Descending Locomotion in Primates

by

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Dissertation submitted in partial fulfillment of
the requirements for the degree of[Doctor
of Philosophy in the Department of
Evolutionary Anthropology in the Graduate School
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2019

ABSTRACT

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Abstract

Primates are an order of mammals that lack claws. Therefore, arboreal primates must apply opposing pressures with their digits to grasp supports and move through their habitats. This requirement may affect the mechanics of specific aspects of arboreal travel, such as descent, in the locomotion of primates compared to clawed non-primates, and may have influenced the evolutionary selective pressures that primates experienced over time. It has been hypothesized that larger primates are less likely to descend supports headfirst than smaller primates and clawed non-primates, however, this phenomenon has never been considered in a comparative context. Knowing how body size, anatomical proportions, and environment interact to affect locomotor behaviors is central to linking morphology with behavior, such as when evaluating hypotheses of primate origins.

This thesis analyzed descending locomotion in nine species of strepsirrhine primates that occupy four locomotor categories: large arboreal generalists, representing above branch quadrupeds weighting over 1 kg; small arboreal generalists, representing above branch quadrupeds under 1 kg; slow climbers; and vertical clingers and leapers. Primates were video recorded moving on supports ranging from horizontal to vertical in 15° increments. I tested specific hypotheses about gait and kinematic changes in response to declines that have been observed in primates moving down supports as steep as approximately 30°

to see if these patterns would be replicated in primates moving on steeper support orientations.

I found that primates under 1 kg always used headfirst descent on all supports. For primates above 1 kg, body size appeared to be an important factor in determining behavior, but it also appeared that anatomical differences might have enabled one of the largest species in the sample, *Varecia variegata*, to perform vertical headfirst descent, while relatively smaller species like *Lemur catta* were not observed to use this behavior on supports greater than 45°. Within these large arboreal generalists, increases to individual age also seemed to drive behaviors away from headfirst descent in favor of tail first descent. Frequencies of headfirst descent were compared to other mechanisms of descent, such as tail first descent, were scored for a total of 3139 observed descents. These observations were incorporated into a Bayesian multilevel model that included information on the support condition (including orientation and diameter), morphological information for each species (average intermembral index and foot proportions), as well as individual mass and age. The model was then used to predict the probability of headfirst descent on various supports in simulated ancestral primates that exemplified different hypotheses of primate origins. It was found that features including body mass, support orientation, and foot and limb proportions greatly affected the predicted probabilities of headfirst descent. Large primates with lower intermembral indices and smaller feet were least likely to use

headfirst, especially as supports became more steeply angled. Species that were smaller, with relatively longer arms or larger feet tend to use headfirst descent most frequently, even on vertical supports. The model predicted less headfirst descent in the very smallest primates on near horizontal supports, driven by observations of leaping in the smallest species in this sample.

Headfirst descents were analyzed for footfall patterns to evaluate temporal aspects of gait, and to test the hypothesis that limb phase should decrease as supports become steeper and that contact period with the support should increase, and relatively more so for the forelimbs than hind limbs. It was found that limb phase did significantly decrease across the sample as support orientation became steeper, and that both forelimb and hind limb contact times increased as proportion of the total stride period, although the forelimb did not increase relatively more than the hind limb in many species.

Headfirst descents were then analyzed for changes to kinematic aspects of gait including effective limb length, joint angles at key points during the stride, limb excursions, and velocity. I found that as supports became steeper primates across the sample reduced trunk inclination bringing the body parallel to the support and reducing the distance of the center of mass from the support, consistent with pitch-avoidance strategies. The forelimb remained compliant and highly protracted with increasing support orientation; the hind limb did not remain complaint and instead became significantly retracted in primates travelling on

supports of 60° and steeper. Speed was generally reduced as support orientation increased.

Overall this study demonstrated that strepsirrhine primates capable of headfirst descent span a range of body masses up to approximately 4 kg in this sample. Across this range of body masses common strategies for traveling headfirst on supports included adopting slow trotting gaits with extended periods of hind limb retraction and forelimb protraction. Species that did not perform headfirst descent may have been limited in their ability to perform this behavior by aspects of their anatomy, such as having relatively short arms or less developed muscles for pedal grasping compared to species that were more adept at headfirst descent.

Placing these results into an evolutionary context, a small primate ancestor would be least impacted in its ability to navigate using headfirst descent on supports of all angles, whereas a larger ancestral primate might have been limited in the arboreal supports it could have navigated headfirst. Leaping may have been an alternative to grasping mediated headfirst descent in very small early primates, while alternatives to headfirst descent, such as tail first decent, that were only observed in larger species might have emerged later as various primate lineages increased in body mass but retained the characters of primate origins, grasping feet and nails.

Dedication

To my favorite primates: my family and friends.

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Chapter 1: Introduction

“One wonders if…*primates are locomotion*: end of story,” – Rosenberger (2008).

It has been argued that the morphological transition to grasping feet with nails instead of claws was a critical ‘moment’ in the evolution of primates (Cartmill 1974a; Bloch and Boyer 2002; Gebo 2004; Sargis et al. 2007), presumably because it aided in navigating and thriving in a terminal branch environment. However, this transition may have also resulted in barriers to early primates attempting to navigate outside this environment (Orkin and Pontzer 2011). Nevertheless, it is known from the fossil record that early Eocene primates underwent widespread dispersal across the northern hemisphere (Smith et al. 2006; Beard 2008), including into environments that are reconstructed as open forests (Secord et al. 2008), which would have required navigating into open environments and an ability to move between discontinuous terminal branch environments.

Primates closest living relatives, the colugos (dermopterans) and treeshrews (scandentians), descend from arboreal supports using gliding and rotating clawed hindfeet, respectively (Jenkins 1974; Byrnes et al. 2008, 2011). Primates, lacking a specialized patagium or primitive claws, must instead actively grasp onto supports to descend. However, there is a limit to the size of a support they can subtend (either with a single-foot or single-hand grasp or with the arms

or legs in opposition to each other, Cartmill 1979), and as body size increases, fewer primates are observed to descend supports headfirst (Curtis and Feistner 1994).

This dissertation asks, simply, 1) what kinds of supports can primates navigate using headfirst descent, and 2) what alternative behaviors do they employ in situations where they do not use headfirst descent? To evaluate these questions, this study analyzes a comparative sample of extant primates with grasping feet and nails, and lacking prehensile tails, descending supports of varying orientation and diameter to analyze how factors such as body mass and morphology influence descending differences between species. From this comparative data, scenarios on how the locomotion of stem primates might have changed while undergoing the replacement of nails with claws and adoption of grasping feet are evaluated.

In this chapter, I review the literature on primate evolution, including hypotheses of primate origins and the fossil record of early primates, extant primate locomotion, with specific reference to species included in this study, and finally, the theoretical mechanics of arboreal travel on declines, including a review of the experimental literature on this topic. The chapter concludes with the major hypotheses and predictions of this study.

1.1 Primate Evolution

1.1.1 Hypotheses of primate origins

Primates closest relatives include the scandentians (treeshrews) dermopterans (colugos, or flying lemurs), and extinct Plesiadapiformes, which together form the clade Euarchonta, a sister group to the Glires (rodents and lagomorphs) (Murphy et al. 2001; Silcox et al. 2007; O'Leary et al. 2013). The earliest fossil evidence of this group is represented by the North American plesiadadapiform *Purgatorius* from approximately 65 million years ago (mya) during the earliest Paleocene following the Paleogene-Cretaceous (K-Pg) boundary (Chester et al. 2015). *Purgatorius* has been interpreted to have a highly mobile ankle and is reconstructed as occupying an arboreal niche (Chester et al. 2015).

The earliest true primates, or euprimates, appear approximately around 56 mya at the boundary of the Paleocene and Eocene, immediately following a brief and intense global warming event known as the Paleocene-Eocene Thermal Maximum (PETM) (Smith et al. 2006). These euprimates are distinguished by a morphological suite of features including an opposable hallux with a flattened nail, and relatively large brains featuring reduced olfaction and highly developed vision with a complete bony post orbital bar (Martin 1990, p. 202). These features have inspired several hypotheses of the selective pressures on primate origins, though the appearance of some of these key primate traits in the fossil record – such as nail bearing divergent hallux observed in carpolestid plesiadapiforms

(Bloch and Boyer 2002), or relatively small brain size in early Eocene euprimates (Harrington et al. 2016; Silcox and Lopez-Torres 2017) – call into question both the timing and sequence of trait acquisition during the evolution of primates. With that in mind, the major hypotheses of primate origins are briefly summarized below.

Arboreal Hypothesis – The Arboreal Hypothesis is one of the earliest hypotheses concerning primate origins, outlined by Smith (1924) and Jones (1916) and later by Le Gros Clark (1934, 1959). In this hypothesis, arboreality is the selective pressure for primate features from a terrestrial mammalian ancestor. Criticisms of this hypothesis include the observation that many other arboreal animals do not share primate traits (Cartmill 1974a; Orkin and Pontzer 2011), and that improvements to systematics recognize that primates' closest relatives are also arboreal indicating that the common ancestor would have also been arboreal prior to the derivation of primate traits (c.f. Cartmill 1992).

Vertical Clinging and Leaping Evolutionary Hypothesis (VCLH) – Napier and Walker (1967) formally describes vertical clinging and leaping (VCL), a specialized locomotor mode used by extant tarsiers, galagoes, and some lemurs, in which primates leap to and from vertical supports. Napier and Walker (1967) argue that the postcranial elements associated with Eocene primates reflect VCL specialization, and that this form of locomotion was basal in primates. Though challenged and largely dismissed as a hypothesis for primate origins, the VCLH was revisited by Gebo (2011) who argues that leaping does seem to be

ubiquitous in Eocene primates, though vertical support use seems to be an early strepsirrhine specialization and absent in early Eocene haplorrhines – although recent analysis by Boyer et al. (2017) suggests otherwise – making VCL as envisioned by Napier and Walker (1967) an unlikely behavior in the common ancestor of all primates.

Visual Predation Hypothesis (later Nocturnal Visual Predation, NVPH) – In contrast to the VCLH, Cartmill (1972, 1974a) proposes a much different view of early primates and their locomotion. The visual predation hypothesis focuses upon key shared derived primate features that are absent in many other arboreal animals, namely forward-facing eyes and the grasping hallux, to understand the selective pressures that might have acted on these features early on in primate evolution. Cartmill (1974a) focuses on the importance of the terminal branch niche as the shaping factor for primate grasping, and predation as the driving force for orbital convergence. Together, these shape a view of the common ancestor of primates moving deliberately through terminal branches in pursuit of insects; in response to criticisms of this hypothesis, Cartmill (1992) further developed his hypothesis into the Nocturnal Visual Predation hypothesis, given the observation that nocturnal predators are more likely to have convergent eyes than diurnal predators.

Angiosperm Co-Evolution Hypothesis (ACEH)– Sussman and Raven (1978) agree with Cartmill (1974a) that the terminal branch habitat was an important selective pressure for shaping primate features but disagree on

selective pressure driving primates into this niche. Instead of insect predation, Sussman and Raven (1978) argue that angiosperm consumption (e.g. nectar, flowers, fruit) was the selective basis for early primate radiation into the terminal branch niche. Later iterations of this hypothesis detailed by Sussman (1991, et al. 2013) incorporate features like color vision and hypothesized diurnality in the earliest primates into the argument.

Grasp-Leaping Hypothesis (GLH) – Szalay and Dagosto (1980, 1988) and Szalay (2007) describe the Grasp-Leaping hypothesis of primate origins using a concept of “morphotype locomotor mode” to encompass aspects of locomotion, posture, and manipulative behaviors that may have made up an ancestral condition for primates to understand how extant behaviors might have arisen through analogy or by homology. Their framework emphasizes the importance of understanding phylogeny, not just morphological similarity, in understanding the form-function relationship of an evolved trait. In this framework, locomotor categories are but one component of a morphotype locomotor mode.

Szalay and Dagosto (1980) detail several diverse morphotype locomotor modes hypothesized to characterize extant primates and their ancestors – claw climbing, grasp-leaping, vertical clinging and leaping, grasp clinging and creeping, ground walking and running, leaping and claw climbing, brachiating, knuckle walking, and bipedalism – including extant species that exemplify the behavior, habitat and evolutionary hypotheses for each. Grasp-leaping behavior is described by Szalay (2007) as “regular practice of bounding leaps and landing

with a hindfoot/forefoot grasp" (pg. 472), and Szalay and Dagosto (1980) point to this as the shared morphotype locomotor mode of euprimates, coming from a claw climbing non-primate ancestor.

Grasp-leaping is described as a causal behavior for the selection for visual stereoscopy to judge distance in rapid leaping behaviors (Le Gros Clark 1959; Crompton 1995) and is divorced from dietary based arguments like the NVPH or ACEH. According to Szalay and Dagosto (1980) the claw-clinging ancestor to primates would have been limited in its ability to traverse long and narrow flexible supports (terminal branches) in an "agile, economical, and secure manner", while a grasp leaping euprimate would enjoy a more rapid and secure travel through an arboreal environment. However, some primate features, including nails and convergent orbits (which have been found to be helpful, but not strictly necessary for depth perception) are absent in other arboreal leaping animals (Crompton 1995), which has been used as evidence against the grasp-leaping hypothesis.

Narrow Niche Hypothesis (NNH) – One of the most recent primate origins hypotheses is the Narrow Niche Hypothesis of Orkin and Pontzer (2011). Like the grasp-leaping hypothesis, NNH does not make explicit assumptions about the diet of early euprimates. NNH proposes that the suite of primate features is explained by selection for a terminal-branch niche to the exclusion of pressures for locomotion through other environments.

1.1.2 Body Mass in early primates

The size of ancient primates is an important aspect of understanding primate evolution with reference to the locomotor ecology of primates since moving along a support may be a much different experience at 10 g compared to 1000 g. The earliest primates are often envisioned as small, with Gebo (2004) suggesting a lower bound of 10 to 15 g. Boyer et al. (2013) found support for a 75-100 g ancestor compared to 10 g from an ancestral state reconstruction that incorporated extant and fossil specimen. However, Soligo and Martin (2006) have hypothesized that the earliest primates were 1000 g or more based on ancestral state reconstruction using an extant sample of arboreal mammals. They reason that claws are not as adaptive as nails at larger body sizes (Soligo and Müller 1999; Soligo and Martin 2006). However, it should be noted that convergence of nails on multiple digits is observed in animals including *Tarsipes rostratus*, the honey possum, which weighs only 11 g (Soligo and Martin 2006).

1.1.3 Fossil evidence of early primates

The earliest putative euprimates, *Altiatlasius*, from the latest Paleocene of Morocco (Sigé et al. 1990), and *Altanius*, from the early Eocene of Mongolia (Dashzeveg and McKenna 1977), are currently represented only by teeth. The earliest postcranial material attributed to euprimates comes from *Donrussellia*, *Cantius*, *Teilhardina* and *Archicebus*, all of which have been inferred to show morphology consistent with leaping (Boyer et al. 2013a, 2017; Ni et al. 2013). It appears that euprimate fossils from between 56 and 55 mya found through

Europe, Asia, and North America support the Grasp-Leaping hypothesis' interpretation of the earliest euprimate morphotype locomotor mode (Smith et al. 2006; Beard 2008).

In contrast, euprimates from India – *Asiadapis*, *Marcgodinodius*, *Vastanomys*, herein referred to collectively as the Vastan euprimates – are dated at 54.5 mya and are interpreted as lacking morphological specializations for leaping by Dunn et al. (2016). Dunn et al. (2016) argue that the overall similarity of these early omomyids and adapiforms, and the lack of strong morphological signal for leaping, is evidence that the most recent common ancestor of strepsirrhines and haplorrhines also lacked leaping specialization. However, this interpretation has been questioned given the inferred phylogenetic positions of these fossils and the potential of a shared environment driving convergences in the morphology of the Vastan fossils (Boyer et al. 2017). The strength of the argument for leaping at the base of the euprimate radiation is the presence of leaping specializations in the ankle across a wide geographic area in the basal members of adapiforms (*Donrussellia*, *Cantius*), omomyiforms (*Teilhardina*), and haplorrhines (*Archicebus*) (Boyer et al. 2013a, 2017). However, the Vastan euprimates and the earlier occurring plesiadapiform *Carpolestes*, each possess a grasping nail-bearing phalanges (at least on the hallux) but do not show morphology consistent with specialized leaping (Bloch and Boyer 2002; Dunn et al. 2016), weakening the position of the Grasp-Leaping hypothesis' proposed functional link between grasping and leaping.

Although *Carpolestes* and the Vastan primates lack traits clearly associated with specialized leaping, it should be noted that leaping behaviors are widespread in extant primates that engage in generalized above-branch arboreal quadrupedalism. Leaping is distinguished from passive dropping behaviors in that it is muscularly driven by the hind limbs and from bounding locomotion in that it has a significant aerial component (Fontaine 1990; Hunt et al. 1996). While specialized leaping primates can cover great distances with their leaps (Napier and Walker 1967), many anthropoids and strepsirrhines are still capable of using leaping as a gap-crossing mechanism within arboreal environments (Hunt et al. 1996) despite lacking the morphological markers of dedicated leapers (e.g. those discussed in Boyer et al. 2013a, 2017). Therefore, when considering fossils like the Vastan primates, it is difficult to fully exclude all leaping behaviors from the behavioral repertoire of these animals.

It remains unclear from the fossil record what the last common ancestor of primates might have looked like with respect to locomotion and if they were arboreal generalists (e.g. *Tupaia*- or *Ptilocercus*-like, modeled by Sargis et al. 2007), terminal branch specialists (e.g. *Caluromys*-like, modeled by Rasmussen 1990 and Schmitt and Lemelin 2002), or dedicated leapers (Szalay and Dagosto 1980, 1988; Boyer et al. 2013a, 2017), at the base of the radiation (Figure 1.1).

1.1.4 Paleoecology of Fossil Primates

Hypotheses of primate origins make implicit predictions about the ecology of the earliest primates. Unfortunately, there's little direct evidence about what

their environments looked like. However, by understanding global climatic trends occurring during the sequence of primate evolution, it may be possible to infer the types of environmental pressures that may have been acting on primates and their relatives as they dispersed and diversified.

The common ancestor of euarchontans survived through the Chicxulub impact, which is hypothesized to have been a key driver of the K-Pg extinction event; this has been modeled to have dropped global mean surface air temperature substantially within the first few decades following the impact event (Brugger et al. 2017). It is argued by Longrich et al. (2016) that Mesozoic mammals faced high extinction rates during this event (modeled at 93% from analysis of the Western Interior of North America), but that subsequent mammalian recovery was rapid during the earliest Paleocene. This mass extinction may made new niches available to the ancestor of primates.

Euarchontans first appear in the fossil record following the K-Pg extinction, with the plesiadapiform *Purgatorius*, in North America. Plesiadapiforms are reconstructed as being primarily arboreal and small in body size (Silcox 2007), although they become quite diverse later in their radiation. Euprimates appear in the fossil record following the Paleocene-Eocene Thermal Maximum (PETM, 56 mya), which was a global warming event occurring over an approximately 20-thousand-year period (Woodburne et al. 2009). It is hypothesized that the warm temperatures of the PETM might have expanded the northernly range of euprimates like *Teilhardina* allowing them to disperse around the northern

hemisphere (Smith et al. 2006; Beard 2008). Following this dispersal of euprimates, euprimates diversified into major adapiform and omomyiform lineages during the Early Eocene Climatic Optimum (EECO) across the northern hemisphere (Woodburne et al. 2009; Gingerich 2012).

Extant primates are primarily found in the tropics, with the highest species diversity found along the equator (Arbour and Santana 2017). Given the distribution of extant euarchontans in rainforests, these environments are often inferred to be the habitats of the earliest euprimates and have influenced interpretations on selective pressures for the origin of primates. For example, Jablonski (2005) states that leaping may have been selected for transportation through rainforest environments, and that a dependence upon leaping may have even led to the eventual extinction of some lineages of Eocene euprimates as environments cooled and changed following the EECO. However, the perceived importance of continuous rainforest environments for early euprimate dispersal (Smith et al. 2006) has not been supported by the paleoenvironmental record. The Bighorn Basin of Wyoming – an important locality bearing some of the earliest euprimate fossils (Beard 2008) – has been reconstructed as a warm-temperate to subtropical environment during the early Eocene, with open canopy structure, based on carbon-isotope analysis by Secord et al. (2008).

The geographic origins of Euarchonta is reasoned to be North America based on the density and antiquity of fossil evidence from that region by Silcox et al. (2005). However, given their close genetic relationship with glires, evidenced

by fossils to be Asian in origin (Asher et al. 2005), and the restricted distribution of extant non-primate euarchontans, treeshrews and colugos to South East Asian rainforests, some have argued for an Asian origin of Euarchonta (c.f. Silcox et al. 2005). At this time, it is difficult to say whether the earliest primates evolved in closed canopy rainforests (Jablonski 2005) or in drier and more open and scrubby environments, as reconstructed for early N. American environments where *Cantius* and *Teilhardina* lived (Secord et al. 2008). The potential differences between these hypothesized environments should be considered when evaluating hypotheses for primate locomotor adaptations at the base of the clade, since extant primates, while sharing a tropical range, occupy many different microhabitats, and even show behavioral frequency differences within species depending on seasonal or spatial variation in their habitats (Gebo and Chapman 1995; Gabriel 2013).

1.1.5 Summary of primate evolution

Primates closest relatives are colugos, treeshrews, and extinct plesiadapiforms, collectively the Euarchontans. The earliest fossil evidence for this group is a small arboreal plesiadapiform, *Purgatorius*, from approximately 66-65 MYA (Chester et al. 2015). Plesiadapiforms are well known from N. America between 65 and 55 MYA, though there are no other crown Euarchontans present there during this time, and presumably the ancestors of extant Euarchontans lived in Asia (Beard 2008) (Figure 1.2). Euprimates appear throughout the northern hemisphere between 56 and 55 MYA and have been

argued to have potentially an Asian or N. American origin (Smith et al. 2006; Beard 2008). These earliest euprimates share characters like nail bearing grasping hands and feet and leaping adaptations (Ni et al. 2013) and might have lived in open canopy environments in certain locations (Secord et al. 2008). However, slightly later occurring primates from India at 54.5 MYA have grasping extremities without strong morphological evidence for leaping and are inferred to have lived in coastal marshy environments (Dunn et al. 2016). Based on current fossil evidence it appears that the earliest recognized euprimates share grasping feet, but may not have shared leaping, which is more prevalent in euprimate fossils found far dispersed from SE Asia and apparently absent in Indian primates (Figure 1.2). This fossil evidence has fueled debate as to whether terminal branch adaptations or leaping characterize the common ancestor of strepsirrhines and haplorrhines, and leaves open questions concerning what traits are shared from a stem primate ancestor and what traits may have converged or been lost in the roughly 10 million years between the appearance of Euarchontans and the appearance of euprimates (Dunn et al. 2016, Boyer et al. 2017).

1.2. Primate Locomotion

1.2.1 Extant Primate Locomotor Diversity

Extant primates display a wide variety of behaviors and are often broadly classified into seven locomotor categories: arboreal quadrupedalism, terrestrial quadrupedalism, slow climbing, vertical clinging and leaping, brachiation, knuckle

walking, and bipedalism (Napier and Napier 1967; Napier and Walker 1967; Fleagle 2013). While these are useful behavioral categories for considering primate locomotion, it is critical to recognize that within each category species exhibit a variety of behaviors (Oxnard et al. 1990; Hunt et al. 1996) and vary in behavioral frequencies (Mittermeier and Fleagle 1976; Gebo 1987). There may also be a considerable amount of overlap of common behaviors utilized by primates across these categories.

This dissertation is focused on a sample of strepsirrhine primates that are all primarily arboreal and can be further classified into distinctive patterns of specialized behavior. This sample will be broken into four categories: small (<1 kg) generalized arboreal quadrupeds, large (>1 kg) generalized arboreal quadrupeds, slow climbers, and vertical clingers and leapers, described below:

Small Arboreal Quadrupeds (≤1 kg) (S-AQ) – These species engage in above branch quadrupedal movements including walking, running, climbing and leaping and fit the size range of the hypothetical ancestral primate (Oxnard et al. 1990; Gebo 2004; Soligo and Martin 2006). Small bodied animals tend to frequently utilize asymmetrical gaits and fast speeds while moving relative to larger bodied animals (Dagg 1973; Shapiro et al. 2016).

Genera in sample: *Cheirogaleus, Microcebus*

Large Arboreal Quadrupeds (≥1 kg) (L-AQ) – These species regularly engage in above branch quadrupedal movement including walking, running, climbing and leaping (Gebo 1987).

Genera in sample: *Daubentonia, Eulemur, Lemur, Varecia*

Slow Climbers (SC) – These primates are characterized by high frequencies of slow quadrupedalism and climbing (Oxnard et al. 1990), and leaping behaviors are absent (Gebo 1987). In addition to climbing, these primates engage in bridging and cantilevering behaviors to cross gaps (Hunt et al. 1996; Nekaris and Stevens 2007). Despite the 'slow' name, speed may be context specific in these species. It has been proposed that their slow locomotion is a cryptic adaptation, possibly used as an anti-predator strategy (Nekaris 2014). Lorises have been observed moving quickly in some conditions by Nekaris and Stevens (2007) who report that *Loris tardigradus* species regularly engage in a rapid scramble behavior, reaching maximum velocities of 1.2 (m/s), though duration of these behaviors were not reported.

Genus in sample: *Nycticebus*

Vertical Clingers and Leapers (VCL) – These genera are characterized by their ricochetal leaps to and from vertical supports (Napier and Walker 1967; Oxnard et al. 1990). Most of the behaviors observed in these species include leaping and climbing, with infrequent use of bimanual and bipedal locomotion, and quadrupedal walking (Gebo 1987; Granatosky et al. 2016).

Genus in sample: *Propithecus*

1.2.2 Gait Classification

Gait describes the respective progression of limb movement. A major influence on the study of animal locomotion was the systemization of gaits by

Milton Hildebrand. Hildebrand (1965) categorized symmetrical gaits by the timing of footfalls, which can be further broken into the following metrics: Duty Factor, a measure of hindfoot contact time with the support, and laterality, a measure of how the limbs move in sequence. Laterality is synonymous with diagonality (Cartmill et al. 2002), gait number (Shapiro and Raichlen 2005), and limb phase (Hesse et al. 2015); the term limb phase will be used here.

Duty Factor (S_H), which is calculated as a percentage of total hind foot contact time across the stride period, ranges from 0 (fully aerial) to 100 (not moving) and correlates to relative speed of movement. Values between 0 and < 50% indicate relatively little contact with the support, and can be interpreted as a running gait, while values between 50 and 100% indicate relatively longer contact with the support and are interpreted as walking gaits. Duty factor can also be measured for the forelimb (S_F). The ratio of hind limb to forelimb duty factor is known as the Duty Factor Index (SI) (Cartmill et al. 2002).

Limb phase is measured as the percentage of time that the touchdown of the hindfoot of interest (e.g. the right hindfoot) precedes the touchdown of the ipsilateral (same side) forefoot across the stride period. Duty factor of the hind limb and limb phase are conventionally displayed together to visualize gaits, after the style used by Hildebrand (1967) (Figure 1.3). Values for limb phase (*D*) correspond to categories of symmetrical gaits including the pace (*D* = 0 or 100), a two-foot gait in which the ipsilateral fore and hind feet touchdown simultaneously, and the trot (*D* = 50), a two-foot gait in which contralateral fore

and hind feet touchdown simultaneously. Following the convention of Hildebrand (1967) and Schmitt et al. (2006), limb phases between 0 and 5, and 95 and 100 are interpreted as paces, and limb phases between 45 and 55 are interpreted as trots (indicated as gray bars in Figure 1.3).

Limb phase also provides information on the sequence or order of footfalls, and the couplets of limbs moving in time. Lateral sequence (LS) gaits (D <50) are those in which the right forefoot (RF) follows the right hindfoot (RH) in time, while diagonal sequence gaits (D ≥50) are those in which the left forefoot (LF) follows the RH. An example of footfall progression for a LS gait would be RH/RF/LH/LF, while a DS gait would progress as RH/LF/LH/RF. A lateral couplet (LC) is when the ipsilateral feet are touching down close in time (D < 25, D > 75), and a diagonal couplet (DC) is when the contralateral feet touch down closer in time (25 < D <75). Limb phases of exactly 25 and 75 are single foot (SF) gaits (LSSF and DSSF respectively) (Cartmill et al. 2002; Shapiro et al. 2016).

When walking and running quadrupedally, primates tend to use diagonal sequence (DS) gaits, a preference that has been noted as unusual among quadrupedal mammals, which typically engage in lateral sequence (LS) gaits, since the 1800's, when the scientific study of animal locomotion was pioneered by Muybridge (1887). Muybridge (1887) described the baboon as "an animal that apparently disregards the law governing the walk" (pg. 30).

It has been hypothesized that DS gait preference in primates is for stability in terminal branch environments, including for the testing of compliant supports

(Cartmill et al. 2002; Schmidt 2005a; Stevens 2006, 2008). In support of this hypothesis, it has been found that DS gaits help to reduce peak substrate reaction forces in primates moving on arboreal supports compared to LS gaits by Wallace and Demes (2008). Non-primate mammals with pedal grasping, such as the wooly opossum (*Caluromys philander*) and feathertail glider (*Acrobates pygmaeus*) also use DS gaits on thin arboreal supports, which suggests a convergent link between pedal grasping and use of DS gaits (Schmitt and Lemelin 2002, Karatanis et al. 2015). Empirical data also supports the argument that hindfoot grasping may be more important for maintaining stability than forefoot grasping (Chadwell and Young 2015; Patel et al. 2015).

However, there is not consensus about the functional significance of primate DS gait use. Shapiro and Raichlen (2005) have proposed that lateral sequence lateral couplet (LSLC) gaits confer equal, if not greater, stability compared to a diagonal sequence diagonal couplet (DSDC) gait for the testing of unstable supports with the forelimb. Shapiro and Raichlen (2005, 2007) argue that the LSLC gait both increases the area of the base of support and allows the body to be supported by contralateral fore and hind limbs at the moment of forelimb touchdown (Figure 1.4).

The point made by Shapiro and Raichlen (2005, 2007) about the size of the base of support created by LS gaits is only applicable to a flat terrestrial surface and does not necessarily translate to a thin arboreal support, which would restrict the base of support regardless of gait sequence (Prost 1969). This

still leaves open the question of whether stability at the moment of forelimb touchdown on an untested support is improved by an ipsilateral (as in DSDC) or a contralateral (as in LSLC) fore/hind limb pair (Shapiro and Raichlen 2007), or if gait use is linked with support testing at all.

Non-human adult primates do not often utilize LS gaits; in his landmark paper on primate gaits, Hildebrand (1967) documented a strong preference for trotting and diagonal sequence diagonal couplet (DSDC) gaits in apes, lemurs, and monkeys. Juvenile macaques and adult lorisids in his study were observed to trot and utilize lateral sequence diagonal couplet (LSDC) gaits. Observations of lateral couplet gaits (LSLC and DSLC) were very uncommon in primates (Hildebrand 1967). DSLC walking gaits are rarely observed across all tetrapods, and are argued to be inherently unstable, but LSLC gaits are common in non-primates (Hildebrand 1980). The potential issue with using a LSLC gait that is not addressed by Shapiro and Raichlen (2005, 2007) is the relative duration of time spent on ipsilateral bipods is proportionally greater than in a DSDC gait (Hildebrand 1980), and how this may impact an animal on an arboreal support differently than an animal on a terrestrial support with respect to craniocaudal torque (roll).

1.2.3 Biomechanics of Locomotion

When an animal travels on a support, it exerts force against the support through each point of contact (the hands and feet) and receives equal and opposite reaction force, felt through these limbs (Biewener 2003) (Figure 1.5a).

The force exerted by an animal maintaining a static posture is the product of gravity (-9.8 m/s^2) and the animal's mass. The animal's center of mass (CoM) is the average location of the total mass.

The CoM is distributed across each limb in contact with the support (referred to as the base of support, Figure 1.5b), and when a quadruped is moving the proportion of mass supported by each limb will change with respect to the number of limbs on the ground (Biewener 2003). Additionally, through active muscular action, the position of the CoM can be shifted anteriorly towards the forelimbs or posteriorly towards the hind limbs during locomotion (Vilensky and Larson 1989). Therefore, understanding differences in dynamic CoM location may be more informative for interpreting locomotion differences than just the static CoM location differences between species (Young et al. 2007).

Reaction forces are experienced at the joints as external moments that are balanced out by internal moments driven by muscular force during locomotion (Biewener 2003). Effective mechanical advantage (EMA) describes the relationship of the reaction forces, and the internal and external joint moments generated by muscular action; when in equilibrium, these forces should be balanced (Biewener 2003). It is generally observed that as body mass increases, limb posture tends to become more erect, hypothesized as a means of improving EMA (Biewener 1989). Primates are unusual in that they show relatively greater limb compliance than non-primate mammals of similar body mass especially in arboreal settings, which Schmitt (1999) hypotheses is a

mechanism for reducing stress on the limbs from reaction forces in an arboreal environment. Additionally, limb flexion helps to bring the center of mass close to a support, which can help to reduce pitch and roll (medio lateral and craniocaudal torque, respectively) on arboreal supports (Cartmill 1985).

Arboreal environments are argued to be inherently poor for efficient travel by Alexander (1991) because of the loss of mechanical energy an animal experiences when its weight causes a supporting branch to bend (Bonser 1999; Young et al. 2016). For primates moving on terminal branches, which are small relative to the animal's size (Cartmill 1985), they must not only resist torque along their cranio-caudal axis (or roll), but also deal with changes to the mechanical environment as compliant supports bend downward under their weight, effectively becoming oblique supports, or declines. The locomotion of primates on declines is therefore the central focus of this thesis since encountering declines is an important and sometimes unavoidable aspect of arboreal travel on thin branches.

As animals move down declines, important changes occur to movement as a result, including increasing the braking force applied by the animal, and an increased potential for forward pitch around a pivot point created by the forelimb's contact with the support (Birn-Jeffrey and Higham 2014). When moving down declines, animals can reduce the potential for forward pitch by bringing their center of mass close to the support (Birn-Jeffrey and Higham 2014). However, maintaining crouched postures during locomotion is associated

with an increased cost of transport relative to non-crouching locomotion (Horner et al. 2016), especially in larger animals (Biewener 1989).

1.2.4 Summary of Primate Experimental Decline Studies

Relatively few studies have analyzed decline locomotion compared to horizontal and inclined locomotion (Birn-Jeffrey and Higham 2014), and of this small number of studies only a few have considered primates. Beginning with Rollinson and Martin (1981), which conducted observational study of the behavior in eight species of captive cercopithecoids moving down oblique supports within a zoo enclosure, it was observed that on declines primates increasingly utilize lateral sequence gaits, especially in juvenile individuals. Rollinson and Martin (1981) hypothesized that this shift in infant individuals might have been driven by a relatively more anterior placement of the center of mass created by the relatively large heads in juveniles; in their model, diagonal sequence gait use on inclines was hypothesized to be driven by a posteriorly situated center of mass in adult primates (see also Prost and Sussman 1969; Reynolds 1985).

This hypothesis, that weight position influences gait sequence (Iwamoto and Tomita 1966; Rollinson and Martin 1981), is one of several arguments for why primates uniquely use diagonal sequence gaits. However, while primates are often conceived of as being ‘hind limb dominant’ relative to more ‘forelimb dominant’ non-primate mammals (Kimura et al. 1979; Reynolds 1985), the weight placement and gait hypothesis has been critiqued by Vilensky and Larson

(1989), who reason that center of gravity position should not influence gait choice (pg. 25) and find little evidence to link active posterior weight shifting with diagonal sequence gaits. Demes et al. (1994) did not find unique difference in primates hindlimb driven propulsion compared to felines that would explain gait differences in these groups. Similarly, Schmitt and Lemelin (2004) recorded increased peak vertical forces in the forelimbs of *Loris* using diagonal sequence gaits on horizontal poles.

Despite the mixed relationship of weight placement and gait selection in primates and non-primates, the hypothetically link between them remains an intuitive explanation for the correlation of primate gait use and support orientation given the relationship between center of mass and the base of support (Figure 1.5) and an increase of LS gaits on declines and DS gaits on inclines (Rollinson and Martin 1981).

The shift towards lateral sequence gaits on declines was replicated by Vilensky et al. (1994) in *Saimiri* (n = 3) moving at a fast walking speed (1.17 m/s) on treadmills. Vilensky et al. (1994) reported that it was difficult to get animals to run down the steeper declines (-16°, -28°) but observed a mix of lateral sequence, trotting, and diagonal sequence gaits. While the exact frequencies of each symmetrical gait observed were not reported, these were averaged for each animal, and it was found that on horizontal and declined supports these *Saimiri* primarily used lateral sequence gaits (Vilensky et al. 1994).

Vilensky et al. (1994) interpreted their observed increased use of diagonal sequence gaits used on inclines as potentially driven by active muscular shifting of the weight posteriorly but did not comment extensively on the use of lateral sequence gaits on declines since they also observed high frequency of lateral sequences during horizontal travel in this species. However, this hypothesized connection between active weight shift and gait sequence could not be directly tested by Vilensky et al. (1994), and eventually was not supported experimentally by Schmidt (2005a). Schmidt (2005a) found that *Saimiri* did shift their weight posteriorly but used diagonal sequences, not lateral sequence gaits, when walking horizontally on a pole. Wild observation of *Saimiri* by Shapiro et al. (2011) has also found that diagonal sequences are frequently used by these animals for most travel on natural supports, regardless of diameter or orientation. Both Schmidt (2005) and Shapiro et al. (2011) speak to the importance of the role of experimental setup in influencing primate gaits, specifically fixed speed flat treadmills compared to self-selected speed on arboreal supports.

Posterior weight shifting in *Daubentonia* was hypothesized to occur on declines by Krakauer et al. (2002) and then confirmed using pressure pads by Kivell et al. (2010). *Daubentonia* is hypothesized to use this posterior weight shift to reduce stress on their highly derived and gracile digits, especially on declines, when the center of mass is predicted to naturally shift anteriorly relative to the forelimb placement (Birn-Jeffrey and Higham 2014). Unfortunately, neither Krakauer et al. (2002) nor Kivell et al. (2010) comment directly on the gaits

observed in their studies; however, it would be predicted that *Daubentonia* would use a diagonal sequence gait if there is a link between posterior weight shifting and DS gait.

Further testing of this link has been explored by Nyakatura et al. (2008) and Hesse et al. (2015) in *Saguinus*. Initial observation of *Saguinus* moving with increasingly lateral gaits on declines in an experimental setting using poles to simulate a natural environment by Nyakatura et al. (2008) was followed up with wild observation of the same pattern by Nyakatura and Heymann (2010). Force data on *Saguinus* collected by Hesse et al. (2015) found that peak reaction forces experienced by hind limbs decreased with increasing support orientation (≤45°) on declines while support reaction forces on the forelimbs increased. Above this angle (60°), it was found that the hind limb began to pull upon the support, and that peak reaction force on the forelimbs was decreased relative to a 45° support. While not explicitly commented on by Hesse et al. (2015), they did not observe lateral sequence gaits on this 60° decline, a pattern potentially explained by the hind limb helping to shift the weight posteriorly off the forelimb on this steep support.

Additional studies have also found an increase in trotting and lateral sequence gaits on declines including Stevens (2003) who conducted a dissertation on six species of strepsirrhines (*Cheirogaleus medius, Eulemur rubriventer, Eulemur fulvus, Loris tardigradus, Nycticebus coucang,* and *Miriza coquereli*) moving on a variety of supports. Stevens (2003) reported findings in

strepsirrhines like observations of anthropoids (Rollinson and Martin 1981; Vilensky et al. 1994), including increased forelimb and hind limb protraction at touchdown. Increased protraction of the forelimbs was hypothesized to increase the anterior breadth of the base of support of the animals, and to function to increase braking by the forelimbs on declines (Stevens 2003).

Data from Stevens (2003), specifically on *Eulemur*, was later compared to wild observation of *Eulemur cinereiceps* by Stevens et al. (2011); this study replicated findings of increased forelimb and hind limb protraction at touchdown, as well as increased hind limb retraction at takeoff in wild animals traveling on declines. Gait type was not reported on for wild animals, so it is unclear whether the wild animals also shifted to trotting or lateral sequence gaits in this field study (Stevens et al. 2011).

From these studies, there appears to be a consistent trend of primates, both anthropoids and strepsirrhines, generally decreasing the frequency of use of diagonal sequence gaits when moving on moderate (≤ 35°) and steep (60°) declines (Rollinson and Martin 1981; Vilensky et al. 1994; Stevens 2003; Nyakatura et al. 2008; Nyakatura and Heymann 2010; Stevens et al. 2011; Hesse et al. 2015). However, this relationship has not been found in the smallest strepsirrhines to be experimentally analyzed, *Microcebus murinus*, by Shapiro et al. (2016). Instead when moving on declines, *Microcebus* was shown to utilize very high frequencies of asymmetrical gaits (all but 1 observation). Given this species small body mass and the frequent utilization of asymmetrical gaits by

small mammals (Dagg 1973), this observation is difficult to attribute to support orientation (Shapiro et al. 2016). Other studies, apart from Hesse et al. (2015), do not include mention of asymmetrical gait use; Hesse et al. (2015) briefly comment that asymmetrical gait use increased with increasing support orientation angle, but similarly to *Microcebus* this could also be a product of the small body mass of *Saguinus*. It is unclear at this time if primates with larger body mass also increase their use of asymmetrical gaits on declines.

No experimental studies have been published that feature primates descending supports steeper than 60°. Part of this may be because of the difficulty of getting primates to travel headfirst on such steep supports (Stevens 2003). Behaviors outside of headfirst descent have not been experimentally analyzed. Body mass appears to be an important factor in determining whether a primate will descend headfirst, given that larger species tend not to engage in headfirst descent (Curtis and Feistner 1994). Field research on apes has also found that older (and therefore heavier) primates tend to use rear first descent on supports in which juvenile conspecifics use headfirst descent (Thorpe and Crompton 2006; Sarringhaus et al. 2014). However, there is no hypothesis for predicting the steepest support any given primate will attempt to descend headfirst.

1.2.5 Vertical Support Use and Direction of Movement

Many primates, especially strepsirrhines, utilize vertical supports, but there is little data on vertical descent in primates, and animals generally (Birn-Jeffrey and Higham 2014). On vertical supports, it is expected that the mechanical environment is quite different from a non-vertical support in that the animal is no longer creating a base of support that can capture the center of gravity.

It has been reasoned that there is an upper weight limit on primates that are able to descend vertical supports headfirst by Curtis and Feistner (1994), based on the observation that *Daubentonia* is the largest (average mass 2.5 kg, Smith and Jungers 1997) non-prehensile tailed primate that regularly engages in headfirst descent. Curtis and Feistner (1994) attributed this ability to the robusticity of the shoulder and humerus of *Daubentonia*. Curtis and Feistner (1994) do not describe whether their observations were of *Daubentonia* descending large diameter or small diameter supports, and it is not reported how this species gracile digits interact with supports during descent. Tilden (1990) observed *Eulemur rubriventer* (species average mass 1.96 kg; Smith and Jungers 1997) also descending large supports headfirst and attributed this ability to claw-like nails in this species. Smaller primates, including the cheirogaleids, callitrichids, lorisids, and galagids, are the only other non-prehensile tailed primates noted to regularly engage in headfirst descent (Tattersall 1982; Gebo 1987; Tilden 1990; Curtis and Feistner 1994). Much larger primates with prehensile tails are also capable of headfirst descent of small supports using

their tail as an anchor, such as in *Alouatta seniculus* (species body mass range: 5.2-7.6 kg; Smith and Jungers 1997) observed by Youlatos and Gasc (1994).

Most research on primates using vertical supports is focused on ascending behaviors. Cartmill (1974b) and Jungers (1976) present a mechanical model for the forces experienced by a primate during ascent of a vertical support (Figure 1.6a). A formula for how these forces and moments are balanced is given as:

$$MG*X_A = B_V*(X_A - X_B) + B_H*Y$$

> Weight * Moment arm between superior support and Center of Mass = (Vertical reaction force for inferior contact*Horizontal distance between superior and inferior points of contact) + (Horizontal reaction force for the inferior contact*vertical distance between the superior and inferior contacts) (Cartmill 1974b, 1985; Jungers 1976, 1978).

In this model of ascent, the hands form a superior point of contact with a support that places the forelimb under tension, while the feet form an inferior point of contact, which places the hind limbs under compression. Each point of contact experiences a rotational force, or torque, which is the product of the perpendicular distance (moment arm) of that point from the center of gravity and the force of gravity that acts upon the mass of the animal (weight) (Figure 1.6a).

Torque (specifically pitch) is experienced in the same direction (e.g. clockwise) by both the hands and feet (Figure 1.6b). During *ascent*, this torque either sends the animal towards the support, in cases where only the hands (superior) are in contact, or away from the support, when only the feet (inferior) are in contact. These would be reversed during *descent*, when the feet would provide the critical superior support for the animal (Figure 1.6b). To avoid critical falls, animals should ensure that they are always able to maintain a secure superior hold on a support whether they are ascending or descending and try to reduce the moment arm at the inferior hold as much as possible (Cartmill 1974b).

To achieve this on a large substrate, as modeled by Cartmill (1974b, 1985) and Jungers (1976, 1978), animals with long arms can help to bring the mass close to the support and adducted foot postures to minimize the inferior moment arm, X_B. It is predicted that animals should utilize postures that keep $X_B < X_A$, however this may not be possible on a thin support, in which these distances may be equal (as in Figure 1.6c).

Changes to the normal force exerted at the inferior support (B_H) are expected to produce an equal but opposite change to the normal force at the superior support (A_H) (Figure 1.6a), as in the more an animal presses into a support with its feet, the more it will need to pull upon the support with its hands to maintain a secure hold during ascent. In this model, the distance between the hands and feet (Y) determines the normal force acting on the inferior support

(B_H), assuming all other variables are held constant, such that maximizing Y will reduce B_H, and minimizing Y will increase B_H.

Changes to B_H will influence the available friction at the inferior point of contact. Friction is the product of B_H*μ, or the coefficient of friction, which is a dimensionless variable determined by the material properties of the objects in contact with each other, i.e. the feet and the support (Brinckmann et al. 2002). For a grasping animal, generating the friction needed to avoid inferior slipping from a support comes at the cost of potentially increasing the pull on the superior support (A_H).

To understand headfirst descent, the Cartmill and Jungers model can be inverted (Figure 1.6c). In this scenario, the feet become the critical anchor point of the body, because if their grip fails the resulting torque would potentially wrench the body away from the support (Figure 1.6b). Many non-primate animals that regularly descend supports headfirst possess mobile ankles that allow for rotation of the foot, thus enabling the claws to be oriented in a manner that interlocks with the support (Jenkins 1974; Jenkins and McClearn 1984; Cartmill 1985). Headfirst descent is presumably favorable to tail first descent because the animal can see its path, which may be especially important in discontinuous arboreal environments.

Some primates, especially gumnivores that exploit relatively large diameter vertical supports, show convergent morphology including secondarily claw-like nails and mobile ankles (Nash 1986; Hamrick 1998). However, primates

that lack such adaptations must actively grasp with the feet, which limits the maximum diameter of the support that can be navigated (Cartmill 1974a, 1974b, 1979, 1985). Alternatively, on a support that is too large for a single foot to grasp, primates could potentially hold the hind limbs in an oppositional grip against each other (Lammers and Gauntner 2008), however this strategy requires powerful adduction of the hindlimbs and would still be limited in the maximal diameter of a support that could be negotiated in this manner.

1.2.6 Locomotion Summary

Extant primates display a wide variety of locomotor repertories, and many primates spend significant amounts of time in trees. Arboreal primates must deal with dynamic environments filled with compliant supports (Alexander 1991), which may influence how they hold their bodies relative to non-primates (Schmitt 1999). It is hypothesized that certain gait types may offer special advantages in arboreal environment, however there is disagreement as to why DS gaits are more prevalent compared to LS gaits (Cartmill et al. 2002, Shapiro and Raichlen 2007).

LS gaits are commonly observed in primates moving on declines (Rollinson and Martin 1981; Vilensky et al. 1994; Stevens 2003; Nyakatura et al. 2008; Nyakatura and Heymann 2010; Hesse et al. 2015). One reason these observations of LS gaits generate so much interest is because they seem to contradict the hypothesis that DSDC gaits are a product of the grasping feet and terminal branch use (Cartmill 1974; Schmidt 2005; Cartmill et al. 2002; Schmitt

and Lemelin 2002; Karantanis et al. 2015). Given that as primates travel on increasingly steep declines they will encounter greater risk of forward pitch, they are expected to counteract with their grasping feet, which would seem to predict a greater reliance on DS gaits rather than less if DS gaits are linked to grasping feet. Several hypotheses have been put forward to explain primate use of LS gaits on declines, but it is unclear at present if this pattern is a function of body size, body mass distribution, and/or morphology since this has not been replicated in very small primates (Shapiro et al. 2016) and not reliably replicated in wild populations (Shapiro et al. 2011).

1.3 Hypotheses, Predictions, and Study Outline

Primates likely evolved from a generalized arboreal ancestor that had claws into an animal with nails and grasping feet (Jones 1916; Smith 1924; Cartmill 1974a; Jenkins 1974; Gebo 2004; Sargis et al. 2007). Claws provide secure attachment for an animal on large vertical supports, while grasping feet allow animals to resist medio-lateral torque, or roll, within a fine-branch environment (Cartmill 1972, 1974a, 1974b, 1985). However, these primate adaptations for movement on fine-branches would appear to limit movement outside of these environments in the absence of other gap crossing mechanisms (Orkin and Pontzer 2011). Despite this, it is recognized that euprimates had a relatively rapid and widespread dispersal in the earliest Eocene, including into environments that are reconstructed as being open rather than closed and continuous (Secord et al. 2008). This pattern of dispersal indicates that at least

some of the earliest euprimates found success in environments that did not consist of continuous fine-branch habitats. This dissertation is interested in one specific aspect of arboreal locomotion: descent, and the ways in which derived primate features – specifically nail bearing, grasping hands and feet, relatively long legs, and body mass increases – influence this aspect of arboreal locomotion, and may have affected primates throughout the evolution of this lineage.

Hypothesis: The morphological features of primates for movement in a terminal branch niche, specifically the loss of claws and selection for grasping-specialized nail-bearing digits, create a biomechanically challenging for descending locomotion. In particular, maintaining a secure connection to the support to resist forward pitch may be more difficult for primates than claw interlocking animals on certain substrates. The best method for descent in a primate is likely affected by support size, orientation, and the distribution of mass in the animal. Primates may engage in alternatives to headfirst descent – e.g. leaping, tail first descent – as a locomotor trade-off between the need to descend and doing so safely or efficiently. Under this hypothesis, the following predictions are expected to apply:

Prediction 1: Body mass should influence the relative frequency of gross descent behavior (e.g. headfirst descent, tail first descent, leaping). In addition to body mass, aspects of skeletal proportions are also anticipated to influence descent. As body size increases, the frequency of headfirst descent is expected to decrease as supports become steeper based on the observed relationship of

these variables in observational studies of behavior (Tilden 1990; Curtis and Feistner 1994; Thorpe and Crompton 2006; Sarringhaus et al. 2014). To test this prediction, primates that span a range of body masses, intermembral indices, and foot sizes, were selected for the sample including those above the hypothesized limit on headfirst descent in non-prehensile tailed primates, 2.5 kg, proposed by Curtis and Feistner (1994). The occurrence of headfirst descent on various support orientations is described for each species, and any behaviors used as an alternative mode of descent are presented in Chapter 3: Use of Headfirst Descent and Support Orientation.

Prediction 2: Gait sequence and timing of footfalls during headfirst descent is predicted to change in response to support orientation. Primates are observed to increase use of lateral sequence gaits on declines (Rollinson and Martin 1981; Vilensky et al. 1994; Stevens 2003; Nyakatura et al. 2008; Hesse et al. 2015). It is predicted that limb phase should decrease (become more lateral) as support orientation increases. To test this prediction, limb phase will be compared across support orientations. Additional temporal aspects of gait including duty factor will be analyzed. Frequency of asymmetrical gait use will be compared across body masses to test if this is a feature of only small species (Shapiro et al. 2016), or if this is a generalized trend in primates. These results are presented in Chapter 4: Gait kinematics and Support Orientation I: Temporal Variables.

Prediction 3: Primates will make kinematic adjustments to body posture in response to support orientation. As supports increase in steepness, there will be

an increased risk of forward pitch (Birn-Jeffrey and Higham 2014). Primates are expected to resist this torque as supports become steeper, which is expected to translate into kinematic changes within species between support conditions. One key mechanism for reducing the risk of forward pitch is to reduce the distance between the center of mass (COM) and the support (Birn-Jeffrey and Higham 2014). Therefore, it is predicted effective limb length will be reduced to lower the COM. This is expected to occur via increases in joint flexion. To test this prediction, joint angles and effective limb lengths will be collected and compared between support conditions. Another feature of arboreal primates are their relatively long legs, or low intermembral indices (IMI). Primates with especially low IMI are predicted to have to flex the hind limb relatively more than the forelimb to keep the trunk relatively parallel to the support to avoid pitch. To test this, primates representing the full range of IMIs in strepsirrhines were selected for the sample. In response to declines, both increases and decreases to speed have been found by experimental studies of vertebrates (Birn-Jeffrey and Higham 2014). Absolute velocity and Froude number will be compared within this sample across support orientations to test whether primates generally speed up or slow down. These results are presented in Chapter 5: Gait kinematics and Support Orientation II: Spatial Variables

The present study involves nine species of strepsirrhine primates – *Cheirogaleus medius, Daubentonia madagascariensis, Eulemur coronatus, Eulemur mongoz, Lemur catta, Microcebus murinus, Nycticebus pygmaeus,*

Propithecus coquereli, and *Varecia variegata* – from a captive sample housed at the Duke Lemur Center (Durham, NC, USA). These species were selected for their variation in body size and limb proportions; this sample also covers a broad range of arboreal locomotor specializations. These species are discussed in further detail in Chapter 2, which also covers the experimental design and data collection procedures.

