THE ECOMORPHOLOGY AND MUSCULOSKELETAL KINEMATICS OF WILD WESTERN LOWLAND GORILLAS

(*GORILLA GORILLA GORILLA*)

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A thesis submitted to the University of Birmingham

for the degree of

DOCTOR OF PHILOSOPHY

School of Biosciences

College of Life and Environmental Sciences

University of Birmingham

March 2024

ABSTRACT

Western lowland gorillas are the largest and most sexually dimorphic ape. Their heavily robust musculature and adaptations towards terrestrial quadrupedal locomotion makes them suitable models for understanding the relationship between morphology, ecology and behaviour in arboreal environments. The arboreal environment is characterised by supports that vary in availability, size and compliance, but it was not previously understood how western lowland gorillas find solutions to the challenges of feeding and travelling in the trees. This thesis addresses this gap in our knowledge by presenting new comprehensive data on the arboreal locomotor repertoire of wild western lowland gorillas. A group of fully habituated wild western lowland gorillas were followed for twelve months in the Loango National Park, Gabon. Walking and vertical climbing dominated the gorillas' arboreal locomotor repertoire, but gap-crossing behaviours made up a considerably larger proportion of their locomotor repertoire than expected. Overall, the gorillas minimised the risk of falling in the supports and hand postures they used when addressing the ecological challenges of accessing different heights, moving in the canopy and dealing with discontinuity.

Despite being phylogenetically close, great apes vary in postcranial morphology and the ecological niches that they inhabit. In order to identify what separates, and what links the locomotor ecology of great apes, focus was then directed towards comparing the arboreal locomotor repertoire of the gorillas with wild chimpanzees and orangutans. The orangutans engaged mostly in suspension, whereas the chimpanzees mostly used vertical climbing, and the gorillas engaged mostly in walking. Interspecific comparisons of support use for gorillas and orangutans revealed that each species differed in the size, type and number of supports that they used when addressing different ecological

challenges. Body size also influenced the arboreal locomotor behaviours of the great apes, but in patterns that did not align with classic predictions. Overall, the results suggested that evolutionary selective pressures have shaped the locomotor behaviours used in complex arboreal environments to reduce energy expenditure. However, the variation in support use reflected many aspects, including their morphology, ecological niche, degree of arboreality and strategies to mitigate the risk of falling.

The next step in developing an understanding of how great apes interact with their environment is to study their locomotor biomechanics in natural habitats. Kinematic analysis of great ape locomotion is used to understand the mechanisms of movement. Recent technological advances in deep learning software to recognise and track objects is revolutionising the way in which we can study animal locomotion. Pose estimation uses this framework to detect body landmarks but very few studies have applied this framework in wild settings. Using video footage of wild gorillas, two open-source markerless pose estimation frameworks were compared to manual identification of body landmarks to assess the accuracy of machine learning software packages, DeepLabCut and Open Ape Pose. Overall, it was determined that they are not yet ready to be applied to wild footage because of the complexities of natural habitats and focus should now be directed towards exposing these software packages to more wild footage so that this can be possible in the future.

These studies highlight the importance of studying primates using the ecomorphology framework. Furthermore, by integrating data on the arboreal locomotor behaviour of apes with locomotor kinematics, this makes them suitable referential models for understanding the evolution of hominoid locomotion.

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my PhD supervisor, Susannah Thorpe. Thank you for teaching me how to write and encouraging me to think about the bigger picture. Your input and encouragement have been invaluable.

Thank you also to Jackie Chappell, for the continued support and advice you have given me throughout my PhD.

I would also like to thank Bill Sellers at the University of Manchester. Thank you for sharing your knowledge of biomechanics and for teaching me that writing code is not as scary as I had thought.

Thank you to the Anatomical Society for funding this research and your continued support. Thank you for giving me the opportunity to present my research at Anatomical Society conferences and for encouraging my career development.

I am very grateful to Martha Robbins at the Max Planck Institute of Evolutionary Anthropology. Thank you for giving me the opportunity to conduct this research at your field site, for which I feel incredibly fortunate. Thank you for teaching me about wild gorillas and for your continued support.

I am extremely grateful to the team in the field. Thank you to all the guides and trackers who kept me safe in the forest and for pulling me out of swamps when I was stuck to my waist. Thank you for teaching me about the animals and plants of the forest. Your

enthusiasm was contagious. I would also like to thank Cristian, Mathilde, Koro, Deb, Maddy, Fanny, Matthew, Gabrielle and Tatiana, who became my good friends. Thank you for sharing laughs, especially when we were stuck in swamps and fishing for our crocs in the mud.

I would also like to thank Robin Crompton, who has been enthusiastic and supportive throughout my PhD. I have enjoyed sharing fieldwork stories with you.

Many thanks go to my PhD colleagues in the Locomotor Ecology and Biomechanics Lab for lots of helpful conversations about great apes. I would like to say thank you in particular to Lelia Bridgeland-Stephens, who has been incredibly important to me since we started our PhD journey together. This process would not have been the same without you.

I am extremely grateful to my family for their encouragement. Thank you to my parents, for supporting me throughout my studies. Thank you, Dad, for always being available to help me with my coding errors.

