


RESEARCH ARTICLE

Sexual dimorphism and growth in *Alouatta palliata* based on 20+ years of field data

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Abstract

Objectives: *Alouatta palliata* patterns of growth and sexual dimorphism are evaluated using 20 plus years of field data. Comparisons are made to other species of *Alouatta* and other New World primates.

Materials and methods: Records of 92 *A. palliata* from Guanacaste Province, Costa Rica, were used to generate growth curves for body mass and linear measurements. Timing of growth for the properties was compared, and males and females were contrasted. Slopes and elevations for periods of rapid growth were evaluated. Growth allometry and proportion ratios were also explored.

Results: Body mass growth is rapid during the first 2 years. Males and females begin to diverge around a year of age as male growth increases and female growth slows. Adult mass for both is reached about 4 years of age. Linear measurements show rapid growth the first 18 months for both sexes. Differences develop as males continue the same rate of linear growth while female growth slows. Adult size is reached for head and body length around 3 years, and for hind-foot and tail lengths around 2 years.

Discussion: *A. palliata* males grow in mass more rapidly than females, while both grow similarly in linear dimensions, so that dimorphism is more pronounced in mass. This pattern is seen in other dimorphic New World primates. Male *A. palliata* may grow more rapidly than *A. seniculus*, reflecting earlier emigration for *A. palliata* males. Linear dimensions reach adult proportions earlier than body mass. For hind-foot and tail, this is probably an adaptation for gripping.

KEYWORDS

Alouatta palliata, growth curves, sexual dimorphism

1 | INTRODUCTION

In this article *Alouatta palliata* sexual dimorphism and growth are explored by analyzing field data collected from 1972 to 1999 in Guanacaste Province, Costa Rica. The population is described in Glander (1992) and the sample in the present study includes over 250 records linked to approximately 100 individuals of known ages. Data include ages, body masses, and linear measurements. Analysis focuses on information derived from growth curves but also considers

ontogenetic scaling and changes in body proportions with growth. Results are interpreted in light of what is known of the timing of lifespan events. Comparisons are made to published information for other *Alouatta* species and other New World primates.

Alouatta is a sexually dimorphic genus with females averaging 70 to 85% of male body mass (Thorington Jr., Ruiz, & Eisenberg, 1984). Generally, *A. palliata* is less dimorphic in size than *A. caraya* and *A. seniculus* (Thorington Jr., Rudran, & Mack, 1979). Life history for both male and female howling monkeys includes

emigration from natal troops while very young, with later immigration into established groups or the formation of new groups (Azkarate, Dunn, Balcells, & Baro, 2017; Crockett & Pope, 2002; Glander, 1992; Rumiz, 1990). Solitaries, satellite individuals, and adults that secondarily emigrate/immigrate also occur. Table 1 provides a summary of adult masses, ages at emigration, and ages of maturation for *A. palliata*, *A. seniculus*, and *A. caraya*. The information is further explored for each species below.

A. palliata males are physiologically mature as subadults at 3.5 years of age, but do not reach their adult size of about 6 kg for another 3 years (Glander, 1980). Juvenile and subadult males usually emigrate (average age 22 months—Glander, 1992) and finish morphological development as solitaries (Azkarate et al., 2017; Glander, 1992). Body mass is critical for successful immigration because potential immigrants must defeat a fully adult resident alpha male that averages 6 kg. This means that successfully immigrating males spend a long period of time maturing without membership in an adult-based group.

A. palliata females, are sexually mature as subadults at 3 years of age, and may have their first young around 3.5 years of age (Glander, 1980). Adult females average 5 kg (Glander, 2006). Almost

all females leave their natal groups as older juveniles (Glander, 1992), averaging 33 months of age. Like males, development continues while living as solitaries (Azkarate et al., 2017; Glander, 1992). Females immigrate into a troop when at least 40 months old by subordinating resident females (Glander, 1980; Glander, 1992). This process can involve physical fights (Azkarate et al., 2017; Clarke & Glander, 1984; Glander, 1992). As females often have their first infant while establishing rank, these infants always die (Glander, 1980). Females are not related to each other, and may attack infants of other females, and infants can be knocked off of their mothers during agonistic interactions (Clarke & Glander, 1984; Glander, 1980). With age, females move down in rank, but infant survival rate improves (Clarke & Glander, 1984; Glander, 1980).

Alouatta seniculus differs in several regards from *A. palliata*. Notable among these differences is that *A. seniculus* males usually emigrate much later than *A. palliata* males—around 4 years of age, or as subadults (Crockett & Pope, 2002). They may also wait until adulthood before emigrating or remain in their natal troops. Males first reproduce at 6 years of age, roughly 2 years later than the earliest observed for *A. palliata*, and may be slightly bigger with a reported average of 6.5 kg (Thorington Jr. et al., 1979). Female *A. seniculus* first reproduce around 4 years of age, roughly 6 months later than *A. palliata* (Crockett & Pope, 2002). *A. seniculus* females average 4.5 kg as adults (Thorington Jr. et al., 1979), slightly lighter than the *A. palliata* average. Like *A. palliata*, *A. seniculus* females emigrate from their natal troops as juveniles, between 2 and 4 years of age (Crockett & Pope, 2002). In contrast, they usually do not take over or otherwise join preexisting troops, and their survival rate is low. However, roughly 20% of females do not leave. *A. seniculus* females seem less aggressive with one another (Rudran, 1979) than *A. palliata*. Adult females may pull an infant off its mother, but without apparent intent to harm it, even occasionally carrying it during travel (Mack, 1979).

Alouatta caraya also differs from *A. palliata*. *A. caraya* males are sexually mature around 4.5 to 5 years of age (Rumiz, 1990; Thorington Jr. et al., 1984), intermediate in timing between *A. palliata* and *A. seniculus*. Average male adult mass is 6.7 kg, but individuals over 8 kg are reported (Thorington Jr. et al., 1984), which is notably heavier than *A. palliata*. Males emigrate from their natal groups as subadults or young adults (Rumiz, 1990; Thorington Jr. et al., 1984). Female *A. caraya* emigrate also, typically as subadults or young adults (Rumiz, 1990). Females reach adulthood later than *A. palliata* at roughly 4.5 years of age, and adults average around 4.3 kg (Rumiz, 1990). Rumiz (1990) reported that females are less likely to disperse than males, but Oklander et al. (2010) found that female dispersal is affected by habitat.

Growth curves are a means of displaying the magnitude of a variable at progressively increasing ages, assuming a sample of immature individuals. Tanner (1951) distinguishes three categories of data used to generate growth curves: cross-sectional, longitudinal, and mixed longitudinal. Cross-sectional data include one record per individual, so that each year of age includes entirely different individuals than other years. For longitudinal data sets, each individual is measured each year so that each has their own growth trajectory, as well as contributing

TABLE 1 Highlights of *Alouatta* species differences^{a,b,c}

Species	Adult body mass (kg)	Age at emigration	Comments
Males			
<i>palliata</i>	6.0	Average 22 months (juvenile)	Full adult size at 6.5 years Earliest reproduction at 4 years
<i>seniculus</i>	6.5	Subadult to adult	Earliest reproduction at 6 years
<i>caraya</i>	6.7, some as large as 8.0	Subadult to adult	Sexually mature 4.5–5 years of age
Females			
<i>palliata</i>	5.0	Average 33 months (older juvenile to subadult)	Earliest reproduction 3.5 years
<i>seniculus</i>	4.5	2–4 years (older juvenile to subadult)	Earliest reproduction 4 years
<i>caraya</i>	4.3	Subadult to adult	Adulthood at 4.5 years

^aSee text footnote regarding body mass variability within species and between seasons.

^bInformation is restricted to that available from the literature. For example, “adulthood” is not assumed to be the same as “earliest reproduction.”

^c*A. palliata* sources are Azkarate et al., 2017; Clarke & Glander, 1984; and Glander, 1980, 1992, and 2006. *A. seniculus* sources are Crockett & Pope, 2002; Mack, 1979; Rudran, 1979; and Thorington Jr. et al., 1979. *A. caraya* sources are Oklander, Kowalewski, & Corach, 2010; Rumiz, 1990; and Thorington Jr. et al., 1984.

to a population curve. Obviously, collecting longitudinal data is very challenging (Tanner, 1986). Mixed longitudinal data sets include individuals who are measured a plurality of times, but these individuals enter or exit the data at varying times (Tanner, 1951). This means that membership at successive ages is partially similar.

Growth curves for measurements such as weight and height are clinically used for humans (see https://www.cdc.gov/growthcharts/clinical_charts.htm), and there also are a myriad of human-focused studies within the field of biological anthropology. Such topics include the effects of ancestry and socioeconomic status in Guatemalan children (Bogin, Sullivan, Hauspie, & MacVean, 1989), the relationship between mechanical loading and growth in long bone section moduli (Ruff, 2003), and a comparison of growth patterns between precontact Pueblo Indians and modern U.S. children (Schillaci, Nikitovic, Akins, Tripp, & Palcovich, 2011). Among nonhuman Old World primates, gorillas, baboons, and macaques have been well-studied (Coelho, 1985; Galbany et al., 2016; Hamada, Hayakawa, Suzuki, & Ohkura, 1999; Leigh, 2009; Newell-Morris & Fahrenbruch, 1985; Schillaci et al., 2007 and Sirianni, 1985).

Growth data for New World primates are available for *Saimiri* (Garber & Leigh, 1995; Long & Cooper, 1968), *Cebus* (Fleagle & Samonds, 1975; Fragaszy & Adams-Curtis, 1998; O'Brien & Robinson, 2002), and *Alouatta* (e.g., Crockett & Pope, 2002; Thorington Jr. et al., 1984). Adult size and reproductive age information has been published for *Lagothrix*, *Ateles*, and *Brachyteles* (Fooden, 1963; Nishimura, 2003; Peres, 1994; Schmitt & Di Fiore, 2014; Strier, 1992; Strier, 1996). In a wider study, Ford and Corruccini (1985) analyzed a large volume of NMNH (Smithsonian Institution) measurements, including juveniles, providing a reference for a diverse array of platyrrhines.

In the present analysis, it is hypothesized that male *Alouatta palliata* body mass will grow at a faster rate than that of female *A. palliata* as males emigrate younger and become larger adults. The prediction comes from examination of published *A. seniculus* and *A. caraya* growth curves (Crockett & Pope, 2002; Thorington Jr. et al., 1984). Some degree of bimaturism, where one sex has a longer duration of growth than the other (Shea, 1986), may be apparent as body mass growth curves for *A. caraya* in Leigh (1994) seem to show both bimaturism and rate differences. Froehlich, Thorington Jr., and Otis (1981) show an *A. palliata* male body mass growth curve that appears to be biphasic, with rapid infant growth, then slower juvenile growth, and then an adolescent growth spurt (p. 213). With this in mind, the Hacienda la Pacifica data set will be evaluated for possible biphasic growth.

In comparison to other species of *Alouatta*, it is expected that male *A. palliata* will show earlier and/or faster growth than male *A. seniculus* and male *A. caraya* because they need to be independent sooner (Table 1). Females do not differ as much in the timing of emigration so they are not expected to diverge from each other.

It is hypothesized that linear measurements will outpace body mass because subadult mammals in general appear slimmer and longer-limbed than adults. Ruff (2003) found that for humans, peak growth in stature occurs before that in body mass. Jungers and

Fleagle (1980) found that limb bone lengths scaled with positive allometry relative to body mass in *Cebus*.

