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Ontogeny of postcranial morphology and locomotor behavior in *Propithecus verreauxi* coquereli and *Lemur catta*

Stephanie Ann Wolf
James Madison University

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Ontogeny of postcranial morphology and locomotor behavior in *Propithecus verreauxi coquereli* and *Lemur catta*

Stephanie Ann Wolf

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This thesis is dedicated with sincere gratitude to my mother, Debra Wolf.

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I. Introduction

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Abstract

Despite living under the same environmental pressures and sympatrically in many cases, *Propithecus verreauxi* and *Lemur catta* have evolved very different strategies for survival in stochastic environmental conditions. *P. verreauxi* show slow somatic growth, low maternal investment, and rapid dental growth while *L. catta* show faster somatic growth, high maternal investment, and slower dental growth. *P. v. coquereli* are highly specialized for vertical clinging and leaping (VCL) among lemurs, while *L. catta,* the most terrestrial of lemurs, use a wider variety of locomotor types including quadrupedalism, climbing, and leaping. *P. v. coquereli* have unusually long legs and muscular thighs while *L. catta* have more similar limb lengths and muscular proximal limb segments (Lessertisseur and Jouffroy, 1973; Jouffroy, 1975). Little is known of the ontogenetic trajectories by which these adult forms are acquired. Because selection acts on the entire life cycle of an animal, it is important to investigate the morphological and locomotor changes occurring early in development. These changes might be important components to each species' survival strategy that allow infant primates to travel with a group of larger adults and survive to adulthood.

I examined changes in locomotor behavior and limb morphology from 0-2 years in *L. catta* and *P. v. coquereli.* Limb segment lengths, limb segment circumferences, and body mass were recorded every 2 weeks in infants and every 4 weeks in yearlings at the Duke Lemur Center (DLC). Locomotor data were collected on infants transitioning to locomotor independence and yearlings of each species in free-ranging enclosures at the DLC using locomotor bout sampling.

Results indicate that both species are born with upper limb lengths similar to lower limb lengths, whereas only *P. v. coquereli* dissociates upper- and lower limb growth to reach adult limb proportions. *P. v. coquereli* transitional infants and yearlings use similar overall locomotor behavior and undergo rapid postcranial growth to achieve the limb proportions necessary for VCL by the time of locomotor independence. Relative to upper limb length, lower limb length is even longer in juveniles first leaping independently than in yearlings and adults. Relatively long hindlimbs may allow juveniles to achieve leaping take-off velocity similar to adults despite absolutely smaller size. *L. catta* transitional infants exhibit a different distribution of locomotor behavior than yearlings despite similarities in limb proportions.

Much like *P. v. coquereli* juveniles are "ecological adults" in terms of their rapid dental development, they seem to also be "ecological adults" in terms of locomotor behavior. Because of the demand for using VCL at a young age, and despite overall slow postcranial growth, *P. v. coquereli* transitional infants are on a rapid growth trajectory towards achieving the limb proportions necessary for specialized leaping. Lowest IMI values at locomotor independence, increased leap frequency paired with decreased leap distance, and high positive allometric growth of the tail are three key findings that provide evidence as to how *P. v. coquereli* transitional infants are able to display similar locomotor repertoires as yearlings in order to keep up with the group to survive, despite being absolutely smaller.

Chapter 1

Introduction

Natural selection does not only act on adults, but plays a critical role at all stages of an organism's lifecycle (Stearns, 1992). Juvenile lemurs, who are undersized and inexperienced relative to adults, have to travel in the same environment to keep up with the group, likely making the juvenile period a time of great locomotor demand (Hurov, 1991; Carrier 1996; Wells and Turnquist, 2001). Little is known, however, about the biomechanical and behavioral consequences of staying small yet needing to travel with a group led by larger adults. This issue is particularly profound for lemurs, who 1) exhibit a complex array of locomotor behaviors including arboreal and terrestrial quadrupedalism, leaping, brachiation, bipedalism, and vertical clinging and leaping (VCL) to negotiate an intricate arboreal environment and 2) have adaptive strategies that sometimes leave small animals moving independently using acrobatic forms of locomotion such as VCL.

Primates can be classified as either haplorhines (higher primates and tarsiers) or strepsirrhines (Fleagle, 1999; Figure 1.1). Strepsirrhine primates are the primary focus of this study as I specifically analyze members of two of the eight extant lemur families: one indrid and one lemurid (Figure 1.1 & 1.2). Coquerel's sifaka (*Propithecus verreauxi coquereli*)[1], a member of the indrid family, is one of six species of sifaka and one of two subspecies of *Propithecus verreauxi*, while ring-tailed

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[1] *Propithecus verreauxi coquereli* and *Propithecus verreauxi verreauxi* are indentified in this study as two distinct subspecies of *Propithecus verreauxi* (Yoder, 1997; Pastorini et al., 2001; Rumpler et al., 2004). This subspecies grouping will be used throughout the remainder of the study because of morphological similarities displayed in both animals rather than recent publications which identify the animals as two distinct species due to genetic differences; *Propithecus verreauxi* and *Propithecus coquereli* (Mayor et al., 2004; Mittermeier et al., 2006). It is of note that most long-term wild studies of *P. verreauxi* have been on *P. v. verreauxi*, while the captive studies typically examine *P. v. coquereli*.

lemurs (*Lemur catta*) are of the lemurid family and are the only members of their genus (Yoder, 1997; Pastorini et al., 2001; Rumpler et al., 2004; Figure 1.2). Strepsirrhines are distributed throughout the old world, but lemurs, and thus *P. v. coquereli* and *L. catta* are isolated to the island of Madagascar (Fleagle, 1999; Figure 1.3). *Propithecus verreauxi* travel in groups of 3 to 10 members and live in the dry and spiny forest of western and southern Madagascar (Jolly, 1966; Richard, 1974, 1975, 1976, 1992; Richard et al., 1975; Ravosa et al., 1993). *L. catta* reside in the dry south of Madagascar, traveling with an average group size of 9 to 14 members (Jolly, 1966; Jolly et al., 2002; Gould, 1990; Gould et al., 2003; Sussman, 1991; Sauther, 1991, Sauther et al., 1999). Both species are diurnal, are native to Madagascar, travel in groups, and are similar in adult size.

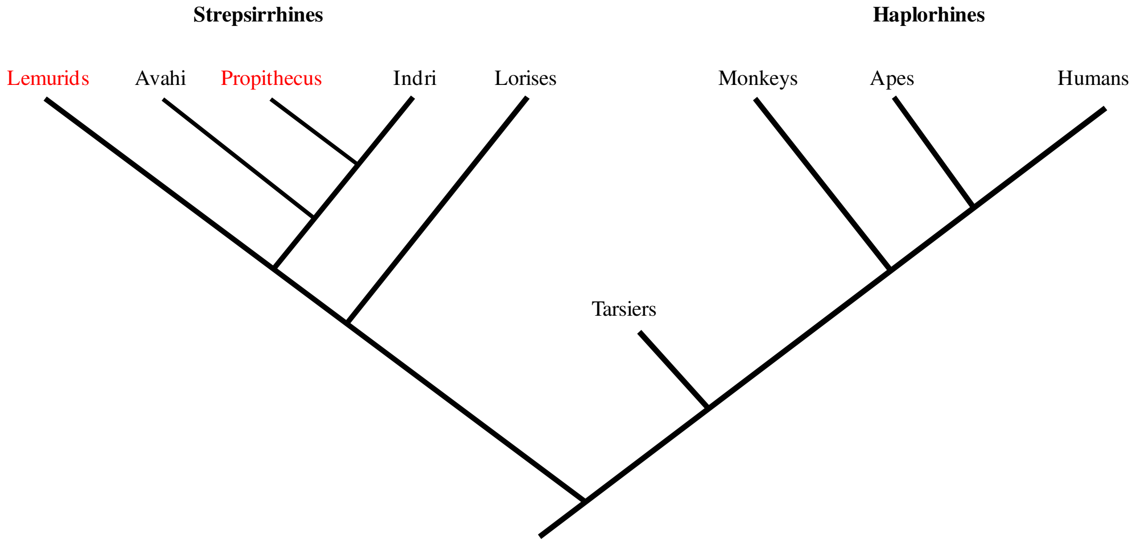

Figure 1.1: Phylogenetic organization of primates into haplorhines and strepsirrhines. *L. catta* and *P. v. coquereli* are members of the strepsirrhines.

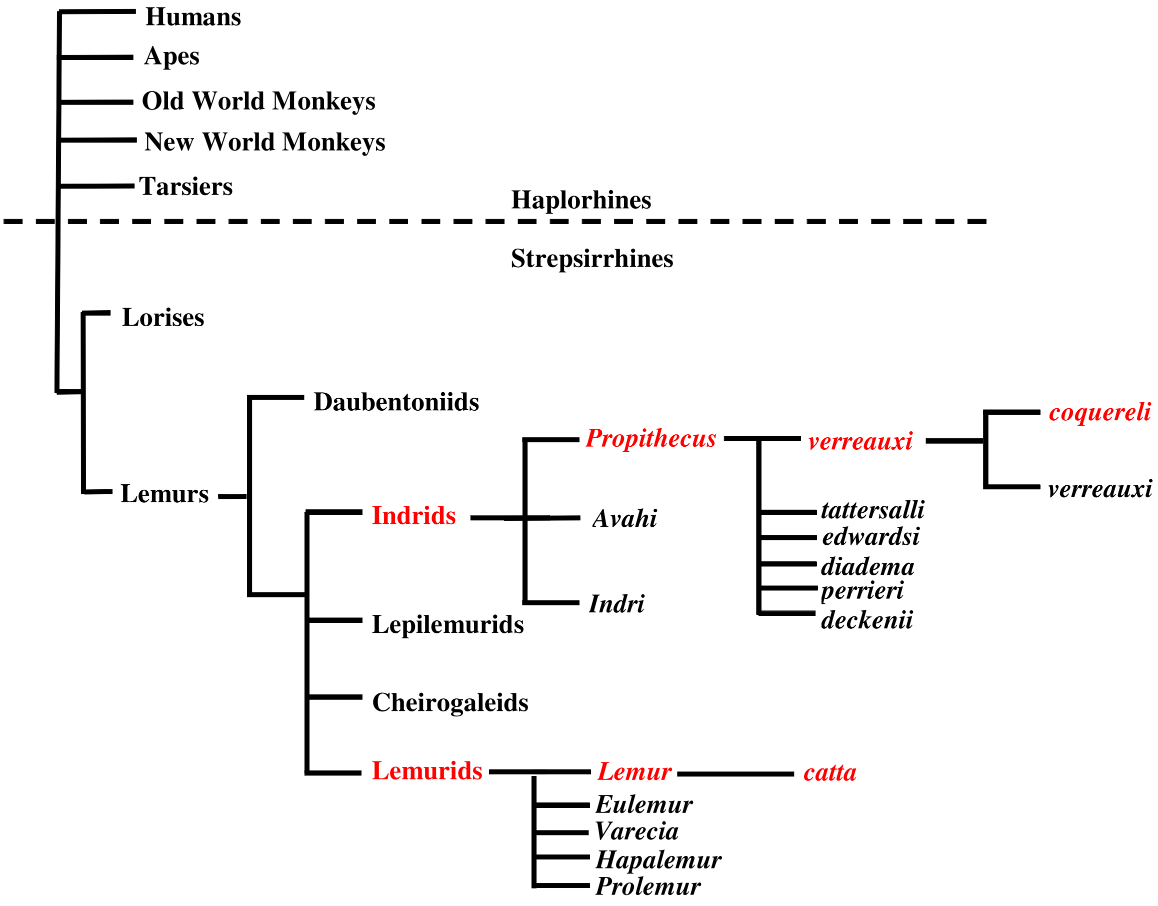

Figure 1.2: Division of primates and breakdown of extant lemur families by genetic distances (Yoder, 1997). The indrid family is specifically highlighted here as many intra-family/intra-genus comparisons are made in this study.

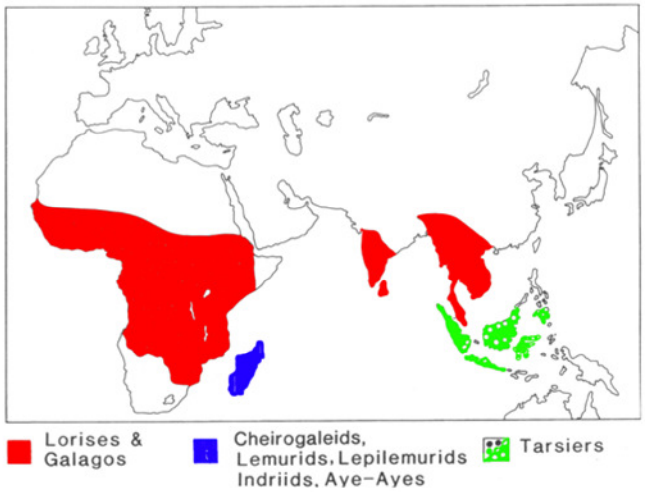

Figure 1.3: Distribution of extant strepsirrhines and tarsiers throughout the world. The lemurid and indrid families (in blue) are isolated to the island of Madagascar off the coast of Africa. Figure taken from Fleagle, 1999.

Because of Madagascar's highly seasonal environment which is prone to intra- and interannual droughts and thus unpredictable patterns of fruiting and flowering, both species have evolved adaptive strategies and specialized features to survive in stochastic environmental conditions (Morland, 1991; Hemmingway, 1995; Powzyk, 1997; Godfrey et al., 2004). Despite living under the same environmental pressures and sympatrically in many cases, these two species of lemur have evolved very different strategies for survival. *P. verreauxi*, a member of the indrid family, shows slow somatic growth, low maternal investment, and rapid dental growth while *L. catta* shows faster somatic growth, high maternal investment, and slower dental growth. Additionally, *P. verreauxi* is a folivore which relies on low maternal input and slow returns, while *L. catta* is a frugivore which relies on a strategy of high maternal input and fast returns (Godfrey et al., 2004). Perhaps the most impressive of these strategies is that *P. v. coquereli* undergo rapid dental growth that allow juveniles to be "ecological adult" at an early age, despite being undersized as juveniles. These life history strategies will be discussed in greater detail in the life history section of this introduction.

The two lemurs also differ largely in their locomotor repertoire and adult limb proportions. *P. verreauxi* is a highly arboreal, specialized vertical clinger and leaper (Napier and Walker, 1967; Demes et al., 1991, 1996, 1998, 1999), while *L. catta* is the most terrestrial of the extant strepsirrhines and uses a wide variety of locomotor types, most commonly quadrupedalism (Ward and Sussman, 1979; Terranova, 1996). As adults, *P. verreauxi* have unusually long lower limbs, while *L. catta* have more similar limb lengths (Lessertisseur and Jouffroy, 1973; Jouffroy, 1975). Adults specialized for

VCL are equipped with specialized morphology (i.e. long lower limbs compared to upper limbs) compared to quadrupeds or less specialized leapers, but the manner in which they attain this specialized morphology in comparison to species that are less specialized for VCL remains unclear.

Because selection acts on the entire life cycle of an animal, it is important to investigate the morphological and behavioral changes that occur early in development. These changes might be important components to each species' survival strategy that allow infant primates to survive to adulthood. In this study I will investigate these relationships as they apply to the postcranial skeleton and locomotor behavior. Specifically, I will investigate the relationship between limb growth allometry and locomotor changes in the earliest stages of locomotor development.

To provide the necessary background information for this study I will start by reviewing the following concepts for each species: adult locomotor behavior and morphology, life history, locomotor development, postcranial skeletal growth, postcranial muscle growth of leapers and quadrupeds, the ontogeny of locomotion in primates in general, and methodological considerations. This information will provide the necessary foundation under which predictions are made for this study.

Adult Locomotor Behavior and Morphology

Linking an organism's locomotor behavior with its underlying functional morphology allows for deeper insight into the selective pressures acting on an organism through ontogeny. *Propithecus verreauxi coquereli* is highly specialized for VCL, while *L. catta* is more generalized in its locomotion, most commonly using quadrupedalism (Napier and Walker, 1967; Ward and Sussman, 1979; Terranova, 1966). During VCL, *P.*

v. coquereli leap in a rapid ricochetal tree-to-tree manner, and have been seen to leap over 10 meters in linear distance (Petter, 1962 in Napier and Walker, 1967, Napier and Walker, 1967; Oxnard et al., 1981; Demes et al., 1996). *Propithecus* have also been observed to use a unique form of bipedal galloping when they are on the ground (Napier and Walker, 1967; Wunderlich and Schaum, 2007); however ground locomotion is much more prevalent in *L. catta*, which are the most terrestrial of all living strepsirrhines (Ward and Sussman, 1979; Gebo, 1987). *Lemur catta* spend about 30% of their overall time and 65% of their traveling time on the ground in the wild (Ward and Sussman, 1979). They travel mostly by quadrupedal walking and running, but also use leaping to cross any gaps in their path (Ward and Sussman, 1979; Gebo, 1987; Terranova, 1996). Engaging in locomotor behavior at great heights in the canopy entails high risks associated with falling, especially when using forms like VCL wherein animals are frequently in an aerial phase leaping from one vertical support to another.

Leaping is a gap-crossing movement in which the hindlimbs are used as the principle propulsors (Hunt et al., 1996). VCL occurs when an animal is initially resting in an orthograde clinging posture on a vertical substrate and uses its hindlimbs together to propel itself to another vertical substrate, landing by making contact with the hind feet first (Napier and Walker, 1967). Both *P. verreauxi* and *L. catta* use this type of VCL and land from jumps with the hindlimb making first contact (Demes *et al.*, 2005). VCL involves either thigh- or foot-powered lower limb propulsion, tail- or arm-initiated body rotation, and high take-off and landing forces associated with increased anteroposterior femoral rigidity (Demes and Gunther, 1989; Demes *et al.*, 1996, 1999).

Within strepsirrhine primates, interspecific size differences in adult morphology and VCL kinematics exist. All living indrids (*Propithecus*, *Avahi*, and *Indri*) are thigh-powered leapers, rather than tarsal-powered leapers; the feet contribute little or nothing to propulsion, as they do in other families of small-bodied leapers such as tarsiers and galagos (Gebo and Dagosto, 1988; Demes *et al.*, 1996). Indrids exhibit a number of morphological specializations for increasing leap distance and reducing the high skeletal loads associated with this unique form of leaping. Longer thigh length contributes to the potential for long acceleration times and thus greater take-off velocities during leaping (Demes *et al.*, 1996). Long acceleration times are advantageous to large-bodied leapers who have relatively smaller thigh musculature for producing leaping force. Consequently, large-bodied vertical clingers and leapers have elongated proximal hindlimb segments (femurs), where as small-bodied ones like galagos and tarsiers, which have relatively large thigh musculature for producing leaping force, have elongated distal segments (calcaneus) (Jouffroy and Lessertisseur, 1979), allowing for a fast take-off due to an increased load arm to lever arm ratio at the ankle. Small-bodied leapers (i.e. galagos and tarsiers) thus have disproportionately elongated feet (most specifically due to the elongated distal calcaneus and navicular) to maximize the time (and distance) to generate sufficient change in momentum for take-off (Demes and Gunther, 1989). In addition to long thigh length, *P. verreauxi* use high hip and knee angular excursions to increase the time for acceleration before take-off (Demes *et al.*, 1996). In smaller species that have shorter thigh length and higher muscle area to body mass ratios, hip and knee angular excursion and acceleration time might be expected to be less (Demes and Gunther, 1989).

Aerial body rotation is necessary in VCL to rotate the body 180º to bring the hindlimbs into landing position (Demes et al., 1996). Larger indrids, like *P. v. coquereli,* use their arms to enhance take-off force and initiate body rotation while airborne, while smaller leapers, like tarsiers, rely more on their tails (Niemitz, 1984; Peters and Preuschoft, 1984; Demes *et al.*, 1996). Larger VCL species exhibit reduced tail size, and the largest member of the Indrids, *Indri*, has almost lost its tail completely (Demes et al., 1996).

Leaping has also been associated with high femoral and reduced humeral rigidity, especially in the sagittal plane (Connour et al., 2000; Demes and Jungers, 1993). This high femoral rigidity is likely a response to the heavy loads placed on the hindlimbs of leapers (Connour et al, 2000). Data from large leapers, such as indrids, show that peak take-off forces can reach up to 10 times body weight, whereas landing forces reach around 7 times body weight (Demes et al., 1995). Larger-bodied indrids leap with lower take-off and landing forces over a longer amount of time than smaller-bodied indrids which use higher take-off and landing forces over a shorter amount of time (Demes *et al*., 1999; Demes and Gunther, 1989). Within *P. v. coquereli,* yearlings tend to exert relatively higher peak take-off and landing forces than adults (Demes et al., 1999). *Lemur catta* generate and absorb higher forces in leaping than the more specialized *P. v. coquereli* (Demes et al., 1999).

