

Dissertation Advisor: Jesse W. Young

Much research on arboreal primate locomotion focuses on the morphological and locomotor adaptations that allow primates to navigate supports that vary in diameter, orientation, continuity, and other physical properties. However, sensory and cognitive processes also affect locomotion. Some studies have cited risk avoidance as cause for certain locomotor behaviors, but in this dissertation, I make the first concerted efforts to quantify risks and measure risk avoidance. In my first study, I determined whether increased height – which would correspond to increased risk of injury after a fall – affected the gait of wild lemurs: *Eulemur rufifrons*, *Eulemur rubriventer*, *Hapalemur aureus*, and *Lemur catta*. I found that height alone did not induce more stable forms of locomotion in most species of lemur, even those that traveled highest in the trees. However, one lemur species – *E. rubriventer* – did increase stability as they increased height, suggesting that lemurs may be sensitive to height but in conjunction with other variables. In my next study, I analyzed the locomotion of wild primates – *Cercopithecus ascanius*, *Papio anubis*, *Eulemur rubriventer*, and *Lemur catta* – as they crossed gaps between branches. I found that while the size of branches that primates preferred for crossing gaps differed among species, all species – regardless of size – were highly proficient at bridging and leaping to cross those gaps. Some subtle patterns did emerge: *C. ascanius* species tended to wait longer to leap across a gap when carrying an infant. Both of these chapters on wild primates address potential ways primates use their vision to effectively guide locomotion. In my last chapter, I examine the effects of light availability – i.e., reduced visual information – on the gait of captive lemurs: *Varecia rubra* and *variegata*, *Lemur catta*, and *Eulemur flavifrons*. These lemurs varied in overall body size and possession of a tapetum lucidum, a reflective tissue layer

behind the retina which would augment vision in dim light. All lemurs made some adjustments to gait that increased stability when they moved in dim light; however, the most pronounced changes were found in the largest bodied lemurs without a tapetum lucidum (*Varecia*). Altogether, these findings indicate that primates are effectively able to perceive risks and often make subtle changes to their locomotion to maneuver through situations that researchers may perceive as risky. The methods applied here will be useful for examining the development of such robust locomotor repertoires in the future.

PRIMATE ASSESSMENT OF RISK DURING ARBOREAL LOCOMOTION

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by

Nicole M. Schapker

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Dissertation written by
Nicole M. Schapker
B.A., Miami University, 2019
Ph.D., Kent State University, 2025

Approved by
Jesse W. Young, Chair, Doctoral Dissertation Committee
Jesse W. Young, Ph.D.

Tobin L. Hieronymus, Members, Doctoral Dissertation Committee
Tobin L. Hieronymus, Ph.D.

Merri J. Rosen
Merri J. Rosen, Ph.D.

Christopher J. Vinyard
Christopher J. Vinyard, Ph.D.

Karen E. Adolph
Karen E. Adolph, Ph.D.

Karin G. Coifman
Karin G. Coifman, Ph.D.

Accepted by
John D. Johnson, Director, School of Biomedical Sciences
John D. Johnson, Ph.D.

Mandy J. Munro-Stasiuk, Dean, College of Arts and Sciences
Mandy J. Munro-Stasiuk, Ph.D.

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PREFACE

Chapters 1 and 3 through 5 are original text written for the purpose of this dissertation.

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For previously published material, data collection was performed by J. Janisch, L.C. Myers, and myself. Original study design for the recording of wild primates was conceptualized by L.J. Shapiro and J.W. Young, with original contribution from me for the recording of branch height. Data curation and analysis were led by me with contributions from T. Phelps, I. Barry, and A. Hottensmith. The manuscript was written by me with feedback from co-authors and anonymous reviewers.

These same contributors helped with video recording and data curation for Chapter 3. Video coding was performed by myself, J. Pham, and A. Matar. For Chapter 4, I designed the project, did all video recording and data curation, and led analyses. Video coding was performed by myself, A. Boghdady, and A. Miller.

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CHAPTER 1: OVERVIEW

Introduction

The primary goal of the following research is to investigate how primates use their senses of vision and touch to guide safe locomotion through the trees.

The mechanisms by which primates maintain stability while moving through their arboreal habitats have been of great interest for decades. Arboreal animals must navigate networks of locomotor supports that simultaneously vary in their physical properties – e.g., diameter, orientation, and compliance. For animals that move between terminal branches, like many primates do, a miscalculation could lead to falls from great heights, meaning that maintaining stability should be a driving pressure for behavioral and morphological adaptations. However, most research on primate locomotor adaptation has been conducted within theoretical frameworks that tend to bypass the cognitive and sensory processes that also govern behavior.

The research presented in Chapters 2 and 4 in this dissertation uses standard methods in locomotor biomechanics to address novel questions about how environmental factors assessed via vision – height in the tree canopy and light availability – may influence the locomotion of wild and captive lemurs. In Chapter 3, I designed and carried out new analytical methods adapted from the field of motor development in human psychology to investigate how primates assess the safety of untested supports while crossing gaps in the trees. The present introductory chapter aims to provide further context for readers about the relevant literature on primate gaits, decision-making in primate locomotion, and the primate subjects chosen for these studies.

Gait, arboreal locomotion, and primate adaptations

Gait analysis

Chapters 2 and 4 of this dissertation use gait analyses to assess the locomotor performance of lemurs. Generally, gaits are cyclical forms of locomotion which can be described via the different ways the body is supported by the limbs. Following the large body of comparative gait analyses done by Hildebrand (Hildebrand, 1966, 1976, 1977), gaits may be divided into two broad categories: symmetrical gaits, where the timing of the footfalls of forelimb and hindlimb pairs are evenly spaced during a gait cycle, and asymmetrical gaits, where those pairs of limbs are unevenly spaced. Examples of symmetrical gaits include walks and trots, while asymmetrical gaits include gallops and bounds.

Primates use a variety of both symmetrical and asymmetrical gaits, though their relative usage can vary among species. For instance, asymmetrical gaits are more common among small-bodied primates like callitrichids (marmosets and tamarins; Chadwell & Young, 2015; Dunham et al., 2020; Nyakatura et al., 2008; Young, 2009). The primate subjects in Chapters 2 and 4, however, were larger-bodied and predominantly used symmetrical walking gaits. Walking gaits occur at low speeds and therefore do not have an aerial phase (i.e., at least one limb is always in contact with the support). They consist of alternating patterns of limb support that may be further categorized: lateral sequence and diagonal sequence gaits (Hildebrand, 1967, 1976). Lateral sequence gaits proceed in this order: reference hindlimb, ipsilateral forelimb, contralateral hindlimb, contralateral forelimb. An example sequence of contacts may go left hindlimb, left forelimb, right hindlimb, and right forelimb. Diagonal sequence gaits proceed in the following order: reference hindlimb, contralateral forelimb, contralateral hindlimb, ipsilateral forelimb. An example sequence beginning with the same left hindlimb would then follow with the contact of the right forelimb, then right hindlimb, and end with the left forelimb.

In order to further discuss the connections between gait and later arguments made about primate locomotion, it is helpful to first discuss some parameters which are commonly

used to mathematically describe gaits (summarized in Table 1.1). A stride is the unit of a gait cycle which is defined as the subsequent contacts of a reference limb, and it can be described by both its length (distance crossed between contacts) and frequency (reciprocal of duration). The period over which a single limb is in contact with a locomotor support as a percentage of stride duration is known as duty factor (Hildebrand, 1966). Duty factor is negatively correlated with speed such that walking gaits have relatively high duty factors whereas running gaits have low duty factors. Limb phase, or diagonality, is a measure to quantify the relative timing of the contacts of the limbs during a gait cycle (Cartmill et al., 2002; Hildebrand, 1967). Limb phase indicates the time passed between the contact of a hindlimb and the contact of an ipsilateral forelimb, measured as a proportion of the stride duration of that hindlimb. One can see how limb phase then relates to gait sequence – lateral sequence gaits will have lower limb phase below 50% of stride duration while those limb phase values will be above 50% for diagonal sequence gaits. Finally, related to both duty factor and limb phase is the mean number of supporting limbs, or the average number of limbs in contact with the support over the course of the stride (Shapiro et al., 2014; Shapiro & Young, 2012). The mean number of supporting limbs contains both information about contact time with the support (like duty factor) as well the relative timing of footfalls (like limb phase).

Table 1.1 Common terminology and definitions used in gait studies

Gait property	Definition
<i>Speed</i>	The distance traveled over a unit time. Presented as relative to body length (Chapter 2) and in meters per second (Chapter 4)
<i>Stride frequency</i>	The number of strides per second (Hz), the reciprocal of stride duration in seconds
<i>Stride length</i>	The distance traveled between subsequent touchdowns of the reference limb
<i>Duty factor</i>	Proportion of limb contact duration and stride duration. May be reported for single limbs, within limb pairs, or averaged over all limbs.
<i>Limb phase</i>	The percent of a stride that elapses between the touchdown of the reference hindlimb and the ipsilateral forelimb.
<i>Mean number of supporting limbs</i>	Average number of limbs contacting the support at any instance during the stride

Behavioral adaptations of arboreal primates

Theories regarding primate locomotor adaptation and evolution often center around the idea that primates must navigate a fine branch niche. This term describes the spaces in arboreal habitats at the distal ends of branches where supports are narrow, compliant, and often angled. Being able to traverse through such spaces may provide foraging opportunities and increase locomotor efficiency by being able to form more straight paths between resources (Cant, 1992; Sussman, 1991; Sussman et al., 2013). Maintaining stability atop narrow, compliant, and angled supports ultimately requires reducing mediolateral torques about the center of mass which could require extra musculoskeletal effort to correct lest the animal topple from the branch (Cartmill, 1985; Lammers & Gauntner, 2008; Larson & Stern, 2006). Features common among many primates – grasping hands and feet, gracile limbs, and long, mobile tails – may be especially helpful for making those corrections during locomotion (Granatosky, 2020;

Larson, 2018; Mincer & Russo, 2020; Schmitt, 2010; Young et al., 2021).

Primates are unusual compared to other clades of tetrapods because diagonal sequence gaits predominate (Hildebrand, 1976). Cartmill and colleagues have argued that diagonal sequence gaits are advantageous on narrow arboreal supports because it places the primate's grasping hindlimb on a tested support where it can anchor the body before the contralateral forelimb touches down on an untested segment of the branch (Cartmill et al., 2002, 2007). The mechanical predictions behind this idea still require further testing (Shapiro & Raichlen, 2005, 2007; Stevens, 2006, 2008), but there is supporting and mitigating evidence to the idea that gait sequence is important for further understanding of arboreal locomotor adaptions. First, the fact that many non-primate arboreal species also use diagonal sequence gaits supports further research into this question (Wimberly et al., 2021; Young, 2023). However, primates do engage in lateral sequence gaits as well, often on more angled substrates, and so a deeper understanding of the contexts in which diagonal sequence gaits may be useful is required (Dunham et al., 2019; Nyakatura et al., 2008; Nyakatura & Heymann, 2010; Stevens, 2006; Young, 2012). Chapter 4 briefly discusses the prevalence of diagonal and lateral sequence gaits recorded in those three genera under study.

Besides gait sequence, primates are also thought to adopt compliant gaits as a behavioral adaption for arboreal locomotion, moving in a way that smoothens the trajectory of the center of mass and aids in stability (Schmitt, 1999; Schmitt et al., 2006). These gaits are characterized by slower speeds, reduced stride frequencies, and increased stride lengths, all aided by the increased angular excursions of their long limbs. Many studies not exclusive to primates have indeed indicated that make these changes to their gaits on thin, oblique supports are common strategies for increasing stability (Gaschek et al., 2019; Karantanis et al., 2015; Lemelin et al., 2003; Shapiro et al., 2014; Shapiro & Young, 2010, 2012; Wallace & Demes, 2008; Young, 2023). Shared strategies should not be misinterpreted as shared competency, however. Comparing the locomotor performance of the arboreal *Petaurus breviceps* to the

terrestrial *Monodelphis domestica*, Shapiro and colleagues (Shapiro et al., 2014) found that the two shared some kinematic changes to gait in response to changes in branch diameter and orientation but the response from *Monodelphis* was more exaggerated. Similarly, though marmosets and squirrel monkeys are both arboreal primates, squirrel monkeys (*Saimiri boliviensis*), with their more generalized primate body plan, change their gait little when moving from safe supports (broad and stiff) to precarious supports (narrow and compliant), in comparison to marmosets (*Callithrix jacchus*) who are more specialized for feeding on broad tree trunks (Schapker et al., 2022; Young & Chadwell, 2020).

On narrow and compliant supports, increasing duty factors and the mean number of supporting limbs may increase stability by reducing peak impulses on the support (thereby reducing unpredictable oscillations of the branch) and providing more time for corrective torques to be exerted by the limbs (Chadwell & Young, 2015; Dunham et al., 2019; Karantanis et al., 2015; Shapiro & Young, 2012; Young & Chadwell, 2020). However, squirrel monkeys (*Saimiri boliviensis*) did not make these same adjustments to duty factors and mean number of supporting limbs, suggesting that the grasping appendages and long limbs of these animals may facilitate robust locomotor performance.

Risk perception and behavioral analysis

Safe movement requires an understanding of one's affordances, or the behaviors available to an animal given its physical environment (Gibson, 1979). In an arboreal environment, this might mean seeing that a branch is relatively thin and anticipating the branch's displacement after being loaded by the animal's body mass (Adolph & Young, 2021; Hunt et al., 2021; Lee et al., 2025). In the precarious fine branch niche, accurately assessing the limitations to one's locomotor capabilities should be important for avoiding accidents and increasing fitness (Wheatley et al., 2021). Affordances, because they depend on the relationship between animal and environment, can change when either experiences a change in properties.

In most cases, the perception of affordances begins with sight. Human infants and toddlers focus their gaze on the obstacle that needs to be crossed (a gap, a bridge, a slope, etc.), then gather information haptically by touching and testing the support (Adolph, 1995, 1997; Adolph et al., 2018; Adolph & Robinson, 2015; Kretch & Adolph, 2017). Sometimes they fail to accurately assess those affordances, but when a toddler misjudges a slope in a research context, an adult is there to catch them. By the time humans reach adulthood, the ability to accurately perceive affordances may be achieved with quick glances (Adolph & Franchak, 2017; Franchak & Adolph, 2014). Discontinuities between locomotor supports are encountered continuously in the tree canopy, forcing primates to visually assess untested supports (Cannon & Leighton, 1994; Cant, 1992; Druelle et al., 2020; Graham & Socha, 2020; McLean et al., 2016; McNamara et al., 2019). Chapter 3 uses a quantitative behavioral approach adapted from these studies on human motor development to investigate how primates varying in body mass and locomotor repertoires assess the safety of untested supports as they move through the trees.

Arboreal primates, for their part, have committed to using sight even in very low light conditions (Heesy, 2009; Kirk, 2006). The large eyes and reflective tapetum lucidum of nocturnal species such as aye-ayes (*Daubentonia*), tarsiers (*Tarsius*), and owl monkeys (*Aotus*) supports this idea. However, among lemurs, cathemeral activity cycles – cycles that do not adhere to strict diurnal-nocturnal boundaries – are common, even though not every species has a tapetum lucidum (Bray et al., 2017; Colquhoun, 1998; Peichl et al., 2019; Schwitzer et al., 2007; Tattersall, 1987; Valenta et al., 2016). In Chapter 4, I investigate whether the absence of the tapetum lucidum in *Varecia* and *Eulemur* subjects leads to the use of more stable gaits in dim light conditions.

Though compliant, discontinuous branches might describe the physical setting of a low bush, the added element of height above the ground perhaps confers the most risk to arboreal living. A fall from several meters up can mean serious injury or death, and documentation of injuries sustained to long bones in primates suggest that injuries due to falls are rather common

(Jarrell, 2011). Despite the increased risk of injury after falling from increased heights, there are several reasons primates may be found moving at a given height in the canopy. Larger monkeys tend to use larger supports, and the distribution of support size in the canopy depends on the age of the forest and the plants it contains (Cant, 1992; Fleagle & Mittermeier, 1980; McGraw, 1996, 1998). Foraging opportunities may also encourage a group of primates to disperse around the crown of the tree to feed. However, it is unclear whether animals are changing behavior on a stride-to-stride basis based on their height above the ground. In Chapter 2, I analyze the gaits of four species of wild lemur to determine whether height above the ground influences their locomotion.

In summary, the following research serves as a bridge between different ways researchers understand primate movement. By being arboreal, primates must contend with biomechanical challenges posed by the locomotor supports available to them. However, primates may also be nocturnal, diurnal, and cathemeral, meaning they move with different levels of ambient light to help guide their paths. They forage and travel at many levels of the tree canopies they inhabit, meaning the risks posed by failure constantly fluctuate. Primates also vary considerably in their body sizes and locomotor repertoires, meaning the risks they encounter also vary on an individual and species-level. My goal with the following research and future work is to better understand how risk perception and risk avoidance behaviors may form part of the suite of adaptations that many primates possess for arboreal life.

Primate subjects

Chapter 2 and 3 investigate the locomotion of wild primates. The predominant group of primates in these two studies are lemurs (Lemuridae), which comprise a family of primates native only to Madagascar. Chapter 3 includes two species of cercopithecoid monkeys found in western Uganda. Lastly, Chapter 4 focuses on four species (discussed as three genera) of captive lemur housed at the Duke Lemur Center. See Figure 1.1 for phylogenetic relationships.

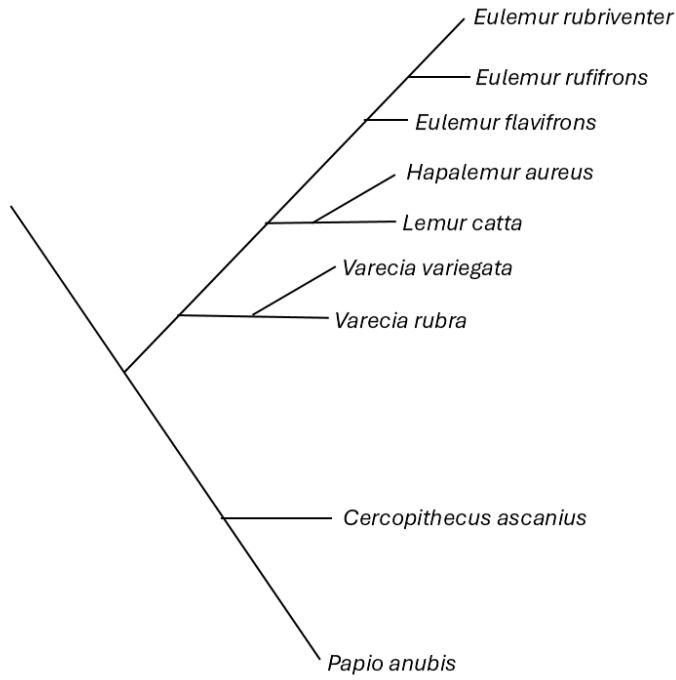


Figure 1.1 Phylogenetic relationships between taxa in this dissertation. Based on (Fleagle et al., 2013; Markolf & Kappeler, 2013).

Lemurs

Lemur catta

Commonly referred to as the ring-tailed lemur, *Lemur catta* is the most terrestrial lemur, though they do engage in some arboreal quadrupedalism and leaping (Ward & Sussman, 1979). They possess a tapetum lucidum (Valenta et al., 2016). This was considered unusual, as they were thought to be diurnal, though some research indicates that some populations may be cathemeral as well, or active at both day and night (Donati et al., 2013; Tattersall, 1987). This species is the only species found in each research chapter of this dissertation and is represented by the color gray where interspecies analyses are performed. The wild ring-tailed lemurs in Chapters 2 and 3 were recorded at the Anja Community Reserve in southeast Madagascar. Three individuals housed at the Duke Lemur Center were used in experiments for

Chapter 4 and future work.

Eulemur spp.

The genus name *Eulemur* means “true lemur,” and this group is the most speciose of the family (Fleagle, 2013). The red-fronted brown lemur, *Eulemur rufifrons* (previously *E. fulvus rufus*) and the red-bellied lemur, *E. rubriventer*, were recorded in Ranomafana National Park in Madagascar. These lemurs are strictly arboreal, and they use a mixture of quadrupedalism and leaping during locomotion (Dagosto & Yamashita, 1998; Overdorff, 1996). These two species are both in Chapter 2 and *E. rubriventer* is also present in Chapter 3.

The blue-eyed black lemur, *E. flavifrons*, is critically endangered in the wild, and so knowledge about their locomotor repertoires is limited (though see Schwitzer et al., 2007 for considerations of their activity cycles). Nonetheless, they are of similar size to *Lemur catta* and other *Eulemur spp.*, and data from the closely related black lemurs suggest that in the wild they would also use quadrupedalism and leaping as predominant forms of locomotion (Colquhoun, 1998).

Hapalemur aureus

The golden bamboo lemur, or *Hapalemur aureus*, inhabits the bamboo forests of Ranomafana National Park. Considering that such forests have relatively few horizontal or obliquely oriented supports, *H. aureus* tends to be a more prolific leaper than the other lemur species considered here (Glander et al., 1992). However, we were able to record the walking gaits of these animals, and those data are included in Chapter 2.

Varecia spp.

The red ruffed lemur, *Varecia rubra*, and the black and white ruffed lemur, *Varecia variegata*, are both relatively large quadrupedal lemurs (Pereira et al., 1988). They lack a tapetum lucidum (Valenta et al., 2016), and they have been historically considered diurnal, though some evidence points to their potential for cathemeral activity as well (Bray et al., 2017; Wright, 1999). Individuals from both species were involved in experiments in Chapter 4 at the

Duke Lemur Center given their morphological and behavioral similarities (Vasey & Tattersall, 2002).

Cercopithecoids

Cercopithecus ascanius

Also known as the red-tailed monkey, *Cercopithecus ascanius* travels in large groups and is a very arboreal species (Gebo & Chapman, 1995). Slightly more massive than lemurs, these monkeys were still on the low end of the ranges of body masses of sympatric monkeys living in Kibale National Park, Uganda. This species is included in the analyses of Chapter 3.

Papio anubis

The olive baboon, *Papio anubis*, represents the opposite end of the size range of monkeys in Kibale National Park. These baboons occupy a range of habitats across central Africa, and while highly terrestrial, will often forage and rest in trees when they occupy densely forested areas like those in the national park. This species is included in the analyses of Chapter 3.

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CHAPTER 2: FROM SUCH GREAT HEIGHTS: THE EFFECTS OF SUBSTRATE HEIGHT AND THE PERCEPTION OF RISK ON LEMUR LOCOMOTOR MECHANICS

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Abstract

An accident during arboreal locomotion can lead to risky falls, but it remains unclear the extent to which primates, as adept arborealists, change their locomotion in response to the perceived risk of moving on high supports in the tree canopy. By using more stable forms of locomotion on higher substrates, primates might avoid potentially fatal consequences. Using high-speed cameras, we recorded the quadrupedal locomotion of four wild lemur species – *Eulemur rubriventer*, *Eulemur rufifrons*, *Hapalemur aureus*, and *Lemur catta* ($N=113$ total strides). We quantified the height, diameter, and angular orientation of locomotor supports using remote sensors and tested the influence of support parameters on gait kinematics, specifically predicting that in response to increasing substrate height, lemurs would decrease speed and stride frequency, but increase stride length and the mean number of supporting limbs. Lemurs did not adjust stride frequency on substrates of varying height. Adjustments to speed, stride length, and the mean number of supporting limbs in response to varying height often ran counter to predictions. Only *E. rubriventer* decreased speed and increased the mean number of supporting limbs on higher substrates. Results suggest that quadrupedal walking is a relatively safe form of locomotion for lemurs, requiring subtle changes in gait to increase stability on

higher – i.e., potentially riskier – substrates. Continued investigation of the impact of height on locomotion will be important to determine how animals assess risk in their environment and how they choose to use this information to move more safely.

Introduction

Arboreal environments are complex matrices of substrates that vary in diameter, obliquity, compliance, and connectedness. Many studies on arboreal locomotion have connected the biomechanical challenges posed by these physical characteristics to potential locomotor and morphological adaptations that increase stability and survival (e.g., Cartmill et al., 2002; Larson, 2018; Larson et al., 2000; Schmitt, 1999; Shapiro et al., 2014, 2016; Shapiro & Young, 2010; Young and Chadwell, 2020). The present study proposes that adding another physical characteristic of locomotor substrates – their height above the ground – could shed light on the types of information primates gather and process to make locomotion less risky.

Unlike diameter, obliquity, compliance, or connectedness – substrate properties which can be seen and touched – substrate height is only judged visually. “Visual cliff” studies affirm the importance of height perception for safe locomotion (Gibson & Walk, 1960). In these studies, animals are placed on a ledge and encouraged to cross a platform made of glass, or from the subject’s perspective, encouraged to step over an apparent cliff. The common pattern of infant and juvenile animals refusing to cross an apparent chasm suggests sensitivity to height is an important conserved trait among various species (Adolph et al., 2014). Indeed, in a visual cliff study done with neonatal rhesus macaques (*Macaca mulatta*), monkeys responded to heights as early as 3 days after birth, a level of precociality that the authors attributed to primate arboreality (Rosenblum & Cross, 1963). This study focuses on how adult primates may respond to perceived risk while traveling at higher points in the tree canopy.

Including approximate height measurements has been standard in primate locomotor studies for decades, but these studies tend to use height to broadly describe different canopy

usage of conspecific primate taxa (Cannon & Leighton, 1994; Fleagle & Mittermeier, 1980; McGraw, 1996, 1998; McLean et al., 2016; Off & Gebo, 2005; Palminteri et al., 2012) or the preference for certain forest structures while animals engage in particular locomotor patterns (Cheyne et al., 2013; Fan et al., 2013; Garber & Pruetz, 1995; MacKinnon & MacKinnon, 1980; Walker, 2005). Moreover, such studies are methodologically limited for the purposes of understanding the moment-by-moment interaction of sensory systems, cognition, and locomotor output. Most often, the heights at which different bouts of locomotion occur are visually estimated within a given stratum (e.g., 0-10m, 11-20m, etc.; per Richards, 1952), though the use of LiDAR (Light Detection and Ranging) has emerged recently to provide more accurate and detailed information about canopy structure (McLean et al., 2016; Palminteri et al., 2012). Advances in video recording for fine-grained locomotion analysis, coupled with the use of remote measurements of branch morphology, permit careful evaluation of how the perception of risk at increased substrate heights might affect locomotion on a stride-by-stride basis (Dunham et al., 2018).

Falling is the mechanism that makes height a potential selective pressure (Wheatley et al., 2021). The risk of injury or severity of injury should be greater at higher levels in the tree canopy because potential energy (PE) increases linearly with height ($PE=mgh$, where m is body mass, g is gravitational acceleration, and h is height above the ground), but this risk is only actualized in the event of a fall. If a fall does not directly result in death, injuries may affect reproductive fitness of an individual through a loss in rank and reduced capacity for agile locomotion (Lovell, 1991). Fall rates in primates are, to our knowledge, yet to be systematically documented. Researchers studying the sympatric monkeys of Kibale National Park, Uganda, have discussed the contribution of falls to the inventory of injuries they documented (Arlet et al., 2009), and Struhsaker and Leakey (1990) reported witnessing several falls of red colobus monkeys (*Piliocolobus tephrosceles*), including three that were fatal. More substantively, in a study on 1,672 primate skeletons, 223 individuals collectively had 300 fractures of their long

bones attributed to falls (Jarrell, 2011). Fracture rates were similar across a broad sample of arboreal primates including representative strepsirrhines, platyrhines, and catarrhines, though larger primates and primates who tend to live higher in the canopy had higher fracture rates of proximal limb elements (humerus or femur) than primates who are smaller or live lower in the tree canopy.

Regardless of the actual risk, animals may adjust their behavior in response to perceived risk. Using forms of locomotion that improve stability on arboreal substrates may reduce fall rates and therefore the risk of such fractures. One strategy to increase stability common among arboreal mammals is to reduce speed on more precarious substrates (e.g., Dunham et al., 2020; Gaschk et al., 2019; Karantanis et al., 2015; Lammers & Biknevicius, 2004; Shapiro et al., 2014; Young, 2023). Adjustments in speed may be variable (Shapiro et al., 2016), and increasing speed may reduce mediolateral fluctuations of the center of mass during locomotion (Young, 2023). Some studies have shown that, controlling for speed, animals may synchronously lengthen strides and decrease stride frequency, which is thought to decrease peak forces exerted on compliant arboreal substrates (Larson et al., 2000, 2001; Schmitt, 1999; Shapiro et al., 2014; Young, 2023), though this is not always consistent (Granatosky & McElroy, 2022; Karantanis et al., 2017; Schapker et al., 2022). Another strategy to improve stability is to increase net contact with the support. In this study, we focus on the mean number of supporting limbs and the constituent limb support configurations that this measure summarizes. The mean number of supporting limbs is a summary measure of the combined proportions of a stride where the body was supported by one, two, three, or four limbs, respectively. This measure is related to other spatiotemporal variables such as duty factor, defined as the relative duration of limb contact, and limb phase, a measure that describes the relative timing of footfalls within a stride. Stability should increase as the mean number of supporting limbs increases (Shapiro et al., 2014; Shapiro & Young, 2016), but where only two limbs are in contact with the substrate, contralateral limb stances should be more stable than ipsilateral ones, as the likelihood that the

center of mass tips over the narrow support of a branch should decrease (Cartmill et al., 2002, 2007). Figure 1 depicts four moments in time during a stride captured from *L. catta*, illustrating how limb stances change over time during a gait cycle.