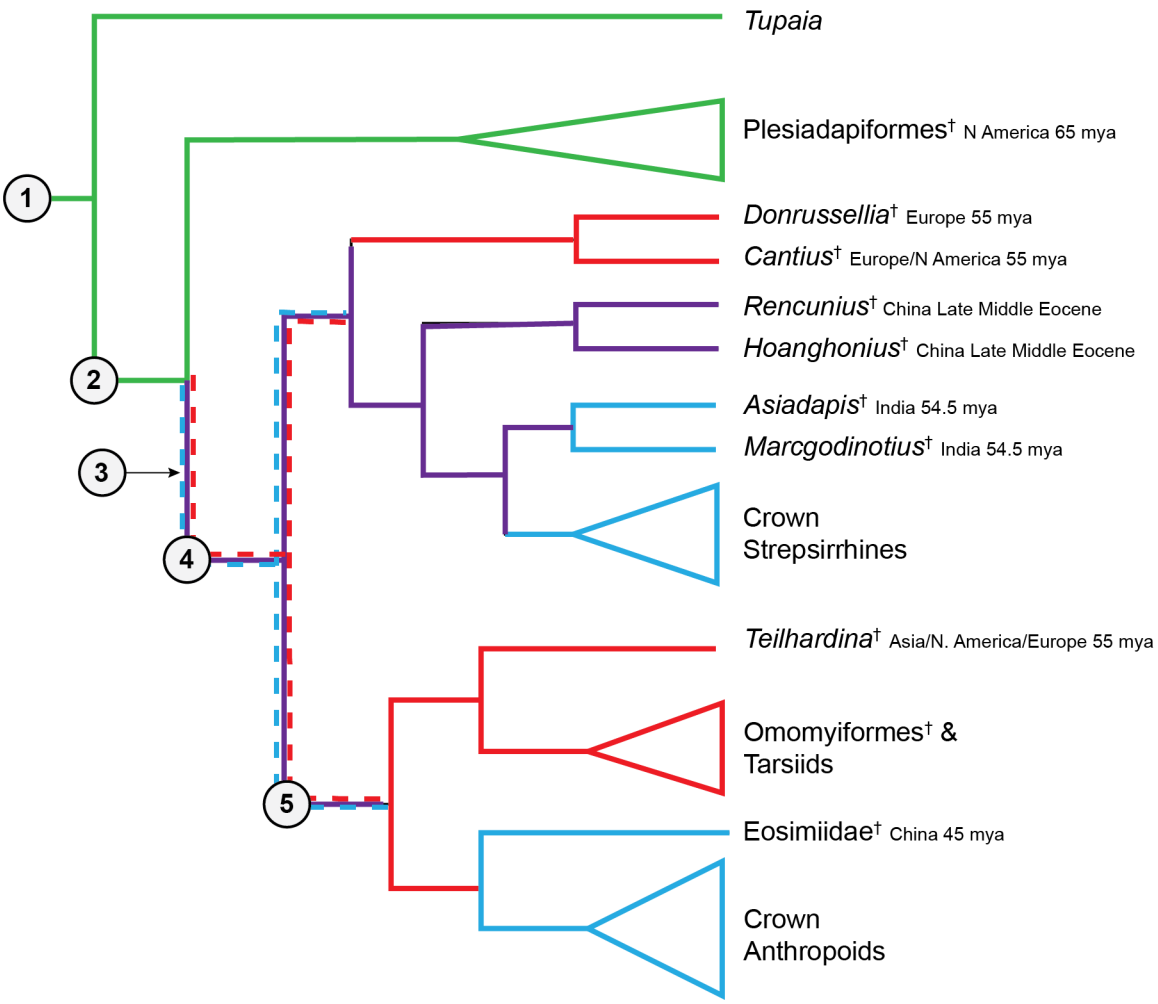


Figure 1-1: Relationships of Early Primates and Major Transitions in Primate Locomotor Evolution. Phylogenetic relationships are adapted from the analysis of Boyer et al. (2017). Numbers indicate hypothesized transitions in primate morphology and/or behavior; 1 – Last common ancestor of all euarchontans, 2 – Last common ancestor of primates and other euarchontans, hypothesized to be relatively small in mass, ≤ 100 g (Gebo 2004, Boyer et al. 2013a), 3 – Selection towards grasping, nail-bearing appendages (Sargis et al. 2007), 4 – Last common ancestor of Strepsirrhines and Haplorrhines, 5 – inferred leaping ancestry at the base of Haplorrhines based on *Eosimias* tarsal elements (Gebo et al. 2015). Legend: Green indicates primitive condition of clawed arboreal locomotion with little to no grasping ability; Blue – generalized above branch quadrupedalism with grasping abilities, absence of specialized leaping in common ancestor; Red – specialized leaping; Purple – no direct evidence for locomotor behavior; Blue dashed line – NVP hypothesis-like locomotion (Cartmill 1974a ,1992; Dunn et al. 2016); Red dashed line – Grasp-leaping hypothesis locomotion (Szalay and Dagosto 1980, Boyer et al. 2017).

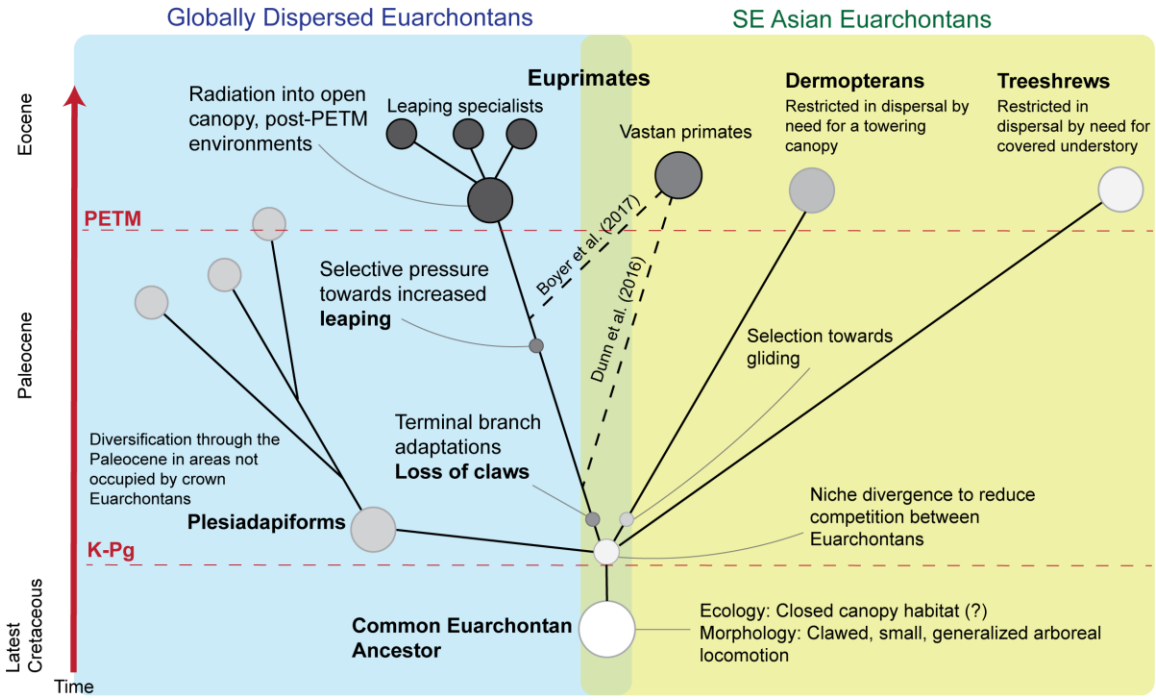


Figure 1-2: Synthesis of Evolutionary Argument. Under this scheme, primate synapomorphies – grasping, nail bear hallux – evolve prior to and independent of leaping adaptations for the exploitation of a terminal branch environment. Leaping adaptations in early far dispersing primate taxa might have been critical in the success of primate dispersal into open post PETM environments.

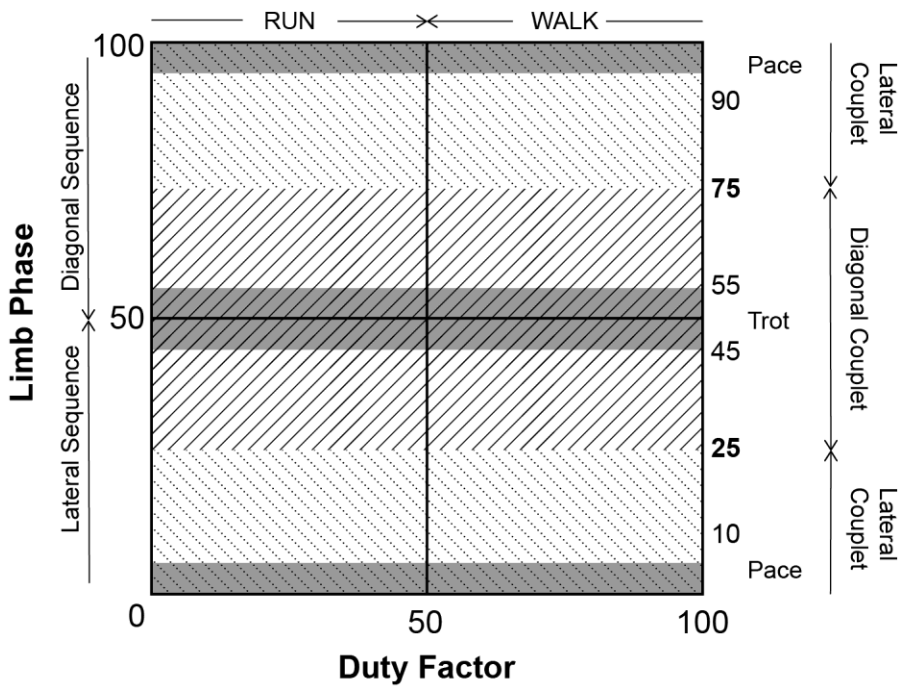


Figure 1-3: Hildebrand (1967) style chart for comparing symmetrical gaits. Duty factor, or the measure of the percentage of hind limb contact time throughout the stride, is plotted along the x-axis and connotates a relative measure of speed, with values below 50 representing running, and values above 50 representing walking. Limb phase, the percentage of the gait cycle in which the forefoot follows the placement of the ipsilateral hindfoot, is plotted along the y-axis and can be broken into several types of gait sequence and couplets.

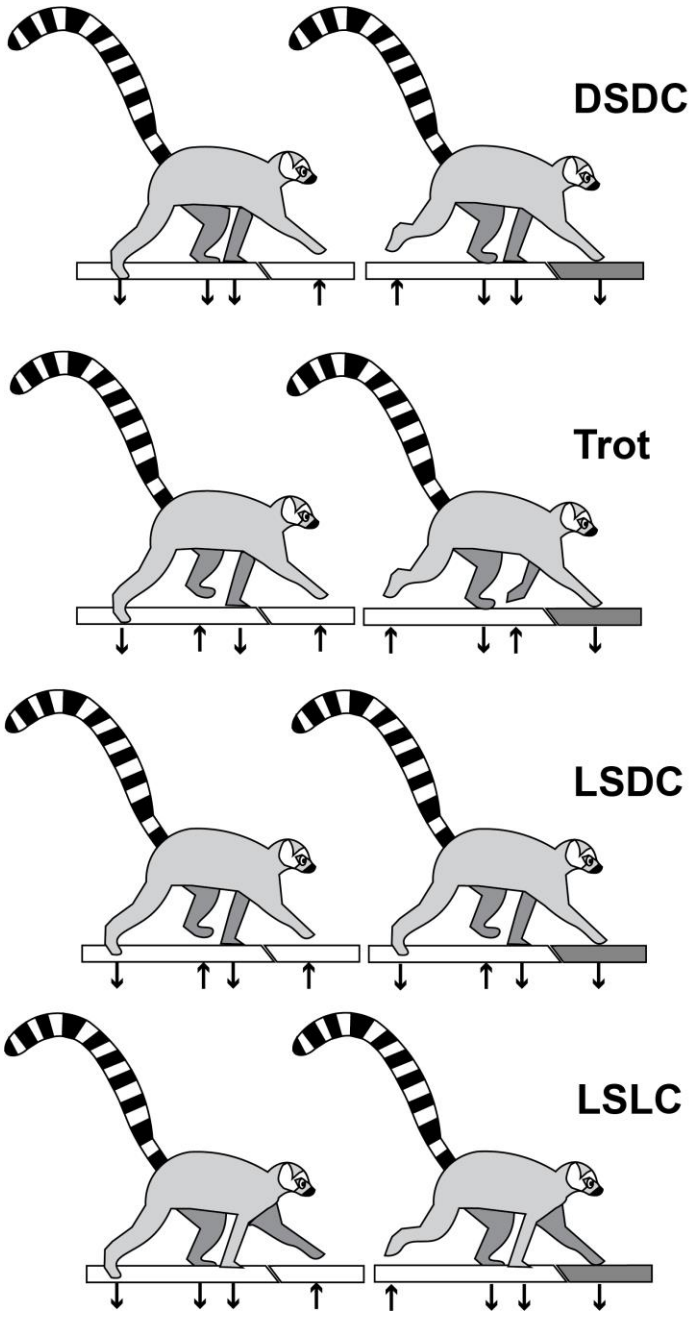


Figure 1-4: Position of hands and feet when allowing forelimb to touchdown on an untested support This a visualization of the debate between Cartmill et al. (2007) and Shapiro and Raichlen (2007) about the utility of DSDC gaits as a mechanism for testing unsteady supports during arboreal locomotion. In this framework, DSDC and LSLC gaits provide the same advantage of a hind limb in contact with the support beneath the center of mass, while trots and LSDC confer less stability.

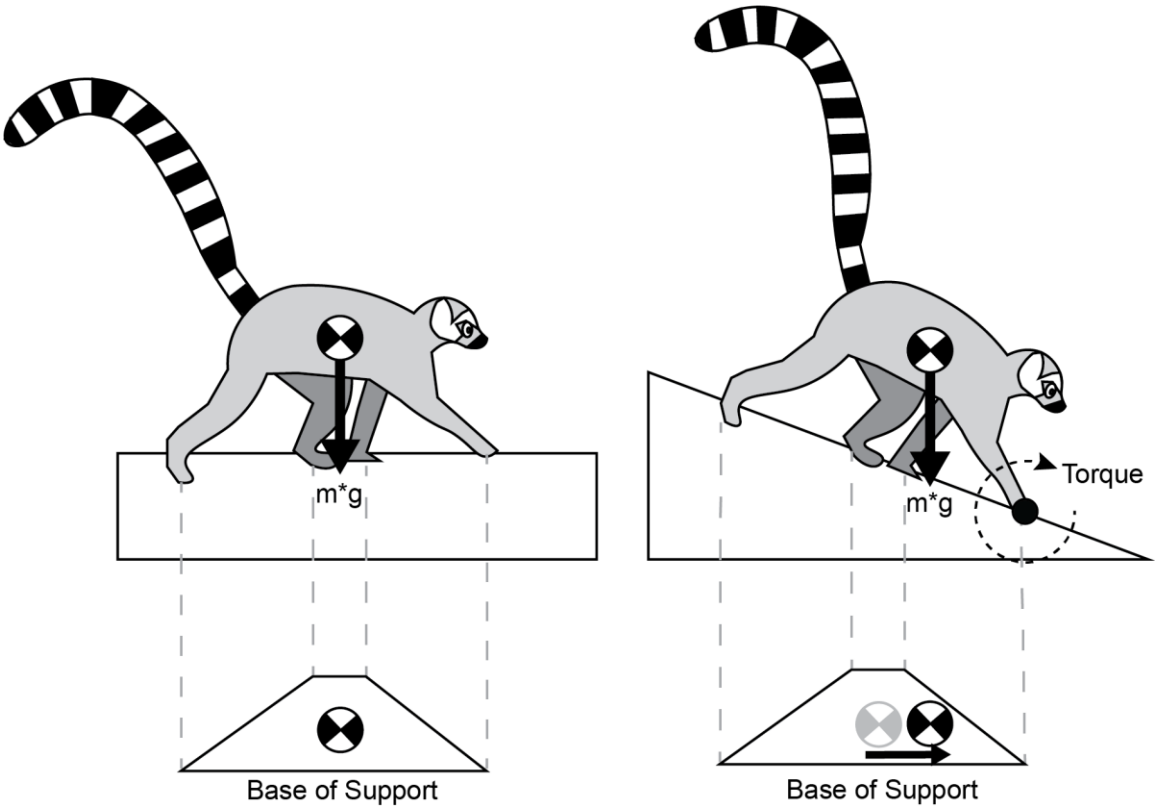


Figure 1-5: Changes to mechanical forces on level supports and declines. It is hypothesized that as animals move on declines, the center of gravity moves anteriorly (towards the hands) within the base of support formed by the hands and feet in contact with the support. As animals move on oblique supports, the risk of toppling motions caused by mediolateral torque, or forward pitch, is increased around a pivot created by the inferiorly placed limb in contact with the support (the hands during headfirst descent). Static friction also decreases as the angle of inclination increases and is expected to disappear at approximately at supports of 34° and steeper (Vilensky et al. 1994).

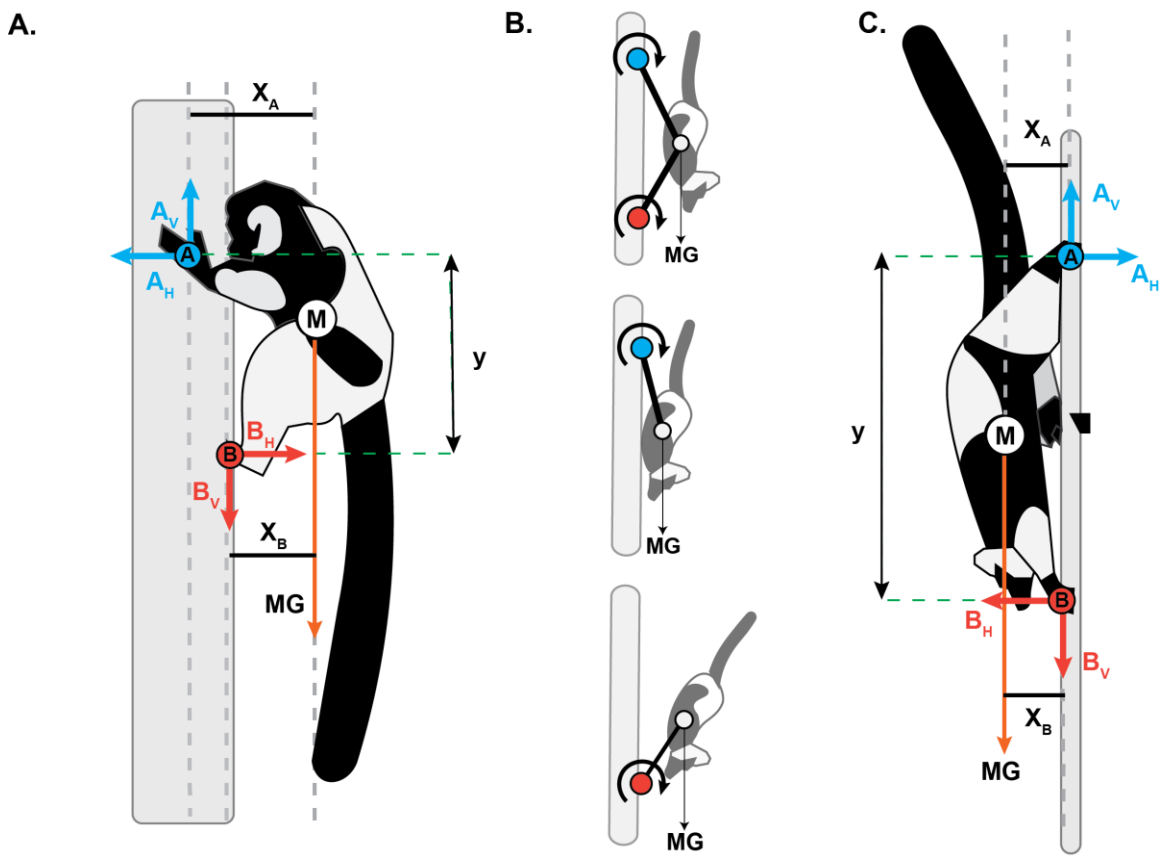


Figure 1-6: Model of Forces experienced during vertical descent. A) Adaptation of Cartmill (1974b) and Jungers (1976) models for ascending a relatively large diameter support. B) Direction of torque is clockwise around the point of contact (e.g. hands, feet); when the superior point of contact is hanging onto the support, the body is rotated towards the support, and when the inferior point of contact is holding onto the support, the body is rotated away from the support. C) An inversion of the Cartmill (1974b) and Jungers (1976) model for descending a vertical support. Legend: M = center of mass, MG = weight vector, A = superior point of contact (hands for ascent, feet for descent), Av and AH – vertical and horizontal components of the reaction force on A, B = inferior point of contact (feet for ascent, hands for descent), Bv and BH – vertical and horizontal components of the reaction force on B; Xa = moment between the superior contact and the center of mass; Xb = moment between the inferior contact and the center of mass; y = distance between the superior and inferior points of contact.

Chapter 2: Sample and Experiment

2.1 Introduction

This chapter outlines the sample and methods used in the present study for testing predictions outlined in the previous chapter. This includes a description of the study sample by locomotor group followed by a description of the experimental design, both in its pilot stage (2015-2016) and the full experiment (2017-2019). Data collection and processing are described. The chapters that follow will contain any methods specific to that portion of the study, such as statistical analyses.

2.2 Primate Sample Overview

This study utilizes a sample of strepsirrhines, which are a morphologically and ecologically diverse group of extant primates found in Africa, Asia, and Madagascar (Fleagle 2013). Strepsirrhines have historically covered a broad range of body masses, from the tiniest living primates, the mouse lemurs, to the large recent subfossil lemurs, e.g. *Archaeoindris*, which is reconstructed as weighing as much as 200 kg (Fleagle 2013). Extant strepsirrhines include taxa often used to model the earliest euprimates, the Cheirogaleidae (Gebo 2004), as well as taxa that include extreme morphological specialization – e.g. the low intermembral indices of *Propithecus*, or the highly derived hands of *Daubentonia* – and a mix of substrate preferences, such as the high degree of terrestriality observed in *Lemur catta* (Ward and Sussman 1979) that mirrors increased terrestriality in some species of anthropoid primates.

While several species of strepsirrhines have been included in previous decline research – *Microcebus murinus* in Shapiro et al. (2016), *Daubentonia madagascariensis* in Krakauer et al. (2002) and Kivell et al. (2010), and finally Stevens (2003) observations of *Eulemur fulvus, Eulemur rubriventer, Loris tardigradus, Nycticebus coucang, Miriza coquereli,* and *Cheirogaleus medius* (n = 12 individuals) – the sample used in the present study represents the greatest diversity of strepsirrhine primate species (n = 9 species, n = 36 individuals) covering the broadest range of average adult body masses (<0.1 to 3.7 kg), and locomotor specializations (arboreal quadrupeds, vertical clingers and leapers, and slow climbers) tested on declines using the same methodology.

The primate sample used in the present study is comprised of captive strepsirrhines housed at the Duke Lemur Center (DLC, Durham, NC, USA) (Figure 2.1). Species include eight Malagasy lemuriforms: *Daubentonia madagascariensis, Lemur catta, Eulemur coronatus, Eulemur mongoz, Varecia variegata, Propithecus coquereli, Microcebus murinus*, and *Cheirogaleus medius*, and one south Asian lorisiform, *Nycticebus pygmaeus* (Figure 2.1). Species have been sorted into four locomotor categories: large arboreal quadrupeds, small arboreal quadrupeds, vertical clingers and leapers, and slow climbers. Descriptions of each species follows:

2.2.1 Species profiles by locomotor category

2.2.1.1 Large arboreal quadrupeds (L-AQ)

Large arboreal quadrupeds (L-AQ) are defined here as arboreal primates that primarily move quadrupedally above branches, with average adult mass greater than 1 kg. Within this sample, these primates span a range of IMI from the high 60's to low 80's, with most species around 70-72 (Figure 2.1).

Family Daubentoniidae

Daubentonia madagascariensis (Gmelin 1788)

The aye-aye is a nocturnal strepsirrhine that is very distinctive in many respects; in terms of postcrania it is most well-known for its unusually derived hands which feature long gracile digits (Fleagle 2013). How *D. madagascariensis*, argued to be one of the largest non-prehensile tailed primates to regularly descend vertical supports headfirst (Curtis and Feistner 1994), manages forces incurred by these gracile digits during descent has generated much interest (Lemelin 1996; Krakauer et al. 2002; Kivell et al. 2010). Lemelin (1996) observed *D. madagascariensis* descending large (7-8 cm diameter) oblique supports and sometimes aligning their hand along the axis of digits III (the highly derived digit) and IV (the longest digit in strepsirrhines, Tattersall 1982), but predominantly these animals grasped with digits I and II, curling the other fingers. To investigate the frequency of these hand postures this further, Krakauer et al. (2002) performed a specific study on descent and ascent in *D. madagascariensis* on supports of approximately 30° to observe the frequency of

these finger curling grasps, and found that individuals (n = 3) either curled digit II or all digits II-V. In contrast when ascending, *D. madagascariensis* typically gripped the support with all manual digits. Further analysis by Kivell et al. (2010) found that *D. madagascariensis* actively shifts pressure away from the digits of the hands when traveling on flat declines, which is consistent with descriptions of them walking terrestrially with extremely dorsiflexed manual digits (Tattersall 1982).

In contrast, the feet of *D. madagascariensis* are considered more generalized, and feature what Gebo (1985) identified as a I-V grasp based on their bony morphology. Gebo (1985) hypothesizes that this pedal arrangement represents the primitive grasp-type for primates, in which the opposition of the foot occurs primarily between the hallux (digit I) and remaining four digits and is driven by musculature concentrated around the hallux and digit V; this grasp is also shared by tarsiers, cheirogaleids, and lorisids (Gebo 1985). This is contrasted against what Gebo (1985) identified as a I-II grasp that appears to be derived in the Lemuridae and Indriidae. Gebo (1985) hypothesized that the I-V grasp is not as mechanically advantageous for holding onto vertical supports at larger body sizes as a I-II grasp based on positional behavior and comparative myology.

This brings up the question of how *D. madagascariensis* can successfully descend headfirst at a relatively large body mass despite possessing potentially disadvantageous pedal grasp. One hypothetical mechanism to facilitate this

behavior are the superficially claw-like nails of *D. madagascariensis* (Tattersall 1982; Tilden 1990; Ancrenaz et al. 1994), which would have to interlock with the support to be useful during decent (Cartmill 1985). However, Krakauer et al. (2002) found no strong evidence that *Daubentonia* were interlocking with the natural support used in that study, although the support angle used was relatively shallow, theoretically allowing these primates to walk rather than climb (Preuschoft 2002), which may not necessitate interlocking. Additionally, to interlock during headfirst descent, *D. madagascariensis* might be expected to possess a highly mobile ankle capable of reversal as seen in other clawed mammals that regularly engage in headfirst descent (Jenkins 1974; Jenkins and McClearn 1984; Cartmill 1985). While Meldrum et al. (1997) share evidence of hindlimb suspension in *D. madagascariensis* on a relatively thin and horizontal support, they make a special note of the limited plantarflexion they observed in this species, in contrast to genera like *Varecia* that display hindfoot reversal.

D. madagascariensis is described as slow and cautious when ascending, descending and bridging, however unlike typical slow climbing primates, *D. madagascariensis* also leaps (Tattersall 1982). Ancrenaz et al. (1994) reported that the *D. madagascariensis* they followed in Mananara-Nord Biosphere Reserve (NE Madagascar) most often utilized supports between 3 and 10 cm in diameter and were more often observed on oblique supports than either horizontal or vertical ones. These authors also report that larger (> 10 cm) supports and tree trunks accounted for approximately a quarter of supports used

by this species, and that descent was both headfirst and tail first on tree trunks (Ancrenaz et al. 1994). In a study of captive free ranging *D. madagascariensis* kept at the Jersey Wildlife Preserve Trust (Jersey, UK), Curtis and Feistner (1994) found that headfirst descent happened at a greater frequency of total locomotion (9%) than tail first descent (1%). Curtis and Feistner (1994) did not report on any specific support diameters descended by the animals in their study but made special note of the role of *D. madagascariensis'* grasping hallux during descent, suggesting that these supports were small enough to grasp with a single foot. Further support of this is provided by Pollock et al. (1985), who describe and photographed *D. madagascariensis* descending through a dense patch of bamboo headfirst.

In terms of intermembral index (IMI), Fleagle (2013) reports a value of 71 for *D. madagascariensis*, possibly derived from Mollison (1911), which is the source used by Napier and Napier (1967), who also report the same IMI. However, later studies conducted by Jouffroy and Lessertisseur (1979), Sterling (1993), and Glander (1994) report much higher average intermembral indices: 82.4 (n = 5, range 79.3-85.5), 77 (n = 7), and 77-81 (n = 7) respectively. These samples were osteological (Jouffroy and Lessertisseur 1979), wild living (Sterling 1993), and captive living specimen (Glander 1994). I will err on the side of Glander (1994) since my sample is also from the DLC and use the osteological measures of Jouffroy and Lessertisseur (1979) rather than Mollison (1911). Apart from *Daubentonia*, the measures of Jouffroy and Lessertisseur (1979), which are

presented at the genus level, are in much closer agreement with IMIs recorded in Fleagle (2013) for other species in this sample.

Family Lemuridae

Lemur catta (Linnaeus 1758)

The ring-tailed lemur is widely considered to be the most terrestrial extant lemur species and is reported to spend more than half its time on the ground (Ward and Sussman 1979; Gebo 1987), but feed in arboreal settings (Gabriel 2013). In comparison to a more arboreal species, *Eulemur fulvus*, Ward and Sussman (1979) found that *L. catta* had significantly shorter distal foot proportions and a less mobile ankle, which the authors linked to frequent terrestrial support use. Of the large arboreal quadrupeds in this sample, *L. catta* possesses the lowest ratio of foot length to hindlimb length (Jouffroy and Lessertisseur 1979).

Eulemur coronatus (Gray 1842) and *Eulemur mongoz* (Linnaeus 1766)

There are many *Eulemur* species, which share a common body plan with low IMI (68-72) and range in average body mass from 1.2-2.3 kg (Fleagle 2013). The crowned lemur (*E. coronatus*) is arboreal and has been reported to engage in petrous locomotion in Ankarana (N. Madagascar) by Wilson et al. (1989), having to vertically descend 5 m to reach a waterhole located in a cave during the dry season, which gave them access to the waterhole to the exclusion of a sympatric population of *Eulemur fulvus sanfordi*. The mongoose lemur is also

arboreal but is described as not frequently climbing, and instead seems to exhibit more quadrupedal travel in the wild (Curtis and Zaramody 1999).

Varecia variegata (Kerr 1792)

Varecia is the largest of the extant lemurid genera and is described as quite primitive in its behaviors (Fleagle 2013). The black and white ruffed lemur has a derived foot morphology that allows it to frequently engage in suspensory postures relative to other strepsirrhines (Meldrum et al. 1997). It is highly arboreal and possibly restricted to patches of forest with continuous canopies (Fleagle 2013).

2.2.1.2 Small arboreal quadrupeds (S-AQ)

Small arboreal quadrupeds (S-AQ) are recognized here as arboreal primates that often move quadrupedally above branches, with average adult mass below 1 kg. Like the large arboreal quadrupeds, they range in IMI from the upper 60's to low 70's (Fleagle 2013) (Figure 2.1).

Family Cheirogaleidae

The cheirogaleids, or dwarf and mouse lemurs, represent the smallest living strepsirrhine primates and share many aspects of locomotion. Gebo (1987) reports that members of this group are capable of vertical clinging and leaping behaviors, and cantilevering. Jouffroy and Lessertisseur (1979) found that within the lemurs, cheirogaleids have some of the longest feet relative to their femoral length (Figure 2.1).

Cheirogaleus medius (Geoffroy 1812)

The lesser, or fat-tailed, dwarf lemur, derives its genus name from the Latin for ‘hand weasel’, which is evocative of the species’ relatively long trunk, short limbs, and grasping appendages. Petter (1962) observed this species regularly traveling on large horizontal supports and occasionally small branches. This species is quite distinctive for storing large amounts of fat in its tail for extended periods of torpor, and this increase in tail mass has been experimentally shown to alter some kinematic aspects of quadrupedal locomotion by Young et al. (2007).

Microcebus murinus (Miller 1777)

The gray, or lesser, mouse lemur is a fast-moving species described as agile and plastic in its behavior by Oxnard et al. (1990) and moving frequently through very thin branches (Petter 1962). It is described as frequently scurrying, including during vertical ascent, and often leaping (Oxnard et al. 1990). The descending abilities of *M. murinus* have been directly assessed by Shapiro et al. (2016) who found very high frequencies of asymmetrical gaits in this species, which appears to be common in small animals generally (Dagg 1973). *Microcebus* is often invoked as a model of early primate locomotion (Gebo 2004).

2.2.1.3 Slow Climbers (SC)

Slow Climbers (SC) are arboreal primates that are characterized by slow locomotion used in part of a cryptic strategy. These primates typically have relatively high IMIs amongst the above branch arboreal quadrupeds, ranging from the 80s to 90s (Fleagle 2013).

Family Lorisidae

Nycticebus pygmaeus (Bonhote 1907)

The pygmy slow loris is a nocturnal primate that lives in SE Asia, often occupying bamboo forests, forest edges, and dense scrub areas (Nekaris and Bearder 2007). *N. pygmaeus* is reported to eat insects as well as nectars and gums, the later suggesting access to tree trunks despite lacking claw-like nails that appear in other exudate feeding primates (Hamrick 1998; Nekaris and Bearder 2007).

2.2.1.4 Vertical Clingers and Leapers (VCL)

Vertical Clingers and Leapers (VCL) are primates specialized for leaping from and landing on vertically oriented supports. VCL primates typically have relatively long legs compared to their arms (Napier and Walker 1967), with IMI's typically being in the range of 55-65 (Fleagle 2013).

Family Indriidae

Propithecus coquereli (Milne-Edwards 1867)

Coquerel's Sifaka is a large bodied VCL primate. Sifakas have been recorded traveling for 10 m within a single leap and often travel in a bipedal hopping fashion when on the ground (Napier and Walker 1967). Granatosky et al. (2016) studied the kinematics of quadrupedal behaviors in this species, which are uncommon, and concluded that *P. coquereli* adopt the typical primate-like diagonal sequence diagonal couplet gait when moving quadrupedally on horizontal supports. *P. coquereli* has been observed to descend from arboreal to

terrestrial substrates using vertical leaps (Wallace et al. 2016). This species possesses the longest arms relative to their legs (IMI = 62) within this sample.

2.2.2 Individual Subject Information

A total of 40 individuals were video recorded at the Duke Lemur Center (DLC) beginning in June of 2015 and ceasing in June 2019. All research was approved by the Duke University Institutional Animal Care and Use Committee (IACUC, protocol registry numbers A122-15-04, A075-18-03). Individuals included in the study successfully participated in two or more research trials (Table 2.1). Individuals were omitted from the study if they were prematurely removed from the experiment after the initial first or second research trials by the DLC technicians (n = 4 individuals), which was done in the case of animals displaying stress inside the research room or not moving on the experimental structure. One individual (VVF2) was included in both the initial pilot study and the full study. The final sample consists of 36 individuals that were used in the data analysis of this study (Table 2.1).

2.3 Experimental Procedure

2.3.1 Pilot Study (2015-2016) Data Acquisition

A pilot study was conducted beginning in 2015. This setup involved a single sized pole for each species (Table 2.2), with diameters selected on the recommendation of the Duke Lemur Center (DLC) staff for each species. Four support orientations were considered: 0°, 30°, 60°, and 90°. Species included in the pilot study (in order of filming) are *Eulemur coronatus* (n = 4), *Varecia*

variegata (n = 4), *Nycticebus pygmaeus* (n = 2), *Microcebus murinus* (n = 4), and *Daubentonia madagascariensis* (n = 4).

Research was conducted in the research room of the DLC for *E. coronatus, V. variegata*, *N. pygmaeus*, and *D. madagascariensis*. A large diameter vertical pole with a platform at its top (height 213.4 cm) was connected to either a shorter support or the floor by a PVC pole (Figure 2.2). Support orientation was set using a commercially available adjustable flagpole bracket (United States Flag Store, USA). Supports were coated in a polyurethane finish mixed with sand to increase the roughness of the surface. The total support length was 185 cm long. *M. murinus* was video recorded in a wood framed box, with one side made of a mesh grating and the other a plexiglass panel (Figure 2.3), within their enclosure rooms to prevent escape of the animals. The support, which was wood coated in the same polyurethane finish/sand mixture, was angled between two platforms and spanned approximately 91.4 cm. The box was rotated 90° from what is pictured in Figure 2.3 to make 60° and 90° support orientations possible.

Nocturnal species (*N. pygmaeus, D. madagascariensis*, and *M. murinus*) were filmed under red lighting using a Sony Handycam model HDR-SR11 (Sony Corporation, Tokyo, Japan) at 60 frames per second (fps). Diurnal species (*E. coronatus, V. variegata*) were filmed under fluorescent lighting using a GoPro Hero 3+ (GoPro, Inc., San Mateo, CA; USA) at 120 fps. All GoPro cameras used in this study were modified by Back-Bone (Back-Bone, Ottawa, ON) to allow for

the use of interchangeable lenses on the camera without a fish-eye distortion of the image.

2.3.2 Main Study (2017-2019) Data Acquisition

The main study was conducted beginning in 2017. Not all individuals from the original study were available for research for the second study. In addition to the pilot study sample species, *Lemur catta, Propithecus coquereli*, and *Cheirogaleus medius* were added to the sample while *Eulemur mongoz* was used in place of *Eulemur coronatus* because of the skittish nature of the later within the research space during the pilot. These two *Eulemur* species are broadly similar in their ecology and morphology.

In this study, seven support orientations 0°, 15°, 30°, 45° 60°, 75°, and 90° were tested using a single support diameter for each species. This diameter was determined by the foot span of each species, which was collected from living animals undergoing routine veterinary work whenever possible. For smaller species, the foot was pressed against a plexiglass panel with scale against it and photographed (*Eulemur mongoz*, *Cheirogaleus medius*, *Microcebus murinus, Nycticebus pygmaeus*); for larger species (*Lemur catta*, *Propithecus coquereli*), individuals that happened to be sedated for other procedures had their feet manipulated to grasp around a paper wrapped pole, a marker was then used to draw the extent of the foot's grasp around the pole. The paper was then removed and measured flat. If there was not an opportunity to measure a species pedal grasp span at a veterinary exam (*Daubentonia madagascariensis*, *Varecia*

variegata), measures were estimated from osteological specimen by summing the measures of the first and fourth metatarsals and phalanges. Additionally, several inked footprints collected from captive individuals or from wild animals in the field and archived by the DLC were made available by Dr. Erin Ehmke; these were measured to verify accuracy of osteological measures.

After pedal grasp span was measured, the pole diameter was selected such that the subtending angle of the first and fourth digits would be approximately 180°. This was considered the 'medium' pole (pedal grasp is approximately ½ of support circumference) and is reported in Table 2.2 for each species. Two additional supports, thin, and thick, were determined using a 270° subtending angle (thin, pedal span is approximately ¾ of support circumference) and a 124° subtending angle (thick, the smallest subtending angle modeled for a single hand grasp by Cartmill 1979). The closest sized commercially available pole for each subtending angle was used in the experiment. The thin and thick support were tested at orientations of 0°, 45°, and 90° in diurnal species and *C. medius* only.

All supports were coated in a mix of polyurethane finish and sand to increase surface roughness. Support length used for large species (> 1 kg) varied from 213.4 to 304.8 cm, while small species (<1 kg) moved on a 121.9 cm long support. Smaller species (*C. medius, N. pygmaeus*) were filmed moving within a plexiglass box (Figure 2.4) that was 121.9 x 60.9 x 60.9 cm. As in the

pilot study, this box was rotated 90° to accommodate the steeper (> 45°) support orientations.

Two vertical poles with platforms connected by a PVC pole were setup for *L. catta* and *P. coquereli*, as in the pilot. For the 0°, 45°, and 90° conditions, all three support sizes were set up in the space at once; this produced an unintended ‘goldilocks’ effect in which animals stuck to a pole that was ‘just right’ on the 45° angle. This effect was not observed at 0° or 90° in which the DLC technicians were able to prompt animals to travel on all three poles at relatively equal frequencies. To account for this, each pole size was then considered individually at the 45° condition for species that would descend such supports headfirst (*L. catta*) and the protocol was changed to film each diameter separately in *V. variegata* and *E. mongoz*.

The research space at the DLC underwent major renovation during the winter of 2017-2018. When research resumed, a new setup was built that complied with the new building requirements for the space. These changes included using a single vertical structural support anchored posteriorly to a concrete wall using threaded steel, and inferiorly using a 5-gallon bucket filled with sand to act as a ballast. A PVC pole was then attached to this and the angle was set using a custom holder (Figure 2.5) that could accommodate varying support diameters and rotate to specific orientations. The PVC pole was then anchored at a second point to the wall using threaded steel to minimize any movement while animals were traveling on the support.

Upon testing individuals (DMF2 and DMF4) on a PVC pole coated with sand (diameter = 6.35 cm), both displayed great difficulty in moving on this support without slipping and appeared to be stressed during transport to and from the research area. Therefore, to test these individuals filming was conducted within their enclosures on straight, natural (wood with bark, with any off-shooting branches removed) supports of a maximum diameter of 6.35 cm. These supports were non-compliant and fixed in place to avoid rolling.

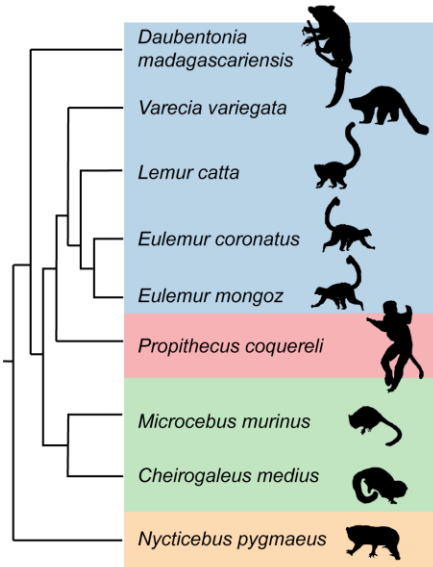
As in the pilot study, nocturnal species (*C. medius, N. pygmaeus*) were filmed under red lighting and diurnal species (*L. catta, P. coquereli, E. mongoz, V. variegata*) were filmed under fluorescent lighting. For these species a GoPro Hero 3+ and/or a GoPro Hero 4 (GoPro, Inc., San Mateo, CA; USA) at 120 fps were used. For *D. madagascariensis*, filming was done on a Sony Handycam model HDR-SR11 (Sony Corporation, Tokyo, Japan) at 60 frames per second (fps) in red lighting.

2.4 Data Processing

All videos were watched from start to finish and notes were taken on all descents observed up to 20 passes per support condition to document frequencies of descending behaviors used. The analysis of these frequencies is further described in Chapter 3.

Videos were then edited into clips of individual bouts of locomotion across the length of the pole using GoPro Studio (GoPro, Inc., San Mateo, CA; USA) or PlayMemories Home (Sony Corporation, Tokyo, Japan) for video shot on the

GoPros or Handycams respectively. These individual clips were saved as individual Audio Video Interleave (*.AVI) files. This was done for continuous bouts (e.g. when the animal did not appear to be coming to a stop), and non-obviously asymmetric strides (e.g. gallops were excluded). From these bouts, frames of footfalls were recorded to calculate temporal gait parameters, which are described in further detail Chapter 4. Strides were digitized with anatomical markers using DLT DataViewer (Hedricks 2008) in Matlab (Mathworks, Natick, MA; USA). From these markers, spatial gait parameters were calculated, which is described in detail in Chapter 5.



Species[1]	Average Body Mass (kg)[2]	Intermembral Index[3-7]	Foot Length /Hindlimb Length[3,7]	Locomotor Category
Daubentonia madagascariensis	M: 2.62; F: 2.49	82.4	32.4	Large Arboreal Quadruped
Varecia variegata	M: 3.47; F: 3.51	72.7	30.1	
Lemur catta	M: 2.21; F 2.21	70	27.9	
Eulemur coronatus	M: 1.69; F: 1.62	69	28.0*	
Eulemur mongoz	M: 1.63; F: 1.61	71.7		
Propithecus coquereli	M: 3.70; F: 4.28	62	27.1*	Vertical Clinging and Leaping
Microcebus murinus	M: 0.125; F: 0.111	72	33.3*	Small Arboreal Quadruped
Cheirogaleus medius	M: 0.283; F: 0.282	68.8	32.6*	
Nycticebus pygmaeus	M: 0.462; F: 0.376	89.2	32.2	Slow Climbing

Figure 2-1: Primate sample included in the present study.1. **Cladogram adapted from the phylogeny of McLain et al. (2012), 2. Species average male (m) and female (f) body mass, using captive data whenever available, from Smith and Jungers (1997); Species average intermembral index ([humeral + radial length]/[femoral + tibial length]) and foot length/hindlimb length as reported in 3. Jouffroy and Lessertisseur (1979), 4. Fleagle (2013), 5. Jungers (1979), 6. Ravosa et al. (1993) and 7. Streicher (2007). * Indicates when specific species level information was unavailable, in these cases, a genus average was used.**

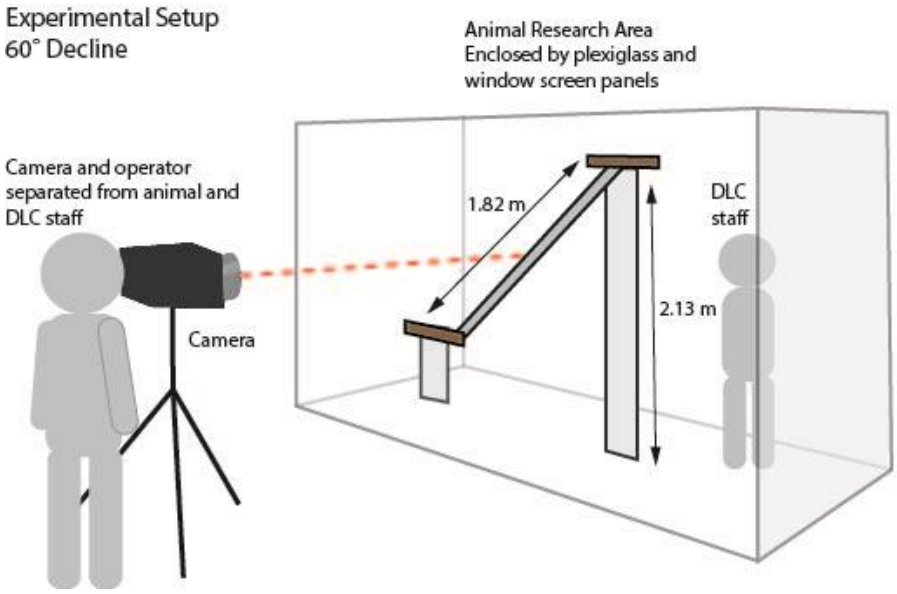


Figure 2-2:Photograph and diagram for room setup used in pilot study for larger bodied animals.

Figure 2-3: Photograph of structure used for filming *M. murinus* in the pilot study.

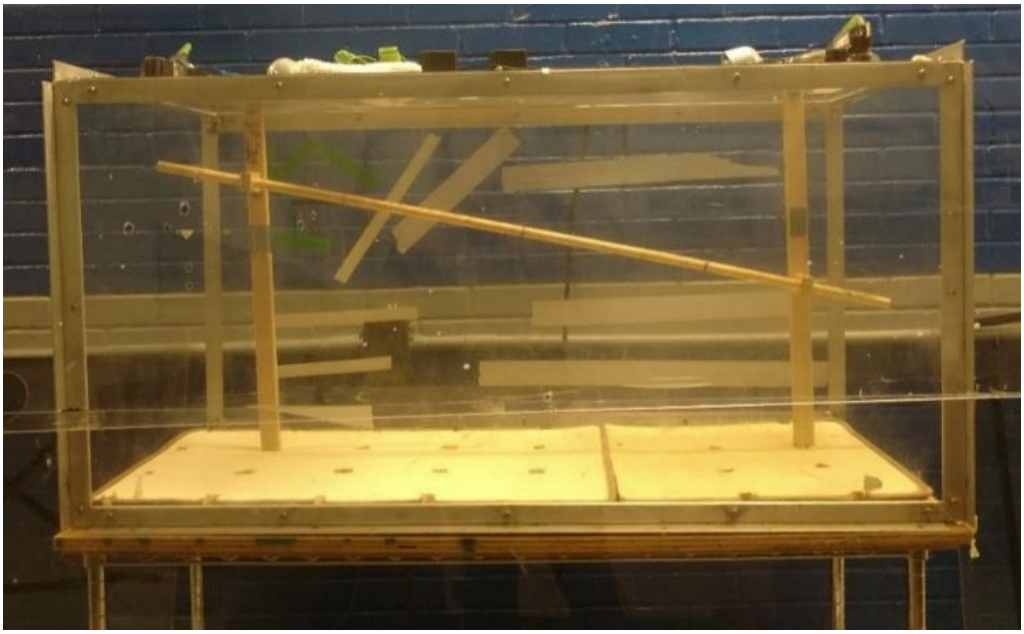


Figure 2-4: Photograph of experimental setup for *Cheirogaleus* and *Nycticebus* during main study.

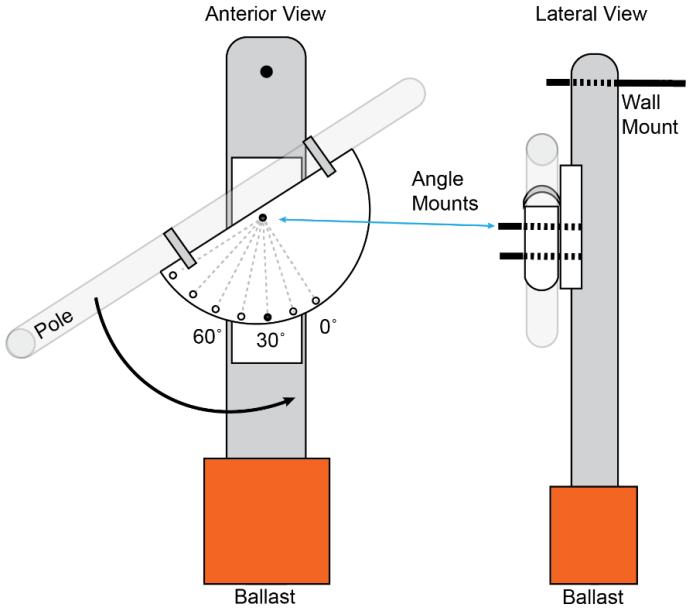


Figure 2-5: Photograph and diagram of experimental setup for primates > 1 kg in main study.

Table 2.1: Individual primates included in the sample. Age and mass for each individual correspond to the age at the start of their participation in the pilot and/or main experiment, and mass at the most recent official weigh in prior to the start of the experiment. Two individuals (DMF1 and VVF2) were sampled in both the pilot and main studies.

Animal ID	Species	DLC Name and ID	Date of Birth	Dates filmed (initial month, year)	Age (yrs)	Mass (g)
CMM1	*Cheirogaleus medius*	Crow 7124	8/9/2012	05/2018	5.7	190
CMM2	*C. medius*	Jaegar 7125	8/9/2012	05/2018	5.7	210
CMM3	*C. medius*	Domestic Chicken 7161	6/26/2013	05/2018	4.8	208
CMF1	*C. medius*	Kiwibird 7190	8/7/2014	05/2018	3.7	251
MMF1	*Microcebus murinus*	Wasabi 7030	5/30/2008	03/2016	7.8	97
MMF2	*M. murinus*	Snap Dragon 7052	7/3/2011	03/2016	4.6	100
MMM2	*M. murinus*	Hurtleberry 7038	6/10/2010	03/2016	5.8	73
MMM3	*M. murinus*	Gobo 7110	7/3/2012	03/2016	3.7	67
DMF1	*Daubentonia madagascariensis*	Lucrezia 6786	7/20/2001	09/2016; 05/2019	15.1 17.8	3080; 2980
DMF2	*D. madagascariensis*	Elphaba 7071	11/29/2011	09/2016	4.8	2550
DMF3	*D. madagascariensis*	Ardrey 6674	4/15/1996	09/2016	20.3	2860
DMF4	*D. madagascriensis*	Medusa	10/14/2003	05/2019	15.6	2880
DMM1	*D. madagascariensis*	Grendel 6975	5/23/2013	09/2016	6.3	2780
ECM1	*Eulemur coronatus*	Xonsu 7150	4/21/2013	06/2015	2.2	1540
ECM2	*E. coronatus*	Geb 6478	4/6/1992	06/2015	23.2	1400
ECF1	*E. coronatus*	Tasherit 6800	4/15/2002	06/2015	13.2	1610
ECF2	*E. coronatus*	Aria 7149	4/21/2013	06/2015	2.2	1420
EMF1	*Eulemur mongoz*	Maddie 6907	6/2/2006	08/2018	12.2	1340
EMM1	*E. mongoz*	Ignacio	4/11/2015	08/2018	3.3	1660

		7208				
EMM2	*E. mongoz*	Mico	5/3/2014	08/2018	4.3	1440
		7182				
LCM1	*Lemur catta*	Licinius	3/17/1993	04/2017	24.0	2320
		6528				
LCM2	*L. catta*	Teres	3/23/1995	04/2017	22.0	2480
		6622				
LCF1	*L. catta*	Persephone	4/25/2005	04/2017	11.9	2660
		6861				
LCF2	*L. catta*	Tellus	3/18/2004	04/2017	13.0	2680
		6831				
VVM1	*Varecia variegata*	Herschel	5/21/2013	03/2016	2.3	3180
		7155				
VVM2	*V. variegata*	Magellan	5/24/2010	10/2015	5.3	3720
		6976				
VVF1	*V. variegata*	Halley	5/21/2013	10/2015	2.3	3080
		7154				
VVF2	*V. variegata*	Kizzy	4/17/2005	10/2015;	10.5;	4020;
		6917		10/2018	13.5	3820
VVM3	*V. variegata*	Rees	5/17/2013	10/2018	5.3	4500
		7151				
VVM4	*V. variegata*	Amor Jr.	5/17/2013	10/2018	5.3	3820
		7152				
NPM1	*Nycticebus pygmaeus*	IO Moth	9/17/2010	11/2015	5.1	620
		2936				
NPF1	*N. pygmaeus*	Flea	12/09/1997	11/2015	17.9	460
		2923				
NPF2	*N. pygmaeus*	Junebug	1/7/2007	01/2019	12.0	546
		2932				
PCM1	*Propithecus coquereli*	Gordian	12/17/1995	04/2017	21.3	3360
		6650				
PCF1	*P. coquereli*	Bertha	2/18/2011	04/2017	6.1	4360
		6987				
PCF2	*P. coquereli*	Beatrice	12/19/2012	04/2017	4.3	4720
		7131				

Table 2.2: Support diameters used for experimental data collection.

Species	Pilot Support Diameter (cm)	Thin Support Diameter (cm)	Medium Support Diameter (cm)	Thick support Diameter (cm)
C. medius	N/A	0.9525	1.5875	2.2225
M. murinus	1.905	N/A	N/A	N/A
D. madagascariensis	3.81	N/A	6.35	N/A
E. coronatus	3.175	N/A	N/A	N/A
E. mongoz	N/A	3.175	3.81	6.35
L. catta	N/A	3.175	5.08	8.89
V. variegata	3.81	5.08	7.62	9.52
N. pygmaeus	3.175	N/A	3.175	N/A
P. coquereli	N/A	3.175	6.35	9.52

Chapter 3: Use of Headfirst Descent and Support Orientation

3.1 Introduction

Headfirst descent of vertical supports in arboreal mammals may be facilitated by highly mobile ankle joints which allow animals to rotate the hindfeet into a position that allow the claws to interlock with the support (Jenkins 1974; Cartmill 1974b, 1985; Jenkins and McClearn 1984). This specialized ability, also known as pedal inversion, appears to be present in many clawed arboreal specialists across several extant taxonomic groups including carnivores, rodents, marsupials, and euarchontans (Jenkins 1974; Cartmill 1974b, 1985; Jenkins and McClearn 1984). Jenkins and McClearn (1984) hypothesized based on fossil and comparative evidence that the earliest mammal ancestors, the cynodonts, might have had a highly mobile ankle (Jenkins 1971), and that further specializations for hindfoot reversal have independently evolved, and possibly been lost and re-evolved, in certain extant groups of mammals (Szalay 1984; Jenkins and McClearn 1984). The repeated convergent evolution of this trait highlights the importance of headfirst descent as a potential selective pressure in arboreal non-volant mammals.

