

## RESEARCH ARTICLE

The Ontogeny of Prehensile-Tail Use in *Cebus capucinus* and *Alouatta palliata*

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A study of the platyrrhine prehensile tail provides an opportunity to better understand how ecological and biomechanical factors affect the ability of primates to distribute mass across many different kinds of arboreal supports. Young individuals experience ontogenetic changes in body mass, limb proportions, and motor skills that are likely to exert a strong influence on foraging strategies, social behaviors, support use, and associated prehensile-tail use. In this research, I examine ontogenetic patterns of prehensile-tail use in *Cebus capucinus* and *Alouatta palliata*. I collected behavioral data on activity, positional context, support size, and prehensile-tail use in five age categories of white-faced capuchins and mantled howlers during a 12-month period at Estación Biológica La Suerte in northeastern Costa Rica. Infant and juvenile howlers and capuchins were found to use their prehensile tails significantly more often than adults during feeding, foraging, and social behavior. Prehensile-tail use did not show predictable increases during growth. In both species, adults used their prehensile tails in mass-bearing modes significantly less often than juveniles. Despite differences in tail anatomy in *Cebus* and *Alouatta*, prehensile-tail use was observed to follow an increasing trajectory from infancy, peaking during juvenescence, and then decreasing in older juveniles and adults. In both species, it appeared that adult patterns of prehensile-tail use reflected the demands placed on young juveniles. Am. J. Primatol. 74:770–782, 2012. © 2012 Wiley Periodicals, Inc.

**Key words:** prehensile tail; ontogeny; *Alouatta*; *Cebus*

## INTRODUCTION

The primate tail has long attracted attention due to its roles in support, balance, and stabilization in positional behaviors in both New and Old World primates [Bergeson, 1996; Carpenter, 1934; Dunbar & Badam, 2000; Garber, 2011; Garber & Rehg, 1999; Karrer, 1970; Lawler & Stamps, 2003; Meldrum, 1998; Rose, 1974; Schmitt et al., 2005; Turnquist et al., 1999; Wheeler & Ungar, 2001; Youlatos, 1993, 1999]. Prehensile tails occur in *Ateles* (spider monkeys), *Alouatta* (howling monkeys), *Lagothrix* (woolly monkeys), *Brachyteles* (woolly spider monkeys), and *Cebus/Sapajus* (capuchin monkeys) and this feature likely represents parallel evolution in the Atelines and some Cebines [Rosenberger, 1983]. In this paper, I follow the argument for a two genera classification in the tufted and untufted capuchins. There is a growing consensus that based on recent genetic, biogeographical, and behavioral data that capuchins represent two genera, *Sapajus* (formerly the genus *Cebus* and referred to as tufted capuchins) and *Cebus* (untufted capuchins) [Garber et al., 2011; Lynch Alfaro et al., 2011; Lynch Alfaro et al., in press]. Prehensile-tailed primates and nonprehensile-tailed primates exhibit differences in tail morphology, including length of the tail, number of caudal vertebrae, muscular arrangement,

muscle mass, and joint surface size [Ankel, 1972; Bergeson, 1996; German, 1982; Johnson & Shapiro, 1998; Lemelin, 1995; Organ, 2010; Organ et al., 2009; Organ et al., 2011]. For example, in primates with prehensile tails (Atelines and capuchins) proximal caudal vertebrae are greater in number, are shorter, and tail muscles such as the extensor caudae longus and flexor caudae longus cross fewer caudal vertebrae allowing greater total angular excursion in flexion and extension [Ankel, 1972; Lemelin, 1995].

Important morphological differences in skeletal and muscular features in the limbs and tail are exhibited between the atelines (family Atelidae) and capuchins (family Cebidae). In *Alouatta* and *Ateles*, tails are heavier than the forelimbs, elongated, and contain between 27 and 31

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caudal vertebrae) [Grand, 1977; German, 1982; Rosenberger, 1983]. In capuchins the forelimbs are heavier than the tail, tails are shorter relative to body length, and tails contain fewer caudal vertebrae ( $N = 25$ ) [German, 1982; Grand, 1977; Garber & Rehg, 1999; Rosenberger, 1983]. Ateline tails feature a bare distal friction pad with mechanoreceptors that allow greater tactile sensation than the fully furred tails in capuchins [Organ et al., 2011]. The tails of capuchins are often considered “semi-prehensile” and therefore intermediate on a prehensile continuum with *Ateles* representing the most derived condition in the order Primates [Carpenter, 1934; Emmons & Gentry, 1983; Lemelin, 1995; Meldrum, 1998; Rosenberger, 1983; Rosenberger & Strier, 1989; Turnquist et al., 1999]. Following Meldrum [1998] and Organ [2010], a prehensile tail is a tail that can suspend the body mass of an adult without aid from the other limbs. The genera *Cebus* and *Sapajus* [Bergeson, 1996; Bezanson, 2009; Garber & Rehg, 1999; Youlatos, 1999] have this ability and therefore the tails are considered prehensile rather than “semiprehensile.” In this paper, I add ontogenetic behavioral data to the rapidly growing understanding of the behavioral/morphological interface that comprises the prehensile tail. I describe differences in tail use among infant, young juvenile, and adult white-faced capuchins (*Cebus capucinus*) and mantled howling monkeys (*Alouatta palliata*). These two primates offer an excellent opportunity to examine tail function and use as they differ in body mass (*C. capucinus*, adult female 2.67 kg, adult male: 3.87 kg, *A. palliata*, adult female: 5.35 kg, adult male: 7.15 kg), foraging strategy (capuchins are described as omnivorous manipulative foragers and howlers are described as energy minimizing folivores), and adult positional behavior is relatively well described [Bergeson, 1996, 1998; Bezanson, 2009; Ford & Davis, 1992; Fragaszy et al., 2004; Gebo, 1992; Garber and Rehg, 1999; Johnson & Shapiro, 1998; Mendel, 1976; Richard, 1970; Strier, 1992]. Research that has focused specifically on age-related differences in tail suspensory behaviors is limited in both genera apart from a brief examination by Russak [2005] and Fontaine [1994] or within the context of describing age-related differences in the positional repertoire [Bezanson, 2009; Prates & Bicca-Marques, 2008]. Therefore, the purpose of this study is to examine more precisely how age influences tail use.