During quadrupedal locomotion, the torso is in a pronograde position (parallel to the ground) on top of supports angled at < 45º from the horizontal plane, and all four limbs typically contact the support in a particular sequence (Hunt et al., 1996). Quadrupeds are known for having more similar limb lengths than leapers or suspensory species and contrary to other non-primate mammals, primate quadrupeds generally support more weight and exhibit higher propulsive forces on their hindlimbs than their forelimbs (Kimura et al., 1979; Reynolds, 1985; Demes et al., 1994; Polk et al., 2000; Hanna et al., 2006). This may be an adaptation to relieve stress on the forelimbs, allowing them to be more mobile (Demes et al., 1994; Schmitt and Hanna, 2004).

Life History

Both *L. catta* and *P. v. coquereli* are found in Madagascar, an island with variable climates with highly unpredictable rainfall (Dewar and Richard, 2007). Such unpredictable rainfall has significant effects not only on the island's fauna, but also on its flora, where fruiting and flowering are confined to a very narrow season of the year (Dewar and Richard, 2007). Despite living under these same environmental pressures, these two species of lemur have evolved very different strategies for survival. *P. verreauxi* is highly folivorous, showing slow somatic growth, rapid dental growth, and low maternal investment, while *L. catta* is mere frugivorous, showing faster somatic growth, slower dental growth, and higher maternal investment than *P. verreauxi* (Godfrey et al., 2004; Richard et al., 2002). No sexual dimorphism exists in wild adult *P. v. verreauxi*, while body weight, leg length, hindlimb length, and forefoot length are significantly greater in wild adult *P. v. coquereli* females than males (Kappeler, 1990; Ravosa et al., 1993). Captive *L. catta* also lack sexual dimorphism in body size (Kappeler, 1990).

Lemurids attain asymptotic adult body mass values more rapidly than indrids of equal adult body mass (Godfrey *et al.*, 2004). Maximum body mass in wild *P. v. verreauxi* is 2.8 to 2.92 kg and is not achieved until 8 years of age (Richard et al., 2002; Lawler, 2006), while captive *P. v. coquereli* reach 3.9 kg by 4.5 years old (Zehr, personal communication; Table 1.1). Maximum body mass in wild *L. catta* is 2.25 kg which is reached by 3 years of age, while captive *L. catta* reach 2.5 kg by 2.5 to 3 years (Sussman, 1991; Koyama et al., 2008; Sarah Zehr, personal communication; Table 1.1). In captivity, postnatal growth rates from birth to weaning average 6.00 g/day in *P. v. coquereli* and 6.15 g/day in *L. catta* (Godfrey *et al.*, 2004; Sarah Zehr, personal communication; Table 1.1). Taking into consideration the adult sizes both animals must reach, *L. catta* are on a much more rapid postnatal growth rate when compared to *P. v. coquereli*.

Table 1.1: Life history comparison of *P. verreauxi* and *L. catta* (Petter-Rousseaux, 1962; Richard, 1976; Richard et al., 2002; Ross, 2001; Van Horn and Eaton, 1979; Sussman, 1991; Godfrey et al., 2004; Garbutt, 1999; Sarah Zehr, personal communication). The abbreviation (na) indicates subject matter was not found in literature.

	Avg. Adult Mass (Age Achieved)	**Postnatal Growth Rate**	**Avg. Litter Size**	**Parental Care**	**Gestation**	**Age at Weaning (Mass)**	**Age at Sexual Maturity**
***P. v. verreauxi* (wild)**	2.92 kg (8 Years)	na	1	Ride	4.3-5 Months	na	6-8 Years
***P. v. coquereli* (captive)**	4.0 kg (4.5 Years)	6.0 g/day	1	Ride	5.2-5.6 Months	5-6 Months (1.16 kg)	2.5-3 Years
***L. catta* (wild)**	2.25 kg (3 Years)	na	1-1.25	Ride	4-4.5 Months	na	3-4 Years
***L. catta* (captive)**	2.5 kg (2.5-3 Years)	6.15 g/day	1.25	Ride	4.3-4.5 Months	4-5 Months (0.72 kg)	1.5-2 Years

Although *L. catta* gains body mass more rapidly than *P. verreauxi* through ontogeny, dental growth is much more precocial in *P. verreauxi* and all the indrids (Godfrey et al., 2004). It is common for folivorous (leaf-eating) lemurs, like *P. verreauxi*, to grow and mature more slowly, while still showing faster dental growth than like-sized frugivorous (fruit-eating) lemurs like *L. catta* (Janson and van Schaik, 1993; Samonds et al., 1999; Godfrey *et al.*, 2001, 2004; Schwartz et al., 2002).

However, indrids have extremely precocial dental development that has been associated with specializations for survival in a highly seasonal environment where young indrids need to be able to eat the same food as adults at a very early age (Janson and van Schaik, 1993; Samonds et al., 1999; Schwartz et al., 2002; Godfrey *et al.*, 2004). There is evidence that all indrids are born with their milk teeth erupted and their permanent molars open, whereas lemurids are born with only the anteriormost milk teeth erupting and molar formation just beginning (Schwartz et al., 2002). Because this precocial dental development allows for the early consumption of adult food, indrids have been coined as becoming "ecological adults" at a young age (Godfrey et al., 2004).

Adult female lemurids exhibit a "higher investment" strategy for caring for their young than do adult female indrids (Godfrey et al., 2004). Maternal investment is a reflection of litter size, pre- and postnatal growth rates, and time of weaning. *P. v. coquereli* typically give birth to one infant at a time (Table 1.1; Jolly, 1966; Klopfer and Klopfer, 1970; Richard, 1976; Van Horn and Eaton, 1979; Koyama et al., 2001). *Lemur catta* give birth to twins approximately 25% and triplets less than 1% of the time in captivity, while multiple births are rarely seen in the wild (Table 1.1; Van Horn and Eaton, 1979; Sussman, 1991; Pereira and Weiss, 1991; Gould et al., 2003; DLC Records). Both species carry their infants rather than parking them in a tree or nest as some lemur species do (Table 1.1; Kappeler, 1998). Infants are fully weaned at 4 to 5 months (0.72 kg) in *L. catta* and 5 to 6 months (1.16 kg) in *P. v. coquereli* (Table 1.1; Klopfer and Boskoff, 1979; Gould, 1990; Meyers and Wright, 1993; Sarah Zehr, personal communication). Sexual maturity is reached around 1.5 to 2 years of age in

L. catta, however wild females tend to give birth for the first time at 3 or 4 years of age (Table 1.1; Jolly, 1966; Van Horn and Eaton, 1979; Godfrey et al., 2004). *P. v. coquereli* are sexually mature at 2.5 to 3 years of age, however wild adult females do not give birth for the first time until 6 to 8 years of age (Table 1.1; Richard et al., 2002; Godfrey et al., 2004).

L. catta are considered to show high maternal investment because they often give birth to twins and even triplets in the wild, which grow at relatively fast rates in terms of body mass compared to their adult size (Table 1.1). *P. verreauxi* are considered to have lower maternal investment than lemurids because they only give birth to a single offspring which shows slower pre- and postnatal growth rates compared to *L. catta* (Jolly, 1966; Richard, 1976; Godfrey et al., 2004; Table 1.1). While the fact that *P. v. coquereli* infants are weaned later than *L. catta* infants may suggest higher maternal investment, these *P. v. coquereli* infants are dentally precocious and equipped with a full set of teeth at the time of birth (Schwartz et al., 2002; Godfrey et al., 2004). Solid foods are tasted exceptionally early in indrids, observed to occur as early as 2 weeks of age in *P. v. verreauxi* (Richard, 1976). This early dental eruption likely aids in the consumption of adult-like food before weaning, contributing an additional source of nutrition other than the mother's milk.

L. catta seem to have evolved a "high maternal input, fast returns" strategy whereby litter sizes are larger and growing faster (Godfrey et al., 2004). Alternatively, indrids like *P. v. coquereli* seem to have evolved a "low maternal input, slow returns" strategy in which smaller litter sizes are produced, postnatal growth is slow, and precocious dental growth occurs making them "ecological adults" at an early age

(Godfrey et al., 2004). Support for the validity of these differing strategies stems from data collected during a prolonged drought period from 1991-1992. During the drought, infant mortality rose in both species, however lactating female mortality was much higher in *L. catta*, than *P. v. verreauxi* (Godfrey et al., 2004). After the habitat recovered, *L. catta* females rapidly reproduced to replenish the population while *P. v. verreauxi* continued to slowly produce low-cost offspring (Richard et al., 2002; Godfrey et al., 2004).

Locomotor Development

Propithecus verreauxi coquereli and *L. catta* mothers carry their infants ventrally at first, and then dorsally; infants are immediately capable of clinging to the mother's fur and climb on them actively (Jolly, 1966; Klopfer, 1974; Eaglen & Boskoff, 1978; Sussman, 1991; Gould 1990). Locomotor independence milestones can be seen at different times in the two species' development; however *P. v. coquereli* achieve complete locomotor independence around the same time but at different body weight relative to adults as *L. catta* (Eaglen and Boskoff, 1978; Gould 1990; Table 1.2).

The first transitions from ventral to dorsal riding occur at 2 weeks of age in captive *P. v. coquereli* (3 to 7 weeks in wild *P. v. verreauxi),* regularly occurring around 5 weeks in captive *P. v. coquereli* (7 to 11 weeks in wild *P. v. verreauxi)* (Jolly, 1966; Eaglen and Boskoff, 1978; Klopfer and Boskoff, 1979; Table 1.2). First attempts to locomote are described as crawling or climbing, followed by branch hanging, short leaping, and hopping in captive *P. v. coquereli* (Eaglen and Boskoff, 1978). *Propithecus verreauxi* infants move increasing distances from their mothers as they develop. First movement away from their mother occurs at 2 weeks in wild *P. verreauxi* (4 weeks in captive *P. v. coquereli*); at 8 to 9 weeks they are regularly moving greater than 1 meter off their mother, making short leaps, followed by longer ones at 11 weeks (Jolly, 1966; Richard, 1976; Eaglen and Boskoff, 1978; Table 1.2). Mothers carry juvenile *P. verreauxi* intermittently for up to six months, at which time the juveniles are only in contact with their mother for 27 to 37% of the time and are weaned (Jolly, 1966; Richard, 1976; Godfrey *et al.*, 2004; Table 1.2).

Table 1.2: Locomotor development (in weeks) in captive and wild *P. verreauxi* and *L. catta* (Jolly, 1966; Klopfer and Klopfer, 1970; Klopfer and Boskoff, 1976, Richard; 1976; Eaglen and Boskoff, 1978; Gould, 1990; Sarah Zehr, personal communication). Trends show captive infants typically start development earlier than wild infants and *L. catta* to start earlier than *P. v. coquereli*. The abbreviation (na) indicates subject matter was not found in literature.

		First Seen Dorsal Riding	**Regularly Dorsal Riding**	**First Movement off Mother**	**Regular Movement (>1 m) off Mother**	**Complete Locomotor Independence**
P. verreauxi	***Wild***	3-4, 7	7, 11	2	8	>24 (1.7 kg)
	Captive	2	5	4	8-9	na
L. catta	***Wild***	<1	1	2	3-4	>20 (1.1 kg)
	Captive	<1	1	2	4	na

Lemur catta are born well developed with eyes open and capable of clinging to the mother's abdomen (Jolly, 1966; Klopfer and Boskoff, 1979). *Lemur catta* show first signs of locomotor independence earlier than other lemurids (Gould, 1990). Regular transitions from ventral to dorsal clinging occur by the first week of age, which is much earlier than in *P. verreauxi* (Jolly, 1966; Klopfer and Boskoff, 1979; Gould, 1990; Table 1.2). *Lemur catta* begin to leave their mothers regularly at 3 to 4 weeks as they are off their mother 16% of the time (Gould, 1990; Table 1.2). At 16 weeks infants still occasionally nurse and are carried dorsally but are off of their mothers 81% of the time (Gould, 1990). At 20 weeks, *L. catta* infants spent only 20% of waking time in contact with their mother (Klopfer and Boskoff, 1979; Table 1.2).

Both species show differential timing of locomotor independence milestones up until 10 weeks of age. *L. catta* start development earlier than *P. v. coquereli*, and captive infants of both species seem to start development earlier than wild infants of both species. Locomotor independence estimates were not found for *L. catta*, although in *P. v. coquereli* it is believed to occur around 24 weeks.

For the purposes of clarity and making comparisons in this study, *P. v. coquereli* and *L. catta* infants that are fully dependent on their mother riding dorsally or ventrally nearly all day are labeled as "dependent infants" and range from 0 to 6 weeks in age (Table 1.3). Infant *P. v. coquereli* and *L. catta* that are 6 to 24 weeks age are labeled as "transitional infants" as they are displaying frequent locomotion off of their mother, but still dorsally riding a large amount of the day (Table 1.3). At 6 weeks, wild infants were off their mother 33% of the time in *L. catta* and at least 30% of the time in *P. v. coquereli* (Gould, 1990; Richard, 1976). Additional records by DLC staff of captive DLC animals confirm the beginning of independent locomotion at 6 weeks of age in both species (Sarah Zehr, personal communication). Infant *P. v. coquereli* and *L. catta* that are fully independent of their mother in terms of locomotion and weaning are labeled "independent infants" and range from 24 to 52 weeks in age (Table 1.3). Lemurs that are 52 to 104 weeks in age are labeled as yearlings (Table 1.3; Lawler, 2006).

Table 1.3: Locomotor categories used in this study.

Category	Age (weeks)
Dependent	0-6
Transitional	6-24
Independent	24-52
Yearling	52-104

Skeletal Growth

Postcranial skeletal size in juvenile *P. verreauxi* lags well behind *L. catta* at standardized stages of dental development (King *et al.*, 2001), which may be partially a result of *P. verreauxi*'s precocial dental growth. In other words, *P. verreauxi* show relatively slower somatic growth than *L. catta* but their dental development is relatively faster, thus both species do not achieve dental and somatic developmental milestones at the same time (Godfrey et al., 2004). Evidence suggests it takes 5 years for *P. verreauxi* to reach adult skeletal size and adult body mass is not attained until 8 years of age (Lawler, 2006). In *Propithecus edwardsi*, slow growth is also observed as body mass increases slower than segment lengths and adult skeletal lengths are obtained at 2 years of age while adult body mass is not obtained until 6 years of age (King et al., 2011). Gaining a better understanding of how *P. v. verreauxi* and *L. catta* obtain these adult lengths through ontogeny may provide a greater understanding of the significance of locomotor performance through ontogeny and to the adaptive strategies adopted by indrids versus lemurids.

A cross-sectional study of sifakas' postcranial ontogeny which used measurements from wild adult and non-adult *P. tattersalli and P. diadema edwardsi* (supplemented with wild adult *P. v. coquereli* and *P. v. verreauxi)* showed primarily isometric trends ranging from slightly negative to slightly positive allometry in limb lengths with respect to body mass (Ravosa et al., 1993). Tail and foot lengths increased with significant positive and negative allometry, respectively, relative to body mass (Ravosa et al., 1993). This cross-sectional study by Ravosa (1993) included sifakas ranging in age from birth to over 5 years, however the sample was only comprised of one animal from 0-6 months of age. Another cross-sectional, ontogenetic study of wild *P. v. verreauxi* yearlings (1-2 year olds) and adults also found upper and lower limb lengths to grow isometrically relative to body mass, although hand and foot lengths increased with significant negative allometry through ontogeny relative to body mass (Lawler, 2006). Thus, the only instances of significant negative allometric bone growth in *P. verreauxi* are isolated to the hands and feet (Ravosa et al., 1993; Lawler, 2006). This means that infants have relatively larger hands and feet at infancy that grow at a slower rate relative to body mass. This likely enables yearling *P. v. verreauxi* to use "adult-sized" substrates (Lawler, 2006). These morphological data are supported by behavioral evidence showing no differences in locomotor behaviors or substrate use between yearlings and adults (Lawler, 2006). Evidence from yearling and adult *P. v. verreauxi* suggest that this negative allometric growth of the hands and feet during ontogeny has been maintained through selection (Lawler, 2006). In contrast to the previous cross-sectional studies, preliminary evidence from a longitudinal study shows all limb segment lengths increase with positive allometry from 0 to 1 year of age in captive *P. v. coquereli* (Wunderlich and Kivell, 2009; Wunderlich et al., 2011).

Intermembral index (IMI) is another common measurement used to compare relative lengths of fore- and hindlimbs during growth and across species. IMI is a ratio of upper limb (humerus and radius) to lower limb (tibia and femur) length, expressed as a percentage. Leaping primates, like *Propithecus*, show more lengthened and strengthened hindlimbs when compared to quadrupedal species like *L. catta* (Oxnard *et al.*, 1981). *Propithecus verreauxi coquereli* and all other indrids are noted for relatively long hindlimbs compared to their forelimbs, displaying a characteristically low adult IMI of 62, which is common in leaping primates (Napier and Walker, 1967; Jouffroy and Lessertisseur, 1979; Ravosa *et al.*, 1993, Table 1.4). The IMI for adult *L. catta* is 67.3, which is characteristic of quadrupedal species (Napier and Walker, 1967; Jouffroy and Lessertisseur, 1979; Table 1.4). The higher IMI in *L. catta* represents more equal hindlimb and forelimb lengths than in *P. v. coquereli*.

Table 1.4: Adult intermembral indices (IMIs) and locomotor behavior for *L. catta* and *P. v. coquereli*. All indices from Jouffroy and Lessertisseur (1979) and Ravosa et al. (1993).

Species	Locomotion Preference	IMI
P. v. coquereli	Vertical Clinging & Leaping, Some Bipedalism	62.0
L. catta	Quadrupedalism, Leaping	67.3

Throughout development, IMI generally decreases with increasing body mass in primates (Schaefer and Nash, 2007), suggesting that upper and lower limb lengths are not growing at the same rates relative to body mass. The only instances of increasing IMI in primates are seen in those whose adult values are above 100, suggesting that IMI moves away from equality throughout ontogeny, as infants are born with more similar limb lengths (Schaefer and Nash, 2007). Evidence of this change in limb proportions through ontogeny was supported in *Galago*, where the IMIs of infants at the initiation of locomotor independence were significantly higher than adult IMI values (Schaefer and Nash, 2007). This presence of higher IMIs early in ontogeny could facilitate a longer upper limb length to increase distance for grasping, which would be beneficial for clinging to their mother during frequent and forceful bouts of locomotion (Ravosa et al., 1993). In both *P. diadema edwardsi* and *P. tattersalli* ontogenetic patterns provide further evidence of a slightly decreasing IMI with increasing body mass (71 to 67 and 67 to 65, respectively) (Rasvosa et al., 1993). This result is contrary, however, to evidence that limb proportions in infant *Propithecus* are thought to be determined prenatally because of only slightly allometric growth (Ravosa *et al.*, 1993).

Interspecially, bone geometry is altered in larger animals as they typically have more robust bones than smaller animals to provide the strength necessary to support their increased body mass (Alexander, 1979; McMahon, 1984; Schmidt-Nielsen, 1984). In indrids (wild adult *Indri indri, P. diadema, P. verreauxi, P. tattersalli,* and *Avahi laniger*) adult long bone cross-sectional dimensions scale close to isometry with respect to body mass (Demes *et al.*, 1991). Ontogenetic studies of non-primates (i.e. emu, goat, oxen, and rabbit) found limb bone cross-sectional dimensions, and thus long bone strength, to exhibit negative allometry during growth with respect to body mass (Carrier, 1983; Heinrich *et al.*, 1999; Lammers and German, 2002; Main and Biewener, 2004). This negative allometry has also been observed in primates, where *Cebus* humeral and femoral safety factors (SF) (limb bone strength relative to the forces experienced) peak at birth, and rapidly decline during postnatal growth due to strong positive allometry in humeral and femoral length combined with isometry of bone strength (Young and Fernandez, 2009; Young et al., 2010). This indicates that young mammals may be born with relatively robust bones for their size, perhaps an adaptation for injury aversion during the initiation of locomotor independence, a time when falling is frequent (Young and Fernandez, 2009; Young et al., 2010). This also highlights once again that interspecific and ontogenetic allometric patterns are not necessarily similar or related.