Hindfoot rotation is present in the closest extant relatives of primates, scandentians, which can fully reverse the hindfoot (Jenkins 1974) and dermopterans, which are capable of a high degree of eversion and inversion of the foot (Youlatos et al. 2019). It is inferred from fossil tarsal elements that the

oldest known euarchontan, *Purgatorius*, was also capable of some degree of pedal inversion (Chester et al. 2015). From this evidence, it appears likely the common ancestor of primates and other euarchontans was capable of headfirst descent via claw-interlocking

In the morphological evolution of primates, claws were lost and replaced with nails, likely starting with the hallux (Bloch and Boyer 2002), and then possibly proceeding to digits IV and V (Boyer et al. 2018), and later extending out to the rest of the digits, perhaps to the exclusion of the pedal digit II, or the grooming claw, of strepsirrhines (Soligo and Müller 1999; Boyer et al. 2018). With the derivation of nails – the selective pressure for which is actively debated (Cartmill, 1974a, 1974b; Sussman and Raven 1978; Soligo and Martin 2006) – the earliest primates would have lost their primitive ability to interlock with supports. This might have excluded them from use of relatively large diameter supports, and limited the types of supports they could descend headfirst.

For an extant primate to descend headfirst, it must establish a secure grasp of a support using its feet, which requires a foot that is both large enough to subtend a substrate, and strong enough to actively support the body weight of the animal. Currently, there is little known about ability to use headfirst descent by primates, other than that there appears to be an inverse relationship between body mass and the use of this behavior in the wild (Curtis and Feistner 1994). Many alternatives to headfirst descent used by primates are described by Hunt et al. (1996), but the comparative frequencies of descending behaviors or the

contexts in which they are employed by primates is not well documented in the existing literature.

In a comparative study of strepsirrhine locomotion, Gebo (1987) makes note that lemurs “climbed downward tail first but would on occasion climb downward head first” (p. 275, describing *Eulemur mongoz*). Gebo (1987) also notes that *Propithecus* descends tail first, while lorisiforms and cheirogaleids descend headfirst, however, Gebo (1987) did not describe the types of supports upon which these behaviors were observed, and descending behaviors were not a focus of that study. While Gebo (1987) provides important insight into the diversity of behaviors exhibited by many strepsirrhine species, the support orientations on when specific descending behaviors are employed by species remains poorly understood.

Curtis and Feistner (1994) observed *Daubentonia* descending vertical supports headfirst and note that such behavior is unusual for a primate of that size (approximately 2.5 kg). However, as in Gebo (1987), there is no information on support size in Curtis and Feistner (1994) to link the use of observed headfirst and tail first behaviors to specific support dimensions. From the literature there is consensus that larger primates do not use vertical headfirst descent, but there isn’t a clear sense of how big a primate must be for this to apply, or how large primate species might transition into different descending behaviors as supports range in orientation from horizontal to vertical.

This question of what determines headfirst descending ability in extant primates bears on interpreting scenarios of primate evolution in which ancestral primates are envisioned as very small at 10 g (Gebo 2004), mouse lemur-sized around 100 g (Boyer et al. 2013a), or above 1 kg in the realm of *Eulemur* sized (Soligo and Martin 2006). As body size increases, the safety factors of skeletal strain and muscle strength scale allometrically (Fleagle 1985; Biewener 1989), and so hypothetically a small animal may exert a relatively stronger grasp for its size compared to a larger animal. The locomotor effects of transitioning from interlocking claws to grasping with nails are therefore assumed to be experienced differently in a 10 g early primate compared to a 1 kg early primate (e.g. Boyer et al. 2013a).

After the loss of claws, primates would have had to use mechanisms other than interlocking for getting down through arboreal habitats including headfirst descent via grasping, tail first descent, or leaping, which again might be employed at different frequency in a very small primate compared to a larger one. The alternative descending behaviors that might have emerged could have in turn prompted further selection away from the ability to headfirst descend (e.g. selection towards specialized leaping with longer hindlimbs could increase the risk of forward pitch on declines).

This study will test the hypothesis that there is a body mass limit on headfirst vertical descent in primates, using the body mass of *Daubentonia* as the prediction for the heaviest mass at which this behavior will occur as has been

suggested by Curtis and Feistner (1994). Further, this study will test if the angle of support orientation for which species abandon headfirst descent is correlated with mass across a comparative sample, with the expectation that as mass increases, the support orientation which an animal will navigate headfirst should decrease. Finally to evaluate the influence of characters hypothesized to affect the ability of a species to descend headfirst – such as an individual's mass, age, intermembral index, etc. – a Bayesian modeling approach will be used to compare the relationship between these variables and the predicted probability that an individual animal will descend a specific support headfirst.

3.2 Methods

The experimental setup and details on individual animals included in this study are described in the previous chapter. Video recordings of experimental sessions were scored for the methods of descent observed as an animal crossed a necessary distance to reach a food reward. Cases in which an animal did not cross the necessary distance – e.g. an individual descended half way down the support and then turned to ascend back to their starting position – were omitted as incomplete bouts.

Complete bouts were scored as headfirst descent, tail first descent, or other. 'Other' behaviors include leaping or dropping a majority of the distance needed to get to the food reward, and various patterns of descending that were not entirely headfirst or tail first in progression. These are identified using the terminology from Hunt et al. (1996) when applicable and described in detail for

each species in the results section. Method of descent was recorded for the first twenty complete descents an individual performed on a given support condition. Instances in which an animal was brought into the experimental room but did not engage with the support are recorded as 0's for all behaviors to indicate that the animal was present for the trial but did not successfully complete the task. Support conditions for which an animal was excluded from that portion of the experiment, usually based on stress displays in a previous session, are omitted from behavioral frequency tables.

In June 2017, two species (*Lemur catta, Propithecus coquereli*) were followed as they free-ranged through forested habitats at the Duke Lemur Center (DLC). Two forested habitats were visited, each containing a family group of each species. Individuals were followed for periods of approximately three hours a day in the mornings around the animals scheduled feeding time. Both species were signaled by a DLC keeper to come to a common feeding area, making it easy to find and follow the animals within the enclosure for the observer. One species would be followed pre-feeding for an hour and a half, and the other species would be followed post feeding for an hour and half; it was alternated whether *L. catta* or *P. coquereli* was followed pre- or post-feeding each day based on the ability of the researcher to initially locate the animals within the enclosure. This was conducted over the course of a week and totals approximately 15 hours of observation.

Observations were audio recorded and later reviewed; all individuals in the view of the researcher were followed for periods of at least 10 minutes before switching between conspecific groups, if applicable, and all observed descending behaviors were noted along with a description of the support the animal was traveling on. The purpose of this observational period was to document the descending behaviors used by individuals traveling on natural supports to verify that behaviors observed in the indoor experiment were used on similarly oriented natural supports

3.2.1 Statistical modeling of probability of headfirst descent

Behavioral outcomes (headfirst or not headfirst) for every video recorded bout (n = 3139) were used to make Bayesian multilevel (or mixed effect) models that predict the probability that an individual would descend a given support headfirst when given information on species anatomy and support geometry (e.g. diameter and orientation). A Bayesian multilevel model is a desirable approach for the present dataset because it can accommodate repeated sampling from the same individuals, uneven sample sizes, and variation within and between species (McElreath 2015).

All models were created using the Stan computation framework (http://mc-stan.org/) through the '*brms'* package for R (Buerkner 2017). All models used the Bernoulli family of tests, which models the probability of an outcome being a 1 or 0; this was chosen in favor of a zero-inflated test because each zero represents a non-headfirst descent, and not a lack of observed data. Each model was tested

using 4 chains of 1000 iterations each. Model comparison was conducted by comparing the Widely Applicable Information Criterion or WAIC (Watanabe 2010) using the '*loo'* package for R (Vehtari et al. 2019).

Bayesian multilevel models allow for the intercepts and/or slopes of specified groups (random effects) to vary within the model (McElreath 2015); individuals and species were treated as random effects in all models considered in the present study. Fixed effects, which are the predictor variables in the model, included grasp-type as identified by Gebo (1985), ln(mass), relative age of the individual (calculated as the individual's age at the start of participation in the experiment as a proportion of species median longevity in captivity, with data on each species from Zehr et al. 2014), species average intermembral index, species average foot size as a proportion of hindlimb length as reported by Jouffroy and Lessertisseur (1979), and the support size relative to mass. The relative support size measure was adapted from Stevens (2003) method for standardizing support diameters to mass and was taken as the actual support diameter over the cube root of the individual's body mass.

All fixed effects were tested for correlation, using the 'cor' function in base R, to calculate the Spearman's correlation coefficient (ρ) between variables, reported in Table 3.1. It was found that the grasp types identified by Gebo (1985) were highly negatively correlated (ρ = -0.86) with foot proportion, such that strepsirrhines with the primitive "V" grasp-type tended to have long feet relative to hindlimb length compared to lemuriforms that possessed a derived "II" grasp-

type. This may reflect the underlying structure of the sample: V grasp-type is heavily represented by the smallest body masses and the II grasp-type is skewed towards higher body masses. Lemelin and Jungers (2007) report that phalanges tend to scale isometrically and the plantar region scales with positive allometry in strepsirrhines which may have further influenced this correlation. Given these high correlations of grasp-type with both foot proportion and ln(mass), it was excluded as a fixed effect in the modeling process.

Fixed effects were centered to a mean of zero and scaled using standard deviation in R for more direct comparisons between the variables; the raw means and standard deviations for each fixed effect used to scale these variables are reported in Table 3.2. Priors inform the posterior probability distribution for any fixed effect and can be used to give relatively more or less weight to a fixed effect within a model (McElreath 2015). Weakly informative priors were selected because they are considered conservative, and at large sample sizes allow the maximum likelihood distribution to shape the posterior distribution (McElreath 2015). Priors were set for each scaled fixed effect as being normally distributed with a mean of 0 and standard deviation of 2. Very strong priors were not used because this would risk overfitting the model to the existing data and because there was no *a priori* reason to assign different weights to the fixed effects. This setup allows the best fitting model's parameters to reveal the relative strength and direction of each predictor's influence on the outcome.

Support orientation was treated as a random effect for which the slope of the mass term vary could vary, that is that the strength of the effect of mass in the model would vary on 15° support orientation compared to a 75° support orientation. Treating support orientation as a random effect with varying slope for mass was found to produce the best fit according to WAIC when compared against models that treated support orientation as a continuous fixed effect, a categorical fixed effect, and a random effect for which intercept but not slope was allowed to vary. This decision to treat support orientation as a random rather than fixed effect was also influenced by the lack of knowledge of how this effect scales in a way that could be built into the model, that is the differences in mechanical environment between a 15° and 30° support compared to a 30° and 45° support may change as available friction decreases. Given this uncertainty, and that only a few selected support angles were tested out of a possible range from horizontal to vertical, allowing orientation to act as an experimental condition rather than a strict fixed effect lends more flexibility to this model. Individuals and taxonomic groupings were also treated as random effects for which intercepts, but not slopes, were permitted to vary.

3.3 Results

3.3.1 Summary of Major Patterns of Headfirst Descent

All primates under 1 kg used headfirst descent when travelling on all support orientations (Figure 3.1). Within species under 1 kg, there was very little behavioral variation with respect to individual age and weight. As individuals in

these species (*Cheirogaleus medius, Microcebus murinus*, and *Nycticebus pygmaeus*) switched from ascending the pole to descending, they were all capable of holding onto the support with the hind limbs and turning around rather than having to go to a horizontally oriented platform the pole was mounted on.

In species above 1 kg, all arboreal quadrupeds except for *Lemur catta* engaged in some headfirst descent of supports between 60 and 90°, however the frequency of observed headfirst descent varied within species. *Propithecus coquereli*, the only vertical clinger and leaper in the study, did not engage in any headfirst descent of supports steeper than 30°, and heavier individuals within this species did not use any headfirst descent on any declined support.

The body mass limit of approximately 2.5 kg on headfirst vertical descent suggested by Curtis and Feistner (1994) was not supported by the present study. The heaviest individuals that continued to perform headfirst vertical descent were *Varecia* that weighed up to 3.82 kg. No individuals over 4 kg regardless of age did any headfirst descent of supports steeper than 60°.

Generally, young adults of relatively low mass for their species were more likely to engage in headfirst descent of support steeper than 60° than conspecific young adults of high mass. Adults of all large species, except for *Daubentonia*, did not perform headfirst descent on the 75° or 90° supports regardless of whether they were heavier or lighter than conspecific young adults that engaged in this descent style, suggesting that body mass alone may not be a physical limit on headfirst descending behavior.

The trend of decreasing headfirst descents with increasing age has been observed in much larger primates including orangutans (Thorpe and Crompton 2006) and chimpanzees (Sarringhaus et al. 2014). These studies have attributed changes in descending behaviors to changes in body mass; the results presented here suggest young adults of large species may be more plastic in their descending behaviors than older individuals in these large species (*E. coronatus, E. mongoz, V. variegata*).

3.3.2 Species specific descent descriptions

3.3.2.1 Cheirogaleus medius

Cheirogaleus medius descended all supports headfirst and above branch (Table 3.3). Animals were observed to leap within the confines of the experimental box (Figure 2.4), but generally this was not done from the support to obtain a food reward. Animals were also observed to turn from ascending to descending while on the support, such that they were always moving headfirst, and did not engage in any sort of tail first or sideways behaviors for descending supports of any orientation. When individuals were tested on the steepest supports, there was a larger flat horizontal supportive structure located superiorly, and individuals tended to stay idle on this and generally avoided the flat bottom of the experimental box. Individuals in the present experiment did not appear to actively avoid any of the various pole diameters.

These observations were consistent with the literature on this species; Gebo (1987) reported that *C. medius* descended supports headfirst. Petter

(1962) described wild *C. medius* as preferring thicker branches and horizontal supports, which individuals in the present experiment appeared to prefer when such supports were available to them.

3.3.2.2 Microcebus murinus

Microcebus murinus descended all supports headfirst and above branch (Table 3.4). Leaping was observed within the experimental box (Figure 2.3), and frequent climbing occurred the grating that made up the back wall of the box. On the 30° support, two individuals (MMF1, MMM2) engaged in occasional dropping from the top of the support to get to the floor of the box, though this was not observed on the 60° and 90° supports, which would have required a greater dropping distance.

When descending vertically, all individuals traveled headfirst however one individual, MMF1, frequently stopped midway down the support and rapidly turned to adopt an upright posture. At 7.8 years, MMF1 was the oldest *Microcebus* included in the sample. When the other individuals (MMF2, MMM1, and MMM2) would pause on the vertical support, they would do so in the direction they were traveling in (e.g. head down when descending). These observations appear consistent with Oxnard et al. (1990) which describes *M. murinus* as frequently engaging in scurrying and leaping behaviors.

3.3.2.3 Daubentonia madagascariensis

Daubentonia madagascariensis individuals used only headfirst descent on all supports of 15° to 45°, and frequently on the 60° decline (Table 3.5, Figure

3.2). Non-headfirst behaviors included tail first descent, which was used at low frequency on non-vertical supports, suspensory postures (only observed once in DMF3), and a third, more common descending behavior in which the body is held perpendicular to the support while the right and left forelimbs, and right and left hind limbs move together as pairs. Downward progression in this style of above-branch descent is achieved by swinging the limb pairs, and largely keeping the axis of the body orthogonal to the support. This mode of locomotion does not appear to be described within the primate locomotor systematic summary by Hunt et al. (1996), in that it appears to be distinctive from sideways vertical descent ("The body is held at right angles to the long axis of the support, the downside fore-and hind limbs provide most of the braking support", Hunt et al. 1996, pg. 379) based on the swinging, as well as distinctive from head-first bounding descent ("Both forelimbs move together, followed by both hind limbs. Hands and feet act as brakes, may grade into a pronograde slide," Hunt et al. 1996, pg. 379) based on the orthogonal position of the body. Instead, this behavior appears intermediate between the distinct descending styles described in Hunt et al. (1996). This intermediate behavior will be referred to as a 'sideways swing' since as a form of descent it does not appear to have been named in any other literature. It is most like the behavior 'transaxial bounding' described for platyrrhines traveling on horizontal and weakly inclined supports by Rosenberger and Stafford (1994), although in that behavior one hind foot is described as landing between the forelimbs and in the present behavior this landing

configuration was not observed. A sideways swing progression (Figure 3.3) was only observed in the context of very steep and vertical supports and was used more often by individuals traveling on the natural wooden support than the PVC support.

Individuals generally avoided the experimental PVC vertical support in the pilot study (diameter = 3.81 cm) or traveled on it primarily using tail first descent. Despite the presence of sand on the surface of the support, it did appear that animal hands and feet were slipping on the experimental PVC pole, indicating that the reduced friction might have been an important factor in their descent locomotion on this support. Individuals also descended on a vertical PVC supporting structure (diameter = 8.89 cm) that was present in the research space but not the focus of the experiment, primarily tail first, but headfirst on one occasion (DMM1). Headfirst descent on 75° and 90° was observed at relatively high frequency on the natural support (Figure 3.2). The only ‘other’ behavior observed in individuals descending the natural support was sideways swinging, which was used at a relatively higher frequency than tail first descent on the vertical support.

Daubentonia is reported to frequently descend vertical supports headfirst in the wild or in free ranging environments (Pollock et al. 1985; Curtis and Feistner 1994; Ancrenaz et al. 1994). It has been suggested by multiple authors that this headfirst descent is aided with claw interlocking, since *D. madagascariensis* has claw-like nails (Tattersall 1982; Tilden 1990; Ancrenaz et

al. 1994). While interlocking was not a focus of the present study, zoomed in video footage (Figure 3.4) does not appear to support the hypothesis that interlocking was used by *D. madagascariensis* in the experiment. Instead *D. madagascariensis* appeared to grasp the support with the hallux in opposition to the four other digits and was not observed to hold the foot in a rotated position that might have enabled any interlocking. This, and the observation of at least one headfirst descent of a PVC pole, suggest that *D. madagascariensis* can exert a pedal grasp capable of supporting its body mass on vertical supports.

D. madagascariensis possesses what Gebo (1985) identified as a primitive grasp-type for strepsirrhines based on the osteological arrangement of its foot. The derived grasp-type he identified was hypothesized to be for vertical support use in relatively large arboreal Indriids and lemuriforms (Gebo 1985). Contrary to the predictions of this hypothesis, *D. madagascariensis* was the only species above 1 kg in this study that regularly used headfirst descent as adults on vertical supports. This suggests that the functional significance of grasp variation in strepsirrhines should be revisited with more behavioral and myological data for *D. madagascariensis*, which was absent from Gebo's (1985) original analysis.

3.3.2.4 Eulemur coronatus

Eulemur coronatus was observed to engage in headfirst descent on all supports (Table 3.6, Figure 3.5). Tail first descents were observed beginning with the 60° support. All individuals used some tail first descents on the vertical

support, with older individuals (ECF1, age 13.2, mass = 1.61 kg; ECM2, age 23.2, mass = 1.4 kg) using this behavior exclusively (Figure 3.5). Other behaviors used by this species were drops, mixing headfirst and tail first progressions within a single descent, and sideways swinging. All the 'other' behaviors were primarily used by the two younger individuals (ECF2, ECM1), and were not as common in the older individuals.

These observations are consistent with field study by Wilson et al. (1989) who observed headfirst vertical descents, bounding descents, and dropping, but at very low frequencies compared to leaping within the canopy. In that study, *E. coronatus* was more frequently moving on horizontal branches rather than on oblique or vertical supports (Wilson et al. 1989).

3.3.2.5 Eulemur mongoz

Eulemur mongoz individuals used headfirst descent exclusively on supports angled at 15° and 30° (Table 3.7, Figure 3.6). On the 45° support individuals continued to utilize headfirst descent, but at different proportions of total behaviors (Table 3.7), EMF1 and EMM2 used headfirst descent exclusively while EMM1, who was the heaviest individual in the *E. mongoz* sample, used a mix of headfirst descent and sideways swinging on the 45° support. On the 60° decline EMM2 continued to use headfirst descent for most passes (75%), while EMF1 and EMM1 ceased using headfirst descent at this angle in favor of tail first descent and sideways swinging.

Headfirst descent of the 75° and 90° supports was only observed in EMM2, at very low frequency (10% observed passes on the largest diameter 90° support, and once after the first 20 bouts of descent of the 75°); the same individual was also observed to use this behavior. Therefore, while headfirst vertical descent is possible in *E. mongoz*, it appeared to be very rare given the experimental conditions.

Tail first descent was reported to be frequently used by captive *E. mongoz* by Gebo (1987). Wild *E. mongoz* were noted to mostly move quadrupedally (78% of observations) and leap (19% of observations), while climbing made up a very small amount of behavior (3% of observations) by Curtis and Zaramody (1999) over a 10-month field study. These observations of both captive and wild *E. mongoz* support the findings of the present study that headfirst descent appears to be very rare in this species as supports become more oblique.

3.3.2.6 Lemur catta

Lemur catta used headfirst descent on supports angled at 15° and 30° (Table 3.8, Figure 3.7). On the 45° decline, a mix of headfirst and tail first descents were observed. The frequencies of these behaviors varied across support sizes, with no *L. catta* engaging in headfirst descent of the thick pole 45° decline (diameter = 8.89 cm). All individuals used some headfirst descent of the moderate (diameter = 5.08 cm) and thin (diameter = 3.175 cm) poles in a 45° orientation. Headfirst descents were not observed on the 60°, 75°, or 90° support orientations by any individuals in this sample.

L. catta frequently engaged in dropping behaviors. Other descending behaviors observed included sideways vertical descents, and descents in which they would progress tail first and then turn to progress headfirst or drop for the rest of the distance at approximately 1 m off the ground. *L. catta* did not engage in the sideways swing behavior observed in *Daubentonia*, *Eulemur*, and *Varecia* during this experiment.

Free ranging family groups of *L. catta* (n = 2 groups) were followed at the DLC for a period of approximately 7.5 hours during June 2017. During this time, *L. catta* were observed to frequently use tail first descents when moving on both thin and thick diameter supports from high in the canopy towards the ground; generally, animals would then drop from supports when they were within 1-2 m above the ground. No free ranging *L. catta* individuals were observed to use headfirst descent of steep or vertical supports.

References to specific descending behaviors exhibited by this species were sparse in the literature, though given their preference for both terrestrial and arboreal substrates, transitioning from tree to ground must make up an important aspect of their locomotion. The observations made in the present study are consistent with observations of frequent leaping as a mechanism of descent (Gebo 1987) and use of tail first descent of a vertical support based on Hosey et al. (1997), who reported that captive *L. catta* descend large diameter man-made piers at a zoo tail first. It is not clear from the literature if this species has ever

been observed using headfirst descent on steep supports (≥60°), or if such behaviors vary with age.

3.3.2.7 Varecia variegata

Varecia variegata used headfirst descent almost exclusively on supports angled at 15°, 30°, and 45° (Table 3.9, Figure 3.8). One individual (VVM1) used quadrupedal suspensory descent on the 30° support, moving in a headfirst direction. No other suspensory behaviors were observed in other individuals, or by VVM1 on steeper supports. On the 60° supports, individuals began to use a mix of headfirst descents and sideways swings on the 3.81 cm diameter support, but not tail first descent, which was observed on the moderate diameter 60° supports (7.62 cm). Vertical headfirst descent was used by multiple individuals on the 90° support; these individuals were all under 4 kg at the time of the experiment and 5.3 years or younger. One individual that used headfirst vertical descent (VVM4) did so on all pole diameters tested, although these represent very few passes (n = 5 total).

Headfirst descent on the 75° or 90° supports was not used by the two largest individuals, VVM3 and VVF2. VVF2 was tested in both the pilot and the second study and changed in mass from 4.02 kg to 3.82 kg between studies, however this weight loss did not appear to result in any increases in headfirst descent on the steeper supports. Instead, during the pilot when tested on a relatively thinner support (3.81 cm) this individual used headfirst descent 100% of the time, compared to only 25% of travel on a larger (7.62 cm) pole, in which tail

first descent was preferred. This individual was the oldest individual in the *V. variegata* sample (age at pilot = 10.5 years, age in full experiment = 13.5 years), and was approaching the median longevity for the species (15.24 years; Zehr et al. 2014) during the second round of observations, suggesting that descending behaviors might subtly change through the lifetime beyond the transition from young adulthood to adulthood.

The observations of the present study are supported by the existing literature on locomotor ecology of *V. variegata*. Captive free-ranging *V. variegata* followed by Pereira et al. (1988) at the DLC were reported to often descend from arboreal supports by bipedally suspending themselves and then bimanually grasping or dropping onto an inferior arboreal support. However, in the case that such horizontal or oblique supports were not present, *V. variegata* were observed to engage in vertical tail first descent and headfirst descent, although the later appeared to only be used when travelling short distances (Pereira et al. 1988). Another behavior in which *V. variegata* descended vertically is described by Pereira et al. (1988) as:

> "On a trunk without branches, a ruffed lemur initially descended feet first while looking back over its shoulder. Its orientation usually changed so that the long axis of the body became almost horizontal. From this position, the hands were released, dropping the upper body below the hips. The hands regrasped the trunk and the feet released, dropping the hips lower than the shoulders before regrasping the trunk. This manner of progression often continued for several meters of descent." (Pereira et al. 1988, pg. 7).

Pereira et al. (1988) did not give a name to this descent, however it appears to be the same 'sideways swing' behavior also observed in *D.*

madagascariensis and *Eulemur* species in this experiment. This behavior may be more common in highly arboreal quadrupedal lemurs of large body size than previously appreciated by the literature.

3.3.2.8 Nycticebus pygmaeus

Nycticebus pygmaeus used headfirst descent on all supports (Table 3.10). No leaping was observed in this species. One individual (NPM1) occasionally engaged in suspensory postures, and in brief stints of tail first descent, as well as tail first ascent of the vertical pole. Both tails first behaviors appeared in the context of the individual backing away from a glove used by the DLC technician – a large welding glove used to handle the animals and prevent bites – and were not used in pursuit of a food reward, and only maintained for very short distances. Tail first behaviors were not observed in this animal when the glove was removed from view.

While most researchers agree that lorisids typically do not leap (Gebo 1987; Oxnard et al. 1990; Sellers 1996), it is reported that wild *N. pygmaeus* quadrupedally run and engage in what Nekaris and Bearder (2007) characterize as ‘mini-leaps’ as a gap-crossing mechanism. Duckworth (1994) characterized *N. pygmaeus* as appear more like *Microcebus* than *Nycticebus coucang* in its locomotion. While *N. coucang* was not observed in the present experiment, *N. pygmaeus* did not behave like the two cheirogaleids species, which moved rapidly with frequent changes in direction and leaps. While *N. pygmaeus*

individuals moved at both slow and fast speeds, they did not leap, and did not change direction quickly.

3.3.2.9 Propithecus coquereli

Headfirst descent was extremely uncommon in *Propithecus coquereli*, and two *P. coquereli* individuals (PCF1, PCF2) were never observed to use headfirst descent (Table 3.11). These individuals were relatively large (4.3-4.7 kg) and rarely engaged in above branch quadrupedal behaviors on the horizontal support (n = 1 by PCF1), instead preferring to bipedally run across it. Descending behaviors observed in these two individuals moving on declines included above branch tail first descent, tail first quadrupedal suspensory descents (in contrast to the headfirst quadrupedal suspensory behavior used by *V. variegata*), and bimanual suspension.

The smaller *P. coquereli* individual (PCM1, mass = 3.36 kg) regularly used above branch quadrupedal behaviors on the horizontal pole and continued to use these to travel on the 15° and 30° supports (Table 3.11). On supports of 45° and greater, all *P. coquereli* ceased using above branch headfirst descent, and all individuals used tail first descent for most passes. In comparing the three support diameters at 45°, it was observed that bimanual suspension was also used in addition to above branch tail first descent on the moderate and thin sized poles, but not the thick pole. While *P. coquereli* often engaged in leaping behaviors and bipedal hopping within the research space, they did not often leap or drop from

the top of the experimental structure to the ground secure their food reward during this experiment.

Free-ranging families (n = 2 groups) of *P. coquereli* at the DLC were followed during June 2017 for an observational period of approximately 15 hours. It was observed that when individuals were traveling through dense vegetation, such as moving from one feeding patch to another, they often engaged in tail first descents or bimanually suspended themselves down to lower branches. When moving through more open spaces or travelling longer distances, groups would travel together using leaping between vertical trunks, and bipedal hopping on terrestrial substrates, consistent with the observation of Wallace et al. (2016) that these species often use leaps to move between arboreal and terrestrial supports. This was true of both adult individuals and juveniles. No *P. coquereli* of any age or body size were observed to engage in headfirst descents during this observation period.

3.3.3 Bayesian Modeling of Headfirst Descent and prediction of headfirst descent in ancestral primates

A null model was generated that held taxonomy and individual as random effects acting on the outcome variable, which was whether descent was headfirst or not. Adding the fixed effect of mass alone did not improve on the null model (Table 3.12). Support orientation was tested as fixed and random effect as described in the methods section of this chapter. After this series of models were created, it was found that the model incorporating mass as a fixed effect and

treating orientation as a random effect with varying slope produced the best fit WAIC value (Table 3.12).

Incorporating anatomical effects – intermembral index and foot-to-hindlimb ratio – did not greatly improve the model on their own compared to just mass but incorporating information along with on support diameter with these variables did (Table 3.12). Adding in relative age also improved the model (Table 3.12). The resulting best fit model for is as follows:

> Headfirst = (4.40) – 1.06 (mass) + 1.58 (IMI) – 0.36 (Relative support diameter) – 0.29 (Relative age) + 1.94 (Ratio of Foot length to Hindlimb length)

This formula is based on the estimated coefficients for population level effects, which ignore random effects in the model (orientation, taxonomic identity, and individual identity), for which intercepts could vary (Tables 3.13, 3.14). All predictor variables were all scaled and centered, such that they had a mean of 0, and priors were held constant so that all fixed effects were assumed *a priori* to have the same weight in the model. This allows the estimated coefficients from the resulting model to be directly compared to each other to understand the relative strength of each effect on the predicted outcome. This information could be used to adjust priors in future studies such that mass might be weighted with a stronger prior than effect like age.

In comparing the coefficients for each fixed effect, it appears that the model put the most weight on the relative size of the foot in determining probability of headfirst descent when information on taxonomic identity and support orientation are unknown; having a relatively larger foot increases the model's predicted probability of headfirst descent. Intermembral index was next most influential effect and having higher values for IMI increases likelihood of engaging in headfirst descent. Mass scaled strongly with a negative effect, such that increasing mass decreases the probability an animal will move headfirst. As a population level effect, mass does not appear as strong as IMI and relative foot size which makes sense in the context of not knowing the support orientation and the only animals in the sample that did not use any headfirst descent were *P. coquereli*, a large bodied, relatively small footed (compared to their long hind limbs), low IMI primate.

When the model is given information on support orientation, the effect of mass is altered. Supports of 15° and 30° had positive slopes for mass, which suggests that large species might be more willing to descend these supports headfirst while smaller species such as *M. murinus* may be more likely to use other behaviors, such as leaping, on these supports. As supports reached 45° and steeper, slopes for mass became increasingly negative and greater in magnitude than the other coefficients for fixed terms in the sample (Table 3.14). While the generally heavier weights of captive primates used in this sample could

bias this model, primates within the sample generally fell within the ranges of wild weights for conspecifics reported by Mittermeier et al. (2010).

Finally, the effects of support diameter and age were small; as supports become larger and animals become older, headfirst decent becomes less likely. The present data does not include a large variation in support size – all supports were graspable by a single foot for each species – and age ranges were limited. Therefore, this model should not be extended to considering supports that might be relatively large or behavior in juvenile individuals since these were not sampled.

3.3.4 Reconstructing Descent in Ancient Primates

The best fit model generated from the extant data was applied to predicting the probability of headfirst descent in an early Eocene fossil primate, *Archicebus achilles*, for which enough skeletal material is known to estimate intermembral index (IMI) (55), relative foot length (36.6), and body mass reconstructed between 44 and 56 g (Ni et al. 2013; Dagosto et al. 2018). *A. achilles* was simulated with its known skeletal proportions, and body mass that ranged from 20 to 4000 g in 10 g increments in the model prediction. All simulated *A. achilles* were set to be the average relative age of the extant sample and moving on the average relative pole size.

The model generated the predicted probability of headfirst descent on all support orientations (Figure 3.13), and as the body mass for simulated *A. achilles* rose, the likelihood of such an animal descending steep supports headfirst

decreased. This effect was most pronounced on the steepest supports, 75° and 90°, falling below a 50% probability of headfirst descent on such supports at the highest masses.

Headfirst descent of 15° and 30° supports increased as simulated body mass increased. While it is unlikely that a 4 kg primate would retain the exact skeletal proportions of *A. achilles*, this simulated dataset demonstrates the weight placed on having relatively large feet by the model for predicting headfirst descent on a given support orientation. The predictions generated for this simulated data at relatively high masses is contrasted against how the model predicted descending in *Propithecus coquereli*, a leaper with relatively short feet compared to its hind limb, for which the model estimated a probability of headfirst descent near 0 for supports of 60-90°. It is critical to note that this model considered total foot length, including the distal calcaneus, and not intrinsic proportions of the foot, which might be expected to change how a model would predict probability of headfirst descent.

A. achilles is argued to be a stem haplorrhine (Ni et al. 2013) and is derived in many characteristics compared to what has often been hypothesized for the morphology of the ancestral primate (Schmitt and Lemelin 2002; Sargis et al. 2007; Bloch et al. 2007; Gebo 2011). To consider the effect of body mass on different hypothetical versions of an ancestral primate, data was simulated for primates ranging in mass from 50 to 1000 g in 50 g increments for a series of 4 different IMI values: 60, 70, 80, and 90. Relative foot length, age, and support

diameter were all held at the average for the extant sample (0 when scaled). The model was then used to predict probability of headfirst descent on various declines (Figure 3.12).

As mass increased, the probability of headfirst descent fell, especially on supports of 60° and steeper across all IMI considered. As IMI increased, primates were predicted to be more likely to use headfirst descent on all support types across a larger range of masses. This model predicts that a *Nycticebus*-like ancestor in IMI (90) would have the highest likelihood of descending all support types headfirst across the full range of body masses.

In an ancestor with a more *Ptilocercus*-like IMI (80) (Sargis et al. 2007; Ankel-Simons 2007), the likelihood of headfirst descent was similar on supports of 15-60°, with a decreased likelihood of headfirst descent on very steep and vertical supports, especially as body mass increased. In an ancestor with a more cheirogaleid-like IMI (70) the probability of descending headfirst on supports of 15-45° was high across body masses but decreased on supports of 60-90° as body mass approached 1 kg.

Finally, in a more leaping ancestor (IMI = 60), the probability of headfirst descent was lowest on supports of 15-45° at low body masses. As body mass increased towards 1 kg, the model predicted increased probability of headfirst descent on supports of 15-30°, with a small reduction in probability for 45°. For low body masses, probability of headfirst descent was low on supports of 60-90°

and dropped even more drastically for these support orientations as mass increased.

3.4 Discussion

In this experiment, small arboreal strepsirrhines (< 1 kg) were able to navigate all supports they encountered using headfirst descent. Species of masses greater than 1 kg tended to show more behavioral variability when it came to how they descended, with younger individuals utilizing a more diverse array of behaviors than older individuals, which tended to use tail first descent on declines of 60° or steeper. It is possible that other mechanisms for descending could have been used by any species, such as leaping, but this might have been limited by aspects of the experimental setup such as forces encountered when landing on a non-compliant floor, or the proximity of humans to the animals during the experiment.

Armed with information about the context of headfirst descending in these species, comparative anatomical hypotheses can now be evaluated. Body mass was not the absolute determinant of ability to headfirst descend based on the inter- and intraspecific variation in headfirst descending ability present in this sample. One of the largest species in the sample, *Varecia variegata*, regularly engaged in headfirst descent of vertical supports while the relatively smaller *Lemur catta* ceased headfirst descent above 45°. Within species, it was not always the lightest individuals that utilized the highest frequencies of headfirst descent, but rather the youngest. This is suggestive of anatomical differences

between large species contributing to headfirst descending ability, and it is possible these might be muscular in nature given the changes to behavior with age.

Both *Eulemur* and *Varecia* are observed to regularly engage in bipedal suspensory behaviors (Meldrum et al. 1997), suggesting that they might be more morphologically suited to supporting their weight using their grasping feet while descending a thin support than a similarly sized species such as *Lemur*, which tends to show shorter foot proportions than more highly arboreal species (Ward and Sussman 1979). Within *Varecia* and *Eulemur*, it also appeared that headfirst descending diminished with age and increases in body mass, both factors of which could conceivably diminish pedal grasping ability. Hind limb suspension ability alone is unlikely to enable headfirst descent given the near absence of this behavior in *P. coquereli*, which regularly employs suspended postures (Meldrum et al. 1997).

Daubentonia, which is reported to regularly headfirst descent vertical supports of varying size in the wild, was observed descending a natural wood support headfirst, but descended PVC supports tail first. It has been suggested that claw like nails help facilitate headfirst descent in *Daubentonia* (Tattersall 1982; Tilden 1990; Curtis and Feistner 1994; Ancrenaz et al. 1994). If *D. madagascariensis* does use interlocking, it would explain a lack of headfirst descent on the vertical PVC pole.

However, in a previous experimental study of descent in this species, Krakauer et al. (2002) found no evidence that *Daubentonia* was interlocking with natural supports. Further, Pollock et al. (1985) observed wild *Daubentonia* vertical descending headfirst on bamboo, which may also be a support in which claws have trouble interlocking with (Cartmill 1974b). Analysis of foot postures used by *D. madagascariensis* during descent of the natural support in the present experiment did not support the hypothesis that interlocking was being used. Instead it appeared that *D. madagascariensis* was grasping the support (Figure 3.4); the PVC poles used in the present experiment might have been too slippery for individuals to securely grasp. This suggests characteristics of volar skin in *D. madagascariensis* play a larger role in establishing a secure grasp than the possibility of interlocking (Cartmill 1979).

It has been hypothesized that lemuriforms have derived foot anatomy that is better suited for vertical grasping at larger body masses by Gebo (1985) than the primitive arrangement shared by *Daubentonia*, lorisiforms, and cheirogaleids. The observations of this experiment do not appear to support this hypothesis. While the derived grasp-type identified by Gebo (1985) may improve static vertical clinging at large sizes or only in upright positions (neither of which are addressed in the present study), it was the species with this grasp-type – *Eulemur, Lemur, Varecia, Propithecus* – that showed the most compromised ability to descend supports headfirst as adults, a behavior that requires a strong pedal grasp.

When considering this observational data in a multilevel Bayesian model, predictors that held the most weight were the relative length of the foot, intermembral index on support orientations of 15°-30°. For supports of 45° and steeper, body mass became the most influential predictor. This model was then used to predict the probability of headfirst descent at various support orientations in different simulated versions of a primate ancestor.

The simulated ancestral primates were varied in mass from 50 g to 1000 g to encompass the hypothesized body masses set forward by Boyer et al. (2013a) and Soligo and Martin (2006). The intermembral indices of the simulated ancestral primates were characteristic of a specialized leaping ancestor (IMI = 60), a cheirogaleid-like ancestor (IMI = 70), a *Ptilocercus*-like ancestor (IMI = 80), and a dedicated terminal-branch specialist (IMI = 90). An actual stem haplorrhine, *A. achilles*, was also simulated at various body masses.

The modeled predictions suggest that as primates transitioned from claw interlocking to grasping, headfirst descent would be most compromised at in an ancestral primate with a lower IMI regardless of mass, assuming an ‘average’ foot size. However, from the fossil record it is known that early primates had relatively long feet (Boyer et al. 2013b). *A. achilles*, despite its very low IMI, was predicted to have comparatively higher probabilities of headfirst descent on steep supports compared to simulated primates of the same size, likely driven by how the model interpreted foot length. Further modeling of intrinsic foot proportions (e.g. those with longer metatarsal regions compared to those with longer

phalangeal region) might change the predicted headfirst descending abilities of a low IMI primate. The current model suggests that a leaping specialist would require relatively long grasping feet to access a terminal branch niche using quadrupedal locomotion, while ancestral primates of relatively higher IMI would only need to be small in mass to travel on the same support orientations using headfirst descent.

Secure headfirst descent through arboreal environments appears to be a behavior that selection has repeatedly acted on in arboreal vertebrates through the selection for rotating hindfeet, a feature seen in extinct Cretaceous Multituberculates (Jenkins and Krause 1983), extant rodents, carnivores, marsupials (Jenkins and McClearn 1984), and even birds (Fujita et al. 2008). Another repeatedly adapted trait that can aid in headfirst descent is a prehensile tail, which is hypothesized to help terminal branch specialists bridge gaps (Cartmill 1974b). Given many selective convergences to enable and improve headfirst descent in arboreal animals, it would be quite novel if stem primates were to completely lose this primitive ability without also adapting alternative means of safe descent.

In the earliest primates, replacement of claws with nails would have removed the ability to use claw interlocking as a mechanism for headfirst descending, but the impact of employing grasping mediated headfirst descent would be experienced differently by stem primates of different morphology and body mass. From the modeled ancestral primates' probability of headfirst

descent, it appears that a relatively small ancestor of low IMI would experience a substantial reduction in ability to headfirst descend compared to an ancestor with a higher IMI. Having a high body mass, as hypothesized by Soligo and Martin (2006), would also compromise ability to headfirst descend across a range of IMI and would require substantial adaptation to the terminal branch niche (e.g. a *Nycticebus*-like IMI, strong pedal grasping) prior to the loss of claws to prevent loss of an ability to headfirst descend steep supports. Given a lack of other gap crossing mechanisms (e.g. a prehensile tail, leaping ability), such a primate would experience further difficulty getting between terminal branch habitats since large diameter vertical supports might become too difficult to navigate. This could be especially problematic if the early Eocene habitats were sparsely vegetated as reconstructed by Secord et al. (2008).

Moving headfirst in an arboreal environment is hypothetically desirable because it allows an animal to observe discontinuities along a path, and enables an animal to continue to progress along compliant branches that may be bending under the weight of the animal without having to change the direction of movement. Further, convergent selection for traits that enable headfirst descent in non-primate mammals are widespread (Cartmill 1974b, 1985; Jenkins and McClearn 1984), while it does not appear that any arboreal animals are specially adapted for tail first descent.

From this study, it is predicted that a small ancestor (≤100 g) with IMI characteristic of generalized arboreal primates and non-primate arboreal

mammals (70-80) (Dunn and Rasmussen 2007; Fleagle 2013) could transition from primitive claw interlocking to derived grasping mediated headfirst descent with the limited impact to headfirst directed behavior within a terminal branch niche. In this ancestral scenario, travel between terminal branch habitats could be facilitated by establishing handholds on rough barky surfaces of tree trunks as observed in modern small primates (Cartmill 1974b), or through generalized leaping in the style of treeshrews (Jenkins 1974) or cheirogaleids.

If specialized vertical clinging and leaping were to evolve prior to adaptation to a terminal branch niche, such an ancestor might have great difficulty moving headfirst in such a niche across a range of body masses. When comparing the modeled probability of headfirst descent in an ancestral primate of an IMI of 60 to behavioral observations of tarsiers by Crompton and Andau (1986), it is reported that *Tarsius bancanus* uses tail first descent, has awkward above-branch quadrupedal locomotion, and rarely travels on supports of 10-45°. Therefore, adaptive scenarios such as the Grasp-Leaping hypothesis that infer selection towards specialized leaping the origin of primate origins should also consider the strength of selective pressures that might be needed to turn a highly specialized leaper in an adept arboreal quadruped in a terminal branch setting.

Finally, this research can be extended into considering non-headfirst descending behaviors to evaluate the hypothesis that such behaviors may only appear in larger lineages that have already undergone selection for traits associated with terminal branch use, including grasping and claw loss. These

alternative descending behaviors, such as tail first descent, may only appear when headfirst descending ability is compromised, either by species specific anatomy and mass, or by individual characteristics like aging. The present experiment has collected comparative observations of tail first descent that can be kinematically evaluated to evaluate if they appear as regular as the quadrupedal gaits of primates, or if they are more variable. Further comparison between headfirst descending and other descending styles will be essential for understanding tradeoffs that may exist between these locomotor behaviors.

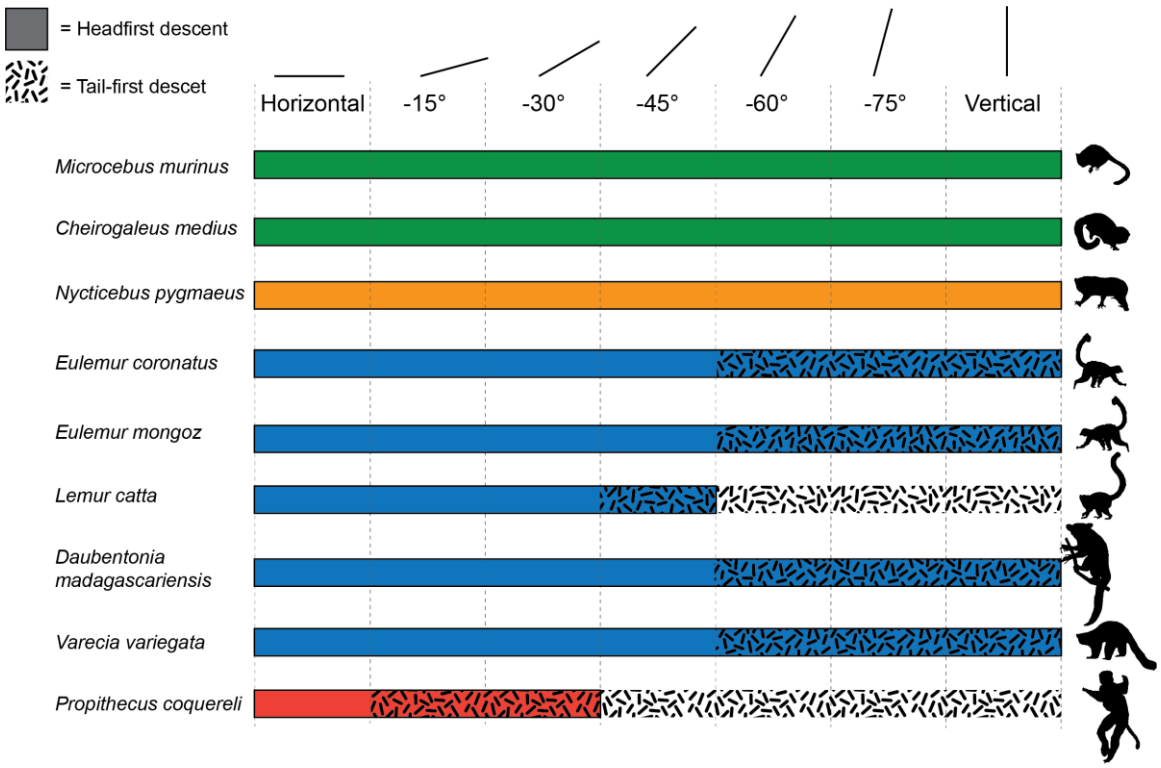


Figure 3-1:Headfirst descending behaviors observed in the sample. Species are arranged in descending order by species average body mass. Colors correspond to the locomotor category (green = S-AQ, yellow = SC, blue = L-AQ, and red = VCL). Solid areas represent support orientations in which at least one individual used headfirst descent, sprinkles correspond to the support conditions in which tail first descent was observed in at least one individual.

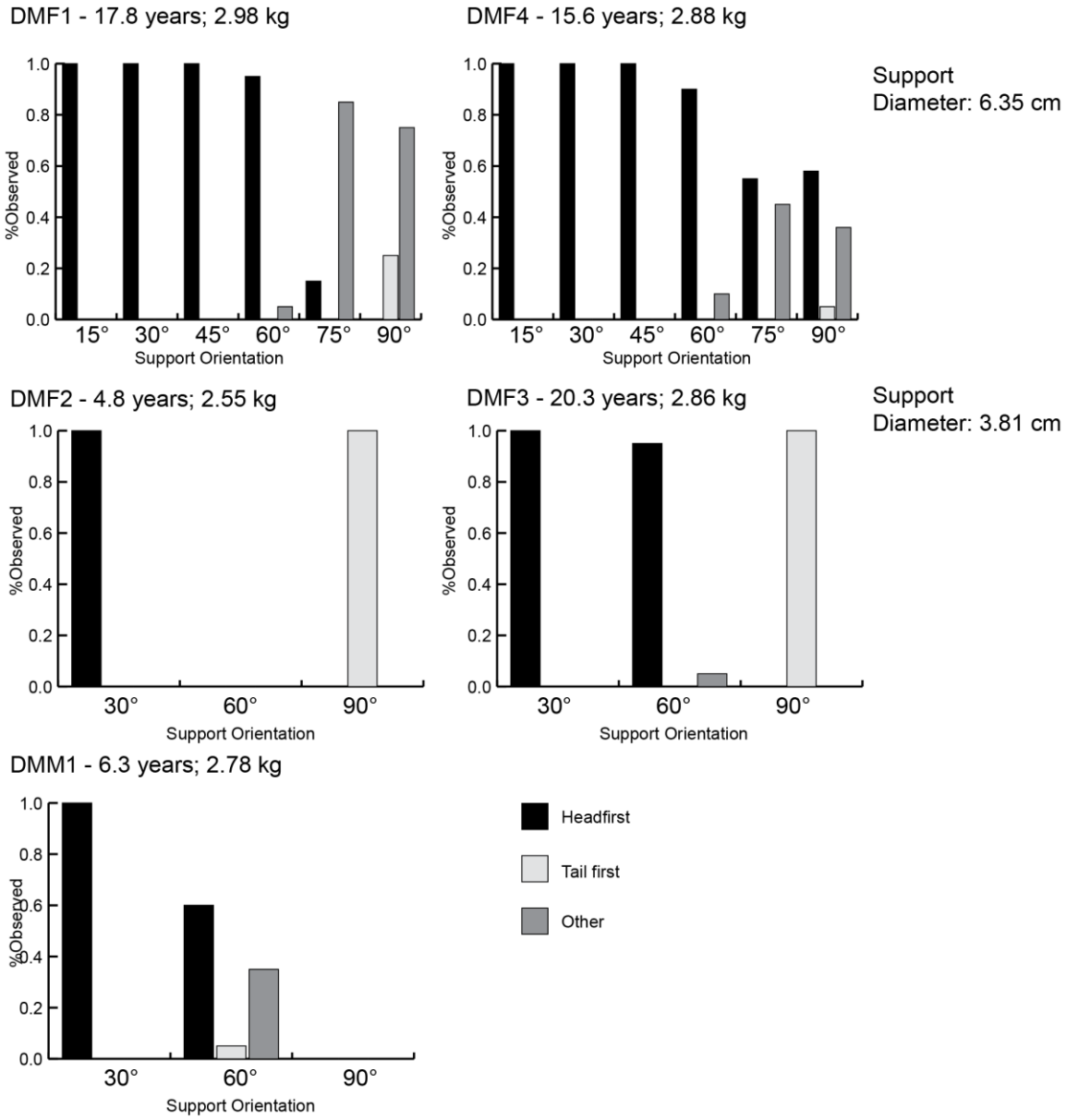


Figure 3-2: Frequencies of Descending Behaviors observed in *Daubentonia madagascariensis* on declines.

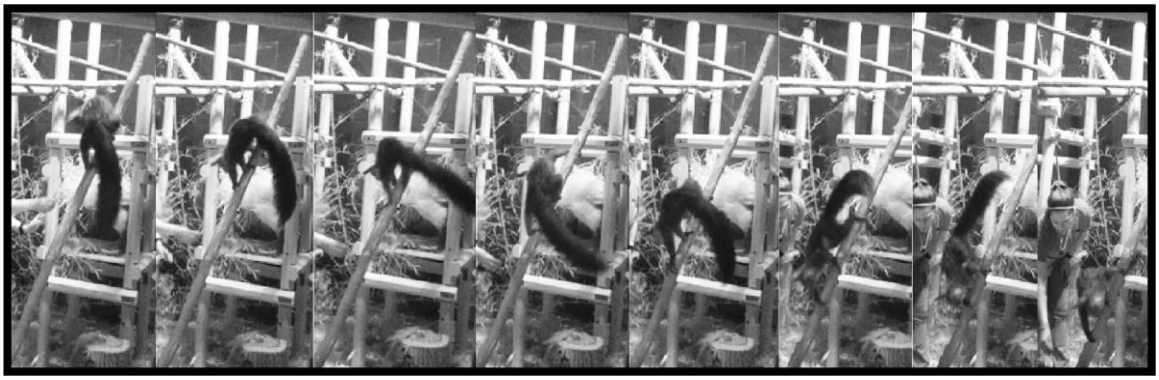


Figure 3-3: Sequence of a sideways swing in *Daubentonia* descending a steep decline. Progression begins with the forearms moving together in time, grasping the pole, and then the hind legs moving together in time. This sequence is then repeated; in the pictured bout, the body of the animal rotated such that it began with its back to the observer and ended with its face towards the observer. This bodily rotation was not observed in every instance of this descent style, e.g. sometimes the animal would remain facing the observer for the whole progression. Images were taken from still frames of video, and have been converted to grayscale and adjusted for brightness and contrast for ease of viewing.

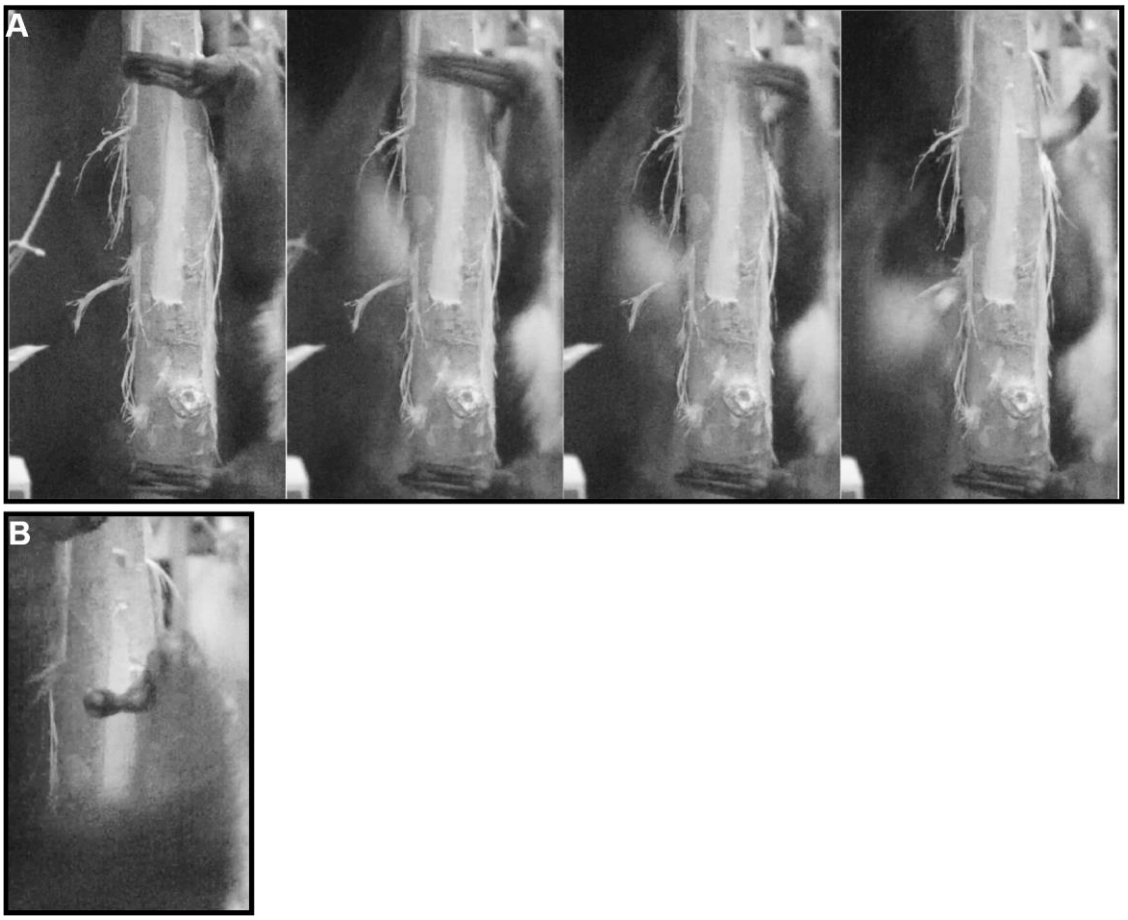


Figure 3-4: Pedal grasping during headfirst vertical descent in *Daubentonia*. A) Sequence of *D. madagascariensis* grasping and releasing a support, the foot is superior in the image and the hand is visible inferiorly. B) View of a grasping hallux during headfirst descent. Images were taken from still frames of video, and have been converted to grayscale and adjusted for brightness and contrast for ease of viewing.