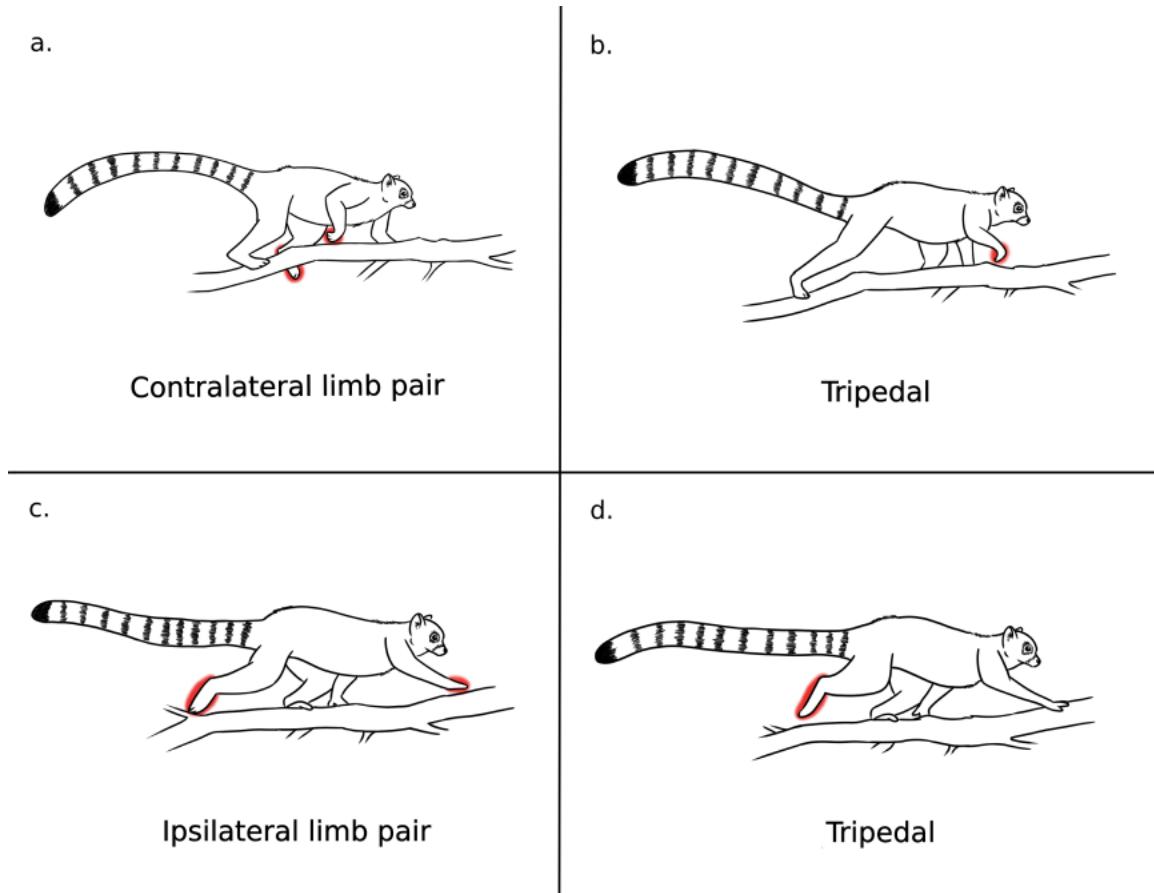


Figure 2.1 An illustrated representation of a video captured of *Lemur catta* walking. The panels sequentially represent the changes in limb stance configurations experienced during a stride. Hands and feet which are in swing phase (i.e., not in contact with the substrate) are highlighted in red for clarity. In this example, *L. catta* started in a contralateral limb pair stance (a.). It transitioned to a tripodal stance (b.). Next it was momentarily supported in an ipsilateral limb pair stance (c.) before returning to a tripodal stance again (d.).

Here, we investigate the effect of substrate height in the canopy – i.e., the vertical distance of a branch or liana from the ground – on the quadrupedal locomotion of four lemur species: *Eulemur rubriventer*, *E. rufifrons*, *Hapalemur aureus*, and *Lemur catta*. These lemurs are of similar mass; *H. aureus* is the smallest at a mean body mass of 1.75kg while *E. rufifrons* is the largest at 2.25kg (Fleagle, 2013). There are some notable morphological and ecological

differences, however. *H. aureus* engages in more vertical clinging and leaping as it navigates bamboo forest, and it has relatively longer hindlimbs compared to *Eulemur* and *L. catta* (Glander et al., 1992). *L. catta* is more terrestrial than the other species (Ward & Sussman, 1979), but a study comparing *L. catta* and *E. rufifrons* (named *E. fulvus rufus* in the study) showed that these two species made similar changes in gait when moving from terrestrial to arboreal substrates (Franz et al., 2005). Despite these differences in morphology and ecology, we predict that all four lemur species should adjust limb kinematics to maximize stability on arboreal substrates and should respond similarly to variation in substrate height.

Following from our hypothesis that lemurs should use more stable gait kinematics as substrate height and its potential for perceived risks increase, we expect the following predicted changes in locomotion. *Prediction 1:* As substrate height increases, lemurs should decrease speed and stride frequency while increasing stride length. *Prediction 2:* As substrate height increases, lemurs should increase the mean number of supporting limbs. Correspondingly, we also expect lemurs to decrease the frequency with which they use single limb stances, and where a pair of limbs support the body, ipsilateral limb pairs should decrease in frequency. *Prediction 3:* If there are differences in response to increasing substrate height among lemur species, *E. rubriventer* and *E. rufifrons* are expected to make the least exaggerated changes in locomotion as they represent more generalized quadrupedal arboreal primates (i.e., not specialized for vertical clinging and leaping, like *Hapalemur*, or terrestrial locomotion, like *Lemur*).

Materials and methods

Data Collection

Free-ranging *E. rubriventer*, *E. rufifrons*, and *H. aureus* were studied at Ranomafana National Park, Madagascar, and *L. catta* was studied at the Anja Community Reserve, Madagascar. Data were collected from June-August 2022. Data collection methods followed the

protocol outlined by Dunham and colleagues (2018). To summarize, lemur locomotion was recorded using modified Backbone GoPro Hero 10s (Back-bone, Ottawa, Ontario, Canada) equipped with a C-mount Fujinon HD 8-80mm Vari-Focal CCTV lens (Fujifilm, Tokyo, Japan). Videos were recorded at 120fps and 1080p resolution. We remotely measured branch obliquity (reported relative to a horizontal line perpendicular to the axis of gravity, accuracy: +/- 2.5°) and key measurements needed to calculate branch diameter (accuracy: +/-1.5mm) using a forestry-grade rangefinder (TruPulse 360R). The rangefinder operates by sending a laser pulse to the object of interest (in this case the branch or liana) and using the time necessary for that light to bounce back to calculate the distance from the instrument. The rangefinder reports the slope distance (the shortest possible distance between two points), as well as the horizontal and vertical distances that compose this vector. The support height above the ground was measured with the rangefinder by either standing directly under the support and adding the height of the measurement-taker (no horizontal distance, so slope and vertical distances are equal), or by recording the vertical distance between support and the ground level (accuracy: +/- 0.2m). Videos were processed using the custom-developed program ClipStride (Dunham et al., 2018) to isolate single strides (N=113, see Table 1 for strides recorded per species). Strides were identified as the successive touchdowns of a reference limb during a gait cycle. GaitKeeper (Dunham et al., 2018) was used to annotate individual frames, track footfalls, and calculate spatiotemporal gait metrics. Both programs were written in MATLAB (Mathworks, Natick, MA) and are available for download at www.younglaboratory.org. Table 2 summarizes the gait parameters analyzed in this study, their definitions, and the predicted changes as substrate height increases.

Table 2.1 Summary of number of strides and lowest and highest substrate heights recorded for each species.

Species	No. of strides	Lowest recorded substrate height (m)	Highest recorded substrate height (m)	Mean substrate height (m)
<i>E. rubriventer</i>	24	0.9	16.6	6.4
<i>E. rufifrons</i>	37	9.1	22.2	15.7
<i>H. aureus</i>	24	2.1	13.7	6.7
<i>L. catta</i>	28	0.5	9.2	4.0

Table 2.2 Predicted changes in gait in response to increased substrate height.

Gait Property	Definition	Expected change on higher substrates
<i>Relative speed</i>	Product of stride frequency and relative stride length	Decrease
<i>Stride frequency</i>	The number of strides per second	Decrease
<i>Relative stride length</i>	The distance traveled between subsequent touchdowns of the reference limb, measured in body lengths	Increase
<i>Mean number of supporting limbs</i>	Average number of limbs contacting the support at any instance during the stride	Increase
<i>Single limb stance</i>	Instances in which the body is supported by only one limb that is contact with the substrate	Decrease
<i>Ipsilateral limb pair stance</i>	Instances in which the body is supported by a hindlimb and a forelimb on the same side of the body	Decrease
<i>Contralateral limb pair stance</i>	Instances in which the body is supported by a hindlimb and a forelimb on opposite sides of the body	Increase relative to ipsilateral limb pair stances
<i>Tripodal stance</i>	Instances in which the body is supported by three limbs in any configuration	Increase
<i>Quadrupedal stance</i>	Instances in which the body is supported by all four limbs	Increase

Statistical Analysis

Before statistical analysis, data were Box-Cox transformed to improve normality. First, a mixed effect ANOVA was used to determine if mean substrate heights were different across species. Next, Tukey's Honestly Significant Difference (HSD) tests were run as a post-hoc analysis to determine which species' means were statistically different ($\alpha=0.05$).

We also ran mixed effects models to test whether support height had a significant effect on the defined gait parameters. Data were not pooled across species but instead used for within-species regression analysis only. The random factor for the models was the individual video clip, as individual animals were not identified. Most video clips contained one stride (average number of strides per video clip was 1.3), some had two or three, and the most was seven. In this particular case, the video captured the movements of four lemurs moving on different substrates. Substrate orientation, substrate diameter, and relative speed (except where speed was a dependent variable) were included as covariates. For each test, we first fit the full model, and then we used backward stepwise term elimination to discern which of our independent variables best predicted the variation in the data. Terms were sequentially eliminated until only significant ones remained. Due to increased variability expected in the quantitative analyses of unconstrained locomotion in natural environments, we recognized significance at $p\leq 0.1$. Data were processed and analyzed in R (version 4.2.2; R Core Team, 2022). Packages used to process raw data were plyr (Wickham, 2011) and dplyr (Wickham et al., 2023). Data visualization was done with ggplot2 (Wickham, 2016), and packages used for the linear models were lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017).

Two types of data categorization were used to understand the role of different limb stance types to overall body support. First, substrate heights were categorized as either high or low relative to their position around the median substrate height for that species. Second, in the high and low categories, we recorded the frequency with which strides contained each limb

stance. Fisher's exact tests ($\alpha=0.05$) were used to discern if these limb configurations occurred in different frequencies at these high or low points in the tree canopy.

Results

Distribution of support heights

Heights at which individual strides were recorded are summarized in Figure 2. *E. rubriventer*, *H. aureus*, and *L. catta* were recorded at relatively low heights – mean 6.4m, 6.7m, and 4.0m, respectively – compared to *E. rufifrons* at a mean height of 15.7m (Table 1). The results of the Tukey HSD (Table 3) analysis indicate that the mean height of *E. rufifrons* was significantly greater than that of the other species ($p<0.01$). The mean height of *L. catta* was also significantly lower than either *E. rubriventer* or *H. aureus* ($p\leq0.024$).

Table 2.3 Results of Tukey HSD analysis comparing the mean substrate heights measured for each species. The mean difference between species is recorded, and the bounds of the 95% confidence interval are reported in brackets.

Species pairwise comparison	Difference [95% CI]	P-value
<i>E. rufifrons</i> – <i>E. rubriventer</i>	1.4 [1.01, 1.87]	<0.001
<i>E. rufifrons</i> – <i>H. aureus</i>	1.3 [0.90, 1.76]	<0.001
<i>E. rufifrons</i> – <i>L. catta</i>	1.9 [1.54, 1.95]	<0.001
<i>L. catta</i> – <i>E. rubriventer</i>	-0.50 [-0.96, -0.05]	0.024
<i>L. catta</i> – <i>H. aureus</i>	-0.62 [-1.08, -0.16]	<0.01
<i>H. aureus</i> – <i>E. rubriventer</i>	0.11 [-0.36, 0.59]	Non-significant

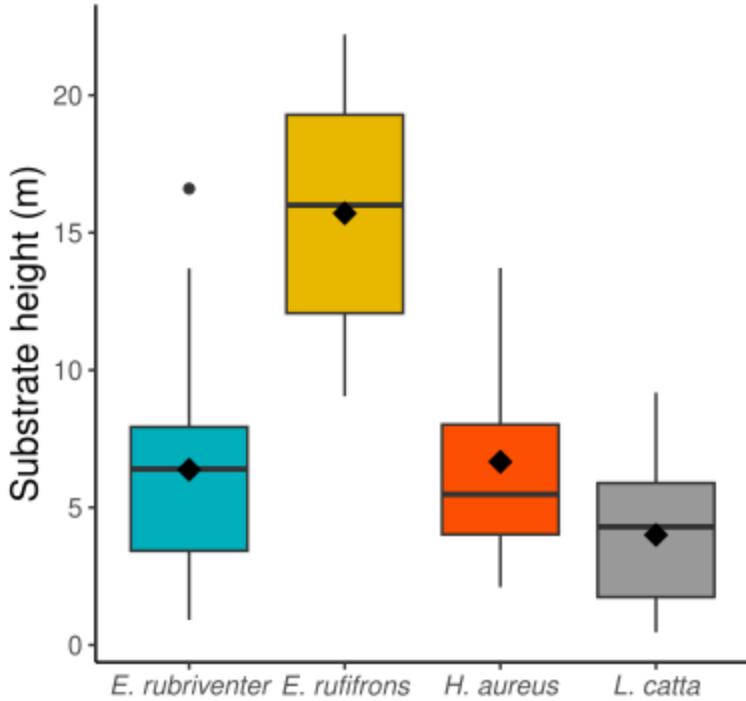


Figure 2.2 Box-and-whisker plot of measured substrate heights from recorded strides of each lemur species. The bolded black line is the median and the box spans the interquartile range. The means are indicated by the black diamonds.

Gait kinematics

Relative speed. Lemurs changed relative speed in response to substrate properties (Table 4, Fig. 3a). *E. rubriventer* decreased speed with increasing height ($p=0.071$). *L. catta* and *H. aureus*, however, increased relative speed on higher substrates ($p\leq 0.052$) and on broader substrates ($p<0.01$). Changes in relative speed also correlated with changes in substrate diameter in *L. catta* and *E. rufifrons*. Both increased relative speed on broader supports ($p\leq 0.054$).

Relative stride length. Only *H. aureus* adjusted relative stride length in response to substrate height, decreasing stride length on higher substrates ($p=0.042$, Table 5, Fig. 3b). The other lemurs did not change relative stride length in response to substrate properties. For all species, relative stride length positively correlated with relative speed ($p<0.001$).

Table 2.4 Effects of substrate properties on relative speed.

Species	Final Model	Estimate	Statistic	P-value
<i>E. rubriventer</i>	Substrate height	-0.41	$F_{[1,22]} = 3.64$	0.071
<i>E. rufifrons</i>	Substrate diameter	0.34	$F_{[1,31]} = 4.00$	0.054
<i>H. aureus</i>	Substrate height	0.56	$F_{[1,22]} = 4.74$	0.052
<i>L. catta</i>	Substrate height	0.47	$F_{[1,27]} = 5.19$	0.032
	Substrate diameter	0.59	$F_{[1,27]} = 7.94$	<0.01

Table 2.5 Effects of substrate properties and relative speed on relative stride length.

Species	Final Model	Estimate	Statistic	P-value
<i>E. rubriventer</i>	Relative speed	0.090	$F_{[1,22]} = 80.7$	<0.001
<i>E. rufifrons</i>	Relative speed	0.61	$F_{[1,33]} = 30.1$	<0.001
<i>H. aureus</i>	Substrate height	-0.48	$F_{[1,22]} = 5.08$	0.042
	Relative speed	1.4	$F_{[1,22]} = 530$	<0.001
<i>L. catta</i>	Relative speed	0.78	$F_{[1,27]} = 39.7$	<0.001

Stride frequency. No lemurs significantly adjusted stride frequency in response to substrate height (Table 6, Fig. 3c). *E. rubriventer* increased stride frequency on broader substrates ($p=0.075$), but the other species did not change stride frequency in response to substrate orientation or diameter. For all species, stride frequency positively correlated with relative speed ($p<0.001$).

Mean number of supporting limbs. Both *Eulemur* species adjusted the mean number of supporting limbs on higher substrates, though in opposing directions (Table 7, Fig. 3d). *E. rubriventer* increased the mean number of supporting limbs on higher substrates ($p<0.001$) whereas *E. rufifrons* decreased them ($p=0.033$). *L. catta* and *H. aureus* did not adjust the mean number of supporting limbs in response to substrate properties. For all species, the mean number of supporting limbs negatively correlated with relative speed ($p<0.027$).

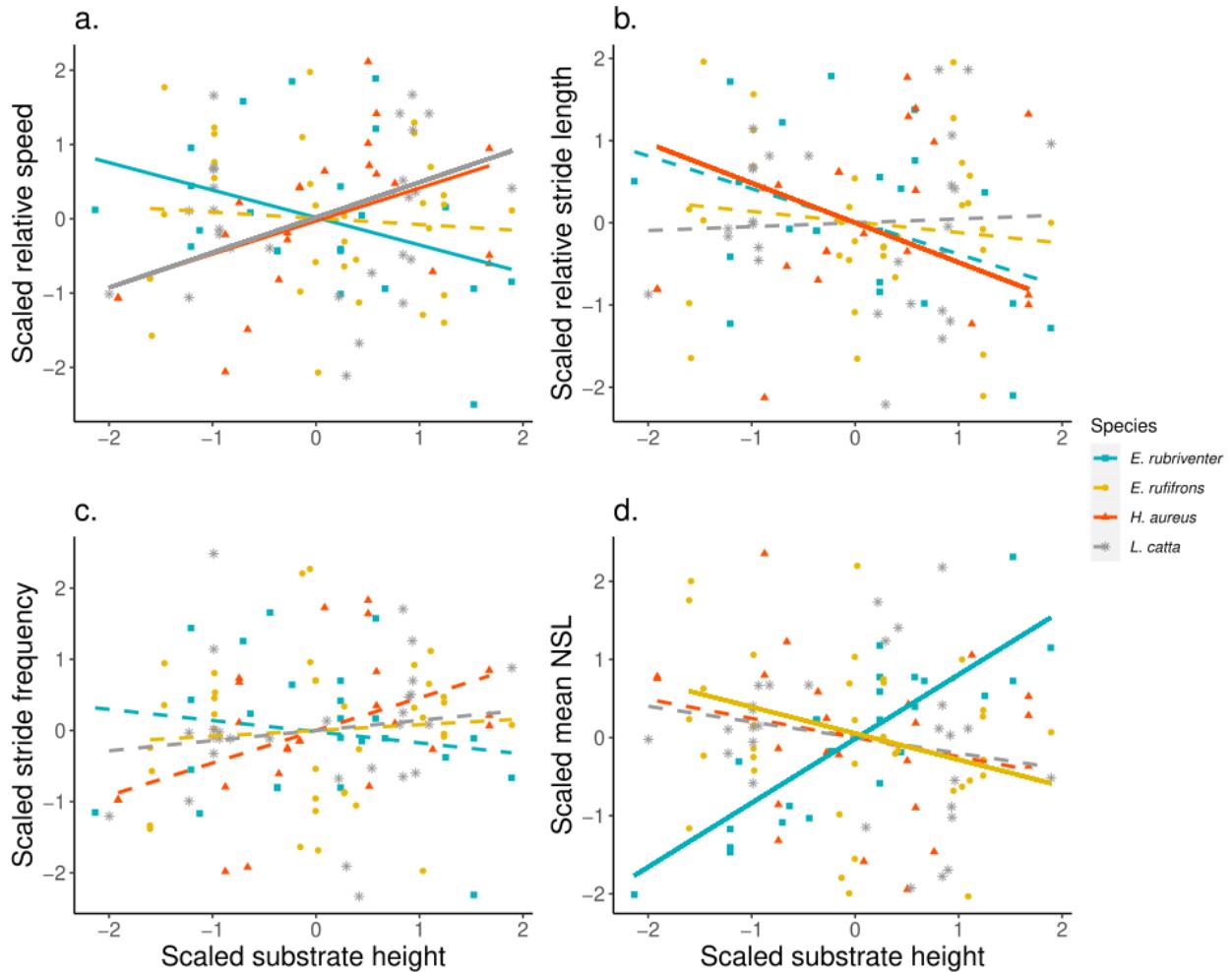


Figure 2.3 Scatterplots of scaled (Box-Cox transformed) gait parameters – relative speed (a.), relative stride length (b.), stride frequency (c.), and mean number of supporting limbs (NSL, d.) – plotted against scaled substrate height, grouped by lemur species. Trend lines indicate reduced maximum likelihood fits from mixed-effects ANCOVA models as reported in Tables 4-7. Dashed lines indicate trends from non-significant regressions, whereas solid lines indicate significant trends.

Table 2.6 Effects of substrate properties and relative speed on stride frequency.

Species	Final Model	Estimate	Statistic	P-value
<i>E. rubriventer</i>	Substrate diameter	0.26	$F_{[1,19]} = 3.56$	0.075
	Relative speed	0.63	$F_{[1,19]} = 21.6$	<0.001
<i>E. rufifrons</i>	Relative speed	0.63	$F_{[1,33]} = 21.6$	<0.001
<i>H. aureus</i>	Relative speed	0.79	$F_{[1,22]} = 35.2$	<0.001
<i>L. catta</i>	Relative speed	0.80	$F_{[1,27]} = 40.5$	<0.001

Table 2.7 Effects of substrate properties and relative speed on the mean number of supporting limbs.

Species	Final Model	Estimate	Statistic	P-value
<i>E. rubriventer</i>	Substrate height	0.82	$F_{[1,19]} = 45.6$	<0.001
	Relative speed	-0.11	$F_{[1,19]} = 13.3$	<0.01
<i>E. rufifrons</i>	Substrate height	-0.34	$F_{[1,30]} = 5.02$	0.033
	Relative speed	-0.52	$F_{[1,30]} = 11.9$	<0.01
<i>H. aureus</i>	Relative speed	-0.82	$F_{[1,22]} = 51.3$	<0.001
<i>L. catta</i>	Relative speed	-0.42	$F_{[1,27]} = 5.56$	0.027

Limb stances. The frequencies of limb stances on low (below median) and high (above median) are reported in Table 8. Though Fisher's exact tests indicated that differences in limb support frequencies are not significant, we nonetheless observed subtle patterns that were in line with predicted responses to increasing substrate height. Contralateral limb pair and tripodal stances were the most common stances, occurring in all strides in the data set (frequency of 1 in Table 8). In *E. rubriventer*, the sole species that increased the mean number of supporting limbs on higher substrates, the proportion of strides with single limb and ipsilateral limb pair stances decreased on high substrates while the proportion of quadrupedal stances increased. In *E. rufifrons*, strides containing single limb stances also decreased in frequency on high substrates while quadrupedal stances increased. Ipsilateral limb pair stances increased marginally in *E. rubriventer* on high substrates as well. Single limb stances increased in frequency when *H. aureus* and *L. catta* moved on high substrates, whereas use of ipsilateral limb pair stances decreased. Strides containing quadrupedal stances decreased on high substrates in *H. aureus*, but *L. catta* did not change the frequency with which it used quadrupedal stances.

Table 2.8 Proportion of strides containing the given limb stances on low and high substrates (above or below median height). Single limb, tripodal, and quadrupedal rows indicate the proportion of strides where the body was at least momentarily supported only by one, three, or four limbs, respectively. Ipsilateral limb pair stances occur when the body is supported by a hindlimb and a forelimb on the same side of the body. Contralateral limb pair stances occur when the body is supported by a hindlimb and a forelimb on opposite sides of the body.

Limb Stance	<i>E. rubriventer</i>		<i>E. rufifrons</i>		<i>H. aureus</i>		<i>L. catta</i>	
	Low	High	Low	High	Low	High	Low	High
<i>Single limb</i>	0.13	0	0.15	0.06	0.23	0.36	0.07	0.29
<i>Ipsilateral limb pair</i>	0.44	0.38	0.45	0.47	0.38	0.27	0.79	0.50
<i>Contralateral limb pair</i>	1	1	1	1	1	1	1	1
<i>Tripodal</i>	1	1	1	1	1	1	1	1
<i>Quadrupedal</i>	0.69	0.88	0.80	1	0.92	0.82	0.50	0.50

Discussion and conclusions

Lemurs were recorded at differing heights in the tree canopy, and locomotion of *E. rufifrons* was recorded at mean height nearly 10m greater than the other species. Following basic principles of ballistic physics where all potential energy is converted to kinetic energy during a fall ($E=mgh=0.5mv^2$, where v is velocity), *E. rufifrons* would incur the greatest velocities upon impact with the ground. Despite this, *E. rufifrons* did not adjust relative speed, relative stride length, or stride frequency in response to higher substrates, and instead they decreased the mean number of supporting limbs as substrate height increased.

In contrast, *E. rubriventer* did increase the mean number of supporting limbs during strides on higher substrates, following our predictions. It appears that this was accomplished by both reducing the frequency that unstable (single limb and ipsilateral limb pair) stances were used while also increasing stable (quadrupedal) stances. Functionally this should mean that over the course of a stride, the limbs are in contact with the substrate more often. This could

reduce perturbations of the substrate itself while also allowing more opportunity to exert muscular force to stabilize the body should its trajectory begin to veer from its intended course. In a study conducted in Ranomafana National Park, *E. rubriventer* was observed using strata lower than *E. rufifrons* during travel (Overdoff, 1996), a distinction in canopy use that mirrors our data. It is possible that *E. rufifrons*, in comparison to the closely related *E. rubriventer*, changed locomotion relatively little because they move more habitually at these higher levels, potentially indicating a difference between these two species in perception of risk at increasing substrate heights.

Like *E. rufifrons*, *H. aureus* and *L. catta* also adjusted gait in response to increasing substrate height in manners counter to our predictions. If lemurs were to vary in their response to increasing perceived risk on higher substrates, these two species were expected to make more exaggerated changes to gait given their ecological and/or morphological differences from the arboreal and more generalized *Eulemur* species. However, *H. aureus* and *L. catta* both tended to increase speed on increasing substrate heights, and *H. aureus* also decreased stride length. These changes are thought to reduce static stability on precarious arboreal substrates, but increasing speed can reduce mediolateral fluctuations of the center of mass, thus providing an alternate, dynamic form of stability (Young, 2023). As speed increases, single limb and paired limb support configurations (i.e., a decrease in mean number of supporting limbs) should be more frequent. And indeed, that is what occurred in *H. aureus* and *L. catta*, who shifted to use more limb configurations that we hypothesized would be statically unstable on higher substrates. More data are needed to assess whether adjustments in speed and subsequent adjustments in limb support configurations are responses to substrate height or demonstrations of robust locomotor performance regardless of substrate height.

The observed subtle changes in locomotion suggest that lemurs move their limbs in ways that already ensure safety, and perhaps only small adjustments are needed to account for variation in the arboreal environment. After all, lemurs do possess long, flexed limbs, grasping

hands and feet, and long, mobile tails – morphological characteristics that are thought to enhance locomotor performance of primates on arboreal substrates (Larson, 2018; Mincer & Russo, 2020; Schmitt, 2010). Whereas the kinematic changes to gait discussed in the present study are common strategies for stable arboreal locomotion, the most pronounced adjustments to increase stability are found in species that, for instance, may have reduced grasping abilities or otherwise do not share the morphological features of typical primates (Shapiro et al., 2014; Young & Chadwell, 2020). Moreover, lemurs in this study generally performed robustly on substrates of varying physical properties. There were some adjustments in response to variations in substrate diameter: *E. rufifrons* and *L. catta* both tended to use lower speeds on narrower, theoretically more unstable, substrates, while *E. rubriventer* tended to use lower stride frequencies. No lemurs adjusted gait in response to variation in substrate inclination. This contrasts with a study on captive mouse lemurs (*Microcebus murinus*) which described the tendency for individuals to increase contact time on oblique substrates (Shapiro et al., 2016). Another study involving several *Eulemur* species showed that lemurs traveling on inclined supports augment elbow and knee flexion to promote stability (Stevens et al., 2011), and primates joint kinematics typically change more in response to varying substrate orientation than varying diameter (Janisch et al., 2024). Future work on the influence of substrate height on locomotion could include analyses of joint kinematics, non-walking gaits, or even tail kinematics as possible avenues of investigation.