Among linear dimensions, tail and hind-foot lengths are expected to either be large at a very young age, and/or to increase at a fast rate during early juveniles stages, compared to head-body length. Three-month old *Alouatta* can suspend by the tail (Mack, 1979), and juveniles travel without being carried before a year of age (Clarke, 1990; Mack, 1979; Raguette-Schofield & Pave, 2015). For *Alouatta* infants, Prates and Bicca-Marques (2008) reported greater frequencies of climbing and bridging behaviors than adults. Tying these behaviors in with foot size and tail length, Jungers and Fleagle (1980) commented on the need for arboreal juveniles to be able to bridge gaps and grab the same branches as adults.

In comparing *Alouatta palliata* to non-atelids *Cebus* and *Saimiri*, it is expected that growth patterns will be similar as they are all sexually dimorphic and arboreal. However, it is known that *Alouatta* differs in positional behavior and diet from these two (Bezanson, 2009; Boinski & Fragaszy, 1989; Gebo, 1992; Glander, 1981), and is much larger (Ford & Corruccini, 1985), so differences will not be surprising.

2 | MATERIALS AND METHODS

The morphological database for this article is described in Glander (1992) and includes 1972 to 1999 seasons. A large number of howling monkeys at Hacienda la Pacifica in Guanacaste Province, Costa Rica, were captured and released, many of them multiple times, during this time period following approved protocols (Duke University IACUC and Costa Rica's Ministerio de Ambiente y Energia). Under sedation, body masses, total body lengths, hind-foot lengths, and tail lengths were measured. For the present analysis, head-body length was obtained by subtracting tail length from head-tail length.

Individuals with known body masses and ages were selected to form samples of 167 female records and 86 male records. These are based on 62 females and 30 males. This sample is referred to as cross-sectional because many individuals contribute only two data points, and five have just one. Table 2 displays individuals and records. Some individuals are missing linear measurements so the linear data sets are slightly smaller than the body mass sets (Table 3).

A subset was identified that contained only individuals with three or more records collected during phases of rapid growth. This forms a mixed longitudinal data set (Tanner, 1951). It includes seven females comprising 24 records, and five males comprising 23 records.

Individuals forming the mixed longitudinal set are also considered individually, although few have a complete growth series. Graphs showing them are in the Supporting Information online because of reliance on color to distinguish individuals. Among females, only Tala and Gollum have records spanning 2 to 4 years of age—the remaining five females either end or begin during this time, which corresponds to the timing of peak female emigration (Glander, 1992). These two left their natal groups around 33 months and were later recaptured as members of other groups (Glander, 1992). Fiona died around 15 years of age, long after the last year included in the present data set (KEG

TABLE 2 Hacienda la Pacifica *Alouatta palliata* sample included in the analysis

Individual	Birth to 0.9 years	1.0–1.9 years	2.0–2.9 years	3.0–3.9 years	4.0–4.9 years	5–5.9 years	6.0+ years
Females							
Amazon							2 records
Amethyst		X		X			
Beanie	X		X				
Bell	X	X	2 records				
Buttercup						2 records	3 records
Charlotte							2 records
Chaya							3 records
Chipper	X	X	X				
Chloe							2 records
Cindy							2 records
Cleo					X	X	X
Diva							2 records
Dorothy							3 records
Eliza							3 records
Elke					X	X	X
ET			X	X			2 records
Fiona				X	X	X	2 records
Garnet							2 records
Gollum			X		X	X	X
Green juvenile			X				
Gremlin	X	X					
Greta	X		X				
Isabel							2 records
Jasmine	2 records						
Juliet							4 records
Kathy							2 records
Lady	X			X			
Lemon							6 records
Lilac					2 records	2 records	X
Lily	X		X				
Lisa	X	X					
Magnolia							2 records
Mariandel							2 records
Masala							2 records
Miki	X	X					
Natasha							4 records
Nicole				X	X		
Nile							2 records
Peach	X			X			X
Pelican					X		X
Pippin	X	X	X				
Pocahantes							2 records
Purple	X						X
Pyrite							3 records
Rachel				2 records			

TABLE 2 (Continued)

Individual	Birth to 0.9 years	1.0–1.9 years	2.0–2.9 years	3.0–3.9 years	4.0–4.9 years	5–5.9 years	6.0+ years
Sabrina	X			3 records			X
Sally							6 records
Schweppes	X					X	
Sherry							3 records
Sifonia							3 records
Simone							3 records
Skipper	X		X				
Sweetie							2 records
Sweetpea			X		X		
Tala			X	X	X		
Tigres							3 records
Topaz II							X
Trinka							3 records
Valencia	X						
Yahtzee	X		2 records				
Yolo	X	X					
Zircon			2 records				
Males							
Bambam	X		X				
Bandit		X	2 records	X		X	4 records
Bart	2 records						
Bilbo							X
Buck							2 records
Bullwinkle							6 records
Casper							2 records
Cherokee							3 records
Chief							2 records
Dano			2 records				
Descartes							2 records
Eli	2 records						
Eric			X		X		
Gabel							2 records
Green infant	2 records						
Haw							2 records
Hernando							4 records
Houdini							3 records
Jose	X	X	X				2 records
Julio		X					2 records
Malachite	X		2 records				
Moses	X		X				
Ringo							X
Roddy	X	X		X	X		
Roo			X	X		X	2 records
Rua pehu							2 records
Scott	2 records	X	X				X
Sidney	2 records						

(Continues)

TABLE 2 (Continued)

Individual	Birth to 0.9 years	1.0–1.9 years	2.0–2.9 years	3.0–3.9 years	4.0–4.9 years	5–5.9 years	6.0+ years
Spud	2 records						
Sri							2 records

TABLE 3 *Alouatta palliata* rapid growth phase regression statistics and ANCOVA comparisons between males and females^a

Sample	N	RMA slope	Slope 95% CI	<i>p</i> -value of correlation	ANCOVA results comparing female and male LS regression lines during rapid growth ^b
Cross-sectional data: Body mass (kg) versus age—Between birth and 3.0 years of age					
Females	47	1.16	1.06–1.27	.000	Slopes differ with <i>p</i> -value of less than .001
Males	35	1.98	1.82–2.14	.000	Y-axis positions differ with <i>p</i> -value of .004 ^c
Cross-sectional data: Head-body length (m) versus age—Between birth and 2.0 years of age					
Females	30	0.12	0.10–0.14	.000	Slopes and elevations do not differ significantly
Males	24	0.13	0.11–0.14	.000	
Cross-sectional data: Hind-foot length (m) versus age—Between birth and 2.0 years of age					
Females	29	0.038	0.030–0.044	.000	Slopes and elevations do not differ significantly
Males	23	0.041	0.035–0.046	.000	
Cross-sectional data: Tail length (m) versus age—Between birth and 2.0 years of age					
Females	30	0.19	0.16–0.22	.000	Slopes and elevations do not differ significantly
Males	24	0.18	0.16–0.20	.000	
Mixed longitudinal data: Body mass (kg) versus age—Between birth and 3.0 years of age					
Females	15	1.11	0.96–1.27	.000	Slopes differ with <i>p</i> -value of less than .001
Males	14	1.94	1.74–2.14	.000	Y-axis positions differ with a <i>p</i> -value of .0007 ^c
Mixed longitudinal data: Head-body length (m) versus age—Between birth and 3.0 years of age					
Females	14	0.08	0.07–0.09	.000	Elevations differ with <i>p</i> -value of less than .001
Males	13	0.09	0.08–0.11	.000	Slopes do not differ significantly
Mixed longitudinal data: Hind-foot length (m) versus age—Between birth and one and a half years of age					
Females	5	0.040	0.013–0.067	.008	Slopes and elevations do not differ significantly
Males	6	0.054	0.017–0.092	.016	
Mixed longitudinal data: Tail length (m) versus age—Between birth and one and a half years of age					
Females	6	0.23	0.11–0.35	.006	Slopes and elevations do not differ significantly
Males	7	0.20	0.10–0.30	.004	

^aTime ranges used were selected to reflect periods of most rapid growth as seen in Figures 1 and 2. “Birth” refers to the youngest age available as no measurements of any individuals were obtained immediately after birth. The age maximums were chosen as those preceding notable declines in slope. Slight curvatures before this point are ignored. If the sexes differ in timing, the younger maximum was used for both. Truly linear regions for each curve were previously identified but were found to be of limited use as they occur within the first year for most variables and thus have small samples and do not provide quantifiable information about trends visible in Figures 1 and 2.

^bANCOVA of least-squares regression lines is appropriate for these comparisons because all correlation coefficients are above 0.96, meaning that RMA and LS slopes are very similar.

^cWhen slopes differ and ANCOVA cannot be used to evaluate elevations, comparisons of samples' Y-axis values relative to a common regression line are made using Fisher's Exact Test as recommended in Tsutakawa and Hewett (1977). Stating that there is a difference in Y-axis position indicates that the majority of data points for one sample plot above the other sample's data points, relative to the a regression line fit through both samples.

unpublished data). In contrast to the females, all five males have records beginning at 2 years or prior, as well as records as adults. Scott has a record at 8 years, although it is not included in Figure S1 because it follows a large time gap. He was presumed dead by 12 years, after the end-date of the data set (KEG unpublished data). Roddy and Roo remained in their natal troops, while Bandit emigrated very young (15 months) but survived to be recaptured in another

group and lived for several years (Glander, 1992). Jose died at 13 years of age, well after his last entry into the data set (KEG unpublished data).

LOWESS curves (SYSTAT Version 13, Systat Software, San Jose, CA) were generated from the cross-sectional data, similar to procedures followed by Leigh, Setchell, and Buchanon (2005), Leigh (2009), and Ruff (2003). Analysis included visual inspection of curves to

evaluate locations where the curves changed relative to age (the X axis variable). Visual inspection of growth data in graphs is utilized in Galbany et al. (2017), Leigh et al. (2005), Leigh (2009), and Ruff (2003).

For the more limited mixed longitudinal data, distance-weighted least squares (DWLS) was used to generate curves (SYSTAT Version 13; SYSTAT, n.d.) as shown in Bogin and Keep (1999). This method more effectively smooths variation in small samples. However, DWLS can erroneously project curves beyond the data set with very small samples, such as with data for individuals. Thus, LOWESS is used for individual trajectories, even though this method links data point to data point without any smoothing in very small samples.

A period of rapid growth was identified for each growth curve and treated as a straight line, although often slightly curved. This made it possible to calculate reduced major axis (RMA) slopes, with associated 95% confidence intervals, and perform analysis of covariance (ANCOVA) of least-squares (LS) slopes to compare male and female samples (SYSTAT Version 13; BIOMstat Version 4.11, Applied Biostatistics, Inc., 1996–2014, Port Jefferson, NY). RMA slope values were preferred over LS slope values because both axes were assumed to have error (Smith, 2009). Field-collected ages of feral animals cannot be exact. Least-squares regression is adequate for ANCOVA because the correlation coefficients for regressions that differ in Table 3 are above 0.96 (see Ruff, 2002, for similar practice). Confidence intervals for RMA slopes do not overlap when ANCOVA indicates that LS slopes differ (Table 3).

When slopes differ, ANCOVA cannot distinguish elevation differences. To determine whether two samples differing in slope are similar in relative Y axis values, Tsutakawa and Hewett (1977) recommend the use of Fisher's exact test to compare data points above and below a common regression line. This method is used in Ruff, Burgess, Ketcham, and Kappelman (2016) and Temple, Auerbach, Nakatsukasa, Sciulli, and Larsen (2008). Differences are referred to as differences in Y-axis position, rather than elevation.

Velocity curves were generated for both cross-sectional and mixed longitudinal data. Calculation of velocity for each successive time increment (i.e., v_1 , v_2 , v_3 ...) yields a data set, which can be plotted to create a velocity curve.