Prehensile tails have evolved in 15 families and 40 genera of mammals [Bergeson, 1996; Schneider & Rosenberger, 1996]. The prehensile-tailed mammals differ in diet, biogeography, degree of arboreality, locomotor patterns, and body size but are similar in that they more commonly occur in Neotropical forests than in African and Asian forests. Emmons and Gentry [1983] suggested that forest structure played a critical role in the evolution of the prehen-

sile tail. Specifically, Neotropical forests are characterized by fewer lianas (average number of lianas per 1,000 m<sup>2</sup> per plot: 71 vs. 92) and more palms (average number of palms per plot: 36.8 vs. 2.5) than African forests. These authors also suggested that vegetation in the Neotropics is more likely to break under the mass of an arboreal mammal. This observation was anecdotally based on the researchers' ability to more easily collect small supports by pulling them down from the canopy in the Neotropics versus Africa and is an assumption that remains untested. Therefore, Emmons and Gentry [1983] suggested that Neotropical vegetation features may have provided the selective context for locomotor adaptations facilitating movement and safer gap crossing on fragile arboreal substrates and climbing on palm leaves. This ecological explanation has attracted attention because it provides a basis for testing the effects of specific habitat pressures on locomotor adaptations [Bergeson, 1996; Garber & Rehg, 1999; Lockwood, 1999; Organ et al., 2009]. If, as suggested by Emmons and Gentry [1983], the prehensile tail is a locomotor adaptation for crossing gaps and climbing on fragile supports, then primates should regularly use their prehensile tails during locomotor behaviors while foraging or traveling. However, studies have shown that *Cebus/Sapajus* and *Alouatta* engage their tails more frequently in postural behaviors than in locomotor behaviors [Bergeson, 1996, 1998; Grand, 1984; Garber & Rehg, 1999; Youlatos, 1998, 1999]. This finding has lead researchers to speculate that a primary role of the prehensile tail is to aid in the distribution of mass while accessing resources in howlers and capuchins [Bergeson, 1996; Grand, 1972, 1984; Garber & Rehg, 1999; Mittermeier & Fleagle, 1976].

In this paper, I address the following questions and hypotheses: (1) During what behavioral contexts do infant, juvenile, and adult *C. capucinus* and *A. palliata* use their prehensile tails? If the primary role of the prehensile tail is to aid in the distribution of mass during feeding and foraging then the prehensile tail should be used more often in larger individuals during these behavioral contexts [Bergeson, 1996; Grand, 1972, 1984; Mittermeier & Fleagle, 1976]. In *A. palliata*, both males and females are reported to reach adult size by 4 years [Glander, 1980]. Comparable data are not available for *C. capucinus*, however, *Sapajus apella* and *C. albifrons* are reported to reach adult body mass at 4 (females) to 6 years (males) of age and for the purposes of this study I assume that white-faced capuchins likely follow a similar pattern [Fleagle & Samonds, 1975; Fragaszy & Adams Curtis, 1998]. Therefore, due to size differences between adult capuchins and howlers, all age categories of *A. palliata* are expected to use their tails more frequently than all age categories of *C. capucinus* and within species, prehensile tail use should increase with age. If

TABLE I. Age Categories and Maximum Sample Sizes for *C. capucinus* and *A. palliata*.

	Number of IARs		Age and estimated body mass/ <i>Cebus</i> (kg)	Age and estimated body mass/ <i>Alouatta</i>
	<i>Cebus</i>	<i>Alouatta</i>		
<i>Infant I</i>	2,354	2,954	Birth to 2 months 0.2–0.5	Birth to 3 months 0.398
<i>Infant II</i>	2,890	4,504	2–6 months 0.5–0.8	3–6 months
<i>Juvenile I</i>	3,248	6,326	6–12 months 0.8–1.1	6–12 months >1.5
<i>Juvenile II</i>	4,332	6,202	12–36 months 1.1–1.8	12–24 months
<i>Adult</i> <sup>b</sup>	11,264	13,270	>7 years 2.54	>4 years 4.0–7.0

Age categories are based on information from Freese and Oppenheimer [1981], Glander [1980], and Fragaszy et al. [2004]. Infant I, Infant II, and Juvenile I individuals were known and identified from birth. Juvenile II categories were identified based on size of the individual, forehead coloration patterns (*Cebus*), and pelage (*Alouatta*) [Bezanson, 2009]. Capuchin body weight estimates based on captive female *C. albifrons* and *S. apella* [Fleagle & Samonds, 1975; Ausman et al., 1982; Jungers & Fleagle, 1980; Fragaszy & Adams-Curtis, 1998; Smith & Jungers, 1997]. *Alouatta palliata* mass estimates combine males and females [Glander, 1980].

<sup>a</sup>IAR = individual activity record

<sup>b</sup>In this analysis, the youngest age classes are compared with adults to avoid confusion between older juveniles/preadults and small adults.

the prehensile tail aids in the distribution of mass on small flexible supports then prehensile-tail use should be more common in adults when using smaller supports than when juveniles use similar sized supports. In addition, larger-bodied *A. palliata* will be observed to use their tails more frequently on small supports than *C. capucinus*. (2) How does prehensile tail use differ among infant, juvenile, and adult *C. capucinus* and *A. palliata*? If functional and biomechanical problems associated with the distribution of body mass on small or fragile supports influenced the evolution of the prehensile tail, then primates of both species will exhibit an increase in tail-use behaviors as body mass increases during growth. Bergeson [1996] hypothesized that in primates, the prehensile tail may be a result of neotenic retention because several Neotropical primates, such as *Saimiri*, *Callithrix*, and *Cebuella*, exhibit tail prehensility during infancy but not during juvenility or adulthood [Bergeson, 1996; Rose, 1974]. If this is the case, tail-gripping behaviors will be observed during the earliest growth stages and decrease in juveniles and adults.

## METHODS

### Study Site and Subjects

Research was conducted at Estación Biológica La Suerte in northeastern Costa Rica (10°26'N, 83°46'W). This 700-hectare site is a tropical premontane wet forest that includes primary forest, advanced secondary forest, and areas that have been selectively logged in the past. Rainfall in this region averages 3,962 mm per year [Garber et al., 2010; Sanford et al., 1994]. Field observations took place for 12 months between March 2002 and August 2003 and behavioral observations were approved by

IACUC and complied with the rules of La Suerte Biological Research Station, the legal requirements of Costa Rica, and the American Society of Primatologists principles for the ethical treatment of primates. The study population included two *C. capucinus* groups (11–17 individuals per group) and three *A. palliata* groups (9–14 individuals per group) from the primate population at La Suerte (see Table I for sample sizes and age categories). In this analysis, the youngest age classes are compared with adults to avoid confusion between older juveniles/preadults and small adults.