While subtle changes in locomotion could be interpreted as robust locomotor performance, lemurs alternatively could be trading energetic efficiency for stability (Miller et al., 2019). Table 8 shows that lemurs used tripodal and quadrupedal stances frequently, regardless of their position in the tree canopy. Strides with more tripodal and quadrupedal stances should be less efficient than strides where paired limb stances predominate (Griffin et al., 2004). Studies in baboons (*Papio anubis*) and chimpanzees (*Pan troglodytes schweinfurthii*) indicate that maneuverability and efficiency are traded for stability when moving from terrestrial to

arboreal substrates (Druelle et al., 2021; Pontzer & Wrangham, 2004). Even the much smaller squirrel monkey (*Saimiri sciureus*) has been shown to make adjustments to limb phase to increase stability on more precarious substrates (Miller et al., 2019).

There are few previous studies addressing how substrate height might directly influence locomotor patterns in other animals. Ornate lizards (*Urosaurus ornatus*) have been shown to decrease speed on higher arboreal substrates, generally, though they *increase* speed on higher substrates while engaging in display behaviors (McElroy et al., 2007). Orangutans (*Pongo spp.*) do not change positional behaviors at different heights in the tree canopy (Thorpe & Crompton, 2006). A later analysis by this research group of only locomotor behavior kept substrate height in the model that best predicted locomotor mode, but in this case, height had the most predictive power when classified as either core stratum – where there is the most continuity among substrates – or peripheral strata – where substrates are relatively discontinuous (Manduell et al., 2011). The present study focuses on lemur locomotion on individual branches, so the relative continuity of substrates was not tested here.

Limitations and Future Directions

The study presented here is an introductory attempt to incorporate additional aspects of arboreal substrate variation into primate locomotion analysis. However, we acknowledge that not all relevant parameters could be accounted for in our analyses. For example, the structure of the lower canopy and forest floor may attenuate some of the risk of a fall by providing cushion or alternative places to land. In physics terms, this would increase the distance over which the falling lemur would decrease its velocity to zero, reducing the force of impact. Such cases would be more likely in Talatakely, the dense forest area of Ranomafana National Park where we studied *E. rubriventer*, *E. rufifrons*, and *H. aureus*. At the Anja Community Reserve, however, where we recorded *L. catta*, the trees were shorter overall but the underbrush was sparse and the ground rocky. Additionally, substrate height may also correlate with other unobserved environmental features like continuity of the substrates (Manduell et al., 2011).

Studying the locomotion of free-ranging animals provides the opportunity to capture more naturalistic variation in the data; however, this also skewed our data in a manner that is difficult to account for. For example, we made assumptions that unmeasured variables or sources of measurement error could have equally affected the quantities used in statistical models. Variation could arise from different reactions to human presence, unknown changes in social dynamics (e.g., intra- or intergroup conflicts), or other effects that altered behavior on that day. Measurements of branch morphology – orientation, diameter, and height – were done from a distance following established protocols (Dunham et al., 2018). While we would often retake measurements to confirm numbers, at times it was more important to capture many measurements quickly so to not lose track of the primate group we were following. Additionally, there are relatively few strides we captured for each species (approximately 25 strides). With smaller sample sizes, these unmeasured factors could have more influence on the patterns we observed.

Lastly, it is difficult – and perhaps unwise – to directly compare the locomotion of these lemurs as they moved at different levels of the tree canopy or in different forests altogether. We recorded *E. rufifrons* on much higher substrates than the other species. While this is reflective of previously recorded differences in habitat use between *Eulemur* species at Ranomafana National Park (Overdorff, 1996), it complicates interpretation. For example, it remains unclear if a relatively terrestrial species like *L. catta* traveling at the same heights as *E. rufifrons* would make the predicted adjustments to gait to improve stability. Furthermore, the studies in lizards (McElroy et al., 2007) and orangutans (Manduell et al., 2011; Thorpe & Crompton, 2006) emphasize the importance of the interacting effects of habitat structure and other behaviors on locomotion. Future work which incorporates more aspects of habitat structure or other types of behavior beyond walking gaits may shed light on potential differences in the perception of risk during locomotion in arboreal primates.

Conclusions

The response to increasing substrate height varied among lemur species. *E. rubriventer* increased the mean number of limbs used to support its body during a stride on higher substrates, whereas other lemurs either did not respond or responded counter to our predictions. Nevertheless, a holistic understanding of primate arboreal adaptation in primates is incomplete without knowledge of the sensory and cognitive processes that govern their movements. Though subtle, the adjustments to gait observed in one species of lemur suggest they may be gathering information about their position in the tree canopy and making decisions to reduce risks.

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CHAPTER 3: LOOK BEFORE YOU LEAP: COMPARING THE SAFETY ASSESSMENT

BEHAVIORS OF WILD PRIMATES DURING ARBOREAL LOCOMOTION

Abstract

Gaps between arboreal supports present two major challenges for locomotion. First, should a primate make a misstep, gaps could cause animals to fall to the ground. Second, primates must make assumptions about the properties of the branch on the other side of a gap, often through visual assessment. Here, I compare the behaviors that primate species use to reduce the risk of falls when crossing gaps. Videos of free-ranging primates were analyzed to quantify duration of pauses (latency) before locomotion as well as gap crossing method, duration, and the relative size of branches used to cross gaps. *Cercopithecus ascanius* was observed using smaller branches to cross gaps; however, individuals that carried infants paused for longer before leaping between those small branches. The sympatric *Papio anubis*, the largest of the primates studied here, used the broadest branches to leap and bridge across gaps. While juveniles and adults were both observed in the trees, more bouts of arboreal locomotion were recorded in juveniles. However, their branch use was similar to that of adults. Two lemur species, *Lemur catta* and *Eulemur rubriventer*, used more varied branch sizes to cross gaps. Common among all species was the tendency to increase gap crossing duration when bridging to narrow supports. Primates may be making subtle adjustments to locomotion to accommodate differences in gap structure, and the paucity of failures or retreats from gap crossings further underscores primate proficiency at addressing these challenges.

Introduction

There are biomechanical challenges to moving in an arboreal environment because supports can vary simultaneously in many physical properties – diameter, compliance, orientation, etc. – which can destabilize an animal in motion. Discontinuity of arboreal supports means poor locomotor performance can lead to falls, but the ability to cross gaps successfully could yield energetic benefits by reducing path lengths to resources (Cant, 1992). Perception of and accurate response to challenges like arboreal gap crossing is key to preventing deadly accidents (Wheatley et al., 2021). An animal's awareness of possible behaviors given their physical environment is an awareness of their *affordances* (Gibson, 1979). Locomotion across gaps in supports is a useful way of examining the adaptive locomotion of primates and their awareness of their affordances as individuals constantly navigate untested supports.

In this study, arboreal “gaps” are most often the small-scale spaces between branches that can be navigated by bridging (as part of generalized arboreal quadrupedalism) or leaps as opposed to large openings in the tree canopy. The biomechanics of crossing gaps are affected by not only the abilities of the animal but also the structure of the gap (Graham & Socha, 2020). Strategies for crossing gaps vary within and between species, likely due to interacting effects of morphology, phylogeny, and ecology (Cannon & Leighton, 1994; Cant, 1992; McGraw, 1998; Walker, 2005). Leaping squirrels use innovative ways to overcome obstacles like compliant take-off supports and variable gap sizes, improving performance with successive leaps (Hunt et al., 2021; Lee et al., 2025). Bonobos have been recorded leaping across gaps over 3.5m wide, using compliant landing branches to slow their fall (Druelle et al., 2020). In the present study, primates traverse less substantial gaps by leaping and bridging across them. Nonetheless, primates may use adaptive locomotor strategies to safely navigate these gaps. Indeed, there are anecdotal accounts of behaviors such as pausing to reorient before leaping (Pariente, 1979). The present study uses video recordings of primates to systematically quantify gap crossing behaviors.

Latency

Primates predominantly use vision to guide their locomotion. During gap crossings, support diameter and compliance may be estimated visually as the two properties are highly correlated across arboreal supports (Dunham et al., 2018; van Casteren et al., 2013). Given the current lack of gaze tracking or three-dimensional analyses of head movement, latency before locomotion is used here as a proxy for visual assessment of the environment (Adolph et al., 1993). The word “latency” as it is used in this dissertation is adapted from studies on human motor development (Adolph, 1995, 1997; Adolph et al., 1993). Human children and infants will take longer to assess their environment before attempting to cross through or over certain obstacles (Adolph, 1997; Adolph et al., 2014). However, adult humans can accurately perceive affordances through quick glances around the environment resulting in rather short latencies or apparently no latencies at all (Adolph & Franchak, 2017; Franchak & Adolph, 2014). Here, as in these studies, latency is the time before an action is taken; i.e., it is the time between bouts of locomotion which could be potentially used to visually explore prior to taking the next steps. I predict that latencies before leaping will be greater than before other types of locomotion, and that latencies will be greater when leaping between smaller supports.

Gap crossing duration

The sense of touch is another way to assess the physical environment. It is crucial because it provides direct feedback to the animal about the properties of its locomotor supports such as diameter and compliance. Touching before committing to bridging across gaps was not prevalent in the data sample (though see later in this chapter for an exception). However, when primates bridge across gaps, the first moments that a forelimb contacts a branch could be serving the same purpose as an isolated touch. Gap crossing durations could be prolonged as the information gained from this contact induces changes in locomotion during the bridging behavior. I therefore predict that the duration of gap crosses will increase on narrower branches.

Subjects

The present study is based on video recordings of four species of wild primates. Table 3.1 summarizes relevant information about the sample. First, I discuss the olive baboon *Papio anubis* and the red-tailed monkey *Cercopithecus ascanius*, sympatric cercopithecoid monkeys in Kibale National Park, Uganda. Overall, both adult and juvenile *P. anubis* display characteristics for efficient terrestrial locomotion. They use more digitigrade postures – where the palms/heels are slightly elevated off the support during stance phase – as opposed to the more commonly seen plantigrade postures – where the palms and heels are in contact with the support. This posture is thought to increase their effective limb length at low speeds, which reduces the cost of locomotion as more distance is traveled per step (Druelle et al., 2021; Patel, 2009). In the related and similarly proportioned species *Papio cynocephalus*, Zeininger and colleagues (2017) found that digitigrade postures were common in adults and juveniles. Additionally, though the hindlimbs are anatomically longer than the forelimbs, *P. cynocephalus* tended to walk with an extended elbow and slightly flexed knee, which may reduce differences in the effective lengths of hindlimbs and forelimbs for more efficient terrestrial locomotion. Lastly, though juveniles are smaller and use more varied postural and locomotor behaviors, they quickly develop adult-like quadrupedal walking mechanics (Druelle et al., 2016, 2017, 2021; Rose, 1977). Contrast these adaptations for terrestrial movement to those of *C. ascanius*, which is a more strictly arboreal primate of small to moderate size. Its ratio of forelimb to hindlimb length (intermembral index) is even lower than that of *P. anubis* – 79 in *C. ascanius* and 97 in *P. anubis* (Fleagle, 2013). While primates that use leaping as a higher proportion of their locomotor activity often have lower intermembral indices (see discussion of lemurs below), *C. ascanius* is documented using high proportions of quadrupedalism and climbing and infrequently leaps (Gebo & Chapman, 1995). Instead, the differences in intermembral indices are better interpreted as an allometric lengthening of the forelimb in the larger-bodied *P. anubis* (Jungers, 1985). *C. ascanius* also possess relatively longer tails (Russo & Shapiro, 2011; Sehner et al., 2008) and longer digits relative to their palm length (higher phalangeal index) compared to *P.*

anubis (Patel & Maiolino, 2016), features which may enhance stability in precarious arboreal settings.

The ring-tailed lemur *Lemur catta* was studied at Anja Community Reserve, Madagascar, and the red-bellied lemur *Eulemur rubriventer* was studied at Ranomafana National Park, Madagascar. These two lemurs are characterized by low intermembral indices – 70 in *L. catta* and 68 in *E. rubriventer* (Fleagle, 2013). They also both have relatively long digits (Patel & Maiolino, 2016) and long tails (Sehner et al., 2018), which aid with stability as they leap and move quadrupedally through the trees. Despite differences in intermembral indices, gait mechanics and the function of the limbs are largely similar between the more terrestrial *Lemur catta* and more arboreal *Eulemur fulvus* as both species move frequently on both terrestrial as well as arboreal supports (Franz et al., 2005). Similarity in the locomotor mechanics – such as ranges of speeds and gait selection – between *L. catta* and *E. rubriventer* were also apparent in Chapter 2. In short, though both *P. anubis* and *L. catta* are described as (semi-)terrestrial primates, *L. catta* does not exhibit the same limitations in arboreal settings as *P. anubis*.

The characteristics of each species sample allow us to address questions of natural variance of body dimensions and ecology and their potential impact on affordance perception and locomotion. I make the following predictions regarding intra- and interspecific comparisons: increased mass – either due to phylogeny, ontogeny, or infant carrying – will correspond to longer latencies, increased use of broad substrates, and longer gap durations.

Table 3.1 Summary of subject information for behavioral coding

Field Site	Species	Locomotion	Mass [†] (kg)	Subcategories
Kibale National Park, Uganda	<i>Cercopithecus ascanius</i>	More arboreal	2.8-4.1	Carrying vs not carrying infant
	<i>Papio anubis</i>	More terrestrial	5-23.4 [‡]	Juvenile vs adult
Ranomafana National Park & Anja Community Reserve, Madagascar	<i>Eulemur rubriventer</i>	More arboreal	1.9	NA
	<i>Lemur catta</i>	More terrestrial	2.2	NA

[†]Obtained from Smith and Jungers (1997)

[‡] A value of approximate 5kg for juvenile baboons was obtained by first estimating age of the youngest juveniles based on Altmann et al. (1981) and matching it to approximate mass obtained from (Druelle et al., 2017). However, the mass of the juvenile baboons is likely slightly overestimated as the data from Druelle and colleagues (2017) were obtained from a captive population where some adult males could reach almost 30kg. This could mean that there is some overlap in the upper range of masses for red-tailed monkeys and lower range for baboons.

Materials and methods

Video recording

The videos used for this study were originally collected in efforts to understand kinematics of primate locomotion, and much work has already been published (Janisch et al., 2024; Schapker et al., 2024; Shapiro et al., 2023). With such recordings, other analyses of naturalistic behaviors may be done (e.g., Myers et al., 2024). These species were initially identified as particularly interesting given their body size ranges and taxonomic diversity, and further investigation revealed their usefulness in tackling other questions about ontogeny and mass fluctuations from infant carrying. Videos were recorded at 120fps with a resolution of

1080p using modified GoPros (Back-bone, Ottawa, Ontario, Canada) equipped with a C-mount Fujinon HD 8-80mm Vari-Focal CCTV lens (Fujifilm, Tokyo, Japan).

Video analysis

Videos were analyzed in Datavyu (Datavyu Team, 2014) in a series of passes (Figure 3.1). During the first pass, coders (myself in collaboration with two undergraduate assistants) would record how long the subject was visible in frame as well as species, age-sex class information, infant carrying status (if applicable), and whether the subject should be included in the study (i.e., whether the subject engaged in locomotion). During the second pass, coders would record locomotor bout duration, type, and whether the bout started and/or ended off-frame. Bouts started with the first lift-off of the first visible limb following initiation of locomotion and ended with the last touch-down of the last visible limb when the animal stopped. Coders aimed for agreement of bout initiation and termination within 2 frames. Locomotor modes were broadly categorized as quadrupedalism/climbing, leaping, and other. Quadrupedalism/climbing encompassed a variety of behaviors that use alternating limb movements for the purposes of above-branch locomotion. This would include a variety of walking and running gaits (Hunt et al., 1996). Climbing was also included with these behaviors as orientation of the branches was often difficult to judge and would create confusion among coders regarding the exact timing of when this behavior would begin. Leaping was any instance where the limbs were used to propel the subject between branches, creating an aerial phase of locomotion where the subject was completely unsupported by branches. Other types of locomotion included any below branch locomotion, slides, and drops (where gravity instead of muscular effort is employed to cross supports). Though positional and locomotor behaviors can be further atomized (e.g., Hunt et al., 1996), it was determined that to address questions about adaptive locomotion in primates that further delineation was unnecessary.

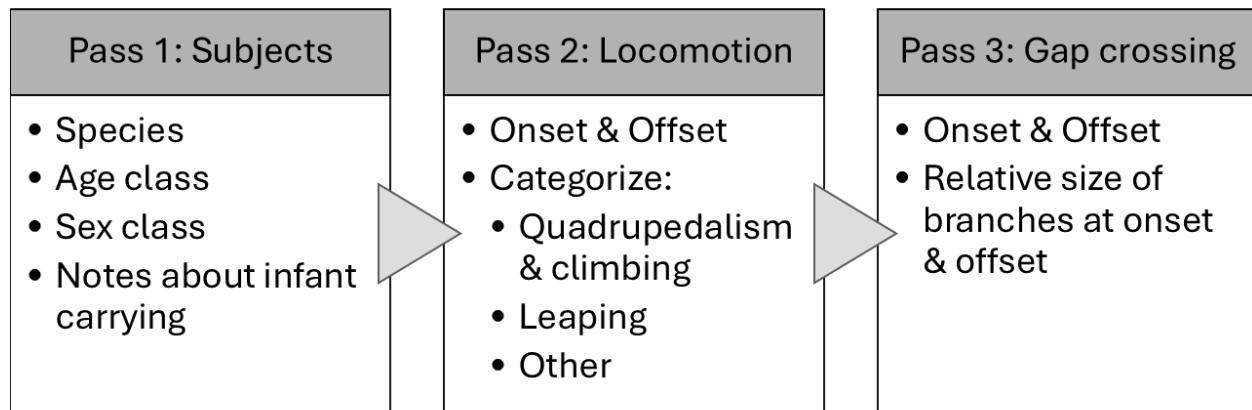


Figure 3.1 Datavyu workflow for analyzing videos of wild primates

I completed the third pass through the videos. Locomotor bouts were checked for consistency with the coding protocol, and then gap crossings were recorded (if applicable). Gap crossings were said to occur when a subject moved so that their body mass was completely supported by a new branch or other locomotor substrate that was yet “untested,” meaning the branch had not been traversed during the locomotor bout in question. In an arboreal environment, large branches proximal to the tree trunk will taper and diverge into many distal branches. An animal moving along this gradient may be able to approximate what the substrate might feel like after the next step; however, an untested branch, even across a fairly small gap, has properties that must be visually judged rather than measured through touch. Leaping by definition is a gap crossing behavior, so for this third pass, recording take-off and landing branch sizes was all that was required (described further below). New gap crossings that were recorded in the third pass were done during bouts of quadrupedalism and climbing, i.e., bridging. If the take-off and landing branches were part of the same parent branch (i.e., two paths of the forking of a tree limb), the subject needed to be at least one body-length away from the node point. Because subjects often rested at these points, creating this rule allowed for clearer demarcation of the onsets and offsets of a gap crossing. The onset of a gap crossing was defined as the

frame in which the first limb to cross the gap lifts off from the take-off branch. The offset was defined as the frame in which the last limb to cross the gap touched the landing branch. The size of the take-off and landing branches were judged qualitatively and categorized relative to diameter of the animal's chest – narrow being <50% chest diameter, medium being ~50%, and broad being >50%.

Statistics

Kolmogorov-Smirnov tests were used to determine whether the distributions of latencies before locomotion are significantly different between groups. As the distributions of the data are not normally distributed (and cluster around zero), Wilcoxon rank sum tests were used to determine whether the median latency before leaping differed significantly from the median latency before bouts categorized as quadrupedalism and climbing. Additionally, because of the considerable skew in the data, comparisons are drawn between those leaps with latencies at or below the median (short latencies) and those with latencies above the median (long latencies). Fisher's exact tests were used to examine the frequencies of branch sizes used by species or groups within species, followed by post-hoc pairwise comparisons also done with Fisher's exact tests. Correction for multiple comparisons was done using the false discovery rate method (Benjamini & Hochberg, 1995).

The change in relative branch size (Δ branch size) is reported on a scale from -2 to 2, where the sign indicates direction of change and magnitude indicates the relative difference between the take-off and landing branches. For example, leaps given a score of 0 were done between branches in the same size category, but a score of -2 occurred between a large take-off branch and a small landing branch. This scale is used for descriptive statistics, but for tests of significance, only the magnitude of change (0-2) was used to reduce the number of factor levels. Simplifying the categorization was necessary to allow for convergence of statistical models.

The durations of gap crossings done via bridging were obtained by subtracting the offset of a gap crossing from its onset. These values were log-transformed to improve normality. Two-way ANOVAs were used to evaluate how durations in time relate to relative branch sizes and species. Where applicable, post-hoc pairwise comparisons were done to interpret the main or interacting effects of relative branch size and species on gap duration.

Visual analysis and statistical testing were performed in R (R Core Team, 2022). Packages used were dplyr (Wickham et al., 2023), ggplot2 (Wickham, 2016), emmeans (Lenth, 2024) and rstatix (Kassambara, 2023).

Results

A summary of the locomotor data obtained from the videos is found in Table 3.2. Videos generally ranged from a few seconds to a few minutes in length, and frequently, only two to three sequential locomotor bouts or gap crossings were obtained from each video. However, longer sequences of locomotor bouts were obtained for each species. The following results are first summarized within species as subcategories vary (e.g., infant carrying vs unloaded and juvenile vs adult). As a note, comparisons between the two predominant bout categories – leaping and quadrupedalism/climbing – are frequently made. Bouts categorized as “other” are infrequent and are briefly described but not included in the statistical analysis.

Table 3.2 Summary of locomotor data collected in four species of primate

Species	Bout totals	Median no. of bouts per video (min, max)	Gap cross totals	Median no. of gap crossings per video (min, max)
<i>C. ascanius</i>	257	2 (1, 10)	111	2 (0, 7)
<i>P. anubis</i>	162	3 (1, 12)	66	2 (0, 11)
<i>E. rubriventer</i>	183	2 (1, 13)	86	2 (0, 8)
<i>L. catta</i>	146	2 (1, 9)	97	2 (0, 11)

Intraspecies analysis

Cercopithecus ascanius

Videos of *C. ascanius* recorded subjects who moved while ventrally carrying infants (n=63 locomotor bouts) and those who moved unloaded (n=194 bouts). Distributions of latencies according to locomotor bout category were similar in both groups (Figure 3.2), where latencies tended to group around 0 and rapidly decrease. A Kolmogorov-Smirnov test shows that the curves are not statistically different ($p=0.36$). In the subset of monkeys carrying infants, the median latency before the onset of quadrupedalism or climbing was 2.1s. Before leaping the latency was 0.6s, but the difference between these values was not significant (Wilcoxon test, $p=0.39$). For those monkeys who were moving without an infant, the median latency before quadrupedalism or climbing was 5.4s, and the median latency before leaping was 0s, indicating that monkeys were identified performing consecutive leaps or leaping after doing another type of locomotion without pausing. For monkeys moving without an infant, the difference between the median latencies before leaping and quadrupedalism was significant (Wilcoxon test, $p<0.001$).

Figure 3.3 is a bar chart showing the distribution of Δ branch size scores for leaps, split into groups by their relative latency duration. The length of an entire bar represents the sum of leaps for all of *C. ascanius* that meet that condition, and the color divisions indicate how many leaps were done by infant carriers versus noncarriers. For instance, among leaps with short latencies, out of the 17 bouts corresponding to a Δ branch size score of 0, 15 were done by noncarriers and two by infant carriers. Monkeys in both groups most frequently leaped between branches in the same size category, and leaps with long latencies only occurred between branches of relatively similar sizes. Figure 3.4 shows the relative size of branches used as take-off and landing supports. These figures show that both infant carriers and non-carriers used a variety of branches for leaping. Infant carriers represent half of the leaps observed with long latencies, and these leaps occurred between narrow and medium-sized branches. Noncarriers

most frequently leaped between narrow branches, but this was observed only once in infant carriers. At these low sample sizes, however, this pattern cannot be declared statistically significant.

When bridging, *C. ascanius* was most frequently observed using take-off and landing branches that were in the same size category (Figure 3.5). For infant carriers, the greatest gap crossing durations occurred when subjects bridged between these similarly sized branches, and movements between branches of different sizes corresponded with shorter gap durations. Similarly for noncarriers, the longest gap durations corresponded to Δ branch size scores of 0 and 1. However, the shortest gap crossing duration also had a score of 1.

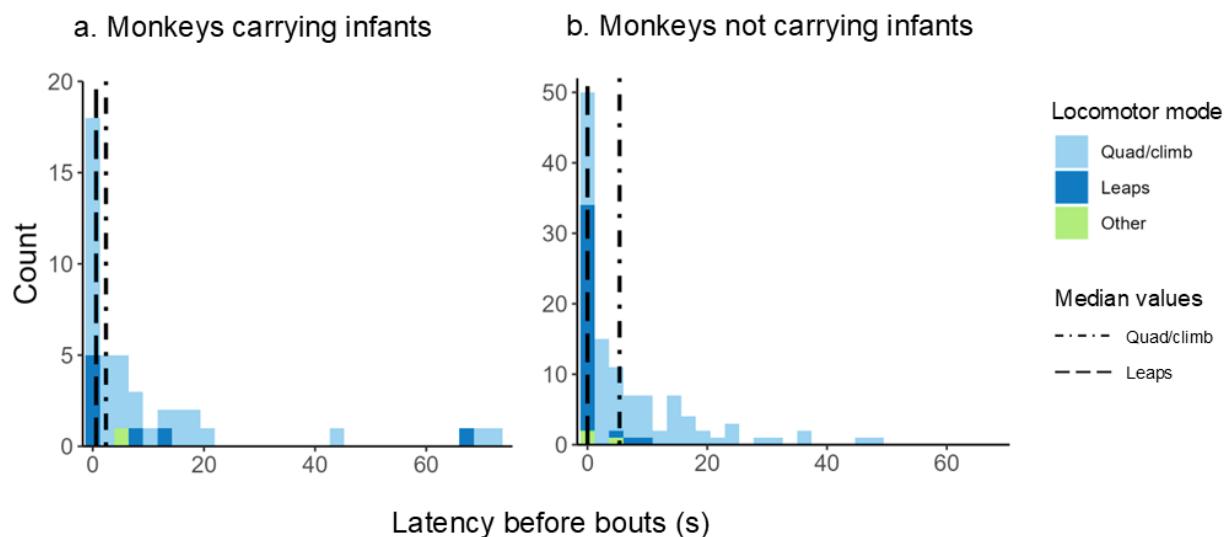


Figure 3.2 Latencies before locomotor bouts in *C. ascanius*. Median latency values are plotted as dot-dashed and long-dashed lines for quadrupedalism/climbing bouts and leaping bouts, respectively. (a) Distribution of latencies during the locomotion of red-tailed monkeys carrying infants. Median values are not significantly different between the two predominant bout types, quadrupedalism/climbing and leaping ($p=0.39$). (b) Distribution of latencies during the locomotion of red-tailed monkeys not carrying infants. Median values are significantly different between bout types ($p<0.001$).

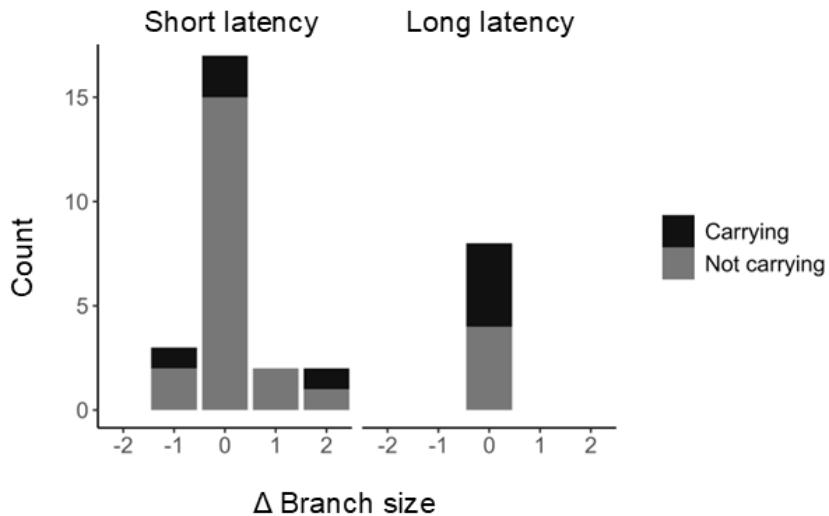


Figure 3.3 Distribution of Δ branch size during leaps in *C. ascanius*, grouped by infant carrying status and latency. Latency duration categorization (short versus long) is relative to the median latency for the group (carriers versus noncarriers).