Postcranial Muscle Growth

The greater the cross-sectional area of muscle, the greater force it can generate. In isometric growth, muscle cross-sectional area, which is proportional to the square of the linear measurement (x^2), does not increase at the same rate as body mass, which is proportional to the cube of the linear measurement (x^3). Consequently, larger animals will have less muscle force per unit mass than smaller animals if muscles growth is isometric (Demes *et al.*, 1996; Young, 2005). If locomotor functional equivalence is to be achieved through ontogeny, either muscle mass should increase with positive allometry (Hurov, 1991; Atzeva *et al.*, 2007), and/or muscle mechanical advantage should increase during growth (Main and Biewener, 2004; Young, 2005; Main and Biewener, 2006). Mechanical advantage has been observed to increase with increasing body size across and within primate and non-primate taxa (Main and Biewener, 2004, 2006; Young, 2005). Ratios of muscle mass over body mass in captive *P. v. coquereli* were found to be consistently smaller in neonates than in adults, suggesting neonates are relatively poorly muscled and muscle mass must increase with positive allometry during growth (Atzeva *et al.*, 2007). In *Propithecus*, limb circumferences (which may be an indicator of muscle cross-sectional area) increase with positive allometry through ontogeny, being highest in the thigh (Ravosa et al., 1993). This suggests that infants are in fact poorly muscled and not overbuilt at birth.

Muscle group ratios of adult strepsirrhines are specialized according to type of locomotion (Demes *et al*., 1998). The proportion of hindlimb propulsive musculature in specialized leapers, like *P. v. coquereli*, is greater than in generalized quadrupedal lemurs like *L. catta* (Demes *et al*., 1998). Quadriceps muscles in *P. v. coquereli* are enlarged, whereas in quadrupedal species, the quadriceps are smaller, compensated for by larger hamstring muscles (Demes *et al*., 1998). Leaping neonates also have much larger quadriceps muscles than quadruped neonates before the onset of locomotion (Atzeva *et al*., 2007). This similarity in the distribution of muscle mass between fore- and hindlimbs through ontogeny suggests that young strepsirrhines may be on a growth trajectory towards achieving the morphology necessary for adult locomotion.

Evidence also exists, however, showing that infants may have different muscle proportions than adults. Distal flexors and extensors are important for grasping supports, thus a larger distal mass of these muscles suggests a greater reliance on arboreal supports (Raichlen, 2004; Hanna and Schmitt, 2011). In studies of quadrupedal macaques and baboons, distribution of limb mass was found to be more distally concentrated in infants, which are clinging to their mother, whereas it was more proximally concentrated in adults (Grand, 1981; Turnquist and Wells, 1994; Raichlen, 2005a, 2006). This shift from distal to proximal limb mass concentration may be an important indicator of the shift from dependent to independent locomotion (Raichlen, 2005b). This alternatively supports the idea that young primates seem to be adapted to early locomotor behaviors.

Ontogeny of Locomotion in Primates

While numerous studies address primate locomotion and positional behavior, studies that examine positional behavior from an ontogenetic perspective are limited, particularly in strepsirrhines. The most important findings in strepsirrhines thus far have indicated that wild *P. v. verreauxi* yearlings and adults use similar locomotor types despite differences in body size (Lawler, 2006). More specifically, climbing, leaping, VCL, and quadrupedalism frequencies were not significantly different between yearlings and adults (Lawler, 2006). The only significant differences occured in the orientation of supports used; yearlings utilized more obliquely oriented supports, where adults used more horizontally oriented supports (Lawler, 2006). The similarity in locomotion and support use between yearlings and adults may be related to negative allometric growth seen in hands and feet; yearlings use their relatively larger hands and feet to traverse similarly sized supports as adults (Lawler, 2006).

Some of the first studies comparing juvenile to adult locomotion illustrated that major changes in locomotor behavior do occur through ontogeny (Doran, 1992, 1997). A study of capuchin monkeys (arboreal quadrupeds) shows *Cebus apella* juveniles (aged 6 months to 6 years) show a greater percent of climbing and leaping compared to adults which spent more time walking (Wright, 2005). Macaques also show greater amounts of climbing and leaping in younger animals than adults, and younger macaques are more arboreal than adults (Rawlins, 1976; Wells and Turnquist, 2001). Infant macaques employ a lower center of gravity and more widely abducted limbs than adults, likely to broaden their contact with a support (Wells and Turnquist, 2001).

Despite these ontogenetic studies, few studies exist that compare changes in locomotor behavior during early development, when locomotor independence is first occurring.

Methodological Considerations

Studies of ontogeny typically use cross-sectional data, which is collected from many individuals of different ages to piece together the growth trajectory (Carrier 1983, Ravosa et al., 1993; Lawler, 2006). These studies are extremely valuable and commonly found in the literature due to their ease in data collection. The disadvantage of cross-sectional studies, however, is that they may not answer questions about details of growth as well as longitudinal studies, which measure the same individuals repeatedly over time. Compared to longitudinal data, cross-sectional data may not account for the variation that exists within individuals and as a result, misrepresent the overall growth trend of the species (Fiorello and German, 1997). For example, Figure 1.4 illustrates that when growth variation occurs between individuals of the same species, a cross-sectional study can easily misrepresent the true growth trajectory of the species.

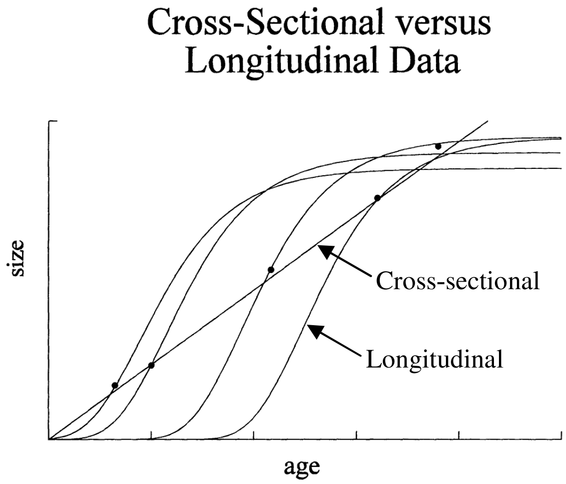

Figure 1.4: A comparison of longitudinal and cross-sectional growth data. Individual variation is ignored by using cross-sectional data. As a result, the overall growth trend of the species may be misrepresented. Figure taken from Fiorello and German, 1997.

To date, only cross-sectional analysis of skeletal growth of *Propithecus* and preliminary longitudinal growth data on *P. v. coquereli* have been collected from birth to one year of age (Ravosa et al., 1993; Wunderlich and Kivell, 2009; Wunderlich et al., 2011), the period when many lemurs are first moving independently and experiencing greatest changes in morphology. In addition, few if any longitudinal studies of lemurids exist that simultaneously compare locomotor behavior to the underlying morphology.

Overall Objectives and Predictions

In order for transitional infants to keep up and travel independently with groups comprised of yearlings and adults, transitional infants should either use similar locomotor behavior as yearlings and adults, facilitated by ontogenetic differences in postcranial morphology, or instead use different locomotor behaviors. These abilities should additionally reflect each species' strategy for survival. Many studies have revealed morphological differences between juveniles and adults, however only a few exist that evaluate differences between transitional infant and yearling morphology and locomotion. I will examine the relationships among growth, morphology, and locomotor behavior. First I will compare differences in locomotor behavior and support use between species (*L. catta* and *P. v. coquereli*) and age classes (transitional infant and yearling). Second, I will compare patterns of limb growth in *P. v. coquereli* and *L. catta* using four different age categories relevant to important locomotor behavior milestones through ontogeny (0 to 6 weeks, 6 to 24 weeks, 24 to 52 weeks, and 52 to 104 weeks). With these results I will compare changes in postcranial morphology to locomotor behavior during the transition from infant to adult in order to better understand lemurid and indrid postcranial growth strategies in the context of their different life history and dental growth patterns.

Locomotor Behavior and Substrate Use

My null hypothesis for locomotor behavior and substrate use is that they will be similar between infants and yearlings of both species. I specifically predict similar frequencies of locomotor behaviors and support use in transitional infants and yearlings of each species. This prediction is based on the fact that yearling and adult *P. verreauxi* exhibit similar locomotor behavior and support use despite differences in body size in the wild (Lawler, 2006). This similar locomotor behavior is likely the only way in which younger animals, which are absolutely smaller in size, are able to keep up with a group of adults, especially those using complex forms of locomotion like leaping. Additionally, most primates are born with relatively large hands and feet which may aide in efficient gripping and grasping (Jungers and Fleagle, 1980; Lawler, 2006; Lemelin and Jungers, 2007). Having relatively large hands and feet at birth would allow for the use of relatively large supports by infants as they are travelling the same arboreal pathways as yearlings and adults (Jungers and Fleagle, 1980). This may also allow infants to exhibit similar overall locomotion and support use despite differences in body size (Lawler, 2006). I also predict that between species, the more terrestrial transitional infant and yearling *L. catta* will show greater frequencies of terrestrial quadrupedal locomotion than transitional infant and yearling *P. v. coquereli*, which will have greater frequencies of arboreal VCL and leaping locomotion.

Skeletal Morphology through Ontogeny

My null hypothesis for postcranial growth is that it will be consistent throughout ontogeny. I specifically predict that limb lengths and limb muscle cross-sectional areas will all grow with similar allometric coefficients through ontogeny, regardless of the locomotor age category examined. This would indicate that infants are born with adult-like proportions, and limb segment lengths and muscle cross-sectional areas are increasing consistently with respect to one another through ontogeny. I make these predictions for three reasons. First, isometric growth was observed in all limb segment lengths from 0 to 5+ years of age in cross-sectional growth studies of *P. verreauxi* (Ravosa et al., 1993). This indicates that all limb segments are growing at similar rates to each other in comparison to body mass. Second, preliminary evidence from 0-1 year old *P. v. coquereli,* a much younger study sample, shows positive allometric limb growth from 0-1 year in all limb segment lengths of *P. v. coquereli,* indicating that limb segments are still growing similarly to each other, but with greater allometric coefficients than seen in Ravosa (1993) (Wunderlich and Kivell, 2009; Wunderlich et al., 2011). Third, volumetric measurements increase faster than linear or squared measurements. This means that if infants are not born with disproportionately long limb lengths or high muscle cross-sectional areas, they must grow with positive allometry in order for functional equivalence to be reached.

Between species I hypothesize that the differing life history strategies of each species will reflect postcranial growth differences. Therefore, I predict to see overall greater positive allometry early in development in *L. catta* than *P. v. coquereli*. *L. catta* have overall higher maternal investment and thus faster overall somatic growth than *P.*

verreauxi which have lower maternal investment and relatively slower overall somatic growth (Godfrey et al., 2004). If *L. catta* is increasing body mass much faster through ontogeny and is receiving higher maternal input, it may have the ability to increase limb segment lengths and cross-sectional areas relatively faster as well. *P. v. coquereli* infants on the other hand which have lower maternal input and slower growth in terms of body mass will correspondingly show relatively slower postcranial growth than *L. catta* through ontogeny. Additionally, *L. catta* is a frugivore which means that after weaning, it is consuming a high energy diet, seemingly more capable of producing relatively more rapid postcranial growth than the folivorous *P. v. coquereli* which is consuming a lower energy diet.

Chapter 2

Materials and Methods

Location and Subjects

All data were collected at the Duke Lemur Center (DLC) in Durham, North Carolina, on two species of lemurs: *Lemur catta* and *Propithecus verreauxi coquereli*. Morphological data were collected from 13 animals between the months of December 2009 and March 2011 (Table 2.1). Locomotor data were collected between the months of May and August 2010 in large outdoor free-ranging enclosures in the Duke Forest on six of the thirteen lemurs studied (Table 2.1). Group sizes were variable throughout the study ranging from 6 to 10 in *L. catta* and 4 to 5 in *P. v. coquereli*. For this study, infants were defined as any animal less than a year old and yearlings were referred to as any animal between 1 and 2 years of age. Adults were defined as reproductively mature animals, usually greater than 1.5 to 2 years of age in *L. catta* and 2.5 to 3 years of age in *P. v. coquereli*.

Behavioral data were only collected when animals were in the large outdoor free-ranging enclosures located in the Duke Forest in Durham, NC. The enclosures were comprised mostly of deciduous forest ranging from 1.4 to 3.3 hectares in area simulating their natural habitat and providing ample space for the animals to move freely. Enclosures had a variety of forest densities including some areas rich in trees and others that are more sparsely distributed, allowing observation of both arboreal and terrestrial travel. Not all infants and yearlings were free-ranging, limiting the behavioral study to 4 *L. catta* (2 infants, 2 yearlings) and 2 *P.v. coquereli* (1 infant, 1 yearling) (Table 2.1). Because animals had access to both indoor and outdoor enclosures *ad libitum*, data were only collected when the animals were outdoors. Data were collected on each animal for 4 to 12 days throughout the study period.

Table 2.1: Animals used in each component of the study including species, sex, birth date, and behavioral study site. A (*) indicates that morphology data are from Wunderlich et al., 2011. (*L. catta*=*Lemur catta*, PVC=*Propithecus verreauxi coquereli*, NHE=Natural Habitat Enclosure.)

Name	Species	Sex	Date of Birth	Behavior Study Site
Limerick	LC	M	3/17/2009	NHE2
Hibernia	LC	F	3/17/2009	NHE2
Alastor	LC	M	7/8/2009	
Crystal Light	LC	F	3/20/2010	NHE9
Capri Sun	LC	F	3/20/2010	
Edelweiss	LC	F	3/25/2010	
Schweppes	LC	M	4/26/2010	NHE9
Johan	LC	M	5/3/2010	
Conrad	PVC	M	12/31/2008	
Pompeiia	PVC	F	2/14/2009	NHE9
Rupert	PVC	M	12/15/2009	
Willhemena	PVC	F	12/25/2009	
Romulus	PVC	M	2/3/2010	NHE7
Charlemagne*	PVC	M	1/2/2007	
Matilda*	PVC	F	1/21/2007	
Irene*	PVC	F	1/27/2007	
Agripinna*	PVC	F	2/7/2007	
Gaius*	PVC	M	1/3/2008	
Martin*	PVC	M	1/25/2008	

Morphological Data Collection

Body mass, limb segment lengths and circumferences, and trunk and tail length were measured every two weeks during the first year of life and every month for the second year in both *Lemur catta* and *Propithecus verreauxi coquereli* in accordance with Wunderlich et al. (2011, Table 2.2). Lengths and circumferences were measured to the nearest 0.1 cm while body masses were measured to the nearest gram. No preference was given to the left or right side of the body for measurements as we assumed symmetry in the animals' bodies. Our sample included 8 *L. catta* (5 infants, 3 yearlings) and 5 *P. v. coquereli* (3 infants, 2 yearlings) (Table 2.1). All animals were measured while under manual restraint by DLC animal handlers. Previously sampled morphological data from Wunderlich et al. (2011) was included to increase sample size where possible, contributing measurements of 6 additional captive DLC *P. v. coquereli* from birth to 1.5 years of age (Table 2.1). All individuals collecting data were trained by the same person for reliability. Additional age and body mass data for both species were obtained from the DLC records.

Table 2.2: Morphological measurements and landmarks (Wunderlich et al., 2011).

Measurement	**Description**
Body Mass	
Thigh Length	Greater trochanter to lateral condyle; in young animals where greater trochanter was not yet present it was estimated to the joint center
Mid-thigh Circumference	Circumference at midpoint of thigh measure
Leg Length	Fibular head to lateral malleolus
Mid-leg Circumference	Circumference at midpoint of leg measure
Foot-Toe 4	Calcaneal tuberosity to distal fourth toe
Foot-Toe 1	Calcaneal tuberosity to distal first toe
Arm Length	Greater tubercle to lateral side of capitulum
Mid-arm Circumference	Circumference at midpoint of arm measure
Forearm Length	Lateral epicondyle to radial styloid process
Mid-forearm Circumference	Circumference at midpoint of forearm measure
Hand Length	Carpal midline to distal fourth digit
Tail Length	Distal tip of last caudal vertebrae to proximal tip of first caudal vertebrae
Trunk	Occipital protuberance to proximal end of tail
Upperlimb	Arm length added to forearm length
Lowerlimb	Thigh length added to leg length

In its entirety, this longitudinal study consists of 9081 individual measurements of age and body mass, 4974 of which are *P.v. coquereli* (2258 female, 2716 male) and 4107 of which were *L. catta* (1959 female, 2148 male). Of those measurements, individual segment lengths were measured 256 times; 106 in *L. catta* (41 female, 65 male) and 150 in *P.v. coquereli* (73 female, 77 male), while individual limb circumferences were measured 174 times; 106 *L. catta* (41 female, 65 male) and 68 *P.v. coquereli* (31 female, 37 male). (Table 2.3)

Table 2.3: Summary of Morphology Data Distribution

	Body Mass/Age			**Segment Lengths**			**Limb Circumferences**		
	Male	**Female**	**Total**	**Male**	**Female**	**Total**	**Male**	**Female**	**Total**
L. catta	2148	1959	4107	41	65	106	41	65	106
P.v. coquereli	2716	2258	4974	77	73	150	37	31	68
Totals	2757	2323	9081	118	138	256	78	96	174

Changes in limb proportions were examined using common indices. Intermembral index was calculated by dividing the sum of the humerus and radius lengths by the sum of the femur and tibia lengths, multiplied by 100. Crural index was calculated by dividing femur length by tibia length multiplied by 100, while brachial index was equal to humerus length divided by radius length multiplied by 100. Humerofemoral index is equal to humerus length divided by femur length times 100, while radiotibial index is equal to radius length divided by tibia length multiplied by 100. Indices were averaged for each locomotor category to examine changing intra- and interlimb proportions through ontogeny and between species. Under the assumption that limb segments are cylindrical in shape, limb segment cross-sectional area was calculated from limb circumference (C) using the equation $\pi(C/2\pi)^2$ and limb segment volume was calculated using both the limb circumference (C) and length (L) using the equation $L*\pi(C/2\pi)^2$.

Four age categories were defined in order to examine the different phases of locomotor ontogeny: dependent infant, transitional infant, independent infant, and yearling stages. The dependent stage (0 to 6 weeks) in both *P.v. coquereli* and *L. catta* is when the animals are riding dorsally or ventrally on their mother nearly all day. The transitional stage (6 to 24 weeks) in both *P. v. coquereli* and *L. catta* is when the infants begin to leave their mothers regularly and are starting to become independent but are still riding on their mother for the majority of the day. Because behavioral data collection did not begin until after the initiation of this stage, the start date (6 weeks) was determined from literature showing infants were off their mother 33% of the time in *L. catta* and at least 30% of the time in *P. v. coquereli* (Gould, 1990; Richard, 1976). Additional records by DLC staff of DLC animals confirm the beginning of independent locomotion at 6 weeks of age in both species (Sarah Zehr, personal communication). The independent stage is from 24 to 52 weeks in *P.v. coquereli* and *L. catta*, the time when they are fully locomotor independent and rarely seen riding on their mother. Just before the initiation of this period the mothers are frequently seen biting the hands of infants attempting to ride dorsally. The yearling stage is from 24 to 52 weeks.

Behavioral Data Collection

Behavioral data in the form of all-day focal animal sampling were collected on six animals from May to August 2010, a period when the infants began to leave their mother. During focal animal bout sampling, one animal was followed each day, and data collection focused on all locomotor behaviors displayed (Doran, 1992). Variables consisted of locomotor behaviors and postures as well as distance travelled, height in the canopy, and size, orientation, and part of tree used (i.e. trunk, secondary branch, tertiary branch) for take-off and landing supports. An example of a data collection sheet is shown in Figure 2.1. Definitions of locomotor, postural, and support categories followed Hunt et al. (1996) (Tables 2.4, 2.5, & 2.6).

Locomotion Measurements								
Animal ID	**Locomotor**		**Identification**		**Support Size and Orientation**			**Height in Forest at Take-Off**
	Type	**Distance**	**Bout**	**Series**	**Take-Off**	**Landing**	**Part of Tree**	

Figure 2.1: Focal animal bout sampling locomotor measurements. Support orientation scored as: vertical (|), horizontal (--), and oblique (/). Support size scored relative to size of adult animal's foot: 1 to 5.

Table 2.4: Locomotor definitions from Hunt et al. (1996); "Hop" and "Climb Over" added here.

