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POLSKIE TOWARZYSTWO ANTROPOLOGICZNE

The ontogeny of the postcranial skeleton in saddle-back tamarins, *Leontocebus fuscicollis* and callimicos, *Callimico goeldii* (Callitrichidae, Primates)

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Abstract: Ontogenetic studies of callitrichid anatomy are limited to research focused mainly on postcranial skeleton of adults. The goal of this study is to compare the ontogeny of postcranial skeletal development in Goeldi's monkeys (i.e., callimico; *Callimico goeldii*) with the corresponding data on saddle-back tamarins (*Leontocebus fuscicollis*). The intermembral, humerofemoral, brachial, crural, and ulna-radius indices of callimicos and saddle-back tamarins were calculated and compared among different age classes in order to assess the implications for their ecology and behavior. Ontogenetic trajectories, including age at growth cessation, were also calculated. It is shown that for a given hindlimb length, *L. fuscicollis* has longer forelimbs compared to *C. goeldii*, maintaining this proportion across all age classes. A relatively elongated forelimb observed in *L. fuscicollis* may have a mechanical role in reducing the force of impact when landing on large vertical substrates. In contrast, hindlimb length and pattern of hindlimb development (such as derived features of the ankle that enhance stability) in callimicos appear to play a critical role in propulsion during trunk-to-trunk leaping. These differences may affect niche partitioning, foraging strategies, and substrate use.

Key words: allometry, growth, limb proportions, New World primates, ontogeny, postcranial skeleton.

Original article

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Introduction

Research studies on ontogeny (i.e., the course of growth and development of individuals to maturity) and allometry (i.e., the study of size and its implications) in individual primate species facilitate better understanding of the evolutionary adaptive histories of the Primate order (Fleagle 1985; Shea 1995; Marroig and Cheverud 2009; for hominid primates: Gould 1977; Leigh 1996a; Nelson and Thompson 1999). Thus, research on the postcranial skeleton, and on the fore- and hindlimbs specifically, offers an opportunity to address questions concerning variation in locomotor patterns and body size among primates (Jungers 1985; Falsetti et al. 1993; Leigh 1996b; Leigh and Shea 1995). In this sense, the diversity of primate limb skeletons is related to natural selection and may reflect the variability in the use of different forest substrates (Chiu and Hamrick 2002).

Regarding the Callitrichidae family (Rylands et al. 2016), there have been few studies that emphasized the importance of postcranial development (e.g., Glassman 1983; Falsetti and Cole 1992). For example, Bicca-Marques et al. (1997, 1998) and Bicca-Marques (1999) compared data on hand morphology among different species of callitrichids, illustrating the relevance of hand shape in relation to their feeding ecology and niche partitioning. However, as indicated by Falsetti and Cole (1992), these data were mainly derived from adult individuals. In contrast, only few studies have taken into account the relevance of studying the ontogeny among callitrichids in order to understand their implications regarding behavioral ecology and positional behavior of this group (Falsetti and Cole 1992; Garber and Leigh 1997; Garber and Leigh 2001a).

Positional and foraging behavior of callitrichids is adapted to the use and preference of low forest substrates (Terborgh 1983; Yoneda 1984; Garber and Teaford 1986; Heymann 1997; Garber and Leigh 2001a, 2001b). The aim of this study is to describe the ontogeny of the postcranial skeleton of callimicos (*Callimico goeldii*) and saddle-back tamarins (*Leontocebus fuscicollis*), and to determine its implications for understanding the development of their positional behavior. These two callithichid taxa are reported to be the most frequent trunk-to-trunk leapers within this primate group (Garber and Leigh 1997; Garber and Leigh 2001) and are sympatric in the wild. This paper aims to provide further information on the postcranial skeleton proportions of the Callithrichidae following the comprehensive work of Davis (2002).

This research has the following objectives: (i) to calculate and compare proportional indices of postcranial skeletons in *C. goeldii* and *L. fuscicollis* immatures/matures; (ii) to determine whether there are intra- and interspecific differences or similarities between both species and between age-classes in terms of their ontogenetic and allometric histories; (iii) to reconstruct the ontogeny of these primates using fore- and hindlimbs; and (iv) to evaluate the relationships between the morphology of the postcranial skeleton and the behavior of both species. Relating morphology and behavior offers insight into the ecological adaptability of these New World primates.