Thank you, Dan, for always being there for me. Thank you for your patience and for listening to me talk about gorillas so much over the last few years.

Finally, I thank the gorillas for giving me this incredible experience.

THESIS CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER ONE

GENERAL INTRODUCTION

1.1 Primate locomotor ecology

Primates are found in a diverse range of habitats across the world and vary considerably in their size and social structures. However, all primates are driven by the ecological needs of acquiring nutritional resources, finding mates and escaping predators (Cartmill, 1972; Cartmill, 1974; Gebo, 2004). All primates face predation, even large-bodied gorillas (from leopards), so in order to avoid predators, primates must be able to escape by employing strategies such as climbing into the canopy, running away or using group cohesion to intimidate or fight off predators (Isbell, 1994; Treves, 1999; Stanford, 2002). If primates cannot escape predators, they will not achieve evolutionary success. All primates are also driven by the requirement to find mates and maintain social relationships. Although some primates, such as orangutans and tarsiers, live semi-solitary lifestyles (Cant, 1987; Gursky, 2005), in order to reproduce, they must be able to interact and communicate with other individuals. Generally, primates are highly social and they rely on complex social organisations and hierarchies to coordinate feeding strategies and deal with intergroup competition (Eisenberg, Muchenhim & Rudran, 1972; Van Shaik, 1996;). Their survival relies on their ability to effectively communicate with others. In order to achieve these ecological needs and to acquire nutritional resources, primates will often exploit both terrestrial (ground) and arboreal (off-ground) environments (Cartmill, 1972; Cartmill, 1974; Gebo, 2004). However, whilst terrestrial environments are less variable, when moving in arboreal environments, primates have to contend with unpredictability and the risk of falling. Arboreal environments are characterised by considerable variation in support type, size, compliance, and continuity, which make them highly complex (e.g. Cartmill, 1974; Walker, 1974; Fleagle et al., 1981; Susman, 1984). This affects the solutions that primates have to find in order to achieve ecological and evolutionary success including the locomotor behaviours that they use.

Primate locomotion is extremely diverse, and includes various types of behaviours such as walking, suspension, leaping, climbing, and running. Many primates specialise in modes of locomotion which best equip them to handle the challenges in arboreal environments (Blanchard & Crompton, 2010). Vertical clinging and leaping (VCL) is typical among the strepsirrhine primates as a strategy to move between vertical supports (Crompton et al., 2010; Gebo, 2011). Brachiation, typical for *Hylobates* (gibbons and siamangs) is used to move through the forest canopy on small supports to escape predators and move between feeding sites quickly (Fleagle, 1974). Compliant quadrupedalism (when the limbs are flexed) is used by larger primates to travel on relatively small supports in order to access the periphery of the tree crown, where nutritional resources are often located (Larney & Larson, 2004). The way in which primates move in their natural habitat, and how locomotion is linked to their morphology, behaviour and ecology is defined as their locomotor ecology (Channon & Leighton, 1994; Warren & Crompton, 1997).

1.2 Body size in arboreal environments

One of the biggest differences between primates, which dictates how they attend to the challenges in arboreal environments is body size (Fleagle, 1985; Cant, 1992). Within the primate order, body size varies considerably. The silverback gorilla (*Gorilla*) weighs up to 190kg, weighing considerably more than the mouse lemur (*Microcebus*) which weighs only 50g (Fleagle, 1977). Large primates experience challenges in accessing and moving around the canopy because of their absolute size relative to the supports available. A support is only ‘large’ or ‘stable’ relative to a primates body size, but for larger primates, there are less large and stable supports (Avis, 1962). In a study of New World monkeys, Rosenberger (1992) discussed the implication of body size on feeding opportunities. It was found that smaller monkeys were able to use canopy niches and hang from thin branches compared to larger species, which were restricted in their to peripheral canopy niches because of their larger size. Body size is also linked to the locomotor behaviours that primates use. Fleagle and Mittermeier (1980) found that larger Surinam monkeys leaped less but climbed more and used larger supports than smaller Surinam monkeys. This was one of the first interspecific primate studies that examine the influence of body size on arboreal locomotion. Following on from this, Harvey et al., (1986) found that larger siamangs used suspension more than the smaller *H. agilis* (agile gibbon), a prediction made by Cartmill and Milton (1977) that increased body size would be accompanied by increased suspension. Furthermore, in a study of six sympatric Old World monkeys (*Colobus* and *Cercocebus*), McGraw (1998) found that body size did not consistently predict leaping and climbing behaviours, as for Surinam monkeys (1980), but showed that larger monkeys frequented areas containing the highest density of large supports, whereas smaller monkeys were more diverse in their canopy use. In a study of *Pan*, Doran (1993) found that bonobos, which are much smaller than chimpanzees, engaged in less climbing and scrambling, but more suspension than chimpanzees (Doran & Hunt, 1994; Doran, 1996). Body size evidently plays a role in shaping arboreal behaviour.