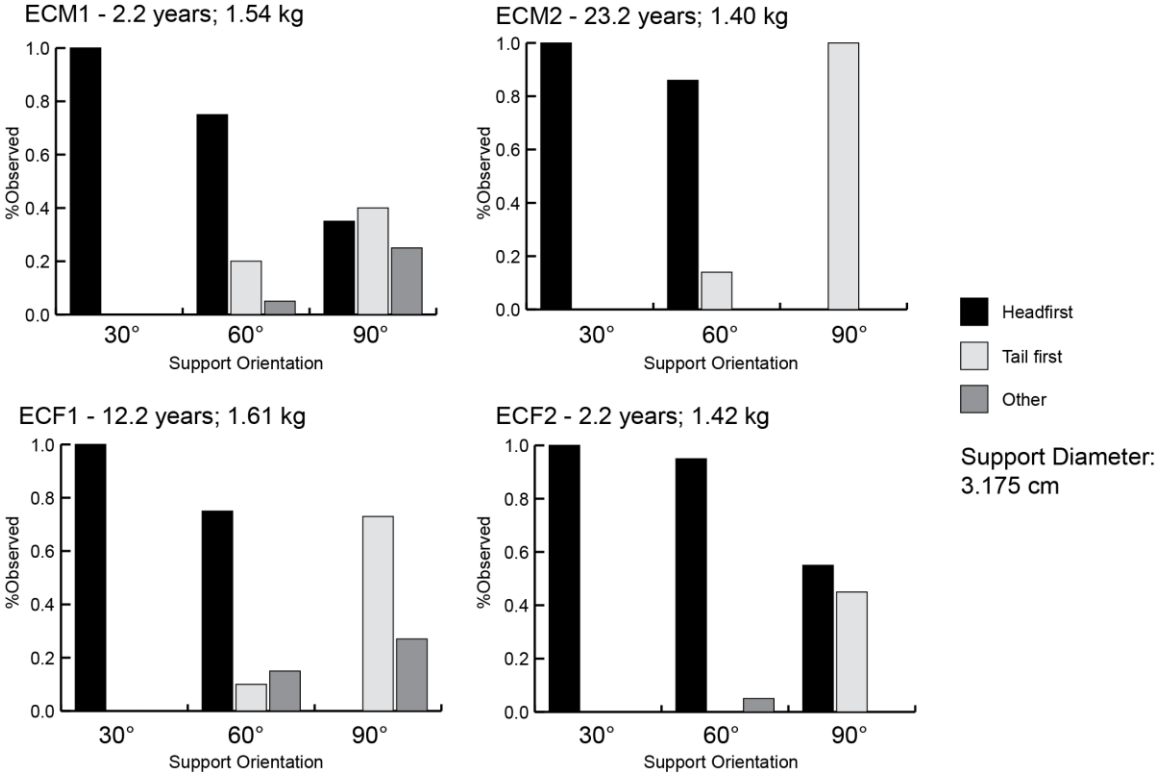


Figure 3-5: Proportions of Descending Behaviors observed in *Eulemur coronatus* on declines.

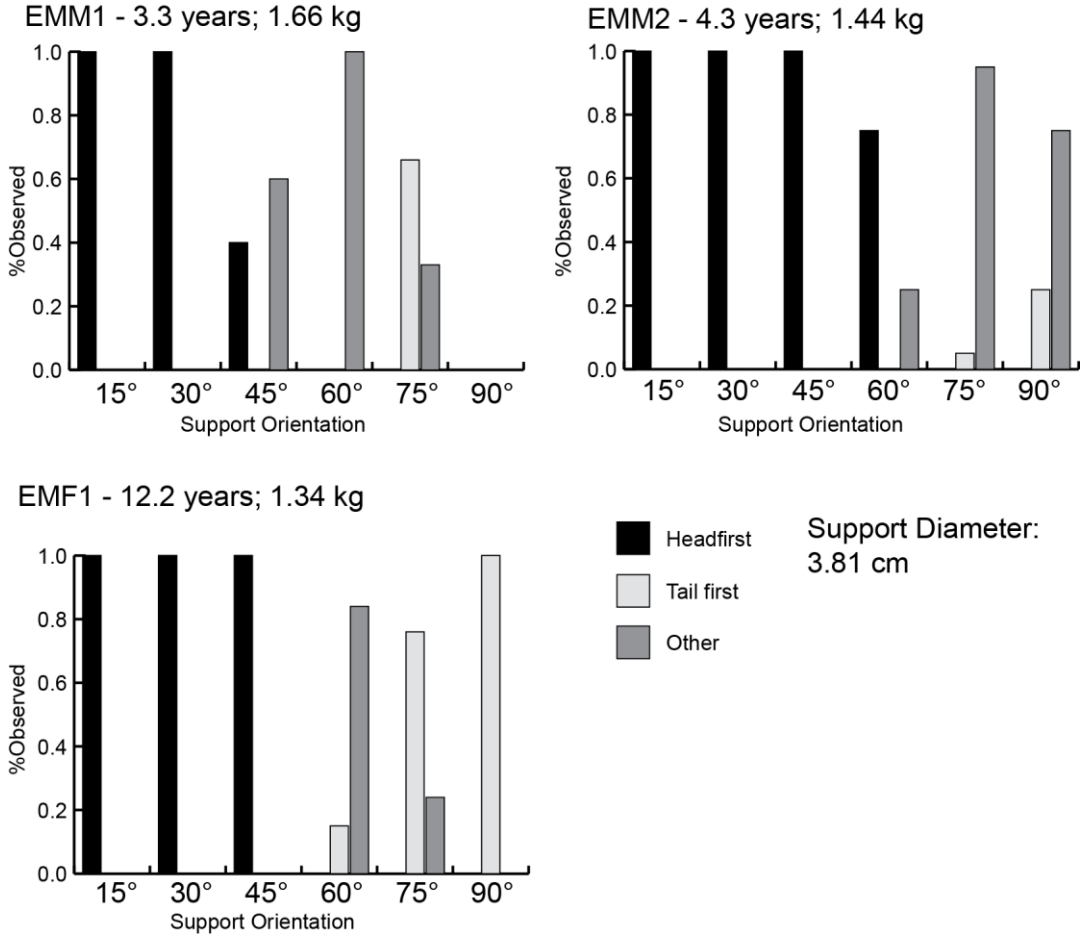


Figure 3-6: Proportions of Descending Behavior observed in *Eulemur mongoz* on declines.

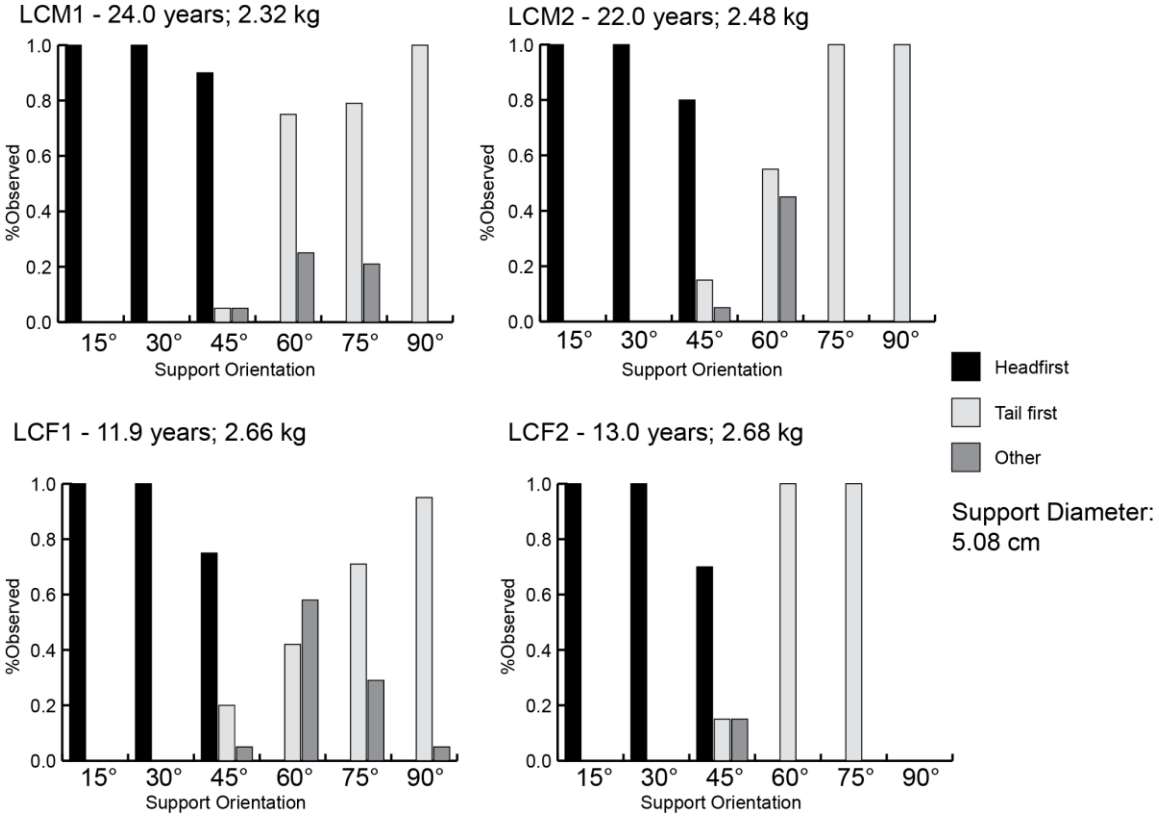


Figure 3-7: Proportions of Descending Behaviors observed in *Lemur catta* on declines.

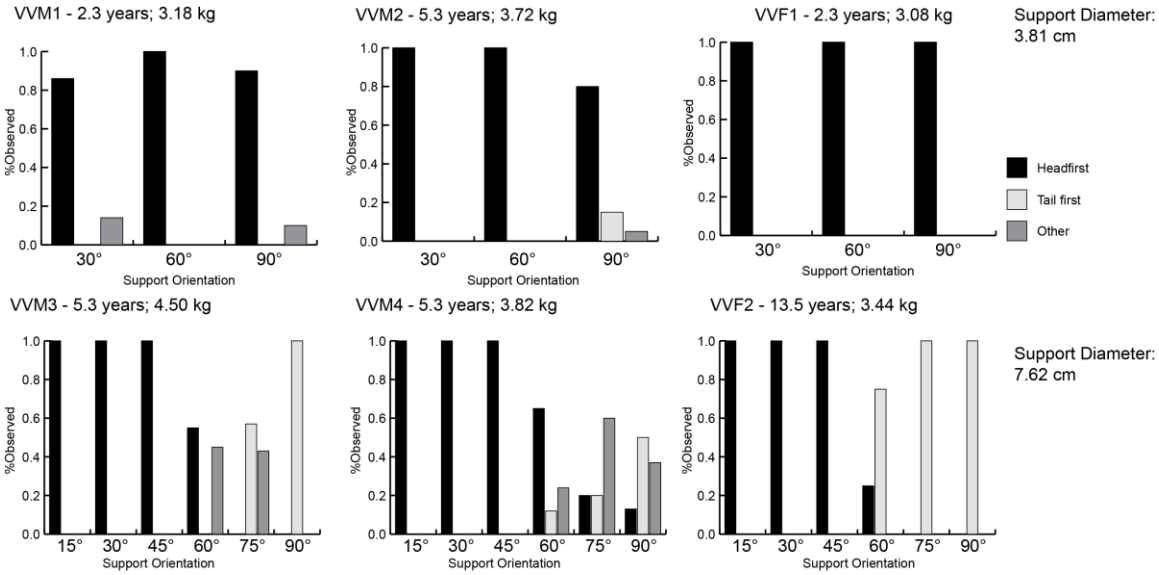


Figure 3-8: Proportions of Descending Behaviors observed in *Varecia variegata* on declines.

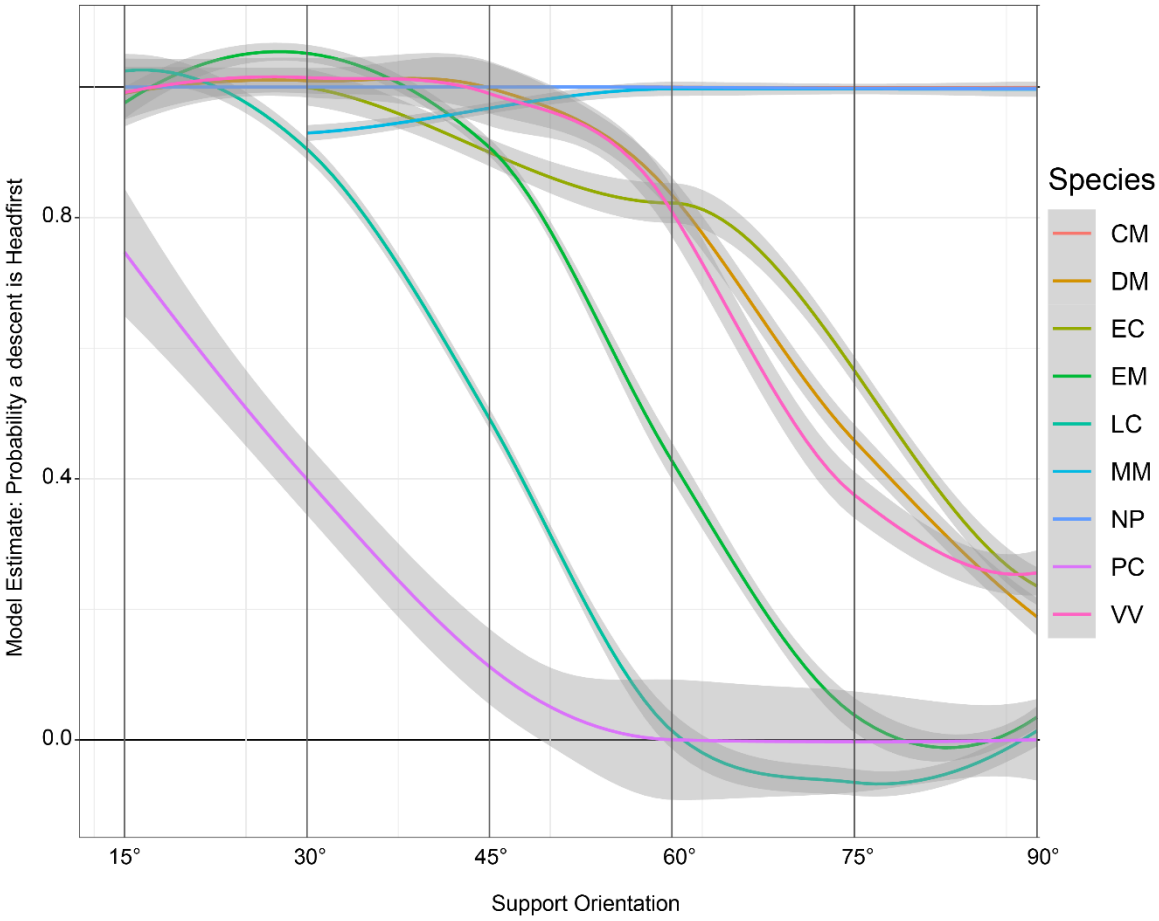


Figure 3-9: Estimated fit of favored Bayesian Multilevel Model of Headfirst Descent. A smooth Loess curve with error intervals was fit to the relationship of support orientation and model estimated probabilities of headfirst descent for each individual. The model infers that all species start with a relatively high probability of descending supports headfirst, and that as supports increase in steepness, this probability decreases at different rates across species.

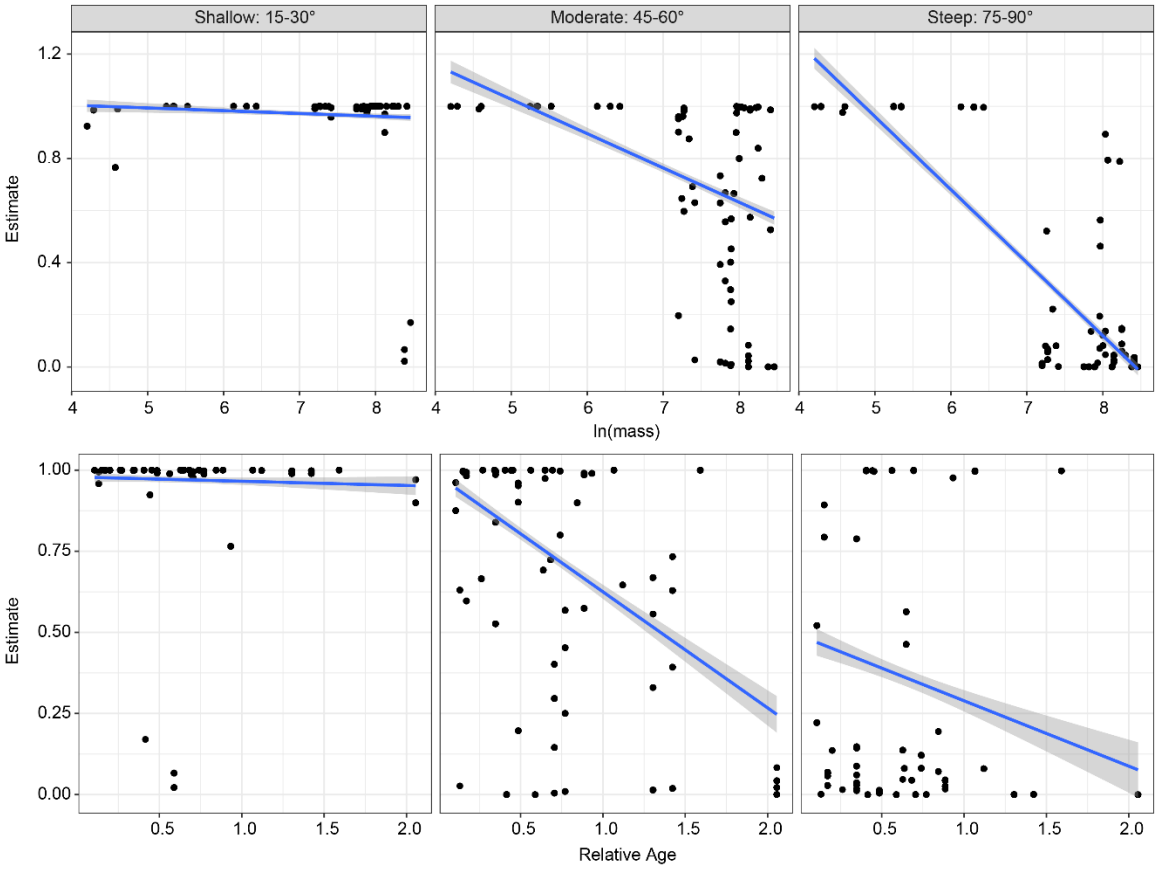


Figure 3-10: Estimate fit of Bayesian Multilevel Model against mass and age. Model estimates are plotted against mass (top) and age (bottom) and fit with a linear line to show the general relationship of these predictors with the outcome. On supports of 15-30°, age and mass increases do not have much effect in this model. On supports of 45-60°, as mass and age increases, the estimated probability of using headfirst descent begins to decrease, and this trend continues upon the steep and vertical 75-90° supports.

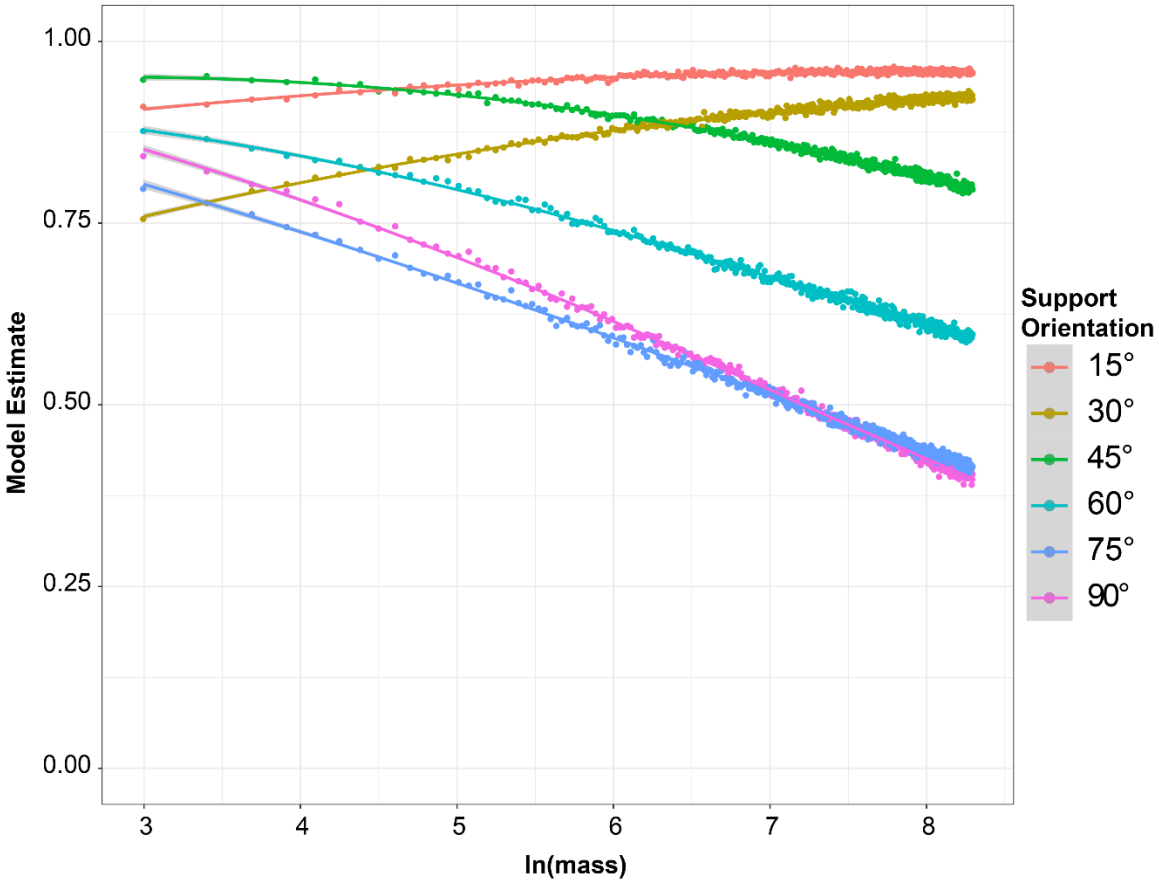


Figure 3-11: Model predictions for headfirst above branch descent on various support orientations by *Archicebus achilles* at various masses. Masses varied between the minimum reconstructed body mass (20 g) for this fossil species and the size of a large arboreal strepsirrhine (4 kg), and assumes that the skeletal proportions of the animal (IMI = 55; relative foot length = 36.6) stay constant across these sizes and that the support size was graspable. Estimates are fit with a Loess curve.

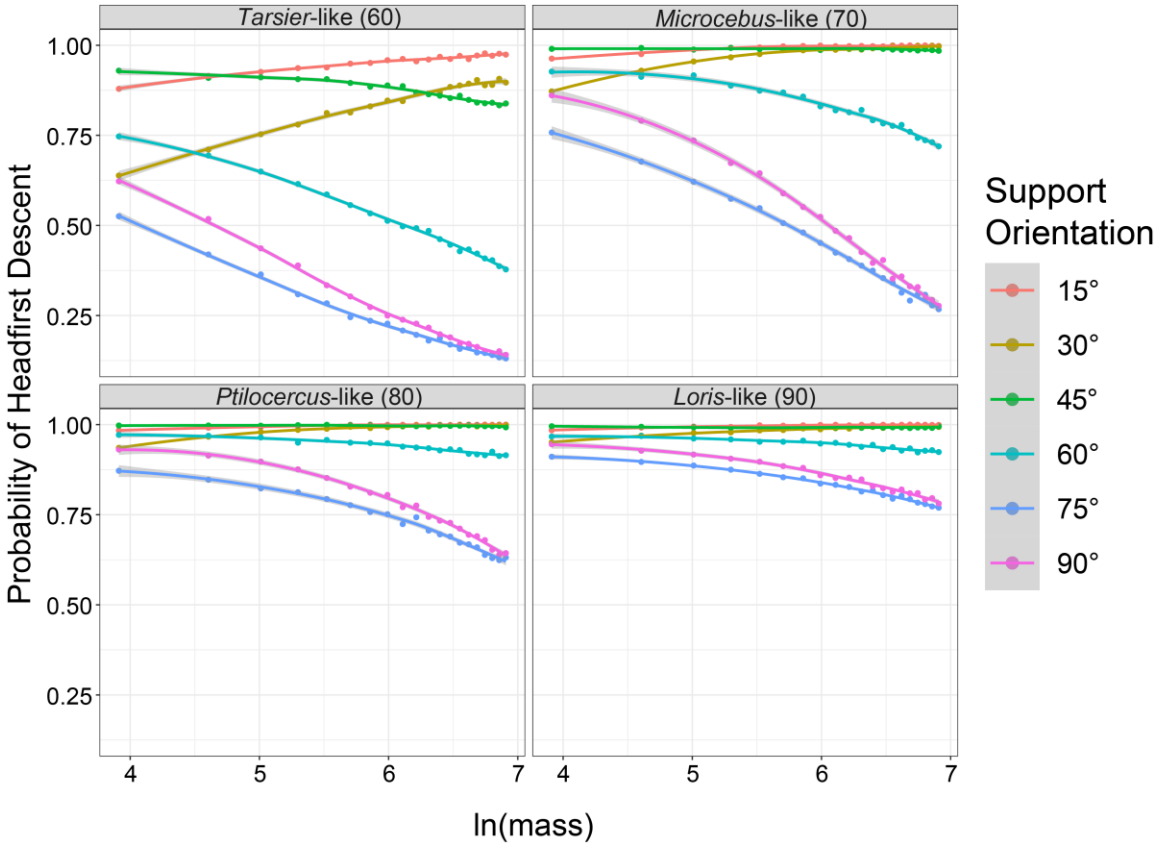


Figure 3-12: Model predictions of headfirst descent in a simulated ancestral primate of varying mass and IMI. Ancestral primates were simulated with an IMI of 60, 70, 80, and 90, all ranging in mass from 50 to 1000 g in 50 g increments. The model was used to predict the probability of headfirst descent on declines ranging from 15° to 90° in 15° increments. Foot ratio, support diameter, and age were all set to the average of the extant sample.

Table 3.1: Correlation of fixed effects present in this sample. Numbers reflect the Spearman correlation coefficient (ρ).

	Relative Foot Length	Intermembral Index (IMI)	Ln(mass)	Relative Age	Relative support size
Grasp type	-0.86	-0.18	0.54	0.00	0.06
Relative Foot Length		0.27	-0.48	-0.27	-0.06
IMI			0.29	0.06	0.33
Ln(mass)				0.09	0.22
Relative Age					0.31

Table 3.2: Summary statistics for fixed effect terms used to center and scale values for Bayesian Multilevel Model.

Variable	Mean	SD
Relative Foot Length	30.12	2.174
IMI	72.6	6.18
Ln(mass)	7.148	1.226
Relative Age	0.652	0.450
Relative Support size	3.612	1.029

Table 3.3: Frequencies of descending behaviors in *Cheirogaleus medius.*

Individual	Support orientation (°) – diameter (cm)	Headfirst descents	Tail first descents	Other descents
CMF1	15 – 1.5875	10	0	0
	30 – 1.5875	17	0	0
	45 – 0.9525	11	0	0
	45 – 1.5875	15	0	0
	45 – 2.2225	19	0	0
	60 – 1.5875	0	0	0
CMM1	15 – 1.5875	20	0	0
	30 – 1.5875	20	0	0
	45 – 0.9525	10	0	0
	45 – 1.5875	20	0	0
	45 – 2.2225	0	0	0
	60 – 1.5875	20	0	0
	75 – 1.5875	20	0	0
	90 – 0.9525	20	0	0
	90 – 1.5875	20	0	0
	90 – 2.2225	18	0	0
CMM2	15 – 1.5875	20	0	0
	30 – 1.5875	20	0	0
	45 – 0.9525	16	0	0
	45 – 1.5875	20	0	0
	45 – 2.2225	15	0	0
	60 – 1.5875	19	0	0
	75 – 1.5875	18	0	0
	90 – 0.9525	20	0	0
	90 – 1.5875	10	0	0
	90 – 2.2225	20	0	0
CMM3	15 – 1.5875	16	0	0
	30 – 1.5875	13	0	0
	45 – 0.9525	17	0	0
	45 – 1.5875	11	0	0
	60 – 1.5875	1	0	0
	75 – 1.5875	0	0	0

Table 3.4: Frequencies of descending behaviors in *Microcebus murinus*

Individual	Support orientation (°) – diameter (cm)	Headfirst descents	Tail first descents	Other descents
MMF1	30 – 1.905	9	0	4
	60 – 1.905	20	0	0
	90 – 1.905	7	0	0
MMF2	30 – 1.905	18	0	0
	60 – 1.905	20	0	0
	90 – 1.905	20	0	0
MMM1	30 – 1.905	20	0	0
	60 – 1.905	20	0	0
	90 – 1.905	20	0	0
MMM2	30 – 1.905	10	0	1
	60 – 1.905	20	0	0
	90 – 1.905	20	0	0

Table 3.5: Frequencies of descending behaviors in *Daubentonia madagascariensis*

Individual	Support orientation (°) – diameter (cm)	Headfirst descents	Tail first descents	Other descents
DMF1	30 – 3.81	20	0	0
	90 – 3.81	0	9	5
	15 – 6.35	13	0	0
	30 – 6.35	20	0	0
	45 – 6.35	20	0	0
	60 – 6.35	19	0	1
	75 – 6.35	3	0	17
	90 – 6.35	0	5	15
DMF2	30 – 3.81	20	0	0
	90 – 3.81	0	2	0
DMF3	30 – 3.81	20	0	0
	60 – 3.81	19	0	1
	90 – 3.81	0	4	0
	90 – 8.89*	0	5	0
DMF4	15 – 6.35	19	0	0
	30 – 6.35	20	0	0
	45 – 6.35	18	0	0
	60 – 6.35	18	0	2
	75 – 6.35	11	0	9
	90 – 6.35	11	1	7
DMM1	30 – 3.81	20	0	0
	60 – 3.81	12	1	7
	90 – 3.81	0	0	0
	90 – 8.89*	1	0	0

**Note:* DMF3 and DMM1 both descended a vertical 8.89 cm pole within the research space instead of the 3.81 cm pole that they were being solicited to descend with a food reward.

Table 3.6: Frequencies of descending behaviors in *Eulemur coronatus*

Individual	Support orientation (°) – diameter (cm)	Headfirst descents	Tail first descents	Other descents
ECF1	30 – 3.175	20	0	0
	60 – 3.175	15	2	3
	90 – 3.175	0	11	4
ECF2	30 – 3.175	20	0	0
	60 – 3.175	19	0	1
	90 – 3.175	11	9	0
ECM1	30 – 3.175	20	0	0
	60 – 3.175	15	4	1
	90 – 3.175	7	8	5
ECM2	30 – 3.175	20	0	0
	60 – 3.175	6	1	0
	90 – 3.175	0	20	0

Table 3.7: Frequencies of descending behaviors in *Eulemur mongoz*

Individual	Support orientation (°) – diameter (cm)	Headfirst descents	Tail first descents	Other descents
EMF1	15 – 3.81	8	0	0
	30 – 3.81	11	0	0
	45 – 3.175	20	0	0
	45 – 3.81	7	0	0
	45 – 6.35	20	0	0
	60 – 3.81	0	2	11
	75 – 3.81	0	13	4
	90 – 3.175	0	18	2
	90 – 3.81	0	12	0
	90 – 6.35	0	10	0
EMM1	15 – 3.81	15	0	0
	30 – 3.81	17	0	0
	45 – 3.81	2	0	3
	60 – 3.81	0	0	1
	75 – 3.81	0	2	1
	90 – 3.81	0	0	0
EMM2	15 – 3.81	20	0	0
	30 – 3.81	20	0	0
	45 – 3.175	20	0	0
	45 – 3.81	20	0	0
	45 – 6.35	18	0	2
	60 – 3.81	15	0	5
	75 – 3.81	0	1	19
	90 – 3.175	0	16	4
	90 – 3.81	0	5	15
	90 – 6.35	2	3	15

Table 3.8: Frequencies of descending behaviors in *Lemur catta.*

Individual	Support orientation (°) – diameter (cm)	Headfirst descents	Tail first descents	Other descents
LCF1	15 – 5.08	11	0	0
	30 – 5.08	20	0	0
	45 – 3.175	0	19	1
	45 – 5.08	15	4	1
	45 – 8.89	0	5	7
	60 – 5.08	0	5	2
	75 – 5.08	0	20	0
	90 – 5.08	0	19	1
LCF2	15 – 5.08	20	0	0
	30 – 5.08	20	0	0
	45 – 3.175	8	3	9
	45 – 5.08	14	3	3
	45 – 8.89	0	3	4
	60 – 5.08	0	13	0
	75 – 5.08	0	8	0
	90 – 3.175	0	4	0
	90 – 5.08	0	0	0
	90 – 8.89	0	0	0
LCM1	15 – 5.08	12	0	0
	30 – 5.08	20	0	0
	45 – 3.175	13	4	3
	45 – 5.08	17	1	1
	45 – 8.89	0	1	7
	60 – 5.08	0	15	5
	75 – 5.08	0	15	4
	90 – 3.175	0	6	0
	90 – 5.08	0	15	0
	90 – 8.89	0	0	0
LCM2	15 – 5.08	20	0	0
	30 – 5.08	20	0	0
	45 – 3.175	10	9	1
	45 – 5.08	16	3	1
	45 – 8.89	0	1	3
	60 – 5.08	0	11	9
	75 – 5.08	0	20	0
	90 – 3.175	0	9	0
	90 – 5.08	0	20	0
	90 – 8.89	0	1	4

Table 3.9: Frequencies of descending behaviors in *Varecia variegata.*

Individual	Support orientation (°) – diameter (cm)	Headfirst descents	Tail first descents	Other descents
VVF1	30 – 3.81	20	0	0
	60 – 3.81	12	0	0
	90 – 3.81	4	0	0
VVF2	15 – 7.62	20	0	0
	30 – 3.81	20	0	0
	30 – 7.62	19	0	0
	45 – 7.62	11	0	0
	45 – 9.52	20	0	0
	60 – 3.81	20	0	0
	60 – 7.62	3	9	0
	75 – 7.62	0	20	0
	90 – 3.81	0	7	0
	90 – 5.08	0	20	0
	90 – 7.62	0	20	0
	90 – 9.52	0	20	0
VVM1	30 – 3.81	12	0	2
	60 – 3.81	20	0	0
	90 – 3.81	18	0	2
VVM2	30 – 3.81	20	0	0
	60 – 3.81	20	0	0
	90 – 3.81	16	3	1
VVM3	15 – 7.62	20	0	0
	30 – 7.62	20	0	0
	45 – 7.62	20	0	0
	60 – 7.62	11	0	9
	75 – 7.62	0	4	3
	90 – 5.08	0	20	0
	90 – 7.62	0	10	0
	90 – 9.52	0	3	0
VVM4	15 – 7.62	20	0	0
	30 – 7.62	20	0	0
	45 – 7.62	20	0	0
	60 – 7.62	11	2	4
	75 – 7.62	4	4	12
	90 – 5.08	2	8	4
	90 – 7.62	1	4	3
	90 – 9.52	2	2	1

Table 3.10: Frequencies of descending behaviors in *Nycticebus pygmaeus*.

Individual	Support orientation (°) – diameter (cm)	Headfirst descents	Tail first descents	Other descents
NPF1	30 – 3.175	20	0	0
	60 – 3.175	18	0	0
	90 – 3.175	20	0	0
NPF2	15 – 3.175	17	0	0
	30 – 3.175	16	0	0
	45 – 3.175	15	0	0
	60 – 3.175	6	0	0
	75 – 3.175	20	0	0
	90 – 3.175	13	0	0
NPM1	30 – 3.175	10	0	0
	60 – 3.175	20	0	0
	90 – 3.175	6	0	0

Table 3.11: Frequencies of descending behaviors in *Propithecus coquereli*.

Individual	Support orientation (°) – diameter (cm)	Headfirst descents	Tail first descents	Other descents
PCF1	15 – 6.35	0	4	3
	30 – 6.35	0	10	2
	45 – 3.175	0	0	1
	45 – 6.35	0	3	2
	60 – 6.35	0	5	0
	75 – 6.35	0	0	0
	90 – 3.175	0	1	0
	90 – 6.35	0	9	0
	90 – 9.52	0	8	2
PCF2	15 – 6.35	0	0	0
	30 – 6.35	0	2	0
	45 – 6.35	0	17	0
	60 – 6.35	0	7	0
	75 – 6.35	0	5	0
	90 – 3.175	0	6	0
	90 – 6.35	0	8	0
	90 – 9.52	0	5	1
PCM1	15 – 6.35	14	0	0
	30 – 6.35	19	0	1
	45 – 3.175	0	0	2
	45 – 6.35	0	5	3
	45 – 9.52	0	6	0
	60 – 6.35	0	13	2
	75 – 6.35	0	15	0
	90 – 3.175	0	8	0
	90 – 6.35	0	3	0
	90 – 9.52	0	7	0

Table 3.12: Bayesian Model Comparison. Fixed effects were scaled to the values presented in Table 3.2. Widely Applicable Information Criterion (WAIC) was used for model comparison, with lower values indicating better fit.

Fixed Effects	Random Effects	WAIC
None	(1|Taxonomy), (1|Individual)	2722.1
Mass	(1|Taxonomy), (1|Individual)	2726.8
Mass, Support Orientation	(1|Taxonomy), (1|Individual)	1120.9
Mass	(1|Taxonomy), (1|Individual), (1|Support Orientation)	1066.9
Mass	(1|Taxonomy), (1|Individual), (1 + Mass|Support Orientation)	967.0
Mass, IMI	(1|Taxonomy), (1|Individual), (1 + Mass|Support Orientation)	967.5
Mass, IMI, Foot Size	(1|Taxonomy), (1|Individual), (1 + Mass|Support Orientation)	966.6
Mass, IMI, Foot Size, Support Diameter	(1|Taxonomy), (1|Individual), (1 + Mass|Support Orientation)	955.2
Mass, IMI, Foot Size, Support Diameter, Relative Age	(1|Taxonomy), (1|Individual), (1 + Mass|Support Orientation)	953.7

Table 3.13: Varying intercept values for the random effects of taxonomy and individual identity

Taxonomy	Individual	Intercept estimate	Estimate Error	CI: 5%	CI: 95%
C. medius		9.455712	5.453579	0.7643014	22.256535
	CMF1	4.5458185	4.152167	-3.59849926	13.177376
	CMM1	4.93818675	3.987146	-2.90211564	12.909689
	CMM2	4.95638111	3.924184	-2.39357167	12.96154
	CMM3	4.59908502	4.109211	-3.77409585	12.323806
M. murinus		3.209898	4.241835	-4.8185751	12.154441
	MMF1	1.42294005	3.498272	-5.49542165	8.336709
	MMF2	5.82859001	3.86902	-1.4108183	13.601128
	MMM1	6.13009818	3.708362	-0.8109744	13.370318
	MMM2	3.70721472	3.565585	-3.07698147	10.868191
D. Madagas-cariensis		1.729135	3.865682	-5.8792422	9.350453
	DMF1	4.35327774	3.491068	-2.36995693	11.527051
	DMF2	2.66099141	3.835116	-4.80416531	10.239705
	DMF3	4.63577961	3.504357	-2.01284304	12.187579
	DMF4	6.53522364	3.471685	0.05507188	13.699916
	DMM1	2.58475029	3.53895	-4.00229678	9.459973
E. coronatus		6.720394	3.235394	0.1156633	13.095932
	ECF1	4.03709834	3.469724	-2.89129976	10.832283
	ECF2	5.94829503	3.493235	-1.01970173	12.804414
	ECM1	4.78703964	3.496943	-2.13570511	11.589113
	ECM2	3.883874	3.531072	-3.3120593	10.951232
E. mongoz		3.012658	3.411554	-4.17025	9.469056
	EMF1	4.449097	3.443376	-2.50377	11.15453
	EMM1	2.103009	3.497318	-5.23865	8.606362
	EMM2	6.286869	3.482007	-0.83913	12.93755
L. catta		2.364573	3.401584	-4.72034	8.878628
	LCF1	3.350327	3.516295	-3.4922	10.27772
	LCF2	4.096082	3.507848	-2.65896	11.17762
	LCM1	4.998301	3.455551	-1.76415	11.71334
	LCM2	4.731794	3.449963	-1.86153	11.5367
V. variegata		7.841312	3.365282	1.074057	14.26956
	VVF1	7.250891	3.678734	0.092912	14.7499
	VVF2	2.288456	3.428508	-4.53671	9.027647
	VVM1	5.880575	3.443987	-0.98737	12.63996
	VVM2	6.426148	3.417863	-0.29133	13.23955
	VVM3	2.208336	3.45928	-4.76033	9.01375
	VVM4	3.528868	3.416128	-3.17328	10.28224
N. pygmaeus		7.876201	5.782131	-1.34124	21.52783
	NPF1	4.644061	4.126027	-3.58641	12.89856
	NPF2	4.839698	3.989877	-2.61946	13.42814
	NPM1	4.582258	4.097771	-3.28335	12.89924
P. coquereli		-1.4831	4.402155	-11.3247	6.582489
	PCF1	0.095964	3.848894	-7.45023	7.524628

PCF2	2.185709	3.952168	-5.39018	9.860982
PCM1	8.969943	3.758618	2.079323	16.55383

Table 3.14: Model Intercept and Slope estimates for Support Orientation.

Support	Intercept Estimate	Estimate Error	CI 5%	CI 95%	Mass Estimate	Estimate Error	CI 5%	CI 95%
15	11.771	3.131	6.409	18.724	0.362	3.034	-6.400	5.559
30	8.277	2.057	4.630	12.939	2.443	1.620	-0.582	5.981
45	6.534	2.088	2.881	11.031	-2.713	2.070	-6.689	1.442
60	1.920	2.001	-1.720	6.298	-2.829	1.664	-5.971	0.543
75	-1.329	2.092	-5.397	3.271	-3.163	1.964	-6.935	0.851
90	-1.244	1.990	-4.951	3.237	-3.914	1.702	-7.163	-0.408

Chapter 4: Gait Kinematics and Support Orientation I: Temporal Variables

4.1 Introduction

Since the late 1800s and the innovative work of Muybridge (1887), who first applied photography to the detailed study of locomotion, primates have been noted to move in an unusual fashion compared to other quadrupeds. What Muybridge (1887) was observing in primates is known as a diagonal sequence (DS) gait and from the extensive comparative work on quadrupedal gaits by researchers in the 1960s and 1970s like Hildebrand (1967), Prost (1969), and Gambaryan (1974), it is now widely recognized that the primate use of diagonal sequence diagonal couplet (DSDC) gaits are distinctive amongst quadrupedal mammals, which typically use lateral sequence gaits (LS). From this foundation, many researchers have pursued an explanation as to why primates appear so unique.

Adaptive hypotheses for primate DSDC gait use have focused on how this gait may improve movement through and promote stability in arboreal environments (Cartmill et al. 2002; Schmidt 2005a; Stevens 2006, 2008; Usherwood and Smith 2018; Miller et al. 2019). Further, when experimental studies were conducted on inclines by Prost and Sussman (1969), they observed that the frequency of DS gait use increased in primates, suggesting a relationship of DS gaits with climbing. Building on this, Rollinson and Martin (1981) demonstrated that LS gaits increased on declines, contributing support to

hypotheses about the relationship of weight distribution in primates and gait sequence.

This pattern of increasing LS gait use on declines has been found in multiple species of cercopithecoids (Rollinson and Martin 1981), platyrrhines (Vilensky et al. 1994; Nyakatura et al. 2008; Nyakatura and Heymann 2010; Hesse et al. 2015) and some strepsirrhines (Stevens 2003). However passive mass-based arguments about gait sequence (Prost and Sussman 1969; Rollinson and Martin 1981; Reynolds 1985) have not held up to scrutiny and comparative study (Vilensky and Larson 1989).

Increasing use of LS gaits on declines also appears to contradict hypotheses that have linked DSDC gaits with grasping feet and terminal branch use by primates (Cartmill 1974a; Cartmill et al. 2002; Schmitt and Lemelin 2002; Schmidt 2005a; Karantanis et al. 2015). As primates travel on increasingly steep declines they will face an increasing risk of forward pitch (Birn-Jeffrey and Higham 2014), which could be counteracted by grasping feet. This would seem to predict a greater reliance on DS gaits rather than less, if these gaits are linked with pedal grasping.

Several alternative hypotheses have been put forward to explain the use of increasingly lateral gaits on declines, including an active posterior shift of the center of mass (Vilensky et al. 1994), and increased braking by the forelimbs causing an increase in forelimb duty factor relative to the hind limb (Nyakatura et al. 2008; Nyakatura and Heymann 2010; Hesse et al. 2015). These hypotheses

predict that limb phase should decrease (become more lateral) with increasing steepness of the support because of the corresponding need to resist pitch and gravity. However, most studies have not tested primates traveling on supports oriented more steeply than approximately 34-36° because at orientations steeper than this there is a hypothesized diminishment of the static friction between primate volar skin and the support (Cartmill 1979; Vilensky et al. 1994).

Two studies have considered steeper supports of 60° (Stevens 2003; Hesse et al. 2015), however Stevens (2003) did not find that all strepsirrhines in that sample switched from DS to LS gaits, and Hesse et al. (2015) reported a decrease in frequency of LS gaits in tamarins moving on a 60° relative to a 30° support. These findings call into question whether frequency of LS gait use increases progressively with support orientation as frictional environment changes. Additionally, the pattern of increased LS gaits was not replicated by Shapiro et al. (2016) in *Microcebus murinus*, calling into question how ubiquitous this pattern is in primates.

To assess the predictions that both duty factor, especially in the forelimb, and gait sequence changes apply across many species moving on a variety of declines, the present study sample includes strepsirrhine species occupying a range different body masses tested upon supports oriented above and below 35°. It is predicted that primates should decrease the limb phase of their gait as supports increase in steepness, and that duty factor index, the ratio of forelimb to

hind limb contact duration during the stride, will increase with support orientation (Nyakatura et al. 2008; Nyakatura and Heymann 2010; Hesse et al. 2015).

4.2 Methods

The experimental setup is described in detail in Chapter 2. For all analyses presented in this chapter, support diameters were restricted to the single poles used in the pilot study and the moderate diameter pole for the full study. Individual clips of bouts of steady headfirst locomotion were imported into VirtualDub (Lee 2012). Any locomotor bouts that appeared to be asymmetrical, such gallops and bounds, were excluded from analysis. Frames corresponding to key points of the stride – initial touch down (TD1), take off (TO) and subsequent touch down (TD2) – were recorded for each limb in Excel (Microsoft, Redmond, WA; USA). A total of n = 1994 individual clips of locomotion containing all twelve points were processed.

After frame numbers associated with footfalls were recorded, the symmetry of the bout was calculated. Gait symmetry is calculated from the timing of hind limb footfalls such that the time between the first hindfoot touchdown and the next (contralateral) hindfoot touchdown should occur approximately midway (50%) through of the total stride period (Cartmill et al. 2002). Following the practice of Schmitt et al. (2006), strides that were within ±5% of perfect symmetry were retained for analysis. A total of n = 1292 bouts were found to be symmetrical.

For all symmetrical strides the limbs from the side of the body (left or right) facing the observer were considered the relevant limbs for calculating temporal gait parameters used in the present analysis (Table 4.1). Gaits were partitioned using discrete categories of limb phase following the nomenclature of Hildebrand (1967) and Cartmill et al. (2002). Duty factor, or the measure of contact time as a percentage of total stride period, for the fore and hind limbs were collected. High hind limb duty factors ($\geq$ 50) indicate longer contact durations, and are considered symmetrical walking gaits, while duty factors under 50 are considered symmetrical running gaits (Hildebrand 1967). Ambles were identified when either the fore- or hind limb duty factor was less than 50 but the other limb's duty factor was at or above 50, and limb phase was not a pace or trot (Schmitt et al. 2006).

Statistical analyses were carried out in R (R Core Team 2000). To evaluate if there were changes to gait parameters between support orientations within species, a non-parametric Kruskal-Wallis test (Kruskal and Wallis 1952) was performed at the species level to see if median values for the following variables: limb phase (*D*) , hind limb duty factor (S_H), forelimb duty factor (S_F), duty factor index (SI), stance phase duration, and swing phase duration, changed between support orientations. If the Kruskal-Wallis test result was significant (α = 0.05), a Dunn's Test (Dunn 1964) was performed using the R package 'FSA' (Ogle 2016), using the Benjamini and Hochberg (1995) correction for multiple tests to adjust the resulting p-value and detect which support orientations were significantly different from each other within each species.

4.3 Results

4.3.1 Distribution of Gaits

As support orientation increased, gaits that were determined to be asymmetrical increased in frequency (Table 4.2). This does not include obviously asymmetrical gaits such as gallops or canters and is therefore likely an underestimate of the actual number of asymmetrical gaits.

Of the 1292 symmetrical strides, 210 were determined to be ambles, 952 were found to be walking strides, and 130 were found to be running gaits (Table 4.2). These gaits are presented in a Hildebrand (1967) style diagram (Figure 4.1) which shows that generally most observations clustered in the typical primate gait space of walking diagonal sequence diagonal couplet (DSDC) gaits. As support orientation increased it was observed the number of running and ambling gaits reduced in frequency across the sample except for in *Microcebus murinus* and *Varecia variegata* (Table 4.2). Both species performed DSDC ambling gaits in which the forelimbs showed relatively lower duty factor (S_F) as the most frequently used symmetrical gait on the vertical support for both species. No other species displayed this strategy on the vertical support, with both *Cheirogaleus medius* and *Nycticebus pygmaeus* using walking gaits on steeper supports and *Eulemur coronatus* using walking and ambling lateral sequence (LS) gaits on the vertical support instead.

4.3.2 Limb Phase Changes on Declines

Pacing, DSLC, and single foot gaits were rarely observed in this sample regardless of support orientation (Table 4.3). When moving on supports angled between horizontal and 30°, most species predominantly used DSDC gaits (Figure 4.1, Table 4.3). As support orientation increased in steepness, median limb phase tended to decrease across the sample (Table 4.4), and significantly changed in all species except for *Microcebus murinus* and *Propithecus coquereli* (Table 4.5). However, a high frequency of gaits used on steep supports were still considered DSDC and walking trotting gaits rather than LS gaits in most species moving on these supports, except for gait used by both species of *Eulemur*, which used high frequencies of LS gaits on declines (Figure 4.1, Table 4.3).

Significant changes to limb phase were primarily observed between the less steep supports (15°, 30°) and steeper conditions (≥45°) (Table 4.4). On supports of 45° and greater, significant differences between the 45° and 90° vertical condition were observed in all species that performed symmetrical headfirst descent on each of these supports (*Cheirogaleus medius*, *Varecia variegata*, and *Nycticebus pygmaeus*). No other significant differences were observed when comparing supports of 45° and greater to each other (Table 4.6).

4.3.3 Hind limb Duty Factor

Hind limb duty factor gradually increased with support orientation (Table 4.4), with significant changes observed in all species except for *Microcebus murinus* and *Propithecus coquereli* (Table 4.5, 4.7). This indicates that generally,

primates extend their relative contact time of the hind limbs as a proportion of the total stride as supports increase in steepness. Most larger primates and *Nycticebus pygmaeus* in this sample adopted walking speeds on all supports ($S_H \geq 50$), while *Cheirogaleus medius* and *Microcebus murinus* tended to use symmetrical running gaits on supports oriented between 0° and 30° (Table 4.3, Figure 4.3).

4.3.4 Forelimb Duty Factor

Forelimb duty factor tended to generally increase with support orientation within the sample (Table 4.4, Figure 4.3). This was significant in all primates except for *Microcebus murinus* and *Propithecus coquereli* (Table 4.5). Forelimb duty was found to and significantly change between the same support orientations for which hind limb duty factor significantly changed within many species (Tables 4.7, 4.8).

4.3.5 Duty Factor Index

Duty Factor Index (SI), which measures hind limb duty factor relative to forelimb duty factor, was predicted to decrease as supports became steeper, indicating a relative higher rise in forelimb duty factor compared to hind limb duty factor, was not observed to change in *Cheirogaleus medius*, *Microcebus murinus*, or *Propithecus coquereli* (Table 4.5). Despite a significant result in the Kruskal-Wallis test, the adjusted results of the Dunn's Test also revealed no significant changes to SI between support conditions within *Eulemur mongoz* (Tables 4.5, 4.9).

In the primates with significant changes to SI – *Daubentonia madagascariensis*, *Eulemur coronatus*, *Lemur catta*, *Varecia variegata,* and *Nycticebus pygmaeus* – increases and decreases were observed between support orientations, rather than gradually decreasing SI with increasing steepness as predicted (Table 4.4, Figure 4.3). Little pattern emerged in the support orientations that were found be significantly different from each other in terms of direction of change across these species (Table 4.7). *N. pygmaeus* was the only species to consistently have SI less than 1, indicating that forelimb contact times were always relatively longer than hind limb contact duration on all supports (Table 4.4).

4.3.6 Stance and Swing phase duration

Stance phase duration was observed to generally increase with support orientation for both the hind and forelimbs, while swing phase duration tended to decrease with increasing support orientation (Table 4.10). This indicates that as duty factor for each limb was increasing in relative proportion of the total stride, contact time was also absolutely increasing in seconds.

Significant differences in duration of stance and swing phases between support conditions within species were found in all species except for *Propithecus coquereli* (Table 4.11). Most species showed significant changes to both limbs in both stance and swing phase duration – as observed *Cheirogaleus medius, Microcebus murinus, Eulemur mongoz, Varecia variegata,* and *Nycticebus pygmaeus* – although significant differences did not always occur

between the same support conditions within species (Tables 4.12, 4.13, 4.14, and 4.15).

