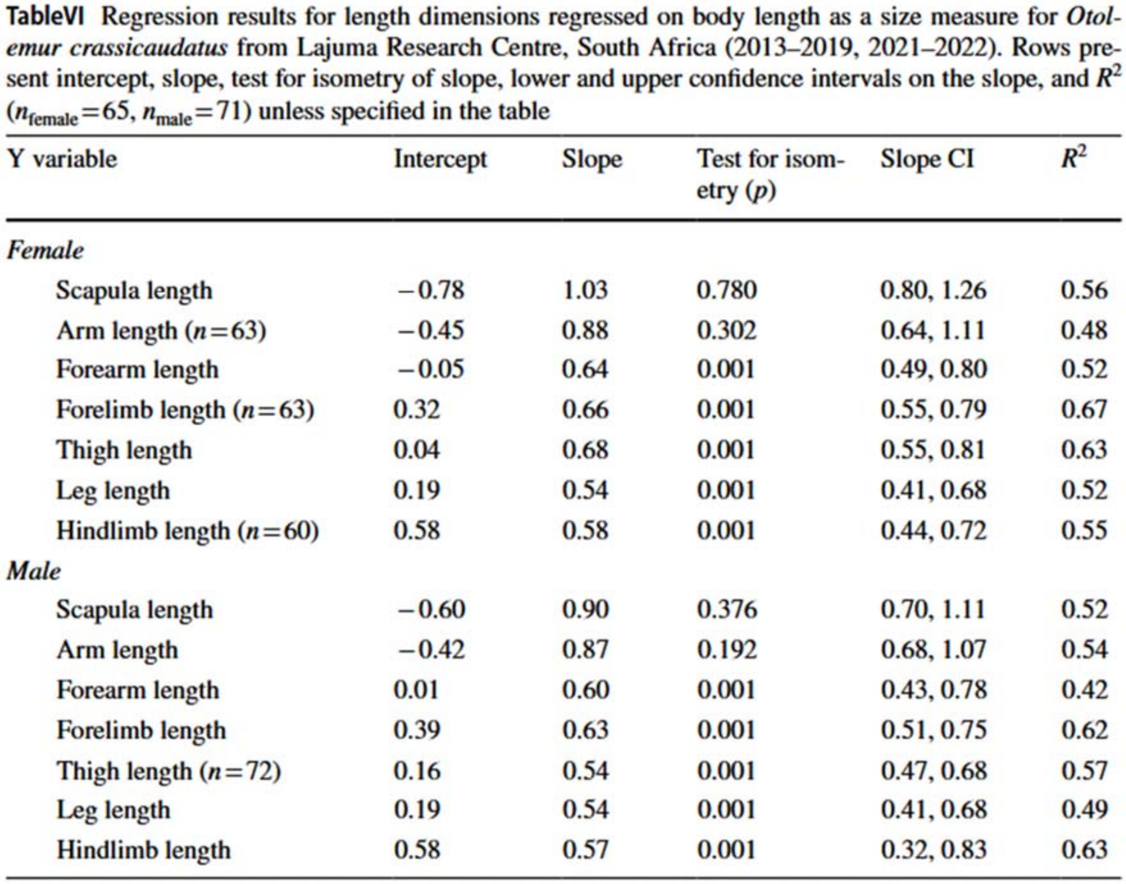

Table VI Regression results for length dimensions regressed on body length as a size measure for *Otolemur crassicaudatus* from Lajuma Research Centre, South Africa (2013–2019, 2021–2022). Rows present intercept, slope, test for isometry of slope, lower and upper confidence intervals on the slope, and R^2 ($n_{female}=65$, $n_{male}=71$) unless specified in the table

Y variable	Intercept	Slope	Test for isometry (*p*)	Slope CI	R^2
Female					
Scapula length	−0.78	1.03	0.780	0.80, 1.26	0.56
Arm length ($n=63$)	−0.45	0.88	0.302	0.64, 1.11	0.48
Forearm length	−0.05	0.64	0.001	0.49, 0.80	0.52
Forelimb length ($n=63$)	0.32	0.66	0.001	0.55, 0.79	0.67
Thigh length	0.04	0.68	0.001	0.55, 0.81	0.63
Leg length	0.19	0.54	0.001	0.41, 0.68	0.52
Hindlimb length ($n=60$)	0.58	0.58	0.001	0.44, 0.72	0.55
Male					
Scapula length	−0.60	0.90	0.376	0.70, 1.11	0.52
Arm length	−0.42	0.87	0.192	0.68, 1.07	0.54
Forearm length	0.01	0.60	0.001	0.43, 0.78	0.42
Forelimb length	0.39	0.63	0.001	0.51, 0.75	0.62
Thigh length ($n=72$)	0.16	0.54	0.001	0.47, 0.68	0.57
Leg length	0.19	0.54	0.001	0.41, 0.68	0.49
Hindlimb length	0.58	0.57	0.001	0.32, 0.83	0.63

Allometry of Linear Dimensions With Body Length

For length dimensions regressed against body length as a size measure, six regressions equal or exceed the correlation threshold of $r = 0.70$ for females, with six above this threshold for males (Table VI). Relative to body length, most male dimensions exceed female dimensions across all size ranges. In other words, male regression lines are transposed above female regression lines, indicating at least slight shape differences between males and females at all sizes (Table VI, Fig. 4).

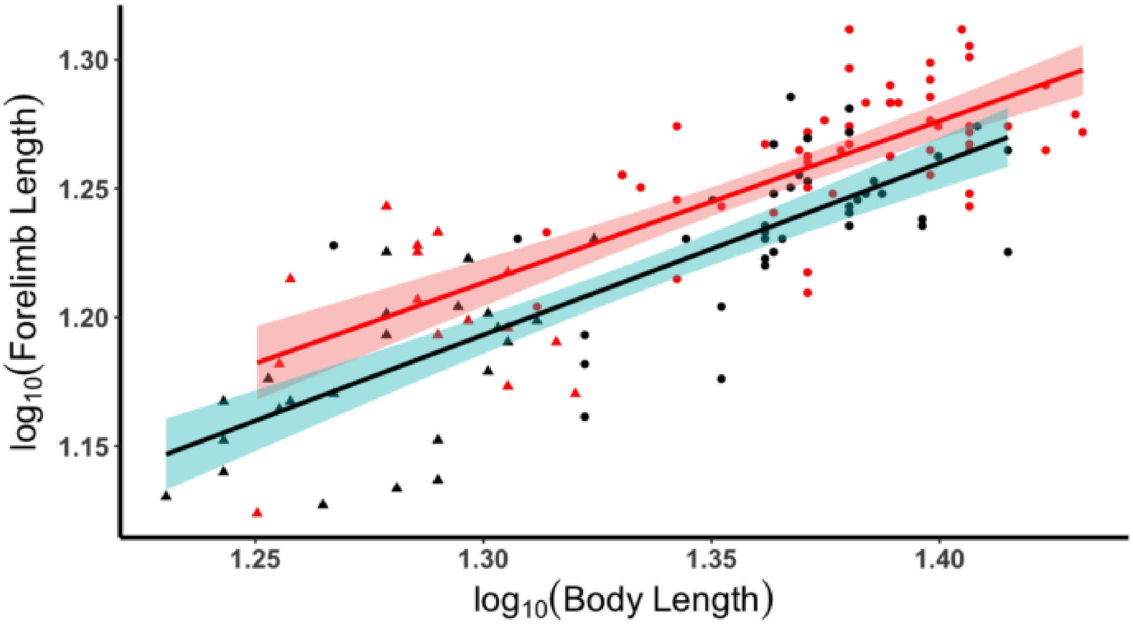

Figure 4. *Female data points are black* and *male data points are red. Triangles* illustrate subadults while *circles* represent adults. OLS regression estimates are bounded by 95% confidence intervals on the slope (*blue* for females, *red* for males).

Scapula length and arm lengths cannot be distinguished from isometry, while forelimb, thigh, leg, and hindlimb lengths are negatively allometric: small animals have relatively long limbs while limbs in larger animals are relatively short (Table VI). Patterns in males for relatively strongly correlated variables parallel those for females, with scapula length and arm length isometric, and thigh, leg, and forelimb lengths returning negatively allometric estimates. For both females and males, correlation analyses show independence of cheiridial dimensions and body length.

ANCOVAs show no significant slope differences for body segment lengths regressed against body length, while male intercepts are significantly higher than female intercepts, except for thigh length (Table VII). Despite overall lack of dimorphism in body dimensions, intercepts for male regression lines consistently exceed those of females in limb dimensions (Table VII, Fig. 4). Thus, males and females present different shapes at common sizes, with considerable overlap between sexes. However, because most dimensions are negatively allometric, the sexes share shapes through much of ontogeny. Even though the largest males are slightly beyond the female size range, negative allometry means that they share shapes with the largest females.