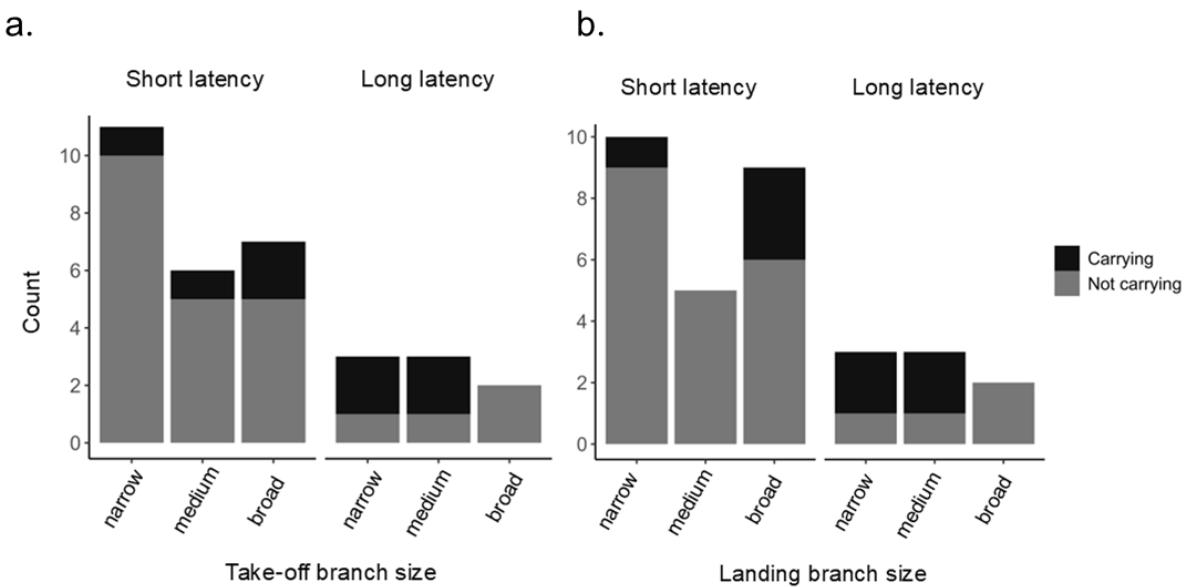


Figure 3.4 Relative size of take-off branches (a.) and landing branches (b.) used by *C. ascanius* during leaps, grouped by infant carrying status and latency. Latency duration categorization (short versus long) is relative to the median latency for the group (carriers versus noncarriers).

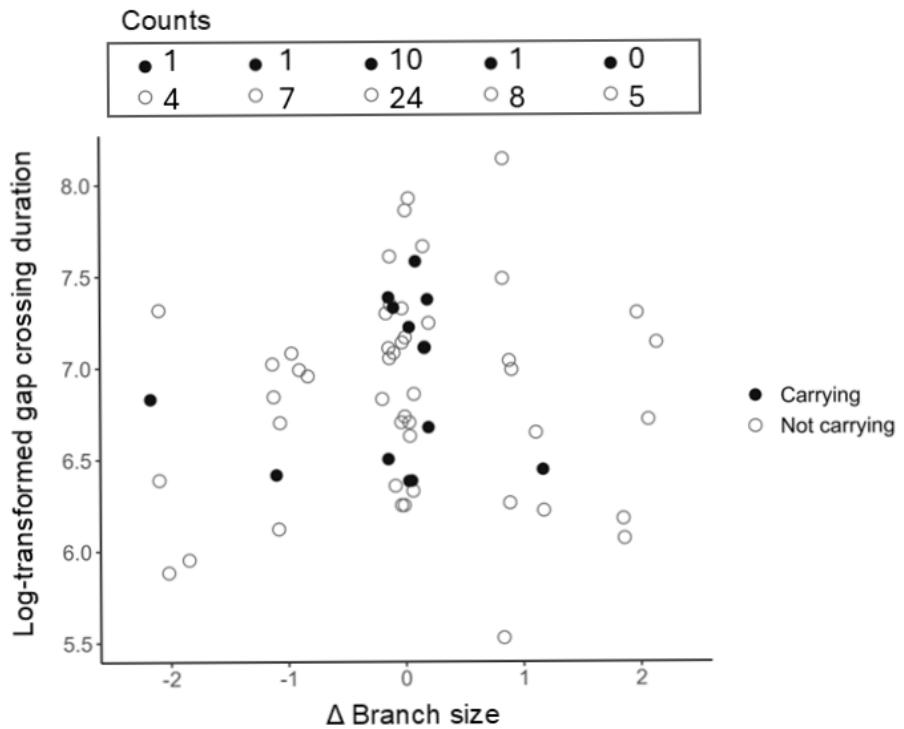


Figure 3.5 Log-transformed duration of bridging gap crosses in *C. ascanius* plotted against Δ branch size, grouped by infant carrier status. Counts for each score are provided in the box above the plot.

Papio anubis

Videos of *P. anubis* recorded subjects that were both adult ($n=38$ locomotor bouts) and juvenile ($n=124$ bouts). Distributions of latencies for the two age categories are similar as determined by a Kolmogorov-Smirnov test ($p=0.85$, Figure 3.6). As a percentage, bouts categorized as “other” are more frequent in juveniles compared to adults (16% compared to 3% respectively). However, a Fisher’s exact test examining the frequency of certain bout types across the age categories indicates this is not significant ($p=0.18$). For both adult and juvenile baboons, the median latency before leaping is significantly lower than before quadrupedalism/climbing (Wilcoxon test, $p<0.001$).

Adult and juvenile baboons most frequently leaped between branches of approximately the same size (Figure 3.7). This pattern holds whether latencies before those leaps are long or short. The most frequent branch size used for take-off and landing were ones that were

relatively large, regardless of age or latency (Figure 3.8). Baboons were also frequently observed using branches of approximately the same size while using quadrupedal walking and climbing behaviors to cross gaps (Figure 3.9). At Δ branch size scores 0 to 2, juveniles used a wide range of gap crossing durations to bridge between supports. For negative scores, durations tended to group closer together. Adults most frequently bridged between branches of similar sizes and gap crossing durations had a similar range to that of juveniles. Adults and juveniles also grouped closely together at bridges scored -2 when crossing durations ranged on the higher end.

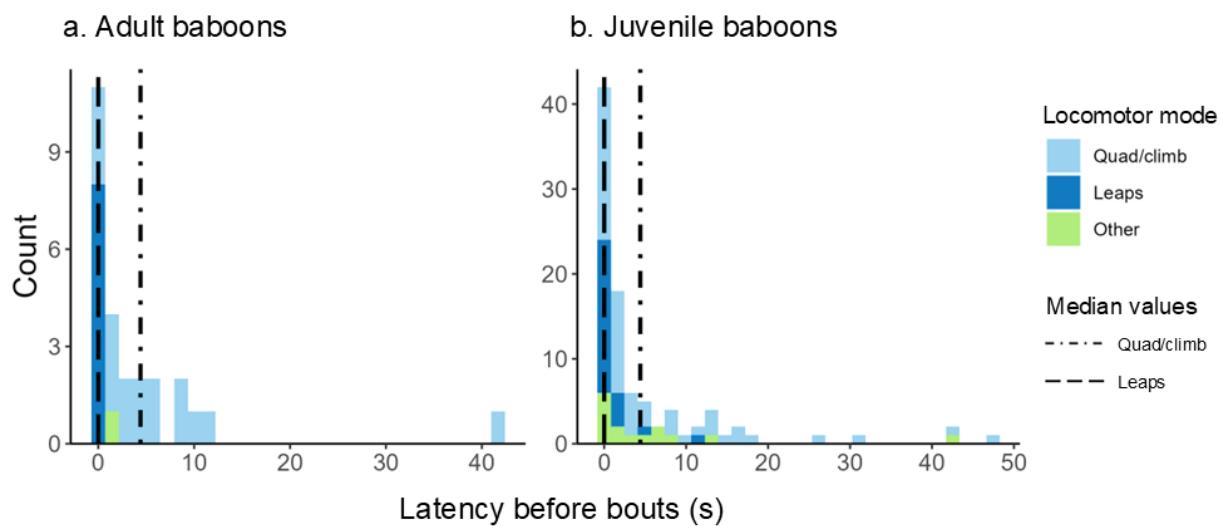


Figure 3.6 Latencies before locomotor bouts in *P. anubis*. Median latency values are plotted as dot-dashed and long-dashed lines for quadrupedalism/climbing bouts and leaping bouts, respectively. (a) Distribution of latencies during the locomotion of adult baboons. (b) Distribution of latencies during the locomotion of juvenile baboons. For both age classes, the median latency before a leap is lower than the median latency before quadrupedalism/climbing ($p<0.001$).

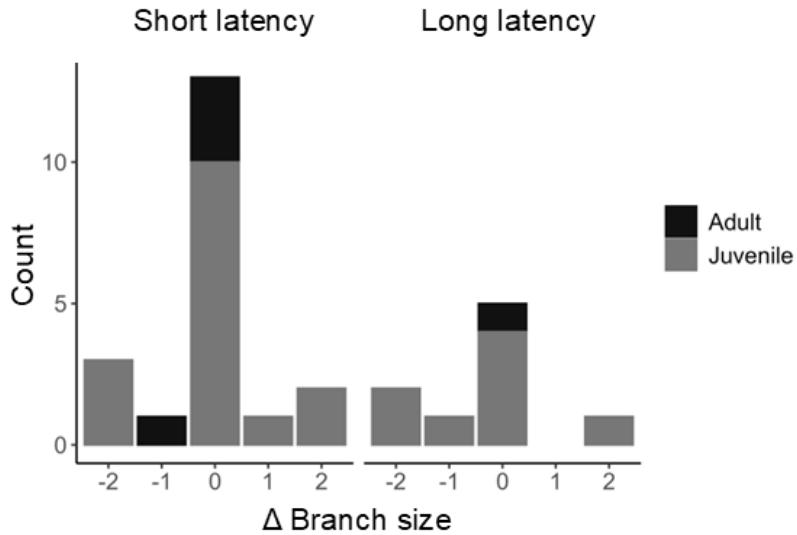


Figure 3.7 Distribution of Δ branch size during leaps in *P. anubis*, grouped by age class and latency. Latency duration categorization (short versus long) is relative to the median latency for the group (adults versus juveniles).

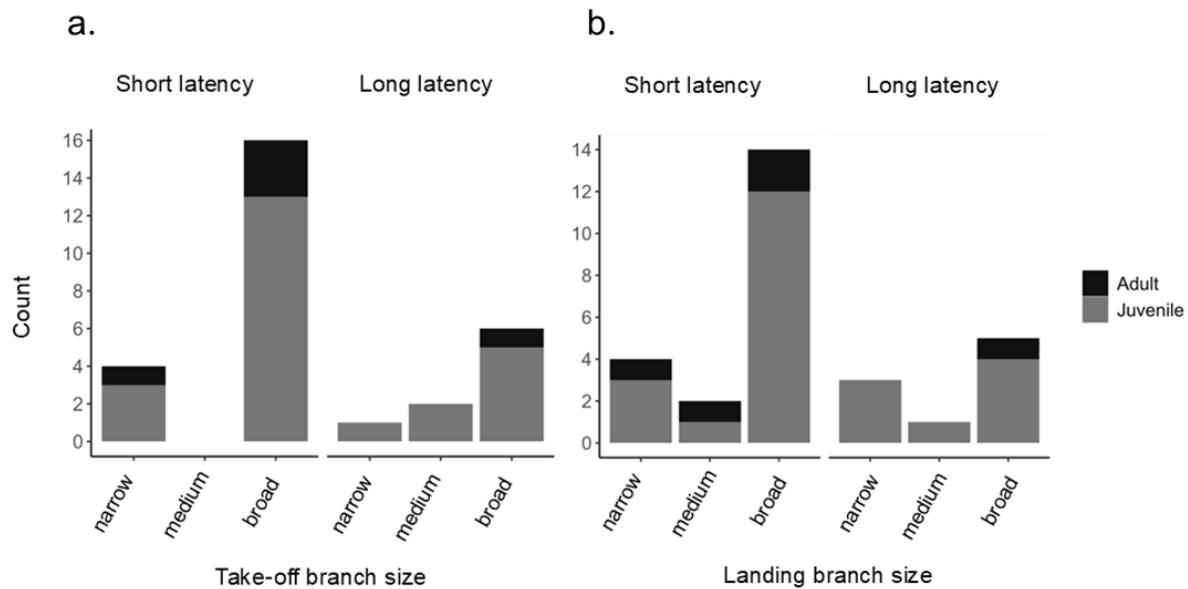


Figure 3.8 Relative size of take-off (a.) and landing branches (b.) used by *P. anubis* during leaps, grouped by age class and latency. Latency duration categorization (short versus long) is relative to the median latency for the group (adults versus juveniles).

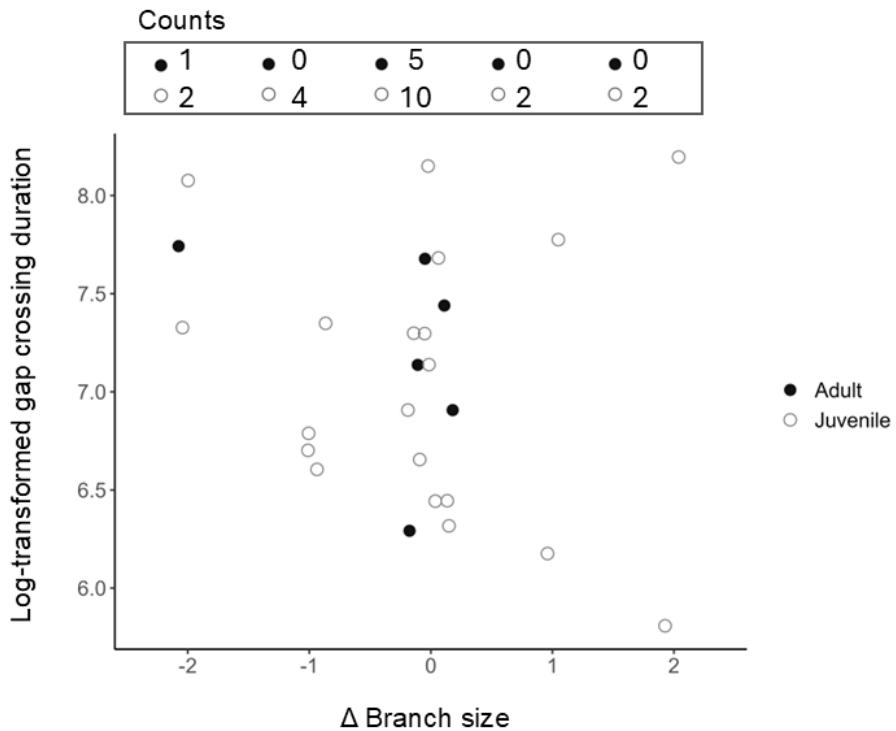


Figure 3.9 Log-transformed duration of bridging gap crossings in *P. anubis* plotted against Δ branch size, grouped by age class. Counts for each score are provided in the box above the plot.

Eulemur rubriventer

Videos of *E. rubriventer* yielded 183 bouts of locomotion (43 leaps and 140 bouts of quadrupedalism/climbing). The median latency before quadrupedalism/climbing bouts was 2.5s and 0s before leaping, which was significantly different (Wilcoxon test, $p<0.001$, Figure 3.10). During leaps, the Δ branch size was most frequently 0, especially when latencies were long (Figure 3.11). When latencies were short, a change in branch size up or down one level was also common. Figure 3.12 shows that red-bellied lemurs tended to use broad branches when leaping, regardless of latency. When latencies were short, medium-sized branches were also frequently used as either take-off or landing branches. When red-bellied lemurs bridged to cross gaps, branches tended to be similar in size (Figure 3.13). The greatest gap crossing durations were observed when individuals crossed from broad to narrow branches (Δ branch size is -2, Figure 3.13). Bridges scored -1 to 2 had similar ranges of gap crossing durations.

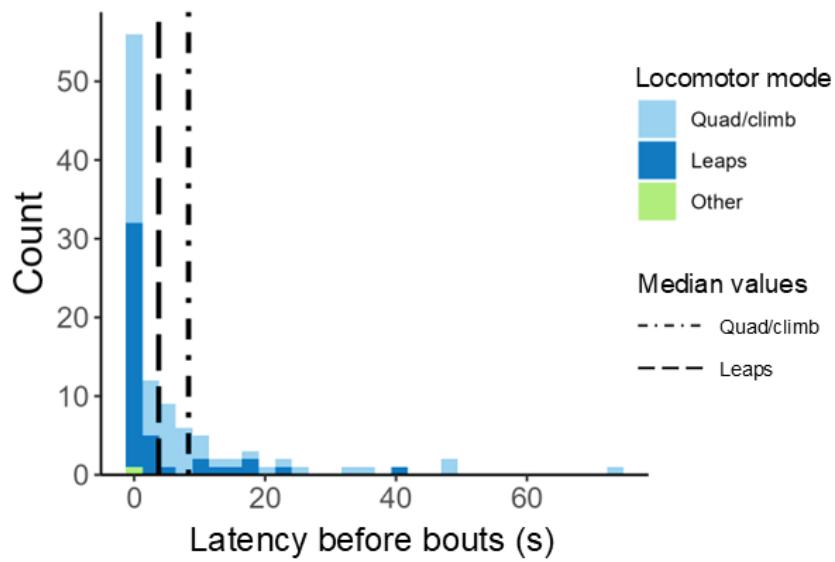


Figure 3.10 Latency before locomotor bouts in *E. rubriventer*. Median latency values are plotted as dot-dashed and long-dashed lines for quadrupedalism/climbing bouts and leaping bouts, respectively.

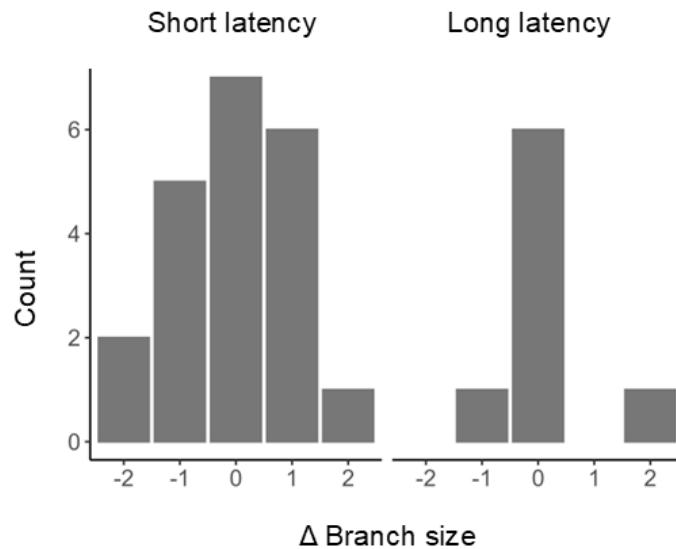


Figure 3.11 Distribution of Δ branch size during leaps in *E. rubriventer*, grouped by latency. Latency duration categorization (short versus long) is relative to the median latency for the species.

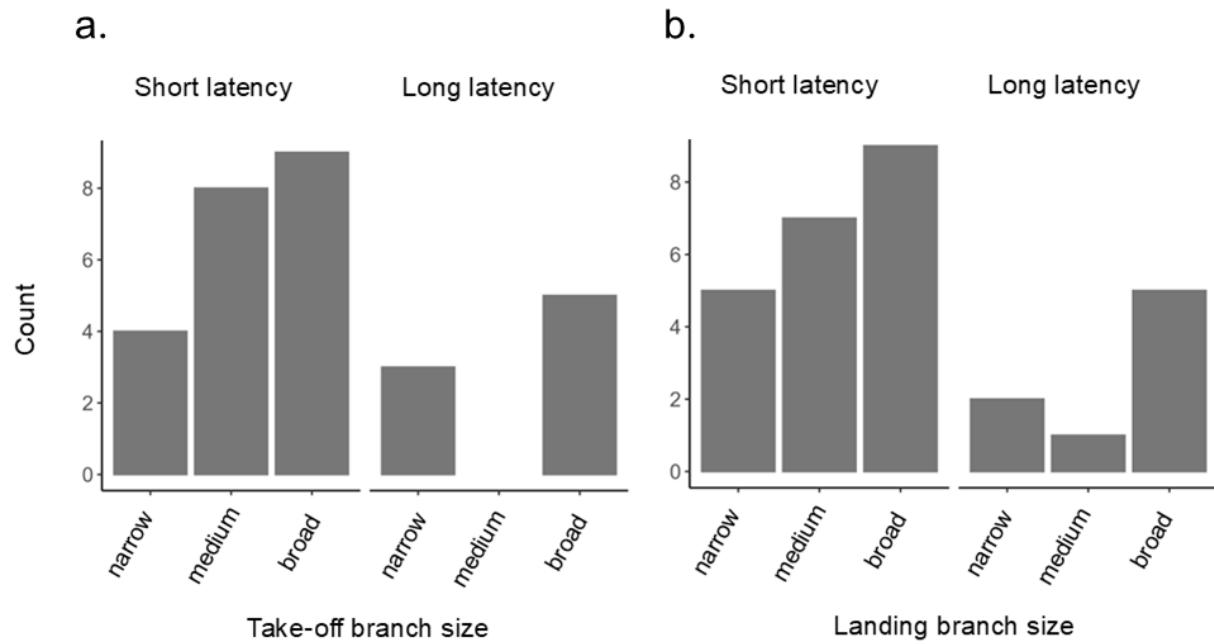


Figure 3.12 Relative size of take-off (a.) and landing (b.) branches used by *E. rubriventer* during leaps, grouped by latency. Latency duration categorization (short versus long) is relative to the median latency for the species

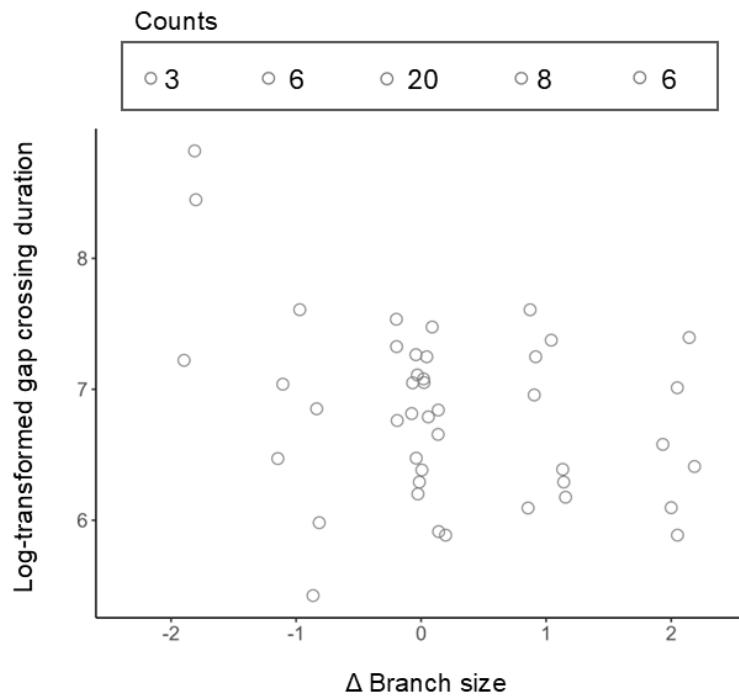


Figure 3.13 Log-transformed duration of bridging gap crossings in *E. rubriventer* plotted against Δ branch size. Counts for each score are provided in the box above the plot.

Lemur catta

Videos of *L. catta* yielded 177 bouts of locomotion (57 leaps and 119 bouts of quadrupedalism/climbing). The median latency before quadrupedalism/climbing bouts is 2.7s and 0s before leaping, which is significant (Wilcoxon test, $p<0.001$, Figure 3.14). When latencies were short, ring-tailed lemurs tended to leap between branches of approximate size (Figure 3.15). However, when latencies were longer, Δ branch size was more evenly distributed. Ring-tailed lemurs used a variety of branch sizes for take-off, though medium-sized ones were most common when latencies were short but the least common when latencies were long (Figure 3.16a). Landing branches were most often broad when latencies were short but narrow when latencies were long (3.16b). When crossing gaps by bridging, *L. catta* most often used branches of approximate size (Figure 3.17).

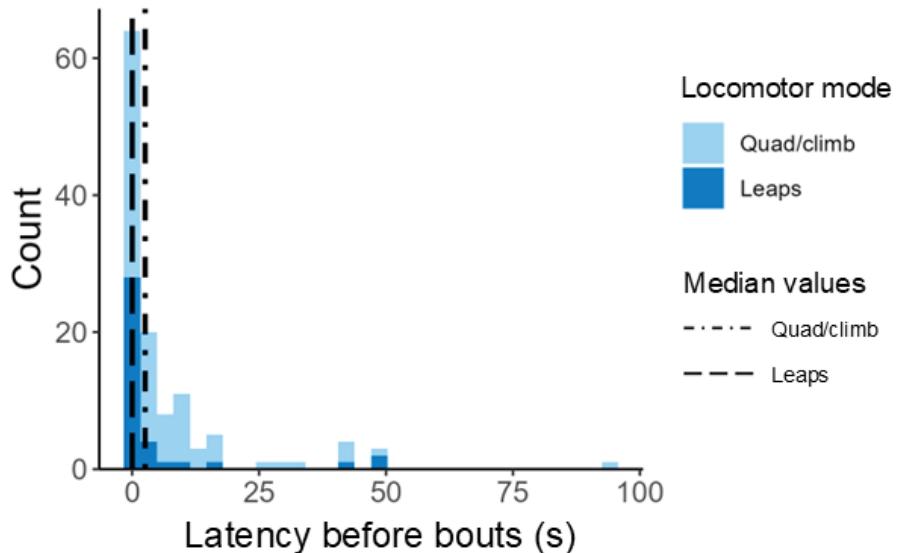


Figure 3.14 Latency before locomotor bouts in *L. catta*. Median latency values are plotted as dot-dashed and long-dashed lines for quadrupedalism/climbing bouts and leaping bouts, respectively.

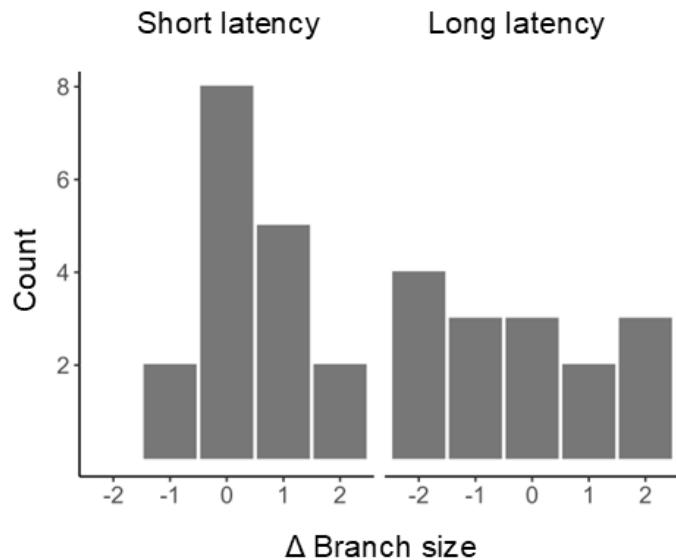


Figure 3.15 Distribution of Δ branch size during leaps in *L. catta*, grouped by latency. Latency duration categorization (short versus long) is relative to the median latency for the species.