4.4 Discussion

Previous studies that have considered the evolution of the primate gait complex have generally focused upon the use of diagonal sequence (DS) gaits on horizontal supports. Only a few studies have considered if and how primates of various taxonomic affiliations use this gait on oblique and vertical supports, and it has been specially noted that primates in these studies shift from using diagonal sequences on horizontal and inclined supports, to lateral sequences on declined and vertical supports by Rollinson and Martin (1981), Vilensky et al. (1994), Stevens (2003), Nyakatura et al. (2008), Hesse et al. (2015), and Granatosky et al. (2019).

This study tested the hypothesis that a shift in limb phase towards lateral sequences would characterize travel on declined supports in strepsirrhines regardless of body size or habitual substrate use. This finding was widely confirmed for declines steeper than 30°, and significantly so in most species included in the sample ranging in species average body mass from 0.2 to 3.5 kg (Tables 4.4, 4.5, and 4.6).

However, while gaits became more lateral in limb phase (*D*), they did not actually cross into the territory of what are recognized as lateral sequence gaits ($D < 45$) for most species moving on non-vertical declines. Instead, within this sample, diagonal sequence diagonal couplet (DSDC; $55 < D < 75$) and trotting

($45 \leq D \leq 55$) gaits were used at much higher frequencies than any lateral sequence gaits on non-vertical supports for all species except for *Propithecus coquereli* and both *Eulemur coronatus* and *Eulemur mongoz* (Figures 4.1, 4.2).

P. coquereli in the present study used higher frequencies of LS gaits on all supports relative to the rest of the sample. These observations were mostly drawn from a single individual (PCM1) and are not consistent with other studies of above branch quadrupedalism on horizontal supports by *P. coquereli* (Granatosky et al. 2016), which report that the gait in this species follow a DSDC pattern. While *P. coquereli* showed the expected trends of decreasing limb phase and decreasing SI on increasingly steep supports, these shifts were not found to be significant, and may not be representative of the typical behaviors of this species (c.f. Chapter 3).

E. coronatus and *E. mongoz* both steadily increased use of lateral sequence diagonal couplet (LSDC) and lateral sequence lateral couplet (LSLC) gaits with significant decreases in limb phase as support orientations increased from 30° to 90°. Stevens (2003) observed two closely related species, *Eulemur fulvus* (n = 2) and *Eulemur rubriventer* (n = 2), on similarly oriented supports (30° and 60°) and found that *E. fulvus* and *E. rubriventer* used mostly diagonal sequences on 30° declines, and that *E. fulvus* used more lateral sequences on 60° (*E. rubriventer* would not symmetrically descend headfirst on that support angle). The results of the present study and Stevens (2003) seem to support that *Eulemur* species regularly engage in lateral sequence gaits on steep supports.

The other species considered by Stevens (2003) include *Microcebus coquereli, Cheirogaleus medius, Nycticebus coucang*, and *Loris tardigradus*. Stevens (2003) reported high within-species variation in gait use, but generally it appeared that DS and trotting gaits were still used at a higher frequency than LS gaits in that study by all but the *Eulemur* and one *C. medius* moving on both 30° and 60° declines (Stevens 2003, page 350). From the present study, Stevens (2003), and Shapiro et al. (2016) it appears that the use of true LS gaits on declines may only characterize certain species of strepsirrhine.

Stevens (2003) suggested that increases to LS gait use might be a result of low intermembral indices (IMI) – which range from 68 to 72 in these four *Eulemur* species (Fleagle 2013) – however, other species from the present sample overlap in the same range of IMI and did not show similar frequencies of LS gaits on the same support orientations. Further, the IMI argument does not appear to be extendable to haplorrhine primates studied on declines given that previously sampled anthropoids tend to have relatively higher IMI (Rollinson and Martin 1981; Vilensky et al. 1994) but are reported to use LS gaits on declines less than 30°.

Hesse et al. (2015) collected kinematic data on tamarins to test the hypothesis that changes to forelimb duty factor relative to hind limb duty factor on declines drives increases to limb phase on inclines and decrease on declines (Cartmill et al. 2002; Stevens 2006). They report compelling evidence for this hypothesis on supports ranging from a 30° decline to a 60° incline. However,

duty factor index was not reported to be different between the declines tested in that study (30°, 45°, and 60°), and LS gaits decreased in frequency on the steeper declines (45° and 60°) when the underlying mechanism for this hypothesis, increased forelimb braking causing the relative increase in S_F, was demonstrated to be highest.

In the present study, duty factor index did not show the same steady decrease with support orientation changes between horizontal and 30° across all species (Table 4.4) as found by Hesse et al. (2015). Hesse et al. (2015) did not find changes to stance duration on declines and reported forelimb stance phases that were generally longer than hind limb stance phases. In contrast, strepsirrhine primates in this sample tended towards having equal or longer hind limb stance phase duration compared to forelimb stance phase durations, with gradual increases in both limbs as supports became steeper (Table 4.10). The locomotion of tamarins observed by Hesse et al. (2015) may just be substantially different from the strepsirrhines of the present sample, especially considering the size and ecological differences between these species, and that may explain these differences.

The results presented here for duty factor index do not support the hypothesis that progressive decreases in SI are driving limb phase changes on declines. It would be predicted that at lower SI, gaits should be more lateral in limb phase based on arguments that higher forelimb duty factors are associated with lateral sequences (Cartmill et al. 2002; Stevens 2006; Nyakatura et al. 2008;

Hesse et al. 2015). However, this was not the case for *Nycticebus pygmaeus* which always had a median SI value below 1, but rarely used LS gaits on supports from 0° to 60°. In contrast, species such as *E. mongoz* were observed to have the same median SI for both slight (15°) and steep (60°) declines but with very different median limb phases (Table 4.4). While mathematically forelimb duty factors are linked to LS gaits (Cartmill et al. 2002; Lemelin and Cartmill 2010), and subtle increases to forelimb duty factor will produce more lateral limb phases (Stevens 2006), these observations seem to point to a more complicated relationship between SI and limb phase, especially on steeper declines.

On vertical supports, only five species in this sample engaged in symmetrical headfirst descent – *Cheirogaleus medius, Microcebus murinus, Eulemur coronatus, Varecia variegata*, and *Nycticebus pygmaeus* – and median limb phase in all these species was significantly decreased relative to a horizontal support apart from *M. murinus* (Table 4.6). This is consistent with reports of limb phase significantly decreasing in primates vertically ascending compared to horizontal travel by Granatosky et al. (2019). Interestingly, for strepsirrhines in that sample (*Loris tardigradus, Cheirogaleus medius, Nycticebus pygmaeus, Eulemur mongoz,* and *Daubentonia madagascariensis*) frequencies of DSDC and trotting gaits still made up most observations despite limb phase significantly lowering (Granatosky et al. 2019).

Granatosky et al. (2019) make a mechanical argument for why both DSDC and LSLC gaits would be potentially disadvantageous during vertical ascent by

pointing out that these gaits maximize time in which the body is only supported by two limbs in close proximity to each other (Figure 1.4). According to models of vertical ascent by Cartmill (1974b) and Jungers (1976), the vertical distance between the limbs in contact with the support will determine the horizontal component of reaction force experienced by the feet. This force can be minimized by spreading the supporting limbs in contact as far apart vertically as possible (Cartmill 1974b; Jungers 1976), and animals may seek to adopt gaits that spread the supporting limbs to minimize risk of falls. Granatosky et al. (2019) point out that an LSDC gait would help to minimize the time in which an animal is supported by two limbs that are spatially close together (Figure 1.4). During descent, a LSDC gait may offer the added advantage of having both forelimbs in contact with the support to provide braking when either hind limb is aerial, a time during which the animal might be at the greatest risk of pitching away from the support. Given these mechanical arguments, it is surprising that LSDC gaits were not more common on steep declines, especially compared to LSLC and DSDC gaits when considering the perceived disadvantages of those two gaits on vertical and near vertical supports (Granatosky et al. 2019).

One gait that has not been well explored yet by the existing decline literature is the trot, even though this gait often represents a higher frequency of the symmetrical gaits used on declines and vertical supports than LS gaits (Stevens 2003; Hesse et al. 2015; Granatosky et al. 2019). In the present sample, trotting was the preferred gait of *M. murinus*, and steadily increased in

frequency in *C. medius*, *D. madagascariensis*, *E. coronatus*, *E. mongoz*, and *V. variegata* with increasing support steepness (Table 4.3). *N. pygmaeus* also used high frequencies of this gait, although these frequencies peaked on the 60° decline and then gradually decreased in favor of LSDC gaits (Table 4.3).

Trotting exists between LS and DS gaits and can be considered a sequence-less diagonal couplet gait, meaning that time spent supported by diagonal bipods is maximized, and time spent supported by three legs is minimized (Gambaryan 1974; Hildebrand 1980; Cartmill et al. 2002). Trotting is rarely observed in primates moving on horizontal supports and lacks the perceived advantage of DSDC gaits that allows for the forelimb to test an untested support while both hind limbs maintain a secure grasp (Cartmill et al. 2002; Schmitt et al. 2006; Cartmill et al. 2007) (Figure 1.4). However, steep and vertical supports may not need testing in the same way as horizontal supports, since they may already be maximally bent beneath the weight of the primate, suggesting that DSDC gaits may only provide advantages in certain arboreal contexts, such as on horizontal supports.

As support orientation increases, it was observed that duty factor in the hind (S_H) and forelimb (S_F) increased (Table 4.4, Figure 4.3), indicating relatively longer contact times for both hands and feet across the entire sample. In this context, trotting gaits with extended contact periods may represent a means by which primates maximize time spent on vertically dispersed diagonal bipods when descending. Trotting also eliminates time in which an animal is supported

only by ipsilateral (same side) limbs (Gambaryan 1974; Hildebrand 1980), which may be an important factor for stability, especially at slower speeds.

4.5 Summary

This study replicated the findings of previous studies that limb phase undergoes gradual decreases in all strepsirrhine primates as they move on steeper supports, and both forelimb and hind limb duty factor increases with support orientation, although duty factor index did not appear to undergo much change in this sample. While limb phase decreased in species in this sample, strepsirrhines observed on declines and vertical supports appeared to use greater frequencies of slow trotting gaits than true lateral sequence gaits, which may provide a mechanical advantage by increasing distance between supporting hands and feet (Cartmill 1974b; Jungers 1976; Granatosky et al. 2019).

When species did engage in relatively high frequencies of LS gaits, it tended to be upon support orientations where non-headfirst descents were also observed, as reported on in the previous chapter. Species that were the most adept at headfirst descent – *Cheirogaleus medius*, *Microcebus murinus*, and *Nycticebus pygmaeus* – did not tend to use LS gaits until the steepest and vertical supports. This may speak to the importance of flexibility in gait at larger body sizes in primates, and the association of diagonal sequence with more horizontal and weakly oblique supports.

Future analyses of primates on declines should be conducted in a more diverse sample of anthropoids moving on supports greater than 30° to test if

general patterns found here in strepsirrhines apply to primates generally. In the next chapter, the spatial aspects of gait – joint yield, limb excursion, stride length and velocity – will be analyzed for changes across support orientations. It is expected that these results will lend context to the understanding the underlying mechanisms that drove the changes to temporal aspects of gait reported on here.

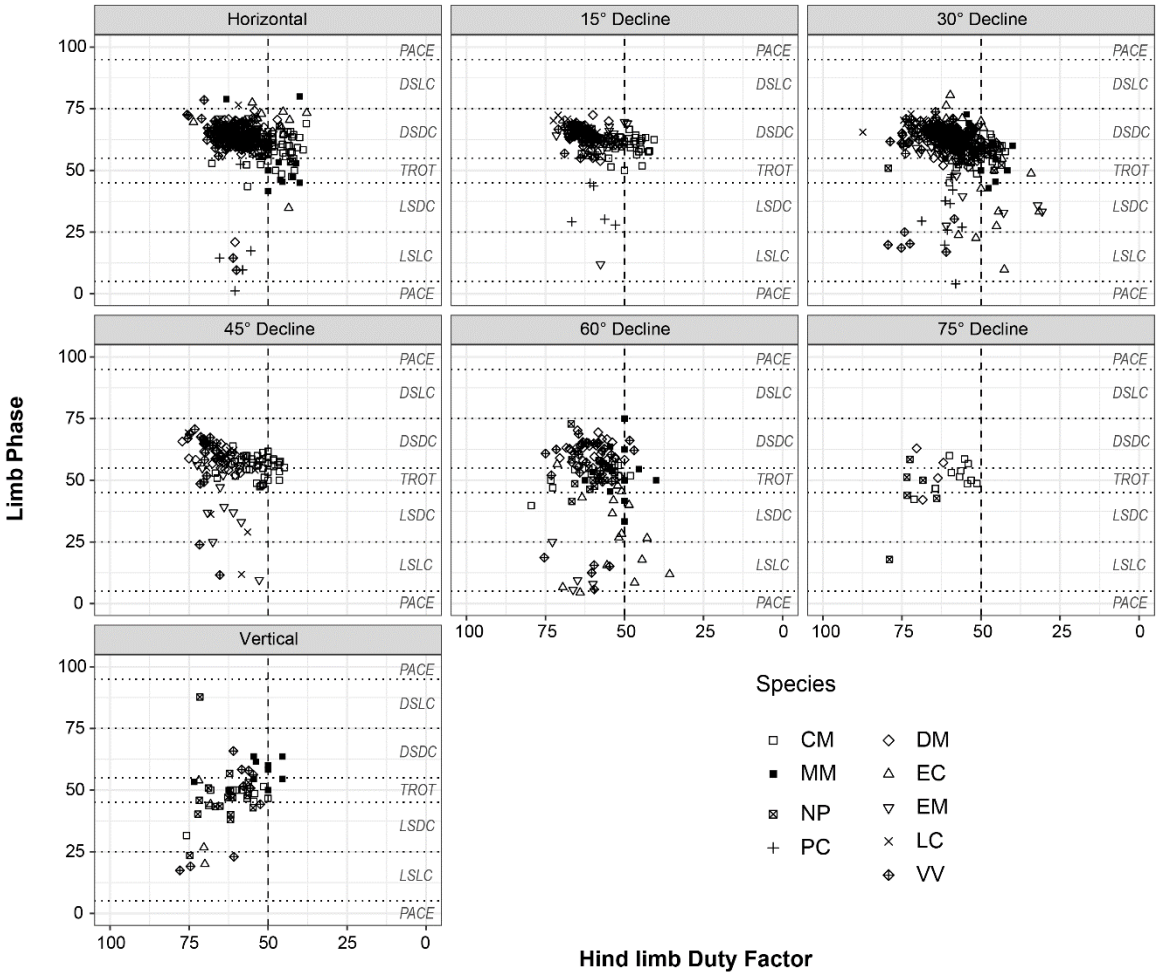


Figure 4-1: Changes to duty factor and limb phase with support orientation steepness for all symmetrical headfirst gaits. Abbreviations: CM – *Cheirogaleus medius*, DM – *Daubentonia madagascariensis*, EC – *Eulemur coronatus*, EM – *Eulemur mongoz*, LC – *Lemur catta*, MM – *Microcebus murinus*, NP – *Nycticebus pygmaeus*, PC – *Propithecus coquereli*, VV – *Varecia variegata*, DSLC – Diagonal sequence lateral couplet, DSDC – Diagonal sequence diagonal couplet, LSLC – Lateral sequence lateral couplet, LSDC – Lateral sequence diagonal couplet.

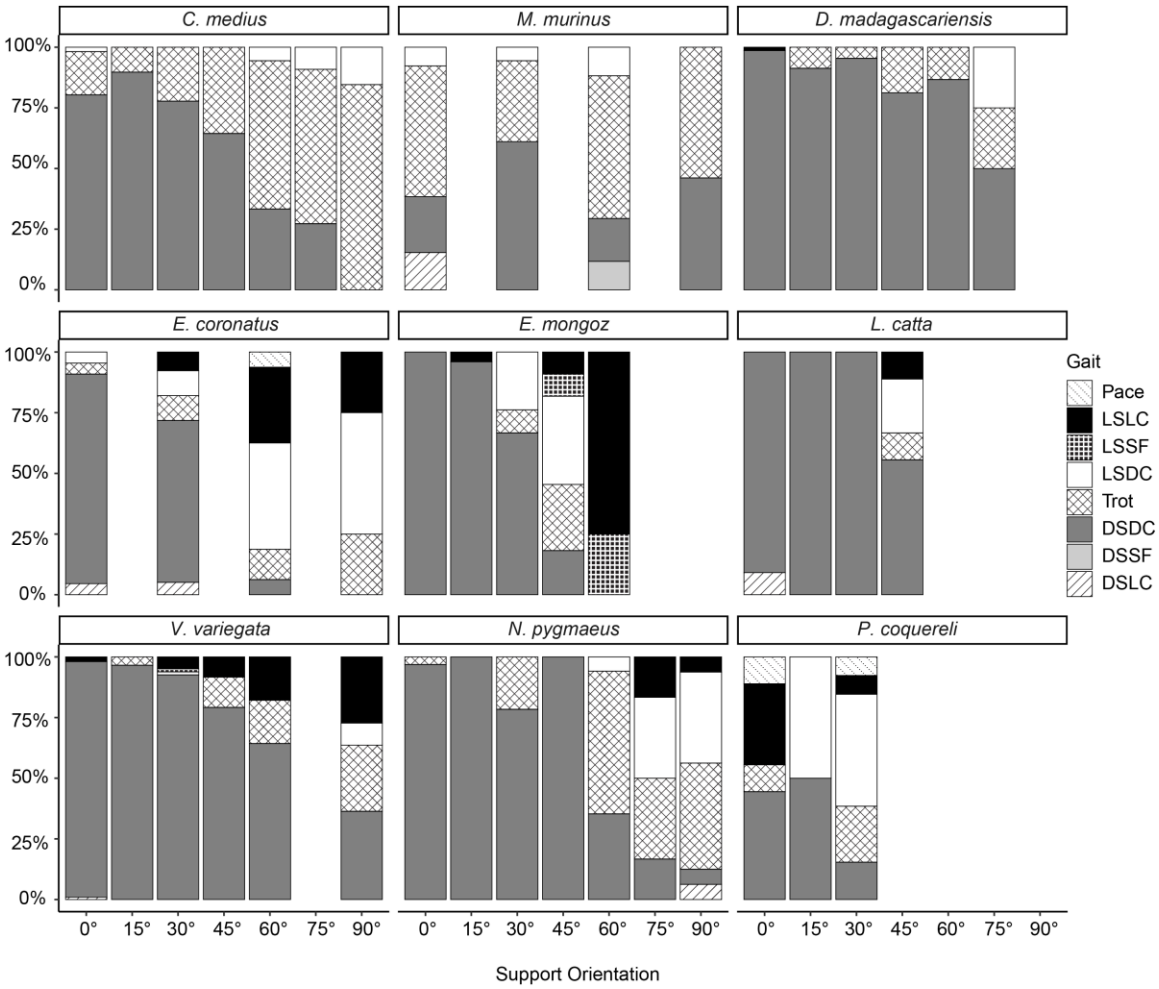


Figure 4-2: Changes to proportions of symmetrical gaits observed on each support orientation by species. Abbreviations: LS – lateral sequence, DS – diagonal sequence, SF – single foot, LC – lateral couplet, DC – diagonal couplet.

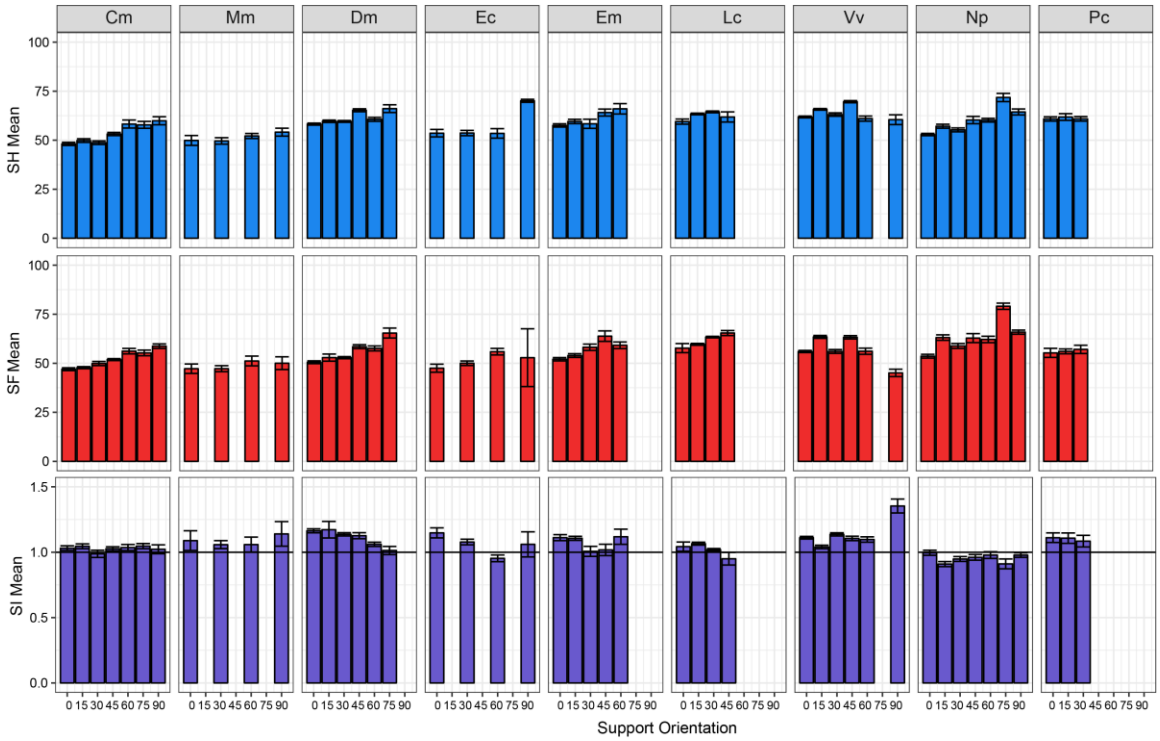


Figure 4-3: Mean duty factor changes across support orientations by species. Duty factor for both the hind (S_H) and forelimb (S_F) increased with support steepness, indicating relative increases in contact time of the feet and hands respectively. Bars represent the mean and standard error around the mean for each measure. The line at 1 for duty factor index (SI) indicates when S_H is equal to S_F. Abbreviations: Cm – *Cheirogaleus medius*, Mm – *Microcebus murinus*, Dm – *Daubentonia madagascariensis*, Ec – *Eulemur coronatus*, Em – *Eulemur mongoz*, Lc – *Lemur catta*, Vv – *Varecia variegata*, Np – *Nycticebus pygmaeus*, Pc – *Propithecus coquereli*.

Table 4.1: Definitions and abbreviations for temporal gait parameters.

Variable	Abbreviation	Definition
Touchdown	TD (1 and 2)	The initial and subsequent points when the HL or FL makes contact with the support
Take-off	TO	The point when the HL or FL leave contact with the support
Stride duration	StrDur	Duration (seconds) between the first and subsequent touchdown of the hind limb (time between TD1 and TD2)
Stance phase duration		Duration (seconds) of contact with the support (time between TD1 and TO)
Swing phase duration		Duration (seconds) when the limb is aerial (time between TO and TD2)
Limb phase	*D*	The percentage of time that the forelimb follows the ipsilateral (same side) hind limb
Stride Symmetry		Frames between the first hindfoot touchdown and the next (contralateral) hindfoot touchdown as a percentage of total stride duration
Hind limb Duty Factor	S_H	Hind limb stance period as a percentage of the total stride duration
Forelimb Duty Factor	S_F	Forelimb stance period as a percentage of the forelimb stride duration
Duty Factor Index	SI	Hind limb duty factor/Forelimb duty factor

Table 4.2: Summary of strides footfalls analyzed for each species on each support.

Species	Support Orientation (Degrees)	# of individuals	Total Strides Analyzed (n)	Asymmetrical Strides (n)	% Asymmetrical	Symmetrical Strides (n)	Walks (n)	Ambles (n)	Runs (n)
C. medius	0	4	85	29	34.12%	56	12	14	30
	15	4	51	12	23.53%	39	9	11	19
	30	4	47	20	42.55%	27	5	12	10
	45	4	58	13	22.41%	45	27	10	8
	60	2	23	5	21.74%	18	16	1	1
	75	2	24	13	54.17%	11	11	0	0
	90	2	23	10	43.48%	13	13	0	0
M. murinus	0	4	33	20	60.61%	13	4	2	7
	30	4	47	29	61.70%	18	6	3	9
	60	4	67	50	74.63%	17	10	1	6
	90	4	47	34	72.34%	13	6	4	3
D. madagascariensis	0	6	86	16	18.60%	70	43	25	2
	15	2	28	5	17.86%	23	18	5	0
	30	6	152	43	28.29%	109	79	28	2
	45	2	44	12	27.27%	32	31	1	0
	60	5	55	25	45.45%	30	26	4	0
	75	2	10	6	60.00%	4	4	0	0
	90	1	9	9	100.00%	0	0	0	0
E. coronatus	0	4	34	12	35.29%	22	9	6	7
	30	4	79	40	50.63%	39	21	12	6
	60	4	51	35	68.63%	16	10	4	2
	90	2	10	6	60.00%	4	3	1	0
E. mongoz	0	3	26	1	3.85%	25	17	8	0

	15	3	29	4	13.79%	25	20	4	1
	30	3	37	16	43.24%	21	17	3	1
	45	3	21	10	47.62%	11	10	0	1
	60	1	7	3	42.86%	4	4	0	0
L. catta	0	2	15	4	26.67%	11	9	2	0
	15	4	51	1	1.96%	50	49	1	0
	30	4	89	7	7.87%	82	82	0	0
	45	4	19	10	52.63%	9	9	0	0
V. variegata	0	6	125	21	16.80%	104	90	14	0
	15	3	34	5	14.71%	29	29	0	0
	30	6	101	20	19.80%	81	64	16	1
	45	3	42	18	42.86%	24	24	0	0
	60	6	67	39	58.21%	28	23	2	3
	90	3	42	31	73.81%	11	3	5	3
N. pygmaeus	0	3	37	5	13.51%	32	23	7	2
	15	1	17	3	17.65%	14	14	0	0
	30	3	49	12	24.49%	37	31	3	3
	45	1	12	8	66.67%	4	4	0	0
	60	3	33	16	48.48%	17	17	0	0
	75	1	9	3	33.33%	6	6	0	0
	90	3	25	9	36.00%	16	16	0	0
P. coquereli	0	2	11	2	18.18%	9	7	0	2
	15	1	15	5	33.33%	10	9	1	0
	30	1	18	5	27.78%	13	12	0	1
Total			1994	702		1292			

Table 4.3: Summary gait types observed in each species on each support condition. Gait types are reported as percentages of all analyzed symmetrical headfirst strides. Abbreviations – LSLC – Lateral sequence; LC – Lateral couplet; DS – Diagonal Sequence; DC – Diagonal Couplet; SF – Single Foot

Species	Support (Degrees)	Strides (n)	%Pace	%LS LC	%LS SF	%LS DC	%Trot	%DS DC	%DS SF	%DS LC
C. medius	0	56	0%	0%	0%	1.79%	17.86%	80.36%	0%	0%
	15	39	0%	0%	0%	0%	10.26%	89.74%	0%	0%
	30	27	0%	0%	0%	0%	22.22%	77.78%	0%	0%
	45	45	0%	0%	0%	0%	35.56%	64.44%	0%	0%
	60	18	0%	0%	0%	5.56%	61.11%	33.33%	0%	0%
	75	11	0%	0%	0%	9.09%	63.64%	27.27%	0%	0%
	90	13	0%	0%	0%	15.38%	84.62%	0%	0%	0%
M. murinus	0	13	0%	0%	0%	7.69%	53.85%	23.08%	0%	15.38%
	30	18	0%	0%	0%	5.56%	33.33%	61.11%	0%	0%
	60	17	0%	0%	0%	11.76%	58.82%	17.65%	11.76%	0%
	90	13	0%	0%	0%	0%	53.85%	46.15%	0%	0%
D. Madagascar-iensis	0	70	0%	1.43%	0%	0%	0%	98.57%	0%	0%
	15	23	0%	0%	0%	0%	8.70%	91.30%	0%	0%
	30	109	0%	0%	0%	0%	4.59%	95.41%	0%	0%
	45	32	0%	0%	0%	0%	18.75%	81.25%	0%	0%
	60	30	0%	0%	0%	0%	13.33%	86.67%	0%	0%
	75	4	0%	0%	0%	25.00%	25.00%	50%	0%	0%
E. coronatus	0	22	0%	0%	0%	4.55%	4.55%	86.36%	0%	4.55%
	30	39	0%	7.69%	0%	10.26%	10.26%	66.67%	0%	5.13%
	60	16	6.25%	31.25%	0%	43.75%	12.50%	6.25%	0%	0%
	90	4	0%	25.00%	0%	50%	25.00%	0%	0%	0%

E. mongoz	0	25	0%	0%	0%	0%	0%	100%	0%	0%
	15	25	0%	4.00%	0%	0%	0%	96.00%	0%	0%
	30	21	0%	0%	0%	23.81%	9.52%	66.67%	0%	0%
	45	11	0%	9.09%	9.09%	36.36%	27.27%	18.18%	0%	0%
	60	4	0%	75.00%	25.00%	0%	0%	0%	0%	0%
L. catta	0	11	0%	0%	0%	0%	0%	100%	0%	0%
	15	50	0%	0%	0%	0%	0%	100%	0%	0%
	30	82	0%	0%	0%	0%	0%	100%	0%	0%
	45	9	0%	11.11%	0%	22.22%	11.11%	55.56%	0%	0%
V. variegata	0	104	0%	1.92%	0%	0%	0%	97.12%	0%	0.96%
	15	29	0%	0%	0%	0%	3.45%	96.55%	0%	0%
	30	81	0%	4.94%	1.23%	1.23%	0%	92.59%	0%	0%
	45	24	0%	8.33%	0%	0%	12.50%	79.17%	0%	0%
	60	28	0%	17.86%	0%	0%	17.86%	64.29%	0%	0%
	90	11	0%	27.27%	0%	9.09%	27.27%	36.36%	0%	0%
N. pygmaeus	0	32	0%	0%	0%	0%	3.13%	96.88%	0%	0%
	15	14	0%	0%	0%	0%	0%	100%	0%	0%
	30	37	0%	0%	0%	0%	21.62%	78.38%	0%	0%
	45	4	0%	0%	0%	0%	0%	100%	0%	0%
	60	17	0%	0%	0%	5.88%	58.82%	35.29%	0%	0%
	75	6	0%	16.67%	0%	33.33%	33.33%	16.67%	0%	0%
	90	16	0%	6.25%	0%	37.50%	43.75%	6.25%	0%	6.25%
P. coquereli	0	9	11.11%	33.33%	0%	0%	11.11%	44.44%	0%	0%
	15	10	0%	0%	0%	50%	0%	50%	0%	0%
	30	13	7.69%	7.69%	0%	46.15%	23.08%	15.38%	0%	0%

Table 4.4: Summary of limb phase and duty factors observed in each species for each support condition. Abbreviations – Med – median; SD – standard deviation.

		Limb phase			Hind limb Duty Factor			Forelimb Duty Factor			Duty Factor Index		
Species	Support (degrees)	Mean	Med	SD	Mean	Med	SD	Mean	Med	SD	Mean	Med	SD
C. medius	0	59.53	60.23	5.40	48.11	48.28	6.06	46.98	46.29	5.28	1.03	1.00	0.13
	15	59.95	60.61	3.82	49.82	48.48	5.75	47.76	47.06	3.35	1.05	1.04	0.12
	30	57.80	58.62	4.76	48.73	47.06	4.82	49.88	50.00	5.45	0.99	0.93	0.14
	45	55.68	56.67	4.05	53.15	51.72	5.36	51.88	51.85	3.35	1.03	1.03	0.10
	60	52.87	54.07	4.27	58.24	54.84	8.71	56.20	54.69	5.89	1.04	1.03	0.10
	75	51.81	51.35	5.33	57.82	56.41	5.75	55.29	53.57	4.72	1.05	1.04	0.07
	90	47.01	48.57	5.15	59.90	58.33	7.37	58.73	60.47	4.17	1.02	1.04	0.12
M. murinus	0	56.29	52.94	12.78	49.89	46.67	9.08	47.23	50.00	8.68	1.09	1.00	0.27
	30	57.88	60.00	8.01	49.61	48.81	6.96	47.24	46.67	6.47	1.06	1.01	0.13
	60	54.34	53.85	10.52	52.14	50.00	5.25	51.16	50.00	10.28	1.06	1.02	0.24
	90	57.10	54.55	4.99	54.10	54.55	7.31	50.04	50.00	11.73	1.14	1.09	0.34

D. madagascariensis	0	64.52	65.00	6.64	58.20	57.79	4.16	50.51	51.32	5.98	1.16	1.14	0.13
	15	62.96	62.50	3.98	59.64	60.00	2.96	52.89	53.85	8.77	1.17	1.09	0.30
	30	62.38	62.79	4.01	59.56	60.34	4.70	52.85	53.49	5.71	1.14	1.13	0.13
	45	58.90	59.28	3.40	65.25	64.93	4.10	58.46	57.89	5.56	1.13	1.11	0.13
	60	60.62	60.09	4.70	60.64	60.56	5.52	57.57	57.84	6.80	1.06	1.04	0.09
	75	53.28	54.03	8.93	66.08	66.03	3.97	65.40	67.48	5.08	1.01	1.03	0.06
E. coronatus	0	65.27	66.04	8.68	53.58	53.23	9.00	47.49	44.51	9.62	1.15	1.13	0.18
	30	57.23	63.24	15.95	53.64	54.24	8.38	50.01	50.59	7.21	1.08	1.10	0.14
	60	28.61	27.54	16.43	53.46	51.98	9.62	55.90	55.21	6.66	0.95	0.94	0.10
	90	36.25	35.53	15.62	70.10	70.15	1.53	52.84	63.54	29.46	1.06	1.02	0.17
E. mongoz	0	64.67	65.88	4.11	57.52	56.34	4.13	52.04	51.39	4.28	1.11	1.11	0.11
	15	62.02	63.93	10.94	59.54	60.22	5.48	53.94	53.62	4.74	1.11	1.11	0.08
	30	52.99	58.02	11.74	58.36	60.99	10.74	58.16	56.96	7.44	1.01	1.04	0.18
	45	40.63	39.18	14.65	64.09	64.23	5.85	63.83	63.33	8.90	1.02	1.01	0.14
	60	12.02	8.73	8.80	66.00	65.58	5.29	59.17	58.51	3.40	1.12	1.11	0.12
L. catta	0	65.23	65.00	5.13	59.48	60.29	4.34	57.72	58.33	7.63	1.04	1.02	0.12
	15	66.41	66.67	2.61	63.37	62.87	3.12	59.67	59.70	3.34	1.07	1.05	0.08

	30	65.81	65.53	2.36	64.43	63.68	4.16	63.35	63.57	3.33	1.02	1.02	0.08
	45	48.81	55.10	18.93	61.84	60.81	7.71	65.42	66.67	3.83	0.95	0.91	0.15
V. variegata	0	63.21	64.04	7.96	61.84	61.26	4.60	55.99	55.80	5.38	1.11	1.10	0.10
	15	64.34	64.46	3.22	65.72	65.43	2.21	63.43	62.31	4.05	1.04	1.04	0.07
	30	61.46	65.09	11.86	63.08	61.76	7.65	56.04	55.45	8.60	1.14	1.12	0.11
	45	58.82	64.09	14.04	69.63	69.99	2.64	63.25	62.95	4.18	1.11	1.11	0.08
	60	52.36	61.27	19.21	61.01	60.08	6.94	56.14	56.90	8.26	1.10	1.10	0.11
	90	45.03	50.82	17.12	60.45	57.81	8.23	45.08	43.48	6.23	1.35	1.37	0.18
N. pygmaeus	0	61.65	62.74	3.69	52.87	53.55	3.30	53.59	54.23	5.50	1.00	0.99	0.11
	15	61.61	62.62	3.06	57.12	58.11	3.78	63.08	65.19	5.21	0.91	0.89	0.07
	30	58.41	58.51	4.21	55.26	54.88	6.00	58.83	57.89	7.63	0.95	0.94	0.11
	45	59.38	59.61	1.80	60.28	59.53	3.73	62.83	62.62	4.55	0.96	0.97	0.04
	60	53.08	51.52	6.85	60.22	58.62	3.91	62.13	63.33	6.78	0.98	0.95	0.10
	75	44.04	46.98	14.00	71.78	72.93	5.09	79.07	79.74	3.87	0.91	0.93	0.09
	90	47.36	46.41	13.12	64.40	62.45	6.10	65.87	65.94	4.22	0.98	0.98	0.07
P. coquereli	0	39.75	52.50	28.27	60.84	60.92	3.21	55.30	56.00	6.98	1.11	1.13	0.11
	15	49.21	50.62	16.34	61.81	60.34	5.37	56.06	56.28	3.89	1.11	1.11	0.13
	30	38.70	37.63	17.80	60.89	59.76	4.07	57.07	57.63	7.62	1.08	1.07	0.16

Table 4.5: Kruskal-Wallis results for hind and forelimb duty factor, duty factor index, and limb phase, within each species between support orientations.Significant values (<0.05) are indicated in bold, indicating differences in median value for each variable between support conditions. Abbreviations: d.f. – Degrees of Freedom; S_H – Hind Limb Duty Factor; S_F – Forelimb Duty Factor; SI – Duty Factor Index.

Species		Limb phase		S_H		S_F		SI	
	d.f.	χ^2	p-value	χ^2	p-value	χ^2	p-value	χ^2	p-value
C. medius	6	76.54	**<0.001**	65.16	**<0.001**	89.83	**<0.001**	9.44	0.15
M. murinus	3	2.69	0.442	4.79	0.1876	1.24	0.743	0.42	0.935
D. madagascariensis	5	51.58	**<0.001**	51.15	**<0.001**	54.38	**<0.001**	21.08	**<0.001**
E. coronatus	3	35.67	**<0.001**	9.84	**0.019**	10.41	**0.015**	15.30	**0.001**
E. monogoz	4	48.03	**<0.001**	14.32	**0.006**	23.55	**<0.001**	9.80	**0.043**
L. catta	3	18.39	**<0.001**	13.53	**0.003**	36.73	**<0.001**	14.86	**0.001**
V. variegata	5	31.68	**<0.001**	51.80	**<0.001**	71.78	**<0.001**	35.69	**<0.001**
N. pygmaeus	6	59.66	**<0.001**	64.19	**<0.001**	54.23	**<0.001**	14.02	**0.029**
P. coquereli	2	1.63	0.443	0.32	0.851	1.35	0.509	0.96	0.618

Table 4.6: Dunn's test results for median differences in Limb Phase within species between support conditions.Comparisons were conducted for species in which the results of a Kruskal-Wallis test detected significant differences between support orientation conditions. P-values are adjusted using the correction of Benjamini and Hochberg (1995). Significant values (<0.05) denoted in bold.

Support Contrast	*C. medius*		*D. madagascariensis*		*E. coronatus*		*E mongoz*		*L. catta*		*V. variegata*		*N. pygmaeus*	
	Z	p	Z	p	Z	p	Z	p	Z	p	Z	p	Z	p
0 to 15	0.383	0.737	-1.854	0.096	*NA*	*NA*	-0.578	0.563	1.694	0.135	0.843	0.499	0.016	0.987
0 to 30	1.352	0.195	3.519	**0.002**	1.968	0.059	3.989	**0.000**	-0.956	0.339	-0.551	0.623	2.570	**0.021**
0 to 45	-3.958	**0.000**	-6.356	**0.000**	NA	NA	-5.014	**0.000**	-2.098	0.072	-0.698	0.560	-0.952	0.448
0 to 60	4.727	**0.000**	4.237	**0.000**	5.548	**0.000**	4.255	**0.000**	NA	NA	3.167	**0.003**	4.674	**0.000**
0 to 75	4.077	**0.000**	3.272	**0.003**	NA	NA	NA	NA	NA	NA	NA	NA	4.139	**0.000**
0 to 90	6.205	**0.000**	NA	NA	3.016	**0.005**	NA	NA	NA	NA	4.172	**0.000**	5.976	**0.000**
15 to 30	1.584	0.140	0.407	0.684	NA	NA	3.437	**0.001**	1.435	0.182	0.441	0.659	1.993	0.075
15 to 45	3.987	**0.000**	3.332	**0.003**	NA	NA	4.562	**0.000**	4.162	**0.000**	1.214	0.337	0.900	0.430
15 to 60	4.775	**0.000**	1.728	0.114	NA	NA	3.952	**0.000**	NA	NA	3.213	**0.004**	3.901	**0.000**
15 to 75	4.173	**0.000**	2.282	**0.048**	NA	NA	NA	NA	NA	NA	NA	NA	3.784	**0.000**
15 to 90	6.214	**0.000**	NA	NA	NA	NA	NA	NA	NA	NA	4.235	**0.000**	5.014	**0.000**
30 to 45	-1.954	0.082	-4.065	**0.000**	NA	NA	-1.701	0.111	-3.559	**0.001**	-1.031	0.412	0.219	0.913
30 to 60	-3.169	**0.003**	-1.870	0.102	-4.372	**0.000**	-2.036	0.060	NA	NA	-3.448	**0.002**	-2.671	**0.018**
30 to 75	-2.874	**0.007**	-2.245	**0.046**	NA	NA	NA	NA	NA	NA	NA	NA	-2.774	**0.015**
30 to 90	4.720	**0.000**	NA	NA	2.123	0.051	NA	NA	NA	NA	4.371	**0.000**	4.042	**0.000**

45 to 60	1.751	0.120	-1.699	0.112	NA	NA	0.818	0.460	NA	NA	1.856	0.119	1.616	0.159
45 to 75	1.642	0.132	0.614	0.578	NA	NA	NA	NA	NA	NA	NA	NA	2.070	0.067
45 to 90	3.550	**0.001**	NA	NA	NA	NA	NA	NA	NA	NA	3.199	**0.003**	2.370	**0.034**
60 to 75	-0.167	0.868	-1.423	0.179	NA	NA	NA	NA	NA	NA	NA	NA	-0.923	0.440
60 to 90	1.729	0.117	NA	NA	-0.328	0.743	NA	NA	NA	NA	1.822	0.114	1.226	0.308
75 to 90	1.380	0.195	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	-0.024	1.000

Table 4.7: Dunn's test results for median differences in hind limb duty factor within species between support conditions. Comparisons were conducted for species in which the results of a Kruskal-Wallis test detected significant differences between support orientation conditions. P-values are adjusted using the correction of Benjamini and Hochberg (1995). Significant values (<0.05) denoted in bold.

Support contrast	*C. medius*		*D. madagascariensis*		*E. coronatus*		*E. mongoz*		*L. catta*		*V. variegata*		*N. pygmaeus*	
	Z	p	Z	p	Z	p	Z	p	Z	p	Z	p	Z	p
0 to 15	1.361	0.228	1.137	0.348	NA	NA	1.376	0.211	2.434	**0.045**	3.668	**0.001**	2.805	**0.013**
0 to 30	-0.409	0.755	-2.040	0.069	-0.271	0.944	-1.916	0.111	-3.384	**0.004**	-0.955	0.392	-1.995	0.088
0 to 45	4.192	**0.000**	6.650	**0.000**	NA	NA	3.104	**0.019**	1.125	0.313	5.887	**0.000**	2.756	**0.014**
0 to 60	-5.035	**0.000**	-2.419	**0.039**	0.051	0.959	-2.671	**0.038**	NA	NA	0.661	0.509	-4.742	**0.000**
0 to 75	-4.507	**0.000**	-2.959	**0.009**	NA	NA	NA	NA	NA	NA	NA	NA	-5.280	**0.000**
0 to 90	-5.224	**0.000**	NA	NA	-3.002	**0.016**	NA	NA	NA	NA	1.242	0.268	-5.994	**0.000**
15 to 30	0.752	0.559	-0.171	0.864	NA	NA	-0.601	0.609	-1.539	0.186	2.906	**0.007**	1.330	0.241
15 to 45	-2.538	**0.019**	-4.191	**0.000**	NA	NA	-2.028	0.142	0.843	0.399	-2.040	0.069	-0.992	0.355
15 to 60	-3.792	**0.000**	-0.918	0.414	NA	NA	-1.948	0.129	NA	NA	3.439	**0.001**	-1.452	0.220
15 to 75	-3.522	**0.001**	-2.304	**0.040**	NA	NA	NA	NA	NA	NA	NA	NA	-2.972	**0.009**
15 to 90	-4.135	**0.000**	NA	NA	NA	NA	NA	NA	NA	NA	3.287	**0.002**	-2.559	**0.022**
30 to 60	4.169	**0.000**	1.044	0.370	-0.300	1.000	1.597	0.184	NA	NA	-1.287	0.270	3.213	**0.005**
30 to 75	3.887	**0.000**	2.374	**0.038**	NA	NA	NA	NA	NA	NA	NA	NA	4.244	**0.000**
30 to 90	-4.480	**0.000**	NA	NA	-2.971	**0.009**	NA	NA	NA	NA	1.666	0.144	-4.525	**0.000**
45 to 30	3.054	**0.004**	5.503	**0.000**	NA	NA	1.494	0.193	-1.655	0.196	5.128	**0.000**	1.862	0.101
45 to 60	-1.883	0.084	3.507	**0.002**	NA	NA	-0.540	0.589	NA	NA	5.299	**0.000**	0.069	0.945
45 to 75	-1.924	0.082	-0.193	0.908	NA	NA	NA	NA	NA	NA	NA	NA	-1.375	0.237
45 to 90	-2.442	**0.024**	NA	NA	NA	NA	NA	NA	NA	NA	4.743	**0.000**	-0.669	0.529
60 to 75	0.319	0.788	1.866	0.093	NA	NA	NA	NA	NA	NA	NA	NA	1.950	0.090
60 to 90	-0.670	0.587	NA	NA	-2.949	**0.006**	NA	NA	NA	NA	0.711	0.511	-1.184	0.292

75 to 90	-0.298	0.766	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1.073	0.330

Table 4.8: Dunn's test results for median differences in forelimb duty factor within species between support conditions.Comparisons were conducted for species in which the results of a Kruskal-Wallis test detected significant differences between support orientation conditions. P-values are adjusted using the correction of Benjamini and Hochberg (1995). Significant values (<0.05) denoted in bold.

Support contrast	*C. medius*		*D. madagascariensis*		*E. coronatus*		*E. mongoz*		*L. catta*		*V. variegata*		*N. pygmaeus*	
	Z	p	Z	p	Z	p	Z	p	Z	p	Z	p	Z	p
0 to 15	0.432	0.699	1.835	0.091	NA	NA	1.430	0.191	0.024	0.981	5.457	**0.000**	4.007	**0.000**
0 to 30	-2.577	**0.016**	-2.354	**0.028**	-0.788	0.517	-3.055	**0.008**	-2.918	**0.005**	-0.595	0.690	-2.612	**0.024**
0 to 45	5.065	**0.000**	5.596	**0.000**	NA	NA	4.277	**0.000**	3.141	**0.003**	4.969	**0.000**	2.303	**0.045**
0 to 60	-5.885	**0.000**	-5.069	**0.000**	-2.831	**0.028**	-2.351	**0.047**	NA	NA	-0.388	0.805	-3.651	**0.001**
0 to 75	-4.793	**0.000**	-3.782	**0.001**	NA	NA	NA	NA	NA	NA	NA	NA	-5.526	**0.000**
0 to 90	-6.369	**0.000**	NA	NA	-1.806	0.142	NA	NA	NA	NA	3.594	**0.000**	-5.308	**0.000**
15 to 30	-2.052	0.056	0.350	0.778	NA	NA	-1.688	0.152	-5.178	**0.000**	4.889	**0.000**	2.082	0.071
15 to 45	-4.223	**0.000**	-2.755	**0.011**	NA	NA	-3.159	**0.008**	-3.878	**0.000**	0.076	1.000	0.110	0.912
15 to 60	-5.280	**0.000**	-2.400	**0.027**	NA	NA	-1.600	0.157	NA	NA	4.014	**0.000**	0.522	0.665
15 to 75	-4.366	**0.000**	-2.775	**0.012**	NA	NA	NA	NA	NA	NA	NA	NA	-2.407	**0.038**
15 to 90	-5.842	**0.000**	NA	NA	NA	NA	NA	NA	NA	NA	6.455	**0.000**	-0.933	0.434
30 to 45	1.685	0.114	4.145	**0.000**	NA	NA	1.728	0.168	1.353	0.211	4.462	**0.000**	1.122	0.344
30 to 60	3.256	**0.002**	3.616	**0.001**	2.425	**0.046**	0.663	0.563	NA	NA	-0.025	0.980	1.587	0.169
30 to 75	2.731	**0.011**	3.111	**0.005**	NA	NA	NA	NA	NA	NA	NA	NA	4.153	**0.000**
30 to 90	-4.020	**0.000**	NA	NA	-1.470	0.212	NA	NA	NA	NA	3.821	**0.000**	-3.324	**0.003**
45 to 60	-2.082	0.056	0.346	0.729	NA	NA	0.482	0.630	NA	NA	3.748	**0.000**	0.226	0.862
45 to 75	-1.685	0.121	-1.415	0.181	NA	NA	NA	NA	NA	NA	NA	NA	-1.916	0.097
45 to 90	-3.007	**0.005**	NA	NA	NA	NA	NA	NA	NA	NA	6.220	**0.000**	-0.723	0.548
60 to 75	-0.036	0.971	1.575	0.144	NA	NA	NA	NA	NA	NA	NA	NA	2.870	**0.012**

60 to 90	-1.006	0.367	NA	NA	-0.093	0.926	NA	NA	NA	NA	3.435	**0.001**	-1.521	0.180
75 to 90	-0.928	0.391	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1.740	0.132

Table 4.9: Dunn's test results for median differences in Duty Factor Index within species between support conditions.Comparisons were conducted for species in which the results of a Kruskal-Wallis test detected significant differences between support orientation conditions. P-values are adjusted using the correction of Benjamini and Hochberg (1995). Significant values (<0.05) denoted in bold.

Support contrast	*D. madagascariensis*		*E. coronatus*		*E. mongoz*		*L. catta*		*V. variegata*		*N. pygmaeus*	
	Z	p	Z	p	Z	p	Z	p	Z	p	Z	p
0 to 15	-1.379	0.252	NA	NA	0.102	0.919	1.264	0.310	-3.062	**0.005**	-3.085	**0.043**
0 to 30	1.281	0.273	1.409	0.238	2.064	0.097	0.596	0.551	-1.751	0.120	2.483	0.137
0 to 45	-1.444	0.248	NA	NA	-2.157	0.103	-1.286	0.397	0.316	0.752	-0.512	0.799
0 to 60	3.959	**0.001**	3.806	**0.001**	-0.175	1.000	NA	NA	0.382	0.752	1.011	0.595
0 to 75	2.630	**0.043**	NA	NA	NA	NA	NA	NA	NA	NA	1.826	0.285
0 to 90	NA	NA	0.825	0.491	NA	NA	NA	NA	-4.133	**0.000**	0.359	0.795
15 to 30	-0.590	0.641	NA	NA	2.162	0.153	3.411	**0.004**	-4.171	**0.000**	-1.240	0.501
15 to 45	-0.086	0.932	NA	NA	2.237	0.253	2.759	**0.017**	-2.590	**0.018**	-1.264	0.541
15 to 60	1.921	0.117	NA	NA	-0.121	1.000	NA	NA	-2.120	0.057	-1.898	0.303
15 to 75	1.884	0.112	NA	NA	NA	NA	NA	NA	NA	NA	-0.361	0.838
15 to 90	NA	NA	NA	NA	NA	NA	NA	NA	-5.516	**0.000**	-2.401	0.114
30 to 45	-0.557	0.619	NA	NA	-0.456	0.927	-1.102	0.325	-0.809	0.523	0.623	0.800
30 to 60	-3.239	**0.009**	-2.946	**0.010**	1.293	0.327	NA	NA	-1.555	0.163	1.010	0.547
30 to 75	-2.271	0.087	NA	NA	NA	NA	NA	NA	NA	NA	-0.484	0.776
30 to 90	NA	NA	0.213	0.832	NA	NA	NA	NA	NA	NA	-1.636	0.357
45 to 60	2.188	0.086	NA	NA	-1.498	0.268	NA	NA	0.550	0.672	0.057	0.954
45 to 75	1.969	0.122	NA	NA	NA	NA	NA	NA	NA	NA	0.838	0.650
45 to 90	NA	NA	NA	NA	NA	NA	NA	NA	-3.402	**0.002**	-0.289	0.811
60 to 90	NA	NA	-1.205	0.342	NA	NA	NA	NA	-3.270	**0.003**	-0.556	0.810
75 to 60	-0.917	0.449	NA	NA	NA	NA	NA	NA	NA	NA	-1.072	0.596

75 to 90	NA	NA	NA	NA	NA	NA	NA	NA	-3.911	**0.000**	-1.468	0.427

Table 4.10: Summary values for hind and forelimb stance and swing phase durations in seconds (s).Abbreviations – Med – median; SD – standard deviation.