Material and Methods

The saddle-back tamarins (*Leontocebus fuscicollis*) specimens used in this study consisted of 22 females and 18 males (total 40 individuals) including 18 immature (<190 days) and 22 mature (>190 days) individuals (according to the age classes provided by Garber and Leigh (1997)). Data on the exact age of death have been recorded in all examined individuals. The skeletal research collection is housed in the Laboratory of Primate Biology of the Department of Anthropology at the University of Illinois at Urbana-Champaign, USA. These saddle-back tamarin (*L. fuscicollis*) skeletons were curated and obtained from the Department of Anthropology at the University of Tennessee-Knoxville, USA and came from the Marmoset Research Center, Oak Ridge Associated Universities, USA. The original tamarin colony was created in the 1960s by N. Gengozian (1969) and used for medical studies. The skeletons used in this study were sampled from captive-born *L. fuscicollis* individuals belonging to three different subspecies (*illigeri*, *nigrifrons,* and *lagonotus*) and their hybrids. As suggested by Garber and Leigh (1997), the small number of *L. fuscicollis* subspecies used in this study could be a limitation. Although the sample size is ample for this genus, it is not large enough to be compared at the subspecific level. The data are pooled at the species level.

The callimicos (*Callimico goeldii*) skeleton collection is maintained by the Barbara E. and Roger O. Brown Primate Research Facility in the Division of Mammals at the Field Museum of Natural History, Chicago, USA. The specimens, eight females and 14 males (totaling 22 individuals), included six immature and 16 mature individuals. All individuals were captive-born at the Brookfield Zoo (Chicago). The ages were recorded and provided by M. Wanerke (1998, 2003: pers. comm.). The *C. goeldii* colony was founded in 1977 to maintain a long-term successful breeding project for this rare New World primate (Beck et al. 1982; Sodaro 2000; see also Palacios et al. 2021).

In order to pursue the objectives of this work, the maximum lengths of the femur (FML), tibia (TML), humerus (HML), radius (RML), and ulna (UML) were measured using the diaphyseal lengths. The measurements were done using a digital sliding caliper, the Mitutoyo™ 500–197, graduated to 0.01 mm. Data from males and females were pooled; there is no significant sexual dimorphism in this primate group (Hershkovitz 1977; Cole et al. 1988; Hanihara and Natori 1988, estimated by standard deviation in this study). While examining questions of ontogeny, the data were analyzed separately between species and age classes. Immature individuals show signs of ossification, as reported for callitrichid infants by Hofmann et al. (2007). The intermembral, humerofemoral, brachial, crural, and ulna-radius indices were calculated for both primates and age classes, considering the average captive adult body weights (Jungers 1985: 350) (for *L. fuscicollis* body weight [= 414.5 g]: Leigh 1994: 25 and for *C. goeldii* body weight [= 607 g]: Wanerke 2003: pers. comm.). Measurements were collected on non-pregnant and healthy animals.

Statistical analysis was performed using the SYSTAT® software package and Microsoft-Excel®. Ontogenetic data were graphically represented for both callitrichid species. An analytical comparison was done using conventional least squares regression analysis. Furthermore, to contrast pairs of variables, *t*-tests were conducted to establish potential differences among the indices of both primates and age classes.

Results

Figure 1 shows absolute differences in the postcranial maximum length (ML) of both callimicos and saddle-back tamarins. The postcranial proportion indices were calculated in order to compare intra- and interspecific variation in shape. As shown in Table 1, no significant differences were observed in any of the measurement taken from immature individuals of *Callimico goeldii* and *Leontocebus fuscicollis*. However, when comparing the ML proportion indices among mature individuals, *L. fuscicollis* shows significantly (99%, p<0.0001) higher intermembral and humerofemoral indices compared to *C. goeldii*. In contrast, *C. goeldii* has significantly higher values of the ulna-radius index compared to *L. fuscicollis* (Table 1; Fig. 2 shows statistically significant limb proportion indices). The species-specific differences of mature individuals are also indicated in several forelimb and hindlimb indices; in all cases, callimicos values are higher than saddle-back tamarins (Table 1).

