Received: 1 February 2024 | Revised: 13 April 2024 | Accepted: 22 April 2024

DOI: 10.1002/ajp.23634

RESEARCH ARTICLE

AMERICAN JOURNAL OF PRIMATOLOGY WILEY

Developmental milestones in captive *Galago moholi*

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Funding information
National Science Foundation, Grant/Award Numbers: BCS-1231350, BCS-1231717, BCS-1728263, BCS-1830894, BCS-1830919

Abstract

Systems of the body develop in a modular manner. For example, neural development in primates is generally rapid, whereas dental development varies much more. In the present study, we examined development of the skull, teeth, and postcrania in a highly specialized leaping primate, *Galago moholi*. Eighteen specimens ranging from birth to adult were studied. Bones, teeth, and the cranial cavity (i.e., endocast) were reconstructed with Amira software based on microCT cross-referenced to histology. Amira was also used to compute endocast volume (as a proxy for brain size). Reconstructions of the wrist and ankle show that ossification is complete at 1 month postnatally, consistent with the onset of leaping locomotion in this species. Endocranial volume is less than 50% of adult volume at birth, ~80% by 1 month, and has reached adult volume by 2 months postnatal age. Full deciduous dentition eruption occurs by 2 weeks, and the young are known to begin capturing and consuming arthropods on their own by 4 weeks, contemporaneous with the timing of bone and ankle ossification that accompanies successful hunting. The modular pattern of development of body systems in *Galago moholi* provides an interesting view of a "race" to adult morphology for some joints that are critical for specialized leaping and clinging, rapid crown mineralization to begin a transitional diet, but perhaps more prolonged reliance on nursing to support brain growth.

KEYWORDS

bushbaby, locomotion, ontogeny, vertical clinger and leaper

1 | INTRODUCTION

Somatic development is frequently viewed within the context of life history. Viewing prenatal and postnatal development as a continuum, life history theory posits that the timing of birth, weaning, growth cessation, and death are adaptive traits (Smith, 1992). In other words, there is a link between natural selection and the pace at which an animal develops (e.g., Williams (1966); Promislow & Harvey, 1990; Janson & Van Schaik, 1993; Bolter & Zihlman, 2007; Leigh & Blomquist, 2007). Body systems may independently vary in the pace of development based on selective forces acting on both the mother and fetus or infant (Smith et al., 2020). Body systems may also vary in developmental pace across the body. Comparative differences can be related to differential usage of limbs throughout ontogeny in some

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Abbreviations: ECV, endocranial volume; MT, metatarsal.

mammals (Young et al., 2020). For example, marsupials are advanced in fore limb relative to hind limb development; this advanced maturation relates to its transient importance to locomotion for nursing (Smith and Keyte, 2020).

As in other mammals, newborn primates are proportionally different than adults. All primates are initially helpless, and may be nest-bound, carried, or "parked" for a variable amount of time. Subsequently, infants crawl or ride adults (Ross, 2001). Somatic and behavioral maturation allowing adult-like locomotion occurs at a highly variable rate; the important locomotor function of feet and manipulative function of hands is preceded by the precocious capacity to grasp the mother's fur (Peckre et al., 2016; Young and Heard-Booth 2016).

In a broad sense, primates are considered precocial mammals, but this is largely an assessment of their highly encephalized state at birth (Halley, 2017, 2018). In musculoskeletal and dental development, primates are more greatly varied in pace of development (Atzeva et al., 2007; Godfrey et al., 2001; Grand, 1992; Smith et al., 1994). The potential for prolonged juvenility may add considerable flexibility for primates (Smith et al., 2020), while demands for specialized locomotion or diet may constrain this flexibility, requiring more rapid development of some body regions or systems (Atzeva et al., 2007; Godfrey et al., 2003; Young et al., 2020).

Prior work has indicated mammals vary in the pace of somatic and neural development (Grand, 1977). In galagids, dental development (e.g., cusp mineralization) is known to be relatively rapid (Paddock et al., 2020), whereas in relative brain size at birth galagids are intermediate among primates (Harvey et al., 1987). In contrast, development of hind limb robusticity may be especially rapid in specialized leaping primates (Young et al., 2020), suggesting that selection for specialized locomotion promotes more rapid somatic development prenatally, though lesser bushbabies (*Galago* spp.) in particular have not been studied in this regard. Here we examine postnatal ontogeny of several somatic systems in a known-age ontogenetic sample of the southern lesser bushbaby (*Galago moholi*). Since considerable behavioral and life history information is available from captive and wild settings, this species presents a unique opportunity to assess the pace of somatic development in a specialized leaping primate. Whereas rapid dental development is already known for this species (e.g., Godfrey et al., 2001), we predict prolonged postnatal brain growth since galagids are not born with large relative brain sizes (Harvey et al., 1987). Because of their specialized mode of locomotion, we predict differential patterns of development of the hind and fore limbs, with more rapid postnatal development of thigh and leg (vs. arm and forearm) musculature and bones based on differential use of limbs (grasping vs. leaping).

2 | MATERIALS AND METHODS

Eighteen *Galago moholi* specimens were studied (Table 1; Supporting Information: Table S1). Thirteen were cadaveric subadults, four were cadaveric adults, and one additional cleaned skull of an adult was

TABLE 1 Cranial and limb measurements of *Galago moholi* across age.

Age (*n*)	ECV (mm3)	CL (mm)	BL (mm)	PL (mm)	CBA	BL1 (mm)	BL2 (mm)	Humerus length (mm)	Radius length (mm)	Femur length (mm)	Tibia length (mm)	IMI (%)
Newborn (5)	1838.01	24.6	15.27	7.55	167.45	10.04	5.23	11.33	11.91	19.46	18.1	62
Early infant (4)	2747.4	27.63	16.38	9.25	167.4	10.99	5.39	12.1	13.26	24.95	21.8	54
Older infant (1)	2964.63	30.42	17.89	10.47	169.8	12.17	5.72	19.17	18.13	33.66	31.3	57
Early juvenile (1)	4143.89	35.42	20.36	12.67	169.3	13.72	6.64	24.74	24.605	44.405	42.2	57
Older juvenile (2)	4266.11	37.88	20.76	13.71	171.75	13.99	6.77	24.25	26	48.7	49.6	51
Adult (5)	4168.64	39.46	23.03	14.31	173.2	15.23	7.8	29.31	31.21	61.1	55.3	52

Abbreviations: BL, basicranial length; BL1, prechordal basicranial length; BL2, postchordal basicranial length; CBA, cranial base angle (degrees); CL, cranial length; ECV, endocranial volume; IMI, intermembral index (expressed as % - humerus + radius/femur + tibia *100); PL, palatal length.

utilized. All use of primate tissues was reviewed and approved by the Institutional Animal Care and Use Committee (IACUC) at Slippery Rock University, and was also consistent with the adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates. Most specimens were µCT scanned at Northeast Ohio Medical University (NEOMED) using a Scanco vivaCT 75 scanner (scan parameters: 70 kVp; 114 mA) and reconstructed with 0.0205–0.025 mm cubic voxels. Most specimens were acquired as cadaveric remains from the Duke Lemur Center (DLC), except the adult skull (CMNH-B0747), which was from the Cleveland Museum of Natural History. All DLC animals died of natural causes and most were immersed in formalin or frozen and then immersed in formalin. One perinatal *G. moholi* was fixed in 70% ethanol. The captive primates were maintained in a seminatural environment that presumably allowed the use of their preferred pattern of locomotion without restriction. Subadult specimens, all acquired after natural deaths in captivity at the Duke Lemur Center, ranged in age from 0 to 97 days. In addition to recorded age in days, specimens were also categorized by dental age. “Newborns” were zero to 7 days old. “Infants” were older than 7 days old (per Smith et al., 2020) and had no fully erupted permanent teeth; our sample included “younger” (15–17 days old) and “older” (30-day-old) infants. “Juveniles” had commenced, but not completed, eruption of permanent teeth. Our sample included “younger” (60-day-old) and “older” (95–97 days old) juveniles. No grossly obvious pathologies, such as limb or limb joint deformities, were found among subadult specimens.