### Sampling Methods

Systematic, quantitative behavioral data were collected utilizing 1-min instantaneous focal animal sampling on habituated groups of howlers and capuchins [Altmann, 1974; Martin & Bateson, 1993]. Each instantaneous activity record (IAR) contained information on the identity of the focal animal, activity pattern (feed, forage, rest, travel, active posture, and social behavior), positional behavior, tail use, and support size when the tail appeared to support equal or greater mass than the other limbs. Activity patterns were defined as the following: *Feed*: The focal animal is eating food resources (ingestion). *Forage*: The search, acquisition, and manual processing of food items. *Travel*: The focal animal is moving (body mass is displaced) without feeding, foraging, or not engaged in socially directed movements (e.g. chasing). *Rest*: Periods of inactivity associated with sleep over extended periods of time. *Active posture*: Short-term pauses in movement (less than 1 min) during travel and foraging bouts. *Social behavior*: The focal animal was observed interacting with one or more group members. Positional categories

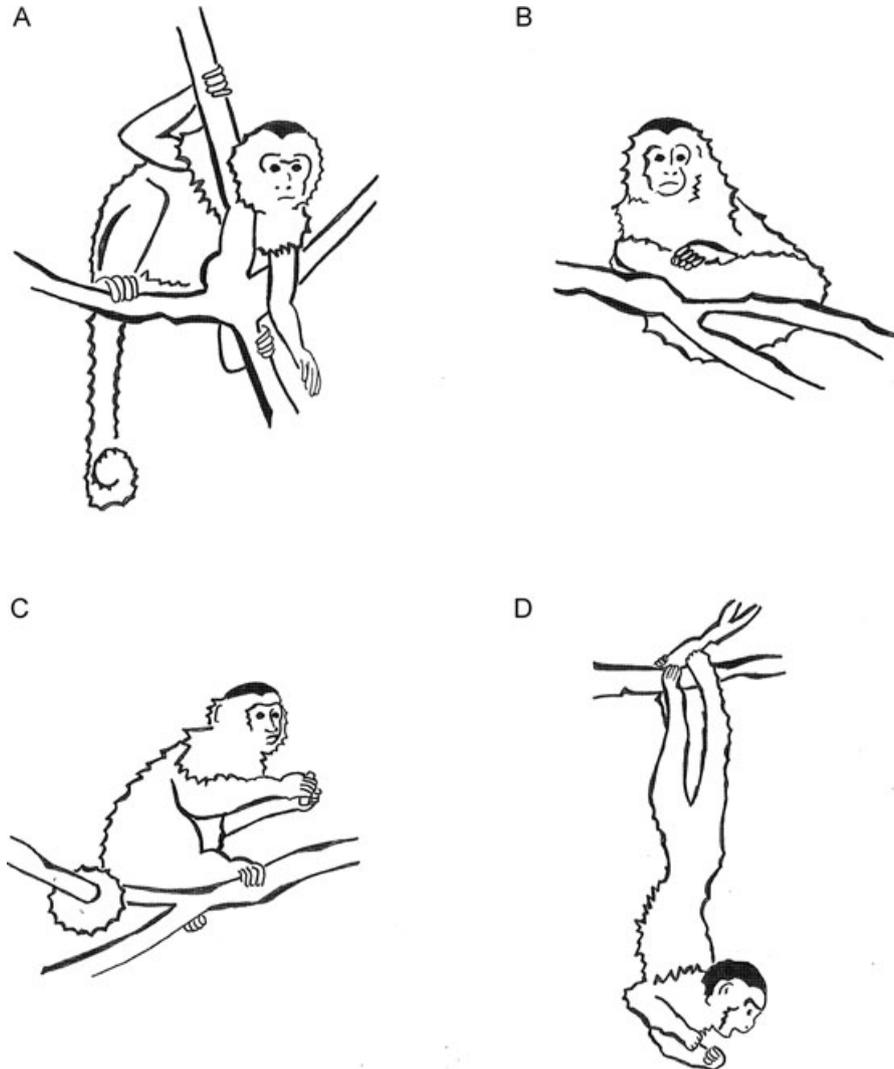


Fig. 1. (A) Tail free (TF): The tail is not touching the support or other substrate. (B) Tail touch (TT): The tail is touching the support or other substrate but not wrapped around it. (C) Tail wrap (TW): The tail is observed wrapped around the support or other substrate and is not bearing significant mass. (D) Tail mass bearing (TMB): The tail appears to be bearing equal or greater mass than the other limbs.

were defined based on Hunt et al. [1996] and are described elsewhere [Bezanson, 2006, 2009; Hunt et al., 1996]. Tail use categories were defined and modified [Bergeson, 1996; Fontaine, 1985; Garber & Rehg, 1999]; *TF* = *Tail free*: The tail was not touching a support or other substrate (e.g. liana, mother's arm, fruit clump); *TT* = *Tail touch*: The tail is touching the support or other substrate but not wrapped around it; *TW* = The tail was observed wrapped around the support or other substrate and is not bearing mass; *TMB* = *Tail mass bearing*: The tail appeared to be bearing equal or greater mass than the other limbs (Fig. 1). The support size that the tail was in contact with as a mass-bearing limb was recorded using predefined estimated circumference categories (small = less than 5 cm, medium = 6–10 cm; large = greater than 11 cm; clumps of small supports). These size

categories were estimated based on their circumference relative to the size of a capuchin hand [Bezanson, 2009]. I collected data on branch orientation but given difficulties in accurately determining branch angle from below the animal, I have not included this information in the present study [Bezanson et al., 2012].

### Data Analysis

The data set presented in this study includes 401.3 hr of data on *C. capucinus* and 554.3 hr of data on *A. palliata* totaling 955.6 hr of data or 57,344 individual activity records. To increase the number of active behavioral samples, I collected more IARs for mantled howlers due to long periods of rest that characterize *Alouatta*. Descriptive statistics

were used to examine proportions of observations of tail use among the different age classes of *Cebus* and *Alouatta*. In addition, statistical analyses were performed using a two-sample randomization procedure written in R-2.3.0, [The R-foundation for Statistical Computing]. Randomization techniques have become increasingly common in studies of positional behavior [Bergeson, 1996, 1998; Dagosto, 1994; Hunt, 1992; Lawler, 2006; Wright, 2005] and involve shuffling of the data set to assure that chance-sampling error is not influencing the results. These tests involve creating a test statistic or the mean differences in the comparisons for each randomization loop through multiple randomizations of the data. This two-sample test is equivalent to the student's *t*-statistic [Manly, 1997]. The *P*-value represents the proportion of values greater than the observed value of all randomization loops. Adams and Anthony [1996] compared 500, 1,000, 2,000, 3,000, 4,000, 5,000, 7,500, and 10,000 randomizations and concluded that variance drops rapidly and then decreases, remaining stable at 4,000 loops and higher. Manly [1997] suggested 1,000 loops to test hypotheses at the 5% level and 5,000 at 1% level. In this study, significance was set at  $P < 0.05$  using 5,000 randomizations. To address issues of multiple pairwise comparisons in each table of *P*-values, I applied a sequential Bonferroni procedure [Holm, 1979].