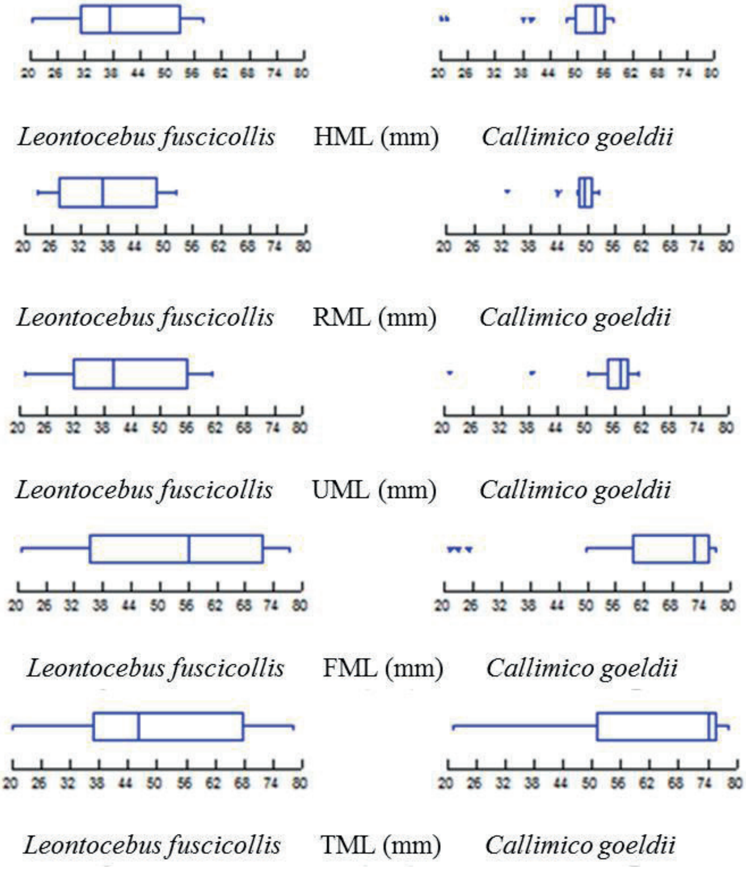


Fig. 1. Box plots for comparison of postcranial skeleton lengths (mm) between mature *Callimico goeldii* and *Leontocebus fuscicollis*

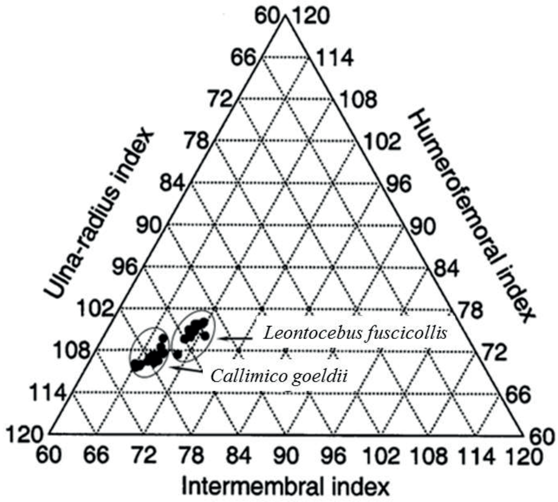


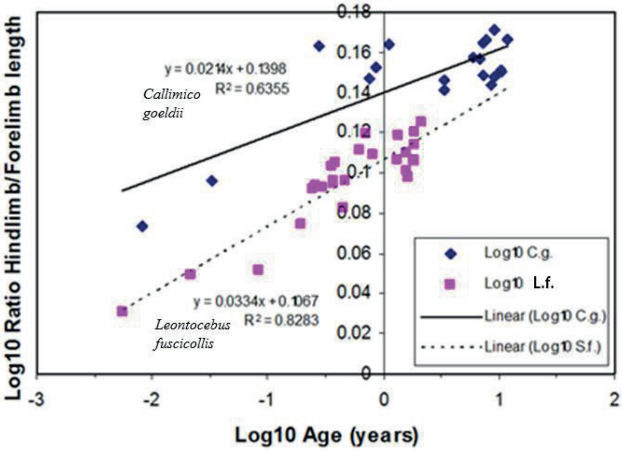
Fig. 2. Triangular plot of the significantly different relative limb proportion (indices) between mature *Callimico goeldii* and *Leontocebus fuscicollis*

Table 1. Comparison of postcranial skeleton proportions (indices) between immature and mature *Callimico goeldii* and *Leontocebus fuscicollis*