Quadrupedal Walk	Locomotion on top of supports angled at <45º; typically all four limbs contact the support in a particular sequence. The torso is pronograde or roughly parallel to the support. Walking is distinguished from running principally by its slow or medium speed.
Quadrupedal Run	Fast locomotion using asymmetrical or irregular gaits and with a period of free flight.
Bipedal Hop	Torso-orthograde bipedal progression where the hindlimbs push off and land roughly simultaneously; there is a period of free flight. Different from leaping in its repetitive, stereotyped progression and orthograde torso.
Hop	Similar to bipedal hop, except torso is near 45º angle to support, where hip and knee are relatively more flexed.
Bipedal Walk	The hindlimbs provide support and propulsion, with only insignificant contributions from other body parts. The hip and knee are relatively extended, in a manner similar to human walking.
Bipedal Run	Same as above, but with a period of free flight.
Scramble (Traverse or Clamber)	Torso-pronograde, non-suspensory quadrupedal progression lacking a regular gait. Typically supports are small, irregularly placed, and variously angled. A locomoting individual may appear quite unstable. Pronograde clamber is most often seen among the terminal branches of trees.
Vertical Climb (Climb Up)	Ascents on supports angled at ≥ 45º. Typically the hindlimb and its contralateral forelimb provide propulsion. The forelimbs help to elevate the body by the extension of the humerus and flexion of the elbow. Limb kinematics follow a diagonal sequence. Torso is held pronograde and nearly parallel to the support.
Vertical Climb (Climb Down)	Same as above, but rump-first descent, where kinematics are reverse of ascent.
Vertical Climb (Climb Over)	Lateral movement on supports angled ≥ 45º.
Brachiate	Hand over hand orthograde suspensory locomotion in which the forelimbs bear more than half of the body weight, but in which some support from the hindlimbs or tail may occur. There is extensive trunk rotation, approaching 180º. The humerus is completely abducted and the elbow is extended, not infrequently completely extended.
Leap	A gap-crossing movement in which the hindlimbs principally are used as propulsors. The flexed hindlimbs and flexed back are forcefully extended, often aided by the forelimbs.
Vertical Clinging and Leaping	Leap begins and ends with a torso-orthograde clinging posture on a relatively vertical support, with push off predominantly hindlimb-powered.
Play	Nonserious use of behavior patterns derived from serious fighting (Pellis and Pellis, 1998). Non-violent, rapid paced movements involving at least one other member of the species. Typically seen in younger animals. Movements were too quick to record each individual bout.

Table 2.5: Postural definitions from Hunt et al. (1996); "Lotus" and "Ventral/Dorsal Cling" definitions added here.

Bipedal Stand	Hip and knee are completely extended, but there is no significant support from the forelimb(s). the trunk is near orthograde.
Dorsal Cling	Flexed limb posture on dorsal side of another lemur, typically mother.
Forelimb-hindlimb-suspend (Horizontal Cling)	Suspension by one or both forelimbs and one or both feet. Limbs are typically extended. Differs from forelimb suspension in the more pronograde orientation of the torso, in in that the forelimb need not be completely abducted.
Forelimb Suspension	More than half of the body weight is borne by one of both of the forelimbs, grasping a support above the animal's center of mass.
Hindlimb Suspension	Suspension from the foot/feet, lacking support from the forelimb.
Lie	Torso orthograde posture on a relatively horizontal supporting stratum, body weight borne principally by the torso. When an individual grasps a support, the extremity bears little more than its own weight. When lying on a side an individual may support the upper body with an elbow.
Lotus (Worship)	Sitting upright on the ground, arms held out from the sides and resting on the Legs extended outward, not crosslegged. Expose stomach to sun, to warm body.
Sit	The ishia bear a substantial portion of the body weight; torso is relatively orthograde.
Stand	Four-limbed standing on horizontal or subhorizontal supports; the elbow and knee are relatively extended and the trunk is near horizontal
Vertical Cling	Flexed limb posture most common on vertical-subvertical supports.
Ventral Cling	Flexed limb posture on ventral side of another lemur, typically mother.

Table 2.6: Ethogram of supports.

Support	**Code**	**Definition**
XS	1	Adult hand can wrap around more than once.
S	2	Adult hand can wrap around one time.
M	3	Adult hand can wrap around half way.
L	4	Adult hand can wrap less than half way around; can wrap adult arms all the way around.
XL	5	Adult arms can fit less than half way around.
Ground	G	Ground.
Multiple Branches	K	Animal was on multiple branches at once, typically smaller.
Horizontal Fence	HF	Horizontal chain link fence.
Vertical Fence	VF	Vertical chain link fence.
Manmade Structure	S	Manmade structure (i.e. roof, bricks, buildings, etc.)
Horizontal	H	Support angled 0 to 30° from horizontal.
Oblique	O	Support angled 30 to 60° from horizontal.
Vertical	V	Support angled 60 to 90° from horizontal.

A bout is continuous locomotion of only one category that begins with that particular type of locomotion and ends when either a new form of locomotion is used or a posture. This study analyses locomotor behavior in frequencies of individual locomotor bouts displayed. Locomotor behavior was described using two methods of locomotor bout sampling. Leaping bouts are quantified in different manners in the literature (Fleagle, 1976; Gebo, 1987; Fleagle and Mittermeier, 1980; Lawler, 2006). One method quantifies the frequency of leaping sets while the other quantifies frequency of individual leaps. As the results of both methods produced similar trends, only the results of locomotor bout sampling as described in Lawler (2006) will be discussed in this section. These locomotor bouts count each leap separately. Locomotor bout sampling as described by Fleagle (1976) quantifies a continuous set of leaps as a bout. The results of these analyses can be located in Appendix A.

A total of 13,999 locomotor bouts were recorded (Table 2.7). The *P.v. coquereli* infant was observed from 4 to 6 months of age, while the yearling was observed from 17 to 18 months of age (Table 2.7). The two *L. catta* infants were measured from 2 to 5 months of age, while the two yearlings were observed from 14 to 16 months of age (Table 2.7). The species have differing birth seasons, however more rapid growth in *L. catta* accounts for stages of locomotor development to be similar within age groups.

Table 2.7: Sample overview for locomotion. (Y= yearling, I=infant, Lc= *Lemur catta*, Pvc = *Propithecus verreauxi coquereli*)

	Age (Months)	# of Total Bouts	# of Postural Bouts	# of Locomotor Bouts
Lc-I	2-5	2822	1350	1472
Lc-Y	14-16	5885	2573	3312
Pvc-I	4-6	3285	1554	1731
Pvc-Y	17-18	2007	984	1023
Total:		13,999	6461	7538

Locomotor bouts and supports used were compiled into frequencies for each species' age class. Locomotor bouts were collapsed into two behavioral categorizations: 'Dominant Limb Used' (hindlimb, forelimb, or all-limb dominant locomotion) and 'Locomotion' (leaping, vertical leaping, climbing, brachiation, quadrupedalism, or bipedalism) (Table 2.8). Postures were not included in any analyses. These two categorizations were made in order to facilitate the analysis and interpretation of such an expansive amount of data. Specifically, the 'Dominant Limb Use' category was created to reflect the biomechanical tendencies of locomotion, while the 'Locomotion' category was created to encapsulate 99% of all the locomotion displayed by both species and for the ease of comparisons with other studies.

Table 2.8: Key to locomotor behaviors and postures for locomotor categories.

Behavior	**Code**	**Conversion 1**	**Conversion 2**
Bipedal Walk	BW	Hindlimb	Bipedalism
Bipedal Hop	BH	Hindlimb	Bipedalism
Brachiation	B	Forelimb	Brachiation
Climb Down	CD	All-limb	Climb
Climb Over	CO	All-limb	Climb
Climb Up	CU	All-limb	Climb
Hop	H	Hindlimb	Leap
Leap	L	Hindlimb	Leap
Quadrupedal Run	QR	All-limb	Quadrupedal
Quadrupedal Walk	QW	All-limb	Quadrupedal
Traverse	T	All-limb	Quadrupedal
Vertical Cling & Leap	VCL	Hindlimb	VCL
Bipedal Stand	BS	Posture	Posture
Dorsal Cling on Lemur	DC	Posture	Posture
Horizontal Cling	HC	Posture	Posture
Lay	LY	Posture	Posture
Lowerlimb Suspension	LS	Posture	Posture
Playing	P	Posture	Posture
Sit	S	Posture	Posture
Stand	ST	Posture	Posture
Suspension	SS	Posture	Posture
Upperlimb Suspension	US	Posture	Posture
Ventral Cling on Lemur	BC	Posture	Posture
Vertical Cling	VC	Posture	Posture
Worship Position	W	Posture	Posture

Statistical Analysis

Spline regression was used to calculate a line of best fit to allow for visual scrutiny of the regression of body mass over age data. However, to more accurately examine these growth trends, OLS linear regression was used to find a line of best fit on subsets of the regression to estimate body mass increase per day. One-way analysis of variance with Tukey's HSD post hoc comparisons were used to examine morphology variables averaged over 2 years to test for sexual differences between species.

To examine patterns of growth among limb elements, allometric coefficients (slope of the best fit line) were calculated by regressing log-transformed trait values on log-transformed body masses, using both ordinal least squares (OLS) and model II reduced major axis (RMA) regression (Smith, 2009). Allometric coefficients for linear length measurements significantly below 0.33 and cross-sectional areas significantly below 0.67, indicated negative allometric growth while positive allometric growth was indicated by allometric coefficients significantly greater than 0.33 or 0.67 for linear and cross-sectional area measurements, respectively. Significant differences between slopes were evaluated using 95% non-overlapping confidence intervals for both OLS regressions and for RMA. All statistical analyses were done using JMP 8.0.2 (SAS Institute Inc., Cary, North Carolina).

Linear regression is a standard technique used in the analysis of growth data. Assumptions of linear regression include: linearity of the data, independence of errors, constant variance of the errors, and normality (Whitlock and Schluter, 2009). While ordinal least squares (OLS) is the traditional method of calculating a best fit line in linear regression, reduced major axis regression (RMA) is used here because it accounts for error of both the dependent and independent variables (Cheverud, 1982; Smith and Jungers, 1997; Jungers, 1979; Leigh, 1996, 2001, 2007; Leigh et al., 1998, 2001, 2007; Lemelin and Jungers, 2007; Ravosa et al., 1993; Lawler, 2006). OLS requires the assumption that X is measured without error, while RMA assumes that it is measured with error (Sokal and Rolph, 2011). This creates two different trend lines: one which takes into account the error only in the y variable (OLS) and the other which incorporates error from both variables (RMA). In this case, RMA may be biased towards slightly steeper slopes than OLS (Smith, 2009). Some mathematicians have cautioned against RMA, however, claiming that users should first take into account the variables' dependence on each other ((a)symmetric relationship) before the presence of error (Smith, 2009). Due to the ongoing debate of this method, both RMA and OLS will be used for analysis in this project.

Regarding locomotor variables, infant and yearling locomotor behaviors and bouts frequencies, support use (size and orientation) frequencies, and leaping distance averages and height in the canopy averages were compared within and between species, as well as to published adult and yearling values described in Lawler (2006). Statistical significance of frequencies were computed using a bootstrap resampling procedure with 5,000 trials where statistical significance is determined by non-overlapping 95% confidence intervals. One-way analysis of variance with Tukey's HSD post hoc comparisons were used to examine differences in leaping distances and height in the canopy.

Chapter 3

Results

Morphology

Body Mass vs. Age

L. catta and *P. v. coquereli* increase in body mass through different growth trajectories. Body mass increases faster in *P. v. coquereli* (6.4 g/day) than *L. catta* (5.2 g/day) from 0 to 6 months (Figure 3.1). *L. catta*'s rate of body mass increase slows down to 1.3 g/day at 6 months of age, immediately after weaning and locomotor independence are achieved (Figure 3.1). This slowed rate in *L. catta* occurs earlier than *P. v. coquereli,* which does not show a decline in rate of body mass increase to 1.6 g/day until 9.5 months of age (Figure 3.1). In these captive animals, body mass begins to level off around 2.5 to 3 years in *L. catta* and 3.5 to 4 years in *P. v. coquereli*, which is about one year after sexual maturity in both species (Figure 3.1). *P. v. coquereli* obtains an overall larger adult body mass, 4.2 kg in females and 3.9 kg in males, than *L. catta,* which reaches 2.5 kg in both males and females (Figure 3.2).

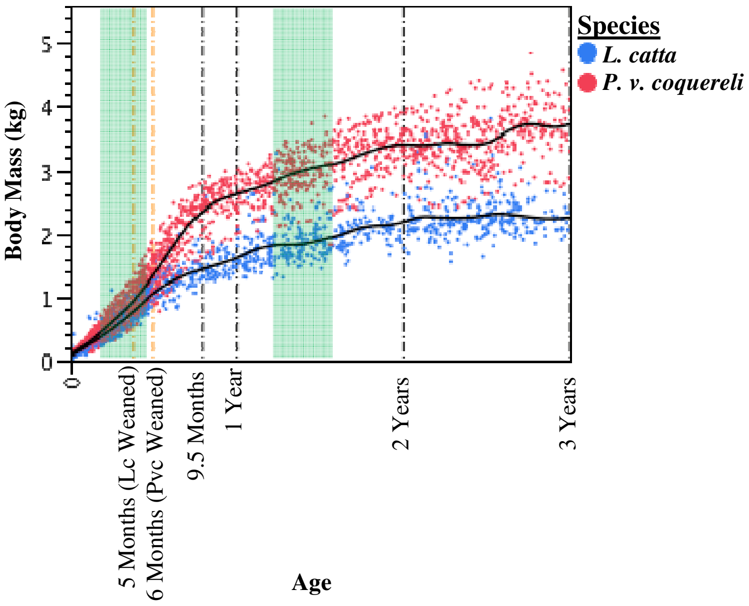

Figure 3.1: Growth of DLC *L. catta* and *P. v. coquereli* from 0 to 3 years of age. Spline regression is used to show *L. catta*'s body mass increase starts to slow at 6 months, while *P. v. coquereli* slows at 9.5 months. Both reach slower rate of growth by 3 years of age. Green shaded areas are periods of behavioral data collection in this study. *L. catta* $R^2=0.905$ and *P. v. coquereli* $R^2=0.954$.

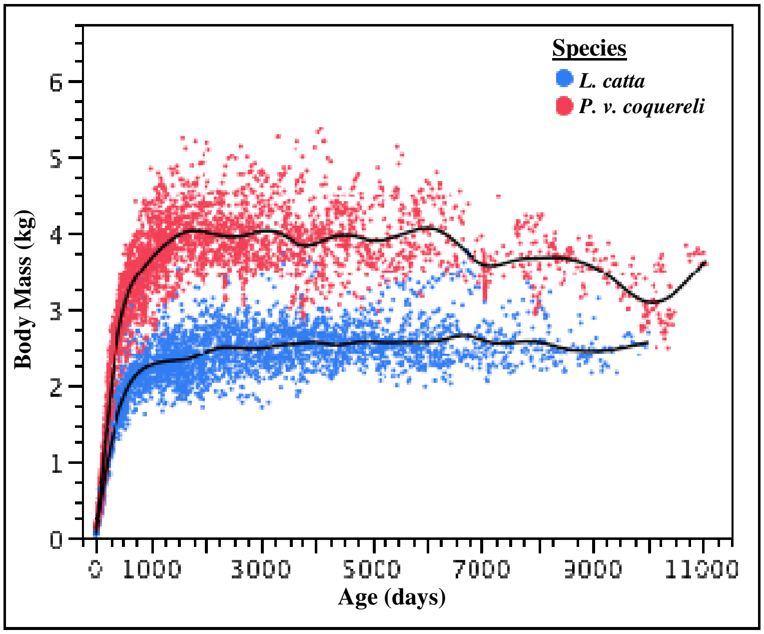

Figure 3.2: Growth of DLC *L. catta* and *P. v. coquereli* from 0 to 30 years of age. Spline regression is used to show *P. v. coquereli* reaches an overall larger body mass which averages 4.2 kg in females and 3.9 kg in males than *L. catta* which averages 2.5 kg for males and females. Both species reach slower rate of growth around 3 years of age. *L. catta* $R^2=0.899$ and *P. v. coquereli* $R^2=0.948$.

Body weights of the lemurs used in this study were compared to all DLC lemurs of the same species using spline regression. Each of the 10 *P. v. coquereli* subjects and 8 *L. catta* subjects used in this study, when examined in a longitudinal manner, exhibited growth trajectories similar to others of their species (Figures 3.3 & 3.4). Very little individual variation is seen in the *P. v. coquereli* subjects measured (Figure 3.3), while in the *L. catta* yearlings measured, Alastor, Limerick, and Hibernia's trendlines lie on the upper and lower edges of the overall species trend but still fit within it (Figure 3.4). Individual lemurs are grouped by species for the remainder of the study.

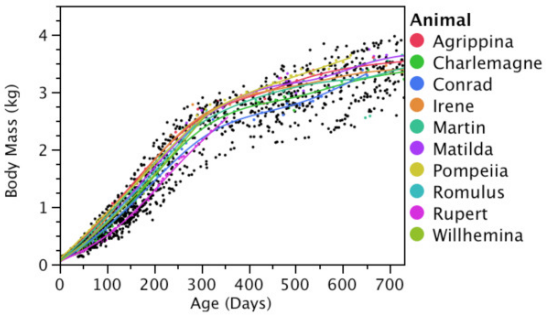

Figure 3.3: Growth comparison of *P. v. coquereli* used in this study. Spline regression was used to create a best fit line. All individuals used fit within the overall subspecies trend. Additional body masses from DLC records. All R^2 values are > .98.

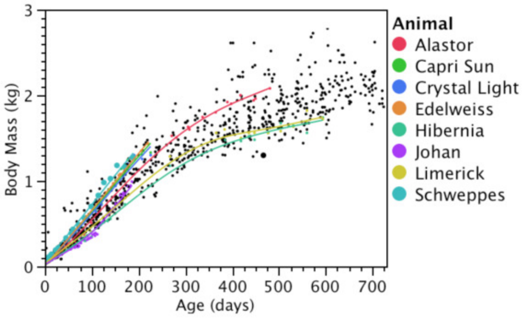

Figure 3.4: Growth comparison of *L. catta* used in this study. . Spline regression was used to create a best fit line. Alastor, Limerick, and Hibernia's trendlines lie on the edges of the plot but still fit within the overall species trend. Additional body masses from DLC records. All R^2 values are > .98.

Males and females of both species exhibited similar growth in body mass. *L. catta* females and males increase in body mass at a similar rate and start to reach asymptotic body masses at about the same time (Figure 3.5). Body mass of *P. v. coquereli* females increases slightly longer than that of males resulting in a slightly larger body mass to adulthood (Figure 3.6). No differences between sexes in 0 to 2 year averages of body mass, average segment lengths, or average limb cross-sectional areas were found in either species using ANOVA.

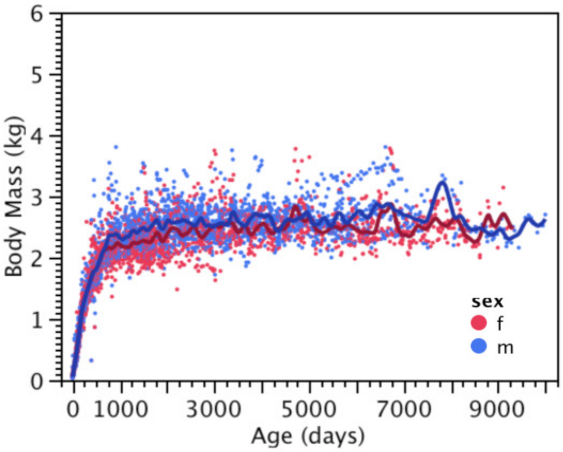

Figure 3.5: Body mass for male and female *L. catta*. Spline regression was used to include a best fit line. Females and males increase body mass similarly with age.

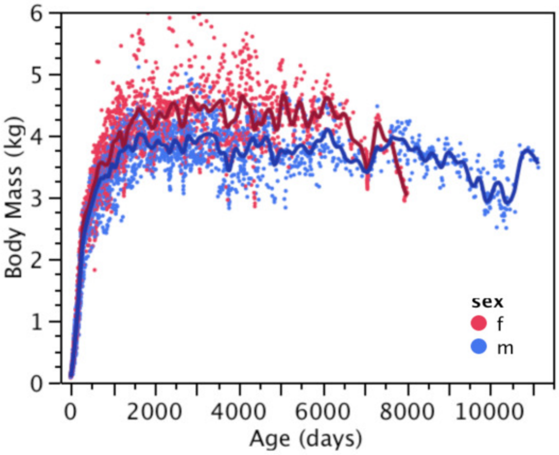

Figure 3.6: Body mass for male and female *P. v. coquereli*. Spline regression was used to include a best fit line. Females increase body mass longer, reaching an overall larger body mass than males.