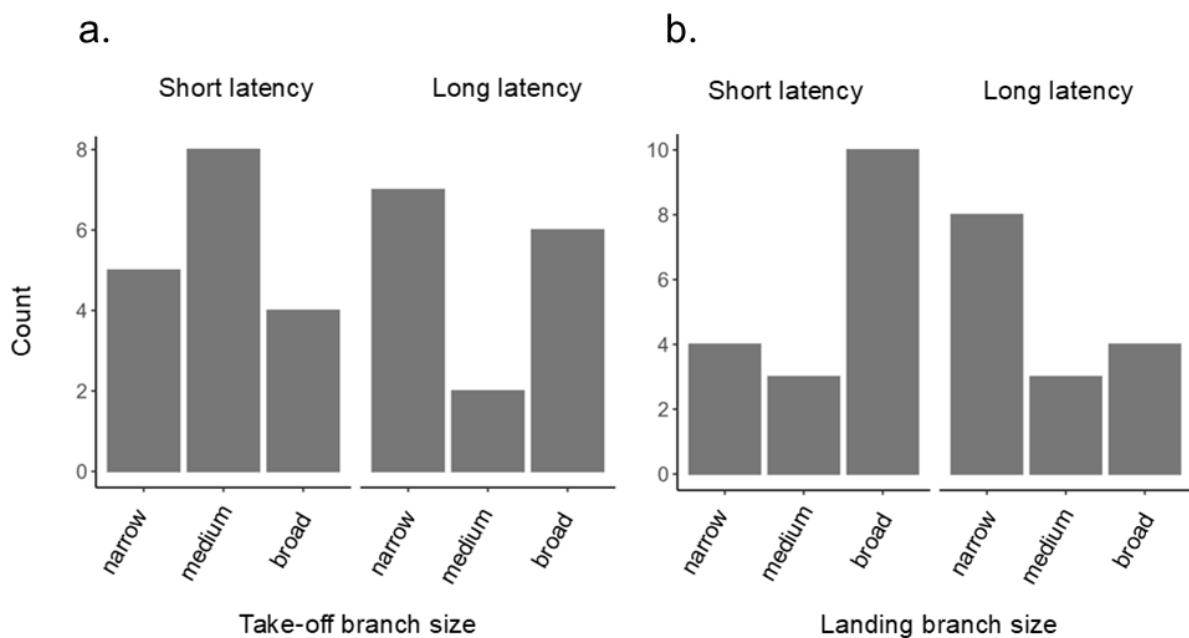


Figure 3.16 Relative size of take-off (a.) and landing (b.) branches used by *L. catta* during leaps, grouped by latency. Latency duration categorization (short versus long) is relative to the median latency for the species.

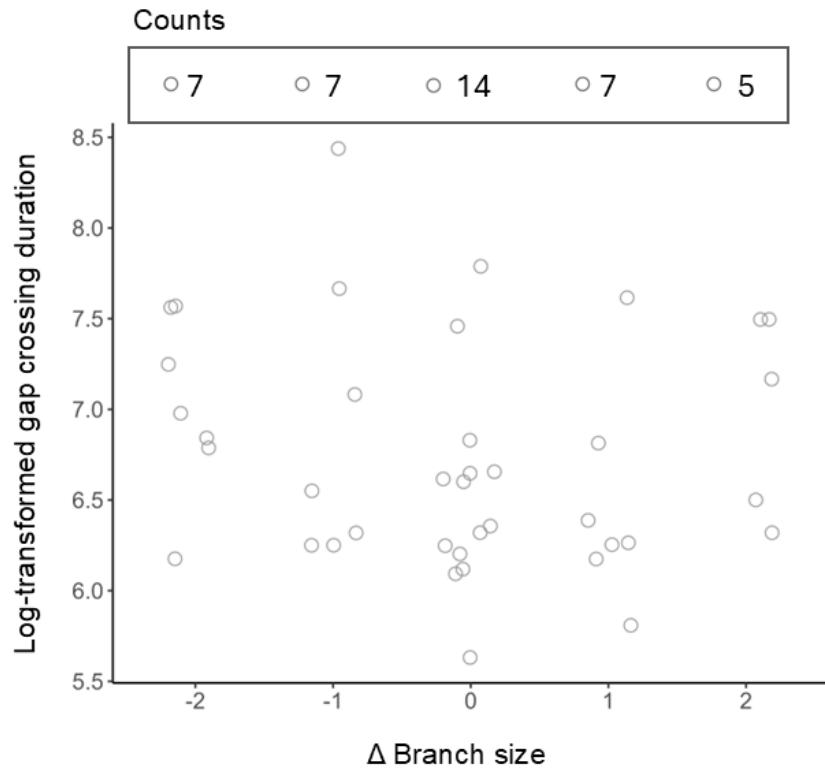


Figure 3.17 Log-transformed duration of bridging gap crossings in *L. catta* plotted against Δ branch size. Counts for each score are provided in the box above the plot.
Interspecies analysis

Leaping

Data were pooled across all individuals within species, irrespective of infant carrying or age group differences. The size of branches that primates used for take-off during leaps varied significantly (Fisher's test, $p=0.0018$, Figure 3.18a). *P. anubis* used significantly fewer medium and more broad branches for take-off compared to *C. ascanius* ($p\leq 0.0099$) and *L. catta* ($p\leq 0.017$). Landing branches did not vary significantly (Fisher's test, $p=0.23$, Figure 3.18b). The single most frequent Δ branch size score was 0 for all species (Figure 3.19). Changes in branch size were significantly different (Fisher's test, $p=0.0035$). Pairwise comparisons indicate that *L. catta* had significantly fewer 0 scores compared to *C. ascanius* ($p=0.035$) and *P. anubis* ($p=0.035$). *L. catta* also had significantly more scores of 2 or -2 compared to *C. ascanius* ($p=0.049$). Most leaps were preceded by short latencies, and the pattern of leaping between

similarly sized branches held regardless of latency except in *L. catta* where Δ branch size scores were evenly distributed (Figure 3.20).

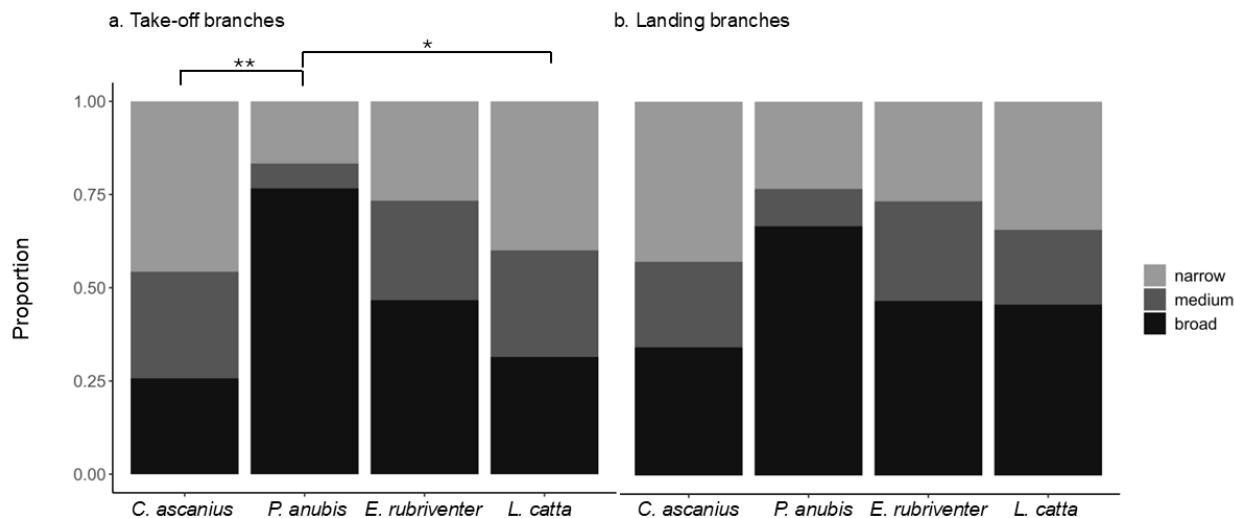


Figure 3.18 Proportions of relative branch sizes used for take-off (a.) and landing (b.) during leaping, grouped by species. Brackets indicate significant differences between groups (**p<0.01; * p<0.05).

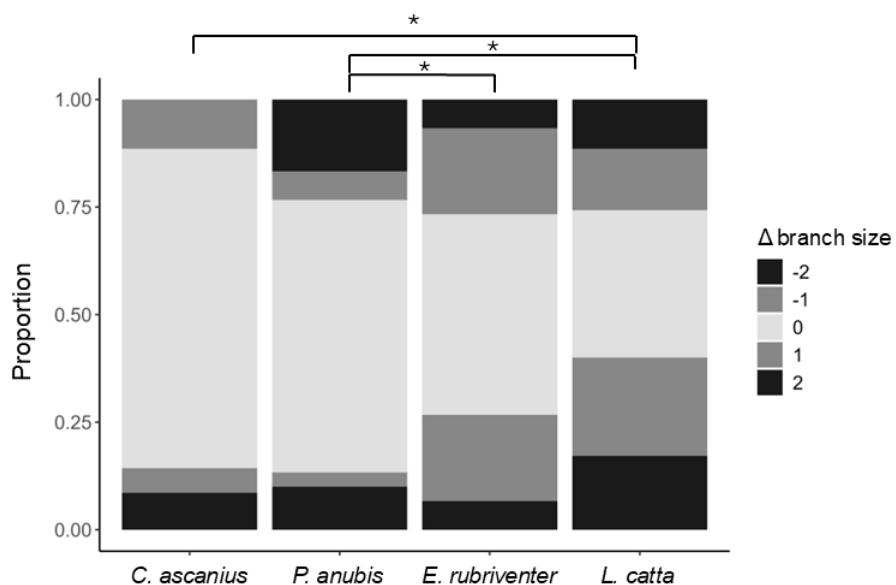


Figure 3.19 Proportional Δ branch size during leaping, grouped by species. Brackets indicate significant differences between species (* p<0.05).

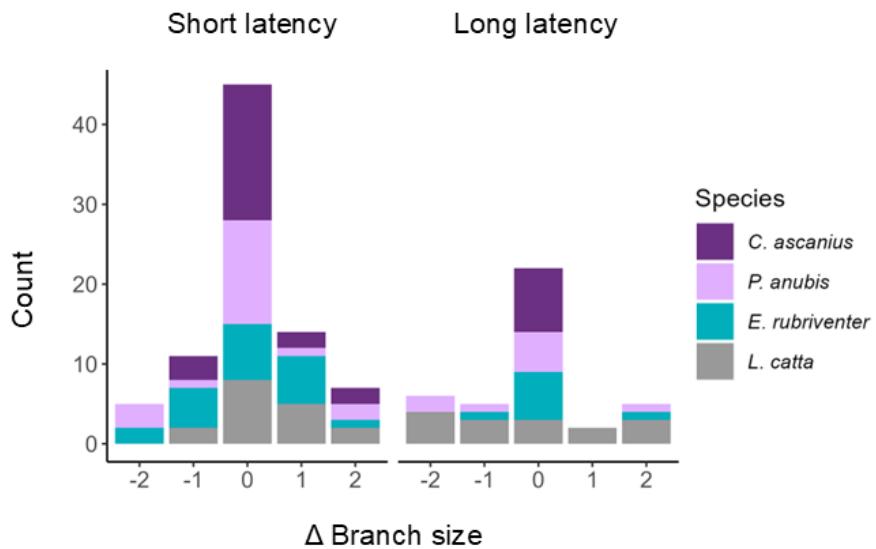


Figure 3.20 Summary of Δ branch size during leaping, grouped by species and compared between latencies.

Bridging

Data were again pooled across all individuals within species. The size of take-off branches used to cross gaps differed significantly among species (Fisher's test, $p=0.025$, Figure 3.21). Compared to *C. ascanius*, both *P. anubis* and *L. catta* used more medium branches for take-off ($p=0.044$). Landing branches did not vary significantly across species (Fisher's test, $p=0.071$). The absolute Δ branch size (scaled from 0 to 2 to reduce levels of comparison) was not significantly different across species (Fisher's test, $p=0.46$, Figure 3.22).

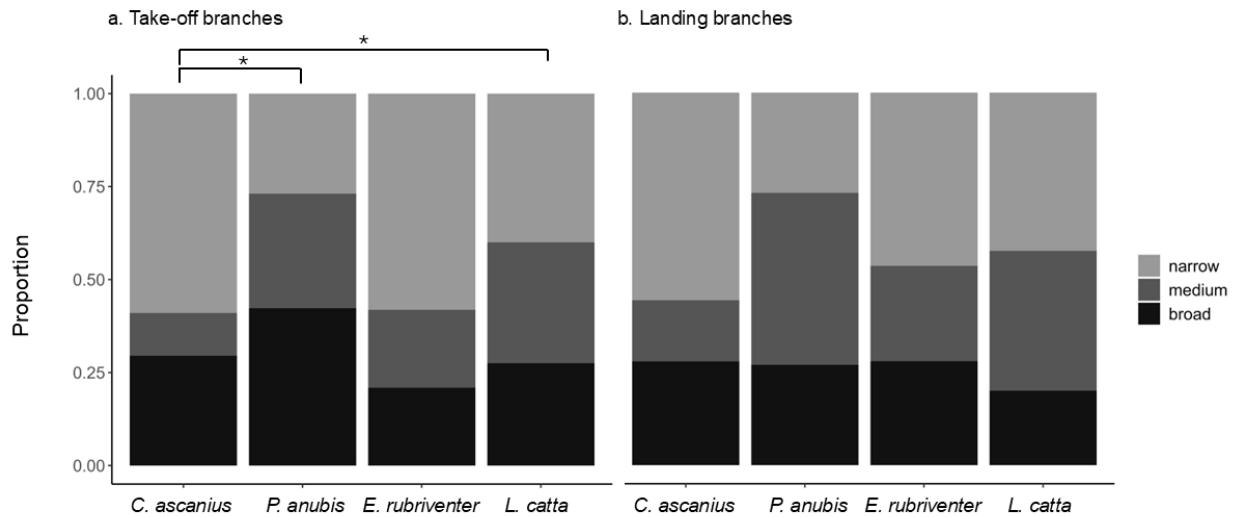


Figure 3.21 Proportions of relative branch sizes used for take-off (a.) and landing (b.) during bridging, grouped by species. Brackets indicate significant differences between groups (* $p<0.05$).

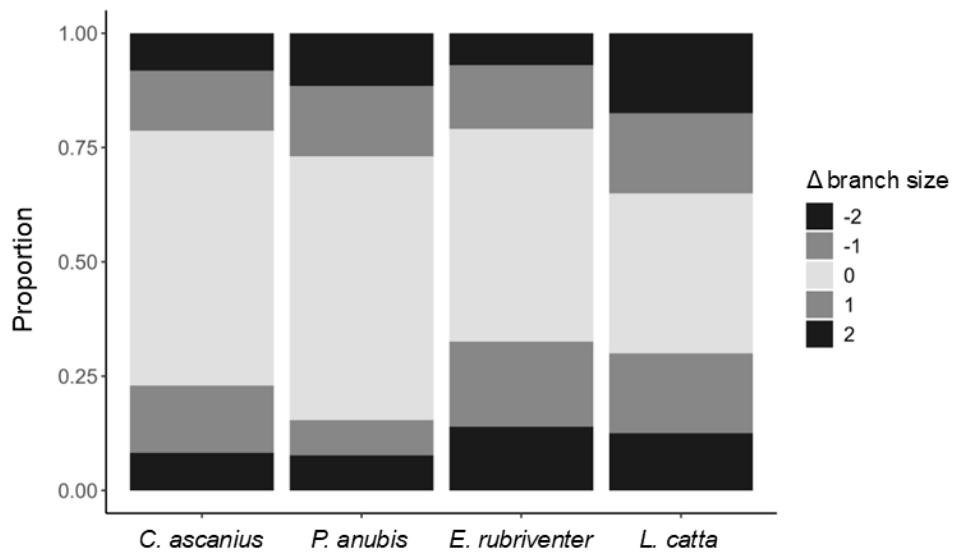


Figure 3.22 Proportional Δ branch size while crossing gaps via bridging, grouped by species.

Analysis of variance in log-transformed gap durations among species and take-off branch size categories showed a significant main effect for branch size ($p=0.038$, Table S1, Figure 3.23) and a significant interaction between take-off branch size and species ($p=0.036$). Within *Cercopithecus ascanius*, individuals took longer to cross gaps on narrow take-off

branches compared to large ones ($p=0.0059$). Other species did not significantly alter gap durations. Within narrow take-off branches, both *C. ascanius* and *P. anubis* had longer gap durations compared to *L. catta* ($p=0.024$). Gap durations did not vary significantly between species within other take-off branch sizes.

Analysis of variance in log-transformed gap durations showed a significant main effect for landing branch size categories ($p<0.0001$, Table S2, Figure 3.24). The effect of species approached significance ($p=0.06$). Gap durations were greater on narrow branches compared to medium ($p<0.01$) and broad branches ($p<0.001$).

Log-transformed gap durations did not significantly vary among absolute Δ branch sizes ($p>0.08$, Table S3, Figure 3.25).

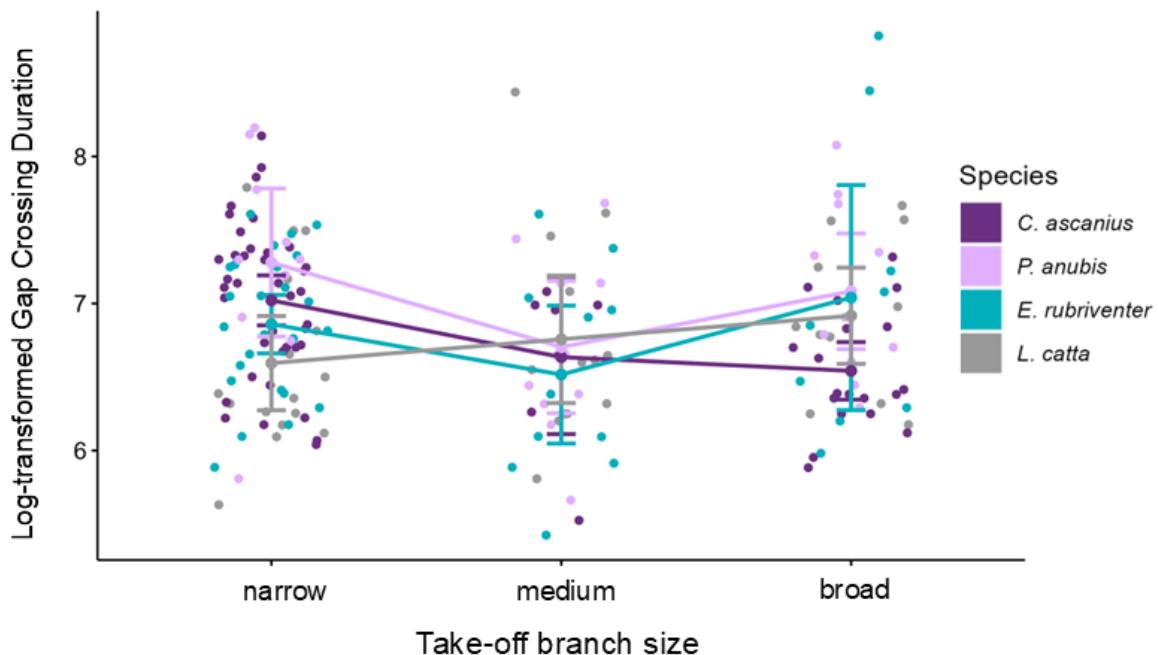


Figure 3.23 Variation in gap crossing durations according to the relative size of the take-off branch. Log-transformed gap durations are grouped by species, and error bars represent 95% confidence intervals.

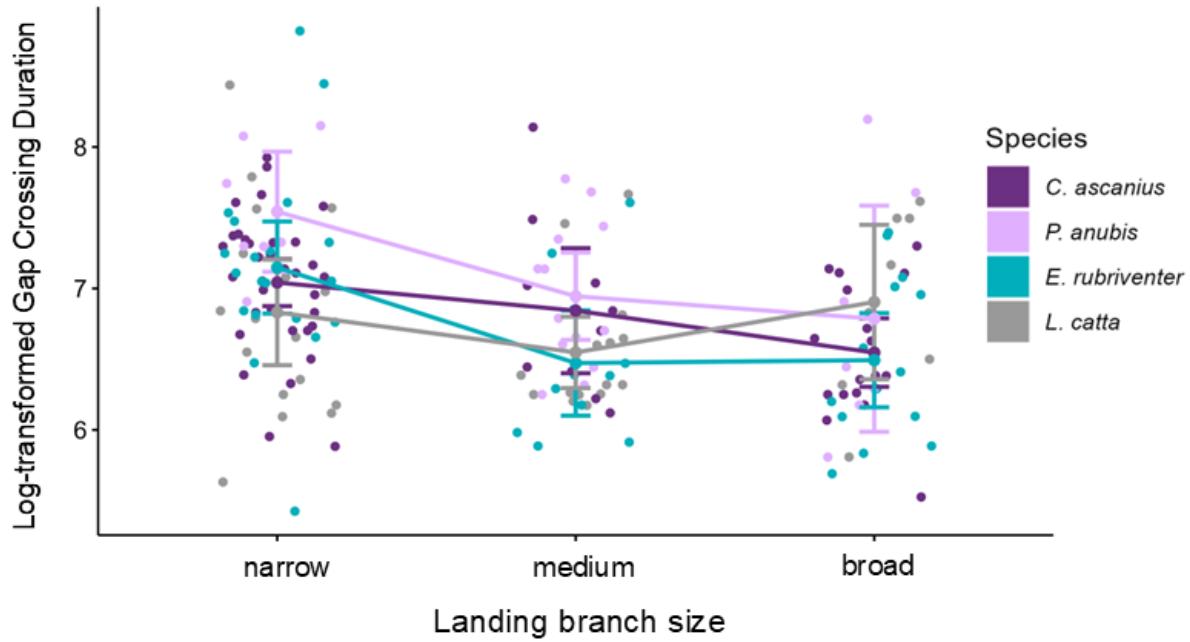


Figure 3.24 Variation in gap crossing durations according to the relative size of landing the branch. Log-transformed gap durations are grouped by species, and error bars represent 95% confidence intervals.

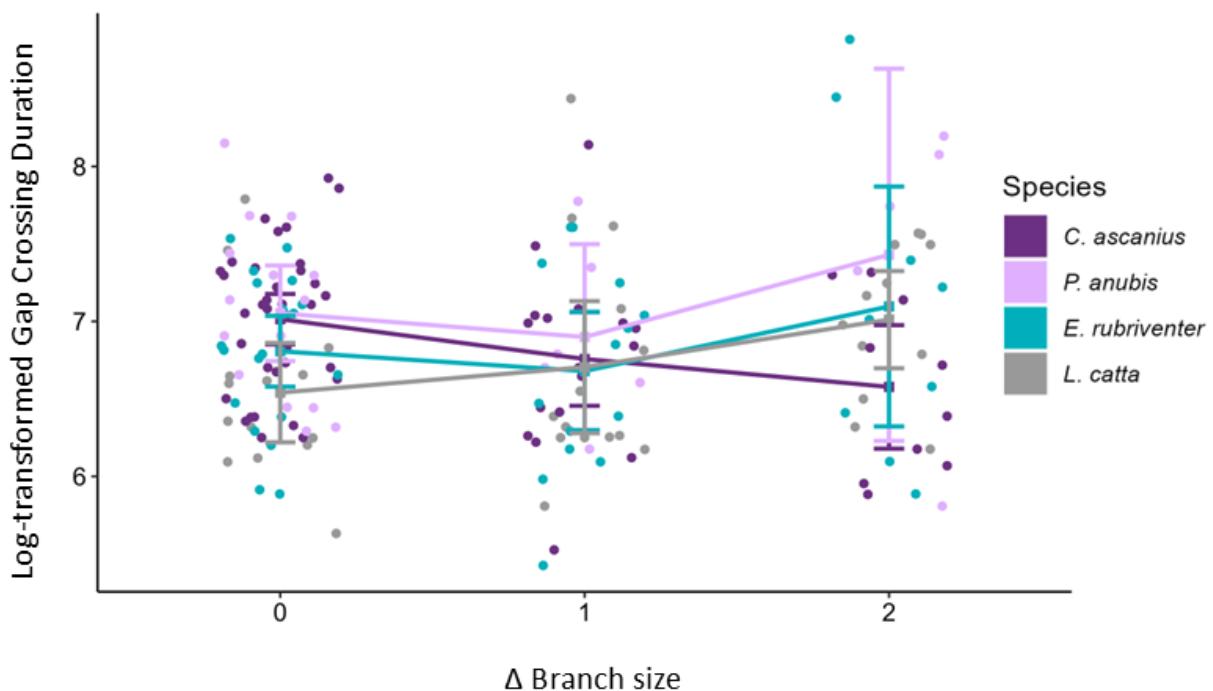


Figure 3.25 Variation in gap crossing duration according to Δ branch size. Log-transformed gap durations are grouped by species, and error bars represent 95% confidence intervals.

Discussion and conclusions

Distributions of latencies are broadly similar across species and groups within species (Figures 3.2, 3.6, 3.10, and 3.14). When primates leaped, they most often did so without pausing. This result means that while individuals were in motion they were often able to gather sufficient information about their environment to successfully navigate it. Mistakes and changes in direction were infrequent – only five such events were observed throughout the 4 hours and 5 minutes of locomotion examined for this study (Table 3.3). When it comes to using vision to guide locomotion, these results align with what is known about human walking – individuals are able map out several steps ahead of their current position (Hollands et al., 2002; Matthis et al., 2018). Further discussion below interprets results of intra- and interspecies analyses of gap crossing behaviors.

Table 3.3 Summary of mistakes and retreats during locomotion

Species	Age-Sex Class	Event
<i>C. ascanius</i>	Adult female (carrying infant)	Uses both forelimbs to partially load weight on very narrow branches, retreats
<i>P. anubis</i>	Juvenile unknown	Falls after unsuccessfully dismounting large trunk
	Juvenile unknown	Trips on narrow branch while walking
<i>E. rufiventer</i>	Adult female	Trips when branch unexpectedly moves
<i>L. catta</i>	Adult unknown	Following group members, leaps onto swaying tree, retreats to leap from a more stable tree

Intraspecies analysis

Cercopithecus ascanius

Red-tailed monkeys were sometimes observed carrying infants, so intraspecies analysis focused on detailing how gap crossing behaviors might have varied during infant carrying versus when the animals were unloaded. The effects of infant carrying on locomotion have been studied in a variety of primates, though not directly in *Cercopithecus ascanius* (Young & Shapiro, 2018). However, it is reasonable to assume that *C. ascanius* fits within the broad

patterns observed in a variety of primates. For instance in callitrichids, travel speed and leaping ability are reduced when carrying infants (Capelos et al., 2012; Schradin & Anzenberger, 2001). In the present study, infant carriers and noncarriers exhibited some similarities in their locomotor profiles: latencies were low, especially before leaping (Figure 3.2) and they frequently used branches of similar size (Δ branch size equals 0) to cross gaps (Figures 3.3). Leaping was hypothesized to be precarious for individuals carrying infants because of the mechanical cost of transporting extra weight. While individuals carrying infants were observed using a range of branches for leaping like unloaded individuals, those carrying infants used proportionally longer latencies before leaps (Figure 3.3), and those leaps occurred more often between narrow and medium-sized branches as opposed to large ones (Figure 3.4). Additionally, the one noticeable retreat identified in this species was of a female carrying an infant who seemed to attempt a gap crossing but retreated (Table 3.3). The individual used both forelimbs to start moving forward and then paused to readjust. After the branches, which were very thin and compliant, moved under the weight of the individual's limbs, it retreated to the large trunk it was resting on previously. It then moved in an alternate direction. Though based on low sample sizes, the observed patterns of branch usage deserve to be more systematically investigated in future research.

Papio anubis

The olive baboon, like most species of baboons, is a highly terrestrial species of primate. Juveniles have been reported to use a greater variety of locomotor behaviors, but by the time they reach adulthood, individuals will predominantly use quadrupedalism to move terrestrially (Druelle & Berillon, 2013; Rose, 1977). The data presented here support this pattern: the bulk of observations of arboreal locomotion was recorded in juveniles, and juveniles also had the most locomotor bouts categorized as "other" (Figure 3.6). These bouts included instances of below branch locomotion and fire-poles slides down very large tree trunks (Hunt et al., 1996). Adults were also observed in the trees, and females were even observed leaping between branches

classified as narrow (Figures 3.9 and 3.10). Adult males, who can be upwards of 10kg larger than adult females (Druelle et al., 2016; Smith & Jungers, 1997), were observed less frequently, accounting for only three bouts of arboreal locomotion. Overall, both adults and juveniles were most often observed crossing gaps where the Δ branch size was zero (Figures 3.7 and 3.9), and branches tended to be relatively large (Figure 3.8).

Juvenile baboons, because of their reduced size and documented tendencies to spend more time engaging in arboreal locomotion, were hypothesized to use overall shorter latencies than adults, especially when leaping between relatively narrow substrates. Instead, adults and juveniles displayed similar patterns of branch usage, preferring broad supports and less frequently using narrow and medium-sized ones. Additionally, the few gap crossing durations calculated in adults also fall within juvenile performance ranges. Understanding the context under which adult baboons opt to use smaller branches will be important for future research. For instance, the baboons in this study were often recorded near the field station, which they are known to frequent. Baboons were observed lower in the trees than many sympatric species (personal observation). Feeding and resting trees may have been determined “safe” through repeated experience at this particular site.