Muscle masses were calculated for most specimens. The same protocol was used for the dissection and weighing of all specimens. Dissection protocol included removal of skin and connective tissue to expose underlying limb musculature. Once the underlying musculature was revealed, muscles were identified and removed individually or in groups. After removal, muscles were grouped according to function and were weighed by a single investigator (DAV). Weights were obtained for the following functional groups: arm extensors, arm flexors, forearm flexors, forearm extensors, and brachioradialis. For the purposes of this study, muscles were combined into four limb segments: arm, forearm, thigh, leg. Intrinsic muscles of the hands were difficult to remove and were excluded from the data. All muscles were removed from bone and connective tissue and blotted dry with paper towel before weighing. Muscle masses were obtained with a Mettler AJ100 scale and were recorded to the nearest 0.001 g for infants and to the nearest 0.01 g for the adult specimens. Muscles/muscle groups were weighed twice and the average of the two recordings was used. In cases of measurement discrepancy exceeding 10%, a third measurement was taken and the outlier thrown out. The data on hind limb muscles were previously published (Atzeva et al., 2007; Baker et al., 2011), and are presented here for evaluation with new data on fore limb musculature.

TABLE 2 Cranial and limb measurements.

1. cranial length: prosthion to inion
2. basicranial length: basion to foramen cecum
3. palatal length: prosthion to posterior-most point of palatine bones
4. cranial base angle: angle between prechordal basicranial line (foramen cecum to middle of sella turcica) and postchordal basicranial line (middle of sella turcica to basion)
5. basicranial line 1: length of prechordal basicranial line
6. basicranial line 2: length of postchordal basicranial line
7. IMI, intermembral index

Cranial and limb bone image data were segmented and then reconstructed using Amira 2019 software. Limb and cranial metric data on older subadults were taken from Amira reconstructions. Cranial metrics included cranial length, cranial base angle, and basicranial length 1 and 2 (Table 2). In smaller subadults, in which epiphyses were unossified, limb measurements were taken directly with digital calipers from cadaveric bones (thus including cartilaginous ends); some were measured already in a prior study (Baker et al., 2011). The relationship of these linear measurements to postnatal age and to body mass (based on records on captive *G. moholi* from the Duke Lemur Center – Zehr et al., 2014; see Supporting Information: Table S2) were examined using least-squares regression. Statistics were done using Excel software; correlation coefficients were considered significant at $p < 0.05$.

Endocasts have been made using bony contours, via µCT scans, including subadults (e.g., Gunz et al., 2010). In the case of the perinatal specimens, unossified skeletal regions may complicate reconstructions of internal cranial spaces (Smith et al., 2023). Here, we overcame this challenge using a comparison of µCT volumes to histology of specimens sectioned in the same plane. The only region that was not ossified sufficiently to visualize was the cribriform plate of newborns. However, that countour was estimated by tracing a line across the right and left frontal bones at the level of the well-ossified endocranial limit of the perpendicular plate of the ethmoid. It was likewise necessary to draw a line between bones that border fontanels.

For a preliminary assessment of age changes in growth plate microanatomy and wrist and ankle ossification, limb joints of one neonate and the 30-day-old were decalcified, paraffin embedded, and serially sectioned at 10 µm in a plane parallel to the long axis of long bones of each joint, and the wrist/hand and foot/ankle. Only specimens that had not been frozen were selected, for optimal preservation (i.e., lack of distortion that can accompany freezing – Wood et al., 2023). Sections were stained with Gomori trichrome, hematoxylin-eosin, or alcian blue-periodic acid-Schiff procedures. In the newborn and 30-day-old, growth plate organization and degree of wrist and ankle ossification were assessed microscopically, using a Leica DMLB compound microscope at magnifications from X25 to X630. Degree of epiphyseal plate fusion and carpal or tarsal ossification in specimens 57 days and older were assessed using µCT and imaged using Amira software.

Behavioral information relating to feeding and locomotion was based on observations of captive lesser bushbabies by Doyle (1979) and Nash (2003). We also contextualize our findings in light of weaning age for *G. moholi*. In a recent compilation of life history data, Zimmermann and Radespiel (2015) provided a range of age at weaning from 45 to 100 days. However, the youngest age is considerably lower than other data the authors list. We therefore use an average that excludes the youngest weaning age. This average, at 92 days, is similar to weaning ages reported for the other lesser bushbaby *G. senegalensis*.

3 | RESULTS

3.1 | Endocranial volume (ECV) and cranial dimensions

ECV is 44% of adult size in the newborn, surpasses 50% during infancy (66% by ~2 weeks; 71% by 1 month), and is fully grown by ~2 months (Table 1; Supporting Information: Figure S1). Based on linear measurements, facial growth lags behind this pace (e.g., by 2 months, basicranial length = 90% adult length; palatal length = 80% adult; Table 1). A qualitative examination of endocasts superimposed over hemisected skulls supports this (Figure 1).

In a cross-sectional age plot of craniofacial metrics (Figure 2), overall cranial length has a higher regression slope than either palatal length or total basicranial length (Figure 2a). Scaling of cranial measurements to estimated body mass for age is very similar (Figure 2b). The prechordal portion of the cranial base (BL1) has a distinctly higher slope than the postchordal segment (BL2) (Figure 2c). Cranial base angle increases across age, from ~168° at birth (average of 2 specimens) to 173° in the adult (Table 1). The angle is quite variable among newborns and early infants, but the older infant, juveniles, and adult cluster closely around a linear regression line (Figure 2d). All metrics are significantly correlated ($p < 0.05$) with postnatal age or body mass (Supporting Information: Tables S2 and S3).