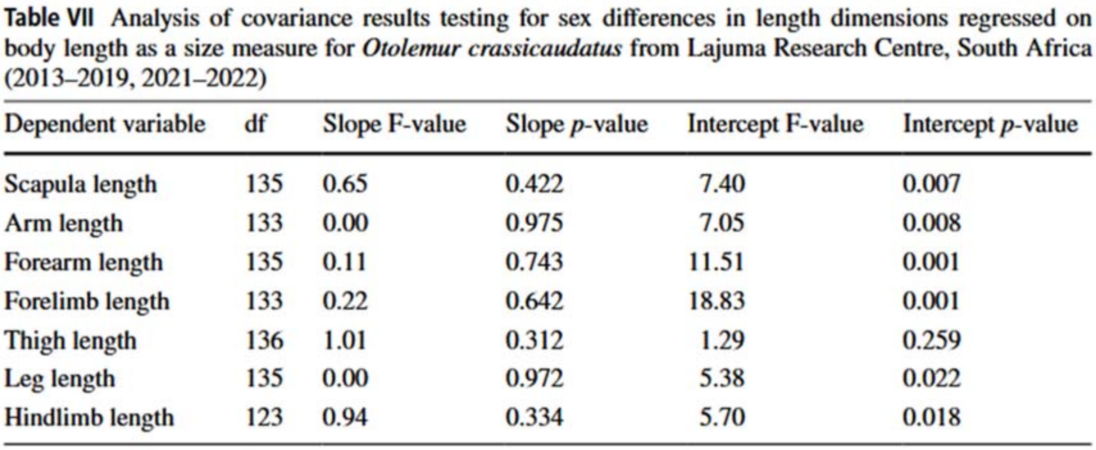

Table VII Analysis of covariance results testing for sex differences in length dimensions regressed on body length as a size measure for *Otolemur crassicaudatus* from Lajuma Research Centre, South Africa (2013–2019, 2021–2022)

Dependent variable	df	Slope F-value	Slope *p*-value	Intercept F-value	Intercept *p*-value
Scapula length	135	0.65	0.422	7.40	0.007
Arm length	133	0.00	0.975	7.05	0.008
Forearm length	135	0.11	0.743	11.51	0.001
Forelimb length	133	0.22	0.642	18.83	0.001
Thigh length	136	1.01	0.312	1.29	0.259
Leg length	135	0.00	0.972	5.38	0.022
Hindlimb length	123	0.94	0.334	5.70	0.018

Allometry of Circumferences with Body Mass

Comparatively strong correlations between circumferences and mass probably reflect the contribution of many tissues to both circumferences and body mass, whereas lengths primarily reflect dimensions of skeletal elements. Four circumference regressions are at or above the correlation threshold of $r = 0.70$ for females, with seven above this threshold for males (Table VIII). Male correlations are generally higher than female correlations.

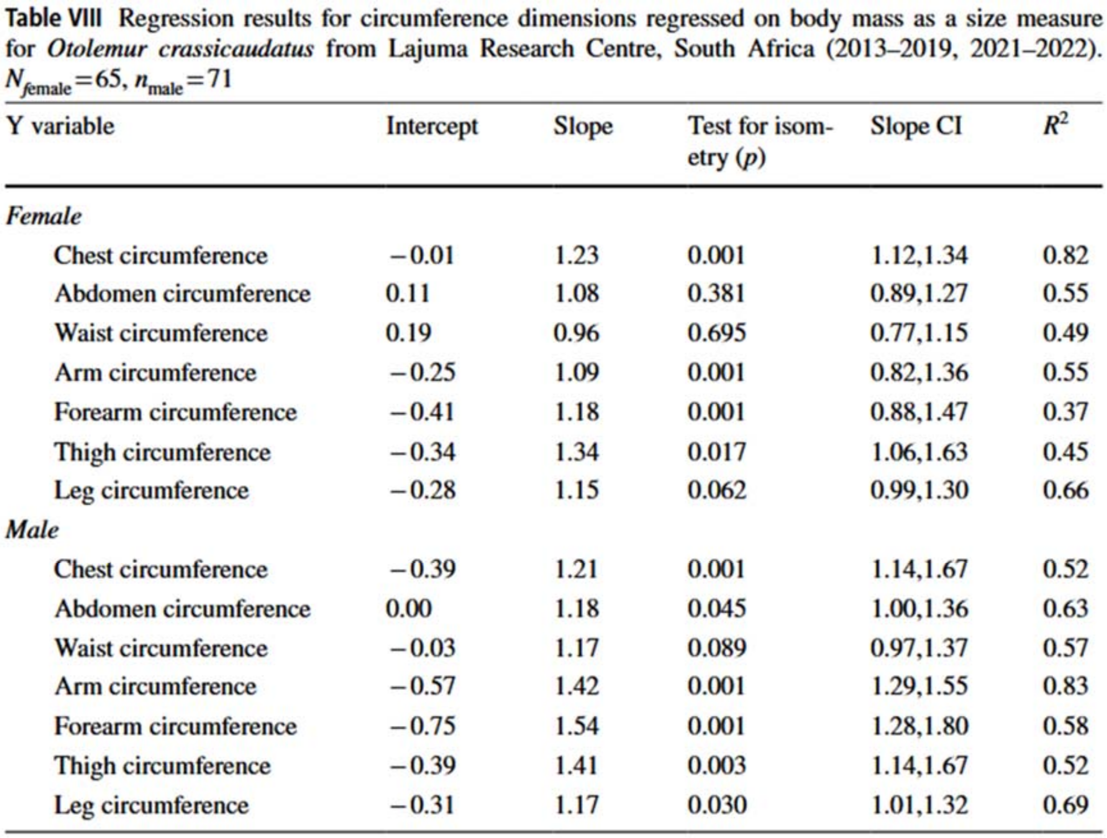

Table VIII Regression results for circumference dimensions regressed on body mass as a size measure for *Otolemur crassicaudatus* from Lajuma Research Centre, South Africa (2013–2019, 2021–2022). $N_{female}=65$, $n_{male}=71$

Y variable	Intercept	Slope	Test for isometry (*p*)	Slope CI	R^2
Female					
Chest circumference	−0.01	1.23	0.001	1.12,1.34	0.82
Abdomen circumference	0.11	1.08	0.381	0.89,1.27	0.55
Waist circumference	0.19	0.96	0.695	0.77,1.15	0.49
Arm circumference	−0.25	1.09	0.001	0.82,1.36	0.55
Forearm circumference	−0.41	1.18	0.001	0.88,1.47	0.37
Thigh circumference	−0.34	1.34	0.017	1.06,1.63	0.45
Leg circumference	−0.28	1.15	0.062	0.99,1.30	0.66
Male					
Chest circumference	−0.39	1.21	0.001	1.14,1.67	0.52
Abdomen circumference	0.00	1.18	0.045	1.00,1.36	0.63
Waist circumference	−0.03	1.17	0.089	0.97,1.37	0.57
Arm circumference	−0.57	1.42	0.001	1.29,1.55	0.83
Forearm circumference	−0.75	1.54	0.001	1.28,1.80	0.58
Thigh circumference	−0.39	1.41	0.003	1.14,1.67	0.52
Leg circumference	−0.31	1.17	0.030	1.01,1.32	0.69

Female and male regression lines overlap extensively for circumferences plotted against mass, although allometric coefficients for males are uniformly higher. Except for waist circumference, all male regressions appear to be positively allometric, probably significantly exceeding isometry. Shapes are generally similar throughout ontogeny, with males extending established scaling relations to larger size ranges (Fig. 5). Specifically, regression lines mostly overlap through the shared size range, then males exceed females in conjunction with larger body size. SSD in circumferences emerges among the largest adults.