The equation below explains how velocity data were generated for both the cross-sectional data and the mixed longitudinal data:

$$\text{Velocity} = \frac{[(\text{average of older year}) - (\text{average of younger year})]}{(\text{number of years apart})}$$

The "number of years apart" was 1 year. Because a whole year is a relatively long time for a juvenile howling monkey, originally 6 months was used as the time increment. This yielded averages based on very small samples and the resulting curves appeared erratic for the cross-sectional data set. Velocity data were graphed using the NEXPO method (SYSTAT Version 13) because it displays curves that follow the data points but which are still smoothed.

Individual growth velocities are included in the Supporting Information online because color is needed to make individuals distinct.

Each data point is calculated as described in Hamada et al. (1999, p. 441):

$$v_1 = (y_2 - y_1) / (x_2 - x_1).$$

Y_1 and y_1 refer to variable magnitudes at two consecutive times, and x_1 and x_2 refer to the corresponding times of measurement.

Allometric analyses were performed for comparisons of linear measurements to body mass, and for linear measurements to each other. Data were transformed by natural logarithm, and include age ranges from close to birth to 14 months. This age maximum was chosen because it corresponds to steepest regions of the linear data in LOWESS curves (Figure 1), and because it allows comparison to other genera with first year data (see below). For linear measurements to body mass, an isometric slope would be 0.33. For linear measurements to other linear measurements, an isometric slope would be 1.00. RMA slopes are evaluated as error is presumed for both axes. Confidence intervals are used to recognize deviation from isometry, and to compare males and females.

Relative tail length (RTL) was calculated using the cross-sectional sample. As shown in Russo (2016):

$$\text{RTL} = (\text{tail length} / \text{head and body length}) \times 100$$

Relative foot length (RFL) was also calculated:

$$\text{RFL} = (\text{hindfoot length} / \text{head and body length}) \times 100$$

Bivariate plots of RTL and RFL versus mass and age were used to identify size ranges where proportions increase with body mass or age (Table 6, Figure 4). These ranges were used to perform RMA regressions. ANCOVA was not performed to compare male and female samples as the correlation coefficients were low enough (between 0.45 and 0.80) that LS slopes differed notably from RMA slopes. Additionally, bivariate plots of the linear properties on body mass, were performed to clarify results.

Because longitudinal data are available for *Saimiri sciureus* (Long & Cooper, 1968, pp. 198 and 203, tables III and V) and *Cebus albifrons* (Fleagle & Samonds, 1975, pp. 42–43, Table 1) for the first year, and because these samples can be extended cross-sectionally to include older specimens from the NMNH database, comparisons were performed with these species. NMNH information was provided with the permission of the National Museum of Natural History, Smithsonian Institution, 10th, and Constitution Ave. N.W., Washington, DC 20560-0193 (2019). (<https://www.nmnh.si.edu/>) Allometric patterns were examined and RTL and RFL were calculated and compared, using the same methods as for *A. palliata*. Additionally, groupings of older and younger individuals were compared using averages and *SD* for all three genera.

Comparisons were also made between growth curves of *A. palliata* (Figure 1) and *A. seniculus* (Crockett & Pope, 2002, figure 8.3, p. 107) and *A. caraya* (Froehlich et al., 1981; Thorington Jr. et al., 1984, p. 362). As these involved no statistics and were

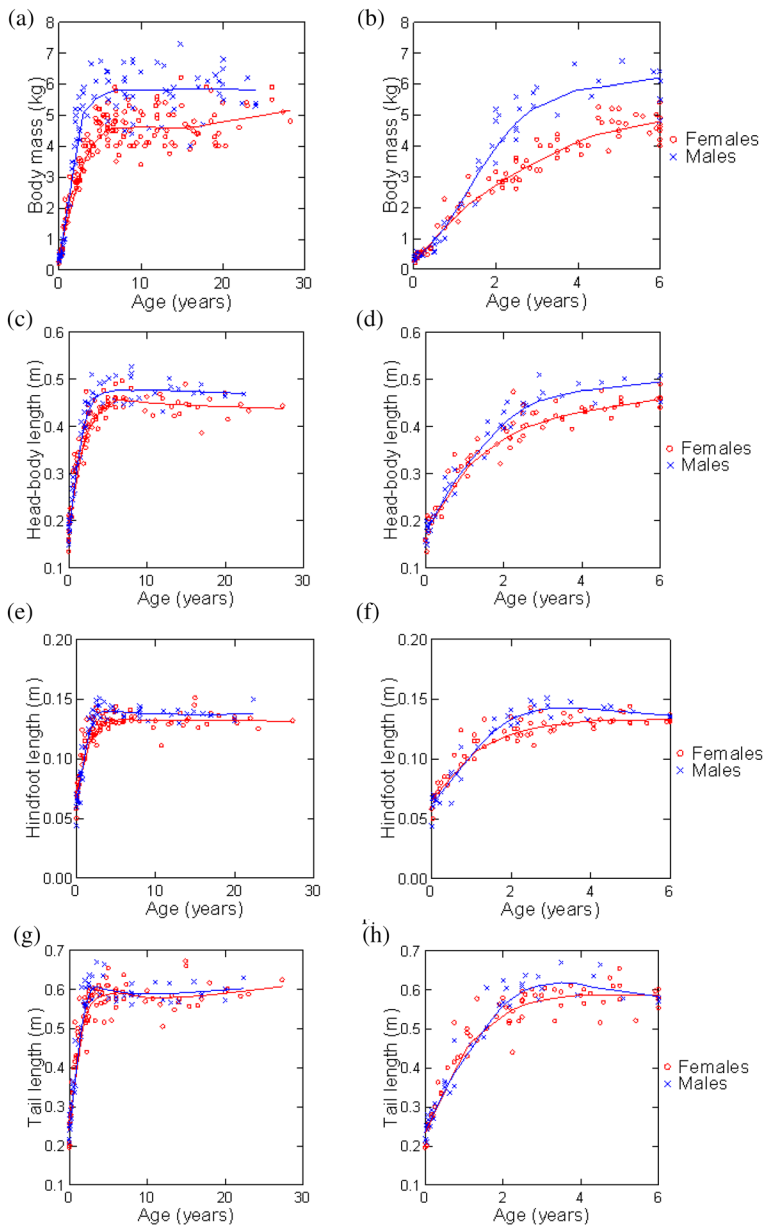


FIGURE 1 Cross-sectional data: LOWESS curves of body mass and length variables versus age in years for *Alouatta palliata*. Figures on the reader's left display the entire age range of the sample, while figures on the right provides a closer view of data for 6 years of age and less. (a,b) show body mass, (c,d) show head-body length, (e,f) show hindfoot length, and (g,h) show tail length. Female N individuals = 62, with 167 records for body mass. Male N individuals = 30 individuals, with 86 records for body mass. Among female records, 93 have linear measurements. Among male records, 55 have head-body and tail measurements, and 54 have hind-foot measurements

mostly limited to visual comparison, the results of these are presented in the "Discussion" section.

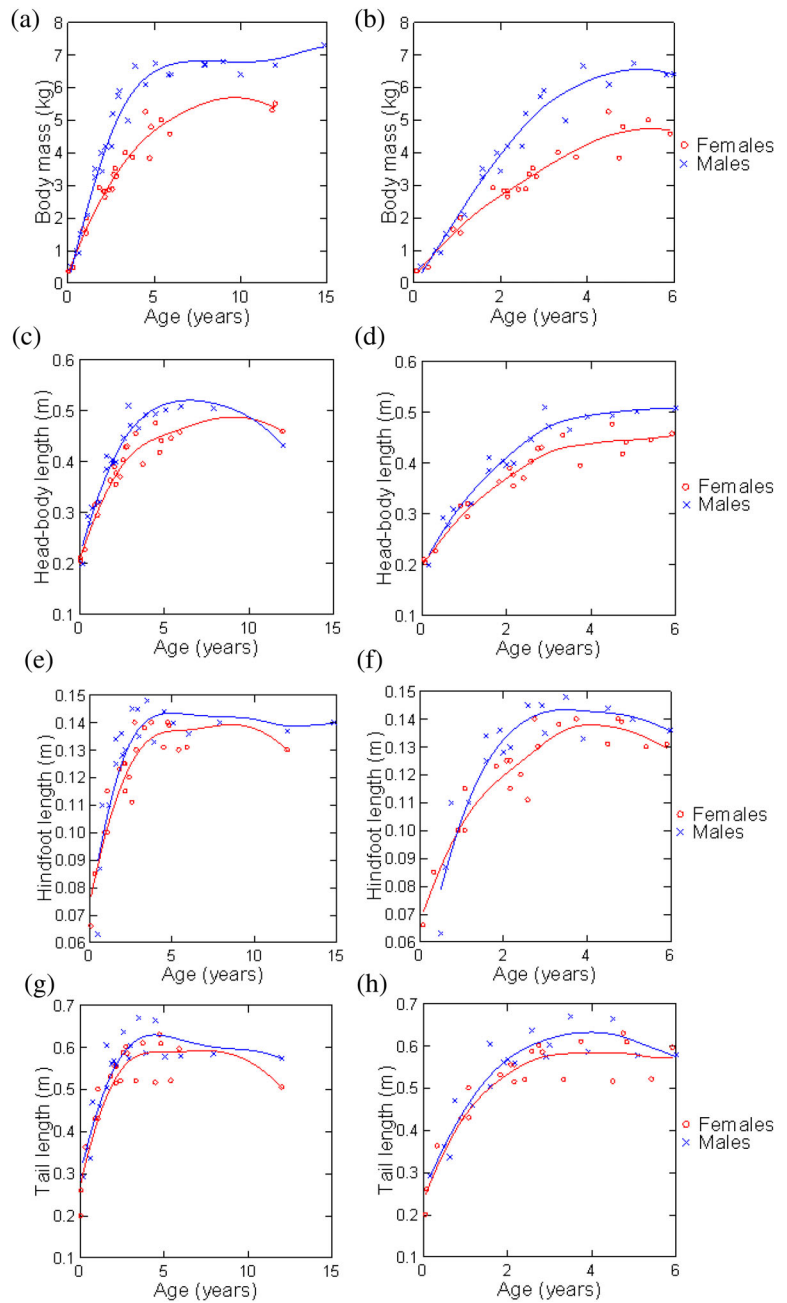
3 | RESULTS

Results are presented in five tables and eight figures, two of which are shown in the Supporting Information online. Figure 1 shows LOWESS curves of body mass on known ages, and linear measurements on known ages for the cross-sectional data set of *A. palliata*. Figure 2 shows DWLS curves for the same variables as Figure 1 but derived from the mixed longitudinal sample. Table 3 shows slopes and related statistics for growth curve phases showing rapid growth in Figures 1 and 2. Figure 3 shows growth velocity curves. Averages used to calculate growth velocities are in Table 4. Growth curves for individuals are shown in Figure S1. Individual growth velocity curves

are shown in Figure S2. Figure 4 shows DWLS growth curves for *Saimiri* and *Cebus* longitudinal data. Table 5 shows *Alouatta*, *Cebus*, and *Saimiri* allometric analysis results for the first 14 months of age. Table 6 shows *A. palliata* results for RTL and relative hind-foot length (RFL) regressions. Table 7 shows RTL and RFL averages and standard deviations for age groupings of all three genera. *Alouatta* data for RTL and RFL are shown in Figures 5 and 6 shows RTL and RFL data for the three genera.