Larger primates also experience higher energetic costs when moving arboreally because they have less muscle force per unit mass, which makes them relatively weaker than smaller primates (Fleagle, 1985; Demes et al., 1996). This influences how they interact with complex arboreal environments as they must be selective in the travel routes that they take and the strategies that they use to reach a goal of feeding and moving in the trees. A gap in the canopy can be crossed by a large-bodied orangutan

(*Pongo*) by reaching across the gap and transferring their weight onto supports on the other side (Thorpe & Crompton, 2005), but for a small-bodied tarsier (*Tarsiidae*), which weighs considerably less, they might cross the same gap by leaping. When travelling horizontally on a small tree branch in the periphery of the canopy, a mouse lemur can walk without deflecting the support underneath them, whereas a chimpanzee (*Pan troglodytes*) will struggle to walk on top of it and may either avoid the support completely or perhaps suspend below it (Cartmill & Milton, 1977; Hunt, 1991). Furthermore, whilst a small capuchin monkey (*Cebus*) can move between different heights in the trees on a single, small, compliant liana, a male mandrill (*Mandrillus* sphinx) which weighs 10 times more, may have to use multiple compliant lianas or a nearby larger tree trunk which can bear his weight.

Body size also affects the consequence of falling from height, as larger primates have a higher chance of fatality because the kinetic energy that the body has to dissipate upon impact increases (Cartmill & Milton, 1977; Preuschoft et al., 2016). Therefore, it is crucial for larger primates to adjust their locomotor behaviours in arboreal environments to mitigate the risk of falling. This might be reflected in the locomotor behaviours that they use, or the supports that they travel on. The way in which large primates are behaviourally and ecologically different to smaller primates is one of the crucial ways to develop an understanding of diverse strategies utilised by primates across various habitat types and evolutionary contexts, especially for the largest arboreal primates, the great apes (Clutton-Brock & Harvey, 1983; Fleagle, 1985; Prost, 1985).

1.3 The great apes

Great apes are a group of primates which belong to the family Hominidae. The first documented account of non-human great apes is believed to be the writings of the Carthaginian explorer Hanno in the fifth century, as he describes the wild, hairy people 'gorillae' in Western Africa (Montagu, 1940; Groves, 2002). The great apes were first properly discovered by Europeans however, during the seventeenth century following the colonial expansion of Southeast Asia and Africa (Van Wyhe & Kjærgaard, 2015). As anatomical explorations of these primates progressed, there seemed to be a simultaneous decline of traditional ape-like ideologies and an increase in scientific interest. The rise of evolutionary scientific theory in the 19th century from the likes of Lamarck and Darwin placed significant emphasis on the biological role, highlighting how adaptations through natural selection and transmutation have shaped modern biodiversity (Van Wyhe & Kjærgaard, 2015; Prost, 1980). In the early 20th century, a new ideology that acknowledged the significance of ecological context started to question the behavioural repertoires of these extant species. Primatological literature by Loomis (1911) and Keith (1915) began to separate the biology from the ecology, presenting the idea that the relationship between primates and their environments should be explored to a much greater extent. Today, most research into the behaviour of great apes is discussed within the ecomorphology framework (Karr & James, 1975), which is crucial in order to fully understand the relationship between morphology, ecology and behaviour both within the Hominidae family and on a species level.

1.3.1 Phylogeny

Extant non-human great apes share 97-99% of their DNA sequence and a myriad of anatomical features with modern *Homo sapiens*. However, the last common ancestor of great apes is dated to approximately 14 million years ago (ma) (Gebo, 1996; Pilbeam, 1996; Crompton, Vereecke & Thorpe, 2008; Chaimanee & Jaeger, 2023). This was the first Hominidae divergence of Ponginae, as shown in Figure 1.1, which today is made up of a single genus *Pongo* (Gagneux & Varki, 2001; Langergraber et al, 2012). The two orangutan species, the Bornean orangutan (*Pongo pygmaeus*) and Sumatran orangutan (*P. abelli*) occupy the Bornean and Sumatran islands of Indonesia and are the most arboreal of the great apes (Cant, 1987; Thorpe & Crompton, 2005; Manduell, Morrogh-Bernard & Thorpe, 2013). Subsequent evolutionary divergence occurred at ~10ma of Gorillinae. The two extant species of gorilla are the western gorillas (*Gorilla gorilla*) and the eastern gorillas (*G.beringei*) (Benedict, 1944). Finally, the *Homininae* split occurred at ~7ma, and is made up today of modern humans and Panini. The two *Pan* species include chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*). The gorillas and *Pan* constitute the African apes and inhabit Central East and West Africa and are sympatric in some parts of Central West Africa.