Eulemur rubriventer

Red-bellied lemurs tended to use broad branches when leaping, though the preference is not as stark as in *Papio* (Figure 3.12). Leaps preceded by long latencies were also often between broad branches, which is counter to the prediction that narrow landing branches would likely need more time for assessment before the animal decided to leap. Like other species, red-bellied lemurs tended to bridge between similarly sized supports (Figure 3.13).

Lemur catta

Ring-tailed lemurs most frequently used short latencies when leaping between similarly sized branches. In contrast, longer latencies were equally likely across all branch categories (Figure 3.15). This pattern contrasts with other species, where Δ branch size scores tend to

follow similar patterns regardless of latency. However, during bridging *L. catta* also tends to bridge between similarly sized branches like other species (Figure 3.17).

Interspecies analysis

Leaping

Differences were observed in the proportional use of relative branch sizes during leaping. *P. anubis* used large branches for take-off much more frequently than *C. ascanius* and *L. catta*, who were the highest users of narrow branches (Figure 3.18a). Even though much of the *P. anubis* sample consisted of juveniles, the estimated age of the juveniles would mean that most, if not all, individuals were more massive than individuals from the other three species in this study. Body-size is a well-documented influence on arboreal locomotion, and larger species tend to use larger substrates for support (Blanchard et al., 2015; Cunha et al., 2006; Fleagle et al., 1981; Gebo & Chapman, 1995; Young, 2023).

Though Δ branch size scores grouped around 0, there were significant interspecific differences in the proportions of those scores (Figure 3.19). However, these proportional differences did not translate to differences in latencies before leaps. Rather, observed differences in both branch size preference and the prevalence of 0 scores for Δ branch size highlight a natural bias in the locomotor data collected: canopy structure. Leaping frequency is often related to several interacting effects of ecology and morphology, depending on the strata where species are likely to be found (Fleagle et al., 1981; Gebo & Chapman, 1995; McGraw, 1996, 1998).

Figure 3.26 depicts some common viewpoints of the primates analyzed in the present study. *C. ascanius* was often observed foraging on the distal ends of tree branches, whereas *P. anubis* was often observed resting on the large boughs of trees where juveniles would play. *E. rubriventer* was recorded in the dense rainforest of Ranomafana National Park. *L. catta* meanwhile was studied at Anja Community Reserve, which is much drier with sparse vegetation. In the previous chapter, these two lemur species were recorded walking at different

heights on average as well, *E. rubriventer* above *L. catta*. However, in both contexts, there were plenty of vertical branches and trunks for lemurs to do a mixture of vertical clinging and leaping (VCL) and torso-pronograde leaping.



Figure 3.26 Isolated video frames of primate locomotion. Top: *C. ascanius* (left) and *P. anubis* (right). Bottom: *E. rubriventer* (left) and *L. catta* (right). Photos are not meant to be entirely summative but illustrative of the basic canopy structure where primates were often observed.

The prevalence of Δ branch size scores at 0 is likely due to the position of the subjects within the tree canopy. If *C. ascanius* was recorded foraging on narrow branch tips, then it is likely that nearby branches will also be narrow. Therefore when leaping to a new branch, primates can likely approximate affordances based on their current position. Nonetheless, the data also show that primates *will* leap between branches of many sizes. For animals like adult baboons or females carrying their infants, understanding the where and when they choose to leap between precarious (e.g., narrow) branches can provide insight into the risks animals are willing to tolerate.

Bridging

Similar to what was observed in leaping, there was a significant difference in the branches that some primates used to initiate bridging movements: *P. anubis* used significantly fewer narrow branches and more broad branches compared to *C. ascanius* and *L. catta* (Figure 3.21). However, gap crossing durations were longer if landing branches were narrow (all species) or if the take-off branch was narrow (*C. ascanius*) (Figures 3.23 and 3.24). It is possible that the mechanics of getting four limbs to come into contact with a narrow and probably compliant branch is in part cause for this relationship. Future passes through the data can include more granular details of the movement of the limbs during this type of gap cross to understand this uncertainty. Regardless, if gap crossing durations are higher when an animal is moving to a narrow branch, it underscores the precariousness of this movement and the importance of having the capacity respond to unexpected perturbations in the branches. The ability to modulate movement of the limbs while traversing gaps is an important element of locomotor flexibility exhibited in primates (McNamara et al., 2019). Slower movement across these gaps may allow for more deliberate placement of the limbs and time to detect the precariousness of the new support.

Limitations and future directions

The present study attempts to repurpose videos to assess whether elemental features such as relative branch size and body size correspond to performance variables like latency and gap crossing durations. Interpretation of the data relied on using these variables as proxies for visual and tactile estimation of upcoming locomotor supports but variation in the timing of these behaviors could occur for several reasons. Locomotor context such as foraging, traveling, or playing could all effect the timing of starts and stops during locomotion. In a familiar environment, it is likely that extended periods of using exploratory behaviors are not often required for robust locomotor performance. Future research would benefit greatly from longitudinal data about a group's typical foraging trees and travel paths – and any potential

changes to these as well. Such data could help determine the likelihood that primates are moving through novel environments and aid in determining the contours of primate affordances.

Other study limitations – such as the short length of many videos – are shared across species and are presumed to affect the presented results in similar ways. However, some species were recorded in more geographically limited areas. *P. anubis* was often recorded opportunistically as they gathered near the Makerere Biodiversity Field Station, and *L. catta* was recorded only over two days in a small area at the Anja Community Reserve. In addition to the proposed study designs above, incorporating videos from other locations – if they exist – may improve our understanding of primate decision-making in different locomotor contexts.

Future research should also aim to include an ontogenetic sample of more species. Analyzing the locomotion of *P. anubis* revealed that juveniles mirror adults in some ways – such as preferred branch sizes – and differ from them in other ways – such as their overall levels of arboreality and locomotor flexibility. As a highly terrestrial and large-bodied species, however, patterns observed in *P. anubis* should not be applied broadly. Additionally, while primates in this study tend to carry their young, some species instead park them while adults forage. Understanding the motor development of primate species, and therefore the cognitive processes that govern adult locomotion, will be greatly enhanced by further comparative and ontogenetic research designs.

Conclusions

Safely navigating arboreal environments is not only a mechanical problem but a cognitive one as well. As far as I am aware, this is the first study of its kind to attempt to quantify the affordances of wild primates. In this study, primates exhibited robust locomotor performance, most often using very short latencies before leaps. Longer latencies often did not correspond to strong patterns of using relatively broad branches or large changes in support size. Only *C. ascanius* carrying infants and *L. catta* might diverge from this pattern, but more data will need to be collected to determine if these are really emerging patterns or circumstantial. When primates

engaged in bridging, gap crossing durations increased when transferring to narrow supports. Primates overall used a variety of behaviors to cross gaps that varied in their structure, highlighting the importance of flexibility and accuracy during arboreal locomotion.

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CHAPTER 4: LEMURS ENHANCE STABILITY ON ARBOREAL SUPPORTS DURING LOCOMOTION IN DIM LIGHT

Abstract

Vision is crucial for guiding the safe locomotion of arboreal primates. Several species of lemur are proposed to be cathemeral, or active on a 24-hour cycle; however, only some have a tapetum lucidum, a reflective tissue layer behind the retina which would augment low-light vision. Here, I investigate how captive lemurs change their gait when moving in ambient light levels mimicking light availability at dawn or dusk. *Varecia spp.*, *Lemur catta*, and *Eulemur flavifrons* individuals were recorded at the Duke Lemur Center as they moved on simulated branches in both bright and dim light conditions. While none of the lemurs adjusted their speed, all made some changes to their gait to increase stability in dim light. *Varecia* used shorter, less frequent strides and higher forelimb duty factors when moving on narrow or declined branches in dim light, in accordance with their large body size and lack of a tapetum lucidum. *Eulemur* used a narrower range of speeds in dim light and trended towards higher hindlimb duty factors. The presence of a tapetum lucidum in *Eulemur* is debated in the literature but we found no apparent eye-shine in these individuals. Finally, *Lemur* increased the mean number of supporting limbs during a stride, which was unexpected as they are smaller and possess a tapetum lucidum. Overall, these results show that in cathemeral lemurs, increasing stability in low-light conditions may be a common strategy regardless of visual capacity.

Introduction

Vision plays an important role in guiding primate locomotion, regardless of daily activity cycles. Because strepsirrhines, and especially lemurs, vary in these activity cycles, researchers have long been interested in how their vision systems influence their social behaviors and signaling, foraging strategies, and other aspects of their ecology (Charles-Dominique, 1975; Pariente, 1976). In the previous chapter, I described the locomotor profiles of four primate species including two species of lemur. In that chapter, the data suggest that generally primates are able to gather sufficient information *while in motion* to safely transition between locomotor modes, leaps, and traverse a complex arboreal environment. Relatively little is known, however, how the mechanics lemur locomotion might change as they move in environments with different levels of ambient light.

In their review on visual systems of lemurs, Valenta and colleagues (2016) document that only nocturnal species of lemur have consistently retained the tapetum lucidum – the reflective tissue layer in the eye that augments low light vision. Meanwhile, members of the genus *Eulemur* are largely cathemeral, or active over a 24-hour period (Colquhoun, 1998; Curtis et al., 1999; Curtis & Rasmussen, 2006; Kappeler & Erkert, 2003; Tattersall, 1987), but they variably possess a tapetum lucidum (Peichl et al., 2019; Valenta et al., 2016). Furthermore, while *Lemur catta* has previously been considered diurnal, they do possess a tapetum lucidum, and substantial evidence suggests that *L. catta* can also exhibit cathemerality in the wild (Donati et al., 2013; LaFleur et al., 2014; Parga, 2011). Additionally, *Varecia rubra* and *variegata* lack a tapetum lucidum and have also been considered diurnal, though there is some anecdotal evidence that they are capable of cathemeral activity patterns (Donati & Borgognini-Tarli, 2006; Wright, 1999). In fact, studies done at the Duke Lemur Center, where this study was also conducted, indicates that *Eulemur*, *Varecia*, and *Lemur* may all exhibit some amount of cathemeral behavior, though activity cycles in these captive groups are highly influenced by human activities and working hours (Bray et al., 2017; Rea et al., 2014).

Activity levels within wild cathemeral species also vary. *Eulemur spp.* have been shown to increase activity levels when the luminosity of the moon is greatest (Colquhoun, 1998; Schwitzer et al., 2007). A similar pattern has also been observed in owl monkeys (*Aotus*; Fernández-Duque et al., 2010). In these studies, locomotor behaviors were not distinguished, so it is unclear the extent to which different types of locomotor behaviors vary. Outside the primate world, one study has shown that the diurnal gecko *Rhoptropus afer* makes a suite of changes to gait – e.g., reducing speed and increasing duty factors – as ambient light levels decrease (Birn-Jeffery & Higham, 2016). Given the variety of activity cycles lemur species use in the wild and the inconstancy of the tapetum lucidum across species, understanding the effects of light availability on the gait of lemurs may provide insight into the interplay between visual anatomy and ecology. This study presents the effects of light availability and support properties on the gait of three genera of captive lemur (Table 4.1).

Table 4.1 Summary of captive lemur subjects

Species	Tapetum lucidum	Activity cycle (wild) [†]	DLC Relative Nocturnal Activity [‡]	Mass (kg)	No. Individuals
<i>V. rubra</i> & <i>variegata</i>	No	Diurnal/ Cathemeral	Intermediate	3.0-3.9	5
<i>L. catta</i>	Yes	Cathemeral	Low	2.0-2.5	3
<i>E. flavifrons</i>	No [§]	Cathemeral	High	2.2-2.8	3

[†]Valenta et al., 2016

[‡]Bray et al., 2016; Relative levels of nocturnal activity reported in the same groups of lemurs housed at the Duke Lemur Center

[§]Published records vary (see Valenta et al., 2016) but attempts to see eye shine produced no apparent reflection

In the present study, lemurs were recorded in bright and dim light settings as they moved across angled poles that varied in diameter. Beyond differences in body mass and eye anatomy, it is helpful to note other differences in the species under study here. In previous Chapters, I

have discussed extensively the morphology and locomotion of *Lemur catta*. *Eulemur flavifrons* is endangered in the wild and relatively little is known about them. However, they do seem equally arboreal as other *Eulemur* species in the wild (Schwitzer et al., 2007). Comparing *Lemur* and *Eulemur* to *Varecia*, the latter genus is characterized by a slightly higher intermembral index due to relative shortening of the hindlimbs (Fleagle, 2013; Jungers, 1985). However, they also use a mixture of quadrupedalism and leaping as forms of arboreal locomotion (Pereira et al., 1988). Despite some differences in ecology, these lemurs are expected to be proficient at the task of above branch quadrupedalism. *Varecia* subjects, because of their size, are expected to make the most pronounced changes to their gait on narrow and declined poles in order to increase stability. I predict that in dim light settings, these changes should be further exaggerated as enhancing stability may increase the amount of visual information that they can process that will further guide locomotion. I also predict that *Eulemur* may increase stability in dim light settings because they also have reduced visual capacity. Lastly, I do not predict *Lemur* to make any changes in response to light availability given that they have a tapetum lucidum.

Materials and methods

Experimental Setup

The lemurs were placed in a testing enclosure measuring 20' x 6' x 10'. Simulated branches were made of PVC, which was coated in paint containing an anti-skid additive. Narrow diameter poles were 2.2cm across and broad poles were 5.8 cm across. Diameters were selected based on the combined length of the palm and third digit (Patel & Maiolino, 2016). Despite differences in body size, hand length was roughly similar among species. On broad poles, hand lengths are approximately equal to one-third of the pole circumference, whereas the hand can wrap completely around the narrow pole. Poles were set at a 25° angle. Based on raw data from Chapter 2, lemurs at Ranomafana National Park and Anja Community Reserve walked on branches ranging from 0 to 60° from the horizontal, and the mean angle was 23°.

Branch diameters ranged from 1 to 10cm, centering around a mean of 4.4cm. While *Varecia* were not studied in Chapter 2, they do live in deeper parts of Ranomafana National Park and have elsewhere been described navigating thin, compliant branches (Pereira et al., 1988). Orange tape was used to divide the pole into even sections around 35cm in length which aided in speed and stride length measurements (see below). Lights in the enclosure room were set on a dimmer. For bright trials, light levels were turned to their maximum. For dim light trials, lights were set at the lowest possible level without turning them off completely. Lux measurements at the pole surface were taken using a light meter (Sekonic, New York, USA). During bright trials, illuminance ranged between 320 and 520 lux at the surface of the poles. During dim light trials, illuminance was between 1 and 7 lux, equivalent to ambient light levels at dawn or dusk. Illuminosity measurements taken in the field for different *Eulemur* species indicate that this range lux values falls within what is experienced by wild lemurs, though lemurs have been recorded moving in even darker conditions around 0.5 lux (Curtis et al., 1999; Kappeler & Erkery, 2003; Schwitzer et al., 2007). For best animal handling practices, increased light levels were desired.

Subjects were trained by DLC staff to do tasks like point follows in the testing enclosure, but they had not been explicitly trained on the substrates used in these experiments. Procedures were approved by Northeast Ohio Medical University IACUC Protocol 22-04-313 and Duke University IACUC Protocol A011-24-01.

Digital Recording

To record lemur locomotion, GoPro cameras were set to record at 120 frames per second and 1080p resolution. GoPro Hero 12 Black cameras were used to record in bright lighting conditions. These newer cameras were useful for their improved image quality and file compression. In dim lighting conditions, videos were recorded by modified GoPro Hero 5s (Back-bone, Ottawa, Ontario, Canada). IR filters were removed and 6mm CS-mount lenses were attached (Arducam, China). Following the advice of Stafstrom and Hoy (2024) infrared

lights (Andoer, China) were placed around the enclosure to increase visibility on the recording. To the human eye, the testing enclosure was still very dark, and animal subjects did not react to the IR lamps' presence.

Video analysis

Videos were processed using the custom program ClipStride (Dunham et al., 2018) to isolate strides across poles (N=290). Clips were analyzed in GaitKeeper to track footfalls and calculate spatial variables. Both programs are available for download at www.younglaboratory.org. Speed was calculated by noting the frames during which the nose of the animal crossed the length of a segment of the pole marked in orange tape. The length of the pole segment was divided by quotient of the time to cross in frames and the frame rate (120fps). Stride length was calculated as the product of speed and stride duration.

Besides speed and stride length, the kinematic parameters assessed in this study were stride frequency, mean number of supporting limbs, and forelimb and hindlimb duty factors. Stride frequency is the reciprocal of stride duration, or the time between successive touchdowns of a reference limb. The mean number of supporting limbs is the average number of limbs contacting the support at any given instance of the stride. Duty factor is the proportion of the stride in which the limbs are in contact with the pole, averaged within the forelimbs and hindlimbs. The frequencies of diagonal sequence and lateral sequence gaits are also reported. Diagonal sequence gaits are those where a reference hindlimb is followed by a contralateral forelimb in the sequence of footfalls during a stride. Lateral sequence gaits are those where the reference hindlimb is followed by an ipsilateral forelimb.

Statistics

Three *Lemur* and five *Varecia* subjects were recorded moving in bright and dim light on narrow and broad angled poles. Because the three *Eulemur flavifrons* subjects were less accustomed to the handling required for this type of research, they were recorded moving on

narrow and broad supports in bright light but only broad supports in dim light. Therefore, statistical tests only compare locomotion on the broad poles in bright and dim light.

Fisher's exact test ($\alpha=0.05$) was used to determine whether the frequencies of gait sequence types varied by light setting. Mixed effect ANOVAs were run to test which variables – diameter, orientation, and light – had the most pronounced effect on gait parameters. Models included individual animal sessions nested within subjects as a random factor. To improve interpretability of the models, tests were run in two iterations. First, all orientations were grouped together to test the effects of light and diameter as cofactors and speed as a covariate (where applicable). Second, all diameters were grouped together to test the effects of light and orientation as cofactors and speed as a covariate (where applicable). In *Eulemur*, where only one diameter could be tested in bright and dim light, only the effect of orientation (along with light and speed) was tested. For each test, the full model was fit, and then nonsignificant interactions between covariates were removed in a stepwise manner.

Data analysis and visualization were performed in R (R Core Team, 2022). Packages used to process raw data were dplyr (Wickham et al., 2023). Data visualization was done with ggplot2 (Wickham, 2016). Linear models were built with lmerTest (Kuznetsova et al., 2017), and post hoc comparisons were run with emmeans (Lenth, 2021).

Results

Table 4.2 summarizes the data collected for this analysis. The predominant form of locomotion was a diagonal sequence walking gait; however, some uses of lateral sequence gaits were observed, especially in *Varecia*. Out of a total 50 strides from *Varecia* that were recorded in bright lighting, 8 were lateral sequence gaits, and 14 out of 64 strides recorded in dim light were lateral sequence gaits. A Fisher's exact test indicated that this slight difference in proportion was not statistically significant ($p=0.48$). The two lateral sequence gaits in *Lemur*

were recorded in dim light, and the single lateral sequence gait in *Eulemur* was recorded in bright light.

Table 4.2 Summary of gait data collected in three genera of captive lemur

Species	No. of Individuals	Stride Total	Gait types [†]
<i>Varecia spp.</i>	5	114	DS (92) LS (22)
<i>Lemur catta</i>	3	114	DS (112) LS (2)
<i>Eulemur flavifrons</i>	3	62	DS (61) LS (1)

[†]DS, diagonal sequence; LS, lateral sequence

Gait kinematics

Speed. Lemurs did not change their average speed in different light conditions (Table 4.3; Supplementary Tables 4-6; Figure 4.1). In both *Varecia* and *Lemur*, the largest range of speeds were observed in dim lighting, including the slowest speeds. In contrast, *Eulemur* used a more limited range of speeds in dim lighting.

Table 4.3 Summary of the influence of light conditions, diameter, and orientation on the gait of three genera of captive lemur

Gait parameter	<i>Varecia</i>	<i>Lemur</i>	<i>Eulemur</i>
Speed	-	-	-
Stride length	Light-Orientation-Speed int. *	-	-
Stride frequency	Light-Diameter-Speed int. *	-	-
Mean NSL	-	Light m.e. *	-
Forelimb DF	Light-Orientation int. *	-	-
	Light-Diameter-Speed int. *		
Hindlimb DF	-	-	Light-Speed int. **
			Light-Orientation int. *

*p<0.05; **p<0.01; int. = interaction; m.e. = main effect

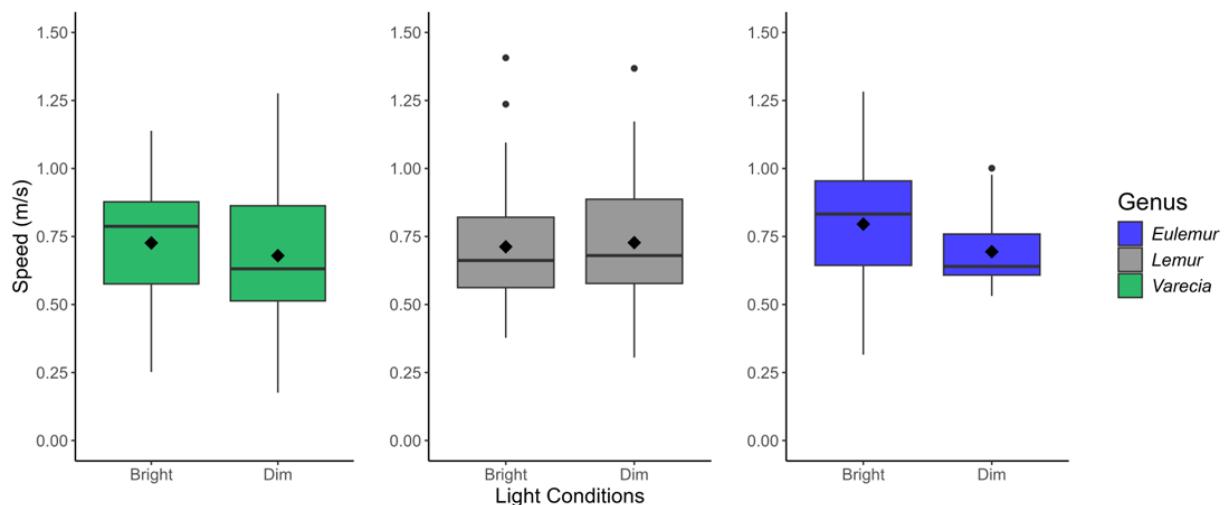


Figure 4.1 Box-and-whisker plot of speeds used by three genera of captive lemur. The bolded black line is the median, and the box spans are the interquartile range. The means are indicated by the black diamonds.

Stride length. *Varecia* subjects adjusted gait in response to changes in light availability (Table 4.3, Supplementary Table 7, Figure 4.2). In analyses grouping all diameters together, stride length was significantly characterized by an interaction between support orientation, light conditions, and speed ($p=0.021$). Post hoc analyses indicate that in bright light conditions when subjects moved slowly, stride lengths were increased on declines compared to inclines ($p=0.0028$). When moving quickly in bright light conditions, strides lengths were reduced on declines ($p<0.0001$). In dim light conditions, there were no significant adjustments to stride lengths when moving slowly ($p=0.36$), but when moving quickly in dim light conditions, stride lengths were reduced on declines ($p<0.001$). Neither *Lemur* nor *Eulemur* altered stride length in response to changes in light availability (Table 4.3, Supplementary Tables 8 and 9, Figure 4.3). For all species, stride length was positively correlated with speed ($p<0.0001$).

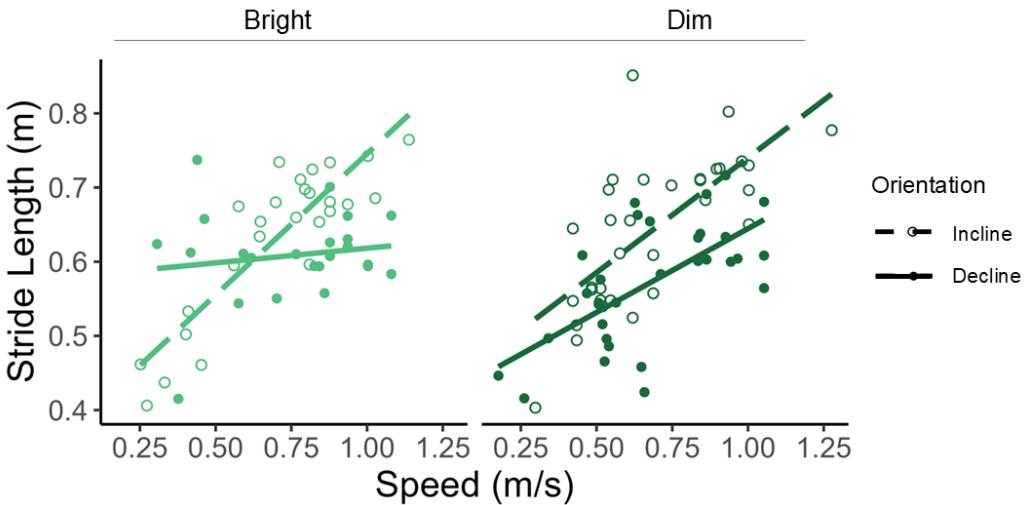


Figure 4.2 Scatterplots of stride length plotted against speed, grouped by support orientation, in *Varecia*. Left panel, strides in bright lighting conditions. Right panel, strides in dim lighting conditions. Trend lines indicate likelihood fits from mixed-effects analyses of covariance models. Solid and long-dash lines indicate groupings by support orientation. Lighter color shades indicate data collected in bright light conditions. Darker color shades indicate data collected in dim light conditions.

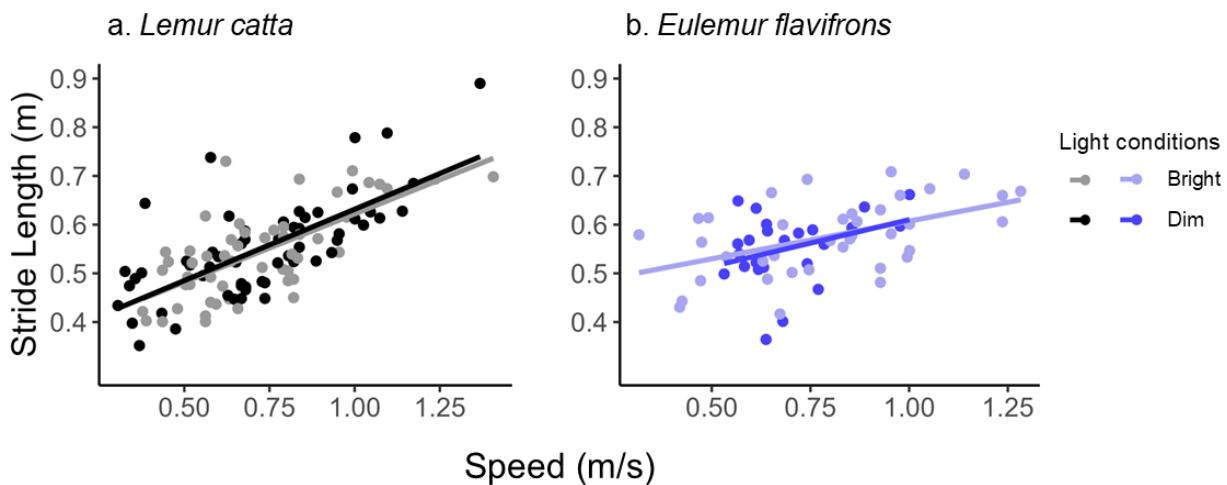


Figure 4.3 Scatterplots of stride length plotted against speed, grouped by lighting conditions, in *Lemur catta* (a.) and *Eulemur flavifrons* (b.). Trend lines indicate likelihood fits from mixed-effects analyses of covariance models. Lighter color shades indicate data collected in bright light conditions. Darker color shades indicate data collected in dim light conditions.

Stride frequency. Only *Varecia* subjects adjusted stride frequencies in response to changes in light availability (Table 4.3, Supplementary Table 10, Figure 4.4). In analyses

grouping orientations together, stride frequency was significantly characterized by an interaction between light conditions, support diameter, and speed ($p=0.039$). Post hoc analyses indicate when lemurs moved slowly in dim light, stride frequency was significantly decreased on narrow supports ($p=0.024$). *Lemur* and *Eulemur* subjects did not significantly alter stride frequency in response to changes in light conditions (Table 4.3, Supplementary Tables 11 and 12, Figure 4.5). For all species, stride frequency was positively correlated with speed ($p<0.0001$).