Figure 1a,b and Figure 2a,b show body mass curves for males and females, with Figures 1b and 2b narrowed to 6 years of age and less. Trajectories for individuals are shown in Figures Ai and Aii (Supporting Information). As expected, adult males are larger than adult females. The difference in size between the sexes appears slightly before a year of age and then becomes more obvious as the male growth curve steepens. In the second year, female average mass is roughly 65% of that for males (cross-sectional sample, Table 4). Full adult body mass

FIGURE 2 Mixed longitudinal data: DWLS curves of body mass and length variables versus age in years for *Alouatta palliata*. All individuals have at least three records collected during growth. Figures on the reader's left display the entire age range of the sample, while figures on the right provide closer view of data for 6 years of age and less. (a,b) show body mass, (c,d) show head-body length, (e,f) show hind-foot length, and (g,h) show tail length. Female N individuals = 7, with 24 records for body mass. Male N individuals = 5 individuals, with 23 records for body mass. Among female records, 22 have head-body measurements, and 21 have hind-foot measurements. Among male records, 17 have linear measurements. Trajectories for individuals are shown in Figure S1



is reached around 4 years of age, with considerable individual variation. Figure 1b indicates that male adult mass is around 6 kg, and adult mass for females is around 4.5 kg. The average cross-sectional sample fifth-year mass for females is 4.7 kg and for males is 6.0 kg, as shown in Table 4, indicating that female weight is roughly 80% that of males.

Table 3 shows regression statistics for the phases of most obvious growth in body mass (between birth and 3 years of age—see Figures 1b and 2b), and ANCOVA results of male–female comparisons. For both cross-sectional and mixed longitudinal samples, the male body mass slopes are significantly higher than that of the females with p -values of less than .001, and the slope confidence intervals do not overlap. The male sample is also higher in Y-axis position.

Figure 3a,b show body mass growth velocity curves for cross-sectional and mixed longitudinal data. Velocity curves for individuals are shown in Figure Bi (Supporting Information). Growth is fastest in the first year for both sexes, and then declines. Male growth is much faster than female growth, especially between the first and second year, until during the third year when rates of growth become similar. Following this, females grow faster than males. Notable especially in Figure 3b which shows mixed longitudinal data, are short-lived prolongings of moderately high growth rates, possibly even slight increases in growth rates, between the third and second years for both sexes.

Head-body length data are plotted versus age in Figure 1c,d using cross-sectional data, Figure 2c,d using mixed longitudinal data, and

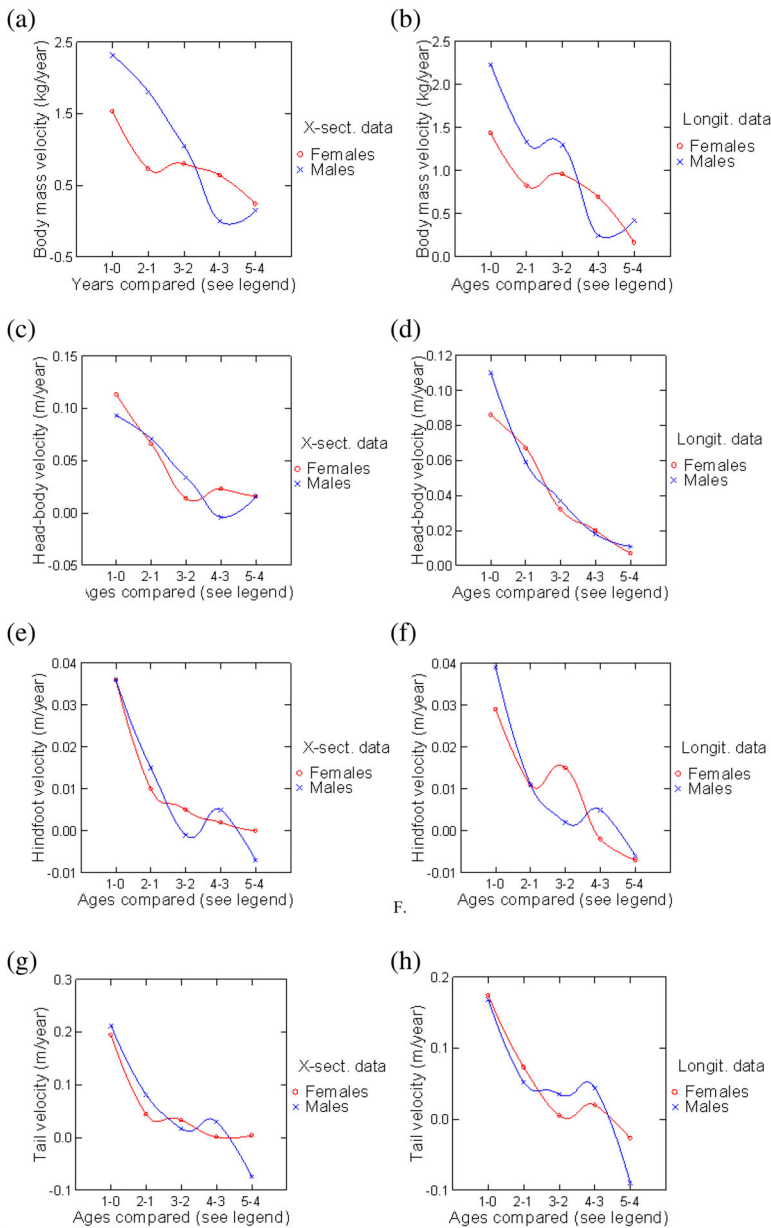


FIGURE 3 Growth velocity curves for *Alouatta palliata*—Velocity curves derived from cross-sectional data (“X-sect.”) are on the reader’s left, and velocity curves derived from mixed longitudinal data (“longit.”) are on the right. (a,b) show rate of change in body mass, (c,d) show rate of change in head-body length, (e,f) show rate of change in hind-foot length, and (g,h) show rate of change in tail length. On the X-axis, 1–0 means the average of individuals under a year subtracted from the average of those that are between 1 and 1.9 years of age. Likewise, 2–1 means the average of individuals 1–1.9 years of age subtracted from the average of individuals 2–2.9 years of age, and so forth, for the remainder of the years compared. NEXPO smoothing method (SYSTAT Version 13) was used as it best fits the data visually. Table 2 displays the averages used in calculating the velocity curves

Figures Aiii and Aiv for individuals (Supporting Information). The growth curve regions with the steepest slopes indicate males and females grow at similar rates until around 1 year of age, after which female growth slows while male growth continues at the same high rate until roughly 2 years of age, and then slows down. At roughly 2 years, females average around 90% of males (Table 4). Both sexes are close to adult body length at around 3 years of age. RMA slope confidence intervals and ANCOVA comparisons of mixed longitudinal data indicate that males and females are similar in slope but that males are higher in elevation (Table 3), which can be observed in Figure 2c,d.

Velocity curves for head-body length in Figure 3c,d differ between cross-sectional and mixed longitudinal data sets. The cross-sectional velocity chart shows very low female growth between the second and third years, with male growth ending (reaching zero) slightly later. However, the mixed longitudinal velocity chart indicates that males and

females are very similar in the rate of body length growth and both do not completely stop growing in length until the fourth year. With mixed longitudinal data, there is no abrupt leveling off, but rather a steady decline in body length growth rate. The conflicting results from the two data sets probably results from using averages from different individuals (See Tanner, 1986, for discussion of growth curve issues).

Individual velocity curves for head-body length are shown in Figure Bii (Supporting Information). These support the cross-sectional results (Figure 3c) in that a cessation of growth is shown between the third and fourth years. Also shown are possible juvenile growth spurts for Bandit and Bell between the second and third years.

Hind-foot length growth curves are shown in Figure 1e,f for cross-sectional data, in Figure 2e,f for mixed longitudinal data, and in Figures Av and Avi (Supporting Information) for individuals. Both sexes are very similar up to roughly 1.25 years old, and there are no slope or

TABLE 4 Averages used in calculating growth velocities with associated sample sizes

Group	0.0–0.9 years (N)	1.0–1.9 years (N)	2.0–2.9 years (N)	3.0–3.9 years (N)	4.0–4.9 years (N)	5.0–6.0 years (N)
Body mass (kg)						
Females—X-sect.	0.75 (20)	2.28 (9)	3.0 (14)	3.8 (11)	4.45 (10)	4.69 (17)
Females—Longit.	0.71 (4)	2.14 (3)	2.97 (7)	3.92 (2)	4.62 (3)	4.78 (2)
Males—X-sect.	0.68 (14)	2.99 (5)	4.8 (11)	5.85 (3)	5.85 (2)	6.00 (6)
Males—Longit.	0.98 (4)	3.22 (4)	4.55 (5)	5.85 (3)	6.1 (1)	6.52 (3)
Head-body length (m)						
Females—X-sect.	0.22 (19)	0.34 (9)	0.40 (14)	0.42 (7)	0.44 (8)	0.46 (10)
Females—Longit.	0.24 (4)	0.33 (3)	0.39 (7)	0.43 (2)	0.45 (3)	0.45 (2)
Males—X-sect.	0.23 (14)	0.37 (5)	0.44 (9)	0.48 (3)	0.47 (2)	0.49 (3)
Males—Longit.	0.27 (4)	0.38 (4)	0.44 (4)	0.48 (3)	0.49 (1)	0.51 (2)
Hindfoot length (m)						
Females—X-sect.	0.08 (18)	0.116 (9)	0.126 (14)	0.131 (8)	0.133 (8)	0.133 (10)
Females—Longit.	0.084 (3)	0.113 (3)	0.124 (7)	0.139 (2)	0.137 (3)	0.131 (2)
Males—X-sect.	0.074 (13)	1.125 (5)	0.140 (9)	0.139 (3)	0.144 (2)	0.137 (3)
Males—Longit.	0.087 (3)	0.126 (4)	0.137 (4)	0.139 (3)	0.144 (1)	0.138 (2)
Tail length (m)						
Females—X-sect.	0.31 (19)	0.51 (9)	0.55 (14)	0.58 (7)	0.58 (8)	0.59 (10)
Females—Longit.	0.31 (4)	0.49 (3)	0.56 (7)	0.57 (2)	0.59 (3)	0.56 (2)
Males—X-sect.	0.31 (14)	0.52 (5)	0.60 (9)	0.62 (3)	0.65 (2)	0.58 (3)
Males—Longit.	0.37 (4)	0.53 (4)	0.59 (4)	0.62 (3)	0.66 (1)	0.58 (2)

Note: For several categories, the same individuals were measured twice during a year so their measurements are included twice if the time between measurements was at least 6 months. The term “X-sect.” refers to data from the cross-sectional sample. The term “longit.” refers to data from the mixed longitudinal sample. Members of the mixed longitudinal sample are subsumed within the cross-sectional sample so the samples are not independent, but the cross-sectional samples are generally much larger.

elevation (or Y-axis position) differences during this shared phase of rapid growth (Table 3). Following this, females level off in growth while males continue at what appears to be the same rate until roughly 1.75 years old. There is some slow growth after this for both sexes, but hind-foot length appears to be almost finished at 2 years of age.

Velocity curves for hind-foot growth (Figure 3e,f; Figure Biii of Supporting Information) decrease sharply for females between the second year and the first year, matching growth curve observations made above. The cross-sectional and individual curves show a slow decrease to zero after this. Mixed longitudinal data show a temporary increase between the third and second year. This is not considered a genuine growth pattern, however, as Table 4 indicates the three and four year old female cohorts used for the mixed longitudinal curve have larger feet than most adult females. Male growth appears to slow slightly at the same age as for females (between years one and two), but reaches zero growth rate a year later. The apparent shrinkage of Bandit's foot length between third and fourth years (Figure Biii) is due to a low measurement taken during his fourth year that was probably an error.