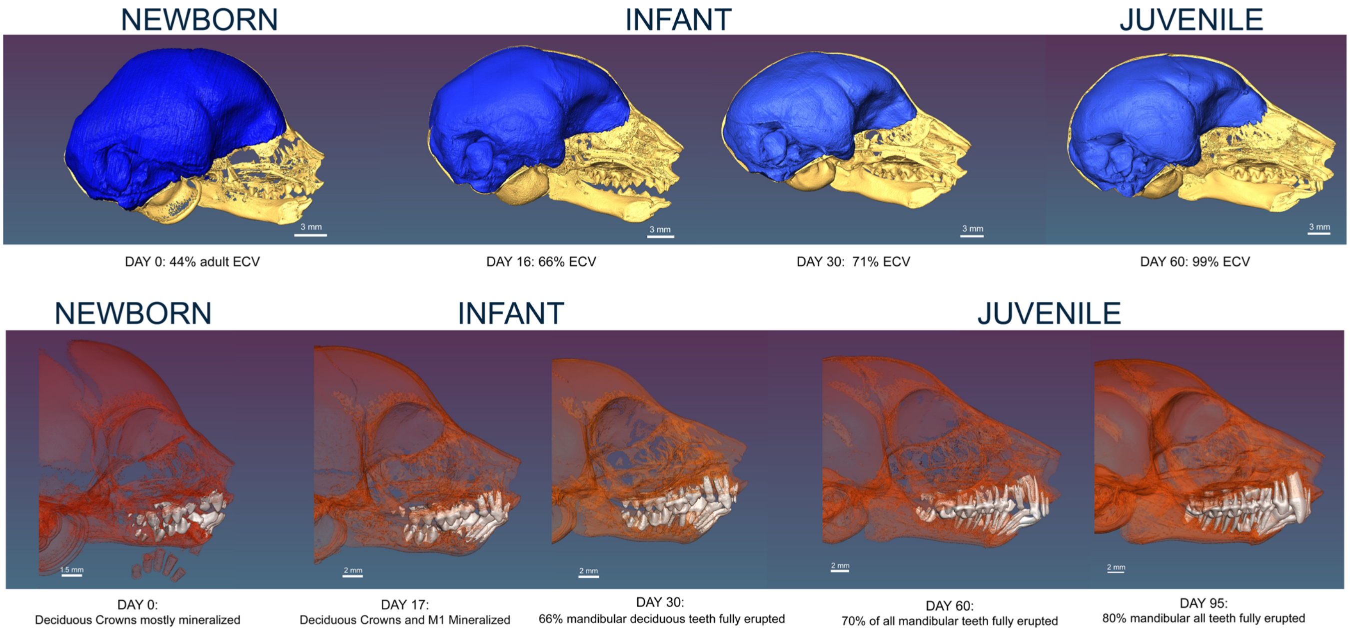
3.2 | Dental development

At birth, deciduous crowns are mostly mineralized but only the incisors have fully erupted (Table 3). Deciduous tooth crowns and M1 are nearly completely formed (though perhaps not fully mineralized) at ~2–3 weeks (see Figure 1). Full eruption of deciduous mandibular tooth crowns is complete by 30 days; by 60 days, M1 has also erupted. Full eruption of all mandibular tooth crowns is delayed beyond weaning (Table 3). The oldest juveniles, approximately of weaning age, have ~89% of mandibular primary teeth in full eruption, and ~87% of all mandibular teeth (primary and successional) erupted. The eruption of primary teeth, expressed as a percentage, increases gradually across the age range. But in terms of total dentition (primary and successional combined), the starkest contrast in number of erupted teeth is seen between the 30- and 60-day-old specimens (Table 3; Supporting Information: Figure S1), implying the pace of dental eruption increases between these time points.

3.3 | Limb development

3.3.1 | Fore- and hind limb musculoskeletal ontogeny

Indices of limb bone length and limb muscle mass in newborns versus adults reveal that hind limbs have accelerated growth in linear bone length and muscle mass relative to the fore limb (Figure 3; Tables 4 and 5). Proportions of muscle mass in the hind limb change between newborns and adults. In neonates, the thigh



DAY 0: 44% adult ECV

DAY 16: 66% ECV

DAY 30: 71% ECV

DAY 60: 99% ECV

DAY 0:
Deciduous Crowns mostly mineralized

DAY 17:
Deciduous Crowns and M1 Mineralized

DAY 30:
66% mandibular deciduous teeth fully erupted

DAY 60:
70% of all mandibular teeth fully erupted

DAY 95:
80% mandibular all teeth fully erupted

FIGURE 1 Comparative Amira software imaging from different stages of development in the newborn, infant, and adult *Galago moholi*. Dentition and facial development is delayed in comparison to growth of endocranial volume.

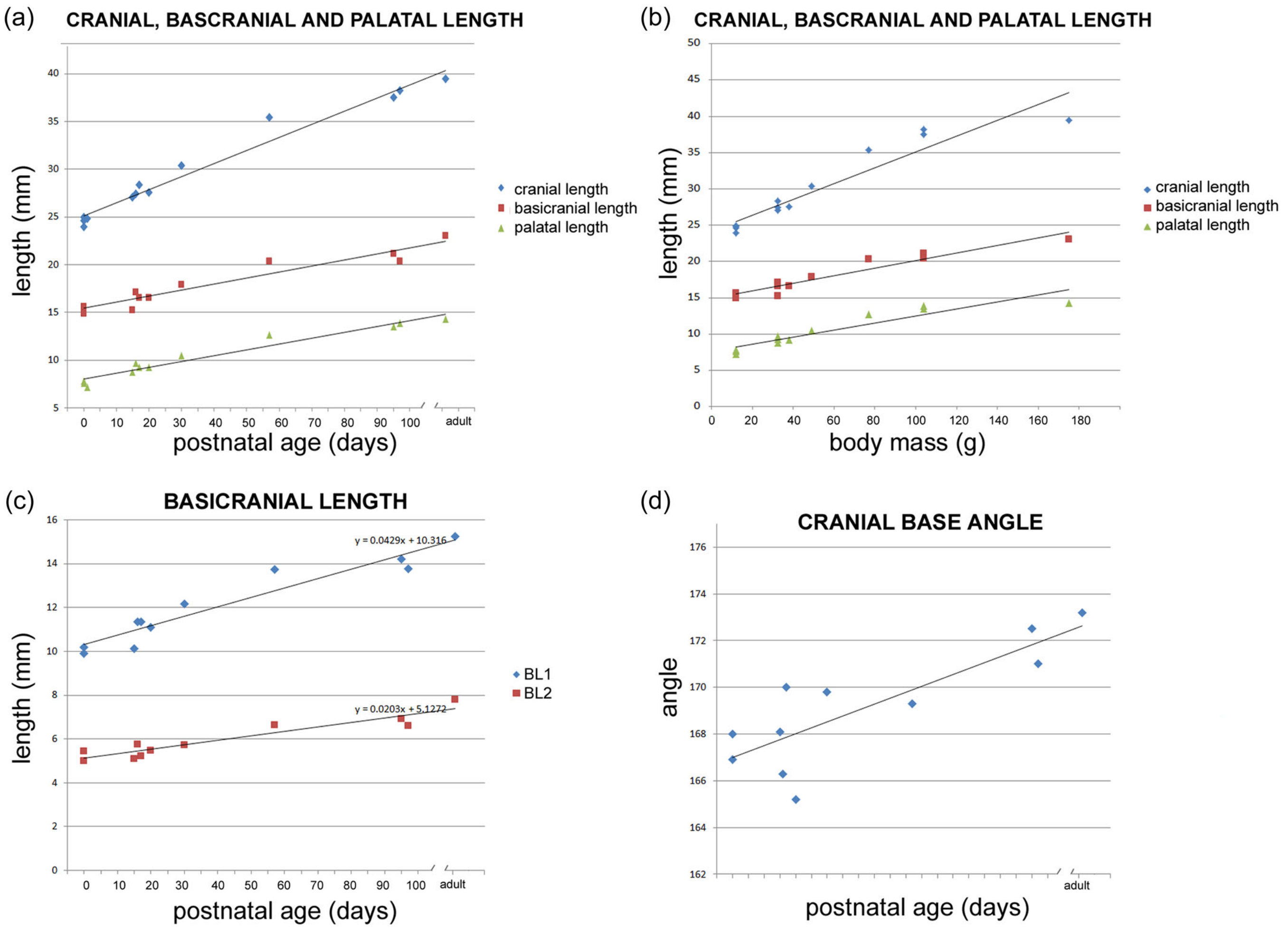


FIGURE 2 Linear regression plots of cranial measurements (see Table 2) against postnatal age in days and body mass in grams (g). (a) cranial length, basicranial length 2, and palatal length plotted against postnatal age. (b) cranial length, basicranial length 2, and palatal length plotted against body mass. (c) basicranial length 1 and 2 plotted against postnatal age. (d) basicranial angle plotted against postnatal age.

TABLE 3 Mandibular dental eruption of teeth by class.