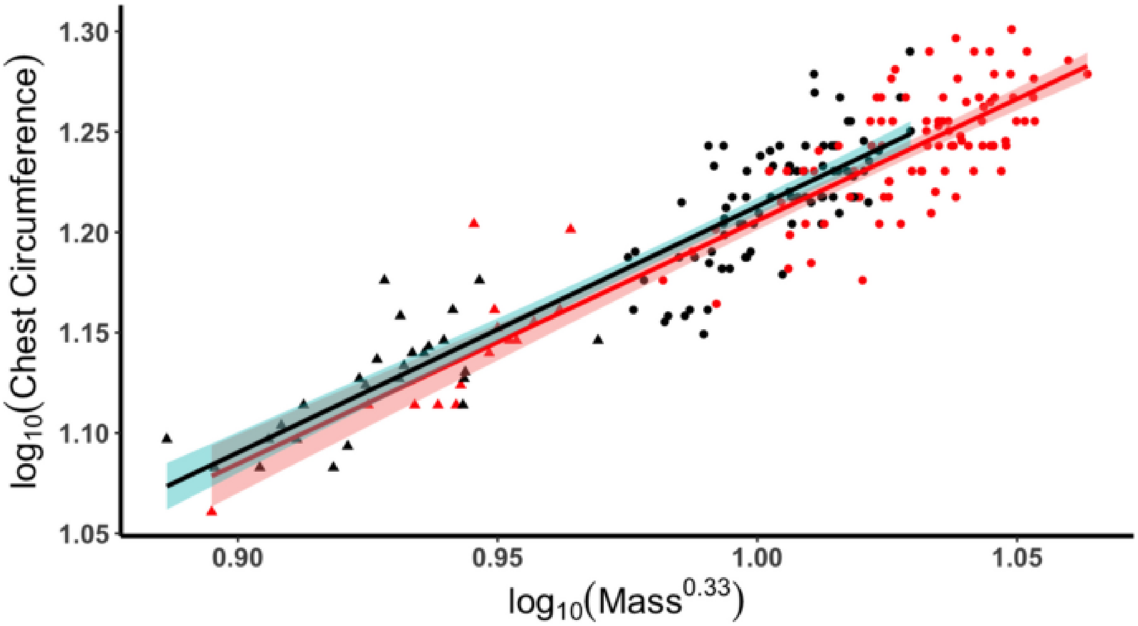

Fig. 5. Chest circumference regressed against body mass for *Otolemur crassicaudatus* from Lajuma Research Centre, South Africa (2013–2019, 2021–2022). *Female data points are black* and *male data points are red*. *Triangles* represent subadults while *circles* represent adults. OLS regression estimates are bounded by 95% confidence intervals on the slope (*blue* for females, *red* for males).

Positive allometries indicate that circumferences change shape substantially in males, in contrast to females, and males experience disproportionately large increases. This is particularly the case for arm circumference plots (Fig. 6), with limited overlap between males and females, and males extending well beyond the female distribution. The largest two dozen males (approximately 25% of the adult male observations) exceed all female points. These allometric trajectories produce exceptionally "bulky" males at all sizes as body mass increases. In addition, differences between females and males are most notable in the chest, arm, and forearm circumferences. Consequently, male circumference regressions differ substantially from those of females, thus producing clear SSD.

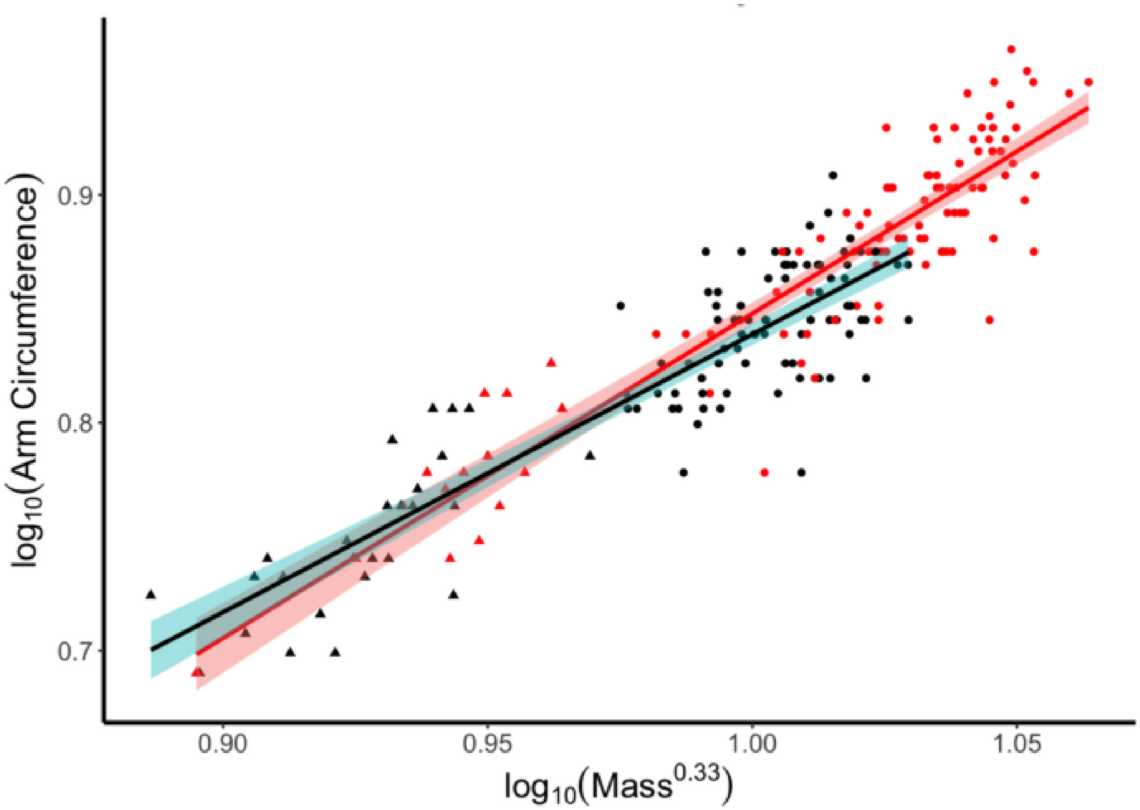

Fig. 6. Arm circumference regressed against body mass for *Otolemur crassicaudatus* from Lajuma Research Centre, South Africa (2013–2019, 2021–2022). *Female data points are black* and *male data points are red*. *Triangles* represent subadults while *circles* represent adults. OLS regression estimates are bounded by 95% confidence intervals on the slope (*blue* for females, *red* for males).

ANCOVAs show variation in the relations between female and male regression lines (Table IX). Arm regressions show significant differences in both slope and intercept, with males exceeding females. Slopes for chest, waist, and forearm circumferences against body mass for females and males cannot be distinguished from one another, while male intercepts exceed female intercepts for these variables. Regression lines cannot be distinguished by sex for the abdomen, thigh, and leg, although male adults extend beyond the female size range.

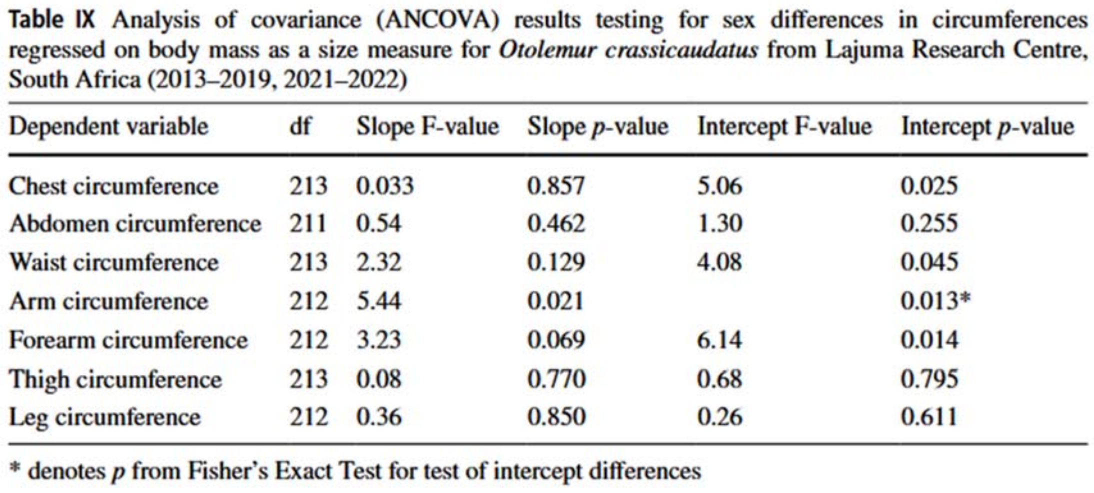

Table IX Analysis of covariance (ANCOVA) results testing for sex differences in circumferences regressed on body mass as a size measure for *Otolemur crassicaudatus* from Lajuma Research Centre, South Africa (2013–2019, 2021–2022)

Dependent variable	df	Slope F-value	Slope *p*-value	Intercept F-value	Intercept *p*-value
Chest circumference	213	0.033	0.857	5.06	0.025
Abdomen circumference	211	0.54	0.462	1.30	0.255
Waist circumference	213	2.32	0.129	4.08	0.045
Arm circumference	212	5.44	0.021		0.013*
Forearm circumference	212	3.23	0.069	6.14	0.014
Thigh circumference	213	0.08	0.770	0.68	0.795
Leg circumference	212	0.36	0.850	0.26	0.611

* denotes *p* from Fisher's Exact Test for test of intercept differences

Allometry of Circumferences with Body Length

Most circumference dimensions and body length show correlations near or above 0.70 (Table X). For females, regressions illustrate negative allometry, with male regressions ranging from negative allometry to slope values at either at or slightly above isometry (Table X). Low SSD and limited size change in body length drive negative allometries, with circumferences changing minimally relative to length. ANCOVAs indicate similarities in regression slopes, with significant intercept differences, except for waist circumference. Intercept differences indicate that males generally present larger circumferences throughout the size range (Table XI).