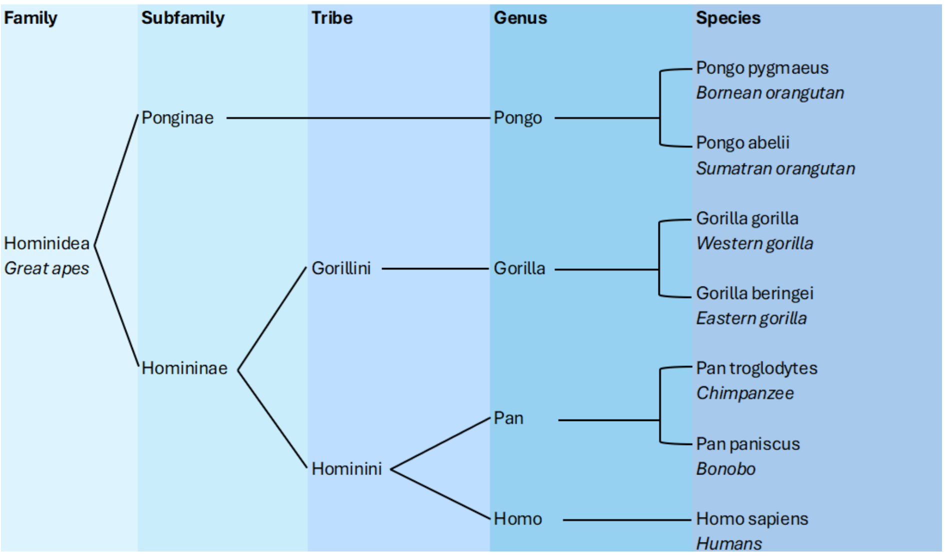

Figure 1.1: Phylogenetic tree showing the divergence of the great apes.

1.3.2 Postcranial morphology

As a result of their shared evolutionary ancestry, the great apes possess shared traits. Many of these specialisations are thought to have developed for suspension and vertical climbing (Hunt, 2016). Skeletal adaptations, as presented in Figure 1.2, include a cone-shaped thorax to reduce the compressive force on the ribcage during forelimb suspension, large iliac blade surface area for the gluteal muscles which are used to extend the hip during vertical climbing (Fleagle et al., 1981), large, round femoral head but long femoral neck to increase hip mobility (Schultz, 1969; MacLatchy & Bossert, 1996) abductible hallux for gripping small supports during vertical climbing (Susman, 1983; Hunt, 2016) and relatively long forelimbs which facilitate greater reach in above-head forelimb postures (Zihlman et al., 2011). In their musculature, the great apes are notable in their large physiological cross-sectional areas (PCSAs) of muscles of the forelimbs (Oxnard, 1967; Myatt et al., 2012; Goh et al., 2017). These muscles are active, and powerful, when engaging in both suspensory and vertical climbing locomotion.