Age	Primary teeth	Successional teeth	All mandibular teeth
Newborn	2/9	0/6	2/15
Early infant	4/9	0/6	4/15
Older infant	6/9	0/6	6/15
Juvenile 1 (57 days)	7/9	2/6	11/15
Juvenile 2 (~95 days)	9/9	4/6	13/15

musculature is >50% of the total hind limb mass, whereas the arm musculature is <50% of the total fore limb mass. The thigh becomes proportionally bigger in the adults, whereas fore limb proximal to distal muscle mass distribution is unchanged between age groups. Specifically, the thigh is 75.1% of total hind limb muscles mass in newborns, compared with 83.3% in adults (Figure 4).

3.3.2 | Fore- and hind limb skeletal ontogeny: Cross-sectional age changes

Intermembral indices suggest three age cohorts are distinct: newborns, infants/younger juvenile, and older juveniles/adults. The index is highest at birth (62%). All infants and the younger juvenile are within a range of 54%–57%. The older juveniles and adults have the lowest indices, at 51%–52%, reflecting the adult hind limb morphology that significantly exceeds the length of the adult fore limb. A plot of hind limb length (excluding the foot) and fore limb length (excluding the hand) against postnatal age suggests a pronounced divergence occurs between early infant and early juvenile stages (Figure 5), with hind limb length greatly outpacing the fore limb length (Table 1).

3.3.3 | Fore limb ossification

Secondary ossification centers for long bones and carpal ossification centers do not appear at birth, but are present in early infants (15–20

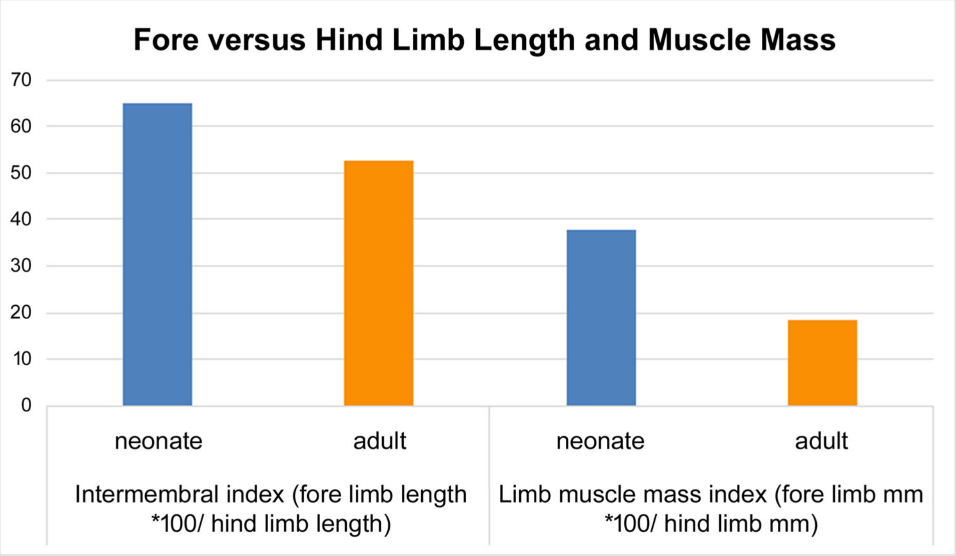


FIGURE 3 Indices of segments (brachium vs. total and thigh vs. total) comparing neonates and adults in linear bone length (intermembral index) and muscle mass.

TABLE 4 Muscle weights (in g) of the fore limb in *Galago moholi*.

Muscle/muscle group	Neonate	Adult
Arm flexors	0.013	0.28
Arm extensors	0.021	0.45
Forearm, flexor comp.	0.028	0.71
Forearm, extensor comp.	0.019	0.28
Brachioradialis	0.007	0.13

TABLE 5 Muscle weights (in g) of the hind limb in *Galago moholi*.[a]

Muscle/muscle group	Neonate	Adult
Hamstrings	0.98	12.46
Sartorius	0.14	3.3
Quadriceps femoris	1.18	52.26
Adductors	0.68	9.29
Superficial plantarflexors	0.4	7.76
Deep plantarflexors	0.45	3.97
Dorsiflexors	0.44	5.27
Lateral compartment	0.27	3.7

[a] From Baker et al. (2011).

days of age). In this age group, most carpals have commenced ossification. The trapezoid and os centrale are the smallest ossification centers at this age; the os centrale is also the smallest nodule in the older infant (Table 6). Secondary centers of ossification for metacarpals and proximal phalanges are present in early infants; in the older infant secondary centers for the middle phalanges have appeared. Early infants have ossified distal epiphyses of the radius and ulna, the proximal epiphysis of the humerus, and that for the greater tubercle. By late infancy, all carpals are ossified, although histology shows both carpals and tarsals retain cartilaginous parts (Figure 6; Supporting Information: Figure S2).

In juveniles, most carpals appear fully ossified. However, the pisiform is not elongated in the early juvenile, but is so in older juveniles. In juveniles, all secondary centers are ossified. In the older juveniles, most epiphyseal lines are visible (Supporting Information: Figure S3); only epiphyseal lines remain and the proximal ulnar head is completely fused. In a younger juvenile specimen (60 days) forearm and arm bones are mostly adult-like in morphology, except for the trochlea. The trochlea is adult-like in the older juveniles.

3.3.4 | Hind limb ossification

Tarsals are notably more advanced in ossification at birth compared with carpals, with well-ossified navicular and calcaneal centers, and the talus is present at least as a small nodule (Figure 6). No secondary centers of long bones of the ankle are ossified at birth, but one newborn exhibits an ossified nodule at the distal tibia. In early infants, ossification centers of all tarsals are present (intermediate cuneiform is the smallest nodule); ossification centers for distal epiphysis of MT III and IV are also present. Secondary centers of ossification for metatarsals and proximal phalanges are present in early infants; in the older infant secondary centers for the middle and some distal phalanges have appeared. All infants have ossified distal epiphyses of the tibia and fibula, as well as the proximal tibia. In the older infant, the proximal fibula also has an ossification center present, and there is an ossification center for the tibial tuberosity (Figure 6, Table 7).

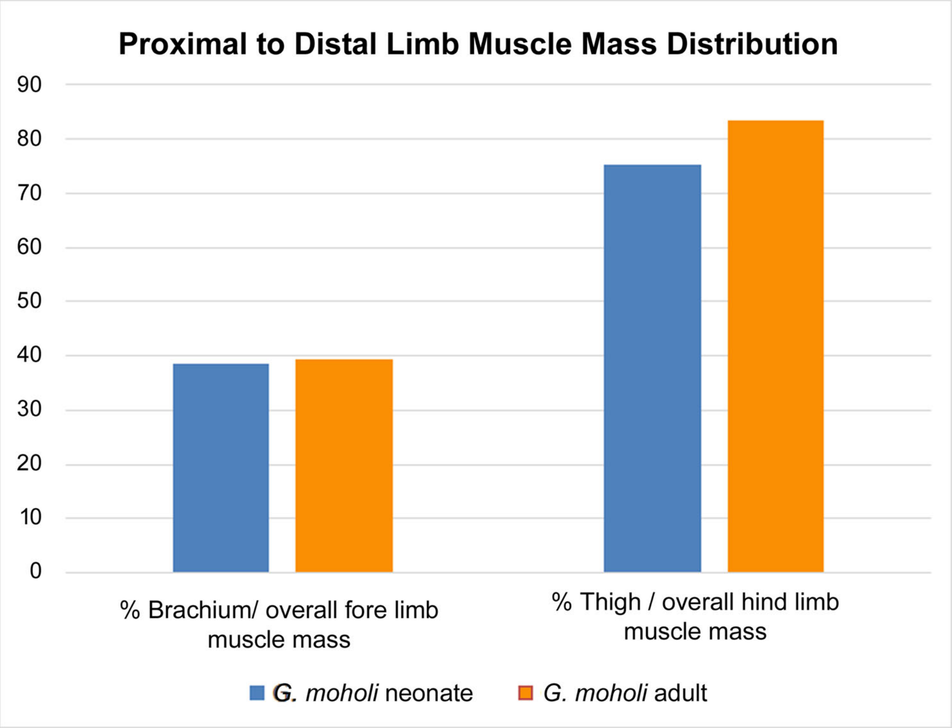


FIGURE 4 Muscle mass distribution in the neonate and adult *Galago moholi*. Measurements demonstrate that the thigh musculature makes up well over 50% of the total mass of the hind limb, while the arm musculature makes up less than 50% of the fore limb. Thigh musculature becomes proportionally bigger during adulthood while fore limb distribution is unchanged between age groups, reflecting a developmental emphasis on leaping for locomotion.