Allometric growth coefficients of segment lengths and limb cross-sectional areas regressed over body mass from 0 to 2 years were similar in males and females (Table 3.1). These results confirm the absence of sexual differences in morphology and postcranial growth. Males and females are therefore pooled in each species for the remainder of this study.

Table 3.1: Allometric coefficients of log-transformed limb lengths to body mass, separated by sex, for *P. v. coquereli* and *L. catta* from 0 to 2 years. No significant differences were observed between sexes in each species (using non-overlapping 95% confidence intervals).

Segment	**Sex**	**0 to 2 Years**			
		L. catta		***P. v. coquereli***	
		OLS	***RMA***	**OLS**	***RMA***
Humerus	Female	0.392	0.398	0.358	0.362
	Male	0.365	0.368	0.339	0.342
Radius	Female	0.322	0.326	0.340	0.341
	Male	0.329	0.330	0.341	0.344
Upper limb	Female	0.370	0.373	0.348	0.350
	Male	0.350	0.352	0.340	0.343
Femur	Female	0.383	0.386	0.410	0.412
	Male	0.375	0.378	0.407	0.409
Tibia	Female	0.351	0.354	0.358	0.360
	Male	0.372	0.373	0.373	0.375
Lower limb	Female	0.351	0.353	0.358	0.362
	Male	0.377	0.379	0.390	0.392
Hand	Female	0.231	0.234	0.336	0.338
	Male	0.250	0.251	0.330	0.333
Foot to Toe 1	Female	0.235	0.237	0.310	0.311
	Male	0.244	0.245	0.332	0.336
Foot to Toe 4	Female	0.244	0.246	0.319	0.321
	Male	0.253	0.254	0.351	0.355
Tail	Female	0.412	0.423	0.433	0.438
	Male	0.392	0.394	0.454	0.456
Trunk	Female	0.435	0.438	0.416	0.420
	Male	0.424	0.426	0.409	0.413
Thigh CS Area	Female	0.942	0 .967	0 .969	0.976
	Male	1.03	1.05	1.05	1.08
Leg CS Area	Female	0.752	0.786	0.571	0.586
	Male	0.752	0 .777	0.613	0.631
Arm CS Area	Female	0.537	0.575	0.528	0.545
	Male	0.535	0 .562	0 .533	0 .597
Forearm CS Area	Female	0.708	0.729	0.790	0.807
	Male	0.716	0.733	0.879	0.967

Limb Proportions

Lower limb lengths increase relatively faster than upper limb lengths from 0 to 2 years in both species; slope values (0.64, 0.60) are not different between species (Figure 3.7a). Increasing lower limb relative to upper limb lengths are also evident in IMI values (upper limb/lower limb*100) where *L. catta* has an initial IMI of 73 which rapidly decreases to 67 at 6 to 24 weeks of age where it remains through adulthood (Figure 3.8a). *P. v. coquereli* has an initial IMI of 69 which decreases to 64 by 52 to 104 weeks of age but actually achieves its lowest value of 61 at 24 to 52 weeks (locomotor independence) (Figure 3.8a)

In the proximal limb segments, femur lengths increase relatively faster than humerus lengths from 0 to 2 years in both species. The slope value of *L. catta* (0.62) is higher than *P. v. coquereli* (0.53) (Figure 3.7b). The humerofemoral index (humerus/femur*100) of *L. catta* fluctuates with increasing age; at 0 to 6 weeks the index value is 64 and by 52 to 104 weeks of age it is 61 (Figure 3.8b). The highest index value for *L. catta* (65) occurs at 24 to 52 weeks (locomotor independence) (Figure 11b). *P. v. coquereli* generally shows decreasing humerofemoral index values with increasing age, however, the lowest values are at 24 to 52 weeks (locomotor independence) and increase slightly back to 58 by 52 to 104 weeks of age (Figure 3.8b).

Distal limb segment lengths display similar trends as proximal lengths, as tibia lengths increase relatively faster than radius lengths from 0 to 2 years in both *L. catta* (0.67) and *P. v. coquereli* (0.66) (Figure 3.7c). Slope values are not different between species (Figure 10c). Radio-tibial indices (radius/tibia*100) decrease with age in both *L. catta* and *P. v. coquereli* (Figure 3.8c). Both *P. v. coquereli* and *L. catta* have lowest index values from 24 to 52 weeks (locomotor independence) rather than from 1 to 2 years of age (Figure 3.8c).

Within the upper limb, radius lengths increase faster than humerus lengths from 0 to 2 years in *P. v. coquereli* (1.1), while *L. catta* (1.0) shows equivalent length changes (Figure 3.7d). Brachial index (radius/humerus*100) values decrease with increasing age in *L. catta* and *P. v. coquereli*, where they reach lowest values from 24 to 52 weeks of age (locomotor independence) rather than 1 to 2 years of age (Figure 3.8d).

Within the lower limb, femur lengths increase faster than tibia lengths in *P. v. coquereli* (0.98), while length increases are equal in *L. catta* (0.89) (Figure 3.7e). Crural index (tibia/femur*100) values remain constant around 100 in *L. catta* while they decrease with increasing age from 104 at 0 to 6 weeks to 95 by 24 to 52 weeks where it remains until adulthood in *P. v. coquereli* (Figure 3.8e).

Table 3.2: Confidence intervals for regressions according to the figure number.

	L. catta			***P. v. coquereli***		
Figure	**Slope**	**Lower**	**Upper**	**Slope**	**Lower**	**Upper**
3.7A	0.64	0.60	0.67	0.60	0.58	0.63
3.7B	0.62	0.58	0.67	0.53	0.50	0.56
3.7C	0.67	0.63	0.7	0.66	0.63	0.69
3.7D	1.0	0.98	1.1	1.1	1.0	1.2
3.7E	0.98	0.93	1.0	0.89	0.86	0.92
3.9	0.33	0.32	0.35	0.53	0.49	0.57
3.10	22.9	21.8	24.1	28.7	26.7	31.0
3.11	0.25	0.24	0.26	0.35	0.33	0.37
3.12	2.0	1.9	2.1	2.1	2.0	2.3

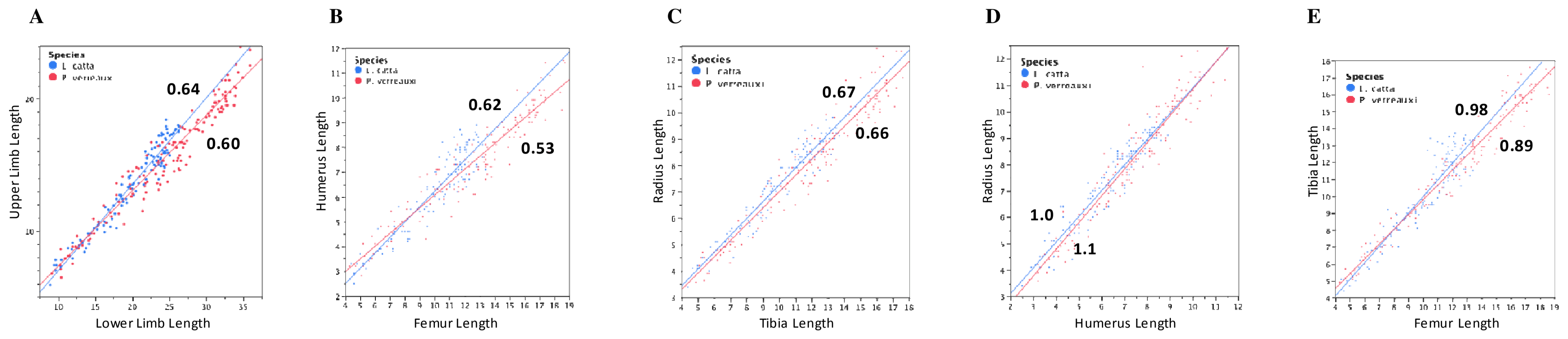

Figure 3.7: Limb segment lengths regressed over limb segment lengths for both *L. catta* and *P. v. coquereli* from 0 to 2 years. Slopes for each species are indicated in bold using RMA regression and 95% confidence intervals to test for significant differences.

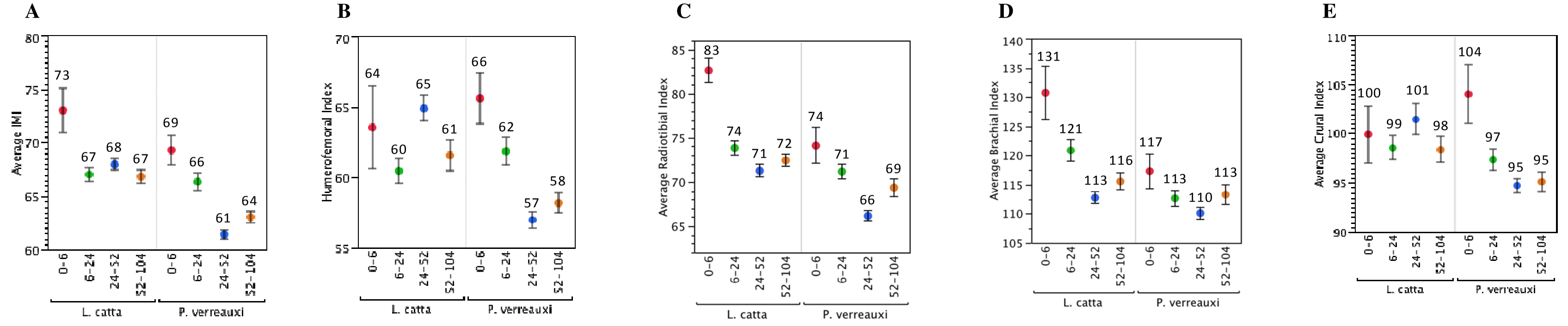

Figure 3.8: Indices averaged for each locomotor category (in weeks) for both *L. catta* and *P. v. coquereli* from 0 to 2 years. Average index values are indicated in bold for indices of each age group. Error bars represent one standard error of the mean.

Limb segment cross sectional areas provide insight about limb segment muscle growth. Lower limb cross-sectional area increases relatively faster that upper limb cross-sectional area in both *P. v. coquereli* and *L. catta*. Upper limb over lower limb cross-sectional area slope values are greater in *P. v. coquereli* (0.53) than *L. catta* (0.33) (Figure 3.9). Comparing proximal to distal cross-sectional areas, proximal cross-sectional areas of both the upper and lower limb increase relatively faster that distal cross-sectional areas of the upper and lower limb in both *P. v. coquereli* and *L. catta* (Figure 3.10). Proximal over distal limb segment cross-sectional area slope values are greater in *P. v. coquereli* (28.7) than *L. catta* (22.9) (Figure 3.10).

Comparison of limb segment volumes may provide insight about limb segment moments of inertia. Lower limb volume increases relatively faster than upper limb volume in both *L. catta* than in *P. v. coquereli* (Figure 3.11). Upper limb over lower limb volume slope values are greater in *P. v. coquereli* than *L. catta* (Figure 3.11). When comparing proximal limb volume to distal limb volume both species increase proximal volume much faster than distal limb volume (Figure 3.12). Both species increase proximal limb volume at the same rate as distal limb volume (Figure 15).

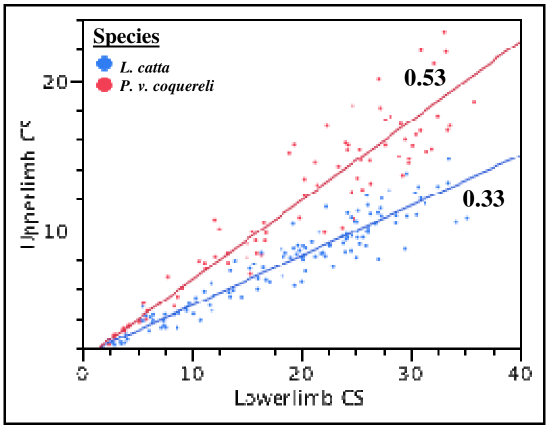

Figure 3.9: Upper limb cross-sectional area regressed over lower limb cross-sectional area from 0 to 2 years in both species.

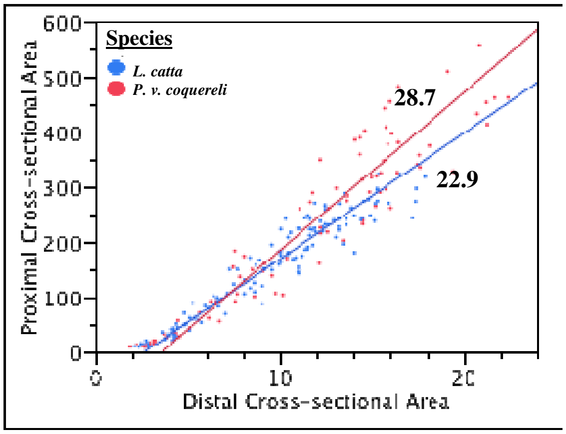

Figure 3.10: Proximal upper and lower limb segment cross-sectional areas regressed over distal upper and lower limb segment cross-sectional areas from 0 to 2 years in both species.

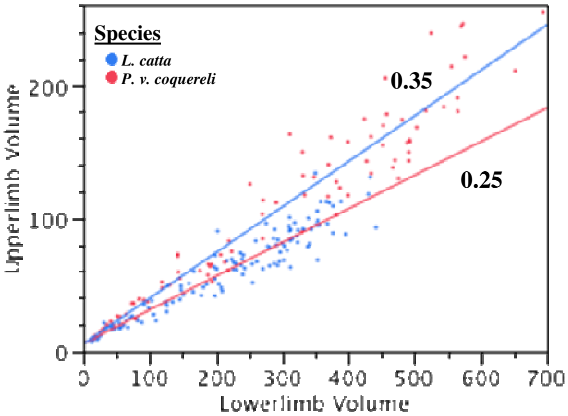

Figure 3.11: Upper limb volume regressed over lower limb volume from 0 to 2 years in both species.

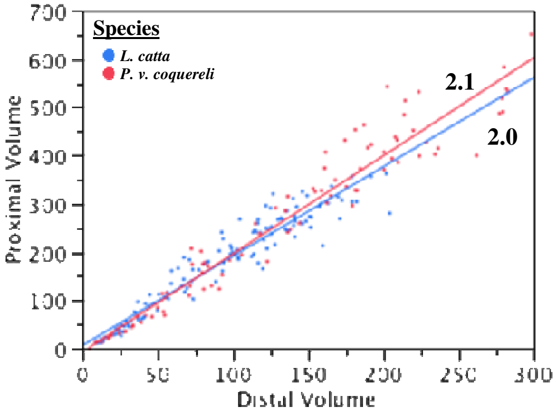

Figure 3.12: Proximal limb segment volume regressed over distal limb segment volume from 0 to 2 years in both species. Both species increase proximal limb volume to distal limb volume at the same rate

Limb Segment Growth: 0 to 2 Years

Allometric growth of limb segment lengths and cross-sectional areas were examined from 0 to 2 years of age. In each individual limb segment, allometry significantly differs within the 0 to 2 year time frame. The slope changes in the regressions of the log-transformed data indicate inconsistent growth rates (Figure 3.13). Breaking down the 0 to 2 year data into smaller, more applicable age categories according to locomotor development is a more appropriate method to examine allometric growth.

Four age categories were defined in order to examine the different phases of locomotor ontogeny: dependent infant, transitional infant, independent infant, and yearling stages. The dependent stage (0 to 6 weeks) in both *P.v. coquereli* and *L. catta* is when the animals are riding dorsally or ventrally on mom nearly all day. The transitional stage (6 to 24 weeks) in both *P. v. coquereli* and *L. catta* is when the infants begin to leave their mothers regularly and are starting to become independent, but still riding on their mother for the majority of the day. The independent stage is from 24 to 52 weeks in *P. v. coquereli* and *L. catta*, the time when they are fully locomotor independent and rarely seen riding on their mother. The yearling stage is from 24 to 52 weeks.

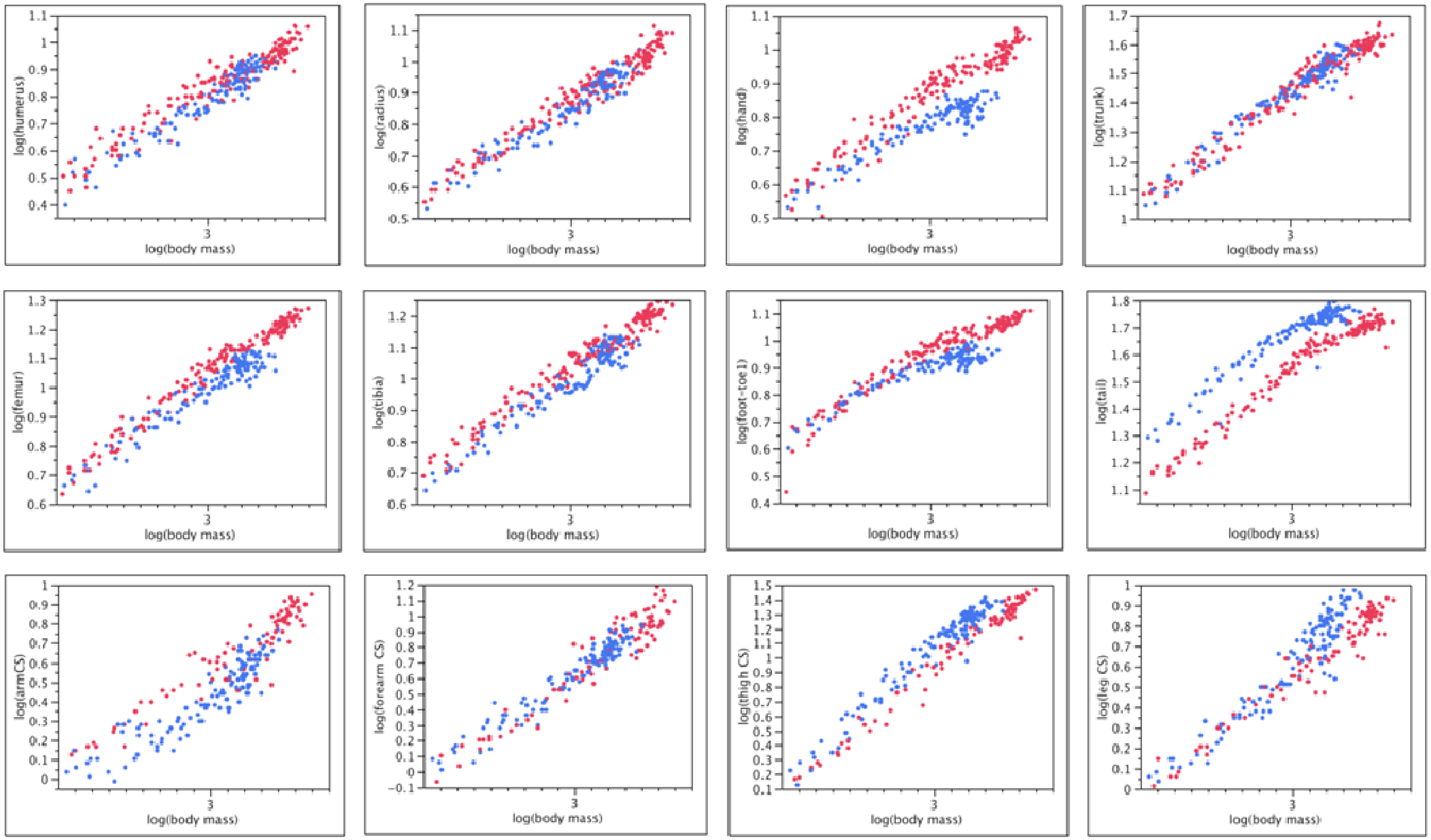

Figure 3.13: Log-transformed limb segment lengths and cross-sectional areas regressed against log-transformed body masses. Plots demonstrate that allometry differs within the 0 to 2 year time frame. Slope changes in the regressions of the log-transformed data giving a somewhat curved appearance in select limb segments.