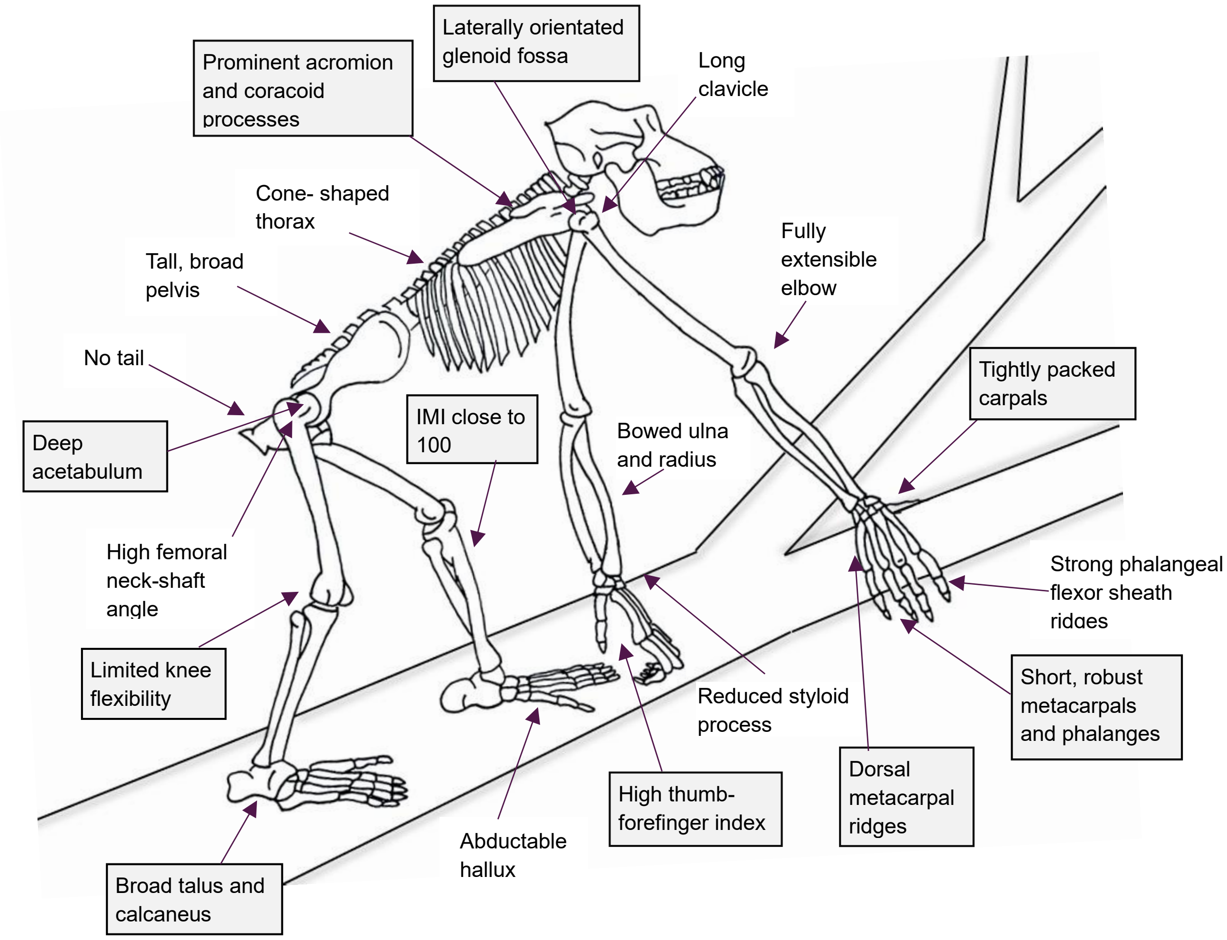

Figure 1.2: Postcranial skeletal specialisations of apes. Shaded boxes describe the postcranial adaptations of gorillas towards terrestrial quadrupedal knuckle-walking (some of which overlap with *Pan*) (Schultz, 1963; Tuttle, 1967; Lewis, 1977; Gebo, 1992; Sarmiento, 1994; Isler, 2005; Kivell & Schmitt, 2009; Williams, 2010; Zihlman et al., 2011; Fleagle, 2013; Hunt, 2016; Sarringhaus, Mitani & MacLatchy, 2022).

Although the great apes share many postcranial morphologies, they have undergone natural selection since their evolutionary split. A complicated array of ecological and environmental conditions has influenced their morphology to develop adaptations towards their local environments (Bock, 1994; Ross et al., 2002; Elton et al., 2016).

Whilst anatomically, chimpanzees, bonobos and gorillas more closely resemble each other than the orangutan, *Pan, Pongo* and *Gorilla* each differ in their morphological design to reflect their respective selective pressures. The postcranial morphology of orangutans is well adapted for arboreality. They possess highly mobile, long and muscular forelimbs (Ashton et al., 1976) which are advantageous for suspensory locomotion and give them a longer reach. They also possess long, curved metacarpals and phalanges along with highly mobile wrist joints which allow for greater grip strength in different above-head forelimb positions (Jungers, 1985). Their lower limbs are relatively shorter (they have the highest intermembral index of the great apes) and have long powerful feet and mobile hip joints which allow for hindlimbs to be used in a range of positions (Sigmon, 1974). The morphology of chimpanzees includes adaptations towards both suspension and quadrupedal knuckle-walking. Similar to orangutans, they have a flexible shoulder joint to facilitate above-head suspension and a high degree of hallux abduction (Susman, 1983; Marzke, 2009) to allow the feet to grip arboreal supports. However, they also share characteristics with gorillas. These include a laterally-orientated glenoid fossa and prominent processes on the scapula to prevent too much humeral head rotation during walking (Zihlman et al., 2011) and shorter (relative to the orangutan) metacarpals and phalanges which allow weight to be borne on the intermediate phalanges when walking (Smith, 1995). However, the morphology of the gorilla differs to that of *Pan*. Gorillas weigh more than twice as much as chimpanzees and considerably more than bonobos, so their adaptations have developed to be able to bear the compressive forces generated when quadrupedal walking on the forest floor (Tuttle, 1967; Zihlman et al., 2011; Matarazzo, 2013). The skeletal features in Figure 1.2 show some of the gorilla-specific traits, which include tightly packed carpals (Kivell & Schmitt, 2009), broad pedal bones to provide a stable weight-bearing area during touchdown (Schultz, 1963; Gebo, 1992) and short, robust manual bones also to increase stability during compression.

There is much evidence to suggest that some of the homogeneous traits of extant apes have undergone parallel evolution; meaning that similar, or equivalent traits have evolved independently in closely related lineages (Schluter et al., 2004). It is generally accepted that the suspensory behaviours of the orangutan evolved independently in orangutans and the African apes (Zihlman et al., 2011). It has also been hypothesised that quadrupedal knuckle-walking in the African apes developed independently in the *Gorilla* and *Pan* lineages: this is based on both morphological analyses of their carpal and manual structures (Inouye & Shea, 2004; Kivell et al., 2009) as well as fossil evidence (Richmond & Strait, 2000). Retained traits versus newly adaptive traits offer clues to what extent a particular structure is utilised during positional behaviour. However, it is still not understood whether shared morphological traits are expressed as similarities in the way they move in arboreal environments.

1.4 The classification of positional behaviour

In order to understand how primates interact with their local environment, we can study their positional behaviour (Prost, 1965). Positional behaviour encompasses two elements: posture and locomotion. The term ‘locomotion’ was defined by Howell (1944) as the act of moving from place to place whilst displacing the centre of mass. Conversely, posture does not include a change in the centre of mass and mostly describes stationary positions. The classification of positional behaviour was standardised by Hunt et al (1996) by distinguishing between biomechanically distinct postures and locomotor behaviours. This classification system became fundamental in the way that positional behaviour could be documented and was built upon by Thorpe and Crompton (2006) in their study of orangutan positional behaviour to incorporate torso-orientation (torso-horizontal or vertical), joint flexion or extension and weight-bearing limbs. By including detailed data on the number of body parts that primates use when engaging in different behaviours and whether the limbs are fully extended or not further reveals the way in which a species interacts with arboreal environments. It can also, to a degree, infer kinematic and functional interpretations of the musculoskeletal system as particular behaviours are assigned based on their anatomical positioning and function. Streamlining the way in which data is collected for wild primates means that comparisons can be made between species' or genera and shed light on whether primates that share characteristics in their habitat or morphology also share similar positional repertoires.