In the younger juvenile, tarsal ossification is progressed and all appear in close articulation; all are fully adult-like in morphology in the older juveniles. An unfused center for the calcaneal tuberosity is present in the younger juvenile. Secondary centers of ossification of all long bones are large and nearly adult-like in morphology in the younger juvenile, although growth plates appear to be patent still. In the older juveniles, epiphyseal fusion is incomplete, but only epiphyseal lines remain visible in the proximal and distal femur (Supporting Information: Figure S4). There is still a small ossification center for the tibial tuberosity at 60 days; it is enlarged in the older juveniles, but still incompletely fused.

3.3.5 | Epiphyseal growth plate differences among long bones during infancy

All growth plates in the serially sectioned neonate are proximo-distally more expansive, in absolute longitudinal breadth, compared with the 1-month-old (Figure 7, showing the distal growth plate of the zeugopod). However, organization of the growth plate appeared to change with age in the hind limb. In particular, in the zones of hypertrophy and proliferation of hind limb growth plates, the columns of dividing chondrocytes are better organized into continuous streams in the 1-month-old compared with the neonate (Figure 7; Supporting Information: Figure S5). This was less true for the distal (Figure 7) and proximal radius.

Although all growth plates examined are more restricted (proximodistally) in the 1-month-old compared with the neonate, this restriction was exaggerated in the fore limb growth plates compared with those of the hind limb (Figure 7). This is particularly evident in the elbow versus the knee. In the proximal radius of the 30-day-old, columns of cells in the zone of proliferation numbered less than 10 on average. The proximal tibia, in contrast, has columns of proliferating chondrocytes numbering from 20 to 32 cells in depth. In the distal femur, proliferating chondrocytes number 26 to 37 cells in depth. Comparisons of the proximal humerus and femur could not be made due to poor orientation of the growth plate in the humerus of the 30-day-old.

4 | DISCUSSION

Altriciality/precociality is considered primarily a measure of neural (especially brain) development at birth (Halley, 2018), but many body systems vary in their functional status at birth. Among mammals, marsupials are born with the least developed musculature to enact adult style locomotion, whereas hooved mammals generally have the most developed limb musculature at birth (Grand, 1977, 1992). Mechanical properties of bone also vary, with greater robusticity being an attribute of more precocial species (Magrini et al., 2023; Wei & Zhang, 2019). The pace of dental development is strongly linked to

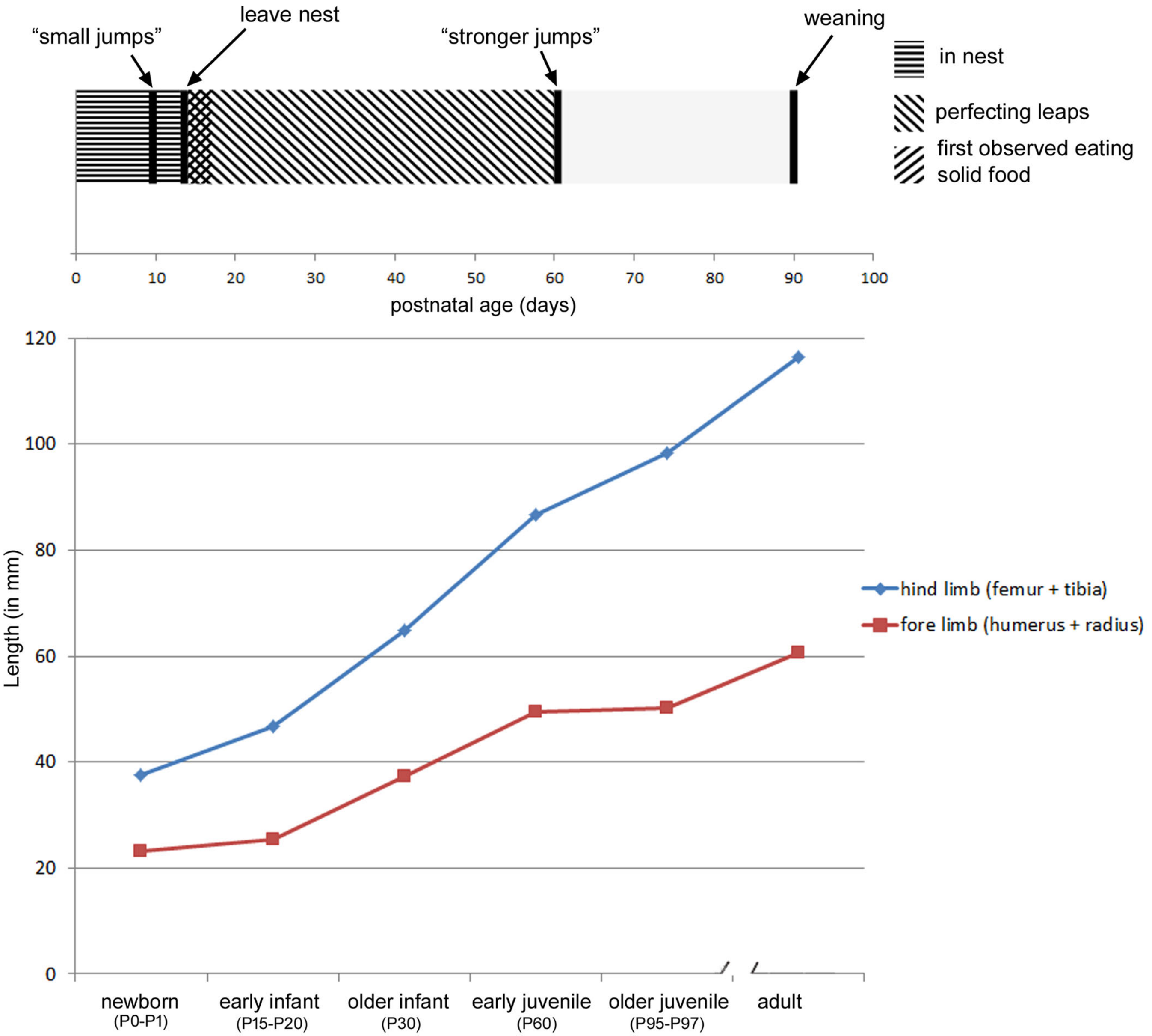


FIGURE 5 Ontogenetic changes in length of fore limb (red) and hind limb (blue) skeletal elements relative to life history milestones shows the association of increased hind limb growth and locomotor milestones related to leaping behavior.

dietary specialization of adults (Godfrey et al., 2001, 2003; Smith et al., 1994; Paddock et al., 2020).

With relatively prolonged juvenility and delayed reproductive maturation compared with many other mammals, primates may be especially well-suited to accommodate variable developmental schedules (Pereira & Fairbanks, 2002). Whereas some species mature far more quickly than others, all primates are highly dependent on adults in their first postnatal days. Subsequently, some primates dispense with deciduous teeth and grow very rapidly, but there is considerable variability in some primates at the family level. In most primates, we lack a broad understanding of the pace of development across different body systems. Here, we establish differential rates of development among and within specific body systems in lesser bushbabies, primates that exhibit highly specialized clinging and leaping locomotor patterns within the first 2 postnatal months (Crompton, 1983; Doyle, 1979; Nash, 2003).