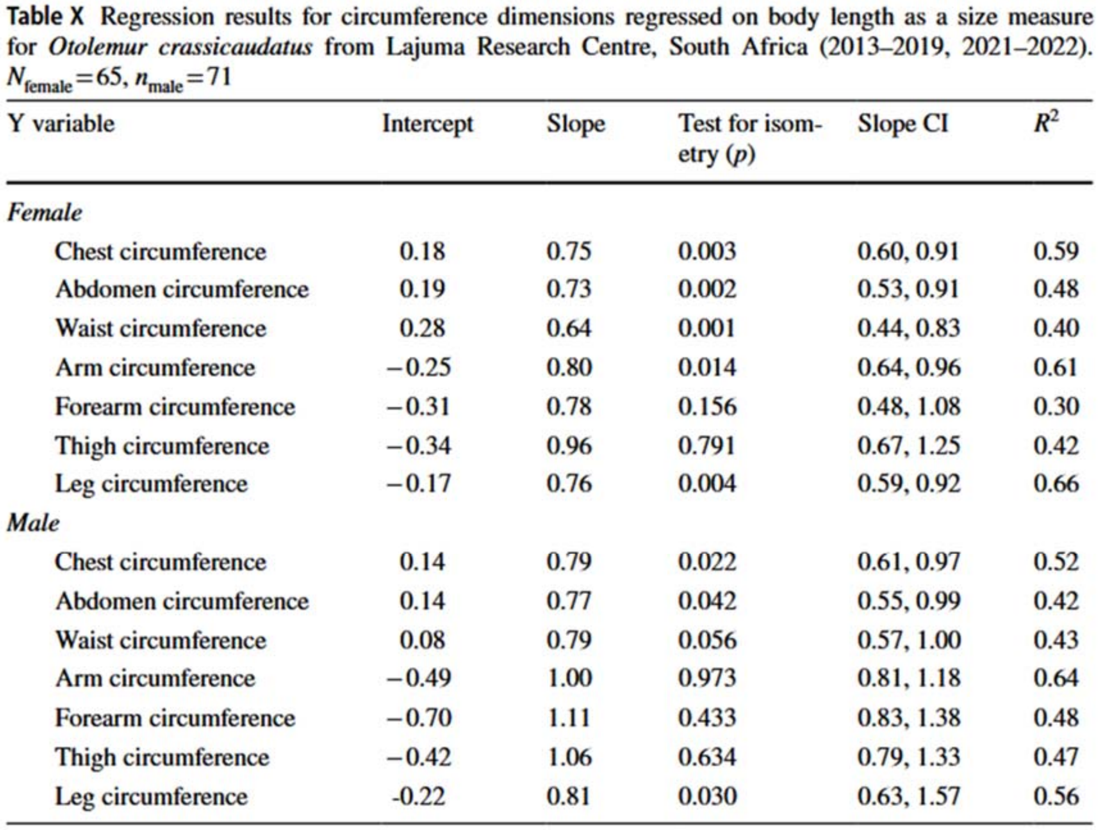

Table X Regression results for circumference dimensions regressed on body length as a size measure for *Otolemur crassicaudatus* from Lajuma Research Centre, South Africa (2013–2019, 2021–2022). $N_{\text{female}}=65$, $n_{\text{male}}=71$

Y variable	Intercept	Slope	Test for isometry (*p*)	Slope CI	R^2
Female					
Chest circumference	0.18	0.75	0.003	0.60, 0.91	0.59
Abdomen circumference	0.19	0.73	0.002	0.53, 0.91	0.48
Waist circumference	0.28	0.64	0.001	0.44, 0.83	0.40
Arm circumference	−0.25	0.80	0.014	0.64, 0.96	0.61
Forearm circumference	−0.31	0.78	0.156	0.48, 1.08	0.30
Thigh circumference	−0.34	0.96	0.791	0.67, 1.25	0.42
Leg circumference	−0.17	0.76	0.004	0.59, 0.92	0.66
Male					
Chest circumference	0.14	0.79	0.022	0.61, 0.97	0.52
Abdomen circumference	0.14	0.77	0.042	0.55, 0.99	0.42
Waist circumference	0.08	0.79	0.056	0.57, 1.00	0.43
Arm circumference	−0.49	1.00	0.973	0.81, 1.18	0.64
Forearm circumference	−0.70	1.11	0.433	0.83, 1.38	0.48
Thigh circumference	−0.42	1.06	0.634	0.79, 1.33	0.47
Leg circumference	-0.22	0.81	0.030	0.63, 1.57	0.56

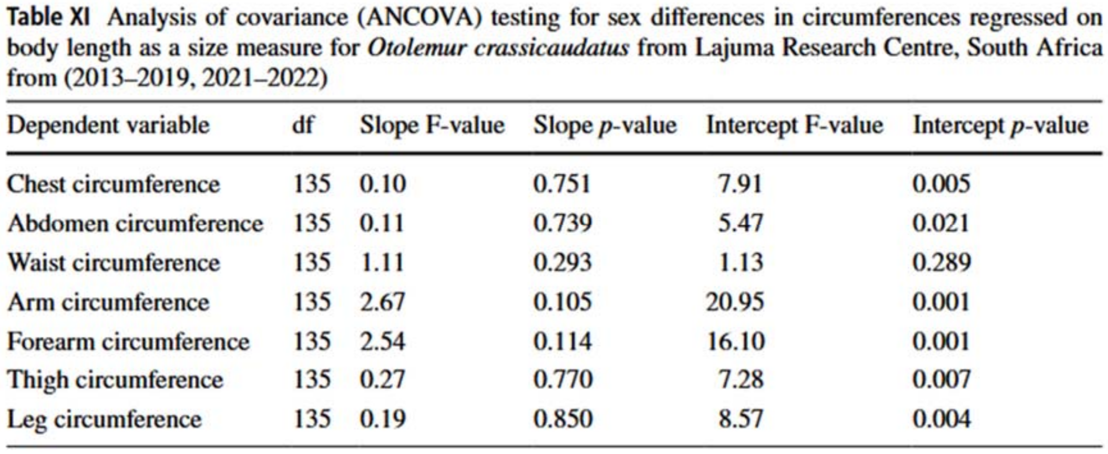

Table XI Analysis of covariance (ANCOVA) testing for sex differences in circumferences regressed on body length as a size measure for *Otolemur crassicaudatus* from Lajuma Research Centre, South Africa from (2013–2019, 2021–2022)

Dependent variable	df	Slope F-value	Slope *p*-value	Intercept F-value	Intercept *p*-value
Chest circumference	135	0.10	0.751	7.91	0.005
Abdomen circumference	135	0.11	0.739	5.47	0.021
Waist circumference	135	1.11	0.293	1.13	0.289
Arm circumference	135	2.67	0.105	20.95	0.001
Forearm circumference	135	2.54	0.114	16.10	0.001
Thigh circumference	135	0.27	0.770	7.28	0.007
Leg circumference	135	0.19	0.850	8.57	0.004

Discussion

Analyses of adult body mass and somatometric sexual size dimorphism (SSD) in *Otolemur crassicaudatus* from Lajuma Research Centre, South Africa reveal variable levels of SSD across body elements in adults. Similarly, allometric ontogenetic analyses of these variables reveal complex developmental bases of adult SSD. Body mass reaches moderately high SSD, while somatometrics uniformly show less SSD, and many body elements lack SSD entirely. Ontogenetic allometric analyses record differences among dimensions in how growth and development lead to adult SSD. Generally, when lengths are scaled against body mass, regressions overlap extensively. When lengths are regressed against body length as a size measure, male regressions are transposed above female regressions. Circumference dimensions are among the most dimorphic, with male circumference dimensions reaching large sizes by extending shared allometric trajectories. Minimal shape changes characterize regressions of circumferences on body length.