	Immature								
	Callimico goeldii			***Leontocebus fuscicollis***					
	n	**Mean**	**S. D.**	**n**	**Mean**	**S. D.**	***p*-value**	**d.f**	
Intermembral index	6	79.015	7.109	17	82.961	4.588	0,021	3	*L. f.>C. g.*
Humerofemoral index	4	80.701	8.839	13	90.122	4.091	0,054	3	L. f.>C. g.
Brachial index	6	90.191	11.037	18	89.268	4.096	0,780	5	*C. g.>L. f.*
Crural index	4	96.762	3.914	13	105.802	3.416	0,043	3	*L. f.>C. g.*
Ulna/radius index	6	111.206	6.167	18	113.733	3.784	0,791	5	L. f.>C. g.
	Mature								
	Callimico goeldii			***Leontocebus fuscicollis***					
	n	**Mean**	**S. D.**	**n**	**Mean**	**S. D.**	***p*-value**	**d.f**	
Intermembral index	16	70.073	1.485	21	77.424	1.441	0,000	12	*L. f.>C. g.**
Humerofemoral index	16	74.576	2.121	13	83.163	2.992	0,000	12	*L. f.>C. g.**
Brachial index	16	90.292	3.230	21	91.512	5.111	0,756	15	*L. f.>C. g.*
Crural index	16	102.479	2.851	13	107.090	4.831	0,019	12	L. f.>C. g.
Ulna/radius index	16	116.173	1.017	22	114.320	1.768	0,003	15	*C. g.>L.f.**
Forelimb index	16	12.072	1.051	21	10.130	2.958	0,000	12	*C.g.>L.f.**
Hindlimb index	16	17.235	1.522	13	14.784	2.471	0,001	15	C.g.>L.f.*

*Significantly different after *t*-test (99%). Abbreviations: *C. g.* (*Callimico goeldi*), *L. f.* (*Leontocebus fuscicollis*).

Mature individuals of *C. goeldii* have longer hindlimbs relative to forelimbs compared to *L. fuscicollis*. In other words, at a given hindlimb length, *C. goeldii* has shorter forelimbs compared to *L. fuscicollis*, and these differences are maintained with age (Fig. 3). These results are supported by the least squares regression analyses (Table 2) as all regression slopes are under the isometric line, indicating that both primate species exhibit differential growth rates. However, the regression slopes also indicate that *C. goeldii* has a lower rate of growth compared to *L. fuscicollis*.



Three *C. g.* weaning (2 two-days old, 1 three-days old) were omitted due to high dispersion.

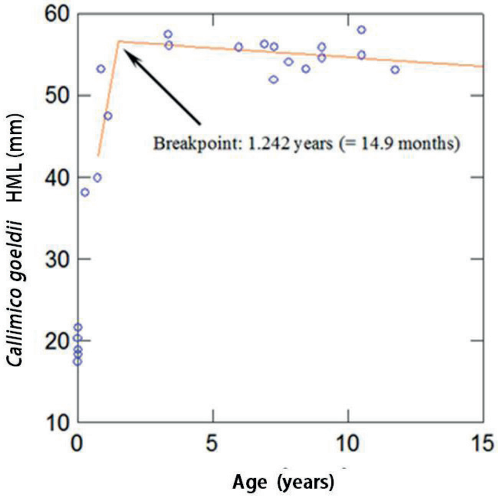
Fig. 3. Allometric comparison of the hindlimb/forelimb length ratio between *Callimico goeldii* and *Leontocebus fuscicollis*

Table 2. Least squares regression analysis between mature *Callimico goeldii* and *Leontocebus fuscicollis*

	X axis	Y axis			
Primate	**(years)**	**(mm)**	**Intercept**	**Slope**	**R²**
Leontocebus fuscicollis	**Age**	**HML**	1.593	0.2372	0.876
	Age	**RML**	1.551	0.2411	0.870
	Age	**UML**	1.610	0.2486	0.875
	Age	**FML**	1.672	0.2729	0.915
	Age	**TML**	1.694	0.2692	0.901
Callimico goeldi	**Age**	**HML**	1.618	0.1530	0.948
	Age	**RML**	1.572	0.1533	0.937
	Age	**UML**	1.632	0.1615	0.944
	Age	**FML**	1.734	0.1698	0.920
	Age	**TML**	1.735	0.1805	0.944

All values in Log10

Piecewise regressions were performed on all immature and mature individuals, absolute *C. goeldi* postcranial maximum lengths were recorded in order to determine the age at growth cessation. Callimicos have an age at growth cessation of 14.9 months (Fig. 4). This age is similar to the one reported for sexual maturity in female callimicos (13–14 months, using radioimmunoassay of urinary steroid hormones), and the earliest recorded among all callitrichids (Dettling and Pryce 1999). Our *L. fuscicollis* data present two cluster groups that do not allow this type of regression. However, Garber and Leigh (1994), using captive-born saddle-back tamarin adult brain size data analyzed by a piecewise regression, reported growth cessation in the cranium at ~13.2 months. Fig. 5 shows scatter plots of maximum lengths *vs*. age with log-transformed trend lines indicating similar growth curves for both primate species.