Limb Segment Growth: 6 to 24 vs. 24 to 52 weeks

When limb segment allometry was broken down into 0 to 6, 6 to 24, 24 to 52, and 52 to 104 week categories, only enough data to make confident comparisons between categories were available for 6 to 24 and 24 to52 week categories. As a result, limb segment growth was examined according to two locomotor development stages: transitional (6 to 24 weeks) and independent (24 to 52 weeks). Minimal differences between RMA and OLS slope values are observed, although it should be noted that RMA slope values tend to be slightly higher than OLS slope values (Table 3.3).

In *P. v. coquereli* from 6 to 24 weeks, limb segment lengths grow with significant positive allometry except the arm, and forearm, which grow isometrically (Table 3.3; Figure 3.14). In *P. v. coquereli* from 24 to 52 weeks, the arm forearm, thigh, and tail grow isometrically, while the hand, foot, leg, and trunk grow with negative allometry (Table 3.3; Figure 3.14). Cross-sectional area increases with positive allometry in the forearm and thigh and isometry in the arm and leg in both 6 to 24 weeks and 24 to 52 weeks of age (Table 3.3; Figure 3.14). Significant differences in allometric growth coefficients in *P. v. coquereli* between 6 to 24 weeks and 24 to 52 weeks are in the thigh, leg, hand, foot, tail, and trunk lengths, while none exist for cross-sectional areas (Table 3.3; Figure 3.14).

From 6 to 24 weeks in *L. catta,* the tail, trunk, and thigh lengths grow with positive allometry; the arm, forearm, and leg lengths grow with isometry; while the hand and foot lengths grow with negative allometry (Table 3.3; Figure 3.15). From 24 to 52 weeks, the leg and forearm lengths grow with positive allometry; the tail, trunk, thigh, foot (toe 1), and arm lengths grow isometrically; while the hand and foot (toe 4) grow with negative allometry (Table 3.3; Figure 3.15). Thigh cross-sectional area increases with positive allometry from 6 to 24 weeks in *L. catta* while all other cross-sectional areas increase with isometry. From 24 to 52 weeks all limb cross-sectional areas increase with positive allometry in *L. catta* except in the thigh which grows with isometry (Table 3.3). Significant differences in allometric growth coefficients in *L. catta* between 6 to 24 week growth and 24 to 52 week growth are in leg length and arm cross-sectional area (Table 3.3).

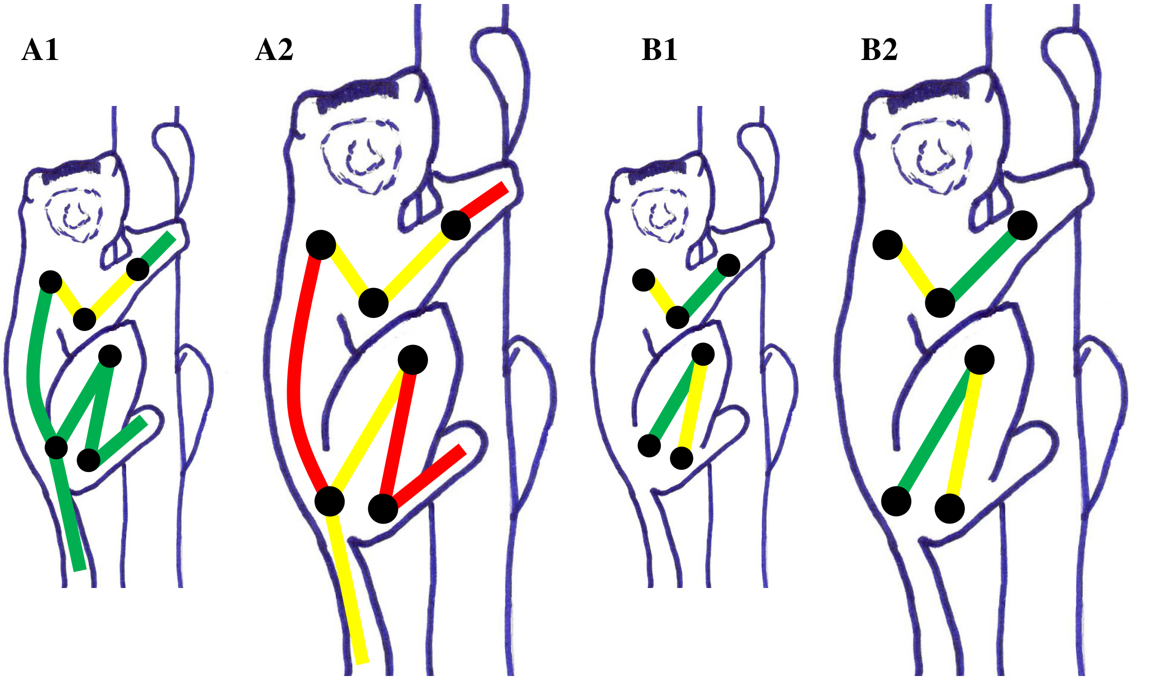

Figure 3.14: Visual representation of *P. v. coquereli* (A) limb segment length and (B) and cross-sectional allometry from 6 to 24 weeks (1) and 24 to 52 weeks (2). Green lines indicate significant positive allometry, yellow lines indicate isometry, and red lines indicate significant negative allometry. From 6 to 24 weeks, positive allometry is seen in limb lengths, but from 24 to 52 weeks isometry and negative allometry is seen. Cross-sectional areas show similar patterns of allometric growth from 6 to 24 weeks and 24 to 52 weeks.

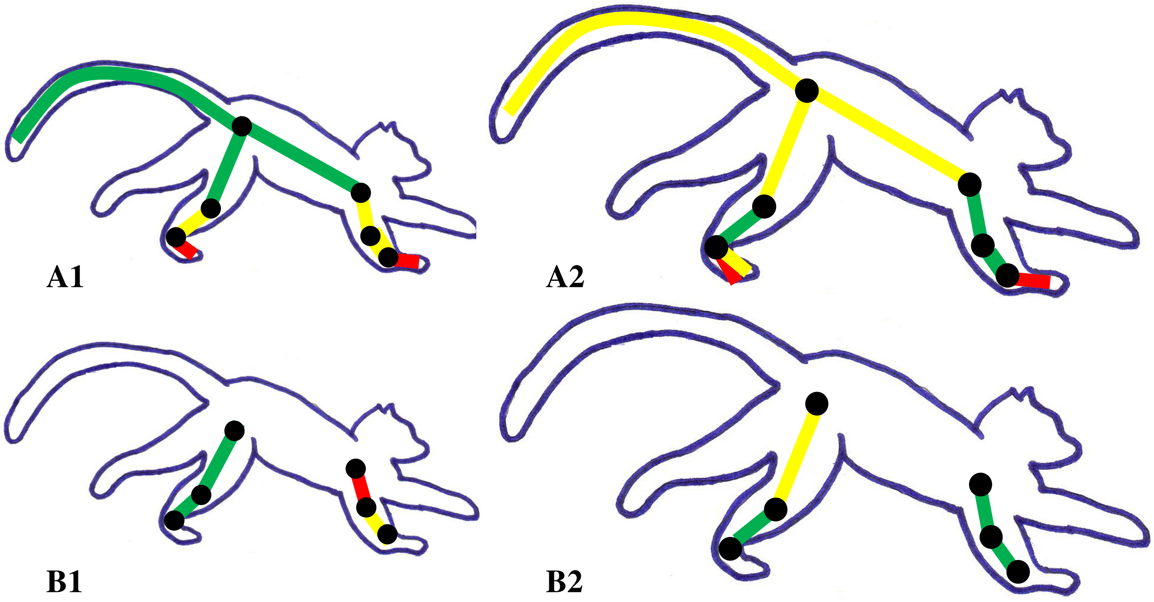

Figure 3.15: Visual representation of *L. catta* (A) limb segment length and (B) and cross-sectional allometry from 6 to 24 weeks (1) and 24 to 52 weeks (2). Green lines indicate significant positive allometry, yellow lines indicate isometry, and red lines indicate significant negative allometry. From 6 to 24 weeks positive allometry and isometry are seen in all lengths except the hands and feet, while from 24 to 52 weeks negative allometry is still seen in the hands and feet, but positive allometry is seen in the distal limb segments. Limb cross-sectional areas grow with different patterns of allometry from 6 to 24 weeks while they all grow with positive allometry from 24 to 52 weeks.

Table 3.3: Allometric coefficients of limb segment lengths and cross-sectional areas from 6 to 24 weeks and 24 to 52 weeks. Length values significantly different from 0.33 and cross-sectional values significantly different from 0.67 are indicated by (*), found using non-overlapping 95% confidence intervals. Significant differences between age classes are indicated by (^) in the species column.

Segment	**Species**	**6 to 24 Weeks**		**24 to 52 Weeks**	
		OLS	**RMA**	**OLS**	**RMA**
Humerus	*L. catta*	0.343	0.350	0.423	0.497*
	P. v. coquereli	0.372	0.384	0.313	0.336
Radius	*L. catta*	0.305	0.310	0.437	0.775*
	P. v. coquereli	0.353	0.358	0.300	0.316
Upper limb	*L. catta*	0.321	0.324	0.435	0.530*
	P. v. coquereli	0.354	0.360	0.306	0.321
Femur	*L. catta*	0.381	0.391*	0.312	0.367
	P. v. coquereli^	0.448*	0.454*	0.297	0.301
Tibia	*L. catta*^	0.343	0.347	0.578*	0.672*
	P. v. coquereli^	0.362	0.367*	0.260*	0.270*
Lower limb	*L. catta*	0.362	0.366	0.446*	0.488*
	P. v. coquereli^	0.416	0.420*	0.277	0.282*
Hand	*L. catta*	0.272*	0.274*	0.116*	0.129*
	P. v. coquereli^	0.365	0.372*	0.167*	0.172*
Foot to Toe 1	*L. catta*	0.280*	0.282*	0.233*	0.252
	P. v. coquereli	0.375*	0.377*	0.200*	0.205*
Foot to Toe 4	*L. catta*	0.300*	0.303*	0.218*	0.231*
	P. v. coquereli^	0.392*	0.394*	0.202*	0.207*
Tail	*L. catta*	0.463*	0.472*	0.327	0.404
	P. v. coquereli^	0.539*	0.543*	0.299	0.305
Trunk	*L. catta*	0.425*	0.431*	0.357	0.412
	P. v. coquereli^	0.479*	0.487*	0.206*	0.223*
Thigh CS Area	*L. catta*	1.10*	1.15*	0.615	0.939
	P. v. coquereli	1.06*	1.12*	0.952*	1.00*
Leg CS Area	*L. catta*	0.733	0.780*	0.665	2.20*
	P. v. coquereli	0.683	0.701	0.663	0.805
Arm CS Area	*L. catta*^	0.455*	0.510*	0.889	1.43*
	P. v. coquereli	0.578	0.625	0.695	1.04
Forearm CS Area	*L. catta*	0.709	0.761	0.712	1.02*
	P. v. coquereli	0.898*	0.971*	1.00*	1.28*

Behavior

Locomotor Behavior

Of all the positional data collected, 54% (7,538/13,999) were locomotor bouts and 46% (6,461/13,999) were postural bouts. Only locomotor bouts were analyzed. *L. catta* transitional infants display <1% brachiation, <1% bipedalism, 22% climbing, 31% leaping, 40% quadrupedalism, and 6% VCL (Table 3.4). *L. catta* yearlings display <1% brachiation, <1% bipedalism, 9.2% climbing, 22% leaping, 68% quadrupedalism, and <1% VCL (Table 3.4). Climbing, leaping, brachiation, bipedalism, and VCL constitute a higher amount of locomotion in *L. catta* transitional infants, while quadrupedalism constitutes a higher percent of locomotion in *L. catta* yearlings (Table 3.4). Yearling *L. catta* leap larger distances (1.10 m) than transitional infant *L. catta* (0.809 m) (Figure 3.16).

Transitional infant *P. v. coquereli* display 4.4% brachiation, 11% bipedalism, 32% climbing, 22% leaping, <1% quadrupedalism, and 30% VCL (Table 3.4). Yearling *P. v. coquereli* display 4.1% brachiation, 14% bipedalism, 37% climbing, 15% leaping, <1% quadrupedalism, and 29% VCL (Table 3.4). In *P. v. coquereli*, leaping constitutes a higher percent of locomotion in transitional infants than yearlings; however yearlings leap larger distances (1.53 m) than infants (1.03 m) (Table 3.4; Figure 3.16). Leaping, VCL, climbing, and brachiation constitute a higher percent of locomotion in *P. v. coquereli* transitional infants and yearlings than *L. catta* transitional infants and yearlings in which quadrupedalism is a higher percent of locomotion (Table 3.4). Additionally, *P. v. coquereli* transitional infants and yearlings leap larger distances than *L. catta* transitional infants and yearlings, respectively (Figure 3.16).

Table 3.4: Frequency of locomotor behaviors used during locomotion. 95% Confidence intervals calculated using bootstrap resampling. (Y=yearling, I=infant, L=*Lemur catta*, P=*Propithecus verreauxi coquereli*)

		Frequency (%)	Lower	Upper	Sig. Dif. From
LI	**Brachiate**	.88	.41	1.4	LY, PI, PY
	Bipedalism	.61	.27	1.0	LY, PI, PY
	Climb	22	20	24	LY, PI, PY
	Leap	31	28	33	LY, PI, PY
	Quadrupedal	40	37	42	LY, PI, PY
	VCL	6.0	5.0	7.0	LY, PI, PY
LY	**Brachiate**	.18	.06	.33	LI, PI
	Bipedalism	.091	0	.21	LI, PI, PY
	Climb	9.2	8.2	10	LI, PI, PY
	Leap	22	20	23	LY, PY
	Quadrupedal	68	66	69	LI, PI, PY
	VCL	.94	.60	1.3	LI, PI, PY

		Frequency (%)	Lower	Upper	Sig. Dif. From
PI	**Brachiate**	4.4	3.5	5.4	LI, LY
	Bipedalism	11	10	13	LI, LY
	Climb	32	30	35	LI, LY
	Leap	22	20	24	LI, PY
	Quadrupedal	.23	.058	.46	LI, LY
	VCL	30	28	32	LI, LY
PY	**Brachiate**	4.1	3.1	5.5	LI,LY
	Bipedalism	14	12	16	LI, LY
	Climb	37	34	40	LI, LY
	Leap	15	13	17	LI, LY, PI
	Quadrupedal	.78	.29	1.4	LI, LY
	VCL	29	26	32	LI, LY

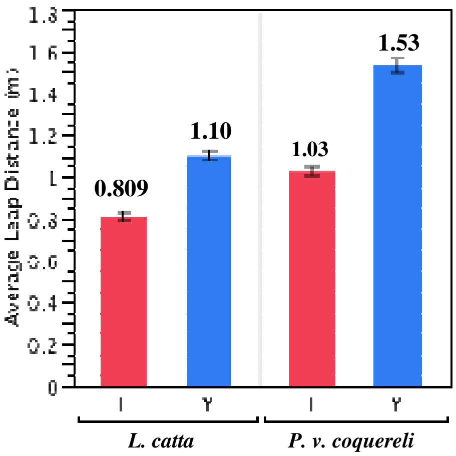

Figure 3.16: Average leap distance (including leaping and vertical leaping) in meters within and between species. Error bars represent 1 standard error of the mean. (Y= yearling, I=infant). Yearlings leap larger distances than transitional infants in each species, while *P. v. coquereli* transitional infants and yearlings leap larger distances than *L. catta* transitional infants and yearlings, respectively.

Locomotion was also categorized according to limb usage. In *L. catta* transitional infants, 63% of all locomotion consisted of all-limb dominant, <1% consisted of forelimb dominant, and 37% was hindlimb dominant locomotion. In *L. catta* yearlings, 77% of all locomotion consisted of all-limb dominant, <1% consisted of forelimb dominant, and 23% was hindlimb dominant locomotion (Table 3.5). *L. catta* transitional infants show significantly more hind- and forelimb dominant locomotion and significantly less all-limb dominant locomotion than yearlings, which is associated with increased amounts of leaping and VCL in transitional infants than yearlings (Table 3.5). In transitional infant *P. v. coquereli,* 33% of locomotion consisted of all- limb dominant, 4.4% of locomotion consisted of forelimb dominant, and 63% was hindlimb dominant locomotion while yearlings show 37% all-limb, 4.1% forelimb, and 58% hindlimb dominant locomotion (Table 3.5). *P. v. coquereli* infants and yearlings show no significant differences from one another in all-limb, forelimb, or hindlimb dominant locomotion frequencies (Table 3.5). Both *P. v. coquereli* transitional infants and yearlings show less all-limb and more hind and forelimb dominant locomotion than both transitional infant and yearling *L. catta* (Table 3.5).

Table 3.5: Frequency of dominant limb(s) used during locomotion. 95% Confidence intervals calculated using bootstrap resampling. (Y= yearling, I=infant, Lc= *Lemur catta*, P=*Propithecus verreauxi coquereli*)

		Frequency (%)	**Lower**	**Upper**	**Sig. Dif. From**
LI	**All-limb**	62	59	64	LY, PI, PV
	Forelimb	.88	.48	1.4	LY, PI, PV
	Hindlimb	37	35	40	LY, PI, PV
LY	**All-limb**	77	75	78	LI, PI, PV
	Forelimb	.18	0.061	.33	LI, PI, PV
	Hindlimb	23	21	24	LI, PI, PV
PI	**All-limb**	33	30	35	LI, LY
	Forelimb	4.4	3.5	5.4	LI, LY
	Hindlimb	63	61	65	LI, LY
PY	**All-limb**	37	34	40	LI, LY
	Forelimb	4.1	2.9	5.4	LI, LY
	Hindlimb	58	55	62	LI, LY

Support Use

Support use was compared between age classes and species for all locomotor behaviors. Frequencies of take-off support sizes/orientations compared to landing support sizes/orientations are similar, thus only take-off supports were examined. *Lemur catta* transitional infants use the ground 30%, horizontal supports 33%, oblique supports 9%, and vertical supports 28% (Table 3.6). *Lemur catta* yearlings use the ground 71%, horizontal supports 14%, oblique supports 6.8%, and vertical supports 7.8% (Table 3.6). *L. catta* transitional infants use the ground significantly less and horizontal and vertical supports significantly more than *L. catta* yearlings (Table 3.6).

Transitional infant *P. v. coquereli* use the ground 12%, horizontal supports 15%, oblique supports 15%, and vertical supports 57% (Table 3.6). Yearling *P. v. coquereli* use the ground 14%, horizontal supports 20%, oblique supports 10%, and vertical supports 55% (Table 3.6). In *P. v. coquereli*, transitional infants use oblique supports significantly more and horizontal supports significantly less than yearlings (Table 3.6). *L. catta* use the ground more often than *P. v. coquereli,* which are using vertical supports significantly more (Table 3.6).

Table 3.6: Support use according to orientation for all locomotion. (Y= yearling, I=infant, L=*Lemur catta*, P=*Propithecus verreauxi coquereli*)

		Frequency (%)	**Lower**	**Upper**	**Sig. Dif. From**
LI	**Ground**	30	27	33	LY, PI, PY
	Horizontal	33	30	36	LY, PI, PY
	Oblique	9.0	7.5	11	PI
	Vertical	28	26	31	LY, PI, PY
LY	**Ground**	71	69	73	LI, PI, PY
	Horizontal	14	12	16	LI, PY
	Oblique	6.8	5.7	8.0	PI, PY
	Vertical	7.8	6.6	9.0	LI, PI, PY
PI	**Ground**	12	11	14	LI, LY
	Horizontal	15	14	17	LI, PY
	Oblique	15	13	17	LI, LY, PY
	Vertical	57	55	60	LI, LY
PY	**Ground**	14	12	16	LI, LY
	Horizontal	20	18	23	LI, LY, PI
	Oblique	10	8.4	12	PI, LY
	Vertical	55	52	58	LI, LY

L. catta transitional infants use extra small supports 15%, small supports 28%, medium supports 18%, large supports 7.6%, extra large supports 2.3%, and the ground 30% (Table 3.7). *L. catta* yearlings use extra small supports 2.8%, small supports 10%, medium supports 8.7%, large supports 3.8%, extra large supports 2.8%, and the ground 72% (Table 3.7). *L. catta* transitional infants use the ground significantly less and extra small, small, and medium supports significantly more than yearlings (Table 3.7).

Transitional infant *P. v. coquereli* use extra small supports 10%, small supports 33%, medium supports 34%, large supports 10%, extra large supports 1%, and the ground 12% (Table 3.7). Yearling *P. v. coquereli* use extra small supports <1%, S supports 15%, medium supports 53%, large supports 14%, extra large supports 3%, and the ground 14% (Table 3.7). *P. v. coquereli* transitional infants use extra small and small supports significantly more than yearlings that use medium supports significantly more than transitional infants (Table 3.7). *P. v. coquereli* transitional infants and yearlings use significantly more medium supports than *L. catta* transitional infants and yearlings that use the ground significantly more (Table 3.7).