4.1 | Brain growth is prolonged and most occurs postnatally

In mammals such as primates, ECV and brain mass bear the same relationship to body mass (Isler et al., 2008). Thus, ECV has long been used as a proxy for brain size, although it does comprise some nonneural structures as well (Maugoust & Orliac, 2023). Ontogenetic samples pose special challenges for the study of ECV, because in

TABLE 6 Summary of fore limb ossification across postnatal age in subadult *Galago moholi*.

Age	Hand and wrist	Forearm	Arm
Newborn	No secondary centers in long bones. No carpals ossified.	No secondary centers	No secondary centers
Early infant	Most carpals have commenced ossification; trapezoid and os centrale are the smallest nodules. Most secondary oss. centers of MCs and proximal phalanges now present.	Distal epiphyses now have oss. centers (ulnar center is smaller).	Proximal epiphysis and greater tubercle of the humerus now have oss. centers. Some early infants have an ossification of the lesser tubercle.
Older infant	All carpals have commenced ossification; os centrale is the smallest ossification center in this specimen. Most secondary oss. centers of middle phalanges now present; one secondary oss. center of distal phalanges present.	Distal epiphyses only.	Distal humeral epiphysis now present.
Early juvenile	Most carpals appear fully ossified. All secondary ossification centers now present, and some growth plate regions narrowed.	Proximal epiphyses of radius and ulna present.	Capitulum now “adult-like” in morphology, but not fused to distal humerus. Trochlear morphology is not yet apparent.
Late juvenile	Pisiform is now dorsoventrally elongated. Epiphyseal lines of MCs and proximal epiphyses of most phalanges are visible.	Radius: epiphyses fused; ulna: Epiphyseal line of proximal epiphysis is visible. Distal epiphysis of ulna fused.	Proximal epiphyseal line is visible; distally, the line is faint.

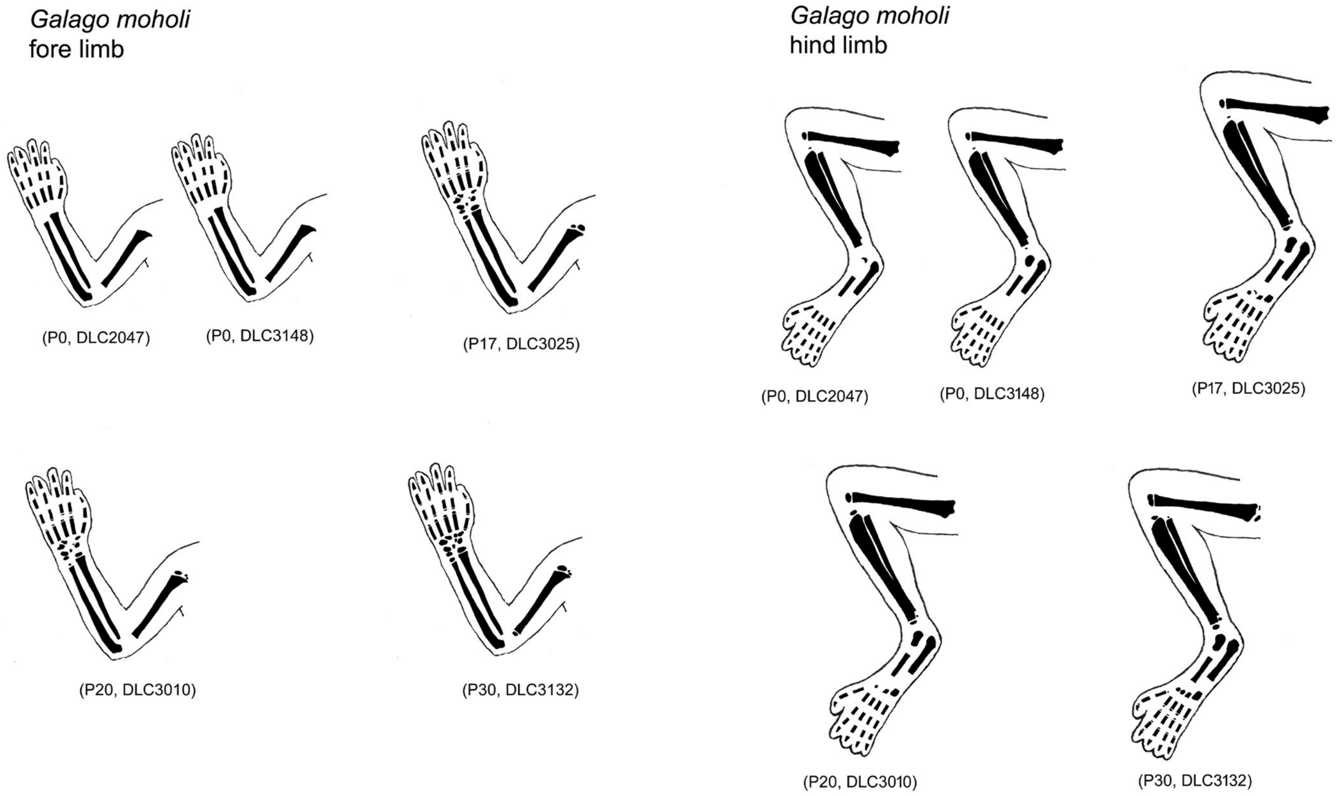


FIGURE 6 Ossification of fore and hind limbs through late infancy in *Galago moholi*.

subadults substantial portions of the chondrocranium may remain cartilaginous; this creates large apertures that make it difficult to measure volume using traditional methods (e.g., beads). Virtual methods can overcome this complication, especially when histology of enhanced scanning techniques can reveal the actual endocranial contours (Smith et al., 2023). Here, we found that lesser bushbabies have relatively well ossified skulls even at birth. In the newborn, even the incompletely ossified ethmoid has a partially ossified

TABLE 7 Summary of hind limb ossification across postnatal age in subadult *Galago moholi*.

Age	Foot and ankle	leg	thigh
Newborn	Ossification centers for calcaneus, talus (small nodule), navicular present.	Secondary center for proximal tibia present; distal tibial center may be present as small nodule.	Secondary center for distal femur present.
Early infant	Ossification centers of all tarsals present (intermediate cuneiform is a small nodule). Ossification centers for distal epiphysis of metatarsal (MT) III and IV are present.	Secondary centers for proximal and distal tibia present.	Same as newborn.
Older infant	All tarsals have enlarged ossification centers compared the younger infants but still spatially separated, especially at talonavicular and calcaneocuboid joints. Ossification centers for distal epiphyses of MT II-V and proximal epiphyses of MT I are present. Ossification centers for proximal epiphyses of proximal phalanges II-IV, intermediate phalanges II-V, and distal phalanx II are present.	The center for tibial tuberosity is present and unfused. Proximal and distal epiphyses are “adult-like” in morphology and unfused.	Proximal epiphysis now ossified as small a nodule. Ossification center for distal epiphysis is larger, greater in diameter compared with the distal diaphysis. Ossification center of greater trochanter now present.
Early juvenile	Tarsals appear nearly fully ossified and in close articulation. The calcaneal tuberosity has an unfused secondary center. Epiphyseal growth plates for proximal epiphysis of MT I, distal MT epiphyses are still patent.	The center for tibial tuberosity is present and unfused. Proximal and distal epiphyses are “adult-like” in morphology and unfused.	All epiphyses and trochanters are now “adult-like” in morphology. Synchondroses (growth plates) of proximal epiphysis and greater trochanter are narrowly patent. The synchondrosis for the distal epiphysis is more widely patent by comparison.
Late juvenile	Tarsals are fully “adult-like” in morphology. Epiphyseal lines for proximal epiphysis of MT I, distal MT epiphyses are still visible. Proximal epiphyses of proximal phalanges are still visible.	Epiphyseal lines are visible proximally and distally. The center for tibial tuberosity is present and unfused. An accessory ossification center is present laterally, and unfused.	Epiphyseal lines of femur are faint proximally and distally. Distally, sesamoid bones (fabellae) are present.

perpendicular plate denoting the endocranial limit of the cribriform plate (Figure 1a). Thus, our ECV estimates can be considered reliable across the entire postnatal period.