Infants were excluded from statistical analyses for several reasons. First, the goal of this research is to assess how growth and development influence tail use. Much infant behavior takes place on the mother with very few observations of locomotion and posture off of the mother. Breaking down the number of observations into different behavioral contexts reduces the number of samples or individual activity records. Therefore, I provide descriptive data for the small number of infant positional modes as an overall pattern of tail use and focus on the differences and similarities observed among juveniles and adults. The adult category combines males and females for both

species. Although *Cebus* and *Alouatta* exhibit varying degrees of sexual dimorphism (25–35%), previous studies have suggested that adult males and females exhibit similar patterns of positional behavior [Garber, 2011; Gebo, 1992]. To be certain this was the case in *Cebus* and *Alouatta*, I tested for differences between females and males in both species during feeding and foraging and found no significant differences. However, females carrying infants exhibited significant differences during travel ( $P < 0.001$ ). Due to low sample sizes of these individuals, I removed these activity records from the adult data set. In addition, the youngest age classes are compared to adults to avoid confusion between older juveniles/preadults (similar body mass) and adults [Bezanson, 2006, 2009].

## RESULTS

### Behavioral Context

Overall, the three most common activities in the capuchin data set were foraging, resting, and traveling (Table II). The majority of capuchin infant behavior occurred either on the mother's body (dorsal or ventral) or within 1 m from the mother (Ride: Infant I [INFI]: 88.8%, Infant II [INFII]: 68.4%). Young Juvenile and adult capuchins were similar in the investment of time devoted to foraging (Juvenile I [JI]: 36.8%, Juvenile II [JII]: 33.8%, Adult [A]: 29.7%) and spent a smaller proportion of their observations resting. Capuchin infants spent a smaller proportion of their total activity budget engaged in social behaviors (INFI: 4.1%, INFII: 2.7%). Social interactions increased in juveniles (JI: 11.4%, JII: 14.2%). Play was first observed in capuchin Infant I (42.3% of social behaviors) individuals and increased in the Infant II category (78% of social behaviors). Capuchin juveniles also played during the majority of social behaviors (play = JI: 80.2%, JII: 78.2%).

TABLE II. Percentage IARs Devoted to Different Activities in *C. capucinus* and *A. palliata*.

Activity	<i>Cebus capucinus</i>					<i>Alouatta palliata</i>				
	Infant I	Infant II	Juvenile I	Juvenile II	Adult	Infant I	Infant II	Juvenile I	Juvenile II	Adult
Feed	4.2	2.1	10.7	11	8.9	0	2.1	7.2	9.2	8.5
Forage	0.2	11.0	36.8	33.8	29.7	0	1.9	16	12.4	5.1
Travel	0.1	0.7	21.6	19.8	20.4	0	2.9	9.5	13.6	7.0
Rest	0.3	1.1	11.1	12.1	16.4	0	25.2	48.7	49.4	74.2
Active posture	0.5	3.7	6.6	8.2	10.2	1.8	1.6	7.1	7.9	3.6
Explore	1.8	10.1	0.4	0	0	1.6	3.7	2.1	2.7	0
Ride	88.8	68.4	0.4	0	0	90.5	56.5	5.2	<0.1	0
Other	0	0.1	1.0	0.8	1.2	0	0	0.3	0.3	0.3
Social behavior	4.1	2.7	11.4	14.2	13.3	6.1	6.2	4.0	4.4	1.3
% of play within social behavior	42.1	78	80.2	78.2	0.1	42.3	68	80.1	76.8	0.2

IAR = individual activity record; "Ride" refers to Infant/Juvenile dorsal and ventral riding on the Mother.

Infant howlers spent considerable time on their mother during infancy (ride: INF I: 90.5%, INF II: 56.5%), primarily leaving the mother during exploration and resting. Although both juvenile and adult howlers devoted considerable time to rest (JI: 48.7%, JII: 49.4%, A: 74.2%), adults rested considerably more than juveniles, and juveniles spent a larger proportion of the day foraging than did adults (JI: 16%, JII: 12.4%, A: 5.1%). In howlers, social behaviors were observed in relatively equal frequencies in the infant categories (II: 6.1%, III: 6.2%) when compared to juveniles (JI: 4.0%, JII: 4.4%) and included interactions with older group members, vocalizing, and play. Play was observed in Infant I individuals (42.3% of social behaviors) and increased in the Infant II category (of social behaviors). These behaviors continued in the juvenile categories (play = JI: 80.1%, JII: 76.8%). Adult howler social behavior included vocalization, sexual solicitation (tongue flick), and copulations, with very rare and brief oc-

currences of aggression (<1%) and play (<1%) with juveniles.

In Table III, I provide the number of IARs and proportion of time engaged in locomotor versus postural modes in *Alouatta* and *Cebus*. In *Cebus*, locomotor activities accounted for 24–31.4% of the positional repertoire in the Infant II through Adult age categories. In all age categories of *Alouatta*, more than 80% of the positional repertoire was dedicated to postural activities and much of this time was devoted to rest. In both species, positional diversity (number of positional modes) increased from the youngest infant stage to the youngest juvenile stage (*Cebus*:  $N = 29$ , *Alouatta*:  $N = 25$ ) and then decreased in adults (*Cebus*:  $N = 21$ , *Alouatta*:  $N = 22$ ). This was especially evident during social behaviors (Table III). I observed an increase in both the numbers of different positional behaviors during social behavior and the number of positional behaviors that employed the prehensile tail as a mass-bearing limb in

**TABLE III. Proportions of Tail-Assisted Positional Behaviors Across All Activities and All Age Classes and Positional Modes During Social Behaviors.**