1.5 Great ape locomotor ecology

1.5.1 Gorillas

Musculoskeletal comparisons between the two geographically distinct species, the eastern gorillas (inclusive of the mountain (*Gorilla beringei beringei*) and lowland (*Gorilla beringei graueri*) subspecies) and western lowland gorillas (*Gorilla gorilla gorilla*) (also including the subspecies, the Cross River gorilla (*Gorilla gorilla diehli*)), have recognised a multitude of variance. These include aspects of their osteology, musculature, physiognomy (facial features) and dental, many of which have significant influence on joint mobility and skeletal capabilities (Schultz, 1934; Gebo, 1996; Remis, 1998; Fleagle, 2013; Jabbour & Pearman, 2016). The differences between the species are greater than those between subspecies or populations within a single species, and all four subspecies can be distinguished from each other based on large multivariate skeletal studies (Jabbour & Pearman, 2016). However, it was not known to what extent these variations drive the differences in their positional behaviour.

The positional behaviour of gorillas was broadly discussed by Tuttle and Watts (1985) for mountain gorillas and Remis (1995) for western lowland gorillas. Tuttle and Watts found that mountain gorillas mostly engaged in quadrupedal walking, and when off the ground, they climbed and walked, but rarely engaged in suspensory behaviours (Tuttle & Watts, 1985). Western lowland gorillas were documented to be more variable in their locomotor behaviours, and the variation in locomotion reflected differences in body size (Remis, 1995). Gorillas exhibit the largest degree of sexual dimorphism out of all the primates. The silverback gorilla can weigh up to 190kg, which is more than twice the weight of adult females, who are approximately 70kg (Zihlman & McFarland, 2000). The female western lowland gorillas used suspensory and bipedal locomotion more and travelled on smaller supports than large adult male gorillas, which suggest that the silverback was constrained in support use because of his size (Remis, 1995). Although these studies offered new insight into the behaviours of gorillas in arboreal environments, they were limited because of the level of habituation of the subjects (Remis, 1995). Therefore, our current understanding of the degree of arboreality and variation in positional behaviour is still limited. It was speculated that mountain gorillas spend approximately 5% of their time arboreally (Tuttle & Watts, 1985; Hunt, 1991), but this figure might be as high as 60% for western lowland gorillas (Crompton, Sellers & Thorpe, 2010). However, it was hypothesised that variation in their behaviours and degree of arboreality is not in fact shaped by the array of musculoskeletal differences, but instead, reflects their habitat variability (Remis, 1995; Remis, 1998). Mountain gorillas in East Africa occupy dense montane forests, which differ in altitude, spatial and temporal availability of vegetation and shrub density between sites (Watts, 1991; Doran, 1998; Doran & McNeilage, 1998; Nkurunungi et al., 2004; Ganas & Robbins, 2005). Conversely, the western gorillas occupy lowland rainforests, which are characterised by mosaic habitat types which include coastal forest, savannahs, swamps, mangroves and primary forests (Poulsen & Clark, 2004; Head et al., 2011). This variation in habitat shapes the distribution of resources and the strategies that gorillas exploit to address ecological needs in the way they feed, reproduce and maintain social relationships.

1.5.2 Chimpanzees

Chimpanzees occupy diverse habitats from the mountains in Mahale, Tanzania, to the open savannahs in the Ivory Coast and the lowland swamp forests of Gabon and the Congo (Poulson & Clark, 2004; Turner, 2006; Lapuente, 2020). In a comparison of chimpanzee subspecies and populations, it was found that the positional behaviour of the two eastern chimpanzee populations (*P. t. schweinfurthii*) from Mahale and Gombe were similar to each other and the female western subspecies (*P. t. verus*) in Taï, but not the adult males in Taï (Doran & Hunt, 1994; Doran, 1996). Sex differences in the eastern populations were not accompanied by significant variation in their arboreal locomotion and were similar overall to the female chimpanzees in the east. Vertical climbing accounted for 58% of their arboreal repertoires, whereas they quadrupedally walked 31% of the time, engaged in suspension 7% of the time, and walked bipedally less than 3% of their time in the trees (Hunt, 1992; Doran & Hunt, 1994; Doran, 1996). Conversely, the males in Taï walked much less but climbed much more, which was hypothesised to be a potential consequence of their larger body size. Vertical climbing seems to be a key component of chimpanzees' arboreal locomotion.