Patterns of Adult Dimorphism

With a male/female ratio of about 1.21, body mass SSD in *O. crassicaudatus* exceeds SSD both in other galagids and most other strepsirrhine primates by a substantial margin (Fleagle, 2013; Gordon, 2006; Kappeler, 1990, 1991; Leigh & Terranova, 1998). Only a few strepsirrhines, including *O. crassicaudatus, Galago senegalensis, Nycticebus pygmaeus*, and *Chierogaleus major*, potentially show levels of SSD at or above 1.20 (Table I), making SSD in our study population among the highest known for the strepsirrhines. Our data may resolve discrepancies among previously published estimates of body mass SSD in *O. crassicaudatus* (Table I).

The achievement of high body mass SSD does not translate to other body dimensions, although circumferences track body mass more closely than linear dimensions. Thus, body mass SSD appears to be "decoupled" from SSD in other dimensions; neither skeletal dimensions nor circumferences reach the level of SSD observed for mass. This suggests that mass is more responsive than other somatometrics to factors driving SSD, most importantly, sexual selection (Darwin, 1871; Fisher, 1930). Sexual selection in this species probably involves fairly high levels of intermale competition, reflected in higher numbers of injuries observed in males *versus* females (Sauther, personal observation). Male *O. crassicaudatus* tend to establish a territory that includes multiple females, and have been observed both tolerating and excluding other males (Clark, 1985), comparable to other galagids (Nekaris & Bearder, 2006). Males also appear to maintain distinct hierarchies of dominant and submissive individuals (Dalton, personal communication). They engage in highly agonistic behavior in experimental circumstances (Bearder & Doyle, 1974). These conditions may favor attempts to monopolize access to females, driving sexual selection.

Beyond mass, other dimorphic dimensions involve forelimb, chest, waist, and thigh circumferences, suggesting that males would appear to have large "upper" bodies and large thighs relative to females. These features could also be interpreted as responses to sexual selection, especially if intermale competition involves grappling with opponents. This pattern may differ from *Propithecus verreauxi verreauxi*, in which larger male leg dimensions seem to reflect selection on males related to chasing behaviors during mating instead of intermale competition (Lawler, 2007). *O. crassicaudatus* presents a "stocky" appearance, possibly driven by high levels of SSD in these dimensions. These features suggest that sexual selection has favored dissociation of mass from other dimensions, while "targeting" specific elements valuable in intermale competition, such as large torso and limb cross-sectional areas and underlying musculature, although female mate choice may certainly be involved in the evolution of this pattern of SSD. However, the mechanisms of sexual selection, including intermale competition, specifics of female mate choice, and sperm competition, remain complex and difficult to investigate, particularly in nocturnal species (Dixson, 1995).

These observations suggest that mass and its main components (muscle, fat, integument, etc.) can respond to sexual selection more readily than other anatomical elements, especially hard tissues. This could indicate that mass responds to sexual selection through elevated growth rates, extended growth, or some combination of these factors. In contrast, skeletal growth does not appear to be as responsive to sexual selection. Without data from known-age animals, these possibilities are difficult to test. However, these results imply that body mass can respond to sexual selection, while skeletal responses to sexual selection may be bounded by functional or biomechanical considerations. In other words, dimorphism in body mass, especially by adding to circumferences, may be the most direct route to sexual dimorphism in *O. crassicaudatus*.

The comparatively high level of *O. crassicaudatus* body size SSD may indicate that they do not face the same kinds of seasonal, life history, and growth duration constraints that appear to limit or preclude anatomical responses to sexual selection in other strepsirrhines (Gordon, 2006; Leigh and Terranova, 1998). Decoupling of skeletal dimensions and mass could suggest the presence of bimaturism (a sex difference in the age of maturation) as a driver of dimorphism, as has been observed in *Galago moholi* and *Otolemur garnettii* (O'Mara *et al.*, 2012) and in *Alouatta* (Mariotto *et al.*, 2024; Runestad Connour & Glander, 2020). Male *O. crassicaudatus* body mass growth "outstrips" growth of skeletal dimensions to produce adult SSD beyond female size ranges, possibly indicating that male body mass increases for a longer period than females. Males appear to grow at least past the size and perhaps age at which skeletal growth ceases for both females and males, given overall similarities and very limited dimorphism in nearly all skeletal sizes between sexes. Similarities in skeletal dimensions would seem to indicate that male and female growth rates are comparable at young ages. Thus, males probably respond at older ages to factors that typically lead to sexual size dimorphism, primarily sexual selection either through intermale competition or female mate choice (Darwin, 1871; Fisher, 1930). However, the skeletal system apparently has not responded to these selective forces, probably because skeletal growth ceases prior to the imposition of the strongest selective forces, thus "decoupling" mass and skeletal size dimorphisms in *O. crassicaudatus*. Unfortunately, the age at which skeletal growth ceases in *O. crassicaudatus* is unknown, either in captivity or in the wild. Older and limited data in captive samples classified as *Galago c. crassicaudatus* fail to show clear sex differences in maturation ages measured as age at first reproduction (Eaglen & Simons, 1980).

Circumference measures suggest that soft tissues influence body mass dimorphism substantially. Obviously, circumferences capture all components of tissue and mass growth (e.g., bone, fat, muscle and fascia, vessels, integument, and organs). Strongly positive forelimb allometries in males would also result in the emergence of SSD at preadult sizes and then throughout the adult size range. Positive allometries would also exaggerate male attributes.

The hypothesis that sexual selection has driven a response in intermale competition in *O. crassicaudatus* is clearly plausible. Dixson reports intermale competition more broadly in nocturnal strepsirrhines (1995). Haplorrhine primates that reach body mass SSD of about 1.20 include species and subspecies of chimpanzees, capuchins, squirrel monkeys, and colobine monkeys (Gordon, 2006). Modest levels of sexual selection via intermale competition would not be considered unusual for these species. In other words, species with dimorphism at about 1.20, such as *O. crassicaudatus*, probably experience at least some level of sexual selection, including obvious intermale competition. However, the possibility that *O. crassicaudatus* is unusual among galagos or strepsirrhines more broadly in attaining a comparatively high level of SSD may indicate the presence of unusual factors that can lead to a more general understanding of sexual selection in primates.

Ontogenetic Allometric Analyses

Scaling analyses investigating either body mass or body length reveal that limited SSD in linear dimensions results either from shared ontogenetic trajectories (regression lines) for body mass regressions that extend to different endpoints, or slight separations of regressions for dimensions in relation to body length. Many female regressions appear to be slightly elevated in regressions of lengths measured against body mass. These nominal differences of regression slopes are probably not biologically significant; we interpret this as a function of the preponderance of females in the smallest size ranges, which should be explored further. If this is not a result of sampling bias, it may reveal slight functional differences, with females typically nearer adult proportions or shapes than males throughout ontogeny. Overall, our findings suggest that male and female linear dimensions follow common allometric trajectories to different endpoints attributable to the attainment of larger body mass in males. While shapes attained by males differ from females, similar pathways produce these shapes. We interpret the attainment of different shapes through similar regression pathways as a “conservative” path to the slight skeletal size dimorphism in *O. crassicaudatus*. Overlapping regressions indicate similar shapes throughout ontogeny, and thus imply comparable functional capacities throughout ontogeny between the sexes.

For several length dimensions, low correlations with body mass reveal limited or even no change in a dimension relative to overall body size during ontogeny. For example, low correlations generally characterize distal limb dimensions, including cheiridia, especially foot, sole, and palm lengths (Jungers & Fleagle, 1980; Lawler, 2006; Runestad Connour & Glander, 2020), while stronger correlations characterize proximal limb elements (thigh, leg; arm, forearm).

In scaling analyses of linear or skeletal dimensions relative to body length, shapes differ between males and females throughout ontogeny, with longer male skeletal dimensions at all body lengths. At a given size, males would appear to have longer limbs than females in relation to length. However, negative allometry of limbs means that males and females share shapes throughout ontogeny; a longer male would have a shape like a shorter female. Similarities between sexes in shape throughout ontogeny may suggest maintenance of functional capabilities across a range of body lengths, despite proportional differences at common sizes. In contrast, large shape or proportional differences between sexes would require consideration of functional differences. For example, this could reflect differences in lever and load arms of limb bones, which could entail performance differences. While biomechanical analyses are beyond the scope of this analysis, similar shapes (at different sizes) in each sex imply functional similarities between sexes.

Scaling analyses of circumferences are more complicated than scaling analyses of length dimensions. Specifically, divergences between female and male regressions lines appear to be more common in circumferences, especially in the forelimb. Scaling of the arm is particularly striking in that a high male positive allometry extends male sizes and shapes well beyond those of females. Ultimately, this leads to higher levels of SSD in the forelimb, with levels of SSD ranking slightly lower than body mass. Scaling of male forelimb circumferences seems to play a relatively important role in contributing to overall SSD, with high regression slopes observed for these dimensions. At larger size ranges, males have relatively larger circumferences in the forelimb, with the arm being especially dimorphic among adults. With positive allometry, both dimorphism and shape differences emerge at smaller sizes than in other dimensions. Negative allometries in circumferences relative to body length indicate limited changes in shape.