	<i>Cebus capucinus</i>					<i>Alouatta palliata</i>				
	INF I	INF II	JI	JII	A	INF I	INF II	JI	JII	A
Locomotor modes	6.5	24.5	31.2	31.1	25.9	6.4	10.4	13.6	16.9	8.3
Tail-assisted locomotor modes	0.0	2.4	1.3	3.5	2.7	0.0	0.0	5.3	5.5	8.8
Postural modes	93.5	75.5	68.8	68.9	74.1	93.6	89.6	86.4	83.1	91.7
Tail-assisted postural modes	12.9	33.1	40.5	27.4	14.9	3.8	30.5	74.5	71.8	54.0
Total positional modes	10	26	29	26	21	4	14	25	25	22
Positional modes during social behavior										
Sit	5.1	13.7	11.1 <sup>a,b</sup>	26.7 <sup>a</sup>	59.7	36.3	19.4	11.8 <sup>a,b</sup>	9.5 <sup>a</sup>	47.2
Squat	0	15.8	8.6	19.7 <sup>a</sup>	7.5	2.2	0	2.7	0.7	4.0
Lie	82.5	22.6	24.5	18.1 <sup>a</sup>	24.4	3.9	7.5	6.3 <sup>b</sup>	3.3	8.5
Quadrupedal stand	2.1	4.1	3.2	4.0	2.4	3.4	5.4	3.1 <sup>a</sup>	1.8 <sup>a</sup>	9.7
Tripedal stand	0	0	0	0	0.1	0	0	0	0	0
Crouch	4.1	5.2	0.7	0.3	2.1	0	0	0.4	0.4	0
Flexed bipedal stand	0	0.7	2.9	0.1	0.1	0	0	0	0	0
Horizontal tripod	0	0.3	0.5	0.4	0.3	0	1.1	3.9	1.1	0
Vertical tripod	0	1.0	0.7	0.7	<0.1	0	0	0	0.7	0
Tail suspend	6.2	12.3	9.8 <sup>a</sup>	8.7 <sup>a</sup>	0.9	37.4	54.3	58.1 <sup>a</sup>	57.5 <sup>a</sup>	6.2
Tail/hindlimb suspend	0	0	0.5	2.0	<0.1	3.9	4.3	3.1	2.6	0
Pronograde tail quadrumanus suspend	0	0	0	0	0	2.8	2.2	2.7	2.9	0
Quadrupedal walk	0	6.2	5.2 <sup>a</sup>	2.6	1.1	0	3.2	0.8 <sup>a,b</sup>	13.7 <sup>a</sup>	22.1
Quadrupedal run	0	6.2	17.1 <sup>a,b</sup>	8.1 <sup>a</sup>	0	0	0	2.3	2.2	0
Flexed-elbow vertical climb	0	2.7	1.2	0	0	0	0	0.8	1.1	2.3
Ladder climb	0	0	0.5	1.0	0.9	0	0	0.8	0.7	0
Vertical scramble	0	4.5	0.9	2.2	<0.1	0	0	0	1.1	0
Bimanual pull-up	0	1.7	0.2	0	0	10.1	0.4	1.6	0.7	0
Fire pole slide	0	1.0	8.6 <sup>a,b</sup>	3.8	0	0	0	0	0	0
Leap	0	1.0	3.6	1.6	0.2	0	0	0	0	0
Hop	0	1.0	0.2	0	0	0	0	0	0	0
Quadrupedal walk	0	6.2	5.2	2.6	1.1	0	0	0	0	0

Tail-assisted modes are those modes where the tail is providing equal or greater support than any limb (TMB) or modes where the tail is wrapped around the support (TW) but not bearing significant mass. Additional details on positional repertoire during feeding and travel can be found in Bezanson [2006, 2009]. Statistical significance is reported for modes that total >5% of the positional repertoire during social behavior.

<sup>a</sup>Statistical significance: significantly different from Adult.

<sup>b</sup>Statistical significance: Juvenile II significantly different from Juvenile I.

Values are significant after comparisons using sequential Bonferroni correction.

juveniles of both species (Table III). Capuchins exhibited the greatest diversity in the number of positional modes in young juveniles (INF I: 5, INF II: 18, J I: 20, J II: 17, A: 16) whereas howlers showed greater diversity in older juveniles (INF I: 8, INF II: 9, J I: 14, J II: 16, A: 7) during social interactions.

### Prehensile-tail Use *C. capucinus*

La Suerte capuchins employed the tail as a mass-bearing fifth limb primarily during feeding, foraging, and social behavior (Table IV). During travel the tail provided no support (*tail free*) during approximately 97% of the total observations in J I, J II, and A. The tail rarely provided support in Infant I individuals while they were clinging to their mother's neck and upper back. While engaged in social behavior, Infant I capuchins primarily exhibited *tail free* (44.4%) followed by *tail wrap* (29.4%) and *tail mass bearing* (5.9%). When riding on mothers during travel, In-

fant II individuals rarely wrapped their tails around the carriers' arm, torso, or tail. In Juvenile Is, the tail was used for mass bearing during 13.9% of feeding/foraging and 1.9% of travel ( $P = 0.002$  compared to adult). During social behavior, the tail modes were *tail free* (38.7%), *tail touch* (33.6%), *tail wrap* (14.5%), and *tail mass bearing* (13.2%). Juvenile IIs exhibited a similar pattern as juvenile Is, with *tail mass bearing* observed during 10.6% of feed/forage and during 1.2% of travel. During social behavior, capuchin juvenile IIs exhibited *tail mass-bearing* behaviors during 10.3% of the observations.

Adult capuchins were observed using their tail as a mass-bearing fifth limb less frequently during feed/forage (6.4%) and social behavior (0.8%) when compared to Juvenile Is, and Juvenile IIs ( $P < 0.001$  in all comparisons). During social behavior, the adult tail was often observed touching a substrate (71.3%) significantly more often than in juveniles ( $P < 0.001$  in both comparisons). This reflected high proportions

**TABLE IV. Prehensile Tail Use (%) in Infant (II and III), Juvenile (JI and JII), and Adult *C. capucinus* and *A. palliata*.**