Growth curves for tail length are shown in Figure 1g,h for cross-sectional data, in Figure 2g,h for mixed longitudinal data, and in Figures Avii and Aviii (Supporting Information). The male and female curves are very similar and overlap for both data sets, although male rapid growth continues slightly longer. Table 3 statistics indicate that the elevations and slopes for phases of most rapid growth for males

and females do not differ. As with hind-foot length, adult length is almost reached at age two. The velocity curves for tail length also show close similarity between males and females (Figure 3g,h; Figure Biv in Supporting Information), although the mixed longitudinal data suggest that males have slightly higher growth rate. Both males and females for both data sets level off in growth velocity close to zero between the second and first year.

For comparison to *Alouatta* Figures 1 and 2, first-year growth curves for *S. sciureus* and *C. albifrons* made using longitudinal data from Long and Cooper (1968, pp. 198 and 203, tables III and V) and (Fleagle & Samonds, 1975, pp. 42–43, Table 1) are shown in Figure 4. Males become greater in body mass than females quite early, with visible differences for *Cebus* by 2 months and for *Saimiri* by 4 months (Figure 4a). Head-body length versus age is shown in Figure 4b. For both genera, male and female lines are close together. *Cebus* males and females seem to diverge around 3.5 months, and *Saimiri* lines appear the same until roughly 9 months when males become longer. At a year of age, *Saimiri* and *Cebus* female average masses are roughly 85% of those of males, while for both genera, female average head-body lengths are around 95% of those of males (data from Fleagle & Samonds, 1975, and Long & Cooper, 1968).

Hind-foot length versus age (Figure 4c) lines diverge slightly at roughly 3 months for *Cebus*, and around 4 months for *Saimiri*. *Saimiri* lines look very close, but some of this is the effect of their small body

TABLE 5 Allometric analysis results for *Alouatta palliata*, *Cebus albifrons*, and *Saimiri sciureus* from birth to 12 months (*Cebus*) or 14 months (*Alouatta* and *Saimiri*)^{a, b, c}

Sample	N	RMA slope	Slope 95% CI	p-value of correlation	Allometry
<i>Alouatta palliata</i>					
Ln head-body length (m) versus Ln body mass (kg)					
Females	23	0.36	0.32–0.40	.001	Isometry
Males	17	0.43	0.34–0.52	.001	Positive allometry
Ln hind-foot length (m) versus Ln body mass (kg)					
Females	21	0.34	0.31–0.37	.001	Isometry
Males	13	0.35	0.29–0.41	.001	Isometry
Ln tail length (m) versus Ln body mass (kg)					
Females	20	0.40	0.37–0.42	.001	Positive allometry
Males	16	0.43	0.37–0.48	.001	Positive allometry
Ln hind-foot length (m) versus Ln head-body length (m)					
Females	22	0.91	0.82–0.99	.001	Negative allometry
Males	13	0.84	0.70–0.98	.001	Negative allometry
Ln tail length (m) versus Ln head-body length (m)					
Females	22	1.10	0.98–1.22	.001	Isometry
Males	17	1.01	0.84–1.18	.001	Isometry
<i>Cebus albifrons</i> (Fleagle & Samonds, 1975)					
Ln head-body length (m) versus Ln body mass (kg)					
Females	10	0.37	0.35–0.39	.001	Positive allometry
Males	10	0.39	0.36–0.41	.001	Positive allometry
Ln hind-foot length (m) versus Ln body mass (kg)					
Females	10	0.42	0.39–0.44	.000	Positive allometry
Males	10	0.42	0.40–0.44	.000	Positive allometry
Ln tail length (m) versus Ln body mass (kg)					
Females	10	0.53	0.49–0.57	.000	Positive allometry
Males	10	0.52	0.49–0.55	.000	Positive allometry
Ln hind-foot length (m) versus Ln head-body length (m)					
Females	10	1.14	1.12–1.16	.000	Positive allometry
Males	10	1.09	1.07–1.11	.000	Positive allometry
Ln tail length (m) versus Ln head-body length (m)					
Females	10	1.44	1.38–1.50	.000	Positive allometry
Males	10	1.34	1.28–1.39	.000	Positive allometry
<i>Saimiri sciureus</i> (Long & Cooper, 1968)					
Ln head-body length (m) versus Ln body mass (kg)					
Females	15	0.37	0.36–0.38	.000	Positive allometry
Males	15	0.35	0.33–0.38	.000	Isometry
Ln hind-foot length (m) versus Ln body mass (kg)					
Females	15	0.32	0.29–0.34	.000	Isometry
Males	15	0.31	0.29–0.33	.000	Isometry
Ln hind-foot (m) versus Ln head-body length (m)					
Females	15	0.86	0.79–0.92	.000	Negative allometry
Males	15	0.88	0.79–0.98	.000	Negative allometry
<i>Saimiri sciureus</i> (NMNH database) ^d					
Ln hind-foot length (m) versus Ln head-body length (m)					
Females and males	13	0.88	0.75–1.02	.000	Isometry

TABLE 5 (Continued)

Sample	N	RMA slope	Slope 95% CI	p-value of correlation	Allometry
Ln tail length (m) versus Ln head-body length (m)					
Females and males	15	1.48	1.10–1.90	.000	Positive allometry

^aAn isometric slope for length to mass comparisons would be a slope of 0.33, and for length to length comparisons it would be 1.00.

^bFleagle and Samonds (1975) and Long and Cooper (1968) data are captive animal averages, and NMNH data are wild-caught individuals.

^cNo tail measurements are available for the Long and Cooper (1968) *Saimiri* sample.

^dNMNH database *Cebus* and *Saimiri* information provided with the permission of the National Museum of Natural History, Smithsonian Institution, 10th and Constitution Ave. N.W., Washington, DC 20560–0193. (<https://www.nmnh.si.edu>). (<https://www.nmnh.si.edu/>).

TABLE 6 Results of relative tail length (RTL) and relative hind-foot length (RFL) regressed on body mass and age for *Alouatta palliata*^{a,b}

Variables compared	Age range (N)	RMA slope	Confidence interval	Comparison of Y-axis positions ^b
RTL versus age (years)				
Females	Birth to 8 years (70)	–4.78	–6.87 to –2.68	No significant difference
Males	Birth to 8 years (44)	–4.53	–6.57 to –2.29	
RFL versus age (years)				
Females	Birth to 5 years (60)	–2.02	–2.54 to –1.51	No significant difference
Males	Birth to 5 years (34)	–2.11	–3.17 to –1.06	

^aRTL refers to the ratio of tail length to head-body length (Russo, 2016) and RFL refers to the ratio of hind-foot length to head-body length.

^bAge ranges were chosen to reflect linearly decreasing regions of Figure 5. Correlation coefficients were low enough (between 0.45 and 0.80) that LS slopes were too different from RMA slopes to use them in ANCOVA analysis, although all p-values were less than .001. Therefore, only RMA confidence intervals were used to compare slopes for different samples. For differences in the Y-axis distributions, Fisher’s exact test as described in Tsutakawa and Hewett (1977) was used to evaluate the relative positions of combined sample data above and below a common RMA-derived regression line.

TABLE 7 Relative tail length (RTL) and relative hind-foot length (RFL) averages for juvenile and adult *Saimiri*, *Cebus*, and *Alouatta*^{a,b,c}

	Body mass range at ½ adult (kg)	Body mass range adult (kg)	Average RTL at ½ adult mass (SD, N)	Average RTL at adult mass (SD, N)	Average RFL at ½ adult mass (SD, N)	Average RFL at adult mass (SD, N)
<i>Saimiri sciureus</i>						
Females	0.36–0.51	0.70–1.00	158.0 (9.7, 4)	148.0 (9.9, 12)	30.9 (0.8, 12)	31.6 (2.5, 10)
Males	0.40–0.75	0.80–1.40	153.1 (6.7, 7)	135.3 (9.1, 11)	31.3 (1.3, 16)	29.9 (1.8, 9)
<i>Cebus albifrons</i>						
Females	0.72–1.09	1.60–2.00	127.3 (10.2, 5)	102.9 (8.9, 9)	34.9 (1.2, 5)	29.2 (2.4, 9)
Males	1.20–1.80	2.50–3.60	117.5 (18.7, 5)	94.9 (7.7, 9)	34.6 (0.9, 5)	28.6 (2.2, 9)
<i>Alouatta palliata</i>						
Females	1.98–2.60	4.00–5.00	145.1 (7.5, 6)	131.2 (7.7, 31)	34.6 (1.7, 7)	29.8 (1.8, 31)
Males	3.30–3.50	5.50–6.80	140.9 (17.4, 3)	122.5 (8.5, 19)	32.5 (2.2, 3)	28.5 (1.5, 19)

^aRTL refers to the ratio of tail length to head-body length (Russo, 2016) and RFL refers to the ratio of hind-foot length to head-body length.

^b“1/2 adult mass” is a range selected around the result of dividing the adult mass by two. Ranges were affected by availability of specimens. In addition, while using half of adult size is an attempt to compare small and large monkeys, it is an exploratory approach. Half of adult mass may not occur at relatively similar points in the growth of the sexes within each genus, or between different genera. For *Alouatta*, fifth-year averages of cross-sectional data from Table 4 were used. For *Saimiri* and *Cebus*, the start of the level region of a LOWESS curve of head-body length versus body mass was used, similar to that seen in Figure 6e,f, except the sexes were separated.

^cIn addition to Long and Cooper (1968, p. 198, 203) *Saimiri* data and Fleagle and Samonds (1975, pp. 42–43) *Cebus* data, *Cebus*, and *Saimiri* data include measurements of wildshot individuals from the Smithsonian database (*Cebus* N = 22, *Saimiri* N = 54), although some are missing measurements. Information provided with the permission of the National Museum of Natural History, Smithsonian Institution, 10th and Constitution Ave. N.W., Washington, DC 20560–0193. (<https://www.nmnh.si.edu/>).

size. Tail length versus age for *Cebus* is shown in Figure 4d. Males and females appear not to diverge at all until at least 8 months of age.

Allometric results in Table 5 include first-year *Cebus* (Fleagle & Samonds, 1975) and *Saimiri* data (Long & Cooper, 1968; NMNH

Database—see “Materials and Methods”), as well as first-year cross-sectional *Alouatta* data. In general, confidence intervals are narrower for Fleagle and Samonds (1975) captive *Cebus* and Long and Cooper (1968) captive *Saimiri*, probably because they are true longitudinal

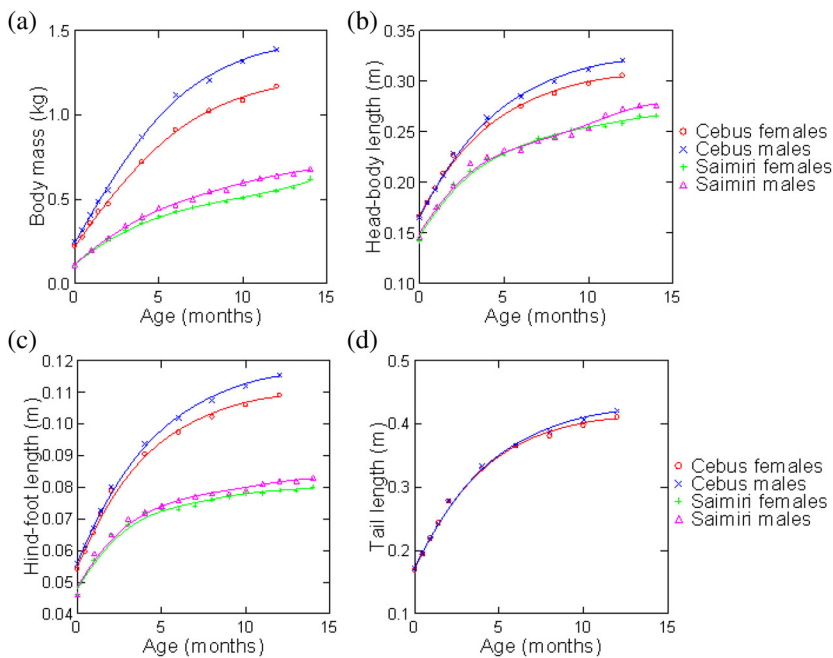


FIGURE 4 DWLS curves (SYSTAT Version 13) showing growth data from birth to 12 or 14 months for captive *Cebus albifrons* from Fleagle and Samonds table 1 (1975, pp. 42–43) and *Saimiri sciureus* from Long and Cooper tables III and V (1968, pp. 198 and 203). (a) shows body mass relative to age, (b) show head-body length relative to age, (c) shows hind-foot length relative to age, and (d) shows tail length relative to age. No tail length data were available for *Saimiri*. *Alouatta* data are not included because they overly and obscure the *Cebus* data. Similar information for *Alouatta* can be seen in Figures 1 and 2

samples. The cross-sectional NMNH feral *Saimiri* sample has wide confidence intervals, and the *Alouatta* sample frequently does too.