Functional Implications

Our results reveal that *O. crassicaudatus* bodies, especially males, are "bulky" in relation to body length and skeletal dimensions, particularly in the forelimb, with positive allometries for circumferences. The implication for SSD is that male soft tissues surround a skeletal system that differs little in size and shape from that of females. Moreover, scaling analyses indicate that circumference size growth, especially positive forelimb allometries, contributes significantly to overall body size dimorphism. Not only would males appear bulky, but the upper limb may also seem especially so, carrying disproportionately more mass than females and with a relatively large share of tissue contributing to body mass located in the forelimb, leading to a "top-heavy" appearance.

Our findings may have biomechanical implications. For instance, differences in mass without comparable differences in skeletal lengths may affect functional capacities by sex, especially if the torso and upper limb are disproportionately large. Simply put, female and male musculoskeletal systems with similar limb dimensions must move animals with substantially different distributions of body mass. This implies that skeletal levers and moment arms are comparable between sexes, with differences in both body mass and the allocation of body mass. Mass distribution may have functional implications beyond locomotion. For example, larger forelimb dimensions may suggest greater forelimb muscle mass, which could affect climbing, intermale competition, leaping, or other behaviors.

These possible functional considerations suggest that generalized quadrupedalism in *O. crassicaudatus* (Charles-Dominique, 1977; Crompton, 1983, 1984; Lewton & Patel, 2020; Walker, 1979) may be compatible with the evolution of relatively strong SSD in this species, contrasting with galagids that leap frequently. Leaping may be incompatible with the shapes of *O. crassicaudatus* (high body mass SSD localized to the "upper" body) in the absence of changes in limb proportions. Thus, decoupling limbs from body mass may be an important factor in the evolution of *O. crassicaudatus* dimorphism. A comparison with sympatric *Galago moholi* may be instructive, given frequent leaping and a much smaller mean body mass than *O. crassicaudatus* (body mass ranges from around 155 g in females to 185 g in males in *G. moholi*, depending on the source [Kappeler, 1991; Smith & Jungers, 1997]).

Developmental evidence may also provide insights into locomotion and SSD in *O. crassicaudatus*. Specifically, subadults leap more frequently than adults (Crompton, 1983). This may indicate that limb proportions and mass distributions of subadults at smaller masses are compatible with leaping. However, the growth of body mass, torso, and limb elements beyond skeletal dimensions may subsequently restrict these behaviors. Overall, there may be a tradeoff between leaping behaviors and sexual dimorphism in *O. crassicaudatus*.

Implications for the Fossil Record

The broad anatomical view of SSD afforded by this study has important implications for understanding SSD in the fossil record, including the difficult task of reconstructing body mass from skeletal dimensions (Elliott *et al*., 2016). Specifically, decoupling of body mass from skeletal dimensions indicates that skeletal lengths may not reliably reflect total levels of body size dimorphism in fossils. While skeletal length sexual dimorphism is generally lower than body mass dimorphism, SSD in the skeleton and dentition can be informative about behavior (Plavcan, 2001). Several of our findings complicate interpretations of SSD in the fossil record. First, decoupling skeletal dimensions and body mass increases the complexity of reconstructing body mass dimorphism. Second, sex differences in the distribution of tissues (e.g., "top heavy" males) may not be clearly reflected by skeletal materials, although we might predict corresponding variation in bone geometry (beyond length) in anatomical regions with more tissue. Third, different scaling patterns related to different independent variables (mass or length) may complicate allometric analyses of fossils. Finally, the possibility of locomotor tradeoffs with SSD could complicate interpretations of SSD in species in the absence of information about locomotor behaviors. Analyses of bone geometry in this species may help tie SSD in mass to the skeleton more closely than the present analyses of lengths (cf. Elliott *et al*., 2016; Niskanen & Ruff, 2018).

Conclusions

This study illustrates complex developmental bases of sexual size dimorphism (SSD) in *Otolemur crassicaudatus* based on allometric ontogenetic analyses from a large sample of individually known, wild animals. We establish that adult body mass sexual size dimorphism (SSD) in *O. crassicaudatus* probably reaches the highest known level for strepsirrhine primates, with male mean body mass approximately 1.21 times larger than female body mass. High body mass dimorphism accompanies lower levels of sexual size dimorphism in other dimensions, including linear dimensions representing skeletal dimensions and body circumferences. Moderate dimorphism in circumferences contributes significantly to overall body mass dimorphism. Body length and other skeletal measures of SSD are decoupled from both body mass and circumference SSDs. Analyses of ontogenetic allometry show that scaling relations between linear dimensions and measures of overall size (body mass and body length) differ by size measure. Circumference allometries result from steeper male regressions compared to female regressions, contributing significantly to overall body mass dimorphism. Sexual selection through intermale competition probably accounts for body mass sexual size dimorphism in *O. crassicaudatus*. The skeletal system does not seem to have responded to sexual selection, so that body mass dimorphism mainly involves larger quantities of soft tissue mass in males than in females. Similarly sized female and male skeletons support different amounts of soft tissue, distributed differentially across the body and localizing SSD. Generalized quadrupedalism, with limited leaping behaviors, may be involved in reducing tradeoffs between sexual selection and the evolution of SSD and locomotor behaviors. Our analyses have important implications for reconstructing both size and SSD in fossil samples.

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Contributions

MLS and FPC conceived of the project, secured funding, undertook field investigations, and collected morphometric data. ASWT and IVW ensured proper veterinary care upon capture. SRL conducted analyses, and, with MLS and FPC, wrote the manuscript.

Conflict of Interest

The authors declare that they have no conflict of interest.

References

Bearder, S. K., & Doyle, G. A. (1974). Field and laboratory studies of social organization in bushbabies (*Galago senegalensis*). *Journal of Human Evolution, 3*, 37–50

Bonduriansky, R. (2007). Sexual selection and allometry: A critical reappraisal of the evidence and ideas. *Evolution International Journal of Organization Evolution*, *61*(4), 838–849. http://www.hubmed.org/display.cgi?uids=17439616

Boulinguez-Ambroise, G., Herrel, A., Berillon, G., Young, J. W., Cornette, R., Meguerditchian, A., et al. (2021). Increased performance in juvenile baboons is consistent with ontogenetic changes in morphology. *American Journal of Physical Anthropology, 175*(3), 546–558. https://doi.org/10.1002/AJPA.24235

Burrows, A.M. and Nash, L. T. (2010). Searching for dental signals of exudativory in galagos. In *The evolution of exudativory in primates. developments in primatology: Progress and prospects* (pp. 211–233). Springer

Charles-Dominique, P. (1977). *Ecology and behavior of nocturnal primates*. Columbia University Press

Cheverud, J. M. (1982). Relationships among ontogenetic, static, and evolutionary allometry. *American Journal of Physical Anthropology,* *59*(2), 139–149. https://doi.org/10.1002/ajpa.1330590204

Clark, A. B. (1985). Sociality in a nocturnal "solitary" prosimian: *Galago crassicaudatus*. *International Journal of Primatology, 6*, 581–600

Crompton, R. H. (1983). Age differences in locomotion of two subtropical galaginae. *Primates, 24*(2), 241–259. https://doi.org/10.1007/BF02381086

Crompton, R. H. (1984). Foraging, habitat structure, and locomotion in two species of Galago. In P. S. Rodman & J. G. H. Cant (Eds.), *Adaptations for foraging in nonhuman primates* (pp. 73–111). Columbia University Press

Darwin, C. (1871). *The descent of man, and selection in relation to sex*. D. Appleton and Co

Demes, B., Jungers, W. L., Gross, T. S., & Fleagle, J. G. (1995). Kinetics of leaping primates: Influence of substrate orientation and compliance. *American Journal of Physical Anthropology, 96*(4), 419–429. https://doi.org/10.1002/ajpa.1330960407

Dixson, A. F. (1995). Sexual selection and the evolution of copulatory behavior in nocturnal prosimians. In L. Alterman, G. Doyle, & M. K. Izard (Eds.), *Creatures of the dark: The nocturnal prosimians* (pp. 93–118). Springer Science + Business Media LLC

Druelle, F., Aerts, P., & Berillon, G. (2016). Effect of body mass distribution on the ontogeny of positional behaviors in non-human primates: Longitudinal follow-up of infant captive olive baboons (*Papio anubis*). *American Journal of Primatology, 78*(11), 1201–1221. https://doi.org/10.1002/AJP.22575