The piecewise regression equation: y = b0+b1*age+b2*(age-bp)*(age>bp) (From SYSTAT© Manual).

Fig. 4. *Callimico goeldii* humerus maximum length growth trajectory with the age of growth cessation

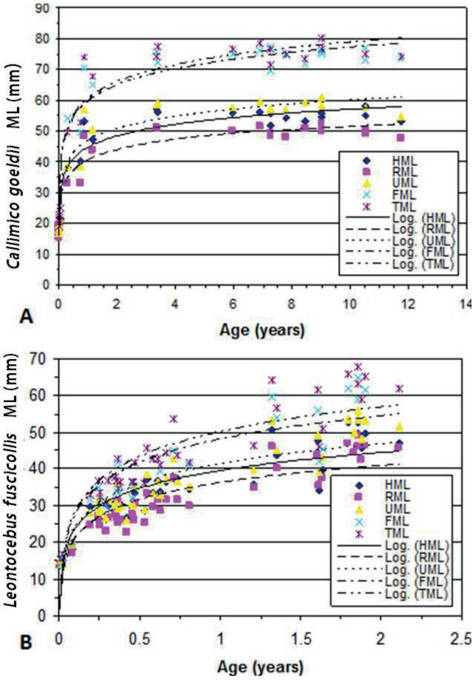


Fig. 5. *Callimico goeldii* and *Leontocebus fuscicollis* postcranial skeleton growth curves

Discussion

The results of the postcranial skeleton in *Callimico goeldii* and *Leontocebus fuscicollis* analyses provide insights into several aspects of their positional behavior. As indicated by Kimura (2003), arboreal primates tend to have longer hindlimbs than terrestrial ones, a feature related to the locomotor behavior adopted by each primate taxon in different environments. Garber and Leigh (2001a) argued that species differences in limb proportions rather than body mass offer a better explanation of differences in positional behavior and patterns of habitat utilization, which appears to be the case for other primate taxa as well (Garber 2007).

Growth trajectories showed in our study are congruent with those reported by Falsetti and Cole (1992), indicating that among callitrichids, saddle-back tamarins (*L. fuscicollis*), cotton-top tamarins (*S. oedipus*), and common marmosets (*Callithrix jacchus*), growth trajectories are also similar. In addition, as shown by Garber and Leigh (2001a) and Falsetti and Cole (1992), *L. fuscicollis* has proportionally longer forelimbs to hindlimbs during ontogeny compared to marmosets (*Callithrix* spp.) and other tamarins (*Leontocebus labiatus*).

Our results also show that, compared with *C. goeldii, L. fuscicollis* exhibits longer forelimbs than hindlimbs. Field studies on the positional behavior of these sympatric primate species suggest that longer forelimbs in *L. fuscicollis* may provide an "advantage by increasing the braking distance available for decelerating the body when landing in a rigid support" (Garber and Leigh 2001a: 28). In addition, in *L. fuscicollis* longer forelimbs might also be an adaptation for foraging, which is in accordance with data reported by Bicca-Marques et al. (1997, 1998) and Bicca-Marques (1999), who found that in this species, longer forelimbs might be an advantage during feeding.

On the other hand, in callimicos, elongated hindlimbs and a pattern of hindlimb development characterized by derived features of the ankle may serve to enhance stability during locomotion (Davis 1996). This has been argued to represent an adaptation for trunk-to-trunk leaping behavior (Garber and Leigh 2001a; Garber et al. 2009).

The differences in the postcranial skeleton and limb proportions in *L. fuscicollis* and *C. goeldii* suggest that different limb proportions, diet, foraging strategies, and patterns of habitat utilization enable these species to exploit different microenvironments in sympatry.

In sum, these data suggest that, in the evolutionary history of the Callitrichidae, differences in limb proportions and growth ontogeny might have played a major role in shaping ecological and behavioral differences between *C. goeldii* and *L. fuscicollis*. These differences include divergence in substrate use (Garber and Pruetz 1995; Heymann and Buchanan-Smith 2000; Berles et al. 2022), niche partitioning, feeding behavior (Bicca-Marques 1999), and positional behavior (Garber and Leigh 2001a, 2001b). It also indicates that limb proportions among callitrichids may be used to distinguish ecologically different taxa. Nevertheless, further research on the energetic cost of leaping, vertical clinging, quadrupedal running, and musculoskeletal design is needed (Warren and Crompton 1998; Polk 2002) in order to fully understand the specific relationships between limb morphology and positional behavior in the Callitrichidae.

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Conflict of interest

The author declared no conflict of interest.

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