RMA slopes and confidence intervals indicate that *Alouatta* head-body length scales isometrically with body mass for females and positively allometrically for males (Table 5). *Cebus* males and females both scale with positive allometry, and *Saimiri* females do as well. However, examination of the actual slope values reveals that female *Alouatta*, and both sexes of both *Cebus* and *Saimiri*, all have slopes between 0.35 and 0.39, so that there is a general pattern of slight positive allometry. Male *Alouatta* have a notably higher slope of 0.43 but the confidence interval overlaps with all other samples.

Hind-foot length scales isometrically with body mass for both sexes of *Alouatta* and *Saimiri*, with slopes ranging between 0.31 and 0.35 (Table 5). *Cebus* males and females are positively allometric (slopes = 0.42), and other than male *Alouatta* and *Cebus*, the confidence intervals do not overlap with the other samples.

When hind-foot length is compared to head-body length, *Alouatta* and *Saimiri* show negative allometry with slopes ranging between 0.84 and 0.91 (Table 5). The NMNH *Saimiri* sample's confidence interval does include isometry, but the slope value is close to that for the Long and Cooper (1968) sample, so it is likely a larger feral sample would also show negative allometry. *Alouatta* and *Saimiri* negative allometry corresponds to slight positive allometry for head-body versus body mass combined with isometry for hind-foot length on body mass, as discussed above. For *Cebus*, foot length on head-body length shows positive allometry (roughly 1.11 for both sexes). Both head-body and hind-foot lengths scale with positive allometry to body mass, but hind-foot length more so, and so this is expected.

Tail length scales with positive allometry relative to mass for both males and females for *Alouatta* and *Cebus* (Table 5). However, *Alouatta* slope values (0.40 and 0.43) are notably lower than those of *Cebus*

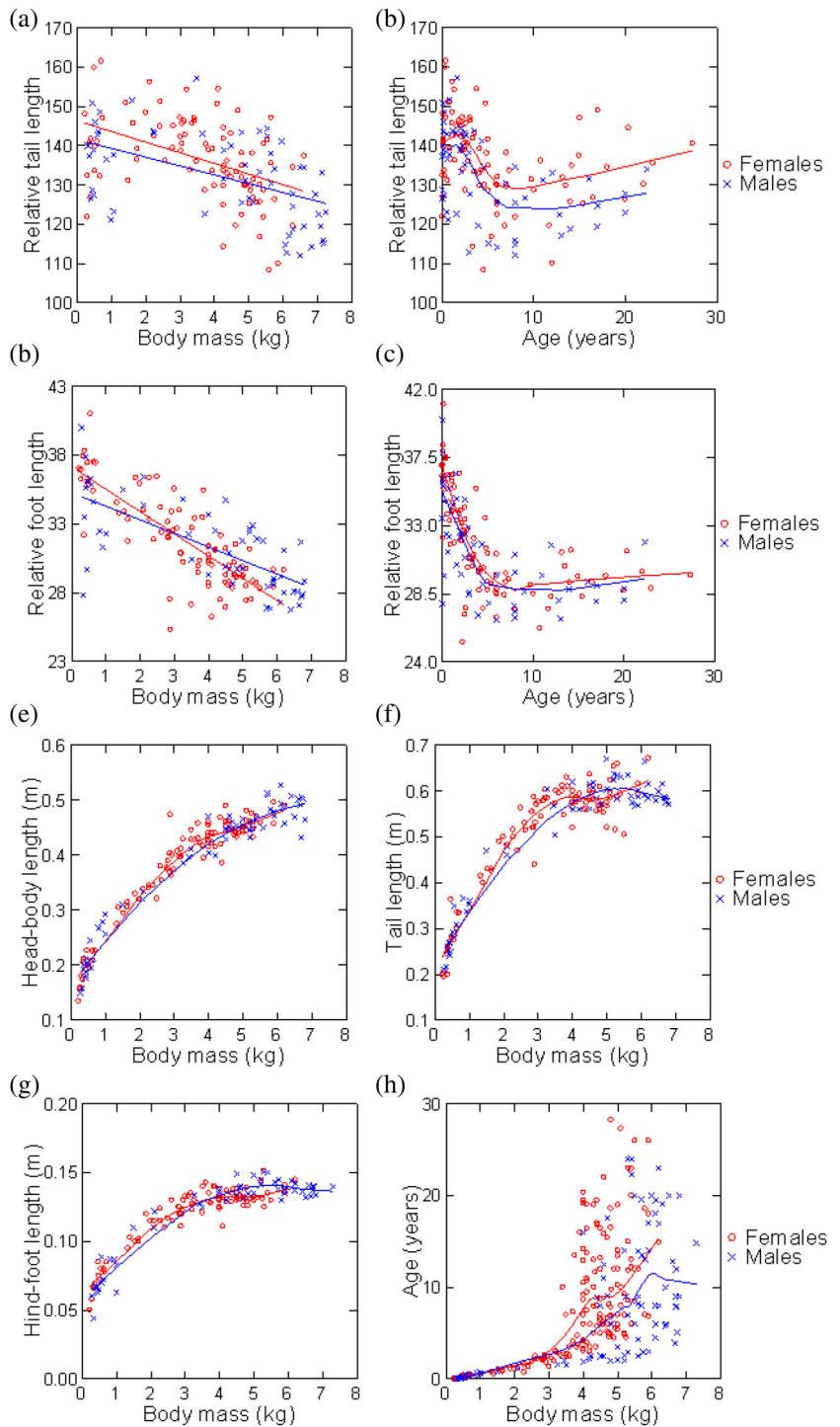
(0.53 and 0.52), and confidence intervals do not overlap. *Cebus* tail length confidence intervals also do not overlap with those for *Cebus* head-body length on mass or *Cebus* hind-foot length on mass. *Saimiri* could not be evaluated for tail length on body mass because the Long and Cooper (1968) sample does not have tail measurements, and although the NMNH sample does, it has few body masses.

Tail length scales with isometry to head-body length for *Alouatta* (Table 5), which is to be expected for males as both properties scale with similar positive allometry to body mass. Female *Alouatta* are almost positively allometric (slope = 1.10), corresponding to isometry for head-body length on mass and positive allometry of tail length on mass. *Cebus* male and female tail length scales with high positive allometry relative to head-body length (slopes of 1.34 and 1.44), which is to be expected as while tail length and head-body length both scale with positive allometry relative to mass, tail length slopes are higher than those for head-body length (see above). The tail length to head-body length slope for NMNH *Saimiri* is clearly positively allometric (1.48), slightly higher than those for *Cebus*.

Table 6 shows regression results for *Alouatta* relative tail length (RTL) and relative foot length (RFL) regressed on age. Related data are shown in Figure 5. While there is much individual variation, curves of RTL versus age and RFL versus age (Figure 5b,d) indicate a decrease in both with increasing age, and then either an upward slope or a leveling of the curve occurs. For RTL, this change occurs at roughly 8 years for both sexes. For RFL, the change occurs at roughly 5 years. The slopes for these comparisons do not differ between males and females, based on their overlapping confidence intervals. Figure 5a,c indicate that RTL and RFL also decrease with body mass, although the male and female correlations are not significant.

Comparisons of head-body length, hind-foot length, and tail length to body mass (Figure 5e,f, and g) show that these properties reach their maxima at different body masses. Head-body length

FIGURE 5 *Alouatta palliata* cross-sectional sample data related to evaluating relative tail length (RTL) and relative foot length (RFL) versus body mass and age. Figure 4a shows RTL versus body mass, Figure 4b shows RTL versus age, Figure 4c shows relative foot length (RFL) versus body mass, Figure 4d shows RFL versus age, Figure 4e shows head-body length versus body mass, Figure 4f shows tail length versus body mass, Figure 4g shows hind-foot length versus body mass, and Figure 4h shows age versus body mass. The last figure shows the inverse of Figure 1a,b, and serves to emphasize the nonequivalence of mass and age. All nonlinear curves in the figure are fit with LOWESS (SYSTAT Version 13)



appears to continue increasing even at the largest masses for both sexes, although not as much for females (Figure 5e). For tail length, females appear to reach maximum length between three and 4 kg (Figure 5f). Male tails appear to reach maximum length around 5 kg. For hind-foot length, female maximum length is around 4 kg, and male maximum length is around 5 kg (Figure 5g).

Figure 6 shows RTL and RFL versus body mass, as well as head-body length, tail length, and hind-foot length versus body mass for *Alouatta*, *Cebus*, and *Saimiri*. Sexes are combined. Samples are

described in “Materials and Methods,” and include NMNH *Saimiri* ($N = 54$) and *Cebus* ($N = 22$) of all maturity levels (see Table 7 foot-notes). The graphs on the left-hand side include the full body mass range of *Alouatta*, while the corresponding graphs on the right-hand side are restricted to X-axis values less than 1.5 kg. This was done to better view *Saimiri* data. Adult *Saimiri* are similar in size to very young *Cebus* and *Alouatta*.