Druelle, F., Aerts, P., D'Aoȗt, K., Moulin, V., & Berillon, G. (2017a). Segmental morphometrics of the olive baboon (*Papio anubis*): A longitudinal study from birth to adulthood. *Journal of Anatomy, 230*(6), 805–819. https://doi.org/10.1111/JOA.12602

Druelle, F., Berillon, G., & Aerts, P. (2017b). Intrinsic limb morpho-dynamics and the early development of interlimb coordination of walking in a quadrupedal primate. *Journal of Zoology, 301*(3), 235–247. https://doi.org/10.1111/JZO.12423

Druelle, F., Young, J. W., & Berillon, G. (2018). Behavioral implications of ontogenetic changes in intrinsic hand and foot proportions in olive baboons (*Papio anubis*). *American Journal of Physical Anthropology, 165*(1), 65–76. https://doi.org/10.1002/AJPA.23331

Eaglen, R. H., & Simons, E. L. (1980). Notes on the breeding biology of thick-tailed and silvery galagos in captivity. *Journal of Mammology, 61*, 534–537

Elliott, M., Kurki, H., Weston, D. A., & Collard, M. (2016). Estimating body mass from skeletal material: New predictive equations and methodological insights from analyses of a known-mass sample of humans. *Archaeological and Anthropological Sciences, 8*, 731–750. https://doi.org/10.1007/s12520-015-0252-5

Feiner, N., Jackson, I. S. C., Van Der Cruyssen, E., & Uller, T. (2021). A highly conserved ontogenetic limb allometry and its evolutionary significance in the adaptive radiation of Anolis lizards. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1953). https://doi.org/10.1098/rspb.2021.0226

Fisher, R. A. (1930). *The genetical theory of natural selection*. Clarendon Press

Fleagle, J. G. (2013). *Primate adaptation and evolution* (Third Ed.). Elsevier, Inc

Gordon, A. D. (2006). Scaling of size and dimorphism in primates II: Macroevolution. *International Journal of Primatology, 27*, 63–105. https://doi.org/10.1007/s10764-005-9004-1

Gould, S. J. (1966). Allometry and size in ontogeny and phylogeny. *Biological Reviews of the Cambridge Philosophical Society, 41*(4), 587–640. https://doi.org/10.1111/J.1469-185X.1966.TB01624.X

Gould, S. J. (1977). *Ontogeny and phylogeny*. Belknap Press of Harvard University Press

Haraway, D. J. (1989). *Primate visions: Gender, race, and nature in the world of modern science*. Routledge

Harcourt, C. (1986). Seasonal variation in the diet of South African galagos. *International Journal of Primatology, 7*(5), 491–506

Jungers, W. L. (1985). Body size and scaling of limb proportions in primates. *Size and Scaling in Primate Biology, 1985*, 345–381. https://doi.org/10.1007/978-1-4899-3647-9_16

Jungers, W. L., & Fleagle, J. G. (1980). Postnatal growth allometry of the extremities in *Cebus albifrons* and *Cebus apella*: A longitudinal and comparative study. *American Journal of Physical Anthropology, 53*(4), 471–478. https://doi.org/10.1002/AJPA.1330530403

Kappeler, P. M. (1990). The evolution of sexual size dimorphism in prosimian primates. *American Journal of Primatology, 21*(3), 201–214. https://doi.org/10.1002/AJP.1350210304

Kappeler, P. M. (1991). Patterns of sexual dimorphism in body weight among prosimian primates. *Folia Primatologica, 57*(3), 132–146. https://doi.org/10.1159/000156575

Klingenberg, C. P. (2007). Heterochrony and allometry: The analysis of evolutionary change in ontogeny. *Biological Reviews, 73*(1), 79–123. https://doi.org/10.1111/j.1469-185X.1997.tb00026.x

Kieser, J. A. (1990). Craniometric allometry in the thicktailed bushbaby *Otolemur crassicaudatus*. *Primates, 31*, 273–281

Kieser, J. A., & Groeneveld, H. T. (1989). Patterns of sexual dimorphism and of variability in the dentition of *Otolemur crassicaudatus*. *International Journal of Primatology, 10*, 137–147

Lawler, R. R. (2006). Sifaka positional behavior: Ontogenetic and quantitative genetic approaches. *American Journal of Physical Anthropology, 131*(2), 261–271. https://doi.org/10.1002/ajpa.20430

Lawler, R. R. (2007). Fitness and extra-group reproduction in male Verreaux's sifaka: An analysis of reproductive success from 1989 to 1999. *American Journal of Physical Anthropology, 132*, 267–277. https://doi.org/10.1002/ajpa.20507

Leigh, S. R. (1992). Patterns of variation in the ontogeny of primate body size dimorphism. *Journal of Human Evolution, 23*(1), 27–50

Leigh, S. R. (1995). Socioecology and the ontogeny of sexual size dimorphism in anthropoid primates. *American Journal of Physical Anthropology, 97*(4), 339–356. https://doi.org/10.1002/ajpa.1330970402

Leigh, S. R. (2007). Homoplasy and the evolution of ontogeny in papionin primates. *Journal of Human Evolution, 52*(5), 536–558. https://doi.org/10.1016/j.jhevol.2006.11.016

Leigh, S. R., & Bernstein, R. M. (2006). Ontogeny, life history, and maternal investment in baboons. In L. Swedell & S. R. Leigh (Eds.), *Reproduction and fitness in baboons: Behavioral, ecological, and life history perspectives* (pp. 225–256). Springer

Leigh, S.R., & Cheverud, J. M. (1989). A finite element scaling study of growth, allometry, and sexual dimorphism in the baboon skull (*Papio* sp.). *American Journal of Physical Anthropology*, *78(2)*, 259–260

Leigh, S. R., & Cheverud, J. M. (1991). Sexual dimorphism in the baboon facial skeleton. *American Journal of Physical Anthropology, 84*(2), 193–208. https://doi.org/10.1002/ajpa.1330840209

Leigh, S. R., Setchell, J. M., Charpentier, M., Knapp, L. A., & Wickings, E. J. (2008). Canine tooth size and fitness in male mandrills (*Mandrillus sphinx*). *Journal of Human Evolution, 55*(1), 75–85. https://doi.org/10.1016/j.jhevol.2008.01.001

Leigh, S. R., & Shea, B. T. (1995). Ontogeny and the evolution of adult body size dimorphism in apes. *American Journal of Primatology, 36*(1), 37–60. https://doi.org/10.1002/AJP.1350360104

Leigh, S. R., & Terranova, C. J. (1998). Comparative perspectives on bimaturism, ontogeny, and dimorphism in lemurid primates. *International Journal of Primatology, 19*(4), 723–749

Lewton, K. L., & Patel, B. A. (2020). Calcaneal elongation and bone strength in leaping galagids. *American Journal of Physical Anthropology, 171*(3), 430–438. https://doi.org/10.1002/ajpa.23970

Li, Y, Huang, Z., Yang, Y., He, X., Pan, R., He, X-B., Pan, R., He, X-M., Yank, G, Wu, H, Cui, L, Xiao, , & W. (2023) Ontogenetic development of sexual dimorphism in body mass of wild black-and-white snubnose monkey (*Rhinopithecus bieti*). *Animals*, *13*(9), 1576). https://doi.org/10.3390/ani13091576

Long, C., Tordiffe, A., Sauther, M., Cuozzo, F., Millette, J., Ganswindt, A., & Scheun, J. (2021). Seasonal drivers of faecal glucocorticoid metabolite concentrations in an African strepsirrhine primate, the thick-tailed greater galago (*Otolemur crassicaudatus*). *Conservation Physiology, 9*(1), 1–15. https://doi.org/10.1093/conphys/coab081

Lumer, H., & Schultz, A. H. (1941). Relative growth of the limb segments and tail in macaques. *Human Biology, 13*(3), 282–305

Mariotto, L. F., Dada, A. N., Campos da Silva, T., Beirith, A., Francisco, S. R. S., de Souza Junior, J. C., et al. (2024). Growth and allometric curves of southern brown howler monkey (*Alouatta guariba*): Insights on its ontogeny and conservation. *American Journal of Primatology, 86*(6), e23675. https://doi.org/10.1002/ajp.23675

Nekaris, K. A. I., & Bearder, S. K. (2006). The Lorisiform primates of and mainland Africa. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. M. Stumpf (Eds.), *Primates in perspective* (pp. 23–72). Oxford University Press