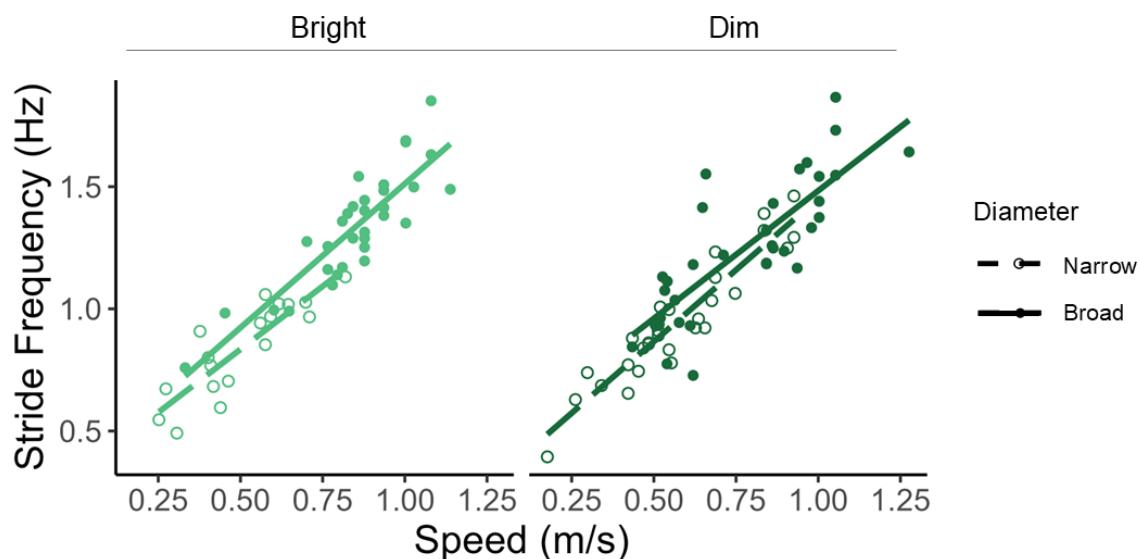


Figure 4.4 Scatterplots of stride frequency plotted against speed, grouped by support diameter, in *Varecia*. Left panel, strides in bright light. Right panel, strides in dim light. Trend lines indicate likelihood fits from mixed-effects analyses of covariance models. Solid and long-dash lines indicate groupings by support diameter. Lighter color shades indicate data collected in bright light conditions. Darker color shades indicate data collected in dim light conditions.

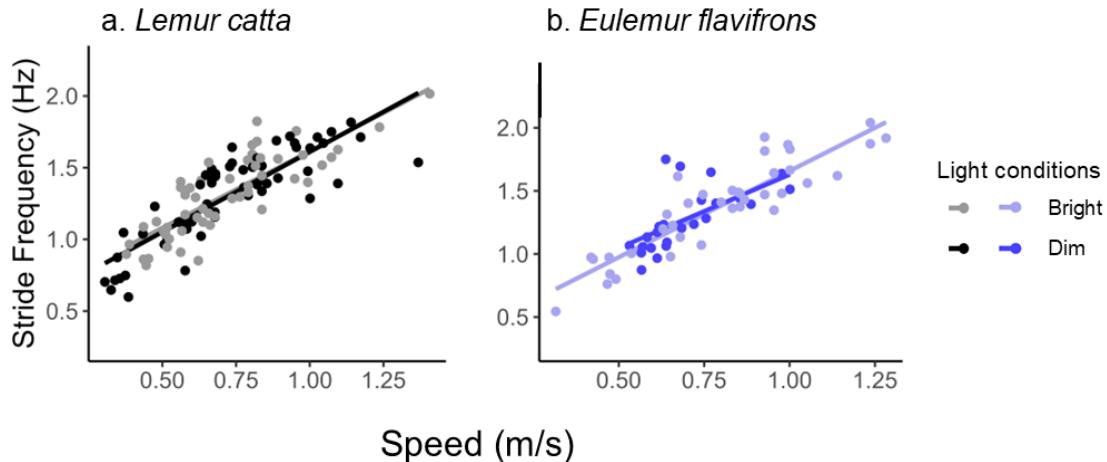


Figure 4.5 Scatterplots of stride frequency plotted against speed, grouped by lighting conditions, in *Lemur catta* (a.) and *Eulemur flavifrons* (b.). Trend lines indicate likelihood fits from mixed-effects analyses of covariance models. Lighter color shades indicate data collected in bright light conditions. Darker color shades indicate data collected in dim light conditions.

Mean number of supporting limbs. Only *Lemur catta* adjusted the mean number of supporting limbs in response to changes in light conditions (Table 4.3, Supplementary Table 14, Figure 4.6b). In the mixed-effects model grouping all diameters together, light conditions remained as a significant main effect ($p=0.030$). In the model grouping all orientations together, light conditions approached significance as a main effect ($p=0.052$). Post hoc analysis indicates that lemurs increased the mean number of supporting limbs during a stride in dim light conditions ($p=0.030$). *Varecia* and *Eulemur* did not alter mean number of supporting limbs in response to varying light conditions (Table 4.3, Supplementary Tables 13 and 15, Figure 4.6a,c). For all species, mean number of supporting limbs was negatively correlated with speed ($p<0.0001$).

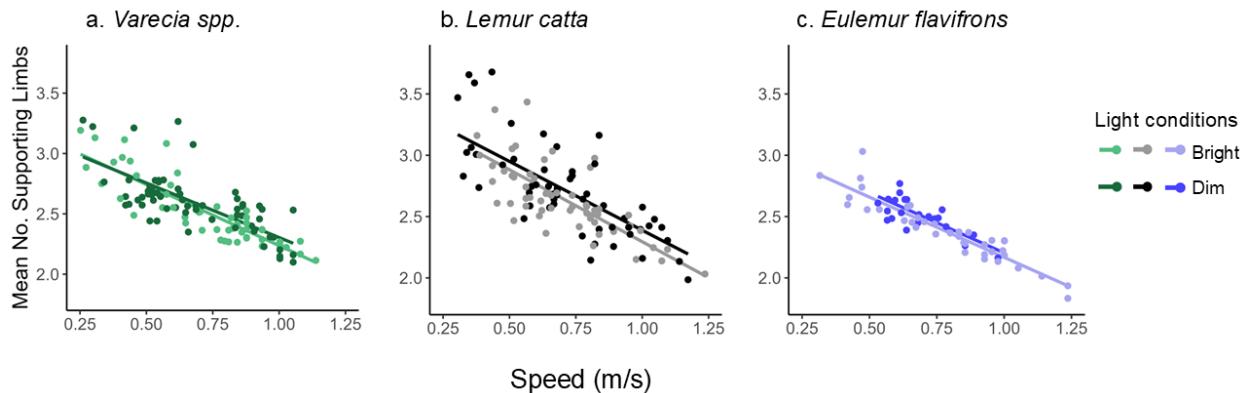


Figure 4.6 Scatterplots of mean number of supporting limbs plotted against speed, grouped by lighting conditions. Trend lines indicate likelihood fits from mixed-effects analyses of covariance models. Dashed lines for *Varecia* (a.) and *Eulemur* (c.) indicate non-significant trends. Lighter color shades indicate data collected in bright light conditions. Darker color shades indicate data collected in dim light conditions.

Forelimb duty factor. *Varecia* altered forelimb duty factors in response to changes in light availability (Table 4.3, Supplementary Table 16, Figure 4.7). In the model grouping all orientations together, forelimb duty factors were characterized by a significant three-way interaction between light, support diameter, and speed ($p=0.015$). Post hoc analyses for this model indicate that when lemurs moved slowly in bright lighting conditions, forelimb duty factors were increased on broad supports compared to narrow ones ($p=0.024$). In the mixed-effects model with all diameters grouped together, forelimb duty factor was significantly characterized by a factor-by-factor interaction between support orientation and light ($p=0.049$). Post hoc analyses for this model indicated that when *Varecia* subjects moved in dim light they increased forelimb duty factors on declines relative to inclines ($p<0.0001$). The effect of moving in bright light followed the same pattern but only approached statistical significance ($p=0.054$). Post hoc analyses examining light effects within orientations were nonsignificant. *Lemur* and *Eulemur* did not adjust forelimb duty factors in response to changes in light conditions (Table 4.3, Supplementary Tables 17 and 18, Figure 4.8). For all species, forelimb duty factor was negatively correlated with speed ($p<0.0001$).

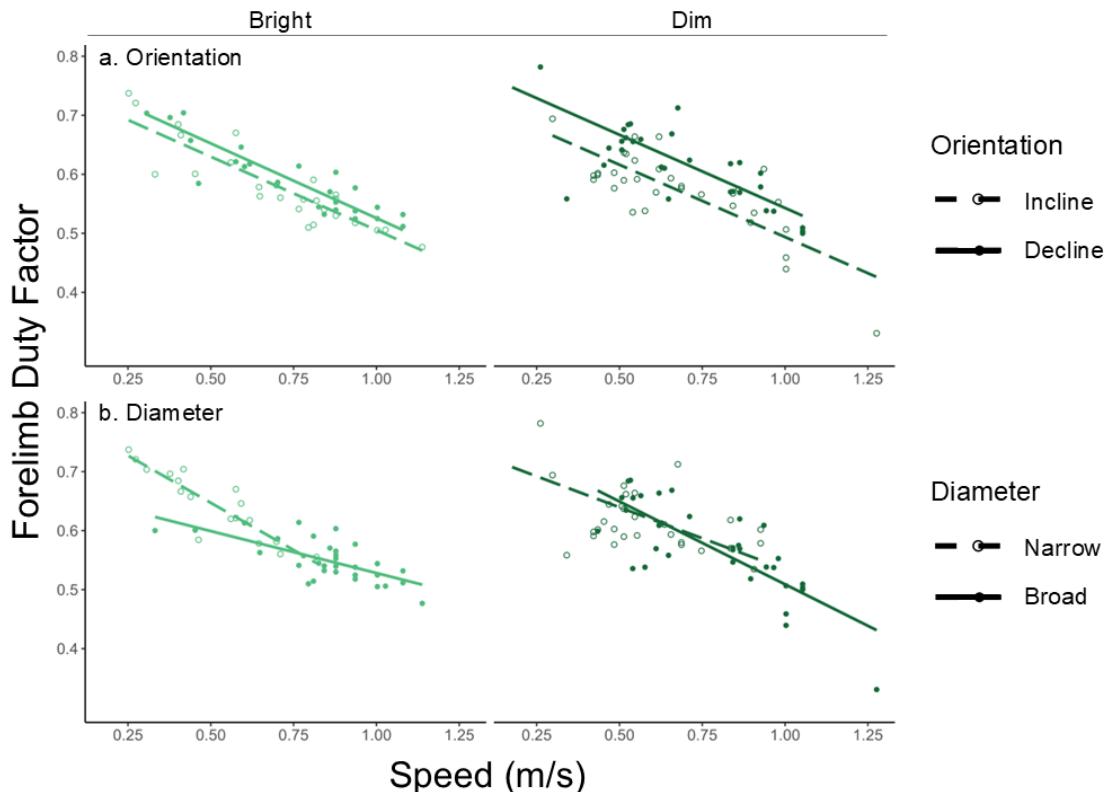


Figure 4.7 Scatterplots of forelimb duty factors plotted against speed in *Varecia*, grouped by Orientation (a.) and Diameter (b.). Trend lines indicate likelihood fits from mixed-effects analyses of covariance models. Line types distinguish inclines from declines in the top row and narrow supports from broad ones in the bottom row. Lighter color shades indicate data collected in bright light conditions. Darker color shades indicate data collected in dim light conditions.

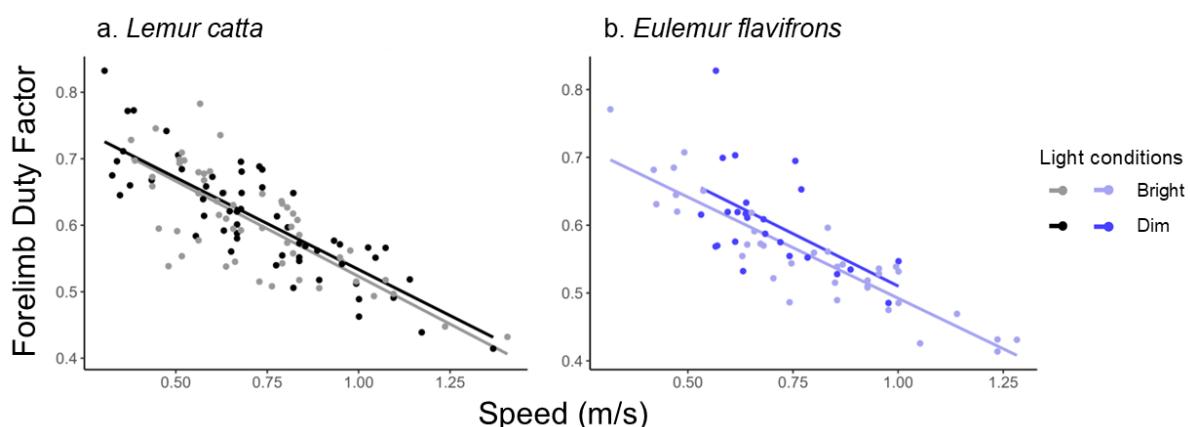


Figure 4.8 Scatterplots of forelimb duty factors plotted against speed in *Lemur* (a.) and *Eulemur* (b.), grouped by light conditions. Trend lines indicate likelihood fits from mixed-effects analyses of covariance models. Trends were nonsignificant and so are indicated by dashed lines. Lighter color shades indicate data collected in bright light conditions. Darker color shades indicate data collected in dim light conditions.

Hindlimb duty factor. *Eulemur* altered hindlimb duty factors in response to changes in lighting conditions (Table 4.3, Supplementary Table 21, Figure 4.9). Hindlimb duty factors were significantly characterized by a factor-by-covariate interaction between light conditions and stride speed ($p=0.0049$) as well as a factor-by-factor interaction between light conditions and support orientation ($p=0.023$). However, post hoc analyses examining the differences in hindlimb duty factors at the minimum and maximum shared speeds in bright and dim light were non-significant due to the constrained ranges of speed in dim light trials ($p=0.90$). Post hoc analyses examining the effects of light conditions within orientations indicate that on inclines, hindlimb duty factors were significantly increased in the in bright light ($p=0.049$). The differences between hindlimb duty factors on declines in different light conditions were not significant. Examining the effects of orientation within light conditions, post hoc analyses that in bright light, hindlimb duty factors were increased on declines ($p=0.022$), but in dim light, hindlimb duty factors were not significantly altered on differently oriented supports. Neither *Varecia* nor *Lemur* adjusted hindlimb duty factor in response to changes in light conditions (Table 4.3, Supplementary Tables 19 and 20, Figure 4.10). For all species, hindlimb duty factor was negatively correlated with speed ($p<0.0001$).

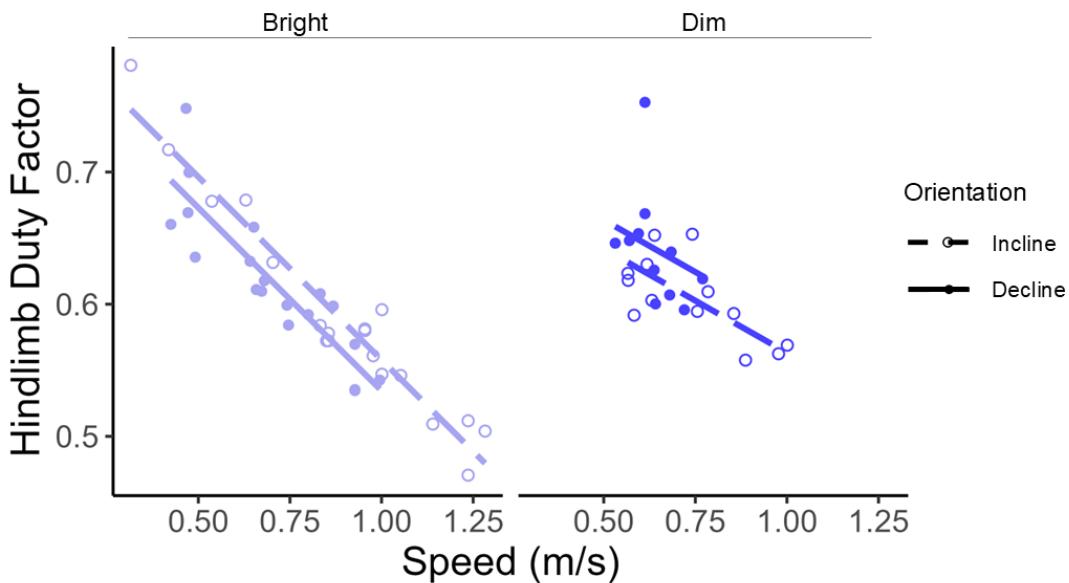


Figure 4.9 Scatterplots of hindlimb duty factors plotted against speed, grouped by support orientation, in *Eulemur*. Left panel, strides in bright light. Right panel, strides in dim light. Trend lines indicate likelihood fits from mixed-effects analyses of covariance models. Trends were significant, so solid and long-dash lines indicate groupings by support diameter. Lighter color shades indicate data collected in bright light conditions. Darker color shades indicate data collected in dim light conditions.

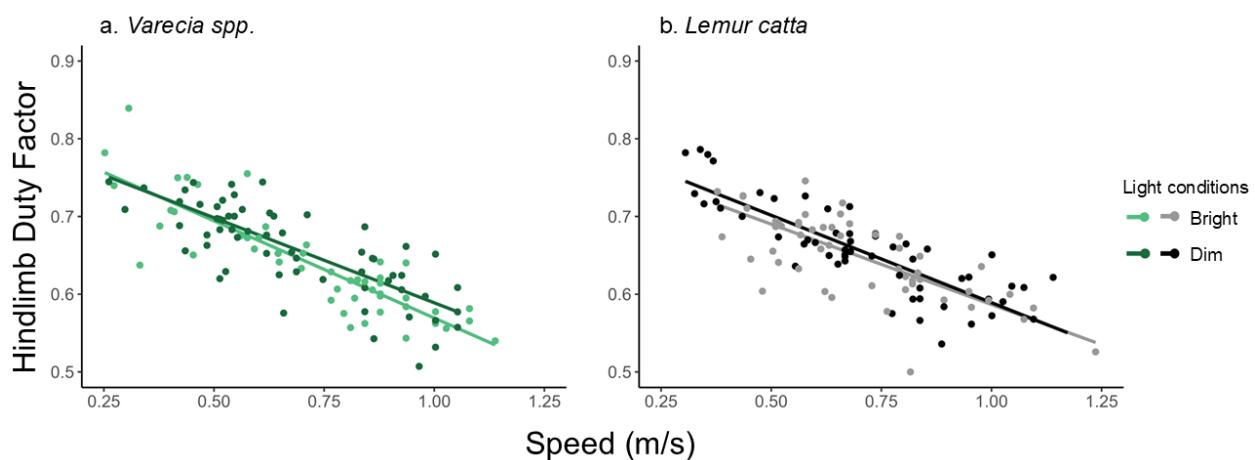


Figure 4.10 Scatterplots of hindlimb duty factors plotted against speed, grouped by light conditions, in *Varecia* (a.) and *Lemur* (b.). Trend lines indicate likelihood fits from mixed-effects analyses of covariance models. Trends were nonsignificant and so are indicated by dashed lines. Lighter color shades indicate data collected in bright light conditions. Darker color shades indicate data collected in dim light conditions.

Discussion and conclusions

Lemurs used a mixture of diagonal sequence and lateral sequence gaits as they navigated simulated arboreal supports in bright and dim light (Table 4.2). In *Varecia*, the genus with the highest proportion of lateral sequence gaits, these gaits were evenly distributed in bright and dim light settings. Since Hildebrand began cataloguing the footfall patterns of a variety of quadrupedal taxa, primates have stood out for their preference for diagonal sequence gaits (Hildebrand, 1967). However, field and laboratory studies have documented that many primate species will also use lateral sequence gaits (see Stevens, 2006 for summary; more recent examples include Dunham et al., 2019; Nyakatura & Heymann, 2010; Young, 2012), perhaps especially on declined substrates when the braking forces of the forelimb could be enhanced (Nyakatura et al., 2008). These results suggest that there is nothing inherent about either gait sequence which would significantly compromise the stability of the gaze or safe placement of the foot during locomotion with limited visual information.

Within gaits, lemurs altered one or many gait parameters in response to changes in light availability during locomotor trials, and *Varecia* changed the greatest number of gait parameters examined here (Table 4.3). However, adjustments to gait were also specific to the subject's speed and the properties of the support. For example, when *Varecia* moved slowly in dim light, they reduced stride lengths on declines (Figure 4.2) Previously in this dissertation, I have discussed some canonical ways of understanding how primates may increase stability in the fine branch niche – where arboreal supports are angled, narrow, and compliant. Generally, primates are predicted to simultaneously increase stride length and contact with the support while decreasing stride frequencies on precarious arboreal supports in order to reduce perturbations of the support that could lead to destabilizing torques (Lammers & Zurcher, 2011; Larson et al., 2000, 2001; Schmitt, 1999; Young, 2023). *Varecia* did reduce stride frequencies on narrow poles when moving slowly (Figure 4.3). However, when examining the interacting effects of light and support orientation, a slightly different pattern emerged. When moving on

declined poles as opposed to inclined ones, subjects reduced stride length (when moving slowly, Figure 4.2) and increased forelimb duty factors (regardless of speed, Figure 4.7a). Such movement may reflect the use of the forelimb as a brake against the forces of gravity acting on the subject moving down the pole (Nyakatura et al., 2008). As a large-bodied lemur without a tapetum lucidum, *Varecia* seems to have used strategies to increase stability when moving on the most precarious supports in dim light.

Lemur and *Eulemur* made fewer adjustments to gait in response to changes in light availability. *Lemur catta* increased the mean number of supporting limbs in dim light settings (Figure 4.6), which is hypothesized to increase stability through greater contact time with the support (Shapiro et al., 2014; Shapiro & Young, 2012). This result was unexpected as *Lemur catta* is smaller than *Varecia* and retains the tapetum lucidum for enhanced dim light vision. While the more exaggerated changes to gait in *Varecia* support previous predictions, the fact that *Lemur catta* also made some slight adjustments to promote stable locomotion suggests that broad environmental changes may produce differences in locomotor behavior regardless. Indeed, some subjects (though not all) from each species seemed more reluctant to perform trained tasks like returning to a carrier while the lights were still dimmed.

While *Eulemur* did not alter mean speed in response to changes in lighting conditions, the range of speeds *Eulemur* used in dim light was more constrained than the speeds they used in bright light (Figure 4.1). Additionally, they significantly altered their hindlimb duty factors such that duty factors tended to increase in bright light and on inclines (Figure 4.9). However, as duty factor and speed are negatively correlated and the lowest *Eulemur* speeds were observed in bright light, this pattern is not surprising. While not significant, hindlimb duty factors in dim light trend higher on declines as opposed to inclines, following the pattern observed in forelimb duty factors for *Varecia*. Future work should continue to evaluate the gait of these animals in bright and dim light to determine whether they pattern more closely to *Varecia*, to *Lemur*, or whether they are forming different strategies.

Previous studies on the activity cycles of these lemurs housed at the Duke Lemur Center, as well as investigations of their wild counterparts indicate that *Varecia variegata*, *Varecia rubra*, *Lemur catta*, and *Eulemur flavifrons* may often be active during the day and night, when light levels were even lower than the (Bray et al., 2017; Donati et al., 2013; LaFleur et al., 2014; Rea et al., 2014; Schwitzer et al., 2007). It is remarkable, then, that only *L. catta* seems to possess a tapetum lucidum. In studies of the visual systems of primates, researchers debate the origins of trichromatic vision and high visual acuity that persist in monkeys and apes (Peichl et al., 2019; Valenta et al., 2016; Veilleux & Kirk, 2009, 2014). These debates are focused on the ability of animals to perceive color differences in potential food items, however, and not their ability to safely move to forage for these items. When it comes to the role of locomotor performance as a part of natural selection in cathemeral lemurs, increasing activity during bright moonlight and adopting the documented adjustments to gait may be sufficient for reducing risk.

Limitations and future directions

Sources of variation are limited in this laboratory study compared to the studies in Chapters 2 and 3. However, there are still some factors not controlled through study design or statistics. Some subjects had variable temperaments, especially because research required transport outside of their home enclosure. Ideally, repeated measurements in the same testing conditions could be made on different days, but time constraints and prioritization of other types of data collection precluded this. Using multiple individuals should alleviate some of these concerns. Additionally, all species had more tolerant individuals, but in the case of *Eulemur*, for instance, subjects were less used to being recruited for locomotion research. Gait data for these individuals is limited and potentially more affected by individual differences.

In their study on the movements of a secondarily-diurnal gecko in various light settings, Birn-Jeffery & Higham (2016) showed that *Rhoptropus afer* made similar adjustments to its gait kinematics to what is observed in these three genera of lemur – reducing stride lengths and stride frequencies and increasing contact with the ground. They suggest that such adjustments

have two primary purposes – increasing the amount of visual information that reaches the eye and providing greater predictability about the location of the support near the touch down of a limb in swing phase. Future work could examine fluctuations in the movement of the center of mass, eyes, and substrate to examine the extent to which lemurs attempt to stabilize their gaze when exposed to reduced visual stimuli. Furthermore, future analyses will examine how locomotion varies as lemurs are freely able to move between simulated arboreal supports. While diurnal species do restrict most of their activities to daylight hours, movements within or between nearby sleeping trees do occur (personal observation). The behaviors that occur when transitioning between supports – stance, exploratory touching, and looking – will provide further insight into the types of information lemurs value. Such work will also be important for further exploring the differences between these lemurs that vary in body size and possession of a tapetum lucidum.

Conclusions

Reducing risk while moving in the trees requires accurate response to visual cues that inform the individual about the movement of their body and the immediate surroundings. To my knowledge, this is the first study to examine the effects that low ambient light levels have on the gaits of arboreal primates. Lemurs adjusted their locomotion in dim light settings in ways that enhance stability and potentially their perceptual capacity. The results have implications for the future studies of the ecomorphology and ecopsychology of these animals.

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CHAPTER 5: CONCLUSIONS AND FUTURE RESEARCH

Conclusions

This research highlighted the behavioral adjustments primates make – or do not make – in response to potential risks in their environment. In Chapter 2, I found that increasing height in the tree canopy was associated with gaits that promoted stability in one species of lemur, but other lemur species either did not respond to branch height or moved in ways that potentially decreased stability. In Chapter 3, I used novel behavioral analyses to determine whether gap crossing behaviors were influenced by the dimensions of untested supports in a primate's path. These two chapters make an important consideration that is rarely explicitly tested in primate locomotion studies: in such visually driven species, visual cues may alter locomotion without requiring direct contact between a support and the primate. I found that responses to such visual cues vary across species, differences potentially driven by ecology and morphology. In Chapter 4, I purposefully altered the visual information captive lemurs could take in by changing the lighting conditions across trials. Though the most pronounced changes to gait were observed in *Varecia*, all lemurs made alterations to their gait. The behavioral flexibility of lemurs has been discussed extensively in previous research in efforts to understand the potential nocturnal origins of primates, and these results suggest that robust locomotor performance in dim light may be achieved through behavioral adjustments even when individuals do not possess a tapetum lucidum.

Limitations in the study of animal behavior

This dissertation adopts a framework shared by many of the researchers cited throughout: The arboreal locomotion of primates is different from their terrestrial locomotion or the arboreal locomotion of other animals because of their behavioral and morphological

adaptations for arborealism. However, the data I present consist only of successful bouts of primate locomotion – ones in which the individual did not fall. Because subjects freely move and we cannot program in certain gait parameters to see their effects on stability, centering the potential for falling as a method of selection and adaptation may be flawed. Addressing selection for energetic efficiency could be the better route.

Recall that the compliant gait model discusses how flattening the trajectory of the center of mass may reduce perturbations of narrow and compliant branches (Schmitt, 1999). Muscular effort could be used to correct any rolling or pitching moments, but this comes at an energetic cost. Miller and colleagues (2019) expand on this idea in a study on the selection of limb phases of squirrel monkeys (*Saimiri sciureus*). They suggest that diagonal sequence gaits reduce rolling torques on narrow arboreal supports, and even small adjustments to limb phase may ultimately reduce muscular effort required to correct mediolateral movements. In an exploratory study on terrestrial versus arboreal walking in *P. anubis*, lateral sequence gaits were associated with more recruitment of distal muscles, potentially for enhancing stability at the cost of efficiency (Druelle et al., 2021). These laboratory studies do not capture the variability of wild primate locomotion; however, they indicate that researchers could make predictions about gait parameters that align with maximized efficiency. Where primates deviate from those models may give us a sense of direction of natural selection for arboreality.

Additionally, Chapters 2 and 3 statistically test hypotheses about the uncontrolled movement of wild animals. In those sections, I discuss some potential sources of error and variability which could limit the interpretability of test statistics that are best used in more controlled, experimental study designs (see Eberhardt, 2003; Stephens et al., 2007). In Chapter 2, I iteratively removed nonsignificant effects from mixed effects models to assess whether height explained a significant amount of variation in lemur gait parameters. However, the interpretability of such an approach is limited by the strength of the models and underlying predictions. For example, lemurs chose the paths that they took to increase their height in the

tree canopy. This would be an unmeasured source of variation – different from an experimental approach where animals are placed at different heights by researchers. Assuming that lemurs are sensitive to support height, this decision-making process may be the feature on which selection is acting, not gait. This is not to throw out the observations that *Eulemur rubriventer*, for instance, seemed to use more stable forms of locomotion at increased heights, but future analyses and study design would be improved by addressing these statistical limitations.