All genera show considerable data scatter for RTL and RFL on body mass (Figure 6a–d), and this is also true if the sexes are

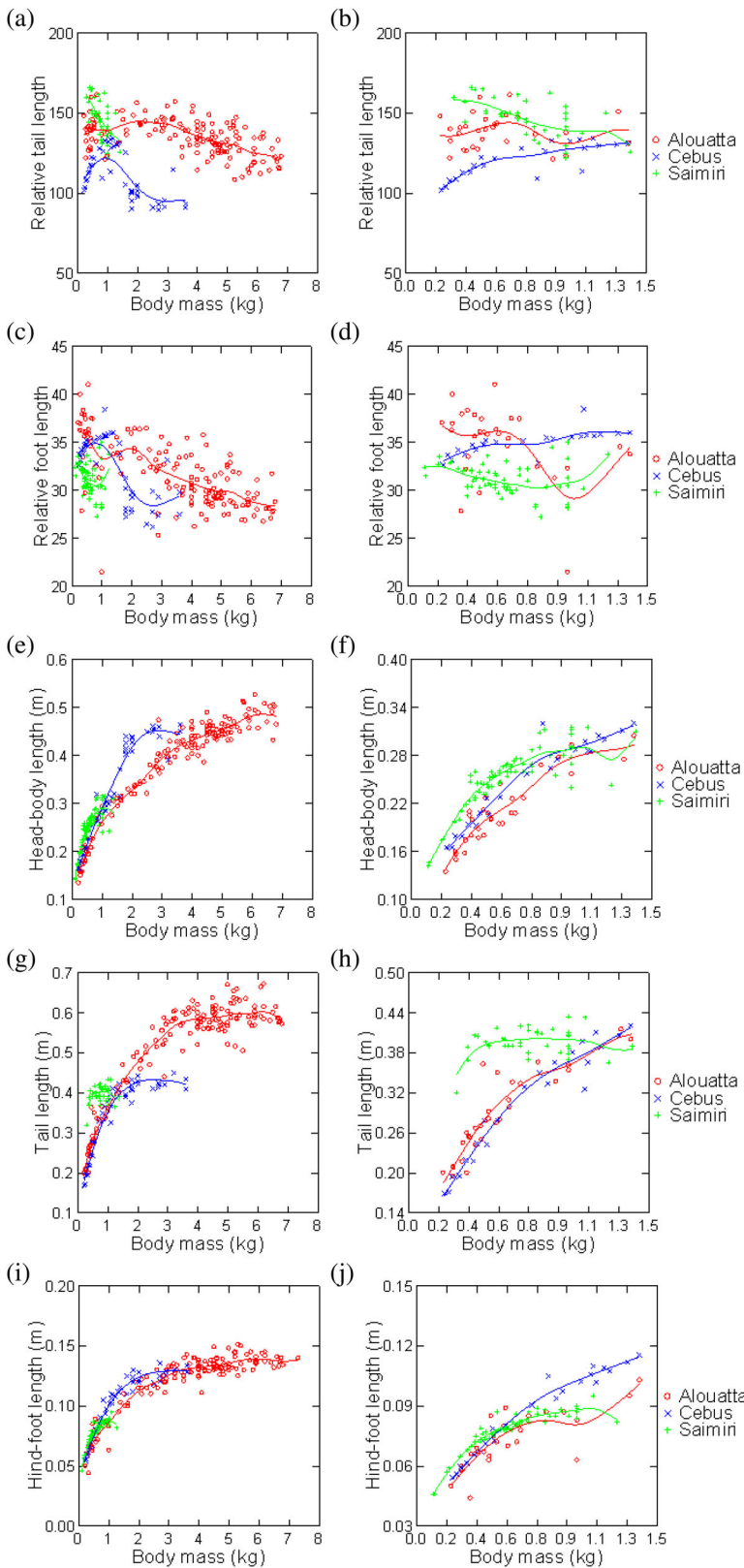


FIGURE 6 *Alouatta palliata*, *Cebus albifrons*, and *Saimiri sciureus* data related to evaluating relative tail length (RTL) and relative foot length (RFL) versus body mass. In addition to Long and Cooper (1968, pp. 198 and 203) *Saimiri* data and Fleagle and Samonds (1975, pp. 42 and 43) *Cebus* data, *Cebus*, and *Saimiri* data include measurements of wildshot individuals from the Smithsonian database (*Cebus* $N = 22$, *Saimiri* $N = 54$), although some are missing measurements. Information provided with the permission of the National Museum of Natural History, Smithsonian Institution, 10th and Constitution Ave. N.W., Washington, DC 20560-0193. (<https://www.nmnh.si.edu/>) (a) shows RTL versus body mass for the full *Alouatta* size range, (b) shows RTL versus body mass for up to 1.5 kg, (c) shows RFL versus body mass for the whole size range, (d) shows RFL versus body mass for up to 1.5 kg, (e) shows head-body length versus body mass for the whole size range, (f) shows head-body length versus body mass for up to 1.5 kg, (g) shows tail length versus body mass for the whole size range, (h) shows tail length versus body mass for up to 1.5 kg, (i) shows hind-foot length versus body mass for the whole size range, (j) shows hind-foot versus body mass for up to 1.5 kg

separated also (not shown). *Cebus* increase in RTL and RFL when still very small (recall positive allometry for first year data in Table 5), then both properties decrease after roughly 1.5 kg. *Saimiri* RTL is the highest of the genera at the smallest body masses, but this ratio falls as they become bigger, and they seem to be intermediate between

the other two genera as adults. *Saimiri* RFL is similar to *Cebus* at smallest body masses, and then decreases with increasing body size so that most of the *Saimiri* scatter is below *Cebus*. *Alouatta* has the highest RFL at the smallest body masses and then decreases until RFL levels are similar to *Cebus* and some *Saimiri*.

Figure 6e–j show direct comparisons of *Cebus* and *Saimiri* linear measurements to those of *Alouatta*. For tail length, *Alouatta* have the longest as adults (Figure 6(g)), not surprisingly. The *Alouatta* curve appears to be a continuation of the *Cebus* curve. As expected, *Saimiri* are much smaller in head-body length and hind-foot length in the absolute sense than the other genera (Figure 6e,f,i, and j). However, *Saimiri* curves for both variables lie slightly above the corresponding curves for the others, suggesting that these properties are a little longer relative to body mass than would be expected. For tail length, the *Saimiri* curve appears horizontal so that it looks like tails reach adult length early. *Saimiri* tails are as long in the absolute sense as those of adult *Cebus* (Figure 6(g)). Unfortunately, the smallest *Saimiri*, limited to the Long and Cooper (1968) sample, do not have tail lengths so the earliest part of the curve is restricted to NMNH *Saimiri*, for which the youngest is probably 3 to 4 months old (estimate from interpretation of *Saimiri* curves in Figure 4a). Possibly very young infants would begin with short tails, and then grow in tail length rapidly.

As an overall pattern, all genera show downward trends in RTL and RFL values with body mass when all ages are included (Figure 6a,c), somewhat similar to that seen for *Alouatta* with RTL and RFL regressed on age (Table 6, Figure 5). *Saimiri* and *Cebus* samples show considerable scatter and the ratios do not correlate with body mass. Therefore, to evaluate the downward trend, it was decided to compare averages for juveniles that are roughly half of adult mass to averages for adults. The body mass ranges, average RTL and RFL values, standard deviations, and sample sizes are shown in Table 7. Adults were selected from the level regions of the head-body length to body mass curve (Figure 6e,f) for *Saimiri* and *Cebus*, or from a range around the fifth-year body mass averages for the *Alouatta* cross-sectional sample (Table 4). Using half of adult mass for the younger age range does not imply that the juveniles are all at the same developmental stage, but it does allow comparison of juveniles to adults for each genus.

Average RTL and RFL values for juveniles in Table 7 are almost all higher than their corresponding adult averages, although younger and older averages are not always two *SD* away from each other. The largest drop appears to be in *Cebus*, with differences between juvenile and adult ratios of over 20. The only exception to the trend of higher juvenile values is RFL in *Saimiri* where juveniles and adult hind-foot ratios are quite similar.

Comparing RTL ratios among genera, *Alouatta* juveniles and adults are intermediate between very high ratios for both age groups of *Saimiri* and relatively low ratios for *Cebus* (Table 7).

Comparing RFL values, *Alouatta* and *Cebus* juvenile averages are similar, ranging between 32.5 and 34.9, and adult averages are also similar, ranging between 28.5 and 29.8 (Table 7). *Saimiri* adults are similar to *Cebus* and *Alouatta* adults, but *Saimiri* juveniles are lower than juveniles of the other genera.

4 | DISCUSSION

Growth resulting in sexual dimorphism has been modeled as either one sex growing faster than the other, or one sex growing for a longer

duration, or both (Leigh, 1992; O'Mara, Gordon, Catlett, Terranova, & Schwartz, 2012; Shea, 1986). Growing for a longer duration is referred to as bimaturism (Shea, 1986). *A. palliata* males become larger than females in body mass predominantly by growing at a faster rate, and not by bimaturism. This is demonstrated visually by LOWESS curves of body mass on age, and also by differences in slopes during the time of most rapid growth (birth to roughly 3 years of age) (Figures 1 and 2, Table 3).

Examination of body mass growth using velocity curves indicates that males and females begin to diverge after 1 year of age and males continue to grow faster than females for the next 2 years (Figure 3). The rate of growth slows between the second and third year, although growth is still on-going for both sexes. For most individuals, the growth rate reaches zero between the fourth and fifth year.

The biphasic male body mass growth curve for a Barro Colorado population seen in Froehlich et al. (1981, p. 213, Figure 2) is not seen in the Hacienda la Pacifica population LOWESS curves. However, body mass velocity curves for both sexes of the mixed longitudinal sample and females of the cross-sectional sample do show rapid early growth, a slow-down, and then a minor older juvenile growth spurt (Figure 3a,b). The later possible growth spurt corresponds to a transition between years three and two. As the average age of male emigration is roughly 2 years of age (Glander, 1992), the timing of this growth increase seems problematic, but it may be the earliest possible within genetic plasticity. Froehlich et al. (1981) note that emigration of males occurs when they seem to be growing the most, often in response to older male aggression (see also Clarke, 1990). They found higher than expected mortality for subadult males in the Barro Colorado population in their article, and cite other sources indicating that young males often suffer from malnutrition. For females, the apparent minor juvenile growth spurt coincides with the average age of emigration of 33 months (Glander, 1992). Being as large as possible before becoming a solitary probably helps with survival.

Body mass growth curves for *Alouatta seniculus* males and females have been published by Crockett and Pope using field data provided by Thorington pers. comm. and Thorington Jr. et al. (1979) (Crockett & Pope, 2002: figure 8.3, p. 107). Similar to *A. palliata*, *A. seniculus* males and females appear close to adult body mass around 4 years of age, with very little growth after this. The two species are also similar in that the divergence between male and female curves first is visible in the graph around 1 year of age, and males appear to grow faster than females.

However, there are differences between male rates of growth. The curve is steepest for *A. palliata* prior to 3 years of age. For *A. seniculus*, the curve appears to be steep until 4 years of age. Using figure 8.3 in Crockett and Pope (2002, p. 107), the slope for *A. seniculus* for this time period is roughly estimated to be 1.4 kg/year (= 5.5 kg/4 years). This is notably lower than the *A. palliata* slope of 2.0 kg/year (Table 3). Thus, it is proposed that the time of rapid growth is slower and more prolonged for male *A. seniculus* than for male *A. palliata*. As male *A. seniculus* typically emigrate after 4 years of age, there is less need to grow as rapidly as *A. palliata*.

Growth curves for *Alouatta caraya* based on field data are shown in Thorington Jr. et al. (1984, figure 5, p. 362). It is difficult to compare

them directly to the ones for *A. palliata* and *A. seniculus* as the age axis is a spectrum of toothwear. Nonetheless, the curves show that *A. caraya* males grow in body mass faster than females, as male slope appears steeper, and that males reach higher adult masses than females. This is similar to the other *Alouatta* species.

A major difference between *Alouatta caraya* and the other species, however, is that the level of adult body mass dimorphism is greater in *A. caraya*. Male and female body mass growth curves in Figure 5 of Thorington Jr. et al. (1984, p. 362), differ by as much as 3 kg at their zeniths. In contrast, male and female *A. palliata* curves differ by roughly 1.5 kg (Figure 1, Table 4), and *A. seniculus* curves by roughly 2 kg (Crockett & Pope, 2002, figure 8.3, p. 107). Captive *A. caraya* data presented in Leigh (1994, p. 509, figure 9) are of known age. Male growth rate can be roughly estimated from the Leigh (1994) graph as $(11 \text{ kg}/5.5 \text{ years}) = 2 \text{ kg/year}$, the same as the rate listed above for *A. palliata*, so rate is not why *A. caraya* are larger. Instead, body mass continues to increase for *A. caraya* for 2 years after it levels off for *A. palliata*, based on Figure 1 of the present article and the Leigh (1994) graph. This age difference for male maturation is also mentioned by Froehlich et al. (1981) citing others.