Niskanen, M. and Ruff, C.B. (2018). Body size and shape reconstruction. In C.B. Ruff (Ed.), *Skeletal variation and adaptation in Europeans: Upper Paleolithic to the twentieth century* (pp. 15–37). John Wiley & Sons. https://doi.org/10.1002/9781118628430.ch2

O'Mara, M. T., Gordon, A. D., Catlett, K. K., Terranova, C. J., & Schwartz, G. T. (2012). Growth and the development of sexual size dimorphism in lorises and galagos. *American Journal of Physical Anthropology, 147*(1), 11–20. https://doi.org/10.1002/AJPA.21600

Penna, A., & Pozzi, L. (2024). Hidden in the Dark: A Review of Galagid Systematics and Phylogenetics. *International Journal of Primatology, 5*, 1–34. https://doi.org/10.1007/s10764-024-00430-w

Pereira, M. E., & Leigh, S. R. (2003). Modes of primate development. In P. M. Kappeler & M. E. Pereira (Eds.), *Primate life histories and socioecology* (pp. 149–176). Univ Chicago Press

Phukuntsi, M. A., du Plessis, M., Dalton, D. L., Jansen, R., Cuozzo, F. P., Sauther, M. L., & Kotze, A. (2020). Population genetic structure of the thick-tailed bushbaby (*Otolemur crassicaudatus*) from the Soutpansberg Mountain range, Northern South Africa, based on four mitochondrial DNA regions. *Mitochondrial DNA Part A: DNA Mapping, Sequencing, and Analysis, 31*(1), 1–10. https://doi.org/10.1080/24701394.2019.1694015

Plavcan, J. M. (2001). Sexual dimorphism in primate evolution. *Yearbook of Physical Anthropology, 44*, 25–53. https://doi.org/10.1002/AJPA.10011

Plavcan, J. M. (2002). Taxonomic variation in the patterns of craniofacial dimorphism in primates. *Journal of Human Evolution, 42*(5), 579–608. https://doi.org/10.1006/jhev.2001.0542

Plavcan, J. M. (2012). Sexual size dimorphism, canine dimorphism, and male–male competition in primates: Where do humans fit in? *Human Nature, 23*(1), 45–67. https://doi.org/10.1007/s12110-012-9130-3

R Core Team. (2022). R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing

Ravosa, M. J. (1998). Cranial allometry and geographic variation in slow lorises (*Nycticebus*). *American Journal of Primatology, 45*(3), 225–243

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

Rehg, J. A., & Leigh, S. R. (1999). Estimating sexual dimorphism and size differences in the fossil record: A test of methods. *American Journal of Physical Anthropology, 110*(1), 95–104

Runestad Connour, J., & Glander, K. E. (2020). Sexual dimorphism and growth in Alouatta palliata based on 20+ years of field data. *American Journal of Physical Anthropology, 172*(4), 545–566. https://doi.org/10.1002/ajpa.24055

SAS Institute, Inc. (2022) JMP® Version 17.0.0. SAS Institute

Sauther, M. L., Millette, J. B., Cuozzo, F. P., Long, C., Msimango, V. H., & Confuron, L. (2024). Environmental effects on nocturnal encounters of two sympatric bushbabies, Galago moholi and Otolemur crassicaudatus, in a high-altitude South African northern mistbelt montane habitat. *International Journal of Primatology*. https://doi.org/10.1007/s10764-024-00427-5

Schaefer, M. S., & Nash, L. T. (2007). Limb growth in captive *Galago senegalensis*: Getting in shape to be an adult. *American Journal of Primatology, 69*(1), 104–112. https://doi.org/10.1002/AJP.20330

Setchell, J. M., Lee, P. C., Jean Wickings, E., & Dixson, A. F. (2001). Growth and ontogeny of sexual size dimorphism in the mandrill (*Mandrillus sphinx*). *American Journal of Physical Anthropology, 115*(4), 349–360. https://doi.org/10.1002/AJPA.1091

Shapiro, L. J., & Raichlen, D. A. (2006). Limb proportions and the ontogeny of quadrupedal walking in infant baboons (*Papio cynocephalus*). *Journal of Zoology, 269*(2), 191–203. https://doi.org/10.1111/J.1469-7998.2006.00082.X

Shea, B. T. (1981). Relative growth of the limbs and trunk in the African apes. *American Journal of Physical Anthropology, 56*(2), 179–201. https://doi.org/10.1002/AJPA.1330560209

Shea, B. T. (1983). Allometry and heterochrony in the African apes. *American Journal of Physical Anthropology, 62*(3), 275–289. https://doi.org/10.1002/AJPA.1330620307

Shea, B. T. (1984). An allometric perspective on the morphological and evolutionary relationships between pygmy (*Pan paniscus*) and common (*Pan troglodytes*) chimpanzees. *The Pygmy Chimpanzee, 1984*, 89–130. https://doi.org/10.1007/978-1-4757-0082-4_6

Shea, B. T. (1985a). The ontogeny of sexual dimorphism in the African apes. *American Journal of Primatology, 8*(2), 183–188. https://doi.org/10.1002/AJP.1350080208

Shea, B. T. (1985b). On aspects of skull form in African apes and orangutans, with implications for hominoid evolution. *American Journal of Physical Anthropology, 68*(3), 329–342. https://doi.org/10.1002/ajpa.1330680304

Shea, B. T., & Bailey, R. C. (1996). Allometry and adaptation of body proportions and stature in African pygmies. *American Journal of Physical Anthropology, 100*(3), 311–340

Smith, R. J., & Jungers, W. L. (1997). Body mass in comparative primatology. *Journal of Human Evolution, 32*(6), 523–559. https://doi.org/10.1006/jhev.1996.0122

Sokal, R. R., & Rohlf, F. J. (1995). *Biometry: The principles and practice of statistics in biological research* (Vol. 3). Freeman

Turcotte, C. M., Mann, E. H. J., Stock, M. K., Villamil, C. I., Montague, M. J., Dickinson, E., et al. (2022). The ontogeny of sexual dimorphism in free-ranging rhesus macaques. *American Journal of Biological Anthropology, 177*(2), 314–327. https://doi.org/10.1002/AJPA.24442

Turner, T. R., Anapol, F., & Jolly, C. J. (1997). Growth, development, and sexual dimorphism in vervet monkeys (*Cercopithecus aethiops*) at four sites in Kenya. *American Journal of Physical Anthropology, 103*(1), 19–35

Turnquist, J. E., & Wells, J. P. (1994). Ontogeny of locomotion in rhesus macaques (*Macaca mulatta*): I. Early postnatal ontogeny of the musculoskeletal system. *Journal of Human Evolution*, *26*(5–6), 487–499. https://doi.org/10.1006/JHEV.1994.1029

van Schaik, C. P., & Isler, K. (2011). Life history evolution. In J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit, & J. B. Silk (Eds.), *The evolution of primate societies*. University of Chicago Press. https://doi.org/10.1016/B978-0-12-383832-2.00066-9

Walker, A. (1979). Prosimian locomotor behavior. In G. A. Doyle & R. D. Martin (Eds.), *The Study of Prosimian Behavior* (pp. 543–565). Academic Press

Wood, B. A. (1976). The nature and basis of sexual dimorphism in the primate skeleton. *Journal of Zoology, 180*(1), 15–34. https://doi.org/10.1111/J.1469-7998.1976.TB04660.X

Young, J. W. (2005). Ontogeny of muscle mechanical advantage in capuchin monkeys (*Cebus albifrons* and *Cebus apella*). *Journal of Zoology, 267*(4), 351–362. https://doi.org/10.1017/s0952836905007521

Young, J. W., Fernández, D., & Fleagle, J. G. (2009). Ontogeny of long bone geometry in capuchin monkeys (*Cebus albifrons* and *Cebus apella*): Implications for locomotor development and life history. *Biology Letters, 6*(2), 197–200. https://doi.org/10.1098/rsbl.2009.0773

Young, J. W., & Heard-Booth, A. N. (2016). Grasping primate development: Ontogeny of intrinsic hand and foot proportions in capuchin monkeys (*Cebus albifrons* and *Sapajus apella*). *American Journal of Physical Anthropology, 161*(1), 104–115. https://doi.org/10.1002/AJPA.23013

Zeininger, A., Shapiro, L. J., & Raichlen, D. A. (2017). Ontogenetic changes in limb postures and their impact on effective limb length in baboons (*Papio cynocephalus*). *American Journal of Physical Anthropology, 163*(2), 231–241. https://doi.org/10.1002/AJPA.23201

Zuckerman, S. (1926). Growth-changes in the skull of the baboon, *Papio porcarius*. *Proceedings of the Zoological Society of London, 96*(3), 843–873. https://doi.org/10.1111/J.1469-7998.1926.TB07131.X