		Hind limb Stance Phase (s)			Hind limb Swing Phase (s)			Forelimb Stance Phase (s)			Forelimb Swing Phase (s)		
Species	Support Orientation	Mean	Med	SD	Mean	Med	SD	Mean	Med	sd	Mean	Med	SD
C. medius	0	0.14	0.13	0.06	0.15	0.15	0.03	0.14	0.13	0.07	0.16	0.16	0.04
	15	0.14	0.13	0.04	0.14	0.14	0.02	0.14	0.13	0.03	0.15	0.16	0.03
	30	0.13	0.12	0.05	0.13	0.13	0.03	0.15	0.13	0.05	0.15	0.13	0.06
	45	0.16	0.13	0.06	0.14	0.13	0.02	0.16	0.15	0.05	0.15	0.13	0.04
	60	0.19	0.14	0.12	0.12	0.12	0.01	0.18	0.13	0.10	0.13	0.13	0.03
	75	0.18	0.17	0.05	0.13	0.13	0.02	0.17	0.14	0.06	0.13	0.13	0.02
	90	0.21	0.18	0.13	0.13	0.13	0.02	0.19	0.18	0.06	0.13	0.13	0.03
M. murinus	0	0.14	0.13	0.05	0.14	0.13	0.03	0.12	0.12	0.04	0.13	0.13	0.04
	30	0.11	0.10	0.06	0.11	0.10	0.04	0.10	0.08	0.06	0.10	0.10	0.03
	60	0.09	0.10	0.03	0.08	0.08	0.02	0.08	0.08	0.02	0.08	0.07	0.02
	90	0.10	0.10	0.03	0.08	0.08	0.02	0.08	0.07	0.01	0.08	0.08	0.03
D. madagascariensis	0	0.42	0.40	0.08	0.30	0.30	0.03	0.37	0.33	0.09	0.36	0.35	0.05
	15	0.46	0.45	0.06	0.31	0.30	0.03	0.44	0.43	0.07	0.42	0.35	0.23
	30	0.44	0.40	0.13	0.29	0.27	0.06	0.38	0.35	0.12	0.34	0.32	0.09

	45	0.48	0.44	0.12	0.25	0.23	0.03	0.40	0.40	0.08	0.28	0.27	0.04
	60	0.41	0.40	0.12	0.26	0.25	0.04	0.38	0.37	0.12	0.27	0.27	0.05
	75	0.52	0.51	0.10	0.27	0.27	0.05	0.46	0.47	0.08	0.24	0.24	0.02
E. coronatus	0	0.29	0.21	0.15	0.23	0.23	0.04	0.24	0.17	0.13	0.24	0.24	0.05
	30	0.30	0.28	0.12	0.24	0.25	0.04	0.25	0.25	0.11	0.23	0.24	0.05
	60	0.30	0.22	0.22	0.23	0.22	0.06	0.21	0.16	0.14	0.15	0.13	0.05
	90	0.54	0.53	0.04	0.23	0.23	0.02	0.32	0.29	0.28	0.22	0.20	0.11
E. mongoz	0	0.37	0.36	0.08	0.27	0.27	0.03	0.33	0.31	0.05	0.30	0.30	0.04
	15	0.38	0.38	0.10	0.25	0.24	0.03	0.33	0.33	0.08	0.28	0.27	0.04
	30	0.45	0.43	0.16	0.30	0.28	0.07	0.39	0.37	0.17	0.26	0.28	0.07
	45	0.59	0.58	0.10	0.33	0.33	0.07	0.40	0.33	0.16	0.21	0.21	0.04
	60	0.46	0.45	0.08	0.23	0.23	0.02	0.22	0.22	0.03	0.16	0.16	0.04
L. catta	0	0.49	0.45	0.16	0.32	0.30	0.08	0.49	0.42	0.18	0.34	0.33	0.05
	15	0.56	0.57	0.09	0.32	0.33	0.04	0.53	0.53	0.08	0.36	0.37	0.05
	30	0.55	0.54	0.11	0.30	0.29	0.05	0.54	0.53	0.08	0.31	0.31	0.06
	45	0.50	0.49	0.18	0.30	0.25	0.09	0.41	0.39	0.10	0.22	0.22	0.06
V. variegata	0	0.60	0.58	0.16	0.36	0.35	0.06	0.54	0.52	0.17	0.42	0.40	0.09
	15	0.73	0.67	0.13	0.38	0.37	0.06	0.69	0.68	0.12	0.40	0.40	0.07
	30	0.58	0.52	0.21	0.32	0.32	0.04	0.50	0.46	0.20	0.37	0.36	0.05
	45	0.61	0.59	0.13	0.26	0.25	0.04	0.51	0.50	0.10	0.30	0.30	0.08
	60	0.49	0.47	0.13	0.30	0.28	0.05	0.38	0.40	0.10	0.29	0.29	0.06

	90	0.42	0.29	0.26	0.24	0.23	0.03	0.28	0.27	0.10	0.34	0.36	0.07
N. pygmaeus	0	0.32	0.33	0.08	0.28	0.28	0.05	0.34	0.32	0.12	0.29	0.27	0.10
	15	0.58	0.47	0.29	0.42	0.37	0.18	0.71	0.55	0.61	0.41	0.32	0.30
	30	0.45	0.30	0.67	0.30	0.25	0.16	0.46	0.32	0.67	0.26	0.23	0.12
	45	0.50	0.50	0.07	0.33	0.33	0.02	0.54	0.55	0.02	0.32	0.32	0.06
	60	0.38	0.32	0.16	0.24	0.23	0.06	0.38	0.35	0.14	0.22	0.22	0.04
	75	2.11	2.10	0.77	0.84	0.70	0.41	2.68	2.57	1.17	0.68	0.66	0.25
	90	0.69	0.55	0.34	0.35	0.33	0.09	0.68	0.58	0.41	0.33	0.30	0.14
P. coquereli	0	0.46	0.43	0.08	0.29	0.28	0.04	0.34	0.35	0.10	0.27	0.26	0.06
	15	0.47	0.46	0.06	0.29	0.29	0.06	0.32	0.32	0.08	0.25	0.25	0.06
	30	0.49	0.47	0.07	0.31	0.30	0.03	0.36	0.30	0.12	0.26	0.25	0.06

Table 4.11: Kruskal-Wallis tests for hind and forelimb stance and swing phase changes within species between support conditions. Significant values (<0.05) in bold indicate differences in median value between support conditions within species. Abbreviation: – d.f. – Degrees of freedom.

		Hind Stance Duration		Hind Swing Duration		Fore Stance Duration		Fore Swing Duration	
Species	d.f.	χ^2	p-value	χ^2	p-value	χ^2	p-value	χ^2	p-value
C. medius	6	25.01	**<0.001**	38.27	**<0.001**	41.46	**0.002**	19.63	**0.003**
M. murinus	3	11.24	**0.011**	24.33	**<0.001**	12.84	**0.005**	20.13	**<0.001**
D. madagascariensis	5	16.74	**0.005**	54.24	**<0.001**	19.46	**0.001**	82.08	**<0.001**
E. coronatus	3	10.48	**0.015**	4.73	0.193	3.60	0.308	20.91	**<0.001**
E. mongoz	4	22.79	**<0.001**	25.32	**<0.001**	9.90	**0.042**	29.58	**<0.001**
L. catta	3	4.79	0.188	8.93	**0.032**	13.84	**0.004**	36.61	**<0.001**
V. variegata	5	53.93	**<0.001**	109.37	**<0.001**	83.99	**<0.001**	93.21	**<0.001**
N. pygmaeus	6	53.34`	**<0.001**	46.26	**<0.001**	50.15	**<0.001**	37.05	**<0.001**
P. coquereli	2	3.42	0.181	3.02	0.221	0.33	0.848	0.24	0.887

Table 4.12: Dunn's test results for median differences in hind limb stance duration within species between support conditions.Comparisons were conducted for species in which the results of a Kruskal-Wallis test detected significant differences between support orientation conditions. P-values are adjusted using the correction of Benjamini and Hochberg (1995). Significant values (<0.05) denoted in bold.

Support	C. medius		M. murinus		D. madagascariensis		E. coronatus		E. mongoz		V. variegata		N. pygmaeus	
Contrast	Z	p	Z	p	Z	p	Z	p	Z	p	Z	p	Z	p
0 to 15	0.22	0.869	NA	NA	2.06	0.098	NA	NA	0.25	0.805	4.03	**0.000**	4.03	**0.000**
0 to 30	1.54	0.198	2.62	**0.027**	0.33	0.792	-1.01	0.374	-1.92	0.136	1.70	0.112	-0.73	0.613
0 to 45	1.55	0.211	NA	NA	2.36	0.055	NA	NA	4.31	**0.000**	0.44	0.658	2.54	**0.023**
0 to 60	-1.48	0.208	3.14	**0.010**	0.82	0.617	0.23	0.814	-1.52	0.215	3.55	**0.001**	-0.71	0.594
0 to 75	-2.81	**0.026**	NA	NA	-1.76	0.131	NA	NA	NA	NA	NA	NA	-4.83	**0.000**
0 to 90	-2.93	**0.024**	2.46	**0.028**	NA	NA	-3.00	**0.008**	NA	NA	3.61	**0.001**	-4.51	**0.000**
15 to 30	1.63	0.198	NA	NA	2.38	0.065	NA	NA	-1.69	0.183	5.07	**0.000**	3.56	**0.001**
15 to 45	-1.21	0.263	NA	NA	-0.03	0.979	NA	NA	-4.12	**0.000**	2.70	**0.010**	-0.09	0.971
15 to 60	-1.25	0.261	NA	NA	2.43	0.075	NA	NA	-1.39	0.236	6.05	**0.000**	2.99	**0.006**
15 to 75	-2.59	**0.029**	NA	NA	-0.76	0.562	NA	NA	NA	NA	NA	NA	-1.75	0.129
15 to 90	-2.67	**0.026**	NA	NA	NA	NA	NA	NA	NA	NA	5.63	**0.000**	-0.24	0.945
30 to 60	2.51	**0.032**	-0.60	0.822	-0.62	0.616	-1.17	0.363	0.45	0.721	-2.30	**0.029**	0.12	0.997
30 to 75	3.61	**0.003**	NA	NA	1.88	0.113	NA	NA	NA	NA	NA	NA	4.48	**0.000**
30 to 90	-3.74	**0.004**	0.03	0.976	NA	NA	-2.59	**0.019**	NA	NA	2.78	**0.009**	-4.02	**0.000**
45 to 30	2.76	**0.024**	NA	NA	2.75	0.088	NA	NA	2.66	**0.026**	1.51	0.150	2.22	**0.050**

45 to 60	-0.33	0.823	NA	NA	2.68	0.055	NA	NA	1.27	0.255	3.08	**0.004**	2.04	0.072
45 to 75	-1.84	0.139	NA	NA	-0.76	0.611	NA	NA	NA	NA	NA	NA	-1.24	0.300
45 to 90	-1.88	0.141	NA	NA	NA	NA	NA	NA	NA	NA	3.42	**0.001**	-0.06	0.951
60 to 75	1.38	0.236	NA	NA	2.04	0.089	NA	NA	NA	NA	NA	NA	4.08	**0.000**
60 to 90	-1.38	0.222	-0.52	0.722	NA	NA	-3.05	**0.014**	NA	NA	1.09	0.293	-3.35	**0.002**
75 to 90	0.06	0.949	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1.60	0.163

Table 4.13: Dunn's test results for median differences in hind limb swing duration within species between support conditions.Comparisons were conducted for species in which the results of a Kruskal-Wallis test detected significant differences between support orientation conditions. P-values are adjusted using the correction of Benjamini and Hochberg (1995). Significant values (<0.05) denoted in bold.

Support	*C. medius*		*M. murinus*		*D. madagascariensis*		*E. mongoz*		*V. variegata*		*N. pygmaeus*	
Contrast	Z	p	Z	p	Z	p	Z	p	Z	p	Z	p
0 to 15	-1.77	0.160	NA	NA	1.21	0.310	-2.48	**0.026**	1.39	0.191	3.41	**0.002**
0 to 30	2.78	**0.023**	2.06	**0.047**	2.67	**0.014**	-1.02	0.344	4.99	**<0.001**	0.43	0.697
0 to 45	-3.55	**0.003**	NA	NA	-5.64	**<0.001**	2.10	0.051	-7.21	**<0.001**	1.16	0.287
0 to 60	5.26	**<0.001**	4.18	**<0.001**	4.60	**<0.001**	2.16	0.052	4.72	**<0.001**	2.10	0.068
0 to 75	2.73	**0.022**	NA	NA	1.46	0.217	NA	NA	NA	NA	-4.01	**<0.001**
0 to 90	3.47	**0.003**	4.17	**<0.001**	NA	NA	NA	NA	NA	NA	-2.04	0.072
15 to 30	1.12	0.343	NA	NA	3.04	**0.006**	-3.39	**0.004**	4.76	**<0.001**	3.82	**0.001**
15 to 45	1.55	0.210	NA	NA	5.46	**<0.001**	-4.04	**0.001**	6.98	**<0.001**	0.84	0.441
15 to 60	3.70	**0.002**	NA	NA	4.67	**<0.001**	0.85	0.393	4.89	**<0.001**	4.78	**<0.001**
15 to 75	1.56	0.228	NA	NA	1.92	0.091	NA	NA	NA	NA	-1.42	0.218
15 to 90	2.18	0.068	NA	NA	NA	NA	NA	NA	6.28	**<0.001**	1.28	0.248
30 to 60	-2.54	**0.029**	-2.33	**0.029**	-2.89	**0.008**	-2.68	**0.018**	-1.21	0.244	-1.79	0.109
30 to 75	-0.70	0.565	NA	NA	-0.67	0.537	NA	NA	NA	NA	4.30	**<0.001**
30 to 90	1.24	0.325	2.43	**0.030**	NA	NA	NA	NA	3.72	**<0.001**	-2.44	**0.039**
45 to 30	-0.24	0.809	NA	NA	-3.95	**<0.001**	1.23	0.272	-3.85	**<0.001**	1.37	0.225

45 to 60	2.56	**0.031**	NA	NA	-0.78	0.502	3.29	**0.003**	-2.26	0.029	2.24	0.053
45 to 75	0.57	0.629	NA	NA	-0.85	0.492	NA	NA	NA	NA	-1.81	0.113
45 to 90	1.14	0.357	NA	NA	NA	NA	NA	NA	0.82	0.410	-0.02	0.985
60 to 75	1.37	0.276	NA	NA	0.48	0.633	NA	NA	NA	NA	5.09	**<0.001**
60 to 90	-0.98	0.404	0.26	0.796	NA	NA	NA	NA	2.61	**0.012**	-3.60	**0.001**
75 to 90	0.41	0.718	NA	NA	NA	NA	NA	NA	6.10	**<0.001**	2.42	**0.036**

Table 4.14: Dunn's test results for median differences in forelimb stance duration within species between support conditions.Comparisons were conducted for species in which the results of a Kruskal-Wallis test detected significant differences between support orientation conditions. P-values are adjusted using the correction of Benjamini and Hochberg (1995). Significant values (<0.05) denoted in bold.

Support Contrast	*C. medius*		*M. murinus*		*D. madagas-cariensis*		*E. mongoz*		*L. catta*		*V. variegata*		*N. pygmaeus*	
	Z	p	Z	p	Z	p	Z	p	Z	p	Z	p	Z	p
0 to 15	0.29	0.901	NA	NA	3.71	**0.003**	-0.08	0.937	1.29	0.236	4.55	**<0.001**	4.23	**<0.001**
0 to 30	-0.10	0.969	2.21	0.055	-0.63	0.663	NA	NA	NA	NA	NA	NA	-0.70	0.596
0 to 45	2.37	0.092	NA	NA	1.82	0.128	0.90	0.460	-1.59	0.222	-0.60	0.549	2.53	**0.024**
0 to 60	-1.67	0.166	3.11	**0.006**	-0.46	0.748	2.49	0.043	NA	NA	4.96	**<0.001**	-0.91	0.478
0 to 75	-2.12	0.143	NA	NA	-2.08	0.139	NA	NA	NA	NA	NA	NA	-4.78	**<0.001**
0 to 90	-3.65	**0.005**	3.16	**0.010**	NA	NA	NA	NA	NA	NA	NA	NA	-4.01	**<0.001**
15 to 30	0.15	0.973	NA	NA	3.47	**0.004**	-1.03	0.607	-3.42	0.004	6.00	**<0.001**	3.77	**0.001**
15 to 45	-1.90	0.174	NA	NA	1.84	0.163	-0.96	0.560	3.17	0.005	3.95	**<0.001**	0.02	0.983
15 to 60	-1.38	0.254	NA	NA	2.86	**0.021**	2.45	0.036	NA	NA	7.59	**<0.001**	3.00	0.007
15 to 75	-1.87	0.143	NA	NA	-0.33	0.794	NA	NA	NA	NA	NA	NA	-1.58	0.170
15 to 90	-3.32	**0.009**	NA	NA	NA	NA	NA	NA	NA	NA	6.97	**<0.001**	0.34	0.809
30 to 60	1.41	0.255	-1.02	0.371	0.02	0.986	-2.98	0.029	NA	NA	-3.25	**0.002**	0.35	0.846
30 to 75	1.89	0.154	NA	NA	1.92	0.166	-0.95	0.486	NA	NA	2.32	**0.025**	4.45	**<0.001**
30 to 90	-3.27	**0.008**	1.20	0.347	NA	NA	NA	NA	NA	NA	3.64	**<0.001**	-3.54	**0.001**

45 to 30	1.86	0.132	NA	NA	1.46	0.242	0.12	1.000	-1.51	0.196	0.90	0.396	2.23	**0.050**
45 to 60	0.08	0.935	NA	NA	1.14	0.348	2.85	**0.022**	NA	NA	3.31	**0.001**	1.92	0.095
45 to 75	-0.67	0.663	NA	NA	-1.29	0.297	NA	NA	NA	NA	NA	NA	-1.22	0.314
45 to 90	-2.06	0.136	NA	NA	NA	NA	NA	NA	NA	NA	3.78	**<0.001**	0.20	0.882
60 to 75	0.65	0.641	NA	NA	1.83	0.145	NA	NA	-0.31	0.759	NA	NA	3.90	**<0.001**
60 to 90	-1.85	0.123	0.25	0.804	NA	NA	NA	NA	NA	NA	1.28	0.230	-2.75	**0.014**
75 to 90	-1.04	0.418	NA	NA	NA	NA	NA	NA	NA	NA	4.77	**<0.001**	1.87	0.098

Table 4.15: Dunn's test results for median differences in forelimb swing duration within species between support conditions.Comparisons were conducted for species in which the results of a Kruskal-Wallis test detected significant differences between support orientation conditions. P-values are adjusted using the correction of Benjamini and Hochberg (1995). Significant values (<0.05) denoted in bold.

Support contrast	*C. medius*		*M. murinus*		*D. madagas-cariensis*		*E. coronatus*		*E mongoz*		*L. catta*		*V. variegata*		*N. pygmaeus*	
	Z	p	Z	p	Z	p	Z	p	Z	p	Z	p	Z	p	Z	p
0 to 15	-0.16	0.920	NA	NA	0.32	0.746	NA	NA	-2.08	**0.047**	0.95	0.344	-0.59	0.597	1.83	0.118
0 to 30	2.48	0.069	1.87	0.092	3.44	**0.001**	0.02	0.985	2.27	**0.033**	1.49	0.165	4.25	**<0.001**	1.76	0.127
0 to 45	-1.57	0.247	NA	NA	-6.23	**<0.001**	NA	NA	-4.51	**<0.001**	-3.50	**0.001**	-6.91	**<0.001**	1.17	0.298
0 to 60	3.05	**0.048**	4.19	**<0.001**	6.64	**<0.001**	3.92	**0.000**	3.88	**0.001**	NA	NA	7.46	**<0.001**	2.76	**0.017**
0 to 75	2.15	0.096	NA	NA	3.84	**<0.001**	NA	NA	NA	NA	NA	NA	NA	NA	-3.14	**0.007**
0 to 90	2.50	0.088	3.22	**0.004**	NA	NA	0.67	0.602	NA	NA	NA	NA	NA	NA	-0.80	0.468
15 to 30	2.19	0.100	NA	NA	2.64	**0.011**	NA	NA	0.29	0.775	4.42	**<0.001**	2.34	0.032	3.22	**0.007**
15 to 45	1.28	0.348	NA	NA	5.15	**<0.001**	NA	NA	2.88	**0.013**	5.21	**<0.001**	5.22	**<0.001**	-0.06	0.950
15 to 60	2.79	0.056	NA	NA	5.51	**<0.001**	NA	NA	2.79	**0.013**	NA	NA	5.53	**<0.001**	3.92	**0.001**
15 to 75	1.98	0.126	NA	NA	3.79	**<0.001**	NA	NA	NA	NA	NA	NA	NA	NA	-1.66	0.144
15 to 90	2.30	0.090	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	2.15	**0.048**	0.93	0.410
30 to 60	-0.81	0.588	-2.55	**0.022**	-4.47	**<0.001**	-4.32	**<0.001**	-2.60	**0.019**	NA	NA	-4.37	**<0.001**	-1.38	0.235
30 to 75	-0.35	0.893	NA	NA	-2.84	**0.007**	NA	NA	NA	NA	NA	NA	NA	NA	4.14	**<0.001**
30 to 90	0.56	0.758	1.60	0.132	NA	NA	0.69	0.739	NA	NA	NA	NA	0.79	0.494	-2.24	0.053
45 to 30	1.10	0.408	NA	NA	-3.99	**0.000**	NA	NA	-2.58	**0.017**	-3.12	**0.003**	-4.02	**<0.001**	1.99	0.089
45 to 60	1.84	0.154	NA	NA	0.47	0.684	NA	NA	0.79	0.479	NA	NA	0.08	0.935	2.61	**0.024**
45 to 75	1.17	0.390	NA	NA	1.21	0.281	NA	NA	NA	NA	NA	NA	NA	NA	-1.20	0.301

45 to 90	1.45	0.283	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	-1.87	0.077	0.67	0.526
60 to 75	0.31	0.883	NA	NA	-0.98	0.375	NA	NA	NA	NA	NA	NA	NA	NA	4.69	**<0.001**
60 to 90	-0.16	0.967	-0.76	0.446	NA	NA	-1.65	0.198	NA	NA	NA	NA	-1.98	0.066	-3.08	**0.007**
75 to 90	0.15	0.881	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	2.79	**0.010**	2.41	**0.037**

Chapter 5: Gait Kinematics and Support Orientation II: Spatial variables

5.1 Introduction

Primates are well differentiated from non-primates in their strong preferences for diagonal sequence gaits, however in addition to footfall timing and sequence, other aspects of primate gaits have been argued to be distinctive among mammals. On level supports, primate gaits are characterized as being relatively more compliant compared to non-primate gaits by Schmitt (1999). This manifests in high limb yield, or change in joint angle from touchdown to takeoff, at the knee and elbow (Schmitt 1999; Larney and Larson 2004). This compliance, which is contrasted against having a relatively stiff limb that will not decrease much in joint angle, and therefore effective length, is hypothesized to contribute to stability and to reduced reaction forces experienced by the limbs when moving in unstable arboreal environments (Schmitt 1999).

On oblique supports, animals are similarly expected to alter their positional behavior and adopt more flexed limbs to bring the center of mass close to the support as a mechanism for avoiding forward pitch (Lammers and Zurcher 2011; Birn-Jeffrey and Higham 2014). Increased flexion of the elbows and knees has been reported on previously in strepsirrhines traveling on declines by Krakauer et al. (2002) and Stevens (2003, et al. 2011). Vilensky et al. (1994) directly considered joint yield and reported increased flexion at the knee throughout the

stride on a 16° decline. This would indicate a relatively stiffer limb, however, primates in that study were moving on flat treadmills so it is not clear how aspects of the experimental setup other than support orientation might have been influencing compliance since primates show relatively higher compliance on arboreal supports (Schmitt 1999).

In support of the relationship of stiffness with declines, goats (Lee et al. 2008) and humans (Dewolf et al. 2016) traveling on terrestrial declines (15° and 9°, respectively) have been found to increases limb stiffness compared to level travel. Lee et al. (2014) further hypothesized that relatively high stiffness in goats compared to dogs moving on similar supports is an adaptation for travel on steep rocky terrain. However, larger and terrestrial animals tend to be relatively less compliant in general and have more erect limbs (Biewener 1989; Larney and Larson 2004). Therefore, it is unclear stiffness is a general response to declines, or if primates should remain compliant when traveling on arboreal declines.

Increased limb flexion is also expected to cause changes to trunk inclination, with Vilensky et al. (1994) reporting a reduction of trunk inclination angle on supports of 28° compared to level supports. Presumably to avoid forward pitch, primates should seek to lower the hip relative to the shoulder during headfirst descent on declines. In support of this It has been reported that *Daubentonia madagascariensis* reduced hip height but not shoulder height when descending a 30° support (Krakauer et al. 2002). It remains unknown how this may vary with intermembral index (IMI), which might drive increased flexion of

the relatively longer hind limb in those primates to maintain a favorable trunk inclination.

In addition to limb compliance and joint yield, primates have also been argued to have distinctive patterns of limb excursion, which is a measure of how far forward the limb lands at touchdown (protraction) and how far back the limb extends at takeoff (retraction) (Larson et al. 2000, 2001, although see Schmidt 2005b for an alternative perspective on the comparison of primates to other mammals). Larson et al. (2001) linked primates relatively large limb excursions to their arboreal milieu, and asymmetries in hind and forelimb excursion to intermembral indices, in that the shorter limb should have a relatively larger excursion to match the longer limb. Most arboreal above branch quadrupedal primates have relatively short arms, including extant strepsirrhines, and would be predicted to have larger forelimb excursions as a result.

As with primate limb compliance, most experimental work on limb excursion has been done on level supports, however several decline studies of primates have reported similar findings on how limb excursions change with support orientation. Stevens (2003), Stevens et al. (2011) and Nyakatura et al. (2008) found increased protraction in both limbs, but especially the forelimb, in strepsirrhines and tamarins. Hesse et al. (2015) replicated the findings of Nyakatura et al (2008) for tamarins traveling on the same support angles (up to 28°), but also reported increased hindlimb retraction on the steepest declines in that study (60°). Hesse et al. (2015) described this increase in hind limb

retraction as a kinematic shift at higher angles and hypothesized that it is related to the hind limbs being held in tension when avoiding forward pitch during headfirst descent of very steep supports.

The present study considers changes to limb kinematics as support orientation becomes steeper in a sample of eight strepsirrhine primates that are diverse in body mass and morphology. It is predicted that as supports become steeper, limbs should become more flexed throughout the stride, resulting in a reduction of effective limb length (ELL), or the distance of the shoulder or hip from the support at midstance (Pontzer et al. 2007).

All primates in this study have relatively longer legs than arms. If previous findings of increased lowering of the hip relative to the shoulder are replicated (Krakauer et al. 2002), then trunk inclination relative to the support should decrease during descent compared to level travel. Changes to limb excursion will be tested, with the prediction that forelimb protraction should increase with support steepness based on previous studies (Stevens 2003, et al. 2011; Nyakatura et al. 2008; Hesse et al. 2015), and that the hindlimb may increase in retraction on very steep supports (Hesse et al. 2015).

Finally, this study will also address absolute changes to speed. Velocity has been hypothesized to either increase on declines, since movement is in the direction of gravity, or decrease, as animals increasingly resist gravity, and studies have not observed a consistent velocity response across animals (Birn-Jeffrey and Higham 2014). In primates there are mixed results: Stevens (2003)

observed no consistent changes to speed within species of strepsirrhines; Nyakatura et al. (2008) and Hesse et al. (2015) found no changes to velocity in tamarins, and Kivell et al. (2010) found decreased speed during descent compared to level or inclined travel in *Daubentonia madagascariensis*. Given the increasing duty factors reported on in the previous chapter, it is predicted that velocity should decrease as supports become steeper.

5.2 Methods

Headfirst symmetrical strides were digitized with eight anatomical markers (Figure 5.1), for all species except *Microcebus* and *Nycticebus* from the pilot study (individuals NPF1 and NPM1), for which video quality was not sufficient to reliably place all markers. Anatomical markers were digitally placed on the side of the body facing the camera at first and second touchdown (TD1, TD2), midstance (MS), and take off (TO) for both the fore and hind limb whenever possible using DLT DataViewer (Hedricks, 2008) in Matlab (Mathworks, Natick, MA; USA).

A total of 417 strides were digitized (Table 5.2). Animals were not shaved or physically marked prior to the experiment, and so to assess the magnitude of observer error in landmark placement, fifteen bouts of locomotion were randomly selected from the sample and digitized 5 times on separate days. Physical markings on the support the animal was traveling on of known length were used to calibrate distance. Digital anatomical markers were used to determine joint angles (Figure 5.2), limb excursions (Figure 5.3), stride length, and effective limb

length (Table 5.1). Trunk length between shoulder and hip was measured at each point during the stride and then averaged for the bout. Trunk inclination was averaged from the inclination at the first hind and forelimb touchdowns (Table 5.1).

Velocity was determined by displacement of the hip from hind limb TD1 to TD2, with time measured by number of frames. To compare speed across all taxa, Froude number (Fr), a dimensionless measure of speed that can be compared across body sizes was calculated using the method of Alexander and Jayes (1983) as follows:

$$Fr = (\text{velocity } (m/s))^2 / (g\ (m/s)^2 * \text{leg length } (m))$$

Froude number was selected because equal numbers reflect dynamically similar gaits between animals of varying size (Alexander and Jayes 1983). Leg length was determined by adding segment lengths of the hip to knee and knee to ankle for each individual at TD1 of the hindlimb on a level support. The average leg length for all level travel was then used to calculate Fr at the individual level. This was selected as the unit of comparative height rather than a measure like hip height at midstance since the latter is predicted to be influenced by support condition. Following Hof (1996), dimensionless measures of stride duration and frequency were also calculated (Table 5.1).

Statistical analyses were carried out in R (R Core Team 2000) using non-parametric Kruskal-Wallis tests to evaluate if changes to median values occurred within species between support orientations for variables of interest (Kruskal and Wallis 1952). For significant Kruskal-Wallis test results, a Dunn's test (Dunn 1964) using the 'FSA' package in R (Ogle 2016) using an adjusted p-value using the Benjamini and Hochberg (1995) correction for multiple tests were used to determine which support orientations significantly differed from each other within species.

5.3 Results

5.3.1 Error Study of Landmark Placement

The standard error for the position of each eight anatomical marker was calculated from the x and y positions of these markers in pixels, and then converted into millimeters (mm) using the markers of known distance in the video. The largest standard error observed among the sixteen coordinates is presented in Table 5.3 for each video. Standard error for each joint angle and trunk length were also measured, and from this it appeared that the ankle joint showed the highest error across the sample (Table 5.3).

5.3.2 Effective limb length (ELL)

Both hind and forelimb ELL decreased as support orientation increased, as predicted (Table 5.4). All species experienced significant decreases to hind limb ELL, but only species that traveled on supports greater than 45° showed significant decreases in forelimb ELL (Table 5.5).

On supports of 60° to 90°, mean hind limb ELL increased in several species (*Cheirogaleus medius, Daubentonia madagascariensis, Eulemur coronatus*, and *Varecia variegata*), although these increases were not found to be significant in any species (Table 5.6). This suggests that while the hind limb gets significantly shorter as supports transition from 0° to 45°, hind limb ELL remains relatively static on steeper angles (Table 5.6).

The effective limb length intermembral index (ELL IMI), which is the ratio of forelimb ELL to hind limb ELL (Table 5.1), was observed to increase towards 1 in several species as supports approach 45° (Table 5.4), indicating that the hind limb and forelimb were becoming approximately more equal in height. On supports of 60° to 90° ELL IMI tended to decrease, which was significant in C. medius and D. madagascariensis on these supports relative to the 45° support (Table 5.7). *N. pygmaeus* was the only species for which ELL IMI did not significantly change in response to support orientation (Table 5.5)

The effect of these changes to ELL on trunk inclination found that mean trunk inclination decreased such that on very steep supports some species were on average negative (Table 5.4), which indicates that the shoulder was held higher than the hip. Trunk inclination relative to the ground showed a significant linear correlation with the angle of support orientation ($R^2 = 0.874$, $p = <0.001$) across the entire sample (Figure 5.5).

5.3.3 Joint Angle Changes

Primates tended to touchdown with increasingly flexed ankles, knees, and hips (Table 5.8a) as support orientations became steeper. Some species experienced extension in the knees at midstance on steeper supports (≥60°) (Figure 5.6, Table 5.8a). This created a situation in which that the hindlimb was effectively short when landing and extending at midstance, indicating a relatively stiffer limb compared to yield on level and less oblique supports (Table 5.8a).

The elbow and shoulder were extended at touchdown and underwent flexion at midstance (Table 5.8b). The elbow at midstance tended to be more extended on level and shallow supports and became increasing flexed at midstance on steeper angles (Figure 5.7). This indicates that the forelimb showed relatively higher compliance than the hind limb as supports became steeper.

Significant changes to the joint angle at touchdown, midstance, and the degree of flexion at midstance were found across the sample for all joints (Table 5.9). More species experienced significant changes in joint angle between touchdown and midstance at the ankle and knee compared to the hip (Table 5.8a). Most species did not show significant differences in the change in shoulder angle from touchdown to midstance with increasing support orientation (Table 5.9).

5.3.4 Limb excursion

Most species increased hind limb protraction as supports transitioned between 0° and 45°, above these angles, protraction was reduced to values near or lower than on level travel (Table 5.10, Figure 5.8). Significant changes to hindlimb protraction were observed in almost every species (Table 5.11). Significant increases to hind limb protraction occurred across all species except *for Eulemur coronatus* between the level and 30° supports (Table 5.12). However as supports transitioned from 45° and up, most species experienced a reduction of hind limb protraction, which was significant in larger species like *Daubentonia madagascariensis* and *Varecia variegata* (Table 5.12). These observations appear consistent with the increasingly flexed postures of the hip and knee at touchdown (Table 5.8a).

Hind limb retraction tended to be relatively constant on supports of 0° to 45°, and then significantly increased on steeper supports (Table 5.10, 5.13, Figure 5.8). This strategy was shared by all arboreal quadrupeds in the sample (Table 5.13); *Nycticebus pygmaeus* also appeared to employ this strategy although not significantly, which may reflect the observation that *N. pygmaeus* tends towards using relatively large limb excursions on all supports compared to the rest of the sample (Table 5.10).

Forelimb protraction tended to increase with support orientation across all species (Table 5.10, Figure 5.8), and significantly changed in all species (Table 5.11). As with hind limb protraction, most significant comparisons within species

were between level and decline supports (Table 5.14), however unlike hind limb protraction, forelimb protraction did not decrease on steeper supports (Table 5.10, Table 5.14). Forelimb retraction showed two general patterns that appear to be associated with body mass. Species under 1 kg (*Cheirogaleus medius*, *N. pygmaeus*) tended to show gradual increases to forelimb retraction on steeper declines, which were significant for comparisons of level supports and declines of 45° and steeper in *C. medius*, and only significant in *N. pygmaeus* when comparing 0° and 45° (Table 5.15). In species above 1 kg, forelimb retraction tended to decrease significantly when comparing supports of 0° to 30° to supports of 45° to 90° (Table 5.15, Figure 5.8).

Together, protraction and retraction are called excursion and increasing protraction will cause a corresponding reduction of retraction if excursion is kept constant. However, in this sample total excursion of the hind and forelimb also significantly changed with support orientation in several species (Table 5.11). For these species in which changes to total excursion occurred (*C. medius, D. madagascariensis, E. coronatus, Eulemur mongoz, Lemur catta,* and *N. pygmaeus*) it was found that generally, most differences were between level and declined travel instead of between different decline orientations (Tables 5.16, 5.17). Generally hind limb excursion increased as supports became steeper up to 60°, and above that hind limb excursions decreased in most species (Table 5.10, 5.16). A similar, but less pronounced, trend was observed in the forelimb (Table 5.10, 5.17).

5.3.5 Velocity and stride length

Velocity tended to decrease as supports became more oblique (Table 5.18). This relationship was significant in *Cheirogaleus medius*, *Daubentonia madagascariensis*, *Varecia variegata*, and *Nycticebus pygmaeus* (Table 5.19). In *C. medius* and *D. madagascariensis*, this significance primarily occurred when comparing declines up to 30°, upon which animals moved faster, to declines steeper than 30°, upon which animals moved more slowly. *N. pygmaeus* moved significantly faster on the level support compared to declines and did not show as many significant decreases in velocity between declines (Table 5.20). Only one species, *V. variegata*, showed consistent and significant increases to velocity as support orientation increased (Table 5.20).

Froude number tended to be similar across species apart from *C. medius* and *Eulemur coronatus*, which tended to move with higher Froude numbers than the rest of the sample (Table 5.18, Figure 5.9). Most species decreased in Froude number as supports became steeper except for *V. variegata*, which consistently increased in velocity and Froude number as supports became steeper. Stride frequency, standardized to leg length, also tended to decrease across the sample (Table 5.18). Stride length, which was standardized to individual trunk length, tended to decrease as supports became steeper but did not significantly change with support orientation in most species (Tables 5.18, 5.19). All species that showed significant changes to stride length were those that traveled on all support orientations (Table 5.18).

5.4 Discussion

Speed tended to generally decrease with increasing support steepness in this sample, likely driven by overall reduction in both stride length and frequency (Table 5.18). Froude numbers of all species except for *Cheirogaleus medius* were below 1 on all supports (Figure 5.9), indicating that animals were largely using walking gaits (Alexander and Jayes 1983; Griffin et al. 2004). Rapid movement is expected in *C. medius* given its small size and general locomotor ecology (Dagg 1973; Oxnard et al. 1990); *C. medius* increased in speed as supports became steeper than 30°, only slowing down into a walking range as supports reached 75°-90° (Table 5.18). This indicates that not only is *C. medius* adept at performing headfirst descent on all supports, but that it also does so with relatively rapid speed compared to the rest of the sample.

It was predicted that animals would seek to reduce effective limb length (ELL) as supports became steeper, and the present study found that effective limb length in primates shortened as supports ranged from 15° to 45°, but above these angles the hind limb did not continue to significantly change. This is a surprising result since the risk of pitch is greatest on steep supports and ELL would be predicted to be minimized at the highest supports.

Hypothetically, having the hip rise high above the shoulder during headfirst descent could cause an increased risk of pitch and primates should adopt postures that minimize this risk. In support of this explanation, the ratio of forelimb to hind limb ELL, or ELL IMI, began to approach 1 as supports

approached 45° (Figure 5.4). This was accompanied by changes to trunk inclination in which trunks progressively less inclined relative to the support (Figure 5.5).

This ELL IMI pattern is consistent with Krakauer et al. (2002)'s observations that the hip was lowering more than the shoulder in *Daubentonia madagascariensis*. Given the low IMI of primates in this sample, it is intuitive that since the hind limb is longer than the forelimb it correspondingly needed to lower more. Patterns of decreasing trunk inclination observed here are also consistent with Vilensky et al. (1994) observing less inclined trunks relative to the support in *Saimiri* as supports became steeper.

As supports rose above 45°, ELL IMI began to fall again in several species, indicating that the leg was relatively longer than the arm at midstance for each limb. This would appear to increase the risk of pitch; however, ELL IMI is not a direct measure of trunk inclination since the timing of forelimb and hind limb midstance may be staggered as a function of limb phase, a measure of the sequence and timing of footfalls. ELL IMI is likely mostly closely approximated to trunk inclination when limb phases approach pure diagonal couplets (trots) or lateral couplets (paces).

When looking at average trunk inclination, which was sampled at fore- and hind limb touchdown, the hip was relatively lower than the shoulder at certain support orientations in *D. madagascariensis, Eulemur coronatus, Lemur catta, Varecia variegata, Nycticebus pygmaeus*, and *Propithecus coquereli* (Figure 5.5).

More analysis is needed to understand if and how much the trunk inclination might be oscillating through the stride, or if the shoulder is rising at hindlimb midstance to keep the body parallel to the support. Further, hind limb ELL might not need to be minimized on the steepest supports if primates are counteracting any increased risk of pitch on these support orientations with strong pedal grasping. There may also be a functional limit to how short the leg can become during locomotion.

To reduce fore- and hind limb ELL, the elbows, knees, and ankles became increasingly flexed with rising support angle (Figures 5.6, 5.7). However, at a certain point many species were touching down with highly flexed hind limbs, and joints were not yielding at midstance (Table 5.8a), indicating that the hind limb became relatively stiff, consistent with observations of Vilensky et al. (1994), Lee et al. (2008, 2014), and Dewolf et al. (2016) in primates and goats traveling on declines.

Observations of the knee in this sample found that on level supports *N. pygmaeus*, *Cheirogaleus medius*, and *D. madagascariensis* did not experience much knee yield; this is consistent with Larney and Larson (2004)'s observations of lorises, and they not have hindlimb data for *D. madagascariensis*, or any observations of cheirogaleids for comparison. Lemuriformes in this sample experienced knee yield on level supports consistent with Larney and Larson (2004) and continued to increase yield on declines until reaching approximately 45°-60° supports, when decreases to yield were observed in these primates. This

may indicate that hind limb compliance is not characteristic of all primates, a conclusion reached by Larney and Larson (2004), and that it may only characterize the hind limb on certain support orientations.

In contrast to the hindlimb, Larney and Larson (2004) supported Schmitt (1999)'s finding that forelimb compliance seems to be a primate-wide trait. The present study found that across the sample the elbow progressively increased in yield with support angle until supports reached approximately 75° to 90° (Table 5.8b). On these vertical and near-vertical supports, the forelimb was still yielding between touchdown and midstance, in contrast to the knee in some species, but showed relatively less yield than on level or oblique supports up to 60°.

Forelimb compliance has been associated with reducing substrate reaction forces (Schmitt 1999). On declines, the forelimb is hypothesized to experience relatively greater reaction forces as a function of bearing a higher proportion of the animal's weight during locomotion relative to level travel when moving headfirst (Birn-Jeffrey and Higham 2014). The increasing elbow yield on declines observed here may be one mechanism by which primates uniformly responded to increases of reaction forces to the forelimbs. Other studies have hypothesized that primates may further reduce reaction forces on the forelimbs through an active posterior weight shift (Vilensky et al. 1994; Krakauer et al. 2002; Kivell et al. 2010), which if happening in the present sample, could be contributing to observed changes in hindlimb stiffness.

Increased limb yield is associated with increased limb excursion and contact time (Schmitt 1999; Larney and Larson 2004). In the previous chapter it was found that forelimb contact periods (both duty factor and stance phase duration) increased with support orientation. Limb excursions tended to progressively increase as declines increased from 0° to 60° for the fore- and hindlimbs in this study (Table 5.10).

Changes to limb excursions observed here fit with the previous literature in that forelimb protraction progressively increased as support became steeper (Vilensky et al. 1994; Stevens 2003; Nyakatura et al. 2008; Hesse et al. 2015). Primates further adopted a general strategy of increasing hindlimb retraction on very steep declines (Hesse et al. 2015), possibly to distance the supporting limbs from each other and from the center of mass (Cartmill 1974b; Jungers 1976), or as a mechanism of extending contact time with the support. This increase of hind limb retraction is an alternative explanation for the flexed hind limbs at touchdown, which may be a mechanism for maintaining total hind limb excursion angles by limiting hind limb protraction in favor of increased retraction.

Hesse et al (2015) measured forces on the tamarin hindlimb on declines and found that at 60° the hind limb began to exert a tensile (pulling) force against the support, hypothesized to be a counteractive measure against pitch. The same extended periods of hind limb retraction observed on steep angles here suggest that the same strategy is being employed by strepsirrhines in the present study. It appears from Hesse et al. (2015) and this data, that primates are

adopting postures during descent of very steep supports that inverts the Cartmill (1974b) and Jungers (1976) model of ascending.

During descent primates that navigate very steep and vertical supports headfirst must establish a strong pedal grip and allow the leg to act as a rope to suspend the body weight, much like a tetherball. If a single-foot grasp is strong enough to support the entirety of the weight during the period in which the contralateral foot is in swing phase, the primate will not topple away from the support. The weight borne by the single foot grasp may additionally be offset by braking forces applied by the forelimb.

5.5 Summary

Many studies to previously consider spatial changes to gait on declines have been focused on supports ranging between 0° and 36° (Vilensky et al. 1994; Krakauer et al. 2002; Nyakatura et al. 2008) with fewer observations of steeper supports (Stevens 2003; Hesse et al 2015). In the present study, spatial changes to gait were primarily significant when comparing level and shallow supports (≤30°) to each and to supports of 45° and steeper, especially in smaller primates that exclusively used headfirst descent (*Cheirogaleus medius* and *Nycticebus pygmaeus*).

On supports of approximately 34° and greater, static friction may no longer be available to primates based on the (Cartmill 1979; Vilensky et al. 1994), which should increase the need for active pedal grasping as supports get progressively steep. A shift from utilizing passive friction to total reliance on

grasping may help to explain why kinematic patterns appear to broadly shift within the sample when comparing supports of 0° to 45° to supports of 60° to 90°, or what Hesse et al. (2015) termed a “kinematic turning point”.

Widely observed primate traits like high forelimb protraction seem to be maintained on declines. On increasingly steep declines, the landing forelimb may act like a strut while extended and a spring through midstance yield to both act as a brake and then reduce peak forces. The hindlimb strategy appears decoupled from this, and instead the ability to maintain a secure single-foot grasp and effectively transform the leg into a rope on a slope may be what separates primates who descended very steep supports headfirst in this study from those that abandoned this behavior in favor of other descent styles. Future analysis of osteological and muscular differences coupled with this behavioral dataset could be used to directly link anatomy with the ability to perform headfirst descent across a wide range of body masses.

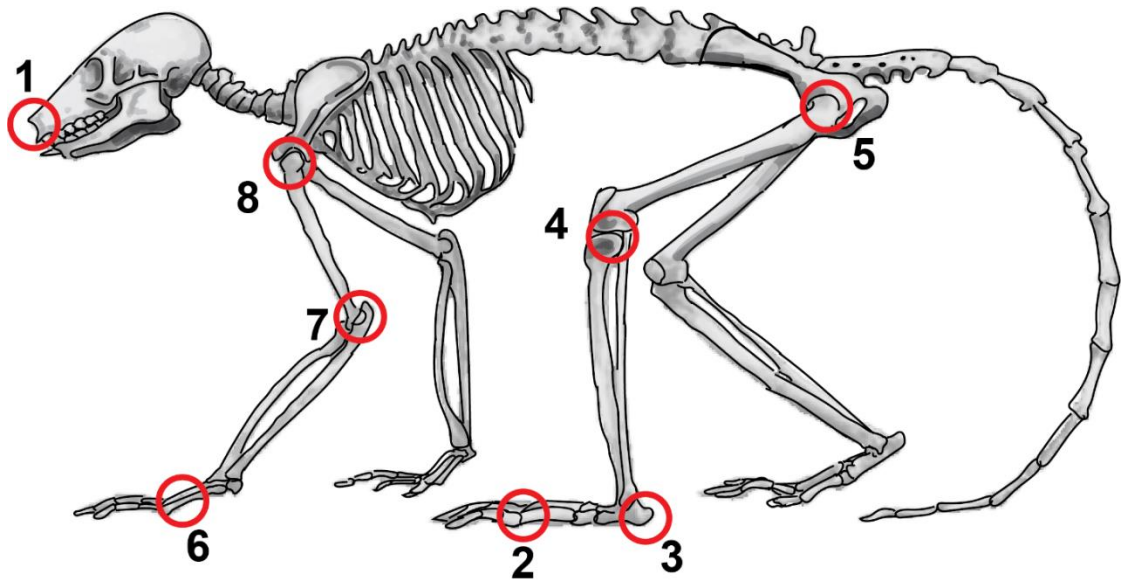


Figure 5-1: Locations of Digitized points. Points correspond to the following: 1. Nose, 2. Foot at metatarsal-phalangeal joint, 3. Distal calcaneus, 4. Knee, 5. Hip, 6. Hand at metacarpal-phalangeal joint, 7. Elbow, 8. Shoulder. Not pictured: two points of known distance on the support.

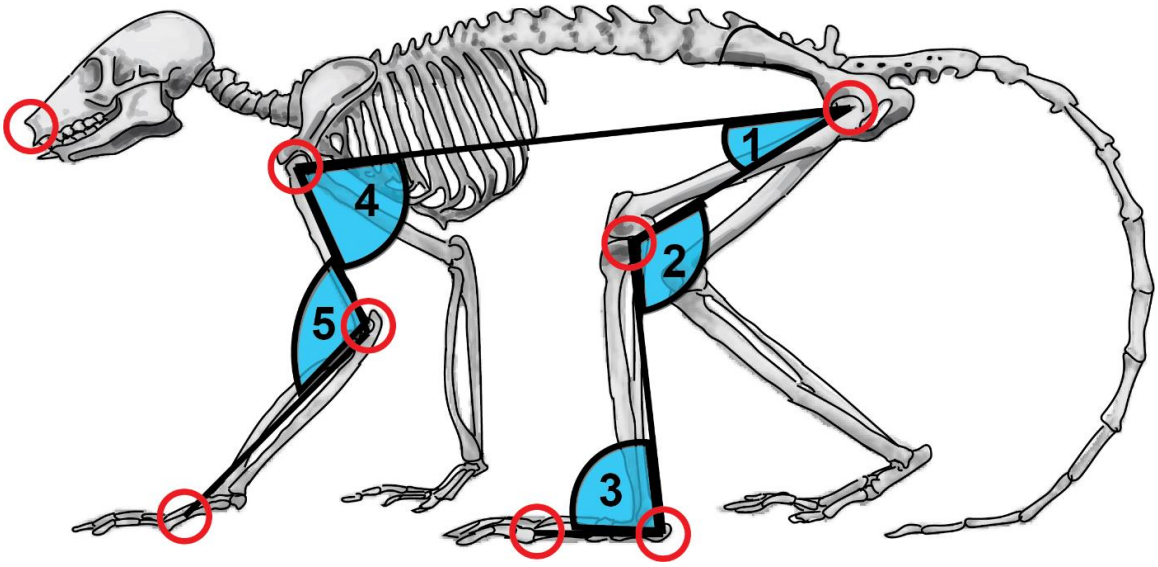


Figure 5-2: Joint Angles measured from anatomical markers. Joint angles are 1. Hip angle from trunk, 2. Knee angle between hip and ankle, 3. Ankle angle between foot, ankle, and knee; 4. Shoulder angle from trunk, 5. Elbow angle between hand and shoulder.

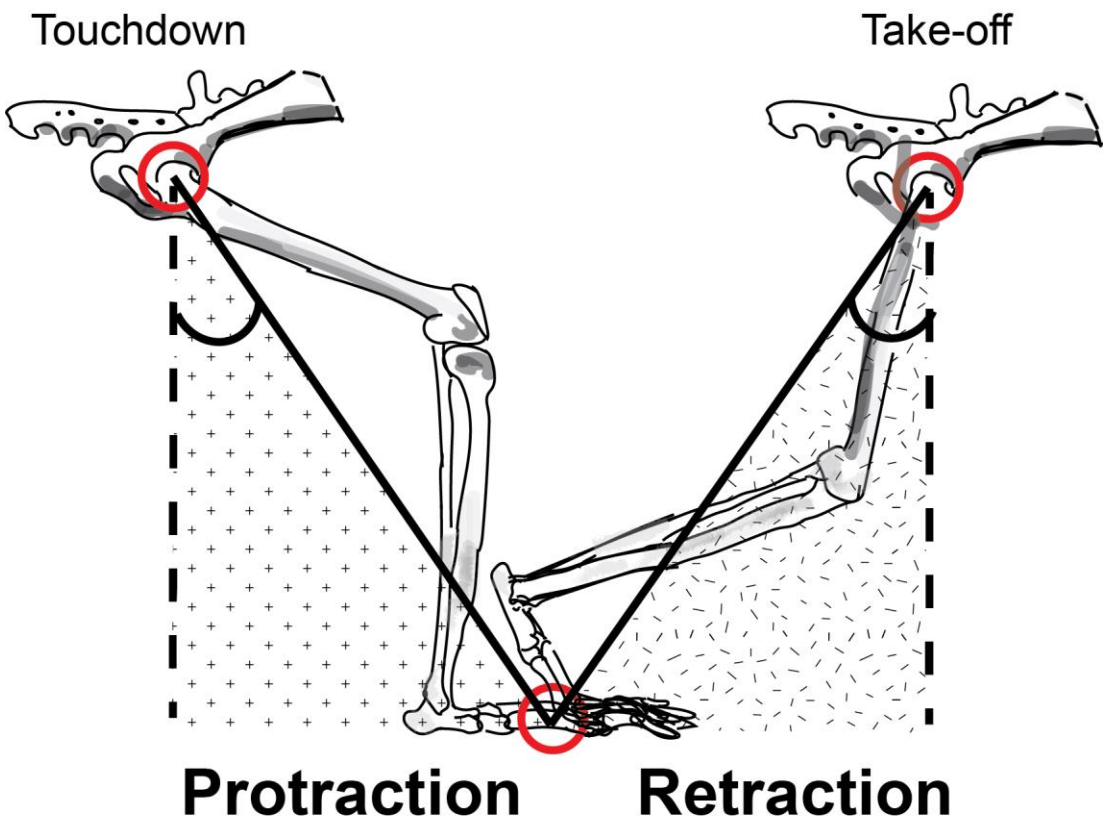


Figure 5-3: Excursion angles measured from anatomical markers. Excursion angles were calculated from the angle created between the shoulder/hand or hip/foot from touchdown to midstance (protraction) and from midstance to takeoff (retraction).

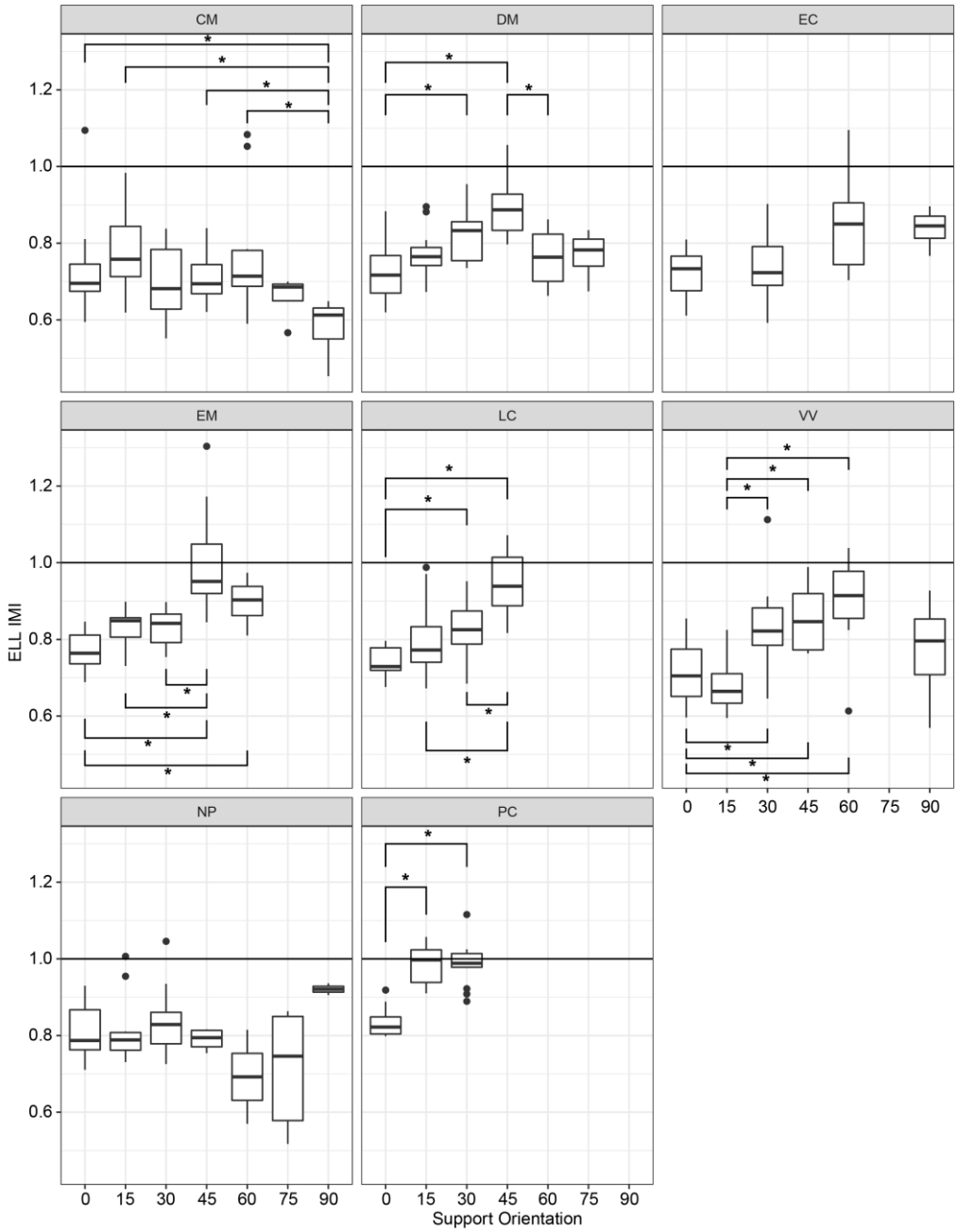


Figure 5-4: Effective Limb Length Intermembral Index changes with support orientation by species. Significant contrasts as found by a Dunn's Test using a Benjamini and Hochberg (1995) correction for multiple comparisons are indicated by asterisks. Abbreviations: ELL IMI – Effective Limb Length Intermembral Index, CM – *C. medius*, DM – *D. madagascariensis*, EC – *E. coronatus*, EM – *E. mongoz*, LC – *L. catta*, VV – *V. variegata*, NP – *N. pygmaeus*, PC – *P. coquereli*.