In Chapter 3, I use statistical tests to compare branch size preference for gap crossing behaviors as well as gap crossing durations as animals move between differently sized branches. These statistical tests are helpful for summarizing observations; however, building comparative predictive models from these observations will require a stricter sampling regime. For instance, while I describe the effects of body size on primate locomotion, it is not the only source of variation. In the case of *P. anubis*, differences in body size were due to age which affects other body proportions, muscular control, and decision-making processes. Lastly, it is important to remember that strategies may be taken to approach the problem of crossing gaps between arboreal supports.

Future directions

Consistently primates demonstrate their robust locomotor performance when presented with the challenges of both simulated and actual variability of arboreal supports. However, we can assert that there are risks primates encounter daily in these habitats. Therefore, one of the main takeaways from this body of work is to consider what primates perceive as risky versus what researchers propose. In the future, the push towards authentic simulation of arboreal habitats in locomotion research should also come with studies of choice – do primates choose to move on less precarious substrates? An excerpt from Fleagle and Mittermeier (1980, p. 307) illustrates how primates are thought to choose routes to make arboreal locomotion safer: “The animals appear to choose regular pathways for travel (often called arboreal highways) that permit long uninterrupted bouts of locomotion on relatively stable supports.” Since then, route

analysis in primates has developed into studies on primate cognition and their capacity to make mental maps and consistently travel through the same places (Janmaat et al., 2021).

The work presented in this dissertation puts forth another avenue of assessing how primates may evaluate the safety of particular routes. Efforts are already underway to expand on the work presented in this dissertation. First, the video database on which Chapters 2 and 3 are based is a valuable resource for examining the naturalistic movements of wild primates. I plan to add more species to the analysis I performed in Chapter 3 to gain a deeper understanding on how body size, phylogeny, and habitat structure guide the safety assessment behaviors of primates. Second, at the Duke Lemur Center, I also recorded lemurs as they moved freely in a testing enclosure with several choices for locomotor substrate in bright and dim lighting conditions. I will assess whether the gait adjustments observed in Chapter 4 correspond to differences in substrate choice. I also aim to quantify three-dimensional head movements of lemurs as they move across these various substrates in an effort to understand how and when they might be visually assessing their next steps or the next support.

Continuing field and laboratory work will be important for untangling questions about risk assessment in primate locomotion. In addition to video recording the locomotion of wild primates, documenting what happens when groups encounter large gaps in the tree canopy could shed light on primate cognition and risk assessment. In Chapter 3, most of the gaps crossed by primates in this study were relatively small (Graham & Socha, 2020), though there were some instances of primates leaping across impressive gaps. Future field work aimed at documenting behaviors around large gaps (requiring either leaps or detours) could assess how different individuals approach such an obstacle. Juveniles, adults carrying infants, and elder group members, for instance, may require more time to assess a leap or watch other individuals proceed. In the laboratory, adult primates may be outfitted with weights to simulate infant carrying. In humans, pregnant subjects and those outfitted with artificial bellies performed similarly in tests of affordance estimates by the end of the trials (Franchak & Adolph, 2014). A

mixture of the behavioral and gait analyses found in this dissertation could tell us more about how primate affordances change during naturalistic changes in body mass and locomotor ability.

In Chapters 2 and 3, I discussed how perception of risks like branch height and morphology are connected to the concepts in psychology of the visual cliff and affordances. In humans and other animals, studies tend to focus on the early stages of development (Adolph et al., 2014; Adolph & Franchak, 2017; Gibson & Walk, 1960). Nonhuman primates similarly must contend with learning to move in a constantly changing body (Young & Shapiro, 2018). However, primate development varies widely. Primates may carry their infants as they cling to an adult's (typically mother's) fur, or they may be parked while the mother forages (Ross, 2001). Overall, age at locomotor independence seems to be related to a host of factors including body size, infant growth rates, and phylogeny (Young & Shapiro, 2018). Variations in exposure to locomotor forces and visual cues may create additional differences in the motor development pathways of different primates. Comparative observational studies in parked and carried infants will contribute greatly to our knowledge.

Lastly, gait analyses predominate in Chapters 2 and 4 of this dissertation. In the field and laboratory studies proposed above, other forms of locomotion should be considered. For instance, lemurs are proficient leapers, including the species considered in this work. Kemp (2024) found that altering the field of binocular vision in the fat-tailed dwarf lemur (*Cheirogaleus medius*) reduced their leaping performance. In the studies of cathemeral lemurs, it is unclear what types of movements they tend to engage in at night (Bray et al., 2017; Colquhoun, 1998; Curtis et al., 1999). Future work should document how variable cathemeral lemur locomotion is, especially in those species lacking the tapetum lucidum.

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APPENDIX: SUPPLEMENTARY TABLES

Supplementary Table 1. Effects of take-off branch diameter and species on duration of gap crossing

Term	Mean Difference (\log_{10} s)	Statistic	P-value [†]
Overall ANOVA			
Take-off branch size	-	$F_{[2,171]}=3.3$	0.038
Species	-	$F_{[3,171]}=1.5$	0.22
Branch-species interaction	-	$F_{[6,171]}=2.3$	0.036
Pairwise Comparison - Species			
<i>Cercopithecus ascanius</i>			
Narrow – Medium	0.46	$t_{[171]}=1.8$	0.12
Narrow – Large	0.55	$t_{[171]}=3.1$	0.0059
Medium – Large	0.093	$t_{[171]}=0.33$	0.74
<i>Papio anubis</i>			
Narrow – Medium	0.58	$t_{[171]}=2.0$	0.12
Narrow – Large	0.20	$t_{[171]}=0.71$	0.48
Medium – Large	-0.38	$t_{[171]}=-1.4$	0.25
<i>Eulemur rubriventer</i>			
Narrow – Medium	0.34	$t_{[171]}=1.5$	0.20
Narrow – Large	-0.18	$t_{[171]}=-0.74$	0.46
Medium – Large	-0.52	$t_{[171]}=-1.9$	0.20
<i>Lemur catta</i>			
Narrow – Medium	-0.16	$t_{[171]}=-0.69$	0.52
Narrow – Large	-0.32	$t_{[171]}=-1.3$	0.52
Medium – Large	-0.16	$t_{[171]}=-0.64$	0.52
Pairwise Comparison – Branch			
Narrow			
<i>C. ascanius</i> – <i>P. anubis</i>	-0.19	$t_{[171]}=-0.84$	0.40
<i>C. ascanius</i> – <i>E. rubriventer</i>	0.23	$t_{[171]}=1.5$	0.22
<i>C. ascanius</i> – <i>L. catta</i>	0.50	$t_{[171]}=2.7$	0.024
<i>P. anubis</i> – <i>E. rubriventer</i>	0.42	$t_{[171]}=1.8$	0.15
<i>P. anubis</i> – <i>L. catta</i>	0.68	$t_{[171]}=2.7$	0.024
<i>E. rubriventer</i> – <i>L. catta</i>	0.27	$t_{[171]}=1.3$	0.23
Medium			
<i>C. ascanius</i> – <i>P. anubis</i>	-0.068	$t_{[171]}=-0.22$	0.84
<i>C. ascanius</i> – <i>E. rubriventer</i>	0.12	$t_{[171]}=0.39$	0.84
<i>C. ascanius</i> – <i>L. catta</i>	-0.12	$t_{[171]}=-0.41$	0.84
<i>P. anubis</i> – <i>E. rubriventer</i>	0.19	$t_{[171]}=0.68$	0.84
<i>P. anubis</i> – <i>L. catta</i>	-0.053	$t_{[171]}=-0.20$	0.84
<i>E. rubriventer</i> – <i>L. catta</i>	-0.24	$t_{[171]}=-0.93$	0.84
Broad			
<i>C. ascanius</i> – <i>P. anubis</i>	-0.54	$t_{[171]}=-2.3$	0.15
<i>C. ascanius</i> – <i>E. rubriventer</i>	-0.50	$t_{[171]}=-2.0$	0.15
<i>C. ascanius</i> – <i>L. catta</i>	-0.37	$t_{[171]}=-1.6$	0.22
<i>P. anubis</i> – <i>E. rubriventer</i>	0.042	$t_{[171]}=0.15$	0.88
<i>P. anubis</i> – <i>L. catta</i>	0.17	$t_{[171]}=0.63$	0.80
<i>E. rubriventer</i> – <i>L. catta</i>	0.12	$t_{[171]}=0.45$	0.80

[†]P-values for pairwise comparisons were corrected using the false discovery rate method (Benjamini & Hochberg, 1995)

Supplementary Table 2. Effects of landing branch diameter and species on duration of gap crossing

Term	Mean Difference (\log_{10} s)	Statistic	P-value [†]
Overall ANOVA			
Landing branch size	-	$F_{[2,162]}=11$	<0.0001
Species	-	$F_{[3,162]}=2.5$	0.060
Branch-species interaction	-	$F_{[6,162]}=1.2$	0.29
Pairwise Comparison – Branch			
Narrow – Medium	0.45	$t_{[168]}=3.8$	<0.001
Narrow – Large	0.49	$t_{[168]}=4.3$	<0.0001
Medium – Large	0.046	$t_{[168]}=0.35$	0.93

[†]P-values for pairwise comparisons were corrected using the false discovery rate method (Benjamini & Hochberg, 1995)

Supplementary Table 3. Effects of relative size difference in take-off and landing branches and species on duration of gap crossing

Term	Statistic	P-value
Overall ANOVA		
Branch Δ	$F_{[2,159]}=1.8$	0.16
Species	$F_{[3,159]}=1.6$	0.19
Branch Δ -species interaction	$F_{[6,159]}=1.9$	0.088

Supplementary Table 4. Effects of support properties and light conditions on speed in *Varecia spp.*

Term	Statistic	P-value [†]
ANOVA – across orientations		
Diameter	$F_{[1,114]}=11.6$	0.014
Light conditions	$F_{[1,114]}=0.25$	0.64
Diameter-Light interaction	-	NS
ANOVA – across diameters		
Orientation	$F_{[1,114]}=0.34$	0.56
Light conditions	$F_{[1,114]}=1.1$	0.33
Orientation-Light interaction	-	NS

[†]Non-significant interactions removed from the models

Supplementary Table 5. Effects of support properties and light conditions on speed in *Lemur catta*

Term	Statistic	P-value [†]
ANOVA – across orientations		
Diameter	$F_{[1,109]}=34.5$	<0.0001
Light conditions	$F_{[1,109]}=2.7$	0.10
Diameter-Light interaction	-	NS
ANOVA – across diameters		
Orientation	$F_{[1,101]}=20.1$	<0.0001
Light conditions	$F_{[1,20.5]}=0.15$	0.70
Orientation-Light interaction	-	NS

[†]Non-significant interactions removed from the models

Supplementary Table 6. Effects of support properties and light conditions on speed in *Eulemur flavifrons*

Term	Statistic	P-value [†]
ANOVA – across diameters		
Orientation	$F_{[1,53.4]}=11.1$	0.0016
Light conditions	$F_{[1,5.1]}=0.88$	0.39
Orientation-Light interaction	-	NS

[†]Non-significant interactions removed from the models

Supplementary Table 7. Effects of support properties and light conditions on stride length in *Varecia spp.*

Term	Mean difference	Statistic	P-value [†]
ANOVA – across orientations			
Speed	-	$F_{[1,114]}=89.6$	<0.0001
Diameter	-	$F_{[1,114]}=11.4$	0.0011
Light conditions	-	$F_{[1,114]}=0.40$	0.53
Speed-Diameter interaction	-	-	NS
Speed-Light interaction	-	-	NS
Diameter-Light interaction	-	-	NS
Speed-Diameter-Light interaction	-	-	NS
ANOVA – across diameters			
Speed	-	$F_{[1,114]}=115$	<0.0001
Orientation	-	$F_{[1,114]}=7.8$	0.0060
Light conditions	-	$F_{[1,114]}=0.27$	0.60
Speed-Orientation interaction	-	$F_{[1,114]}=20.6$	<0.0001
Speed-Light interaction	-	$F_{[1,114]}=0.92$	0.34
Orientation-Light interaction	-	$F_{[1,114]}=8.1$	0.0056
Speed-Orientation-Light interaction	-	$F_{[1,114]}=5.5$	0.021

Pairwise comparisons – across diameters			
<i>Within light conditions</i>			
<i>Min. common speed – Bright light</i>			
Decline-Incline	0.11	$t_{[98.4]}=3.1$	0.0028
<i>Min. common speed – Dim light</i>			
Decline-Incline	-0.027	$t_{[97.5]}=-0.92$	0.36
<i>Max. common speed – Bright light</i>			
Decline-Incline	-0.15	$t_{[98]}=-5.2$	<0.0001
<i>Max. common speed – Dim light</i>			
Decline-Incline	-0.11	$t_{[97.4]}=-4.0$	<0.001
<i>Within orientations</i>			
<i>Min. common speed – Decline</i>			
Bright-Dim	0.083	$t_{[44.3]}=1.5$	0.15
<i>Min. common speed - Incline</i>			
Bright-Dim	-0.055	$t_{[36.2]}=-1.0$	0.31
<i>Max. common speed - Decline</i>			
Bright-Dim	-0.065	$t_{[17.9]}=-1.4$	0.17
<i>Max. common speed – Incline</i>			
Bright-Dim	-0.025	$t_{[18.8]}=-0.56$	0.59

[†]Non-significant interactions removed from the models

Supplementary Table 8. Effects of support properties and light conditions on stride length in *Lemur catta*

Term	Statistic	P-value [†]
ANOVA – across orientations		
Speed	$F_{[1,110]}=89.5$	<0.0001
Diameter	$F_{[1,110]}=5.8$	0.018
Light conditions	$F_{[1,108]}=0.012$	0.91
Speed-Diameter interaction	-	NS
Speed-Light interaction	-	NS
Diameter-Light interaction	-	NS
Speed-Diameter-Light interaction	-	NS
ANOVA – across diameters		
Speed	$F_{[1,40.7]}=44.1$	<0.0001
Orientation	$F_{[1,105]}=1.1$	0.28
Light conditions	$F_{[1,8.3]}=0.28$	0.61
Speed-Orientation interaction	$F_{[1,107]}=4.1$	0.047
Speed-Light interaction	-	NS
Orientation-Light interaction	-	NS
Speed-Orientation-Light interaction	-	NS

[†]Non-significant interactions removed from the models

Supplementary Table 9. Effects of support properties and light conditions on stride length in *Eulemur flavifrons*

Term	Statistic	P-value [†]
ANOVA – across diameters		
Speed	$F_{[1,34.2]}=24.4$	<0.0001
Orientation	$F_{[1,54.4]}=1.9$	0.17
Light conditions	$F_{[1,2.2]}=0.0010$	0.98
Orientation-Light interaction	-	NS
Speed-Light interaction	-	NS
Speed-Orientation-Light interaction	-	NS

[†]Non-significant interactions removed from the models

Supplementary Table 10. Effects of support properties and light conditions on stride frequency in *Varecia spp.*

Term	Mean difference	Statistic	P-value [†]
ANOVA – across orientations			
Speed	-	$F_{[1,114]}=86.2$	<0.0001
Diameter	-	$F_{[1,114]}=3.7$	0.066
Light conditions	-	$F_{[1,114]}=0.74$	0.40
Speed-Diameter interaction	-	$F_{[1,114]}=0.51$	0.48
Speed-Light interaction	-	$F_{[1,114]}=0.16$	0.69
Diameter-Light interaction	-	$F_{[1,114]}=3.1$	0.093
Speed-Diameter-Light interaction	-	$F_{[1,114]}=4.5$	0.039
ANOVA – across diameters			
Speed	-	$F_{[1,114]}=204$	<0.0001
Orientation	-	$F_{[1,114]}=.79$	0.0058
Light conditions	-	$F_{[1,114]}=0.46$	0.53
Speed-Orientation interaction	-	$F_{[1,114]}=26.5$	<0.0001
Speed-Light interaction	-	-	NS
Orientation-Light interaction	-	-	NS
Speed-Orientation-Light interaction	-	-	NS
Pairwise comparisons – across orientations			
<i>Within light conditions</i>			
<i>Min. common speed – Bright light</i>			
Narrow-Broad	-0.11	$t_{[11.5]}=-0.80$	0.44
<i>Min. common speed – Dim light</i>			
Narrow-Broad	-0.31	$t_{[8.8]}=-2.7$	0.024
<i>Max. common speed – Bright light</i>			
Narrow-Broad	-0.25	$t_{[14.3]}=-1.7$	0.11
<i>Max. common speed – Dim light</i>			

Narrow-Broad	-0.012	$t_{[7.8]}=-0.14$	0.90
<i>Within diameters</i>			
Min. common speed – Narrow			
Bright-Dim	0.014	$t_{[7.2]}=0.12$	0.91
<i>Min. common speed – Broad</i>			
Bright-Dim	-0.19	$t_{[14.4]}=-1.5$	0.16
<i>Max. common speed – Narrow</i>			
Bright-Dim	-0.16	$t_{[17.6]}=-1.0$	0.32
<i>Max. common speed – Broad</i>			
Bright-Dim	0.075	$t_{[3.9]}=1.1$	0.35

[†]Non-significant interactions removed from the models

Supplementary Table 11. Effects of support properties and light conditions on stride frequency in *Lemur catta*

Term	Statistic	P-value [†]
ANOVA – across orientations		
Speed	$F_{[1,95.6]}=214$	<0.0001
Diameter	$F_{[1,8.1]}=8.2$	0.021
Light conditions	$F_{[1,6.1]}=0.0074$	0.93
Speed-Diameter interaction	-	NS
Speed-Light interaction	-	NS
Diameter-Light interaction	-	NS
Speed-Diameter-Light interaction	-	NS
ANOVA – across diameters		
Speed	$F_{[1,38.1]}=340$	<0.0001
Orientation	$F_{[1,104]}=7.5$	0.0075
Light conditions	$F_{[1,6.3]}=0.43$	0.53
Speed-Orientation interaction	$F_{[1,106]}=14.6$	<0.001
Speed-Light interaction	-	NS
Orientation-Light interaction	-	NS
Speed-Orientation-Light interaction	-	NS

[†]Non-significant interactions removed from the models

Supplementary Table 12. Effects of support properties and light conditions on stride frequency in *Eulemur flavigrons*

Term	Statistic	P-value [†]
ANOVA – across diameters		
Speed	$F_{[1,57.6]}=123$	<0.0001
Orientation	$F_{[1,56.2]}=5.4$	0.024
Light conditions	$F_{[1,57]}=0.12$	0.73
Orientation-Light interaction	-	NS
Speed-Light interaction	-	NS

Speed-Orientation-Light interaction	-	NS
[†] Non-significant interactions removed from the models		

Supplementary Table 13. Effects of support properties and light conditions on the mean number of supporting limbs in *Varecia spp.*

Term	Statistic	P-value [†]
ANOVA – across orientations		
Speed	$F_{[1,61.9]}=57.2$	<0.0001
Diameter	$F_{[1,8.2]}=2.7$	0.14
Light conditions	$F_{[1,5.7]}=0.45$	0.53
Speed-Diameter interaction	-	NS
Speed-Light interaction	-	NS
Diameter-Light interaction	-	NS
Speed-Diameter-Light interaction	-	NS
ANOVA – across diameters		
Speed	$F_{[1,38.3]}=91.5$	<0.0001
Orientation	$F_{[1,97.5]}=10.0$	0.0021
Light conditions	$F_{[1,4.6]}=1.5$	0.28
Speed-Orientation interaction	-	NS
Speed-Light interaction	-	NS
Orientation-Light interaction	-	NS
Speed-Orientation-Light interaction	-	NS

[†]Non-significant interactions removed from the models

Supplementary Table 14. Effects of support properties and light conditions on the mean number of supporting limbs in *Lemur catta*.

Term	Mean difference	Statistic	P-value [†]
ANOVA – across orientations			
Speed	-	$F_{[1,24.4]}=101$	<0.0001
Diameter	-	$F_{[1,82]}=0.012$	0.91
Light conditions	-	$F_{[1,110]}=3.9$	0.052
Speed-Diameter interaction	-	-	NS
Speed-Light interaction	-	-	NS
Diameter-Light interaction	-	-	NS
Speed-Diameter-Light interaction	-	-	NS
ANOVA – across diameters			
Speed	-	$F_{[1,46]}=97.4$	<0.0001
Orientation	-	$F_{[1,110]}=20.8$	<0.0001
Light conditions	-	$F_{[1,110]}=4.8$	0.030
Speed-Orientation interaction	-	-	NS
Speed-Light interaction	-	-	NS

Orientation-Light interaction	-	-	NS
Speed-Orientation-Light interaction	-	-	NS
Pairwise comparison – Light conditions across diameters			
Bright-Dim	-0.042	$t_{[109]}=-2.2$	0.030

[†]Non-significant interactions removed from the models

Supplementary Table 15. Effects of support properties and light conditions on mean number of supporting limbs in *Eulemur flavifrons*

Term	Statistic	P-value [†]
ANOVA – across diameters		
Speed	$F_{[1,22.7]}=213$	<0.0001
Orientation	$F_{[1,55.4]}=3.7$	0.060
Light conditions	$F_{[1,4.7]}=2.0$	0.22
Orientation-Light interaction	-	NS
Speed-Light interaction	-	NS
Speed-Orientation	-	NS
Speed-Orientation-Light interaction	-	NS

[†]Non-significant interactions removed from the models

Supplementary Table 16. Effects of support properties and light conditions on forelimb duty factors in *Varecia spp.*

Term	Mean difference	Statistic	P-value [†]
ANOVA – across orientations			
Speed	-	$F_{[1,30.1]}=75.1$	<0.0001
Diameter	-	$F_{[1,26.7]}=1.88$	0.18
Light conditions	-	$F_{[1,24.6]}=0.43$	0.52
Speed-Diameter interaction	-	$F_{[1,30.3]}=1.22$	0.28
Speed-Light interaction	-	$F_{[1,30.5]}=0.0083$	0.93
Diameter-Light interaction	-	$F_{[1,22.3]}=7.59$	0.011
Speed-Diameter-Light interactions	-	$F_{[1,28.4]}=6.70$	0.015
ANOVA – across diameters			
Speed	-	$F_{[1,21.7]}=163$	<0.0001
Orientation	-	$F_{[1,100.4]}=24.2$	0.053
Light conditions	-	$F_{[1,6.9]}=0.037$	0.85
Orientation-Light interaction	-	$F_{[1,100.4]}=3.9$	0.049
Speed-Light interaction	-	-	NS
Speed-Orientation-Light interaction	-	-	NS
Pairwise Comparisons – across orientations			

<i>Min. common speed – Bright light</i>			
Narrow-Broad	0.083	$t_{[26.6]}=2.4$	0.024
<i>Min. common speed – Dim light</i>			
Narrow-Broad	-0.023	$t_{[5.8]}=-0.77$	0.47
<i>Max. common speed – Bright light</i>			
Narrow-Broad	-0.035	$t_{[16.6]}=-0.92$	0.37
<i>Max. common speed – Dim light</i>			
Narrow-Broad	0.024	$t_{[6.9]}=0.94$	0.38
Pairwise Comparisons – across diameters			
<i>Within light conditions</i>			
Bright light Decline-Incline	0.022	$t_{[101]}=2.0$	0.054
Dim light Decline-Incline	0.051	$t_{[101]}=5.2$	<0.0001
<i>Within orientations</i>			
Decline Bright-Dim	-0.016	$t_{[19.3]}=-1.3$	0.21
Incline Bright-Dim	0.013	$t_{[17.4]}=1.1$	0.31

[†]Non-significant interactions removed from the models

Supplementary Table 17. Effects of support properties and light conditions on forelimb duty factors in *Lemur catta*

Term	Statistic	P-value [†]
ANOVA – across orientations		
Speed	$F_{[1,71.4]}=118$	<0.0001
Diameter	$F_{[1,105]}=0.12$	0.73
Light conditions	$F_{[1,109]}=1.2$	0.28
Speed-Diameter interaction	-	NS
Speed-Light interaction	-	NS
Diameter-Light interaction	-	NS
Speed-Diameter-Light interaction	-	NS
ANOVA – across diameters		
Speed	$F_{[1,46.2]}=124$	<0.0001
Orientation	$F_{[1,108]}=75.8$	<0.0001
Light conditions	$F_{[1,6.9]}=1.6$	0.25
Speed-Orientation interaction	-	NS
Speed-Light interaction	-	NS
Orientation-Light interaction	-	NS
Speed-Orientation-Light interaction	-	NS

[†]Non-significant interactions removed from the models

Supplementary Table 18. Effects of support properties and light conditions on forelimb duty factors in *Eulemur flavifrons*

Term	Statistic	P-value [†]
ANOVA – across diameters		
Speed	$F_{[1,54.2]}=95.1$	<0.0001
Orientation	$F_{[1,56.5]}=0.41$	0.52
Light conditions	$F_{[1,58]}=1.5$	0.22
Orientation-Light interaction	-	NS
Speed-Light interaction	-	NS
Speed-Orientation	-	NS
Speed-Orientation-Light interaction	-	NS

[†]Non-significant interactions removed from the models

Supplementary Table 19. Effects of support properties and light conditions on hindlimb duty factors in *Varecia spp.*

Term	Statistic	P-value [†]
ANOVA – across orientations		
Speed	$F_{[1,43.4]}=81.1$	<0.0001
Diameter	$F_{[1,29.8]}=6.7$	0.015
Light conditions	$F_{[1,5.0]}=1.1$	0.34
Speed-Diameter interaction	$F_{[1,45.4]}=4.4$	0.041
Speed-Light interaction	-	NS
Diameter-Light interaction	-	NS
Speed-Diameter-Light interaction	-	NS
ANOVA – across diameters		
Speed	$F_{[1,16.7]}=145$	<0.0001
Orientation	$F_{[1,95.9]}=4.6$	0.034
Light conditions	$F_{[1,4.7]}=5.2$	0.075
Speed-Orientation interaction	-	NS
Speed-Light interaction	-	NS
Orientation-Light interaction	-	NS
Speed-Orientation-Light interaction	-	NS

[†]Non-significant interactions removed from the models

Supplementary Table 20. Effects of support properties and light conditions on hindlimb duty factors in *Lemur catta*

Term	Statistic	P-value [†]
ANOVA – across orientations		
Speed	$F_{[1,22.5]}=197$	<0.0001
Diameter	$F_{[1,6.7]}=16.1$	0.0055
Light conditions	$F_{[1,7.9]}=1.1$	0.32
Speed-Diameter interaction	-	NS
Speed-Light interaction	-	NS

Diameter-Light interaction	-	NS
Speed-Diameter-Light interaction	-	NS
ANOVA – across diameters		
Speed	$F_{[1,58.8]}=140$	<0.0001
Orientation	$F_{[1,103]}=13.7$	<0.001
Light conditions	$F_{[1,15.6]}=1.5$	0.23
Speed-Orientation interaction	$F_{[1,105]}=4.9$	0.029
Speed-Light interaction	-	NS
Orientation-Light interaction	-	NS
Speed-Orientation-Light interaction	-	NS

[†]Non-significant interactions removed from the models

Supplementary Table 21. Effects of support orientation and light conditions on hindlimb duty factors in *Eulemur flavifrons*

Term	Mean difference	Statistic	P-value [†]
ANOVA			
Speed	-	$F_{[1,56]}=71.9$	<0.0001
Orientation	-	$F_{[1,56]}=0.011$	0.92
Light conditions	-	$F_{[1,56]}=6.14$	0.016
Orientation-Light interaction	-	$F_{[1,56]}=5.4$	0.023
Speed-Light interaction	-	$F_{[1,56]}=8.6$	0.0049
Speed-Orientation	-	-	NS
Speed-Orientation-Light interaction	-	-	NS
Pairwise Comparisons – Light conditions at two speed levels			
<i>Min. common speed</i>			
Bright-Dim	0.0011	$t_{[5.5]}=0.13$	0.90
<i>Max. common speed</i>			
Bright-Dim	0.0011	$t_{[5.5]}=0.13$	0.90
Pairwise Comparisons – Orientations within light conditions			
Bright Decline-Incline	-0.023	$t_{[53.6]}=-2.4$	0.022
Dim Decline-Incline	0.022	$t_{[53.5]}=1.7$	0.088
Pairwise Comparisons – Light conditions within orientations			
Decline Bright-Dim	-0.021	$t_{[21.3]}=-1.7$	0.10
Incline Bright-Dim	0.024	$t_{[2.1]}=2.1$	0.049

[†]Non-significant interactions removed from the models