What differentiates chimpanzees from gorillas and orangutans is their complex social structure. Chimpanzees live in fission-fusion groups where social rank is highly important (Fritz & Fritz, 1974; Wrangham, 1979). Therefore, when discussing the vertical climbing behaviours of Mahale chimpanzees, Hunt (1994) adjusted for the potential role of hierarchy. It was found that larger male chimpanzees spent more time on the ground and at lower heights than smaller males, suggesting that overall, large chimpanzees will ascend less than smaller chimpanzees (and was further suggested to be true for other large-bodied apes). However, larger chimpanzees used smaller branches more than smaller chimpanzees (when adjusting for social rank) (Hunt, 1992), suggesting that because they use this behaviour less, they bear the costs (if any) of using smaller branches. Chimpanzees are able to use small supports and different locomotor behaviours in arboreal environments, but how these compare to other African apes will be the key in understanding how their distinct social structure and morphology is linked to their arboreal locomotion.

1.5.3 Orangutans

The arboreal locomotion of orangutans has been well documented (Thorpe & Crompton, 2005; Thorpe, Holder & Crompton, 2007; Manduell, Morrogh-Bernard & Thorpe, 2011; Myatt, 2011; Myatt & Thorpe, 2011; Manduell, 2013), and more is understood about how they interact with their environment. Orangutans inhabit highly dense rainforest canopies in Borneo and Sumatra which vary in liana abundance, canopy height and supports of different sizes between peat-swamp forests and lowland forests (Manduell, Harrison & Thorpe, 2012). The orangutans are the most arboreal of the great apes and rarely descend to the ground (Sugardjito, 1982; Cant, 1987; Thorpe & Crompton, 2005). The locomotor repertoire of orangutans was dominated by orthograde suspension, which is facilitated by their postcranial adaptations. However, age-sex differences on their arboreal locomotion were marginal. Thorpe and Crompton (2005) suggested that this reflects the presence of arboreal pathways which were used by individuals of all age-sex categories. They have also exhibited an ability to adopt unique strategies to deal with branch compliance when travelling on small branches and lianas (Thorpe & Crompton, 2005; Thorpe, Holder & Alexander, 2007; Thorpe, Holder & Crompton, 2009; Manduell, 2013). Orangutans use multiple limbs on multiple supports when moving in the trees with long contact times to increase balance and stability (Thorpe, Holder & Crompton, 2009). They also oscillate branches (by using their momentum to sway branches to cross from one support to another) as a strategy to reduce the energetic cost of crossing gaps in the trees (Thorpe, Crompton & Alexander, 2007). Overall, they are highly capable of moving arboreally and dealing with the challenges of small supports and canopy gaps. However, very little is understood about whether the solutions that orangutans have found to deal with challenges in arboreal environments are also used by the African apes.

1.5.4 Interspecific locomotor ecology of great apes

It is notable that only few studies have compared the locomotor repertoires of great apes (Hunt, 1991; Doran, 1996). In a comparison of the positional behaviour of African apes, it was found that *Gorilla* and *Pan* differed in the ways in which they moved in the trees, in the supports that they used and as a result of body size differences (Doran, 1996). Furthermore, in a study of the postural and locomotor repertoires of Hominoidea, Hunt (1991) also found that the variation in arboreal behaviours reflect not only morphological differences, but also habitat differences. However, these studies all predate the standardised descriptions of positional behaviour by Hunt et al (1996) which means that the way in which they classified posture and locomotion was broad and diverse (Tuttle & Watts, 1985; Sugardjito & van Hoof, 1986; Cant, 1987; Hunt, 1991; Hunt, 1992; Doran, 1993; Remis, 1995). Comparative studies are pivotal in understanding the consistencies and differences between the great apes, but at present, these have been based on broad classifications. However, for these comparisons to be meaningful, they must be built on studies that share a classification system of different locomotor behaviours (Hunt et al., 199; Thorpe & Crompton, 2005). By integrating standardised descriptions of locomotor behaviour with detailed data on their morphology and habitats, more can be understood about what shapes the shared and diverse arboreal behaviours of the great apes.

1.6 Ecomorphology

The positional behaviour repertoire of a species can reveal how a species physically uses their environment. However, in order to understand how a species exploits, and addresses the challenges within complex arboreal habitats, it is crucial to fully understand the factors that play a role in influencing their expressed behaviour. What underpins expressed behaviour, specifically positional behaviour, is a complex interplay between morphological structures, environmental factors, and external pressures such as risk minimisation (Arnold, 1983; Pounds, 1988; Bock, 1989), as outlined in Figure 1.3 This approach is defined as ecomorphology (Karr & James, 1975).

Morphological and physiological construction determine how a species can physically interact with their local environment, but the selective pressures to effectively exploit changing environments and cope with external ecological processes also influences its morphological design (Karr & James, 1975; Bock & Wahlert, 1985; Wainwright, 1991). This is a complex balance since, for example, musculoskeletal anatomy that is specialised (i.e. for accessing a particular food type) is ineffective if it restricts the ability to engage in rare but necessary locomotor behaviours. For example, great apes are extremely versatile, but are not generally known for their leaping behaviours. However, if leaping is required to avoid predators or other dangerous situations, they have the retained adaptations in their postcranial morphology to be able to leap (Napier, 1967; Cartmill, 1974). Therefore, it is essential that morphology reflects the most demanding behaviour that a primate will exhibit in their habitat (Morebeck et al., 1997). As the most demanding behaviour is often fundamental for survival, these morphological traits are selected for during evolution. Within the ecomorphology framework, this represents their performance capacity, which dictates how behaviours are expressed in an ecological context (Figure 1.3) (Bennett & Huxley, 1990). Great apes that differ in morphology because of selective pressures within their ecological niche, will also differ in their performance capacity and in turn, lead to differences in the way they interact with their environment.