Prehensile-tail use	<i>Cebus capucinus</i>					<i>Alouatta palliata</i>				
	INF I	INF II	J I	J II	Adult	INF I	INF II	J I	J II	Adult
Feeding and foraging										
N: Feeding and foraging IARs	102	380	1,543	1,937	4,350	0	178	1,554	1,334	1,800
TF	51.3	61.2	54.9 <sup>a</sup>	57.9	68.4	0	20.1	15.0	12.0	14.4
TT	38.6	6.4	10.4	10.8 <sup>a</sup>	10.7	0	2.4	1.1 <sup>a</sup>	2.6 <sup>a</sup>	8.6
TW	10.1	21.5	20.8 <sup>a</sup>	20.7	14.5	0	44.1	47.3	49.1	49.5
TMB	0	10.9	13.9 <sup>a</sup>	10.6 <sup>a</sup>	6.4	0	33.4	36.6 <sup>a</sup>	36.3 <sup>a</sup>	27.4
Travel										
N: Travel IARs	2,094	1,995	717	857	2,298	2,675	2,675	926	862	929
TF	58.4	47.2	97.1	96.8	97.4	49.8	35.2	86.6	81.6	81.0
TT	31.4	37.5	0.1	0.5	0.9	23.7	56.4	2.0	1.6 <sup>a</sup>	4.5
TW	10.2	15.2	0.9	1.5	0.8	26.5	4.9	4.5	4.0	6.1
TMB	0	0	1.9 <sup>a</sup>	1.2	0.9	0	3.5	6.7	12.7 <sup>a,b</sup>	8.4
Social behavior										
N: Social behavior IARs	97	78	366	615	1,495	179	278	255	273	176
TF	44.4	49.6	38.7 <sup>a</sup>	46.0 <sup>a,b</sup>	20.8	29.6	20.6	23.4	18.1	7.1
TT	20.6	20.3	33.6 <sup>a</sup>	30.9 <sup>a</sup>	71.3	3.4	5.6	2.8 <sup>a</sup>	1.6 <sup>a</sup>	26.8
TW	29.4	16.7	14.5 <sup>a</sup>	12.8 <sup>a</sup>	7.1	22.4	16.4	17.1 <sup>a</sup>	20.4 <sup>a</sup>	51.8
TMB	5.9	13.4	13.2 <sup>a</sup>	10.3 <sup>a,b</sup>	0.8	44.6	57.4	56.7 <sup>a</sup>	59.9 <sup>a</sup>	14.3
All behaviors combined										
N: IARs	2,354	2,890	3,248	4,332	11,264	2,954	4,504	6,326	6,202	13,270
TF	57.7	53.5	59.8	59.4	59.9	54.2	37.1	19.0 <sup>a</sup>	28.7 <sup>a,b</sup>	10.3
TT	30.1	20.6	14.9 <sup>a</sup>	21.4 <sup>a,b</sup>	29.1	29.1	35.0	18.1 <sup>a</sup>	16.5 <sup>a</sup>	40.5
TW	11.8	16.2	15.4 <sup>a</sup>	13.5 <sup>a</sup>	8.4	12.3	21.0	44.2 <sup>a</sup>	27.3 <sup>a,b</sup>	39.6
TMB	0.4	9.7	9.9 <sup>a</sup>	5.7 <sup>a,b</sup>	2.6	4.4	6.9	18.7 <sup>a</sup>	27.5 <sup>a,b</sup>	9.6

Travel includes Infant/Juvenile ventral/dorsal clinging. "All behaviors combined": travel, feeding, foraging, social behavior, rest, active posture, explore, and other.

TF (Tail free): the tail is not touching the substrate; TT (Tail touch): the tail is touching the substrate or is wrapped around the body; TW (Tail wrap): the tail is observed wrapped around the substrate and is not observed bearing mass; TMB (Tail mass bearing): the tail is observed bearing equal or greater mass than any single limb.

<sup>a</sup>Statistical significance: significantly different from Adult.

<sup>b</sup>Statistical significance: Juvenile II significantly different from Juvenile I.

Values are significant after comparisons using sequential Bonferroni correction.

of postural modes during grooming in adults. The biggest differences were observed in tail use within social behavior. These differences reflect higher proportions of play in juveniles and higher proportions of grooming in older age groups. For example, the tail provided support (*tail mass bearing*) significantly more often in Juvenile Is and Juvenile IIs compared to adults ( $P < 0.001$  in all comparisons). Juvenile I individuals exhibited significantly more tail mass-bearing modes when compared to Juvenile IIs during social behavior ( $P < 0.001$ ). During feeding and foraging, juveniles exhibited significantly higher proportions of *tail mass bearing* and *tail wrap* than did adults (Table IV).

### Prehensile-tail Use *A. palliata*

Among La Suerte howlers, the use of the prehensile tail as a gripping limb (*tail mass bearing* and *tail wrap*) was highest in the juvenile categories during feed/forage. During feed/forage, the howler tail appeared to be important as additional support during nonsuspensory postures as it was observed wrapped around the substrate during almost half of the observations in all age categories except infants who were not observed to independently feed and forage. During travel, howlers used their tail as a mass-bearing fifth limb relatively more frequently than capuchins (INFII: 3.5%, JI: 6.7%, JII: 12.7%, A: 8.4%) with the only significant differences observed in JII howlers when compared to JI and adult howlers ( $P < 0.001$ ). The use of the prehensile tail as a mass-bearing fifth limb increased (INF I: 44.6%, INFII: 57.4%) during social behavior where below-branch suspensory postures were more common during howler play. Juveniles used their prehensile tail (*tail mass bearing*) significantly more often than adults during social behavior ( $P < 0.001$ , all comparisons) and feeding/foraging ( $P < 0.001$ , all comparisons).

During feed/forage, the tail was observed as a mass-bearing limb during 27.4% of the observations in adults and was wrapped around the substrate during 49.5% of the observations. For adults, the context of social behavior (not including play) seemed to dictate a different pattern of tail use than observed during feed/forage with *tail wrap* (51.8%) and *tail touch* (26.8%) observed more often than *tail mass bearing* (14.3%). Juvenile Is and Juvenile IIs used their tails in mass-bearing modes significantly more often than adults during feed/forage and social behavior while *tail wrap* significantly increased in adults during social behavior (Table IV).

### Support Use (Howlers and Capuchins)

In Table V, I provide support size information for both capuchins and howlers during cases in which the prehensile tail provided support during

mass-bearing, tail-assisted (TMB) positional behaviors during travel and feeding and foraging. During feeding/foraging, infant, juvenile, and adult capuchins used their tails on small supports (75.7–91.1%) most often. Juveniles were observed to use the medium support setting more often than adults (JI: 19.5%, JII: 20.3%, A: 13.2%,  $P < 0.05$  in both comparisons). Howlers exhibited a more varied pattern of substrate use during feeding/foraging with greater exploitation of medium supports (JI: 37.5%, JII: 56.3%, A: 39.0%). In howlers, Juvenile I individuals used smaller supports significantly more often (JI: 60.4%) than did JII and adult categories (JII: 31.3%, A: 35.3%,  $P < 0.001$  in both comparisons). During travel, the tail was observed gripping small supports 30–42% in older capuchins and 47–64% in older howlers. However, these behaviors did not increase proportionately with age (Table V). In both species, the youngest infants primarily traveled by riding on their mothers.