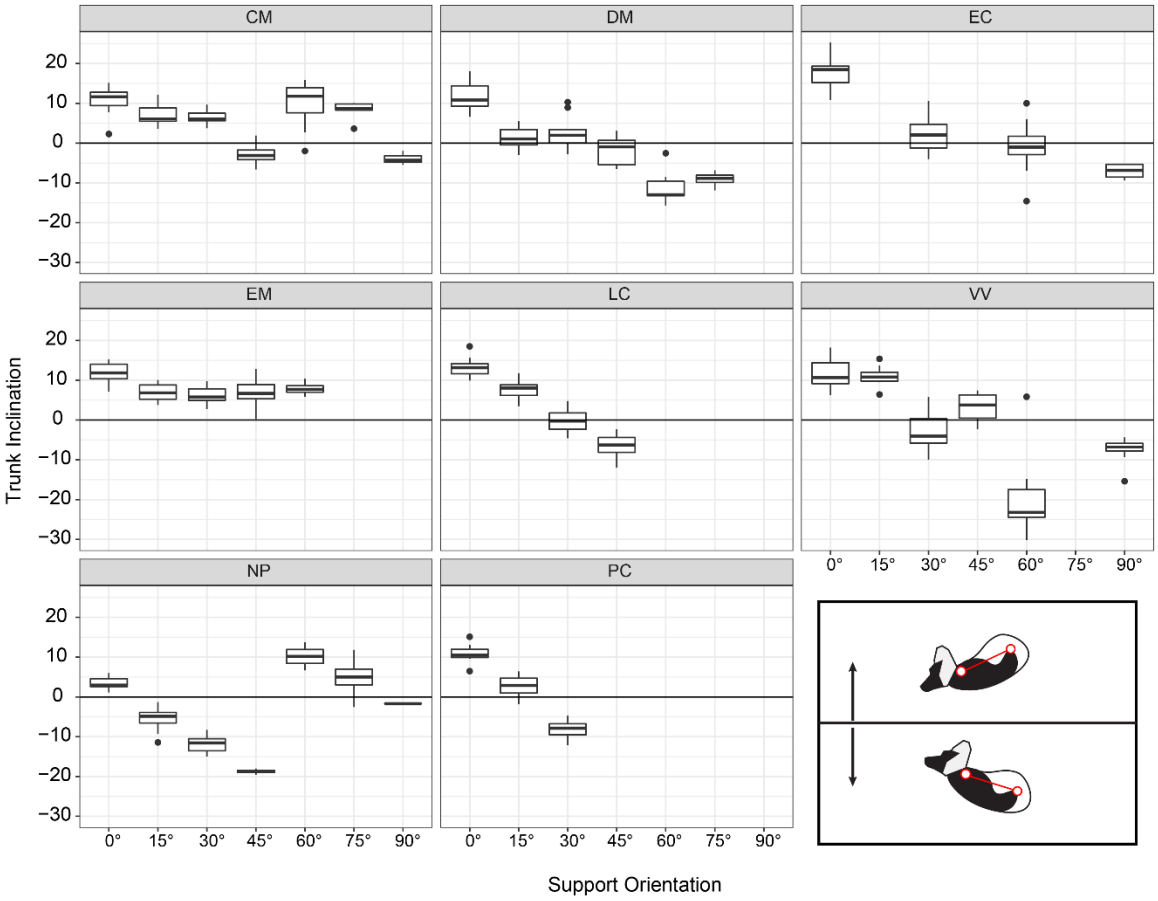


Figure 5-5: Changes to trunk inclination with support orientation. The solid line indicates when trunk inclination, which was the average inclination at touchdown of the fore and hind limb, was approximately equal to support orientation. Values above the line indicate when the hip is relatively farther from the support than the shoulder, and values below the line were when the shoulder was relatively farther from the support than the hip, as illustrated in the bottom right of the figure.

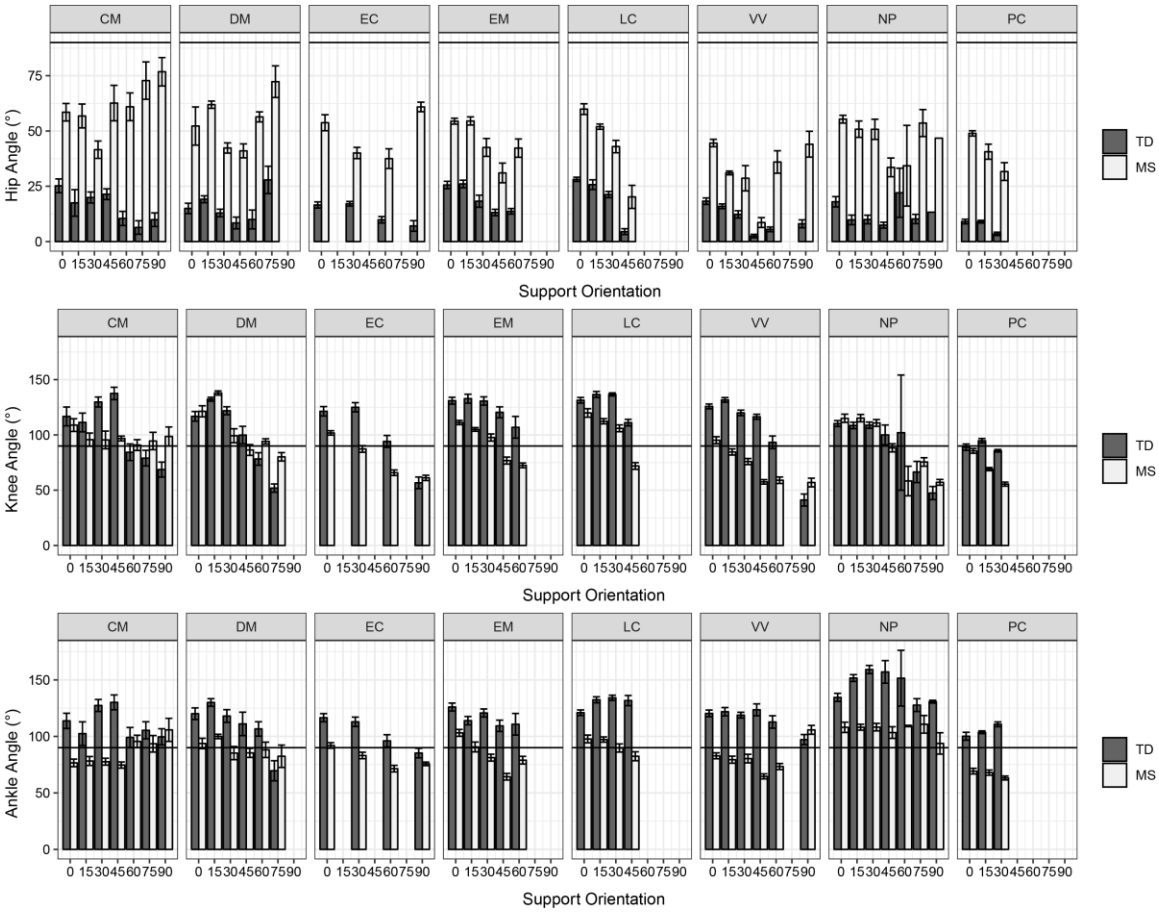


Figure 5-6: Hind limb joint angles at touchdown and midstance for the hip, knee, and ankle. The solid line indicates 90°; flexion is indicated by acute angles and extension by obtuse angles. Abbreviations: TD – touchdown, MS - Midstance, CM – *C. medius*, DM – *D. madagascariensis*, EC – *E. coronatus*, EM – *E. mongoz*, LC – *L. catta*, VV – *V. variegata*, NP – *N. pygmaeus*, PC – *P. coquereli*.

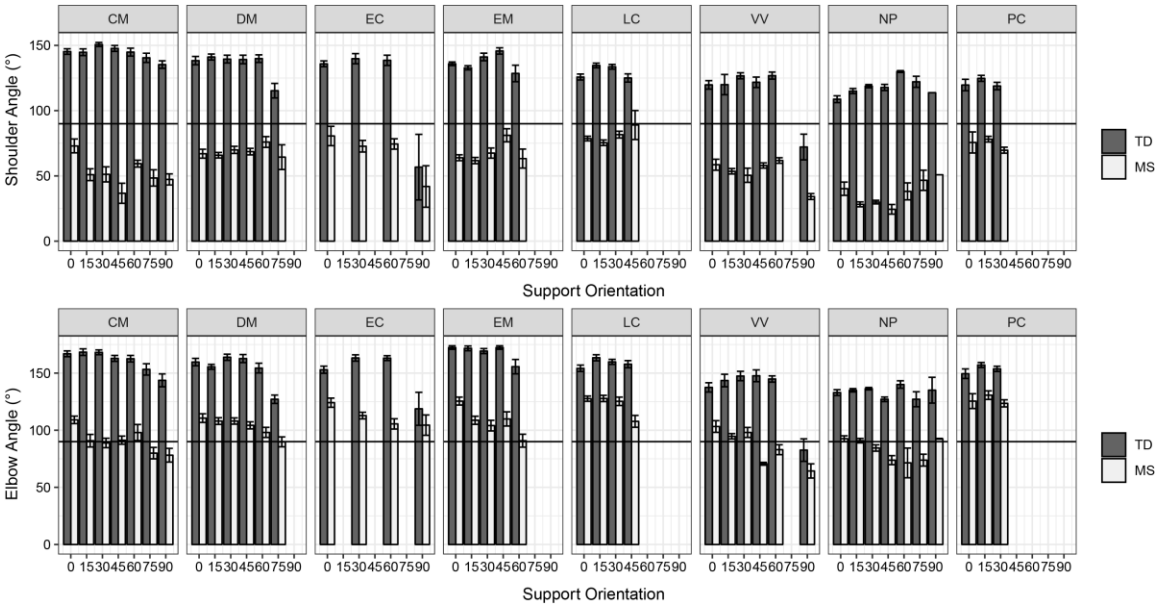


Figure 5-7: Forelimb joint angles at touchdown and midstance for the shoulder and elbow. The solid line indicates 90°; flexion is indicated by acute angles and extension by obtuse angles. Abbreviations: TD – touchdown, MS - Midstance, CM – *C. medius*, DM – *D. madagascariensis*, EC – *E. coronatus*, EM – *E. mongoz*, LC – *L. catta*, VV – *V. variegata*, NP – *N. pygmaeus*, PC – *P. coquereli*.

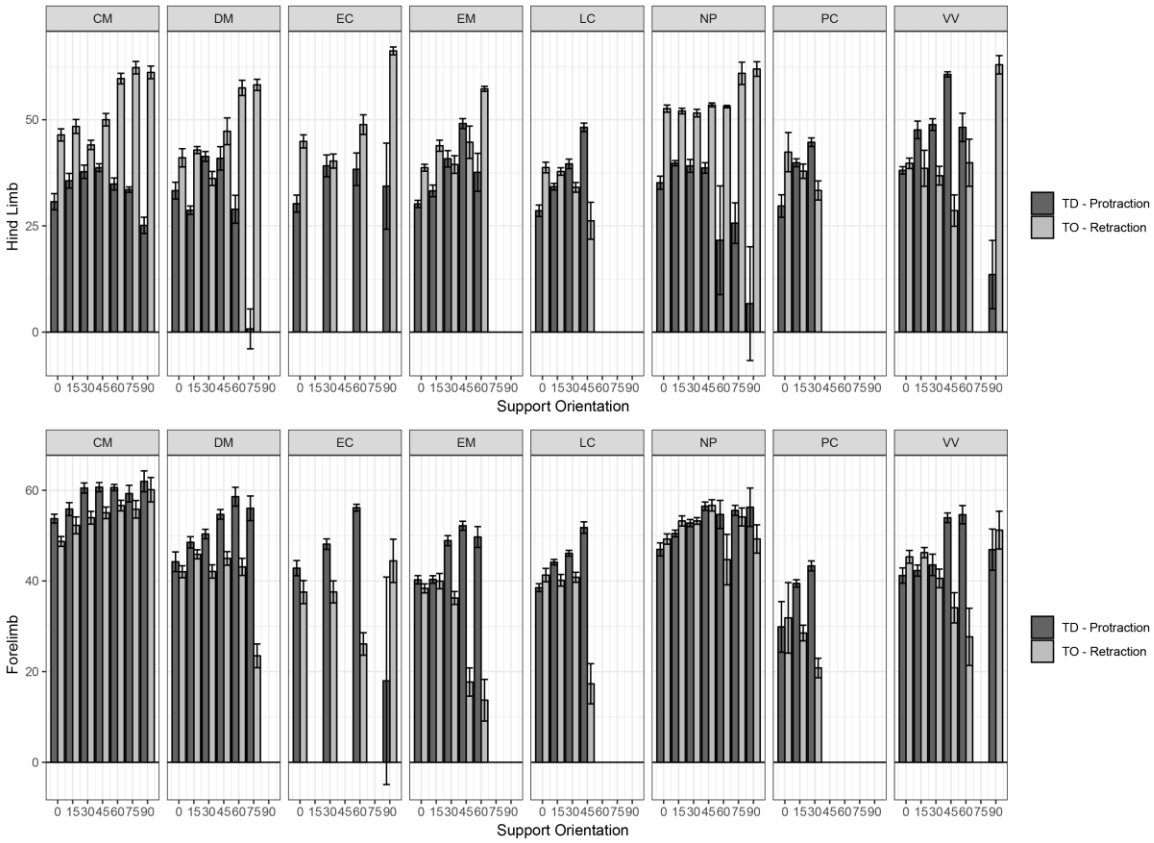


Figure 5-8: Magnitude of hind and forelimb protraction and retraction. Protraction and retraction were measured from the shoulder to hand for the forelimb and from hip to foot for the hind limb. Abbreviations: TD – touchdown, MS - Midstance, CM – *C. medius*, DM – *D. madagascariensis*, EC – *E. coronatus*, EM – *E. mongoz*, LC – *L. catta*, VV – *V. variegata*, NP – *N. pygmaeus*, PC – *P. coquereli*.

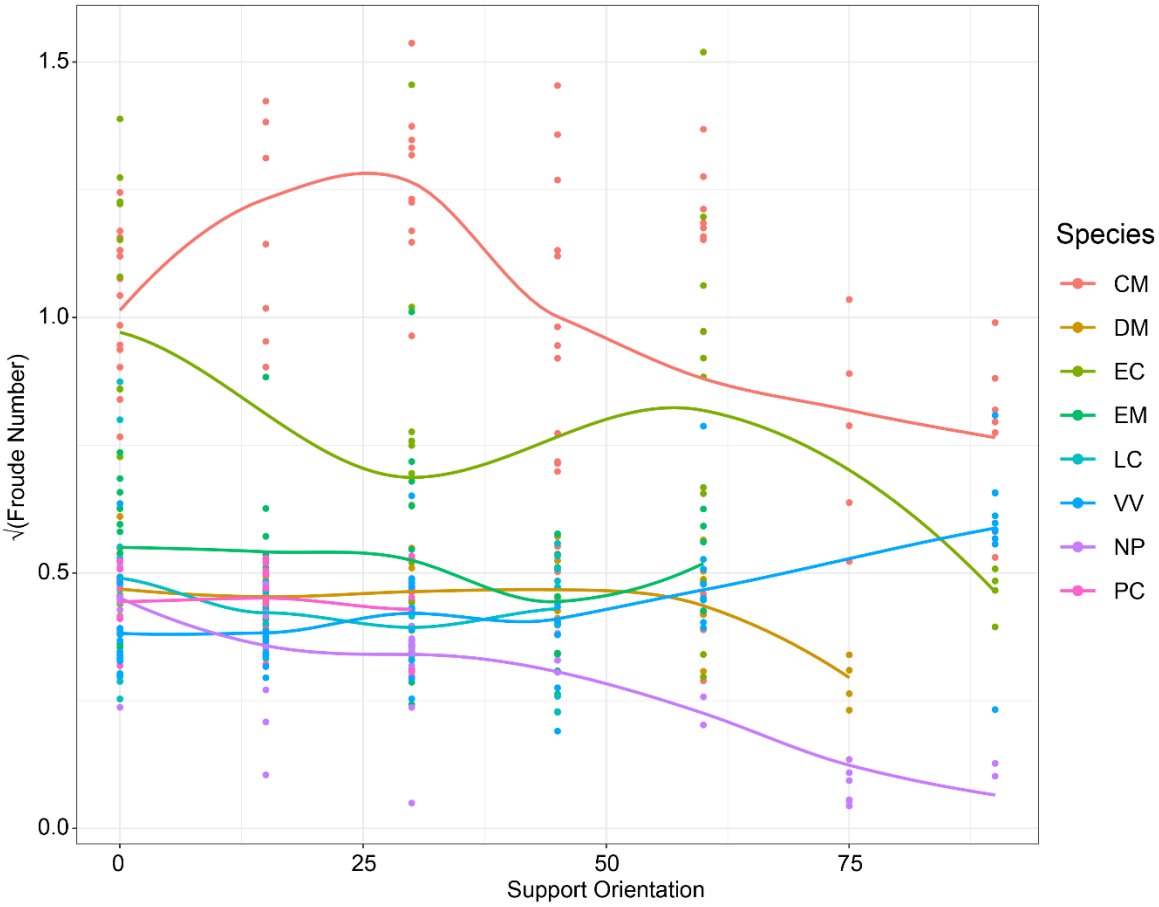


Figure 5-9: Changes to Froude Number with support orientation. Abbreviations: CM – *C. medius*, DM – *D. madagascariensis*, EC – *E. coronatus*, EM – *E. mongoz*, LC – *L. catta*, VV – *V. variegata*, NP – *N. pygmaeus*, PC – *P. coquereli*.

Table 5.1: Definitions of Gait Parameters.

Variable	Abbreviation	Definition
Touchdown	TD (1 and 2)	The initial and subsequent points when the HL or FL makes contact with the support
Take-off	TO	The time when the HL or FL leave contact with the support
Midstance	MS	Midpoint of time between TD1 and TO
Trunk Inclination		Angle measuring the rise of the hip above the shoulder relative to flat ground. Measured at HLTD1 and FLTD1.
Stride length		Measured as the displacement (mm) of the hip from HL TD1 to HL TD2. This was adjusted for each individual by dividing by total hind limb length (mm).
Stride Frequency		Stride frequency is the number of strides over the stride period (seconds). This was transformed into a dimensionless number after Hof (1996) by dividing stride frequency by the square root of gravity over hind limb length.
Velocity (m/s)		Velocity was measured as displacement of the hip from HL TD1 to HL TD2 (m) over time (seconds)
Froude Number	Fr	This measures velocity^2 over gravity (m/s)^2 multiplied by leg length (m) (Alexander and Jayes 1983).
Effective limb length	ELL	The distance (mm) from the limb girdle to the support at midstance. This measure was standardized to individual trunk length (mm).
Effective limb length intermembral index	ELL IMI	The ratio of forelimb ELL to hind limb ELL
Trunk Inclination (°)		The angle created by the shoulder to the hip, relative to the support.
Protraction (°)		The angle of the limb from an imaginary line running perpendicular to the support through the relevant limb girdle, and then from limb girdle to support contact at TD. Illustrated in Fig. 5.3.
Retraction (°)		The angle of the limb from limb girdle to support contact at TO
Total excursion (°)		The total sweep in degrees of the relevant limb girdle during stance phase; measured by adding protraction and the absolute value of retraction

Table 5.2: Sample of symmetrical headfirst descents digitized for the present study.Abbreviations: CM – *C. medius*, DM – *D. madagascariensis*, EC – *E. coronatus*, EM – *E. mongoz*, LC – *L. catta*, VV – *V. variegata*, NP – *N. pygmaeus*, PC – *P. coquereli*.

		Support Orientation (Degrees)						
Species	Individuals	0	15	30	45	60	75	90
CM	CMM1, CMM2	13	7	10	15	11	5	7
DM	DMF1, DMF4	11	14	10	10	7	4	0
EC	ECF1, ECF2, ECM1, ECM2	12	0	12	0	12	0	4
EM	EMF1, EMM1, EMM2	15	10	10	11	4	0	0
LC	LCF1, LCF2, LCM1, LCM2	11	15	14	8	0	0	0
VV	VVF1, VVF2, VVM1, VVM2, VVM3	15	10	15	10	12	0	10
NP	NPF1	12	14	12	4	2	6	2
PC	PCM1	8	10	13	0	0	0	0

Table 5.3: Results of Error Study.

Species	Individual	Angle (Deg)	Maximum SE for point placement (mm)	Trunk Length SE (mm)	Hip Angle SE (Deg)	Knee Angle SE (Deg)	Ankle Angle SE (Deg)	Shoulder Angle SE (Deg)	Elbow Angle SE (Deg)
C. medius	CMM1	60	2.63	2.75	2.68	3.26	2.95	1.50	7.55
D. madagascariensis	DMF1	60	3.98	4.18	1.07	3.36	11.30	1.74	1.82
	DMF4	15	2.65	2.59	1.43	1.22	2.41	1.25	2.06
	DMF4	15	3.94	2.02	2.48	1.16	3.46	1.29	2.14
E. coronatus	ECF1	30	3.32	3.00	1.25	0.44	1.12	1.41	2.20
	ECF2	60	4.03	3.18	1.61	0.97	2.43	2.81	2.08
E. mongoz	EMM2	45	2.79	2.69	0.87	1.19	3.24	1.57	3.20
L. catta	LCF2	45	3.62	2.75	1.15	0.83	3.24	2.14	2.24
	LCM2	30	4.12	1.59	0.92	0.86	3.80	2.61	3.17
N. pygmaeus	NPF2	0	1.63	2.26	1.07	0.95	5.46	1.81	3.61
	NPF2	75	4.25	2.00	4.28	4.43	7.55	1.15	2.24
P. coquereli	PCM1	15	2.01	2.02	0.36	0.52	1.86	0.78	2.20
	PCM1	0	3.42	1.58	1.60	1.30	1.62	1.44	2.82
V. variegata	VVF1	30	3.51	1.54	1.35	1.16	3.70	2.58	3.27
	VVM3	0	3.28	1.78	0.93	0.48	2.64	2.46	3.43

Table 5.4: Summary Statistics for Effective Limb Length and Support Orientation.Fore and hind limb ELL are standardized to individual trunk length. Abbreviations: ELL IMI – Effective limb length intermembral index, CM – *C. medius*, DM – *D. madagascariensis*, EC – *E. coronatus*, EM – *E. mongoz*, LC – *L. catta*, VV – *V. variegata*, NP – *N. pygmaeus*, PC – *P. coquereli*.

		Hind ELL		Fore ELL		ELL IMI		Trunk Inclination (°)	
Species	Support	mean	sd	mean	sd	mean	sd	Mean	sd
CM	0	0.71	0.07	0.56	0.18	0.73	0.13	10.92	3.44
	15	0.64	0.07	0.49	0.05	0.78	0.12	7.21	2.93
	30	0.63	0.09	0.43	0.04	0.70	0.10	6.36	1.87
	45	0.63	0.05	0.45	0.05	0.71	0.06	-2.75	2.37
	60	0.59	0.07	0.45	0.05	0.77	0.16	10.06	5.63
	75	0.64	0.07	0.42	0.04	0.66	0.06	8.10	2.61
	90	0.62	0.06	0.36	0.07	0.58	0.07	-3.97	1.35
DM	0	0.93	0.12	0.67	0.07	0.73	0.08	11.96	3.75
	15	0.97	0.07	0.75	0.06	0.77	0.06	1.28	2.79
	30	0.76	0.06	0.62	0.03	0.82	0.07	2.75	4.09
	45	0.68	0.05	0.60	0.04	0.89	0.08	-1.85	3.50
	60	0.78	0.05	0.59	0.05	0.76	0.08	-10.97	4.35
	75	0.74	0.05	0.57	0.07	0.77	0.07	-9.10	2.11
EC	0	0.89	0.11	0.62	0.06	0.72	0.07	17.67	4.30
	30	0.84	0.07	0.62	0.05	0.74	0.10	2.40	4.56
	60	0.66	0.08	0.55	0.06	0.85	0.12	-0.90	6.22
	90	0.71	0.05	0.59	0.06	0.84	0.06	-7.05	2.12
EM	0	0.95	0.09	0.73	0.09	0.77	0.05	12.04	2.45
	15	0.80	0.04	0.66	0.06	0.83	0.05	7.00	2.27
	30	0.77	0.08	0.64	0.07	0.83	0.05	6.19	2.07
	45	0.68	0.07	0.67	0.08	1.00	0.14	6.96	3.41
	60	0.67	0.03	0.60	0.04	0.90	0.07	7.90	1.87
LC	0	1.03	0.04	0.76	0.05	0.74	0.04	13.26	2.42
	15	1.00	0.06	0.79	0.06	0.80	0.09	7.74	2.10
	30	0.95	0.07	0.78	0.08	0.82	0.07	-0.29	2.89
	45	0.79	0.08	0.74	0.10	0.94	0.09	-6.57	3.26
VV	0	0.79	0.07	0.56	0.07	0.71	0.08	11.85	3.95
	15	0.66	0.06	0.45	0.04	0.68	0.07	11.04	2.47
	30	0.65	0.07	0.54	0.10	0.83	0.11	-3.02	4.46
	45	0.46	0.03	0.39	0.03	0.85	0.08	3.19	3.64
	60	0.52	0.07	0.47	0.08	0.90	0.12	-20.07	9.38
	90	0.57	0.11	0.44	0.09	0.77	0.11	-7.46	3.14

NP	0	0.76	0.05	0.61	0.05	0.81	0.07	3.39	1.55
	15	0.74	0.03	0.60	0.05	0.81	0.08	-5.43	2.64
	30	0.68	0.03	0.57	0.05	0.84	0.09	-11.86	2.16
	45	0.63	0.04	0.50	0.04	0.79	0.03	-18.75	0.68
	60	0.62	0.16	0.41	0.00	0.69	0.17	10.17	4.95
	75	0.58	0.10	0.40	0.06	0.71	0.16	4.89	4.86
	90	0.51	0.07	0.47	0.07	0.92	0.02	-1.69	NA
PC	0	1.02	0.33	0.86	0.28	0.84	0.04	10.86	2.55
	15	0.76	0.04	0.75	0.05	0.99	0.05	2.66	2.61
	30	0.74	0.03	0.73	0.04	0.98	0.06	-8.10	2.08

Table 5.5: Kruskal-Wallis Test results for Effective Limb Length variables of median differences within species between support conditions.Significant values (α = 0.05) indicated in bold. Abbreviations: ELL IMI – effective limb length intermembral index, df – degrees of freedom, CM – *C. medius*, DM – *D. madagascariensis*, EC – *E. coronatus*, EM – *E. mongoz*, LC – *L. catta*, VV – *V. variegata*, NP – *N. pygmaeus*, PC – *P. coquereli*.

		Hind ELL		Fore ELL		ELL IMI	
Species	df	χ^2	p-value	χ^2	p-value	χ^2	p-value
CM	6	14.44	**0.0251**	27.15	**<0.001**	17.69	**0.007**
DM	5	42.48	**<0.001**	33.77	**<0.001**	19.77	**0.001**
EC	3	24.06	**<0.001**	9.66	**0.022**	9.07	**0.028**
EM	4	35.62	**<0.001**	10.93	**0.027**	30.64	**<0.001**
LC	3	21.66	**<0.001**	4.29	0.232	20.51	**<0.001**
VV	5	52.71	**<0.001**	30.26	**<0.001**	28.33	**<0.001**
NP	6	31.37	**<0.001**	32.84	**<0.001**	6.89	0.331
PC	2	17.35	**<0.001**	2.42	0.298	16.33	**<0.001**

Table5.6: Dunn's Test for median differences in Hind limb ELL between support conditions.P-values are adjusted using the correction of Benjamini and Hochberg (1995). Significant values (<0.05) denoted in bold. Abbreviations: ELL – effective limb length, CM – *C. medius*, DM – *D. madagascariensis*, EC – *E. coronatus*, EM – *E. mongoz*, LC – *L. catta*, VV – *V. variegata*, NP – *N. pygmaeus*, PC – *P. coquereli*.

	CM		DM		EC		EM		LC		VV		NP		PC	
Comparison	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj
0 to 15	1.82	0.286	-0.66	0.589			2.35	**0.038**	0.58	0.563	2.24	**0.041**	0.64	0.729	3.05	**0.003**
0 to 30	2.53	0.079	2.95	**0.010**	1.05	0.354	3.12	**0.006**	1.94	0.079	2.78	**0.014**	3.04	**0.010**	4.09	**<0.001**
0 to 45	2.51	0.063	4.65	**<0.001**			5.41	**<0.001**	4.30	**<0.001**	6.44	**<0.001**	3.29	**0.007**		
0 to 60	3.46	**0.011**	2.02	0.072	4.50	**<0.001**	3.93	**<0.001**			5.10	**<0.001**	1.86	0.146		
0 to 75	1.67	0.333	2.55	**0.023**									3.75	**0.004**		
0 to 90	2.58	0.104			2.54	**0.022**					4.21	**<0.001**	3.09	**0.011**		
15 to 30	0.43	0.938	3.75	**0.001**			0.71	0.534	1.45	0.178	0.28	0.776	2.57	**0.027**	0.93	0.352
15 to 45	0.21	0.919	5.54	**<0.001**			2.72	**0.016**	3.97	**<0.001**	3.84	**<0.001**	2.93	**0.012**		
15 to 60	1.16	0.641	2.69	**0.018**			2.12	0.057			2.47	**0.029**	1.55	0.254		
15 to 75	0.04	0.969	3.10	**0.007**									3.37	**0.008**		
15 to 90	0.66	0.969									1.80	0.098	2.80	**0.015**		
30 t 75	-0.34	0.962	0.34	0.732									1.27	0.359		
30 to 45	-0.28	0.912	1.66	0.146			2.00	0.065	2.71	**0.013**	3.86	**<0.001**	1.13	0.420		
30 to 60	0.81	0.881	-0.63	0.567	3.46	**0.002**	1.58	0.142			2.39	**0.032**	0.21	0.873		
30 to 90	0.29	0.952			1.80	0.107					1.66	0.122	1.45	0.283		
45 to 60	1.17	0.723	-2.13	0.061			0.11	0.913			-1.54	0.144	-0.56	0.669		
45 to 75	-0.14	0.930	-0.91	0.493									-0.03	0.979		
45 to 90	0.56	0.929									-2.04	0.063	0.52	0.663		
60 to 75	-1.00	0.740	0.82	0.517									0.58	0.697		
60 to 90	-0.43	0.999			-0.64	0.521					-0.59	0.593	0.94	0.519		
75 to 90	0.57	1.000											0.58	0.740		

Table 5.7: Dunn's Test for median differences in ELL IMI between support conditions.P-values are adjusted using the correction of Benjamini and Hochberg (1995). Significant values (<0.05) denoted in bold. Abbreviations: ELL IMI – effective limb length intermembral index, CM – *C. medius*, DM – *D. madagascariensis*, EC – *E. coronatus*, EM – *E. mongoz*, LC – *L. catta*, VV – *V. variegata*, NP – *N. pygmaeus*, PC – *P. coquereli*.

	CM		DM		EC		EM		LC		VV		PC	
Comparison	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj
0 to 15	-0.896	0.555	-1.243	0.356			-2.128	0.056	-1.693	0.109	0.545	0.627	-3.693	**0.001**
0 to 30	0.636	0.689	-2.548	**0.041**	-0.445	0.788	-2.128	0.067	-2.664	**0.015**	-2.725	**0.016**	-3.495	**0.001**
0 to 45	0.110	0.912	-4.063	**0.001**			-5.356	**0.000**	-4.402	**0.000**	-2.808	**0.015**		
0 to 60	-0.588	0.649	-0.891	0.466			-2.867	**0.010**			-4.039	**0.000**		
0 to 75	1.143	0.483	-0.914	0.492										
0 to 90	3.126	**0.012**			-2.084	0.111					1.542	0.205		
15 to 30	1.396	0.380	-1.479	0.298			0.000	1.000	-1.056	0.291	-2.984	**0.011**	0.430	0.667
15 to 45	1.009	0.506	-3.078	0.016			-2.877	**0.013**	-3.092	**0.006**	-3.062	**0.011**		
15 to 60	0.371	0.746	0.151	0.943			-1.258	0.260			-4.179	**0.000**		
15 to 75	1.745	0.284	-0.058	0.954										
15 to 90	3.528	**0.004**									-1.906	0.106		
30 to 45	-0.553	0.641	-1.481	0.347			-2.877	**0.020**	-2.168	**0.045**	-0.401	0.688		
30 to 60	-1.164	0.514	1.385	0.312	-2.038	0.083	-1.258	0.298			-0.904	0.499		
30 to 75	0.609	0.670	0.979	0.491										
30 to 90	2.431	0.063			-1.805	0.107					0.925	0.409		
45 to 60	-0.712	0.667	2.728	**0.032**			0.879	0.422			-0.933	0.438		
45 to 75	1.084	0.487	2.099	0.108										
45 to 90	3.110	**0.010**									1.207	0.310		
60 to 75	1.562	0.355	-0.164	1.000										
60 to 90	3.529	**0.009**			-0.363	0.716					2.229	0.055		
75 to 90	1.476	0.368												

Table 5.8a: Summary statistics for hind limb joint angles.Bolded values indicate extension of the joint between touchdown and midstance. Values are reported in degrees. Abbreviations: TD – touchdown, MS – midstance, CM – *C. medius*, DM – *D. madagascariensis*, EC – *E. coronatus*, EM – *E. mongoz*, LC – *L. catta*, VV – *V. variegata*, NP – *N. pygmaeus*, PC – *P. coquereli*.

Species	Support	Ankle						Knee						Hip					
		TD		MS		TD to MS		TD		MS		TD to MS		TD		MS		TD to MS	
		mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd
CM	0	113.7	24.2	76.5	12.1	37.2	23.4	116.7	30.7	108.9	20.7	7.8	25.7	25.2	11.2	58.8	6.8	16.2	27.4
	15	102.4	27.7	78.2	10.4	24.2	26.9	111.3	22.3	95.7	15.8	15.6	20.3	17.5	15.9	56.8	14.2	**-39.3**	20.1
	30	127.3	16.7	77.6	9.7	49.7	15.5	129.8	14.3	95.4	25.3	34.3	20.5	19.9	7.9	41.5	7.9	3.3	26.9
	45	130.1	25.3	74.6	10.7	55.5	27.0	137.5	21.6	96.7	8.5	40.8	18.9	21.4	9.4	62.6	16.0	4.7	33.1
	60	99.1	29.3	95.5	18.0	3.5	37.6	84.3	24.9	90.8	16.1	**-6.5**	30.5	10.5	10.6	60.9	16.6	**-28.3**	35.8
	75	105.4	16.9	93.5	16.3	11.9	17.4	79.0	15.8	94.5	17.5	**-15.5**	20.8	6.4	6.8	72.8	18.9	**-66.4**	23.6
	90	99.6	19.0	105.8	27.0	**-6.2**	34.9	68.7	17.9	98.6	22.6	**-29.9**	27.4	9.9	8.2	76.8	17.0	**-66.9**	19.8
DM	0	120.1	16.3	93.7	15.3	26.0	23.9	116.8	13.8	121.3	16.6	**-3.1**	11.5	15.0	7.4	52.2	19.3	**-11.1**	32.8
	15	130.0	12.6	100.0	7.2	30.1	10.3	132.3	6.7	137.9	6.9	**-5.6**	6.7	19.1	5.8	61.9	5.6	**-33.9**	23.4
	30	118.0	17.8	85.2	18.4	32.8	26.8	121.8	10.9	99.2	19.9	21.3	16.2	12.9	5.1	42.3	7.3	**-30.7**	9.7
	45	111.1	31.1	85.4	12.6	28.4	28.0	99.9	22.4	86.4	15.5	16.1	21.5	8.4	7.5	41.0	9.5	**-30.2**	21.2
	60	106.6	16.9	88.1	18.1	18.5	15.7	78.2	14.9	94.2	6.2	**-16.0**	13.2	10.0	11.3	56.4	5.6	**-38.3**	21.9
	75	69.6	17.8	82.4	19.8	**-12.8**	11.5	51.9	7.4	80.2	7.6	**-28.3**	3.4	27.9	12.4	72.3	14.3	**-44.4**	6.2
EC	0	116.5	12.4	92.0	8.6	24.5	13.1	121.4	14.7	101.8	6.8	19.6	18.3	16.5	4.8	53.7	10.2	**-19.3**	29.9
	30	112.9	14.4	83.1	9.9	29.8	14.1	125.0	14.4	87.3	10.4	37.7	13.9	17.1	3.6	40.0	8.5	**-19.6**	14.7
	60	96.1	18.8	71.4	10.1	24.6	24.5	94.1	18.6	65.8	8.6	28.4	22.4	9.9	5.0	37.5	15.4	**-27.6**	14.6
	90	85.3	8.4	75.7	3.1	9.6	10.4	56.6	10.5	61.1	4.8	**-4.5**	12.3	7.1	4.8	60.9	4.3	**-53.8**	8.5
EM	0	126.0	13.6	103.1	11.9	22.9	12.8	131.0	11.8	111.2	7.4	19.8	12.7	25.6	6.4	46.5	15.9	**-20.9**	17.2
	15	113.9	11.7	90.7	13.8	23.3	14.1	132.8	12.7	105.0	5.2	27.8	15.6	26.0	5.4	54.5	5.8	**-28.5**	7.8

	30	120.7	11.3	81.2	9.6	39.5	14.5	130.7	11.9	97.6	10.1	33.0	13.3	18.3	8.6	42.6	12.8	**-24.3**	13.1
	45	109.3	15.8	64.3	9.8	45.3	14.8	120.5	15.6	76.8	10.5	44.5	14.2	13.2	4.5	31.0	14.8	**-19.1**	17.1
	60	110.7	19.1	78.9	6.8	31.8	13.7	106.9	19.6	72.5	4.3	34.4	19.0	13.7	2.5	42.3	8.3	**-28.6**	6.3
LC	0	121.0	8.2	97.7	11.5	23.2	9.1	131.3	8.4	119.9	12.7	11.5	10.3	28.1	3.1	49.2	14.0	**-21.0**	14.1
	15	132.4	10.2	97.2	9.0	35.2	13.8	136.5	10.5	112.4	9.1	24.2	16.2	25.7	8.2	52.0	4.5	**-24.5**	21.3
	30	134.2	8.5	89.8	13.4	44.4	16.0	136.6	5.1	106.0	11.4	30.7	10.0	21.3	5.2	44.0	7.2	**-22.7**	6.3
	45	131.7	12.8	82.4	11.2	49.3	16.6	111.1	8.3	71.9	8.6	39.2	8.4	4.5	3.7	70.3	43.2	**-65.9**	43.1
VV	0	120.3	11.4	82.8	10.1	37.5	14.6	125.8	8.5	95.2	12.1	30.6	11.0	18.3	5.7	41.9	13.6	**-23.6**	14.2
	15	121.8	11.7	79.4	9.9	42.4	16.7	131.7	6.6	84.6	8.8	47.1	13.4	16.0	3.3	31.0	2.7	**-15.1**	3.1
	30	118.8	9.8	80.4	14.3	37.6	12.3	119.9	9.3	75.9	10.3	44.9	10.9	12.3	6.2	25.7	14.6	**-12.5**	16.4
	45	123.5	15.8	64.6	7.0	59.6	14.8	116.4	6.1	57.5	6.3	59.9	8.3	2.5	2.0	8.6	7.0	**-6.9**	8.3
	60	112.7	19.1	73.3	9.3	39.4	19.5	93.3	19.7	59.0	10.1	34.3	22.9	5.5	3.7	26.6	14.7	**-16.6**	17.7
	90	97.2	14.1	105.8	12.4	**-8.6**	18.0	41.1	17.3	57.0	12.5	**-15.8**	20.0	8.1	5.6	44.0	18.5	**-36.0**	22.0
NP	0	134.5	12.4	108.0	15.9	26.5	15.9	110.3	8.8	115.0	12.3	**-5.3**	16.7	18.0	7.7	39.8	13.4	**-20.0**	21.6
	15	151.6	11.3	108.1	9.8	43.5	9.4	108.5	10.9	115.2	12.5	**-6.6**	13.3	9.8	8.1	50.8	12.8	**-33.8**	22.0
	30	159.2	12.5	108.2	11.5	51.0	14.6	108.8	9.9	110.8	10.6	**-2.0**	16.1	10.0	6.8	50.8	15.1	**-36.6**	23.4
	45	157.0	20.0	103.4	10.3	53.6	17.3	100.0	17.9	88.3	7.4	11.7	24.5	7.4	2.7	33.6	8.5	**-26.1**	11.2
	60	151.5	34.8	109.2	0.8	42.3	35.7	102.0	73.7	58.3	18.9	43.7	54.7	22.1	15.7	34.3	25.8	**-12.2**	10.1
	75	127.7	13.9	110.7	19.2	17.0	29.6	66.5	23.5	75.5	9.4	**-9.0**	23.1	10.2	5.2	53.6	15.0	**-43.4**	13.5
	90	130.7	1.7	93.8	13.4	36.9	15.1	47.4	8.4	57.1	3.7	**-9.7**	4.7	13.3	NA	46.8	NA	**-33.5**	NA
PC	0	100.1	9.9	69.2	7.1	30.9	5.0	88.9	8.0	85.6	6.1	3.4	7.6	9.1	2.9	44.8	21.5	**-35.7**	20.3
	15	103.6	3.8	67.9	7.3	35.7	8.1	94.8	6.4	69.1	4.4	25.7	8.5	9.0	2.0	40.6	10.8	**-31.7**	11.1
	30	110.7	7.5	63.2	6.3	47.5	10.8	85.7	4.1	55.5	6.6	30.1	6.7	3.5	2.7	16.0	9.1	**-12.5**	7.3

Table 5.8b: Summary statistics for forelimb joint angles.Bolded values indicate extension of the joint between touchdown and midstance. Values are reported in degrees. Abbreviations: TD – touchdown, MS – midstance, CM – *C. medius*, DM – *D. madagascariensis*, EC – *E. coronatus*, EM – *E. mongoz*, LC – *L. catta*, VV – *V. variegata*, NP – *N. pygmaeus*, PC – *P. coquereli*.

		Elbow						Shoulder					
		TD		MS		TD to MS		TD		MS		TD to MS	
Species	Support	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd
CM	0	166.9	9.2	109.1	11.8	57.8	15.5	145.3	7.4	73.0	13.9	69.2	16.7
	15	168.3	7.6	90.8	14.5	77.5	11.0	144.8	6.9	50.9	11.9	93.9	11.0
	30	168.1	6.7	88.8	13.2	79.3	16.0	150.7	4.9	51.2	11.5	101.6	9.7
	45	162.9	10.0	91.3	13.7	71.6	17.5	147.7	8.8	36.7	15.3	117.3	22.4
	60	162.5	9.5	98.0	23.2	64.6	27.6	144.8	10.1	59.4	7.4	88.6	11.1
	75	153.2	11.0	79.9	11.1	73.3	15.9	140.5	7.9	48.4	14.0	92.0	18.8
	90	143.6	14.9	78.1	15.8	65.5	17.8	135.3	7.6	47.3	11.2	88.0	14.9
DM	0	159.6	10.3	110.6	12.6	47.5	8.4	138.3	9.0	67.0	9.7	71.3	4.1
	15	155.5	8.0	108.0	11.0	47.5	13.8	141.1	8.2	65.8	6.0	76.7	10.0
	30	163.8	8.4	108.1	8.7	55.8	15.0	139.5	8.4	69.9	8.6	66.7	12.4
	45	162.7	11.2	104.3	9.7	58.4	12.2	139.2	9.3	68.6	8.0	69.5	12.3
	60	154.4	11.3	98.1	11.7	56.3	7.8	139.9	7.7	76.0	10.9	63.9	10.8
	75	127.1	7.3	89.8	8.7	37.3	15.7	115.3	11.1	64.4	19.0	50.9	24.1
EC	0	152.9	10.3	124.1	12.7	29.5	16.4	135.9	7.7	80.6	16.5	55.4	20.2

	30	163.2	9.6	112.8	10.1	50.4	10.2	139.8	12.9	72.8	14.7	71.7	5.8
	60	163.1	7.4	105.5	15.5	57.6	14.9	138.6	11.1	74.5	12.6	64.1	9.5
	90	118.7	28.9	104.5	17.8	14.3	42.2	56.7	43.6	41.9	31.8	29.1	60.4
EM	0	172.3	5.9	125.5	13.5	46.8	13.5	135.9	5.4	63.9	5.5	74.6	7.0
	15	171.6	6.5	108.7	11.2	62.9	10.2	132.8	5.1	61.7	7.6	71.1	9.7
	30	169.2	6.9	104.0	14.7	65.2	12.1	141.1	6.5	67.5	12.4	67.4	7.1
	45	172.3	5.0	109.9	20.5	62.5	19.4	145.7	7.3	81.1	15.9	64.3	17.0
	60	155.6	12.6	90.8	11.3	64.8	19.0	128.5	12.6	63.3	14.6	65.2	17.3
LC	0	154.1	9.3	127.6	7.7	26.5	11.0	125.8	7.3	78.6	4.4	49.7	8.4
	15	163.4	10.4	127.8	10.6	35.6	8.7	134.6	7.0	75.4	7.9	59.6	8.2
	30	159.8	8.2	125.3	13.8	34.5	13.0	133.6	6.8	81.6	7.8	55.1	10.6
	45	157.8	8.7	107.7	14.7	50.0	10.5	125.0	8.9	89.0	19.3	43.1	20.2
VV	0	137.5	15.8	103.2	19.9	34.2	23.7	119.7	12.7	58.6	12.6	67.6	13.5
	15	143.5	17.4	94.7	7.4	48.8	17.1	119.9	19.0	53.6	6.6	67.2	17.0
	30	147.4	15.9	98.0	16.4	48.9	27.0	126.7	7.6	50.5	15.4	78.4	12.9
	45	147.6	16.3	70.6	3.8	76.6	17.4	121.7	9.8	58.0	5.5	61.4	13.8
	60	144.8	9.5	82.9	14.3	60.5	17.6	126.8	9.4	61.8	5.2	65.7	7.9
	90	82.6	31.1	64.3	19.6	18.3	35.1	72.1	31.1	34.2	7.1	38.0	27.8
NP	0	132.9	8.9	92.6	8.7	40.3	12.2	108.8	9.0	40.2	10.2	67.2	16.3
	15	134.9	5.4	90.8	7.3	44.1	8.6	115.0	7.2	28.2	7.1	86.8	7.7
	30	136.3	3.7	84.4	9.7	51.9	11.0	118.7	4.3	29.9	4.7	88.8	6.9

	45	127.1	4.0	73.8	7.9	53.3	9.9	117.8	4.7	24.4	7.4	93.4	10.5
	60	140.0	4.5	71.4	18.4	68.6	13.9	129.9	1.0	38.1	9.2	91.8	8.2
	75	127.1	16.1	73.8	11.6	50.9	20.5	122.1	7.4	46.6	15.4	77.0	16.9
	90	135.0	16.0	92.5	0.4	42.6	16.4	113.8	NA	50.9	NA	62.9	NA
PC	0	149.5	11.8	125.5	18.3	24.0	15.1	119.6	11.6	75.6	16.2	38.7	15.5
	15	157.1	6.9	130.7	11.8	26.4	14.5	124.7	7.2	78.1	6.9	46.6	9.2
	30	30.2	12.5	153.7	8.4	123.5	11.3	16.8	37.3	69.7	4.6	52.3	6.3

Table 9: Kruskal Wallis tests for changes joint angles across support orientations.Bolded values indicate significance (α = 0.05). Abbreviations: df – degrees of freedom, CM – *C. medius*, DM – *D. madagascariensis*, EC – *E. coronatus*, EM – *E. mongoz*, LC – *L. catta*, VV – *V. variegata*, NP – *N. pygmaeus*, PC – *P. coquereli*.

Kruskal test for joint angle at HTD1

		Ankle		Knee		Hip		Elbow		Shoulder	
Species	Df	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
CM	6	15.86	**0.014**	36.08	**<0.001**	22.00	**0.001**	21.02	**0.002**	17.32	**0.008**
DM	5	16.65	**0.005**	36.31	**<0.001**	16.21	**0.006**	16.76	**0.005**	10.85	0.054
EC	3	16.47	**0.001**	21.38	**<0.001**	17.00	**<0.001**	13.18	**0.004**	8.47	**0.037**
EM	4	9.49	**0.050**	8.06	0.090	22.38	**<0.001**	9.66	**0.047**	17.04	**0.002**
LC	3	11.16	**0.011**	20.89	**<0.001**	25.62	**<0.001**	7.34	**0.062**	12.59	**0.006**
VV	5	19.00	**0.002**	48.16	**<0.001**	39.23	**<0.001**	28.68	**<0.001**	26.49	**<0.001**
NP	6	23.76	**0.001**	16.57	**0.011**	16.08	**<0.001**	7.33	0.291	16.18	**0.013**
PC	2	6.95	**0.031**	10.19	**0.006**	11.65	0.070	2.75	0.253	1.89	0.388

Kruskal test for joint angle at HMS

		Ankle		Knee		Hip		Elbow		Shoulder	
Species	Df	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
CM	6	20.67	**0.002**	7.42	0.284	13.34	**0.037**	22.25	**0.001**	17.68	**0.007**
DM	5	8.98	0.110	38.50	**<0.001**	29.32	**<0.001**	11.89	**0.036**	4.29	0.508
EC	3	18.27	**0.000**	30.17	**<0.001**	13.77	**0.003**	9.79	**0.020**	4.81	0.186
EM	4	33.48	**<0.001**	35.38	**<0.001**	19.10	**<0.001**	17.00	**0.002**	10.74	**0.029**
LC	3	10.54	**0.015**	25.21	**<0.001**	19.89	**<0.001**	9.05	**0.029**	3.77	0.287
VV	5	32.35	**<0.001**	49.84	**<0.001**	31.02	**<0.001**	36.01	**<0.001**	24.30	**<0.001**
NP	6	3.35	0.765	31.09	**<0.001**	8.43	0.208	20.73	**0.002**	16.13	**0.013**

PC	2	4.13	0.127	24.99	**<0.001**	5.66	0.059	1.40	0.497	3.67	0.159

Kruskal test for joint angle changes between TD1 and MS

		Ankle		Knee		Hip		Elbow		Shoulder	
Species	Df	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
CM	6	29.08	**<0.001**	36.51	**<0.001**	15.54	**0.016**	11.7	0.069	15.16	**0.019**
DM	5	11.41	**0.044**	28.52	**<0.001**	14.21	**0.014**	11.51	**0.048**	7.628	0.178
EC	3	5.478	0.140	12.47	**0.006**	12.88	**0.005**	15.62	**0.001**	4.84	0.183
EM	4	16.17	**0.002**	12.752	**0.013**	8.060	0.09	12.17	**0.016**	3.61	0.460
LC	3	16.12	**0.001**	19.1	**<0.001**	9.23	**0.026**	14.08	**0.002**	3.48	0.322
VV	5	32.08	**<.001**	38.02	**<0.001**	26.79	**<0.001**	24.84	**<0.001**	14.22	**0.014**
NP	6	17.14	**0.008**	5.61	0.468	9.15	0.165	10.65	0.100	10.22	0.115
PC	2	12.84	**0.002**	18.48	**<0.001**	3.39	0.182	0.58	0.744	2.52	0.282

Table 5.10: Summary Statistics for Hind and Forelimb Excursion.Values are reported in degrees. Abbreviations CM – *C. medius*, DM – *D. madagascariensis*, EC – *E. coronatus*, EM – *E. mongoz*, LC – *L. catta*, VV – *V. variegata*, NP – *N. pygmaeus*, PC – *P. coquereli*.

		Hind Protraction		Hind Retraction		Hind Excursion		Fore Protraction		Fore Retraction		Fore Excursion	
species	support	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd
CM	0	30.69	6.86	-46.42	5.15	77.11	6.04	53.74	3.54	-48.71	3.87	102.46	6.34
	15	35.63	4.56	-48.41	4.35	84.04	2.80	55.85	3.78	-52.26	4.93	108.11	6.84
	30	37.74	4.98	-44.07	3.47	81.81	7.21	60.50	3.52	-53.95	4.43	114.45	7.67
	45	38.70	3.54	-50.00	5.68	88.70	5.63	60.69	3.93	-55.03	4.92	115.72	7.64
	60	34.87	4.68	-59.68	4.15	94.54	7.41	60.60	2.14	-56.63	3.69	117.23	4.74
	75	33.54	1.42	-62.25	3.29	95.80	4.56	59.27	4.13	-55.80	4.36	115.07	8.35
	90	25.13	5.07	-61.13	3.94	86.25	6.21	61.98	6.07	-60.12	7.14	122.09	13.02
DM	0	33.31	6.24	-41.03	6.78	74.34	9.83	44.23	6.52	-42.03	3.96	86.26	7.08
	15	28.68	3.72	-42.85	3.09	71.53	4.84	48.52	4.64	-45.87	3.72	94.39	7.28
	30	41.35	3.44	-36.17	4.94	77.52	5.49	50.35	3.28	-42.09	4.62	92.45	5.78
	45	40.90	7.81	-47.29	8.91	88.19	7.31	54.69	3.36	-44.97	4.74	99.66	6.23
	60	28.92	8.70	-57.49	4.73	86.41	10.22	58.59	5.51	-43.10	4.98	101.68	8.78
	75	0.76	9.40	-58.21	2.63	58.97	7.08	56.03	5.44	-23.48	5.23	79.51	0.70
EC	0	30.23	6.99	-44.89	5.35	75.13	7.33	42.82	5.54	-37.54	8.43	80.36	10.78
	30	39.14	8.89	-40.27	5.73	79.41	9.31	48.11	4.06	-37.58	8.42	85.70	9.30
	60	38.34	13.26	-48.85	8.02	87.19	15.73	56.15	2.59	-26.09	8.55	82.25	8.26
	90	34.36	20.26	-66.19	1.88	100.55	21.64	17.97	45.78	-44.44	9.55	62.41	50.78
EM	0	30.16	3.29	-38.70	3.15	68.86	3.70	40.25	3.55	-38.36	3.82	78.61	4.73
	15	33.25	4.35	-43.88	4.15	77.13	6.98	40.32	2.62	-39.96	5.34	80.28	6.41
	30	40.79	6.10	-39.45	6.56	80.25	6.51	48.89	3.53	-36.24	4.51	85.13	6.59
	45	49.09	3.67	-44.69	12.03	93.78	10.67	52.17	3.32	-17.70	10.32	69.87	9.22

	60	37.61	8.97	-57.27	1.19	94.88	8.12	49.69	4.61	-13.69	9.18	63.38	6.47
LC	0	28.57	4.51	-38.74	4.16	67.31	5.34	38.51	2.90	-41.28	4.91	79.80	5.69
	15	34.24	3.01	-37.81	3.42	72.05	3.81	44.14	2.35	-40.14	4.98	84.28	4.58
	30	39.61	4.20	-34.08	4.31	73.68	6.91	46.11	2.36	-40.81	4.13	86.92	4.65
	45	48.20	2.85	-26.21	12.33	74.41	13.98	51.78	3.58	-17.32	12.52	69.09	14.27
VV	0	38.07	3.39	-39.74	4.74	77.81	6.90	41.19	6.51	-45.31	5.46	86.50	10.37
	15	47.60	6.54	-38.56	13.39	86.15	19.19	42.29	3.90	-46.24	3.59	88.53	2.93
	30	48.85	5.15	-36.81	8.25	85.67	8.41	43.54	9.14	-40.56	7.93	84.10	9.96
	45	60.66	1.64	-28.60	9.79	89.26	10.98	53.93	3.36	-34.07	10.56	88.00	10.32
	60	48.19	11.55	-39.87	19.20	88.07	18.51	54.61	6.69	-27.67	20.96	82.28	25.18
	90	13.55	25.41	-62.93	6.85	76.48	27.09	46.90	13.63	-51.21	12.50	98.12	21.24
NP	0	35.16	5.12	-52.60	2.79	87.76	6.58	46.96	4.99	-49.24	3.93	96.20	8.07
	15	39.76	2.29	-52.05	2.45	91.81	3.52	50.47	2.75	-53.24	4.20	103.71	6.20
	30	39.12	5.25	-51.56	3.10	90.69	8.08	52.78	2.71	-53.24	2.52	106.02	3.98
	45	38.64	2.50	-53.47	0.92	92.11	3.34	56.48	1.85	-56.68	2.50	113.16	3.68
	60	21.61	18.10	-53.08	0.41	74.69	18.51	54.67	4.37	-44.71	7.89	99.38	12.26
	75	25.65	11.71	-60.92	6.45	86.57	8.89	55.56	2.69	-54.11	4.88	109.67	7.07
	90	6.70	18.94	-61.93	2.41	68.64	16.53	56.26	6.00	-49.26	4.41	105.52	10.41
PC	0	29.68	7.48	-42.36	13.05	72.04	9.83	29.87	15.80	-31.86	22.00	61.73	11.52
	15	39.85	2.97	-37.88	5.34	77.73	3.02	39.45	2.58	-28.52	5.45	67.97	6.82
	30	44.69	3.66	-33.35	8.11	78.04	5.92	43.32	3.99	-20.80	7.73	64.12	8.62

Table 5.11: Kruskal-Wallis Test results for changes to hind and forelimb protraction and retraction with support orientation.Significant values (<0.05) denoted in bold. Abbreviations HL – hind limb, FL – forelimb, CM – *C. medius*, DM – *D. madagascariensis*, EC – *E. coronatus*, EM – *E. mongoz*, LC – *L. catta*, VV – *V. variegata*, NP – *N. pygmaeus*, PC – *P. coquereli*.