Table 3.7: Support use according to size for all locomotion. (Y= yearling, I=infant, L=*Lemur catta*, P=*Propithecus verreauxi coquereli*, G=Ground, XS= extra small, S=small, M=medium, L=large, XL=extra large diameter support)

		Frequency (%)	**Lower**	**Upper**	**Sig. Dif. From**
LI	**XS**	15	13	17	LY, PI, PY
	S	28	25	30	LY, PI, PY
	M	18	15	20	LY, PI
	L	7.6	6.0	9.1	LY, PY
	XL	2.3	1.5	3.4	
	G	30	27	33	LY, PI, PY
LY	**XS**	2.8	2.1	3.6	LI, PI, PY
	S	10	9.0	12	LI, PI, PY
	M	8.7	7.5	10	LI, PI, PY
	L	3.8	3.0	4.7	LI, PI, PY
	XL	2.8	2.1	3.5	PI
	G	72	69	74	LI, PI, PY

		Frequency (%)	**Lower**	**Upper**	**Sig. Dif. From**
PI	**XS**	10	8.8	12	LI, LY, PY
	S	33	31	36	LI, LY, PY
	M	34	31	46	LI, LY, PY
	L	10	8.4	11	LY
	XL	1.0	.55	1.5	LY, PY
	G	12	11	14	LI, LY
PY	**XS**	.93	.41	1.5	LI, LY, PI
	S	15	13	18	LI, LY, PI
	M	53	50	56	LI, LY, PI
	L	14	11	16	LI, LY
	XL	3.0	2.0	4.1	
	G	14	12	16	LI, LY

In *L. catta*, average height in the canopy during locomotion is lower in yearlings (0.93 m) than transitional infants (2.4 m) (Figure 3.17). In *P. v. coquereli*, yearling average height in the canopy during locomotion is higher in yearlings (4.4 m) than transitional infants (2.1 m) (Figure 3.17). Between species, average height in the canopy during locomotion is higher in *P. v. coquereli* than in *L. catta* yearlings, while average height in the canopy during locomotion is lower in *P. v. coquereli* than *L. catta* transitional infants (Figure 3.17).

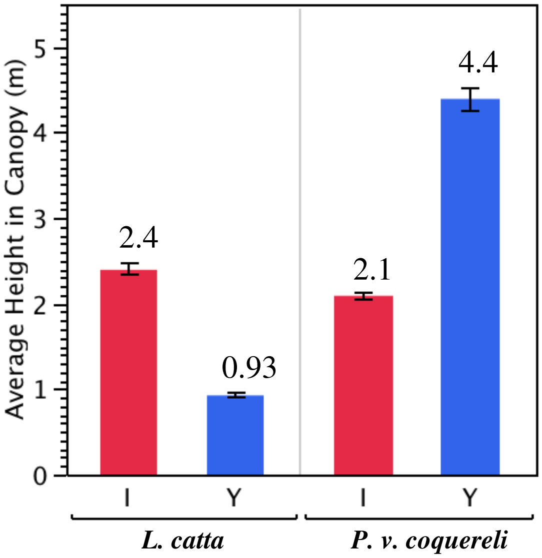

Figure 3.17: Average height in the canopy in meters during locomotion within and between species. Error bars constructed using 95% confidence intervals of the mean. (Y= yearling, I=infant, LC= *Lemur catta*, PVC=*Propithecus verreauxi coquereli*)

Captive vs. Wild Data

In captive *P. v. coquereli* yearlings, climbing constitutes a higher percent of locomotion than in wild *P. v. verreauxi* yearlings, which display greater frequencies of vertical leaping (Table 3.8). Support use differs as well as captive *P. v. coquereli* yearlings display greater frequencies of medium support use and wild *P. v. coquereli* display greater frequencies of small support use (Table 3.8). Captive *P. v. coquereli* yearlings display greater frequencies of vertical and horizontal support use and wild *P. v. coquereli* display greater frequencies of oblique support use (Table 3.8). Leaping distances are similar in distance between wild *P. v. verreauxi* and captive *P. v. coquereli* (Table 3.8).

Table 3.8: Comparison of wild to captive data in adults, yearlings, and infants.

		Wild *P. v. verreauxi* (Lawler, 2006)		Captive *P. v. coquereli* (this study)		Captive *P. v. coquereli* (Williams, 2007)	
		Adult (5+ yrs)	Yearling (1 year)	Yearling (1-2 years)	Infant (3-7 mos)	Adult (3+ yrs)	Juveniles (1-3 years)
Locomotion	Climb	18%	19%	38%	34%	29%	22%
	Leap	29%	32%	30%	35%	15%	22%
	Vertical Leap	53%	48%	30%	31%	53%	54%
	Quadrupedalism	<1%	<1%	<1%	<1%	3%	1%
	Leaping Distance (m)	1.28	1.34	1.53	1.01		
Support Use	**Size**						
	Small	19%	62%	19%	50%		
	Medium	26%	29%	62%	38%		
	Large	55%	9%	19%	12%		
	Orientation						
	Horizontal	19%	12%	24%	18%		
	Oblique	26%	33%	12%	17%		
	Vertical	55%	55%	64%	65%		

Chapter 4

Discussion

P. v. coquereli is highly specialized for VCL among lemurs, while *L. catta,* a terrestrial, quadrupedal lemur, uses a wide variety of locomotor types. Quadrupedalism likely allows for greater flexibility in performance standards during locomotion, whereas VCL performance entails increased risks associated with failure or falling, as the success of the leap is entirely determined by its velocity at takeoff, and large gaps, commonly 6-8 meters in distance, are often crossed with a single leap (Petter, 1962 in Napier and Walker, 1967, Napier and Walker, 1967). *P. v. coquereli* and *L. catta* are born with similar ratios of upper to lower limb lengths (IMI) and achieve lowest IMI values at the beginning of locomotor independence (24-52 weeks). *L. catta* retain these similar proportions throughout the juvenile period and into adulthood, while *P. v. coquereli* exhibit a dissociation of fore- and hindlimb growth (where IMI decreases considerably when lower limb length grows faster than upper limb length) for VCL specialization. This decrease in IMI is due to the rapid hind limb growth observed in transitional infants as positive allometry was seen in the femur and tibia, but isometry was seen in the humerus and radius (Figure 3.14). Although still absolutely smaller, the lower limb length of *P. v. coquereli* is relatively longer than the upper limb length at the initiation of locomotor independence than it is as a yearling or adult.

L. catta transitional infants show a very different locomotor behavior repertoire than yearlings while *P. v. coquereli* transitional infants and yearlings display very similar locomotor behavior repertoires. In *L. catta* infants, selection may not influence infant locomotor behavior, or may favor a variety of different locomotor behaviors to be used at different stages of development. Having the ability to use a wider variety of locomotor behaviors during travel may be advantageous to provide alternate options for crossing gaps that *L. catta* may not be capable of crossing by leaping with the limb proportions they exhibit. Because limb proportions are already similar to adults, this likely results in a less rapid postcranial growth schedule that is more fine tuned to the different behavioral requirements of each locomotor stage. While the IMI values are consistent through locomotor ontogeny, this fine tuning is evident by transitional infants showing greater hindlimb dominant locomotion, supplemented by positive allometric growth in the hindlimb length and muscle cross-sectional area. Yearlings on the other hand, which show more all limb dominant locomotion, supplemented by greater positive allometry in the forelimb length and muscle cross-sectional area.

Because of the demand for using VCL at a young age despite overall slow postcranial growth, *P. v. coquereli* transitional infants seem to be on a rapid trajectory towards achieving the limb proportions necessary for this form of specialized locomotion. Three findings may provide evidence as to how *P. v. coquereli* transitional infants are able to display similar locomotor repertoires as yearlings despite being absolutely smaller: 1) lowest IMI values achieved at the time of locomotor independence (6 months), 2) increased leap frequency, and 3) relatively long tails. I suggest that this rapid growth trajectory to achieve adult like limb proportions may be associated with *P. verreauxi's* distinctive adaptive strategy to the seasonal and stochastic environment that includes slow overall somatic growth (Richard et al., 2002; Godfrey et al., 2004), rapid dental development (Schwartz et al., 2002; Godfrey et al., 2004), and group travel that involves ricochetal leaping dependent on long lower limb lengths.

Survival Strategies: Influences of Locomotor & Postcranial Ontogeny

P. v. coquereli and *L. catta* are native to Madagascar, an island of climatic unpredictability (Dewar and Richard, 2007). Because of Madagascar's highly seasonal environment prone to intra- and interannual droughts and thus unpredictable patterns of fruiting and flowering, both indrids and lemurids have evolved adaptive strategies and specialized features to survive in such a stochastic environment (Morland, 1991; Hemmingway, 1995; Powzyk, 1997; Godfrey et al., 2004). Despite living under the same environmental pressures, these two species of lemur have evolved very different strategies for survival. Previous research has examined these animals' survival strategies in terms of maternal investment, somatic growth, and dental development (Godfrey et al., 2004; Richard et al., 2002; Table 1.1), but here we contribute previously unknown information concerning locomotor behavior and postcranial musculoskeletal proportions through ontogeny.

P. verreauxi shows slow somatic growth, low maternal investment, and rapid dental growth while *L. catta* conversely shows faster somatic growth, high maternal investment, and slower dental growth (Richard et al., 2002; Godfrey et al., 2004; Table 1.1). In terms of somatic growth, lemurids attain asymptotic adult body mass values sooner and have relatively faster postnatal growth rates than indrids (Richard et al., 2002; Lawler, 2006; Godfrey *et al.*, 2004; Sussman, 1991; Koyama et al., 2008; Sarah Zehr, personal communication). Additionally, cranial length grows slower in indrids than like-sized lemurids (Godfrey et al., 2004). Although *L. catta* gains body mass more rapidly than *P. verreauxi* through ontogeny, dental growth is much more precocial in *P. verreauxi* and all the indrids (Godfrey et al., 2004). This extremely precocial dental development in indrids has been associated with specializations for survival in a highly seasonal environment where young indrids need to be able to eat the same food as adults at a very early age (Janson and van Schaik, 1993; Samonds et al., 1999; Schwartz et al., 2002; Godfrey *et al*., 2004). *Propithecus* start ingesting solid foods at 4 to 6 weeks, while *L. catta* don't start ingesting solid foods until 10 weeks of age (Richard, 1976; Gould, 1990; Sussman, 1991; Godfrey et al., 2004) Because this precocial dental development allows for the early consumption of adult food and thus decreased maternal investment, indrids have been said to become "ecological adults" at an early age (Godfrey et al., 2004). Additional factors demonstrating indrids' lower maternal investment than lemurids include slower postnatal growth rates (6.15 g/day in *L. catta* and 6.0 g/day in *P. v. coquereli*) and decreased litter size (Godfrey et al., 2004; Van Horn and Eaton, 1979; Richard, 1976). It seems that this overall "slow and steady" somatic growth and reproduction maximizes survival in *P. verreauxi*, while "fast and hard" growth and reproduction works best for *L. catta*. This life history focus on each species' survival strategy is outlined (in black) in Figure 4.2.

From this study, we additionally recognize that survival strategies for *P. v. coquereli* may include similar infant and yearling locomotor behavior paired with rapid attainment of adult limb proportions by the time of locomotor independence (Figure 4.2). In *L. catta,* survival strategies may involve the use of very different locomotor repertoires between infants and yearlings and more variable musculoskeletal growth with limb length proportions similar to that of adults through ontogeny (Figure 4.2). The relationships of these new ontogenetic findings to previously studied life history survival strategies will be discussed below.

While many primates are specialized for leaping, *Propithecus* and other indrids are unique in that they are much larger in adult size than all other specialized leaping primates (i.e. galagos, tarsiers, and callitrichids) (Fleagle, 1999; Table 4.1). Despite being large in size and therefore having a lower muscle area to body mass ratio, indrids are likely still able to accomplish highly acrobatic long leaps because it is thigh-powered rather than tarsal-powered like it is in smaller primates (Demes et al., 1996). During thigh-powered leaping, indrids use their long thighs to increase the overall acceleration time of the leap (Demes et al., 1996). By increasing this acceleration time during takeoff, the animal is able to increase the takeoff velocity and in principle increase the overall leap distance (Demes et al., 1996). Such a leaping strategy might prove challenging to a small juvenile as they have absolutely smaller limb lengths than adults, and may be relatively poorly muscled early in ontogeny.

Table 4.1: Comparison of *Propithecus* to other specialized primate leapers in terms of body mass (Fleagle, 1999).

Species	**Average Adult Body Mass**
Propithecus	2.2-6.3 kg
Callitrichidae	100-700 g
Galago	95-300 g
Tarsius	58-141 g

P. v. coquereli is a folivore which exhibits low maternal input and slow returns, while *L. catta* is a frugivore which relies on high maternal input and fast returns (Table 1.1; Godfrey et al., 2004). *P. verreauxi*'s larger adult body mass facilitates digestion of a folivorous diet, which is lower in quality, but more predictable and obtainable in such a harsh environment (Godfrey et al., 2004). Indrids, including *P. v. coquereli*, have multiple digestive adaptations that allow for this low quality folivorous diet (Milne Edwards and Grandidier, 1875; Chivers and Hladik, 1980; Campbell et al., 2000). In addition to gut specializations focused on increasing surface area to volume ratios to aid in nutrient absorption, *Propithecus* undergo rapid dental growth that allow juveniles to be "ecological adults" at an early age, despite being undersized as juveniles (Schwartz et al., 2002; Godfrey et al., 2004; Figure 4.2).

Much like rapid dental growth is a specialization for early adult diet consumption and lower maternal investment, the rapid attainment of adult limb proportions may be a specialization that allows *P. v. coquereli* juveniles to be "ecological adults" in terms of locomotor behavior and thus group travel, despite being on a slow growth trajectory and absolutely smaller. The ability of infants to use similar locomotor behavior as yearlings and adults, despite great differences in size through ontogeny is important because they must keep up with the group during travel in order to survive. Three findings of this study suggest important contributions of postcranial growth patterns and locomotor behavior to this ability: 1) the attainment of longest lower limb lengths relative to upper limb lengths at the time of locomotor independence (6 months), 2) decreased leap distance paired with increased leap frequency, and 3) long tail length relative to body mass. *P. v. coquereli* experience strong selection to become "ecological adults" in diet early in life, but selection may also be acting on these animals to be "ecological adults" in terms of locomotor behavior (Figure 4.2). Each of these are discussed below in the context of the different adaptive strategies of indrids and lemurids.

P. v. coquereli infants reach longest lower limb lengths relative to upper limb lengths by the time of locomotor independence (6 months), where gradually decreasing intermembral indices reach their lowest values at 24 to 52 weeks (locomotor independence) (Figure 3.8a). Relatively longer lower limb (specifically the femur) length can increase the leap acceleration distance and time, which increases takeoff velocity (Demes et al., 1999). With the ability to increase leap takeoff velocity the absolutely smaller juvenile animal has the potential to either a) increase overall leap distance or b) decrease the overall time spent in each leap. Preliminary evidence has shown that juvenile and adult *P. v. coquereli* achieve similar takeoff velocities when leaping the same distance (Sean Francis and Caitlin Johnson, personal communication). This suggests that, the relatively longer lower limb length of juveniles may allow for this equivalence of takeoff velocities to be achieved. However, transitional infant *P. v. coquereli* also leap 0.50 meters less per leap than yearlings (Figure 3.16). Because average leap distance in infants was not greater than in yearlings, it is proposed here that an increased takeoff velocity in transitional infants could also serve to decrease the time spent on each leap (Figure 4.1). Lower average leap distance in infants may account for the higher frequencies of leaping used. Increasing the number of leaps used to travel the same overall distance, however, may increase the overall time spent travelling (Figure 4.2). Thus, the infant could make up for the additional time added in increasing leap frequency by increasing each leap's takeoff velocity and decreasing the overall travel time in order to keep up with the group to survive (Figure 4.1).

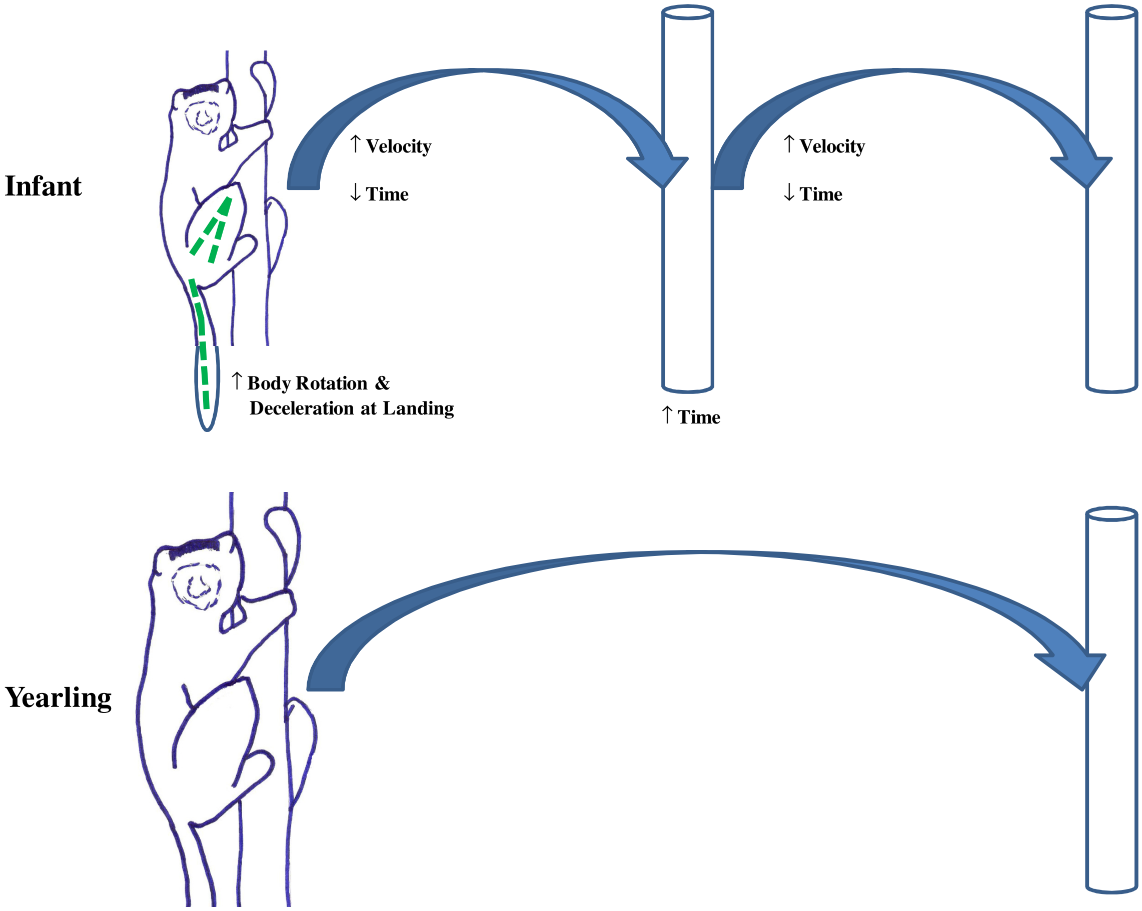

Figure 4.1: Figure representing how infant *P. v. coquereli* may obtain locomotor equivalence to yearlings and adults using an increased leap frequency and decreased leap distance. While the extra support the infant uses may be costly to performance in terms of time, time could also be decreased in each leap due to relatively longer lower limb lengths compared to upper limb lengths at locomotor independence which can increase the leap takeoff velocity. Increased tail length may serve to increase body rotation ability and overall stabilization.

A comparison of subadult (2.3-2.7 kg) and adult (3.8-4.2 kg) *P. verreauxi* found younger animals exert relatively higher peak takeoff and landing forces, in which takeoff forces were greater than landing forces (Demes et al., 1999). Demes (1999) suggests that these differences may be due to shorter acceleration distance and time in subadults and/or the idea that younger leapers are less experienced and “playing it on the safe side.” Here I suggest that greater peak forces in younger sifaka may also be due to increased leap velocity of infants, with their relatively longer hindlimb length to forelimb length at locomotor independence. This increased velocity may be an attempt to ensure adequate leaping distance or to decrease the time spent leaping, which may compensate for the time added by increasing leap frequency. This may allow younger infants to keep a pace similar to the group consisting of larger *P. v. coquereli* in order to keep up with the group to survive.