As ECV increases in this sample, basicranial length increases and cranial base angle progressively flattens. Although all primates have large relative brain size at birth compared with most mammals (Halley, 2018), there is considerable variation among primate families (Harvey et al., 1987) and also among suborders (Leigh, 2004). This variation reflects two strategies: an emphasis on prenatal growth (neonates with the largest relative brain size) or postnatal growth (primates that defer more growth to after birth) (Harvey et al., 1987). Here we show that *G. moholi* defers more than 50% of growth in ECV until after birth. This is a considerable delay relative to limb bone ossification, as well as facial growth. Presumably, the relatively late weaning in *G. moholi* at ~90 days is closely related to this prolonged brain growth.

4.2 | Dentofacial development lags behind growth of the brain and overall cranial length

Among all primates and even among strepsirrhines, galagids exhibit relatively rapid mineralization of tooth crowns (Paddock et al., 2020; Smith et al., 2015). Tooth crowns of all deciduous teeth and M1 are nearly or completely mineralized by 15–17 days, coinciding with the time at which infants are first observed to sample food in captivity (Doyle, 1979). This likely relates to precocious alveolar eruption of teeth (Smith et al., 2015) and early gingival emergence in galagids (Smith et al., 1994).

Whereas dental eruption and crown mineralization may be rapid compared with primates broadly, and even compared with some other strepsirrhines (Godfrey et al., 2001; Paddock et al., 2020), jaw development in *G. moholi* lags behind growth in overall cranial length and also brain growth (as surmised from ECV data—Supporting Information: Figure S1). There are several notable factors that explain this delay. First, development of upper and lower adult canine teeth occurs after day 60 based on our sample (Figure 1); postcanine teeth are also incompletely erupted even in the 95-day-old (Figure 1). Each of these teeth should elongate and add depth to the jaws. In addition, the crescent-shaped perpendicular plate of the ethmoid exhibit pronounced downward growth until early juvenility, likely tracking increased midfacial dimensions, and the rostral side of the bone is advanced at 60 days, suggesting persistence of a growth center, which was histologically shown at 30 days by Wood et al. (2023) in this same sample. Thus, cartilaginous growth likely contributes to “snout” elongation, at least until weaning.

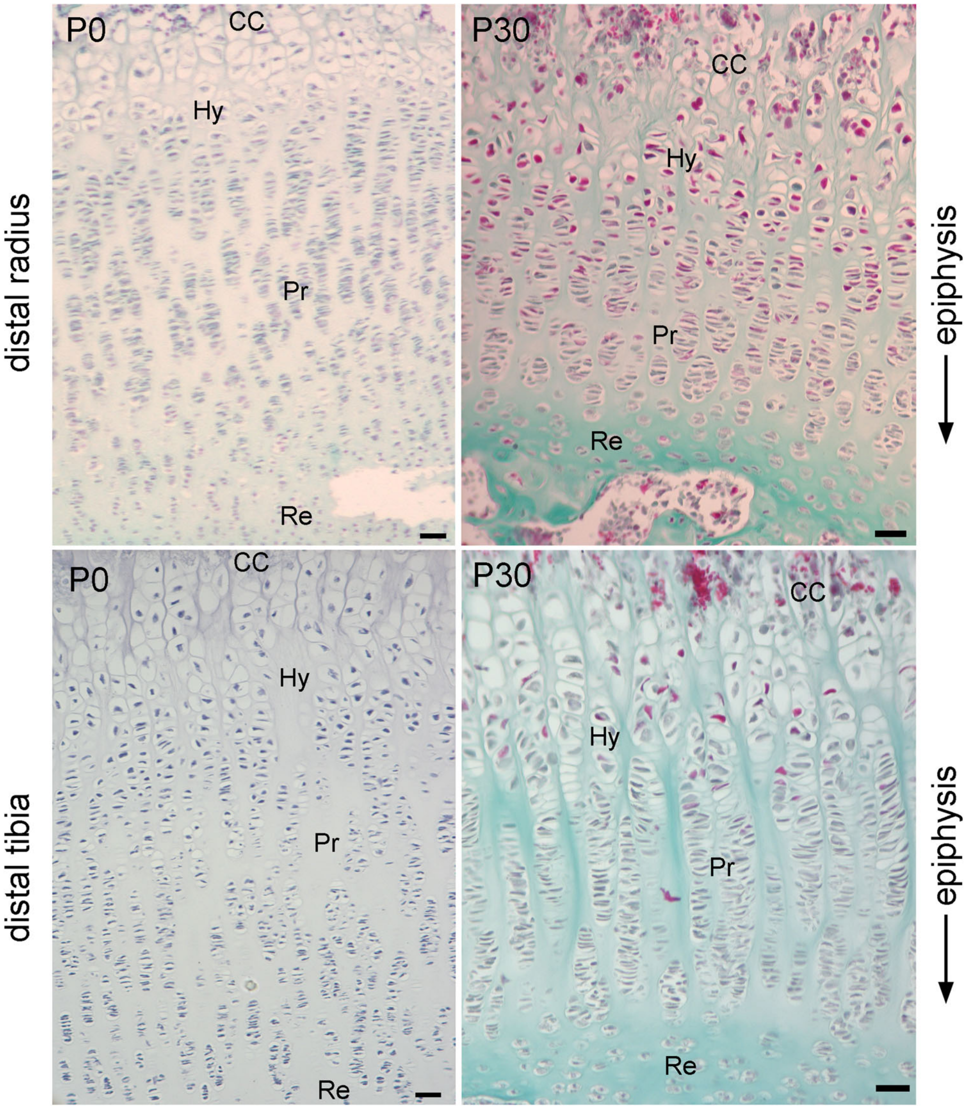


FIGURE 7 Growth plates of the distal end of the radius and tibia in *G. moholi* at birth and 1 month. At birth, the zones of proliferating (Pr) and hypertrophic (Hy) chondrocytes in the radius and tibia are more broadly expanded. Note, however, the radius growth plate becomes more restricted and less organized than the distal tibia at 1 month. CC, zone of calcified cartilage, Re, resting zone. All scales at 30 µm.

4.3 | Limb development closely tracks the time at which bushbabies are perfecting leaps

Detailed data on limb ossification are available for relatively few primates, but more is known of the neonatal stage (see Smith et al., 2020 for detailed review). In fore limb ossification, *G. moholi* is like virtually all known strepsirrhines in possessing no ossified secondary centers of long bones at birth. Except *Nycticebus coucang* and *Otolemur crassicaudatus*, most strepsirrhines (including *G. moholi*) similarly possess no partially ossified carpals at birth. Most haplorhines do possess some ossified secondary centers of selected long bones and carpals at birth. Hind limb ossification is more advanced than in the fore limb at birth in all primates. In particular, all primates studied have initiated ossification of the talus and calcaneus at birth. *G. moholi*, and other galagids, are unusual among strepsirrhines in possessing ossification centers at the knee at birth (see also Glaser, 1970; Smith et al., 2020). Numerous anthropoids possess some ossified secondary centers of long bones of the hind limb at birth, and overall hind limb ossification (including many ossified tarsal bones) is notably advanced in catarrhines and tarsiers. This study is the first attempt to broadly examine measurements relating to somatic and neural development in a strepsirrhine across postnatal age. Although our sample size as well as the limitations of cross-sectional age samples does not establish a specific age at which neural and somatic growth or maturation is complete in this species, the ages of the rare specimens studied here offer broad observations on timing of different anatomical components.