Another major difference between *Alouatta caraya* and the other *Alouatta* species is that *A. caraya* males finish growth later than *A. caraya* females. This can be seen in both the Thorington Jr. et al. (1984) graph and the Leigh (1994) graph. Thus, in addition to growing at a greater rate than females, male *A. caraya* also grow for a longer duration of time. *A. caraya* sexual dimorphism results from both greater male growth rate and bimaturism.

Sexual dimorphism in linear measurements in *A. palliata* seems to mostly result from bimaturism, with longer durations of rapid male growth, coupled with similar rates of rapid growth for males and females, at least during peak growth phases. Head-body length does not show significant rate dimorphism during phases of rapid growth (Table 3), and the longer body length of adult males probably results mostly from a slightly longer period of rapid growth, at least for the cross-sectional sample. The male mixed longitudinal data curve looks like it has a slightly higher slope, although it is not significantly different (Figure 2d). Cross-sectional data indicate that female rapid growth slows after 1 year, and females are close to adult head-body length by 3 years of age. The mixed longitudinal growth curve shows a longer period of rapid growth, up to a little less than 3 years. Cross-sectional data for males show rapid growth continues until around 2.5 years, and mixed longitudinal data indicate it continues until a little after 3 years. Both sexes reach adult length around three and half years. Thus, adult head-body length is reached slightly before adult mass, yielding somewhat lanky subadults.

Head-body length growth curves for *Alouatta caraya* are found in Thorington Jr. et al. (1984), figure 4, p. 362). These show more dimorphism than for *A. palliata*. *A. caraya* male and female curves differ by roughly 6 cm at adulthood. *A. palliata* males and females, in contrast, are separated by roughly 3 cm as adults (Table 4). Whether sexual dimorphism in *A. caraya* results from rate differences, duration differences, or both, is difficult to tell from the graph.

A. palliata hind-foot and tail growth are very rapid in the first year compared to body mass and even to head-body length. Both sexes are similar in the rate of rapid growth during the first year, but males continue rapid growth slightly longer, again exhibiting bimaturism. Hind-foot length and tail length are close to adult lengths by 2 years of age for both sexes, which probably enables them to navigate the same branches that adults use. Clarke (1990) reported on infant and juvenile behavior for the *A. palliata* population used in this study. *A. palliata* actively explore within weeks after birth, and can travel independently before 2 months of age, and are required to do so by 6 months. The timing of predominantly independent travel is earlier than reported for *A. caraya* by Raguette-Schofield and Pave (2015) who report that this species seldom is carried after 9 months. Mack (1979) reports that *A. seniculus* infants were carried only a quarter of the time they traveled when 7 months old. That infant *Alouatta* uses tail suspension in exploration and travel is reported by Mack (1979) who describes the tail as having a gripping region at its end, and that infants can hang by only their tails by the end of the third month of age (Mack, 1979). Related to this tail use, Prates and Biccas-Marques (2008) found that infant and juvenile *A. caraya* have higher frequencies of suspension and bridging than subadults and adults during feeding.

A. palliata growth data were compared to those for *C. albifrons* and *S. sciureus* to provide some understanding of the effects of sexual dimorphism, arboreality, locomotory behavior, and body size during development. All three genera are sexually dimorphic with males larger than females, and arboreal. Data for *Cebus* are from Fleagle and Samonds (1975) and for *Saimiri* are from Long and Cooper (1968), with many additional measurements from specimens listed in the database of the National Museum of Natural History, Smithsonian Institution ("Materials and Methods"). Adult *Alouatta* typically weigh 5–7 kg, adult *Cebus* 1.5 to 3.5 kg, and adult *Saimiri* 0.7 to 1.5 (Table 7).

In locomotory behavior, all three genera can be described as quadrupeds that walk above branches and frequently climb (DuMond, 1968; Fontaine, 1990; Gebo, 1992; Youlatos & Guillot, 2015). *Alouatta* uses bridging and suspensory behaviors more than *Cebus*, with assistance from its prehensile tail (Gebo, 1992; Youlatos & Guillot, 2015). Garber and Rehg (1999) review several works that, in combination, demonstrate that the tail of *Alouatta* is anatomically a specialized locomotory and sensory organ. Bezanson (2009) reports that juvenile *Alouatta* suspend by their tails more than adults, and that adults use more bridging behaviors than juveniles. *Cebus* shows greater leaping frequency than *Alouatta*, with less reliance on bridging to cover gaps (Gebo, 1992). Adult *Cebus* have prehensile tails but, as explained by Fragaszy, Visalberghi, and Fedian (2004) and Garber and Rehg (1999), the tail usually functions in an assisting role and not by itself. Young juvenile *Cebus* utilize leaping and tail suspension more than older juveniles and adults (Bezanson, 2009; Russo & Young, 2011), and can suspend by tail alone (Bezanson, 2009). *Saimiri* adults are frequent and agile leapers and are not reported to suspend by the tail alone (DuMond, 1968; Fontaine, 1990). They do not have prehensile tails, but instead use tails for balance and support, and occasionally to help anchor

themselves (DuMond, 1968; Young, Russo, Fellmann, Thatikunta, & Chadwell, 2015). Unlike adults and older juveniles, infant *Saimiri* have been documented suspending by the tails alone (Rosenblum, 1968).

Growth curves were generated for the first 14 months for *C. albifrons* and *S. sciureus* using data from Fleagle and Samonds (1975) and Long and Cooper (1968) (Figure 4). The curves indicate that body mass diverges very early, while lengths remains close in males and females for most of the first year. This closely resembles results for *Alouatta* during the first year (Figure 1) in that *Cebus* and *Saimiri* body mass curves appear to diverge due to growth rate differences, while linear measurements follow the same rate for the duration of the curves (14 months), suggesting bimaturism for these. Possibly, bimaturism would be manifest with body mass at older ages also if the data were available. LOWESS curves for *Cebus apella* of all ages shown in Leigh (1992) show a marked drop in female growth at roughly three and a half years while male growth continues on the same trajectory (1992, p. 43, figure 8), demonstrating bimaturism. Similarly, growth curves for *S. sciureus* in Garber and Leigh (1995, p. 8, Figure 2) show bimaturism as female growth levels off and males continue to grow.

Allometric analyses were performed for *Alouatta*, *Cebus*, and *Saimiri* for the first 14 months, a period of rapid growth for all three, with tail lengths added for juvenile NMNH *Saimiri* (Table 5). Further information on the scaling of body proportions came from examining relative tail length (RTL) and relative foot length (RFL), an analysis which included samples of all ages. Table 7 shows averages for mid-age juveniles and for adults, both samples include wider age ranges than those used for allometric analysis. For *Cebus* and *Saimiri* samples, additional NMNH specimens were added as described in "Materials and Methods."

Head-body length scales with slight positive allometry bordering on isometry to body mass for both sexes of all the genera except for male *Alouatta* for which it is notably positively allometric. This suggests that relatively taller torsos are part of *Alouatta* bimorphism, but not in *Cebus* and *Saimiri*.

Hind-foot lengths are isometric relative to body mass for the first year, and negatively allometric to head-body length in *Alouatta* and *Saimiri*. For *Cebus*, both regressions are positively allometric. The isometry/negative allometry in *Alouatta* and *Saimiri* may result from having relatively large feet in young infants, which grow only proportionally with mass. RFL ratios of mid-aged juveniles compared to adults indicate that *Saimiri* juveniles and adults have similarly proportioned feet. The positive allometry of *Cebus* foot growth may reflect only a first-year temporary increase in growth rate—curves showing all ages of RFL versus mass suggest this (Figure 6). Mid-aged juvenile and adult RFL averages are similar to those for *Alouatta* (Table 6) with larger juvenile feet. *Alouatta* regressions of RFL on mass also show declining RFL with increasing age up to 5 years. In general, results support previous articles indicating feet are relatively large in young primates (Ford & Corruccini, 1985; Jungers & Fleagle, 1980; Young & Heard-Booth, 2016). Infants explore independently at least occasionally in all three genera and must be able to grab branches (Bezanson, 2009; Boinski & Fragaszy, 1989; Clarke, 1990; Fragaszy et al., 2004; Jungers & Fleagle, 1980).

Tail length scales with positive allometry to body mass in all genera for the first year, and with positive allometry to head-body length in *Cebus* and the NMNH sample of young *Saimiri*. The *Alouatta* regression of RTL on age suggests that eventually, however, tail growth slows, as the slope declines until roughly 8 years of age. Long tails are expected for juveniles exploring arboreal environments, just like long grasping feet, but much growth is apparently needed during the first year in addition to beginning with proportionately long tails.

Saimiri RTL values of 135 (males) and 148 (females) in Table 7 are the highest among adults, and in absolute tail length (Figure 6), *Saimiri* tail lengths are similar to those of *Cebus*. This was unexpected as *Saimiri* does not have prehensile tails, and the *Saimiri boliviensis* average RTL in Russo (2016, p. 137, Table 1) is 116. However, the range for *S. sciureus* in Garber and Rehg (1999, p. 327, Table 1) is 130 to 160, encompassing the ratio values from the present study, so the results are probably not the result of erroneous measurement. *Saimiri* species may differ in tail length. Why *S. sciureus* needs a relatively long tail is open to conjecture. Possibly the tail has a very important role in counterbalancing during leaping. DuMond (1968) describes leaping in an unspecified species of *Saimiri* - landings were observed on branches a quarter of an inch in diameter from 30 ft away, and the animals were observed adjusting direction mid-leap.

In conclusion, *A. palliata* males become larger than females by growing in body mass at a faster rate, while linear measurements in males became larger by growing for a longer period of time (bimaturism). Both males and females are close to adult mass at 4 years of age, while for linear measurements, males have longer phases of rapid growth. Linear dimensions reach adult proportions at earlier ages than does body mass, resulting in lanky older juveniles. There may be a minor growth spurt during mid to late juvenile periods, but this is not consistently apparent. If present, it would occur during or before male emigration and prior to female emigration.

Comparisons to other species of *Alouatta* indicate *A. palliata* males grow at a faster rate than *A. seniculus*. Early rapid growth is probably an adaptation for coping with earlier emigration in *A. palliata* males. Compared to *A. caraya*, *A. palliata* grows at a similar rate but for less time.

Comparisons of *A. palliata* to *Saimiri sciureus* and *Cebus alifrons* for the first year indicate that *Cebus* and *Saimiri* males become larger in mass than females by growing at a faster rate. These results conflict with other sources including all ages that found sexual dimorphism in these genera resulted from bimaturism. In linear measurements relative to age, *Cebus* and *Saimiri* grow in a manner similar to *Alouatta*, exhibiting longer male rapid growth durations.

Examination of RTL supports previous work indicating that infant and juvenile New World monkeys have large feet relative to adults. Positive allometry for hind-foot length in *Cebus* is a probably a temporary first-year event, as RFL falls as *Cebus* reach maturity.

Tail length grows with positive allometry in *Alouatta*, *Cebus*, and *Saimiri* during the first year, after which RTL drops as the animals reach adulthood. *Saimiri* tail lengths are surprisingly long, possibly to help them in control of leaping directionality.

Future research is intended to investigate the effects of environment on *A. palliata* growth. The Hacienda la Pacifica sample encompasses different resource areas, as discussed in Glander (2006) and Teaford and Glander (1996). Additionally, having knowledge of individual life histories may help elucidate the effects of emigration. While these issues are beyond the present article, the greater data set (Glander, 1992) has potential for addressing their relevance for body growth in the future.

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ENDNOTE

¹Body masses listed in this section are intended to provide a general sense of size. As shown in Glander (2006), considerable variation occurs between populations, and for individuals between seasons.

DATA AVAILABILITY STATEMENT

The *Alouatta palliata* data that support the findings of this study are currently stored in an archive managed by Duke University. They can be made available from K.E. Glander upon reasonable request (glander@duke.edu).

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

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