		HL Protraction		HL Retraction		FL Protraction		FL Retraction		Total HL Excursion		Total FL Excursion	
Species	df	χ^2	p value	χ^2	p value	χ^2	p value	χ^2	p value	χ^2	p value	χ^2	p value
CM	6	27.29	**<0.001**	47.04	**<0.001**	23.48	**<0.001**	23.42	**<0.001**	37.83	**<0.001**	26.12	**<0.001**
DM	5	30.26	**<0.001**	30.63	**<0.001**	29.59	**<0.001**	16.98	**0.004**	26.76	**<0.001**	23.02	**<0.001**
EC	3	6.72	0.081	16.891	**<0.001**	22.15	**<0.001**	14.066	**0.002**	10.15	**0.017**	1.56	0.667
EM	4	31.97	**<0.001**	17.39	**0.001**	35.68	**<0.001**	30.82	**<0.001**	32.07	**<0.001**	21.03	**<0.001**
LC	3	33.22	**<0.001**	10.85	**0.012**	33.58	**<0.001**	19.94	**<0.001**	5.53	0.137	15.77	**0.001**
VV	5	40.39	**<0.001**	30.95	**<0.001**	33.04	**<0.001**	28.49	**<0.001**	10.11	0.072	9.67	0.085
NP	6	24.74	**<0.001**	15.28	**0.018**	26.81	**<0.001**	16.65	**0.016**	11.64	0.0705	20.26	**0.002**
PC	2	19.42	**<0.001**	3.37	0.185	16.93	**<0.001**	5.06	0.079	3.1	0.212	1.039	0.595

Table 5.12: Dunn's Test for median differences in hind limb protraction across support orientations.P-values are adjusted using the correction of Benjamini and Hochberg (1995). Significant values (<0.05) denoted in bold. Abbreviations: CM – *C. medius*, DM – *D. madagascariensis*, EM – *E. mongoz*, LC – *L. catta*, VV – *V. variegata*, NP – *N. pygmaeus*, PC – *P. coquereli*.

	CM		DM		EM		LC		VV		NP		PC	
Comparison	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj
0 to 15	-1.688	0.192	1.316	0.235	-1.137	0.319	-1.915	0.055	-2.742	**0.011**	-2.230	0.068	-2.156	**0.031**
0 to 30	-2.678	**0.031**	-2.089	**0.069**	-3.366	**0.003**	-3.808	**0.000**	-3.140	**0.004**	-1.182	0.356	-4.377	**0.000**
0 to 45	-3.454	**0.004**	-1.857	**0.086**	-5.269	**0.000**	-5.366	**0.000**	-4.759	**0.000**	-0.979	0.430		
0 to 60	-1.435	0.265	0.867	0.446	-1.677	0.134			-2.962	**0.007**	1.269	0.330		
0 to 75	-0.680	0.579	2.721	**0.016**							1.900	0.121		
0 to 90	1.487	0.262							0.851	0.494	1.794	0.139		
15 to 30	-0.680	0.613	-3.522	**0.002**	-2.034	0.084	-2.083	**0.045**	-0.115	1.000	1.030	0.424	-2.245	**0.037**
15 to 45	-1.130	0.362	-3.217	**0.005**	-3.771	**0.001**	-3.959	**0.000**	-2.149	**0.043**	0.576	0.697		
15 to 60	0.421	0.674	-0.255	0.856	-0.810	0.464			-0.065	1.000	2.479	0.069		
15 to 75	0.740	0.603	1.879	0.090							3.817	**0.003**		
15 to 90	2.784	**0.028**							3.279	0.003	3.013	**0.027**		
30 to 45	-0.446	0.725	0.162	0.871	-1.737	0.137	-2.164	**0.046**	-2.185	**0.048**	-0.136	0.936		
30 to 60	1.233	0.326	2.752	**0.018**	0.728	0.467			0.051	0.960	1.923	0.127		
30 to 75	1.403	0.259	4.276	**0.000**							2.915	**0.025**		
30 to 90	3.700	**0.002**							3.657	0.001	2.451	0.060		
45 to 60	1.816	0.182	2.527	**0.025**	2.041	0.103			2.168	**0.045**	1.786	0.130		
45 to 75	1.841	0.197	4.068	**0.000**							2.379	0.061		
45 to 90	4.381	**0.000**							5.125	0.000	2.253	0.073		
60 to 75	0.426	0.703	1.887	0.098							-0.014	0.989		
60 to 90	2.657	**0.028**							3.490	0.002	0.404	0.759		

75 to 90	1.801	0.167	0.508	0.713

Table 5.13: Dunn's Test for median differences in hind limb retraction across support orientations.P-values are adjusted using the correction of Benjamini and Hochberg (1995). Significant values (<0.05) denoted in bold. Abbreviations: CM – *C. medius*, DM – *D. madagascariensis*, EC – *E. coronatus*, EM – *E. mongoz*, LC – *L. catta*, VV – *V. variegata*, NP – *N. pygmaeus*.

	CM		DM		EC		EM		LC		VV		NP	
Comparison	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj
0 to 15	0.439	0.731	0.476	0.679			2.040	0.103	-0.350	0.726	-1.181	0.297	-0.291	0.810
0 to 30	-0.911	0.476	-1.336	0.227	-1.414	0.189	0.206	0.930	-2.186	0.058	-0.969	0.384	-1.080	0.534
0 to 45	1.369	0.257	1.402	0.220			2.143	0.107	-2.620	0.053	-2.499	**0.027**	0.869	0.539
0 to 60	4.064	**0.000**	3.422	**0.003**	1.100	0.271	3.619	**0.003**			0.381	0.754	0.442	0.728
0 to 75	3.702	**0.001**	2.922	**0.010**									2.149	0.133
0 to 90	3.875	**0.000**			2.889	**0.012**					3.241	**0.004**	2.017	0.153
15 to 30	-1.195	0.325	-1.897	0.096			-1.674	0.118	-1.996	0.069	0.295	0.768	-0.849	0.520
15 to 45	0.684	0.610	1.055	0.336			0.094	0.925	-2.464	**0.041**	-1.343	0.269	1.102	0.568
15 to 60	3.018	**0.008**	3.217	**0.005**			2.035	0.084			1.470	0.236	0.604	0.674
15 to 75	2.976	**0.007**	2.702	0.017									2.475	0.093
15 to 90	3.014	**0.007**									4.037	**0.000**	2.206	0.144
30 to 45	2.209	**0.044**	2.631	**0.018**			1.768	0.110	-0.760	0.537	-1.693	0.169	1.660	0.291
30 to 60	4.688	**0.000**	4.564	**0.000**	2.514	**0.024**	3.300	**0.005**			1.290	0.269	1.035	0.526
30 to 75	4.256	**0.000**	3.898	**0.001**									3.083	**0.043**
30 to 90	4.464	**0.000**			3.889	**0.001**					4.066	**0.000**	2.620	0.092
45 to 60	2.888	**0.008**	1.974	0.091			1.964	0.083			2.715	**0.017**	-0.194	0.846
45 to 75	2.768	**0.010**	1.738	0.123									0.903	0.550
45 to 90	2.836	**0.009**									5.006	**0.000**	1.204	0.533
60 to 75	0.525	0.699	0.068	0.946									0.920	0.578
60 to 90	0.314	0.791			2.111	0.052					2.746	**0.018**	1.211	0.593

75 to 90	-0.225	0.822	0.563	0.669

Table 5.14: Dunn's Test for median differences in forelimb protraction across support orientations. P-values are adjusted using the correction of Benjamini and Hochberg (1995). Significant values (<0.05) denoted in bold. Abbreviations: CM – *C. medius*, DM – *D. madagascariensis*, EC – *E. coronatus*, EM – *E. mongoz*, LC – *L. catta*, VV – *V. variegata*, NP – *N. pygmaeus*, PC – *P. coquereli*.

	CM		DM		EC		EM		LC		VV		NP		PC	
Comparison	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj
0 to 15	-0.781	0.830	-1.268	0.279			0.028	0.978	-2.933	**0.005**	-0.032	0.974	-1.274	0.327	-2.058	0.059
0 to 30	-3.276	**0.007**	-1.822	0.114	-1.547	0.183	-3.501	**0.002**	-4.168	**0.000**	-1.121	0.328	-2.734	**0.026**	-4.093	**0.000**
0 to 45	-3.789	**0.003**	-3.648	**0.002**			-4.790	**0.000**	-5.482	**0.000**	-4.221	**0.000**	-3.648	**0.003**		
0 to 60	-3.483	**0.005**	-4.337	**0.000**	-4.524	**0.000**	-2.747	**0.012**			-4.127	**0.000**	-2.002	0.136		
0 to 75	-2.287	0.078	-3.112	**0.007**									-3.871	**0.002**		
0 to 90	-2.955	**0.016**			-0.693	0.586					-2.261	0.051	-2.217	0.093		
15 to 30	-2.053	0.105	-0.713	0.549			-3.221	**0.003**	-1.355	0.175	-0.971	0.383	-1.564	0.225	-2.052	**0.040**
15 to 45	-2.337	0.082	-2.739	**0.018**			-4.378	**0.000**	-3.120	**0.004**	-3.824	**0.001**	-2.831	**0.024**		
15 to 60	-2.230	0.077	-3.551	**0.002**			-2.632	0.014			-3.719	**0.001**	-1.359	0.305		
15 to 75	-1.430	0.321	-2.342	**0.041**									-2.940	**0.023**		
15 to 90	-1.907	0.132									-2.046	0.076	-1.577	0.241		
30 to 45	-0.142	1.000	-1.876	0.114			-1.080	0.400	-1.946	0.062	-3.218	**0.004**	-1.714	0.227		
30 to 60	-0.195	1.000	-2.736	**0.016**	-3.043	**0.007**	-0.197	0.937			-3.095	**0.005**	-0.540	0.773		
30 to 75	0.319	1.000	-1.746	0.121									-1.639	0.236		
30 to 90	-0.015	0.988			0.418	0.676					-1.290	0.269	-0.756	0.675		
45 to 60	-0.071	0.990	-1.034	0.377			0.609	0.678			0.194	0.906	0.667	0.707		
45 to 75	0.451	1.000	-0.328	0.743									0.264	0.831		
45 to 90	0.111	1.000									1.675	0.156	0.476	0.740		
60 to 75	0.478	1.000	0.503	0.659									-0.498	0.764		
60 to 90	0.162	1.000			2.570	**0.020**					1.524	0.191	-0.165	0.869		

75 to 90	-0.311	1.000	0.296	0.848

Table 5.15: Dunn's Test for median differences in forelimb retraction between support orientations. P-values are adjusted using the correction of Benjamini and Hochberg (1995). Significant values (<0.05) denoted in bold. Abbreviations: CM – *C. medius*, DM – *D. madagascariensis*, EC – *E. coronatus*, EM – *E. mongoz*, LC – *L. catta*, VV – *V. variegata*, NP – *N. pygmaeus*.

	CM		DM		EC		EM		LC		VV		NP	
Comparison	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj
0 to 15	1.288	0.346	1.959	0.125			0.672	0.557	-0.837	0.604	0.345	0.730	2.416	0.110
0 to 30	2.437	0.062	0.120	0.905	0.358	0.720	-0.672	0.627	-0.618	0.644	-1.570	0.175	2.290	0.116
0 to 45	3.228	**0.009**	1.323	0.309			-4.113	**0.000**	-4.153	**0.000**	-2.471	**0.034**	3.153	**0.034**
0 to 60	3.669	**0.003**	0.354	0.834	-2.601	**0.019**	-3.145	**0.004**			-3.730	**0.001**	-0.490	0.820
0 to 75	2.591	**0.050**	-2.204	0.083									2.090	0.128
0 to 90	3.931	**0.002**			1.082	0.419					1.020	0.355	-0.101	0.966
15 to 30	0.854	0.590	-1.888	0.126			-1.227	0.314	0.218	0.827	-1.749	0.134	-0.040	0.968
15 to 45	1.353	0.370	-0.553	0.726			-4.365	**0.000**	-3.589	**0.001**	-2.571	**0.030**	1.534	0.263
15 to 60	1.906	0.170	-1.422	0.291			-3.455	**0.002**			-3.711	**0.001**	-1.752	0.239
15 to 75	1.297	0.371	-3.812	**0.002**									0.193	0.936
15 to 90	2.318	0.072									0.630	0.567	-1.359	0.281
30 to 45	0.486	0.693	1.237	0.324			-3.109	**0.004**	-3.728	**0.001**	-1.067	0.357	1.533	0.239
30 to 60	1.159	0.398	0.251	0.859	-3.026	**0.015**	-2.528	**0.019**			-2.286	0.042	-1.714	0.202
30 to 75	0.618	0.662	-2.332	0.074									0.220	0.964
30 to 90	1.660	0.254			0.836	0.484					2.380	**0.037**	-1.325	0.278
45 to 60	0.784	0.569	-0.872	0.523			-0.235	0.814			-1.080	0.382	-2.533	0.119
45 to 75	0.272	0.786	-3.266	**0.008**									-1.201	0.322
45 to 90	1.354	0.410									3.132	**0.007**	-2.191	0.120
60 to 75	-0.328	0.780	-2.398	0.082									1.738	0.216
60 to 90	0.608	0.633			2.975	**0.009**					4.251	**0.000**	0.297	0.947

75 to 90	0.819	0.578	-1.374	0.297

Table 5.16: Dunn's Test for median differences in total hindlimb excursion between support orientations.P-values are adjusted using the correction of Benjamini and Hochberg (1995). Significant values (<0.05) denoted in bold. Abbreviations: CM – *C. medius*, DM – *D. madagascariensis*, EC – *E. coronatus*, EM – *E. mongoz*.

comparison	CM		DM		EC		EM	
	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj
0 to 15	-1.517	0.194	0.744	0.489			-2.263	**0.047**
0 to 30	-1.265	0.254	-0.895	0.428	-1.222	0.266	-3.017	**0.009**
0 to 45	-3.780	**0.001**	-2.647	**0.020**			-5.023	**0.000**
0 to 60	-4.895	**0.000**	-2.110	0.065	-2.654	**0.048**	-3.862	**0.001**
0 to 75	-4.356	**0.000**	2.130	0.071				
0 to 90	-2.550	**0.028**			-2.519	**0.035**		
15 to 30	0.364	0.716	-1.684	0.138			-0.689	0.546
15 to 45	-1.575	0.186	-3.528	**0.002**			-2.520	**0.029**
15 to 60	-2.676	**0.022**	-2.912	**0.013**			-2.112	0.058
15 to 75	-2.700	**0.024**	1.679	0.127				
15 to 90	-0.906	0.426						
30 to 45	-2.205	0.064	-1.737	0.137			-1.831	0.096
30 to 60	-3.371	**0.004**	-1.247	0.265	-1.432	0.228	-1.591	0.139
30 to 75	-3.213	**0.006**	2.782	**0.016**				
30 to 90	-1.346	0.234			-1.654	0.196		
45 to 60	-1.443	0.209	0.417	0.677			-0.207	0.836
45 to 75	-1.665	0.168	4.108	**0.001**				
45 to 90	0.518	0.635						
60 to 75	-0.532	0.657	3.670	**0.002**				
60 to 90	1.675	0.179			-0.642	0.521		
75 to 90	1.873	0.128						

Table 5.17: Dunn's Test for median differences in total forelimb excursion between support orientations.P-values are adjusted using the correction of Benjamini and Hochberg (1995). Significant values (<0.05) denoted in bold. Abbreviations: CM – *C. medius*, DM – *D. madagascariensis*, EM – *E. mongoz*, LC – *L. catta*, NP – *N. pygmaeus*.

comparison	CM		DM		EM		LC		NP	
	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj
0 to 15	-1.168	0.463	-2.109	0.075	-0.532	0.595	-1.385	0.249	-2.388	0.089
0 to 30	-3.000	**0.014**	-1.562	0.178	-1.675	0.134	-2.567	**0.021**	-2.855	**0.030**
0 to 45	-3.727	**0.001**	-3.097	**0.007**	2.163	0.051	1.380	0.201	-3.848	**0.003**
0 to 60	-3.927	**0.002**	-3.175	**0.007**	2.601	**0.023**			-0.792	0.692
0 to 75	-2.710	0.028	1.122	0.302					-3.101	**0.020**
0 to 90	-3.733	**0.002**							-1.354	0.410
15 to 30	-1.449	0.309	0.443	0.705	-1.043	0.371	-1.273	0.203	-0.575	0.698
15 to 45	-1.889	0.155	-1.261	0.259	2.462	**0.028**	2.664	**0.023**	-2.261	0.100
15 to 60	-2.241	0.075	-1.510	0.179	2.841	**0.015**			0.443	0.768
15 to 75	-1.500	0.312	2.779	**0.016**					-1.252	0.442
15 to 90	-2.249	0.086							-0.125	0.901
30 to 45	-0.369	0.831	-1.578	0.191	3.530	**0.002**	3.700	**0.001**	-1.829	0.202
30 to 60	-0.872	0.619	-1.791	0.137	3.629	**0.003**			0.734	0.648
30 to 75	-0.300	0.845	2.353	0.047					-0.770	0.662
30 to 90	-0.991	0.563							0.173	0.906
45 to 60	-0.587	0.780	-0.359	0.719	1.036	0.334			1.867	0.217
45 to 75	-0.027	0.979	3.546	**0.003**					1.039	0.523
45 to 90	-0.738	0.691							1.371	0.447
60 to 75	0.412	0.840	3.629	**0.004**					-1.158	0.471
60 to 90	-0.199	0.884							-0.429	0.738
75 to 90	-0.553	0.761							0.633	0.691

Table 5.18: Summary Statistics for Velocity, Froude Number, and Stride length.

Species	Support Orientation	Velocity (m/s)		Froude Number		Stride Length/ Trunk Length		Dimensionless Stride frequency	
		Mean	sd	Mean	sd	Mean	sd	Mean	sd
CM	0	0.84	0.13	1.07	0.29	2.58	0.22	19.98	4.47
	15	0.97	0.17	1.39	0.50	2.59	0.18	23.33	3.54
	30	1.05	0.11	1.62	0.39	2.44	0.09	25.05	3.33
	45	0.75	0.25	0.92	0.59	2.27	0.23	17.06	6.15
	60	0.83	0.35	1.07	0.64	2.27	0.27	18.24	8.40
	75	0.66	0.19	0.63	0.32	2.12	0.27	14.92	4.30
	90	0.64	0.13	0.61	0.24	1.86	0.14	16.25	3.64
DM	0	0.73	0.14	0.23	0.08	2.51	0.21	10.55	1.66
	15	0.68	0.05	0.21	0.03	2.44	0.13	10.78	1.26
	30	0.72	0.13	0.22	0.06	2.04	0.13	12.35	1.71
	45	0.73	0.10	0.22	0.06	2.11	0.22	11.23	1.01
	60	0.70	0.11	0.21	0.07	2.12	0.23	10.52	1.31
	75	0.43	0.07	0.08	0.03	1.45	0.16	9.75	1.84
EC	0	1.35	0.46	1.04	0.59	2.99	0.59	21.80	7.42
	30	0.96	0.43	0.56	0.56	2.45	0.45	16.43	7.68
	60	1.13	0.51	0.80	0.66	2.51	0.41	20.53	9.51
	90	0.64	0.07	0.22	0.04	2.62	0.36	8.46	0.49
EM	0	0.77	0.15	0.31	0.12	2.35	0.27	12.67	2.34
	15	0.76	0.19	0.31	0.18	2.32	0.29	12.00	3.11
	30	0.74	0.34	0.33	0.29	2.47	1.09	11.99	4.04
	45	0.56	0.17	0.17	0.10	2.42	0.61	8.18	1.54
	60	0.77	0.12	0.31	0.09	2.61	0.28	9.68	1.71
LC	0	0.75	0.31	0.28	0.23	2.40	0.30	11.31	4.09
	15	0.65	0.10	0.18	0.06	2.39	0.09	9.43	1.23
	30	0.60	0.08	0.16	0.04	2.26	0.13	9.29	1.41
	45	0.66	0.19	0.20	0.10	2.24	0.49	11.17	3.34
VV	0	0.65	0.15	0.16	0.08	1.99	0.24	8.92	1.67
	15	0.59	0.06	0.13	0.02	1.74	0.11	8.30	1.03
	30	0.74	0.22	0.19	0.11	1.92	0.35	11.41	3.57
	45	0.59	0.17	0.13	0.06	1.53	0.16	8.83	2.24
	60	0.82	0.18	0.26	0.15	1.73	0.72	12.51	3.42
	90	0.96	0.24	0.36	0.15	2.00	0.34	15.25	4.46
NP	0	0.46	0.08	0.21	0.06	2.47	0.10	8.93	1.04

	15	0.37	0.11	0.14	0.07	2.40	0.15	6.64	2.04
	30	0.35	0.11	0.13	0.05	2.19	0.13	6.63	2.11
	45	0.36	0.05	0.13	0.03	2.10	0.08	6.90	1.09
	60	0.23	0.04	0.05	0.02	1.88	0.66	4.33	0.59
	75	0.08	0.04	0.01	0.01	1.52	0.11	1.73	0.69
	90	0.12	0.02	0.01	0.00	1.54	0.25	2.47	0.43
PC	0	0.73	0.12	0.20	0.06	2.39	0.30	11.79	1.88
	15	0.74	0.11	0.21	0.06	2.51	0.32	11.22	1.37
	30	0.71	0.13	0.19	0.06	2.35	0.31	11.34	1.52

Table 5.19: Kruskal-Wallis Tests for median changes to Velocity and Stride Length between support conditions within species.Bold values indicate significant (<0.05) results.

		Velocity (m/s)		Stride Length/ Trunk Length	
Species	Df	χ^2	p value	χ^2	p value
CM	6	22.06	**0.001**	34.15	**<0.001**
DM	5	12.18	**0.032**	37.12	**<0.001**
EC	3	7.56	0.055	7.04	0.071
EM	4	8.63	0.071	2.67	0.614
LC	3	2.55	0.465	5.59	0.133
VV	5	23.08	**<0.001**	15.52	**0.008**
NP	6	28.44	**<0.001**	35.75	**<0.001**
PC	2	0.57	0.753	1.15	0.562

Table 5.20: Dunn's Test for median differences in velocity between support conditions.P-values are adjusted using the correction of Benjamini and Hochberg (1995). Significant values (<0.05) denoted in bold. Abbreviations: CM – *C. medius*, DM – *D. madagascariensis*, VV – *V. variegata*, NP – *N. pygmaeus*.

	CM		DM		VV		NP	
Comparison	Z	P.adj	Z	P.adj	Z	P.adj	Z	P.adj
0 to 15	-1.31	0.284	0.87	0.827	0.80	0.487	2.23	0.077
0 to 30	-2.38	0.074	-0.35	0.993	-1.32	0.309	2.56	**0.044**
0 to 45	0.79	0.529	-0.05	0.964	0.17	0.863	1.86	0.148
0 to 60	-0.65	0.540	0.24	0.867	-2.43	**0.045**	2.48	**0.046**
0 to 75	1.38	0.272	2.99	**0.021**			4.80	**0.000**
0 to 90	1.77	0.162			-3.52	**0.003**	2.96	**0.021**
15 to 30	-0.78	0.509	-1.21	0.561	-1.93	0.100	0.43	0.826
15 to 45	2.00	0.119	-0.86	0.732	-0.48	0.673	0.33	0.823
15 to 60	0.72	0.520	-0.52	0.905	-2.90	**0.014**	1.33	0.294
15 to 75	2.29	0.077	2.49	**0.039**			3.15	**0.017**
15 to 90	2.70	**0.036**			-3.87	**0.002**	1.82	0.143
30 to 45	3.18	**0.015**	0.28	0.970	1.19	0.350	0.03	0.977
30 to 60	1.68	0.179	0.55	0.967	-1.12	0.356	1.10	0.406
30 to 75	3.15	**0.011**	3.21	**0.020**			2.74	**0.033**
30 to 90	3.71	**0.004**			-2.16	0.077	1.59	0.216
45 and 60	-1.43	0.268	0.27	0.907	-2.09	0.079	0.95	0.478
45 to 75	0.82	0.539	2.92	**0.017**			2.09	0.095
45 to 90	1.16	0.347			-2.94	**0.016**	1.38	0.294
60 to 75	1.84	0.154	2.63	**0.032**			0.65	0.681
60 to 90	2.27	0.070			-0.99	0.402	0.37	0.830
75 to 90	0.18	0.859					-0.19	0.890

Chapter 6: Conclusion

6.1 Summary of Findings

The purpose of this research was to document descending behavior at the species level for a morphologically diverse comparative sample of strepsirrhine primates and to test hypotheses surrounding descent locomotion. Few detailed descriptions of descending locomotion in primates exist in the literature despite the necessity of downward movement for navigation through complex three-dimensional arboreal environments. From the literature on captive and wild primates, it is implied that as primates become larger they become less likely to engage in headfirst vertical descent, however what remains an open series of questions are: when does a support become too steep to maneuver headfirst, what behaviors are used as an alternative, and how does this vary in a comparative context?

Experimental studies on descending have primarily analyzed headfirst symmetrical gaits, which have proven difficult to elicit on very steep supports, therefore most of the comparative data that exists only covers supports up to approximately 36° (Rollinson and Martin 1981; Vilensky et al. 1994; Krakauer et al. 2002; Stevens 2003; Nyakatura et al. 2008; Nyakatura and Heymann 2010; Kivell et al. 2010; Hesse et al. 2015). However, the hypotheses that have been generated about primate travel on declines have been extrapolated to all oblique supports. This study set to test commonly held hypotheses from the existing literature on supports angle greater than 30°, which are predicted to have a

different frictional environment than those below 30° (Cartmill 1974b; Cartmill 1979; Vilensky et al. 1994).

The hypotheses addressed by the present study include that there is a body mass limit on vertical headfirst descending in non-prehensile tailed primates (Curtis and Feistner 1994), and that as supports become declined primates will kinematically adjust their headfirst travel by progressively reducing their use of diagonal sequence (DS) gaits in favor of lateral sequence (LS) (Rollinson and Martin 1981; Vilensky et al. 1994; Stevens 2003; Nyakatura et al. 2008; Nyakatura and Heymann 2010; Hesse et al. 2015), relatively increasing the contact time of the forelimb relative to the hind limb (Nyakatura et al. 2008; Nyakatura and Heymann 2010; Hesse et al. 2015), and will hold their body close to the support to mitigate the effects of torque (Krakauer et al. 2002; Birn-Jeffrey and Higham 2014).

6.1.1 Predictions and Outcomes

Hypothesis: There is an upper body mass limit on headfirst descent of steep supports.

Prediction: Body mass will influence the relative frequencies of gross descending behaviors such that large primates will be less likely to use headfirst descent on steeper support orientations relative to smaller primates.

Outcome:

Body mass was an important predictor of headfirst descending behavior, but its effects were strongest only as supports became more steeply angled.

When considered in a Bayesian multilevel model with other predictors, body mass had a relatively weak effect on the probability that a primate would use headfirst descent on a near horizontal support of 15°. On this support, anatomical features including relative foot size and intermembral index had stronger effects than body mass, likely driven by the inclusion of *Propithecus coquereli* in the sample. On supports of 30° and greater body mass became increasingly important, however as supports transitioned from 30° to 45° the effect of body mass switched from strongly positive – that larger primates were more likely to use headfirst descent than a small primate on a 30° support – to negative – that large primates became increasingly unlikely use headfirst descent on supports of 45°-90°. This observation is likely explained by the use of leaping to descend 30° supports by *Microcebus murinus* in this sample, while larger non-indriid primates used headfirst descent almost exclusively on the same support orientation.

The *Daubentonia*-sized limit (approximately 2.5 kg) on headfirst descent of vertical supports as proposed by Curtis and Feistner (1994) did appear to apply to adult and older adult individuals in this sample. However, young adult *Varecia* up to 4 kg regularly engaged in headfirst vertical descent. This and other observations of apparently age-related changes to descending behaviors in *Eulemur* species suggest that mass alone does not determine descending ability within relatively large species. Lemuriforms typically engaged in increasing frequencies of tail first descent on supports of 60°-90°, especially as they increased in relative age.

For species in this sample below 1 kg, headfirst descent did appear to be the preferred mode of travel on all support orientations, although aspects of the experimental setup might have limited use of behaviors such as leaping in *M. murinus* and *Cheirogaleus medius*. Cheirogaleids and lorisids typically changed direction from ascending to descending on the support itself, often rapidly for the cheirogaleids, while maintaining a hold with their hind limbs; this observation parallels descriptions of non-primate arboreal animals changing direction on thin supports including kinkajous (McClearn 1992). This ability to maintain a headfirst progression while changing directions was observed on all support orientation from horizontal to vertical.

Hypothesis: Declines cause specific gait sequence changes in primates

Prediction: Temporal aspects of gait, including sequence and footfall timing, during headfirst descent are predicted to change in response to support orientation such that lateral sequence gaits will become more common on declines relative to level travel.

Outcome:

Previous literature has focused upon increased use of lateral sequence (LS) gaits in primates traveling on declines (Rollinson and Martin 1981; Vilensky et al. 1994; Stevens 2003; Nyakatura et al. 2008; Nyakatura and Heymann 2010; Hesse et al. 2015), and the present study did find that limb phase generally became more lateral in all species as support orientation increased. However, this did not necessarily translate into higher frequencies of actual LS gaits

compared diagonal sequence (DS) gaits on these steeper supports for all species. Instead, walking trots and diagonal sequence diagonal couplet gaits were still frequently used on declines.

Explanations for the decreases in limb phase on declines have considered potential mechanisms including how the center of mass position changes passively on declines in ways that may affect gait (Rollinson and Martin 1981), on active shifting of the center of mass on oblique supports (Vilensky et al. 1994), and to the changing role of the forelimb as a brake linking duty factor index to gait sequence (Nyakatura et al. 2008; Nyakatura and Heymann 2010; Hesse et al. 2015).

If increased weight supported by the hind limb is expected to result in diagonal sequence gaits (Rollinson and Martin 1981; Reynolds 1985), then active posterior shifting of weight on declines should result in fewer observed LS gaits, not more (Vilensky et al. 1994). Similarly, while duty factor index appears to steadily increase on inclines, it has not been found to progressively decrease on declines by Nyakatura et al. (2008), Nyakatura and Heymann (2010), and Hesse et al. (2015). In the present study changes to duty factor index were not significant as support orientations became progressive steep and predicted relationships between duty factor index and limb phase were not met, especially in *Nycticebus pygmaeus* and *Eulemur coronatus*, which used gait sequences opposite of what would be predicted by Nyakatura et al. (2008).

Hypothesis: Mechanical environment changes as support angles become steeper

Prediction: Primates will make kinematic adjustments to the limbs throughout the stride as a function of support orientation that bring the body closer to the support and allow them to counteract gravity and pitch.

Outcome:

Primates were found to increase forelimb protraction on all declines, and hind limb retraction on supports of 60° and steeper, consistent with previous literature (Vilensky et al. 1994; Stevens 2003; Nyakatura et al. 2008; Hesse et al. 2015). Additionally, it appeared that the hind limb became increasingly stiff, interpreted from decreasing yield, as supports became steeper. Forelimb compliance did not appear to become compromised on declines.

Changes to velocity were also largely not significant, consistent with findings by Stevens (2003), Nyakatura et al. (2008) and Hesse et al. (2015). Speed tended to be dynamically similar on supports of the same orientation in lemuriforms and *Daubentonia madagascariensis*, slightly slower in *Nycticebus pygmaeus*, and faster in *Cheirogaleus medius* and *Eulemur coronatus*. *C. medius* was the only species that regularly used running speeds on declines based on comparison of Froude numbers in this sample.

6.2 Anatomical correlates of primate descending behavior

This study has demonstrated the importance of the hind limb in mediating successful headfirst descent of steep supports with a grasping foot that is able to

support the weight while acting like a rope suspending the body weight inferiorly to it. Meldrum et al. (1997) investigated osteological correlates of hind limb suspension in *Varecia,* finding the arrangement of the ankle allows for strong pedal grasping from a variety of foot positions and noting similarity to the morphology of the several non-primates capable of partial and complete hindfoot reversal including the kinkajou, coati, tree squirrels, and margays. In contrast, primates like *Lemur catta* have been shown to have relatively lower muscle mass for digital flexion than more arboreal *Eulemur fulvus* (Ward and Sussman 1979), which may help explain why it abandoned headfirst descent on supports steeper than 45° in the present study.

In addition to powerful pedal grasping, the results of the present study show that primates who regularly engaged in headfirst descent of supports of 60° to 90° tended to highly flex and extend the hind limb during travel. Therefore, it is predicted that these primates who travel on vertical supports – *Cheirogaleus medius, Microcebus murinus, Nycticebus pygmaeus, Daubentonia madagascariensis, Eulemur coronatus*, and *Varecia Variegata* – might show more developed muscles to allow for the leg to support the body mass under tension while in a highly extended posture.

However, features related to hind limb suspension do not necessarily mean a primate is capable of headfirst descent, as illustrated by *Propithecus coquereli* observed in the present study. *P. coquereli* frequently engages in hind limb suspension (Meldrum et al. 1997) and has a large quadratus femoris and hip

extensors specialized for leaping (Demes et al. 1998). However, intermembral index (IMI) is another other important feature that most likely limited descending ability, and *P. coquereli* in this sample may have been limited in its headfirst descending abilities by very short arms. Primates in this study exhibited increasingly protracted forelimbs when moving on declines. Forelimb protraction has been noted as a special feature of primate gait compared to non-primates on level supports (Larson et al. 2001; Larney and Larson 2004), and the degree of protraction is associated with braking forces (Granatosky et al. 2018). It is possible that increasing protraction is related to increasing braking demands on the forelimb during headfirst descent.

Forelimb compliance was also observed to generally increase in this sample with increasing support steepness. High forelimb compliance is another relatively unique trait in primates that is argued to be related to reducing peak forces on the forelimb (Schmitt 1999; Larney and Larson 2004). As primates move on increasingly steep declines, it is predicted that the relative amount of weight supported by the forelimbs increases relative to level travel (Birn-Jeffrey and Higham 2014) and increasing compliance in the forelimb might be a response to that. Additionally, high joint yield allows the body to be held relatively close to the support as a pitch resisting mechanism (Cartmill 1985).

6.3 Anatomical correlates of non-primate mammalian descending behaviors

Convergent adaptations that allow for headfirst descent appear across vertebrates, suggesting that selection has repeatedly acted to enable headfirst descent in arboreal species. These adaptations include hindfoot rotation, or pedal inversion, which allows clawed animals to interlock with a support while descending (Jenkins and McClearn 1984), and prehensile appendages such as tails or feet (Youlatos and Gasc 1994). Advantages of claw interlocking with rotated hindfeet include that it can be used on supports that are relatively large compared to the animal, such as a tree trunk, and it has been hypothesized to be a relatively passive mechanism, based on comparative muscular anatomy of procyonids (Liu et al. 2016).

Hind limb adaptations in eutherians argued to facilitate hindfoot rotation include shared osteological adaptations described by Jenkins and McClearn (1984) that occur at the crurotalar, subtalar, and transverse talar joints in species capable of full hindfoot reversal. As demonstrated by observations of animals like the coati (*Nasua narica* and *Nasua nasua*), even partial hindfoot reversal can still facilitate headfirst descent (McClearn 1992). In species that only possess partial hindfoot rotation, Jenkins and McClearn (1984) found evidence of increased femoral abduction. External rotation of the hip would presumably bring the feet into a favorable position to interlock in these animals.

Scandentians and dermopterans both possess hindfoot mobility (Jenkins 1974; Youlatos et al. 2019). In scandentians, the hindfoot is completely reversable (Jenkins 1974; Jenkins and McClearn 1984). Dermopterans have been shown to hold the foot in a range of everted and inverted postures, although there do not appear to be any reports of use of these foot postures to aid in headfirst descent in this gliding-specialized group (Youlatos et al. 2019). These observations of foot mobility in extant non-primate euarchontans, and fossil evidence from extinct plesiadapiforms (Chester et al. 2015), point to the likelihood that the common ancestor of euarchontans might have been capable of some degree of hindfoot reversal and headfirst descent.

Grasping with tails and feet have also convergently evolved in mammals. It is noted by Cartmill (1974b) that animals that possess prehensile tails are not observed to frequently leap and hypothesized that prehensile tails are an adaptation for crossing discontinuous substrates. However, prehensile tails can also aid in headfirst descent in relatively large species, as observed in anteaters that frequently forage in arboreal settings (*Tamandua mexicana*) (Navarrete and Ortega 2011), and in primates like *Alouatta seniculus* (Youlatos and Gasc 1994).

Prehensile tails also co-occur with hindfoot reversion as observed in the kinkajou (*Potos flavus*) (Jenkins and McClearn 1984; McClearn 1992). However, unlike claw interlocking, any grasping appendage is limited in the size of supports than can be successfully subtended (Cartmill 1974b) indicating that retention of claws may still be necessary for movement on large vertical supports.

Pedal grasping is highly developed in some non-primates, including species of didelphid marsupials, specifically *Caluromys* (Schmitt and Lemelin 2002). Video of *Caluromys philander* collected by D. Schmitt and P. Lemelin (Figure 6.1) shows this animal skillfully descending thin supports headfirst in a manner that appears like observations of *Cheirogaleus medius* in the present study. Didelphid marsupials also possess prehensile tails and appear to diminish in their leaping ability as body mass increases towards 0.2 kg according to experimental comparison by Delciellos and Vieira (2009).

Limited pedal grasping appears to be present in dermopterans (Youlatos et al. 2019) and scandentians like *Ptilocercus* (Sargis 2002), which is suggestive of the presence of primitive grasping ability in the common ancestor of these animals (Sargis et al. 2007). In the fossil record, developed pedal grasping with a nail bearing hallux is apparent in *Carpolestes simpsoni* (Bloch and Boyer 2002), but this is a relatively late occurring adaptation in that lineage and does not appear as a widespread feature of plesiadapiforms, further suggesting that basal euarchontans would have only been capable of limited grasping at most.

6.4 Implications for models for primate origins

Fossil evidence for the earliest primates appears at the start of the Eocene, even though presumably there is a lag in time between when primates diverged from other Euarchontans and when they are firmly recognized in the fossil record (Steiper and Seiffert 2012). Using fossils to calibrate a molecular clock, Steiper and Seiffert (2012) propose that the haplorrhine-strepsirrhine split

might have occurred during the early Paleocene, following the K-Pg extinction event. This leaves roughly ten million years between the hypothetical last common ancestor of strepsirrhines and haplorrhines might have occurred, and the appearance euprimates currently identified with postcrania in the fossil record.

The most primitive stem strepsirrhines and haplorrhines share many dental and postcranial features (e.g. Boyer et al. 2017). Analysis of the talus in one of the most basal strepsirrhines, *Donrussellia provincialis*, by Boyer et al. (2017) interpreted the functional anatomy of this bone as indicating exploitation of relatively large diameter vertical supports and a proclivity towards leaping. The most similar living animal in talar morphology to *D. provincialis* in that study was *Ptilocercus lowii*, which regularly exploits large vertical supports (Stafford and Thorington 1998). Boyer et al. (2017) suggest that *D. provincialis* was not primarily adapted to the terminal branch niche and propose that this habitat was independently invaded by haplorrhines and strepsirrhines rather than their common ancestor.

In support of the adaptive hypothesis of Boyer et al. (2017), other fossil primates from the earliest Eocene show features associated with specialized leaping (Boyer et al. 2013a) including stem haplorrhines like *Teilhardina* (Gebo et al. 2015) and *Archicebus* (Ni et al. 2013), while strepsirrhines and haplorrhines that lack features associated with leaping only occur later (Dunn et al. 2016). The well documented skeletal proportions of *Archicebus* (Ni et al. 2013) are

especially compelling for interpreting highly specialized leaping ability in that species given that the very low intermembral index (IMI) and large grasping foot proportions which appear quite like extant vertical clinging and leaping specialists (Napier and Walker 1967).

However, if support use by *P. lowii* is used to model the use of large diameter vertical supports by *D. provincialis*, it should also be acknowledged that *P. lowii* has a divergent hallux (Sargis et al. 2007), and that euarchontans have been argued to possess primitive hallucial grasping (Youlatos et al. 2017). No other postcranial elements of *D. provincialis* have been published, making it difficult to exclude *D. provincialis* from a terminal branch environment. Additionally, Boyer et al. (2017) point out that the talar morphology of *D. provincialis* is consistent with crouching postures, possibly related to take off positions for leaping, but also useful for bringing the center of mass close to a thin support to reduce pitch and roll.

The hypothesis of Boyer et al. (2017) suggests a convergent invasion of a terminal branch niche and loss of specialized leaping by the Vastan strepsirrhines and haplorrhines, which would have potentially put these primates in direct competition with each other if shared environment was a selective pressure. Further, if *Eosimias*, a stem anthropoid, shares vertical support use with *D. provincialis* (Boyer et al. 2017), a third invasion of the terminal branch niche in primates might have had to occur in the anthropoid lineage.

If low IMI associated with specialized leaping, such as that observed in *Archicebus*, characterizes euprimates adapting to terminal branches, they might encounter great difficulty moving quadrupedally on thin compliant supports that bend beneath their weight and effectively create a declined support. In the predictive model of headfirst descent presented in the third chapter of this study, it was predicted that having very low IMI makes it increasingly unlikely headfirst descent is used on declines, even at low body masses (Figure 3.12). This model assumed that this hypothetical primate had a foot length to hindlimb ratio length of 30.12%; increasing this to the foot proportions found in *Archicebus* of 36.6% (Ni et al. 2013) greatly increased the probability of headfirst descent (Figure 3.11), including at higher body masses.

Therefore, if the association of grasping and leaping occurs independent of a terminal branch environment (Szalay and Dagosto 1980, 1988, Szalay 2007) then a euprimate that already possess grasping appendages as part of a specialized leaping locomotor regime would likely have a much easier time invading the terminal branch niche than a clawed and non-grasping leaper. However, if large vertical supports characterize early primates, which would seem to favor retention of claws (Boyer et al. 2017), it raises the question of what would drive a euprimate adapted for leaping and vertical support use into the terminal branch niche, which demands active grasping to respond to dynamically changing support orientation?

Many small specialized extant leapers have high energy diets such insects and gums (Warren and Crompton 1998). Selection towards arboreal quadrupedalism could be associated with a shift towards a lower quality but easy to acquire diet, as hypothesized to be the strategy of *Otolemur crassicaudatus* by Warren and Crompton (1998). This would seem to favor the angiosperm co-evolution hypothesis (Sussman and Raven 1978) over the nocturnal visual predation hypothesis (Cartmill 1974, 1992) for a dietary based selection of terminal branch use. This scenario could apply to the initial euprimate radiation given the fossil evidence of the Eocene, if not necessarily euprimate origins.

Switching from a high quality but difficult to acquire food source to a lower quality but high availability diet could be related to body mass increases, lending some support to the hypothesis of Soligo and Martin (2006) that nails are only adapted in primates because of a shift towards larger body mass. However, having an increasing body mass also makes headfirst descent increasingly difficult as demonstrated by the present study, and fails to explain the presence of nails in earlier occurring small bodied specialized leapers like *Archicebus* (Ni et al. 2013).

Repeated invasion of a terminal branch niche selecting for arboreal quadrupedalism would also indicate that the shared features of extant primate quadrupedalism may be the product of constrained convergence from shared leaping ancestry. Features attributed to hind limb dominance in the literature could be the product ancestry from lower IMIs associated with leaping under this

evolutionary scenario. However, specialized leaping and large vertical support use does not provide a satisfactory adaptive reason for why these features co-occur with nail bearing grasping hands and feet in earliest euprimate fossils unless relatively small supports also made up a significant aspect of early primate locomotion.

In the present study, a small (≤ 100 g) generalized arboreal quadruped with a *Ptilocercus*-like intermembral index of 80 (Ankel-Simons 2007) at the base of primate origins is predicted to experience the least loss of headfirst descending ability during a transition from a primitive clawed condition to grasping relatively thin supports. However, such a primate would also need a bridge crossing mechanism, or might become restricted to a terminal branch niche, as is the hypothesis for explaining the suite of primate features of Orkin and Pontzer (2011). The narrow niche hypothesis (Orkin and Pontzer 2011) postulates that primates became exclusively adapted to a terminal branch niche, allowing them to lose their claws while other animals that merely pass through a terminal branch niche, like squirrels, must retain such features to move effectively through other environments. This hypothesis forces shared primate features to be the product of terminal branch niche even in the face of competing evidence such as convergent orbits being related to leaping (Changizi and Shimojo 2008), and the absence of these features in other terminal branch specialists.

Other terminal branch exploiting animals with grasping feet have retained claws and variably adapted prehensile tails as a way of navigating discontinuous substrates (Cartmill 1974b; McClearn 1992; Delciellos and Vieira 2009). There is no evidence for tail prehensility at the base of primates. Instead, an alternative gap crossing mechanism could be leaping, which could have been retained from a common euarchontan ancestor given the generalized leaping abilities of extant treeshrews (Jenkins 1974), the presence of adept leaping in many extant primates of moderate IMI such as *Microcebus* (personal observation), and the take-off of dermopteran gliding essentially beginning with a leap (Byrnes and Spenser 2011). Additionally, exploitation of large vertical supports without claws is observed in small extant primates (e.g. *Loris tardigradus*) if the substrate provides sufficient handholds and is not too smooth (Cartmill 1974b), meaning that *D. provincialis* did not necessarily need to retain claws to exploit the supports its ankle morphology appears suited for (Boyer et al. 2017). Extant primates that regularly utilize large supports have secondarily adapted claw-like nails, as in *Phaner* or the callitrichids (Nash 1986; Hamrick 1998), and a similar scenario is conceivable in a Euprimate coming from a nail bearing ancestor.

Rasmussen (1990) sought to reconcile the arboreal (Jones 1916, Smith 1924), visual predation (Cartmill 1974a), and angiosperm co-evolution (Sussman and Raven 1978) hypotheses with a more general terminal branch hypothesis focused on a *Caluromys*-like model. He does not include Grasp-Leaping among the hypotheses of primate origins he sought to reconcile in his study of

Caluromys, possibly because leaping within a terminal branch environment is not part of the Grasp-Leaping hypothesis, and there would seem to be a risk of breaking a thin support if landing on it from a leap rather than cautiously testing it. However, use of a terminal branch habitat is not mutually exclusive from non-specialized leaping in extant primates and in *Caluromys* (Rasmussen 1990).

Leaping as a form of descent on supports that are too large to effectively grasp could make claws redundant and relax the selective pressures that have preserved claws on non-hallucial digits in non-primate terminal branch specialists. Invasion of the terminal branch niche *with* generalized leaping ability by the stem primate might better explain the unique shared characteristics of primate morphology and kinematic aspects of quadrupedalism without overly constraining the types of supports (e.g. both small compliant horizontal supports and large vertical supports) that the earliest primates might have been able to exploit in a way that is not satisfactorily addressed by current iterations of the Grasp-Leaping hypothesis (e.g. Szalay 2007) or various terminal branch hypotheses focused on diet.

Instead, maybe we should consider a “grasping-with-leaping” hypothesis that recognizes the likelihood that some degree of leaping is primitive within Euarchonta, as well as the critical role that the terminal branch niche has played in selecting for grasping feet in non-primates. Earliest Eocene primates spreading through potentially open environments like those that characterize the Bighorn Basin (Secord et al. 2008) might have further selected for increasingly

specialized leaping ability, while those living in more closed or continuous forest environment might have only retained a primitive generalized, and thus difficult to detect morphologically, leaping ability or even relaxed selection to preserve this ability, which could characterize the Vastan primates (Dunn et al. 2016).

6.5 Future Directions

The findings of this study suggest that small primates perform headfirst descent quite adeptly on supports of varying orientation, but that the ability to utilize headfirst descent does not scale directly with body mass. Instead, anatomical feature like strong pedal grasping and moderate intermembral indices may allow very large primates to use headfirst descent even on vertical supports, while relatively smaller primates lacking strong grasping abilities, or primates with very low intermembral indices may be excluded from using headfirst directed travel on the same support orientations.

Building on the behavioral data collected by this study, investigation into anatomical differences that can be associated with specific descending behaviors should be conducted. This could lead to improved linkage of morphological features with demonstrated locomotor abilities.

Additional work on descent in non-primates with pedal grasping, such as *Caluromys* (Figure 6.1) could be informative for identifying shared kinematic responses to declines. Anthropoids traveling on declines steeper than 30° should also be assessed to test if the traits identified as important for headfirst descent in strepsirrhines hold true across primates, and to evaluate if kinematic

responses to declines observed in strepsirrhines here and tamarins by Hesse et al. (2015) occur in old world monkeys and other platyrrhines.

Finally, it would be highly informative to the investigation of primate origins to perform detailed comparative locomotion research on a more specialized small bodied leaper, like *Tarsius* or *Galago*, more generalized small primate such as *Microcebus*, and a non-primate euarchontans like treeshrews. This could be used to evaluate the predictive ability of the model of headfirst descent on specific supports angles presented here and would contribute to a better understanding of how these animals may differ in their kinematics when moving in a terminal branch environment.

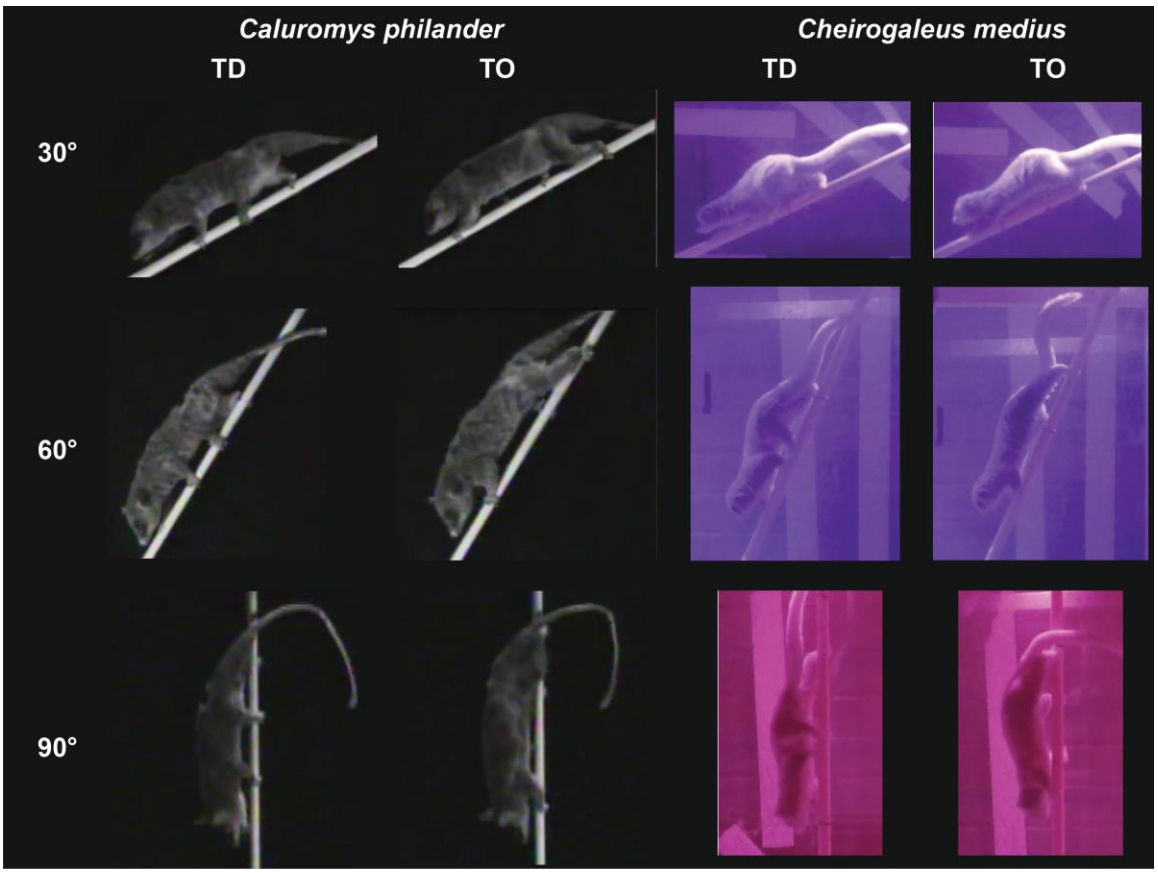


Figure 6-1: Comparison of headfirst descent in *Caluromys philander* and *Cheirogaleus medius* on supports of 30°, 60°, and 90°. Video of *C. philander* was provided by D. Schmitt and P. Lemelin and reproduced here with permission. Video of *C. medius* were collected in the present study.

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Biography

Bernadette Alyce Perchalski grew up in Pennsylvania and attended the Pennsylvania State University, completing both a Bachelor of Science degree in Biological Anthropology and Master of Arts degree in Anthropology in 2013 through the Integrated Undergraduate/Graduate curriculum offered by the Schreyer Honors College. Her thesis research, conducted under the guidance of Dr. Tim Ryan, explored links between femoral head trabecular morphology and arboreal locomotion in strepsirrhines and platyrrhines. She was then a research technician in the lab of Tim Ryan and published research on human bone development.

Bernadette attended Duke University as a Ph.D. student in the Evolutionary Anthropology program beginning in 2014, and graduating in September 2019, advised by Dr. Doug Boyer. In addition to her animal locomotion research, she also contributed to paleontological field research in the Bighorn Basin of Wyoming and collaborated with Doug Boyer on research into the fossil primate species *Notharctus*. Her favorite lemur species is *Varecia variegata*.

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