Prior work on postcranial anatomy has demonstrated that newborn primates are not proportioned, in most respects, similarly to adults (Schaefer & Nash, 2007; and see Smith et al., 2020). Perhaps the most researched metric is intermembral index (IMI). With some exceptions, most primates exhibit a decrease in IMI across age (e.g., Aiello & Dean, 1990; Brizzee & Dunlap, 1986; Falsetti & Cole, 1992; Glander, 1994; Ravosa et al., 1993; Turner et al., 1997; Turnquist & Wells, 1994). Lesser and greater apes appear to be exceptions according to most studies (e.g., Bellisari et al., 2001; Shea, 1981). These exceptions include primates in which the fore limbs are proportionally large compared with other primates, and in the case of lesser apes are recruited for locomotion quite distinctly (i.e., brachiation). The broader trend of decreasing IMI (the hind limbs become proportionately longer) in other primates are thought to facilitate a transition to use of the hind limb as the primary propulsive element (Atzeva et al., 2007; Turnquist & Wells, 1994; and see Young & Shapiro, 2018). Of course, newborn primates do not exhibit adult-like locomotion at birth; an IMI more closely approaching 100% (i.e., more equal limb proportions) is presumably advantageous for crawling in very young infants.

Some prior reports have noted the timing of IMI change parallels the maturation of adult-like locomotion (Turnquist & Wells, 1994; Wells & Turnquist, 2001). Interestingly, Schaefer and Nash (2007) concluded that this is not the case for *Galago senegalensis*. These authors examined IMI in larger samples than we have available, and were able to statistically demonstrate that IMI remained significantly higher in newborn and “older infant” (47 days) compared with adult *G. senegalensis*. However, data on both species agree that decreasing IMI is well underway during infancy, and our findings suggest an acceleration of hind limb growth is occurring from Week 3 until early juvenility (see Figure 5), further supported by our preliminary observations of growth plates. The time frame from late infancy to early juvenility encompasses the entire range of ages in which captive animals are perfecting their leaps (Doyle, 1979; Nash, 2003). Doyle, (1976, 1979) described captive infant *G. moholi* as extremely active in the nest. They make small jumps within 10 days and they continue to become stronger leapers during the first 2 months of age, and jump as frequently as adults by 6 weeks (Doyle, 1979). Our findings demonstrate rapid changes during this time frame, and by 2 months limb bones are essentially “adult-like” in morphology, though the hind limb long bones are still growing in length.

Our data on epiphyseal and tarsal ossification present with some parallels to our data on limb segment measurements. Few primates have been studied using longitudinal or cross-sectional age samples to examine the postnatal pace of limb bone ossification, and only anthropoids thus far, making it difficult to place *G. moholi* in a broad context. A better understanding of the relative pace of limb bone ossification in *G. moholi* will await further ontogenetic studies of other strepsirrhines. For now, we observe that the rate of limb ossification in *G. moholi* appears to correspond well to the timing of development of “adult-like” locomotion.

Results indicate that newborns do not display adequate proximal muscle mass at birth for adult locomotion, requiring a proximal shift in mass, as reported previously (Atzeva et al., 2007; Baker et al., 2011). In this study, we establish that this shift is specific to the hind limb and not the fore limb. Whereas we are unable to track the timing of the muscle mass increase, this finding is consistent with the idea that the hind limb undergoes a significant functional transformation postnatally, whereas the fore limb is primarily a grasping limb at all stages of life. Shifts in limb muscle proportions in a broader range of primates will be required to place these findings in a proper context. For example, it may be predicted that arboreal quadrupeds may exhibit a proximal shift in both limbs, relating to functional transitions. Moreover, the shift may be more profound in primates that ride as infants, reflecting an early emphasis on grip strength to hold their parent's (or alloparent's) fur.

5 | CONCLUSIONS

The results of this study are consistent with the concept of modular growth patterns in developing primates. *G. moholi* has considerably different developmental trajectories among body regions (e.g., neurocranial vs. facial skeleton) and within functional systems (e.g., fore vs. hind limbs of locomotor system). Certain aspects of hind limb development in *Galago* suggest that adaptations for an upright lifestyle (vertical clinging and leaping) are selected for well before infants can ambulate, such as accelerated rates of growth of hind limb bones, and bone growth rates likely accelerate while the animals master their leaps. On the other hand, *G. moholi* prolongs brain growth and even growth of their dentition (Supporting Information: Figure S1), perhaps as a benefit of relatively late weaning. Finally, our results emphasize separate trajectories of muscle ontogeny for fore and hind limbs. Specifically, the fore limb is more stable across development while the hind limb must shift toward more propulsive leaping function through mass shifting from distal to proximal and often from deep to superficial along the limb.

AUTHOR CONTRIBUTIONS

Tim D. Smith: Conceptualization (lead); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); writing—original draft (lead); writing—review and editing (lead); study design (lead); methodology (equal). **Brenna R. McGovern-Lind**: Investigation (equal); methodology (equal). **Kathryn A. Proffitt**: investigation (equal); methodology (equal). **Scot E. E. King**: Investigation (equal); methodology (equal). **Hannah M. Rader**: Formal analysis (equal); investigation (equal); methodology (equal). **Dominic A. Violi**: Formal analysis (equal); investigation (equal); methodology (equal); Writing—review and editing (equal). **Catherine J. Llera Martin**: Investigation (equal); methodology (equal). **Katherine Searight**: Investigation (equal); methodology (equal). **Matthew Kehrer**: Investigation (equal); methodology (equal). **Brandon A. Yeropoli**: Investigation (equal); methodology (equal). **Jesse W. Young**: Conceptualization (equal); Data curation (equal); Writing—review and editing (equal). **Christopher J. Vinyard**: Conceptualization (equal); Data curation (equal); Writing—review and editing (equal). **Valerie B. DeLeon**: Conceptualization (equal); Data curation (equal); funding acquisition (equal); Writing—review and editing (equal).

ACKNOWLEDGMENTS

Some of the data used in the project were collected in prior published reports. We thank the coauthors of these reports, including Jeremy J.

Baker, Madeliene Atzeva Stump, Colleen Shanafelt, and Eric Graham. This is DLC publication # 1587. This work was supported by NSF grant numbers BCS-1830894, BCS-1830919, BCS-1231717, BCS-1231350, and BCS-1728263.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Any scans used in the present study are available on request from the corresponding author (TDS), or from Valerie DeLeon or Chris Vinyard. Interested researchers are encouraged to first check a MorphoSource project page at: https://www.morphosource.org/dashboard/collections/000368935/edit?locale=en& Search for the project "Primate Skeletal Ontogeny" (ID: 000368935). On this project page, µCT scan volumes of whole bodies or heads of specimens used in the present study are freely available for download as TIFF stacks.

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How to cite this article: McGovern-Lind, B. R., Proffitt, K. A., King, S. E. E., Rader, H. M., Violi, D. A., Llera Martin, C. J., Searight, K., Kehrer, M., Yeropoli, B. A., Young, J. W., Vinyard, C. J., DeLeon, V. B., & Smith, T. D. (2024). Developmental milestones in captive *Galago moholi*. *American Journal of Primatology*; e23634. https://doi.org/10.1002/ajp.23634