## DISCUSSION

La Suerte capuchin and howler tail use follows a similar behavioral developmental trajectory with infants and the youngest juveniles exhibiting increased use of the prehensile tail as a fifth limb during feeding/foraging and during social behavior when compared to adults. If prehensile tails in *Cebus* and *Alouatta* represent a neotenic retention [Bergeson, 1996; Meldrum, 1998] then infants and juveniles are expected to use their tails for additional support while riding on their mother and during independent positional behaviors. This was not the case, and therefore is not consistent with a model of neotenic retention. Infant capuchins primarily clung to the dorsal part of their mother's neck and the tail did not appear long enough to reach areas of the mother's arm and torso that could be grasped. However, young howlers were observed to cling the ventral portion of the mother's torso and it often appeared that the tip of the tail was wrapped around a tuft of fur. Once they began clinging dorsally, they often wrapped their tails around the mother's arm or torso. In howler and capuchin JI and IIIs, tail mass-bearing behaviors peaked in the juvenile categories and then decreased significantly in adults. These behaviors do not support the hypothesis of neotenic retention. However, it is important to note that tail wrapping capabilities may not be observable while infants are being carried and this hypothesis warrants further investigation. Thus, in the absence of evidence in support of neotenic retention, I explore the behavioral context of prehensile tail use among different age groups of La Suerte capuchins and howlers.

The prehensile tail was important for mass distribution and stabilization during feed/forage in all age categories of *Cebus* and *Alouatta*. The hypothesis

**TABLE V. Support Characteristics (%) for Mass-Bearing Tail-Assisted (TMB) Positional Behaviors During Feeding/Foraging and Independent Travel in *C. capucinus* and *A. palliata*.**

	<i>Cebus capucinus</i>					<i>Alouatta palliata</i>				
	INF I	INF II	J I	J II	Adult	INF I	INF II	J I	J II	Adult
Branch size: feed/forage										
Clump	0	0	<1.0	<1	1.9	0	0	<1	1.8	5.5
Small	87.8	91.1	78.6	75.7	81.6	100	81.8	60.4 <sup>a</sup>	31.3 <sup>b</sup>	35.3
Medium	12.2	7.8	19.5 <sup>a</sup>	20.3 <sup>a</sup>	13.2	0	18.2	37.5	56.3 <sup>a,b</sup>	39.0
Large	0	1.1	1.8	3.6	3.3	0	0	1.4	10.6	20.2
Branch size: travel										
Clump	0	0	15.4	20	23.8	0	0	1.6	12.8	21.8
Small	0	0	38.5	30	42.9	0	100	64.5	56	47.4
Medium	0	0	15.4	30	14.3	0	0	33.8	25.7	10.3
Large	0	0	30.7	20	19	0	0	0	5.5	20.5

Tail assisted behaviors during travel were rare in all age categories of Capuchins and Howlers and were excluded from statistical analysis.

<sup>a</sup>Statistical significance: significantly different from Adult.

<sup>b</sup>Statistical significance: Juvenile II significantly different from Juvenile I.

Values are significant after comparisons using sequential Bonferroni correction.

that increased tail use would be found in larger bodied *A. palliata* when compared to *C. capucinus* was supported and is not surprising given previous research on positional behavior in the genus *Alouatta* [Bergeson, 1996, 1998; Bezanson, 2006, 2009; Biccamarques & Calegario-Marques, 1993, 1995; Cant, 1986; Mendel, 1976; Richard, 1970; Schön Ybarra, 1984; Schön Ybarra & Schön, 1987; Youlatos, 1993, 1998, 1999]. All age categories of howlers engaged in higher proportions of tail use and the anatomical basis of increased flexion, extension, muscle mass, and strength required for these behaviors has been described in previous studies [Ankel, 1972; German, 1982; Lemelin, 1995; Organ, 2010; Organ et al., 2009; Organ et al., 2011]. Based on the present data, it appears that by age 2, juvenile-mantled howlers exhibit adult-like prehensile tail motor and weight support capabilities. This supports the hypothesis that the prehensile tail plays an important role in balance and the distribution of mass during feeding and foraging postures and may increase a primate's ability to reach resources [Bergeson, 1996; Grand, 1972; Mittermeier & Fleagle, 1976; Youlatos, 1999]. However, direct links between body mass, tail use, and branch use were not found within species. Given that the prehensile tail facilitates the distribution of mass across a broader number of arboreal supports, it was expected that prehensile-tail use would increase during ontogeny as smaller supports are likely to deform under the weight of larger individuals [Fleagle & Mittermeier, 1980; Grand, 1972; Mittermeier & Fleagle, 1976]. The genus *Alouatta* has been described as a cautious and deliberate arboreal quadruped that engages in a variety of below-branch suspensory postures while feeding and foraging [Bergeson, 1996, 1998; Bezanson, 2009; Biccamarques and Calegario-Marques, 1993, 1995; Cant, 1986; Mendel, 1976; Richard, 1970; Schön Ybarra,

1984; Schön Ybarra & Schön, 1987; Youlatos, 1993, 1998, 1999]. If functional and biomechanical problems associated with the distribution of mass influenced the evolution of the prehensile tail then adult-mantled howlers and adult capuchins should be observed to use their tail more often for weight support than infants and juvenile howlers. This was not the case across age groups. In this study, adult howlers used their tail as a mass-bearing limb in 27.4% of feeding behaviors while younger and older juveniles used their tails in approximately 36% of all feeding behaviors. This is similar to previous studies that specifically address prehensile-tail use where adult *A. palliata* were reported to use their tails as a mass-bearing limb during suspensory postures in approximately 30–35% of feeding/foraging positional behaviors [Johnson & Shapiro, 1998; Lawler & Stamps, 2002]. In howlers, the adult positional repertoire involved more sitting postures and fewer suspensory behaviors (e.g. tail suspend and quadrumanus suspend) than observed in the juvenile categories [Bezanson, 2009]. Therefore, adults are not necessarily less efficient foragers than juveniles, rather they use an different set of postures to acquire the same resources. Prates and Biccamarques [2008] describe a similar pattern in *A. caraya*. Adult black and gold howlers adopted more sitting behaviors and juveniles and infants engaged in more bridging and hanging postures.