The other intriguing and functionally unaccounted for positive allometric growth seen in *P. v. coquereli* transitional infants was in the tail length. During adult VCL, the tail is clearly not creating the major thrust in takeoff, however it may play an important role in midflight kinematics, specifically body positioning and landing (Demes et al., 1996). When the tail is used in VCL, it is swung upward to initiate rotation of the body around a transverse axis and bring the hindlimbs forward for landing (Demes et al., 1996). The effect of tail movement on rotation is dependent on its weight in comparison to the rest of the body (Peters and Preuschoft, 1984; Demes and Gunther, 1989; Demes, 1991). This means that if tail length is any indication of tail weight, increased tail length relative to body mass in transitional and independent infants may have a significant role in midflight body rotation during VCL compared to yearlings and adults. This may be especially important since the upper limbs increased only with isometry in both transitional and independent infants and could potentially be relatively small for their body mass in *P. v. coquereli* infants. This notion stems from kinematic differences in VCL across indrids. Larger indrids, like adult *P. v. coquereli,* use their arms to enhance takeoff force and initiate body rotation while airborne, while smaller leapers, like tarsiers, rely more on their tails (Niemitz, 1984; Peters and Preuschoft, 1984; Demes *et al.*, 1996). Younger *P. v. coquereli* that are smaller in size relative to adults may benefit more by using their tail rather than their arms to rotate the body during leaping. In this case, interspecific kinematic differences related to body mass may be reflected in intraspecific growth differences. Future studies should investigate VCL kinematics through ontogeny, specifically focusing on the role of the arms and the tail in body rotation, as well as tail weight in comparison to overall body weight through ontogeny. Furthermore, more data is necessary on takeoff velocities through ontogeny in *P. v. coquereli*. If younger *P. v. coquereli* are showing postcranial growth trajectories that promote relatively fast hind limb growth, increased leap takeoff velocities similar to adults, and overcompensating leaps to reduce risks of falling or failure as discussed previously, then increased methods for body rotation and stabilization may be necessary and highly adaptive (Figure 4.1).

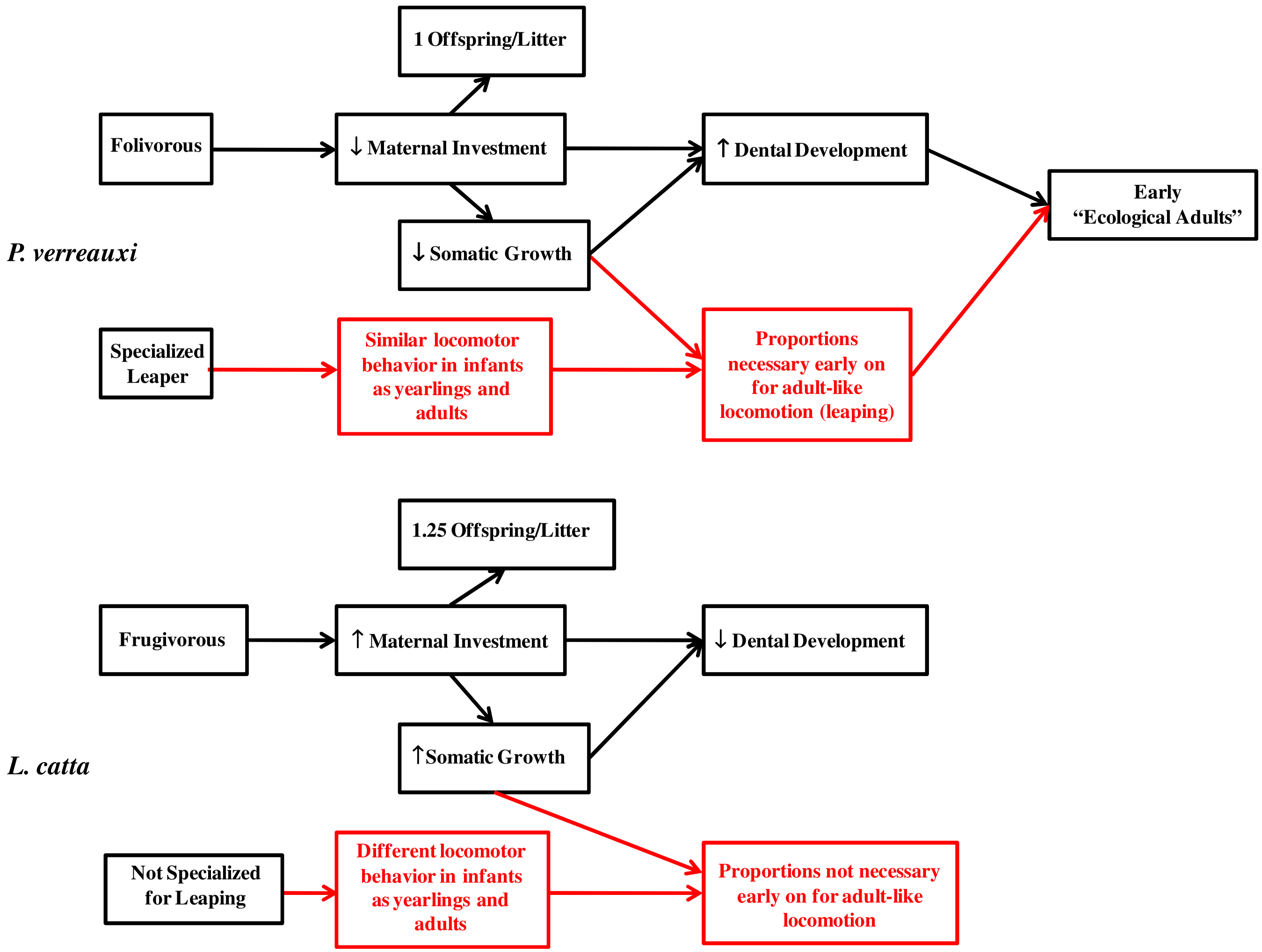

Figure 4.2: Flow chart relating the life history survival strategies (in black, highlighted in Richard et al., 2002 and Godfrey et al., 2004) to locomotor behavior and postcranial morphology through ontogeny (in red) for both *L. catta* and *P. verreauxi.*

Methodological Considerations

Of all the methods and protocols used to obtain data throughout this study, some provided intriguing results worthy of further discussion. Perhaps the most notable is the breakdown of 0 to 2 year growth into smaller categories relevant to locomotion. This technique allowed for the discovery that allometric coefficients differ from one age category to another and therefore postcranial allometric growth is not constant from 0 to 2 years in *L. catta* and *P. v. coquereli* (Figures 3.14 & 3.15; Table 3.2). These differences in limb segment allometric growth highlight the importance of collecting longitudinal data using a complete range of ages. In Ravosa et al. (1993), isometry was observed in sifaka ontogeny using cross-sectional data comprised mostly of adults. In Lawler (2006), using cross-sectional data, isometry was found in all limb segment lengths except the hand and foot which showed negative allometry. This study, which examines *P. v. coquereli* from 0 to 2 years, many lemurs of which were 0 to 6 months in age, reflects these trends, but not coefficients. For example, overall higher allometric coefficients were found in this study, but trends were similar in that where previous studies found isometry, we found positive allometry, and where previous studies found negative allometry, we found isometry. Furthermore, allometric trends were really different within each locomotor category examined, indicating that a single trajectory is not indicative of the growth occurring early in ontogeny (Figure 4.3).

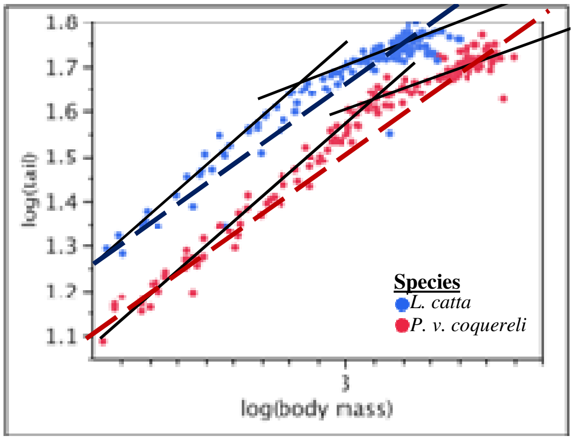

Figure 4.3: Longitudinal log-transformed tail length data regressed over log-transformed body mass for both *P. v. coquereli* (red) and *L. catta* (blue) from 0-2 years. Narrow, solid black lines indicate the two different trends seen for each species' tail segment length. Large dashed lines indicate how the data could be misrepresented by a single growth trajectory.

Future investigations of growth allometry through ontogeny should first critically examine the age distribution of the sample being studied before making concrete conclusions about an animal's growth. It may be more appropriate to break down growth trajectories into smaller categories that are relevant to the species' development. These smaller categories are important because, as observed in this study, different segments of the postcranial skeleton are showing different patterns of growth at different periods of time through ontogeny. Additionally, the use of cross-sectional data may not accurately piece together a species' growth trajectory (Figure 4.4). Not only can cross-sectional data eliminate variation among individuals (Fiorello and German, 1997), but it may mask the idiosyncrasies of postcranial growth. Figure 4.4 represents the longitudinal growth trajectory of a species (in red), but how cross-sectional point sampling at two ends of the spectrum (blue) can create an inaccurate representation of the ontogenetic trend for the same species.

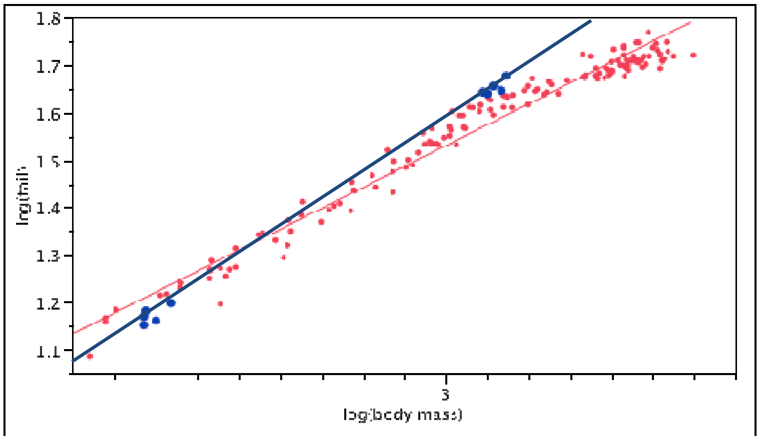

Figure 4.4: Potential cross-sectional (blue) data collection versus actual longitudinal (red) data collection. Cross-sectional data may not accurately represent the growth trajectory of a species as longitudinal data does. All data points were recorded using longitudinal data collection.

In behavioral data collection, another important finding was the potential variation in group behavior. Because the *L. catta* transitional infants observed were not in the same group or enclosure as the yearlings observed, there exists the possibility that locomotor behavior and support use differences result from individual *L. catta* troop preference, which may or may not also be dependent on the variability in each enclosure's forest habitat. To rule out these possibilities, further studies should use animals in the same group and home range. Because all enclosures were comprised of deciduous forest of a relatively large area (2 to 4 ha), the likelihood of environmental variation seems low, however other *L. catta* troops in neighboring enclosures may have had a more particular impact of a social nature on group movements.

Captive data collection versus wild data collection is also a very important methodological consideration. Captive studies offer many benefits that wild ones cannot, including accurate age estimations, animal identification, and convenience and ease of frequent data collection, especially for a longitudinal design such as this one. Among perhaps the most important is that growth studies benefit from measurements that can be taken regularly and frequently. Captivity has the ability to reflect the genetic potential for individual growth in a species, but it may not necessarily reflect the extent to which animals achieve it under natural conditions (King et al., 2011). Previous findings indicate that captivity may accelerate locomotor development and affect absolute size and relative proportions of body segments (Schwandt, 2002 in Schaeffer and Nash, 2007).

In this study, locomotor behavior in captive *P. v. coquereli* is only slightly different than that of wild *P. v. verreauxi* from Lawler (2006). Both species show the same locomotor behaviors, however these behaviors constitute different distributions of their overall locomotion. Captive *P. v. coquereli* use more climbing and less VCL than wild *P. v. verreauxi* (Table 3.7). Support use also differs where captive *P. v. coquereli* use more medium, large, horizontal, and vertical supports than wild *P. v. verreauxi* who use more small and oblique supports (Table 3.7). These deviations may be due to differences in the environment. Wild *P. v. verreauxi* live in the dry deciduous forests of the Beza Mahafaly Reserve in southwestern Madagascar. This reserve is also comprised of an arid spiny forest. Captive *P. v. coquereli* were studied in deciduous forest in Durham, North Carolina. The Beza Mahafaly forest may be less dense in trees relative to the forest at the DLC. These sparser forests that wild *P. v. verreauxi* live in likely require the use of more VCL to cross larger gaps.

Conclusions

Previous research has examined lemurid and indrid survival strategies in terms of life history (Table 1.1;Godfrey et al., 2004; Richard, 2002), but here I contribute previously unknown information concerning the ontogeny of locomotor behavior and postcranial musculoskeletal proportions. This ontogenetic study has undoubtedly demonstrated that postcranial growth is not a single consistent trajectory, but is instead a more variable path from birth to adult forms. Having the ability to study growth at different periods through ontogeny is best executed using longitudinal data. While it may be more difficult to collect data in a longitudinal manner, its ability to display a more accurate representation of growth, which includes the idiosyncrasies and individual variation within a species, are far superior to cross-sectional data collection.

Both *L. catta* and *P. verreauxi,* despite living under the same environmental pressures, have different strategies for survival not only in terms of life history and dental adaptations, but also locomotor development and postcranial growth. Much like *P. verreauxi* are “ecological adults” early on in terms of their dietary habits and rapid dental development, they seem to also be “ecological adults” early on in terms of locomotor behavior. Because of the demand for using VCL at a young age despite overall slow postcranial growth, *P. verreauxi* transitional infants are on a rapid growth trajectory towards achieving the limb proportions necessary for specialized leaping. Lowest IMI values at locomotor independence, high positive allometric growth in the tail, and increased leap frequency paired with decrease leap distance illustrate how *P. verreauxi* transitional infants display similar locomotor repertoires to yearlings despite being absolutely smaller. I suggest that this rapid growth trajectory to achieve adult-like limb proportions may be associated with *P. verreauxi*, and likely all indrids’ distinctive adaptive strategy from that of lemurids to the seasonal and stochastic environment that includes slow overall somatic growth, rapid dental development, and group travel that involves ricochetal leaping that depends on long leg lengths.

Appendix A

This section examines locomotor behavior using an alternative method of locomotor bout sampling which quantifies the frequency of leaping sets, as described by Fleagle (1976), quantifying a continuous set of leaps as a bout. Of all the positional bouts collected, 52% (6,843/13,048) were locomotor bouts and 48% (6,199/13,048) were postural bouts. Only locomotor bouts were analyzed. *L. catta* transitional-infants display <1% brachiation, <1% bipedalism, 23% climbing, 28% leaping, 41% quadrupedalism, and 6% VCL during locomotion (Table A.1). *L. catta* yearlings display <1% brachiation, <1% bipedalism, 9.6% climbing, 19% leaping, 70% quadrupedalism, and <1% VCL during locomotion (Table A.1). Climbing, leaping, brachiation, and VCL constitute a higher amount of locomotion in *L. catta* transitional-infants, while quadrupedalism constitutes a higher percent of locomotion in *L. catta* yearlings (Table A.1).

Transitional-infant *P. v. coquereli* display 4.9% brachiation, 5.8% bipedalism, 40% climbing, 22% leaping, <1% quadrupedalism, and 27% VCL during locomotion (Table A.1). Yearling *P. v. coquereli* display 4.7% brachiation, 9% bipedalism, 43% climbing, 16% leaping, <1% quadrupedalism, and 27% VCL during locomotion (Table A.1). In *P. v. coquereli*, leaping constitutes a higher percent of locomotion in transitional-infants than yearlings (Table A.1). VCL, climbing, and brachiation constitute a higher percent of locomotion in *P. v. coquereli* transitional-infants and yearlings than *L. catta* transitional-infants and yearlings in which quadrupedalism is a higher percent of locomotion (Table A.1). Additionally, leaping constitutes a higher percent of locomotion in *P. v. coquereli* transitional-infants than *L. catta* transitional-infants (Table A.1).

Table A.1: Frequency of locomotor bouts used during locomotion. Locomotor bouts here are characterized by the frequency of leaping sets. 95% Confidence intervals calculated using bootstrap resampling. (Y=yearling, I=infant, L=*Lemur catta*, P=*Propithecus verreauxi coquereli*)

		Frequency (%)	Lower	Upper	Sig. Dif. From
LI	**Brachiate**	0.86	0.43	1.4	LY, PI, PY
	Bipedalism	0.43	0.14	0.79	PI, PY
	Climb	23	21	26	LY, PI, PY
	Leap	28	26	30	LY, PI, PY
	Quadrupedal	41	39	44	LY, PI, PY
	VCL	6.00	4.8	7.2	LY, PI, PY
LY	**Brachiate**	0.19	0.063	0.35	LI, PI, PY
	Bipedalism	0.095	0	0.22	PI, PY
	Climb	9.6	9	11	LI, PI, PY
	Leap	19	18	21	LI
	Quadrupedal	70	69	72	LI, PI, PY
	VCL	0.66	0.41	1.0	LI, PI, PY

		Frequency (%)	Lower	Upper	Sig. Dif. From
PI	**Brachiate**	4.9	3.8	6.1	LI, LY
	Bipedalism	5.8	4.6	7.0	LI, LY
	Climb	40	37	43	LI, LY
	Leap	22	20	25	PY, LI
	Quadrupedal	0.29	0.071	0.57	LI, LY
	VCL	27	24	29	LI, LY
PY	**Brachiate**	4.7	3.3	6.0	LI, LY
	Bipedalism	9	7.2	11	LI, LY
	Climb	43	39	46	LI, LY
	Leap	16	13	18	PI, LI
	Quadrupedal	0.91	0.34	1.6	LI, LY
	VCL	27	24	30	LI, LY

Locomotion was also categorized into categories according to limb usage bouts. In *L. catta* transitional-infants, 65% of all locomotion was considered to use all four limbs, <1% was considered to be forelimb-dominant, and 34% was hindlimb-dominant locomotion. In *L. catta* yearlings, 80% of all locomotion was considered to use all four limbs, <1% was considered forelimb dominant, and 20% was hindlimb dominant locomotion (Table A.2). *L. catta* transitional-infants show more hind- and forelimb dominant locomotion and less all-limb dominant locomotion than yearlings, which is associated with increased amounts of leaping and VCL in transitional-infants than yearlings (Table A.2). In infant *P. v. coquereli,* 40% of locomotion was considered to use all four limbs, 4.9% of locomotion was considered to be forelimb-dominant, and 55% was hindlimb-dominant locomotion while yearlings show 44% all-limb, 4.7% forelimb, and 52% hindlimb-dominant locomotion (Table 5.2). *P. v. coquereli* transitional-infants and yearlings show no differences from one another in all-limb, forelimb-, or hindlimb-dominant locomotion frequencies (Table A.2). Both *P. v. coquereli* transitional-infants and yearlings show less all-limb and more hind- and forelimb dominant locomotion than both transitional-infant and yearling *L. catta* (Table A.2).

Table A.2: Frequency of dominant limb(s) used bouts during locomotion. Locomotor bouts here are characterized by the frequency of leaping sets. 95% Confidence intervals calculated using bootstrap resampling. (Y=yearling, I=infant, L=*Lemur catta*, P=*Propithecus verreauxi coquereli*)

		Frequency (%)	**Lower**	**Upper**	**Sig. Dif. From**
LI	**All-limb**	65	62	67	LI, PI, PY
	Forelimb	0.86	0.43	1.4	LI, PI, PY
	Hindlimb	34	32	37	LI, PI, PY
LY	**All-limb**	80	78	81	LY, PI, PY
	Forelimb	0.19	0.063	0.35	LY, PI, PY
	Hindlimb	20	19	21	LY, PI, PY
PI	**All-limb**	40	38	43	LI, LY
	Forelimb	4.9	3.8	6.1	LI, LY
	Hindlimb	55	52	57	LI, LY
PY	**All-limb**	44	40	47	LI, LY
	Forelimb	4.7	3.3	6.1	LI, LY
	Hindlimb	52	48	55	LI, LY

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