The genera *Cebus* and *Sapajus* have been described as arboreal quadrupeds [Hershkovitz, 1977; Napier & Napier, 1967] that incorporate leaping and tail-assisted suspensory postures [Bergeson, 1996; Bezanson, 2009; Fontaine, 1985; Gebo, 1992; Garber & Rehg, 1999; Johnson & Shapiro, 1998; Oppenheimer, 1968; Wright 2005, 2007; Youlatos, 1998]. Like howlers, adult *C. capucinus* used their tails less often than juveniles (adults:

6.4%, young juveniles: 13.9%, older juveniles: 10.6%). In other studies focusing on the prehensile-tail use, white-faced capuchins have been reported to use their tails as a mass-bearing fifth limb in approximately 16–58% of feeding and foraging postures [Bergeson, 1996; Garber & Rehg, 1999] and approximately (wrapped and mass bearing) 35% of the time across all activities [Bergeson, 1996; Johnson & Shapiro, 1998]. Due to morphological differences and positional patterns observed thus far, adult capuchins have been described as using their tails less often than howlers and to rarely support their full body mass with the tail alone [Carpenter, 1934; Grand, 1984; Lemelin, 1995; Organ, 2010]. However, results presented here and work by Bergeson [1996], Garber and Rehg [1999], and Youlatos [1999]; Bezanson [2009] suggest that tail suspensory postures are more common. For example, in a 3-month study Garber and Rehg [1999] reported that they observed adult capuchins using their tails as the sole support during 18.4% of feeding and foraging postures. In this study, I found that adult capuchins used their tail as a mass-bearing fifth limb during 6.4% of feeding/foraging observations. This is less than Garber and Rehg [1999] found in the same population (18.4%) and less than Bergeson [1996] describes for other populations of *C. capucinus* in Costa Rica (14.3%). This may reflect differences in timing, resources, or age categories. Garber and Rehg [1999] conducted research during January to March and did not observe palm feeding. I observed palm feeding during which the primary posture was sitting on top of a fruit clump (adults 8.1% of feeding/foraging modes, [Bezanson, 2009]). Bergeson [1996:58] included juveniles of unknown age (42.7% of the total age/sex identified sample) in his samples. The inclusion of juveniles is likely to have increased the number of observations of suspensory behaviors. Finally, in both howlers and capuchins, the use of the tail as a mass-bearing fifth limb did not increase when using smaller supports or clumps of small supports. Therefore, data presented here suggest that in these two primate species the prehensile tail serves many roles in support and balance that are not directly linked with increasing body mass when using small supports.

Tail mass-bearing suspensory behaviors were linked to both feeding/foraging and social behavior, especially in howlers and capuchins under 2 years of age, and appear to be disassociated from body mass. Furthermore, the vast majority of prehensile-tailed arboreal mammals are relatively smaller bodied than primates with prehensile tails [Bergeson, 1996; Emmons & Gentry, 1983; Youlatos, 2003]. It is possible that young juveniles develop motor control and strength in their tail earlier than in their forelimbs and therefore rely more on their tail than adults. However, previous studies on the *Cebus* and *Sapajus* have found that long bone lengths scale with

positive allometry while limb bone cross-sectional dimensions scale with negative allometry from birth through the juvenescence [Jungers & Fleagle, 1980; Young et al., 2010]. Behaviorally, these relatively robust bones are argued to allow young capuchins to engage in riskier locomotor behaviors [Young et al., 2010] including suspensory behaviors involving the tail. Russo and Young [2011] examined radiographs of infant *C. albifrons* and *S. apella* and found that young monkeys had stronger and shorter caudal vertebrae than expected for their body size and suggested that the adult locomotor and postural phenotype (as it relates to tail use) reflects demands placed on juveniles rather than adults. While corresponding morphological data on howling monkeys are not available, tail use described in this study and the ontogeny of positional behavior described elsewhere [Bezanson, 2009; Prates and Bicca-Marques, 2008] suggest howlers and capuchins are similar in their early development of complex suspensory behaviors.

Behavioral data from other primate species also suggest a pattern where juveniles exhibit greater positional diversity than their adult counterparts. Rhesus macaque juveniles (10–18 months) exhibited more arboreal positional modes (adults: 35% and juveniles: 49.5%), especially those associated with climbing and leaping than adults [Wells & Turnquist, 2001]. In addition, Dunbar and Badam [1998:543] describe the juvenile period as “the golden age of posture and locomotion” in *Macaca mulatta* (rhesus macaque), *Macaca radiata* (bonnet macaque), and *Semnopithecus entellus* (hanuman langur). In that study, juveniles engaged in more below-branch positional behaviors, especially within the context of play behavior. Fontaine described similar results in five species of New World primates (both captive and wild) including: *A. palliata* (mantled howling monkey), *Ateles geoffroyi* (black-handed spider monkey), *Cacajao calvus* (uakari), *C. capucinus* (white-faced capuchin), and *Saimiri boliviensis* (squirrel monkey). In all five species, he found increased use of complex suspensory behaviors and faster locomotor modes in juveniles. For example, juvenile *A. palliata* engaged in suspensory postures during 86.8% of play behaviors and 12.3% of non-play (feed, forage, travel, rest) behaviors whereas adults used suspensory postures in 4.8% of nonplay behaviors and were not observed to play (Fontaine, 1995). Workman and Covert [2005] emphasize the importance of positional practice during play in captive red-shanked Douc (*Pygathrix nemaeus*), Delacour’s (*Trachypithecus delacouri*), and Hatinh langurs (*Trachypithecus hatinhensis*). The young langur positional repertoire showed increased suspensory, swinging, and leaping categories during play. These results not only illustrate the importance of locomotor development linked to perfecting acrobatic and riskier positional modes that may be beneficial in accessing resources such as fruit and

leaves and avoiding and escaping predators. However, while juveniles engage in more diverse and risky behaviors, infants and juveniles may not match adults in neuromotor control, agility, and stamina [Carrier, 1996]. Finally, results presented here do not support Emmons and Gentry's [1983] contention that the prehensile tail in primates represents a locomotor adaptation in Neotropical forests. Rather, results presented here highlight the importance of the prehensile tail in facilitating survival while engaging in what can be considered relatively riskier behaviors. Future work should consider the interrelated demands and contexts of movement capabilities and behaviors necessary for infant and juvenile survival rather than primarily considering "what it takes" to achieve an adult phenotype.

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