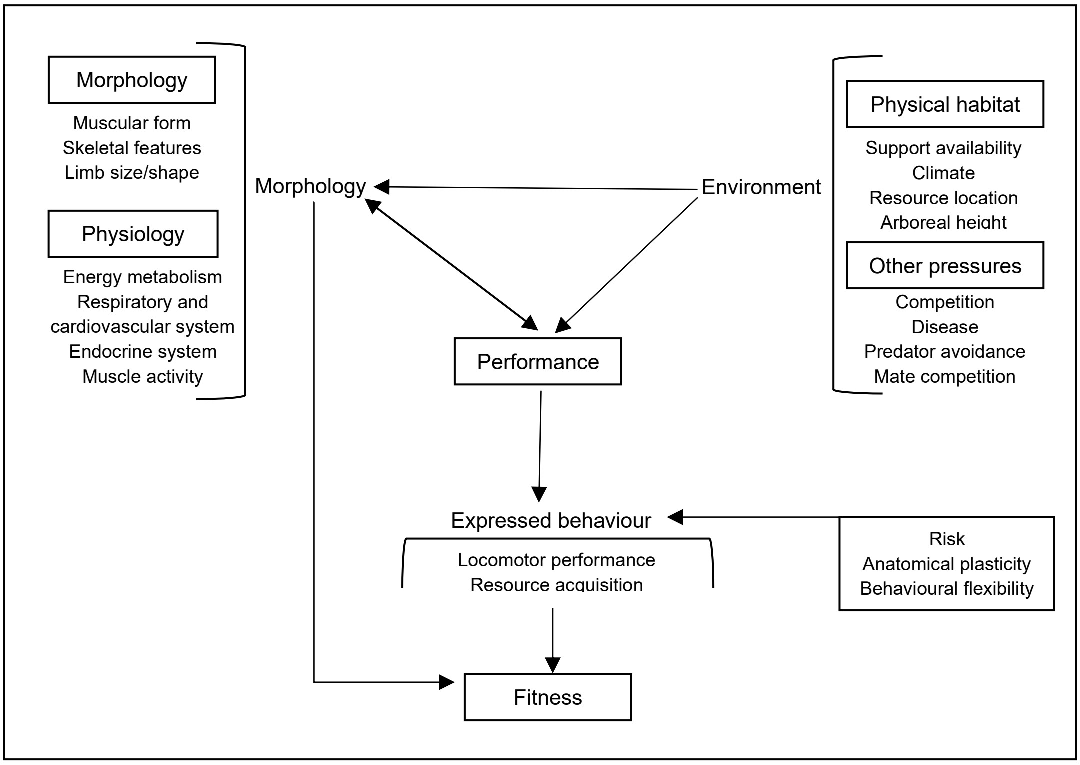

Figure 1.3: The parameters and interactions that comprise the ecomorphology of a species. Developed from Arnold (1983) and Garland and Losos (1994).

A species must have the physiological mechanisms to accomplish ecological needs such as resource acquisition and reproduction, but they must also have the energy capacity to perform behaviours efficiently (Arnold, 1983; Bock & Wahlert, 1985; Wainwright, 1991; Bock, 1994). It would be ineffective if an animal is required to perform a behaviour in their ecological niche which has been anatomically selected for, but they do not have enough energy to do so. Western lowland gorillas, for example, possess adaptations towards terrestrial quadrupedal walking which reduce the energetic demands of this behaviour, but during periods of low resource availability, they must have the energy reserves necessary to travel to sites where they can meet dietary requirements. This is of particular importance for locomotion because of the high energetic demands that underpin movement. However, whilst some primates are highly adapted in their musculoskeletal morphology for particular locomotion in the trees (such as the gibbons (*Hylobates*), which are highly efficient brachiators) (Avis, 1962), large-bodied great apes expend a considerable amount of calories when moving in arboreal environments (Pontzer et al., 2010). The high energetic costs of arboreal travel for great apes dictates that travel routes must be carefully selected. If a feeding site, or destination, can be reached by a travel route using locomotor behaviours and supports that are less energetically demanding, then this will reduce overall energy expenditure, and conserve energy for other highly demanding behaviours. This is vital for great apes that depend on arboreal environments to acquire resources.

What shapes almost every aspect of a primate's life, is their local ecological niche (Cartmill, 1972; Cartmill, 1974; Gebo, 2004). The fundamental niche of an organism represents the suitable theoretical conditions, based on its physiology, morphology and behaviour (Soligo & Smaers, 2016). This represents their ecological optimum, or potential: for primates, this specifies the habitats, food sources, social interactions and behavioural capabilities that allow for survival and reproductive success. However, environmental stochasticity, competition, biotic interactions, resource availability and predation are ecological factors that influence the dynamic interactions between a species and its environment (Bock & Wahlert, 1965). It is not possible to understand the relationship between morphology, ecology and behaviour without understanding all of the complexities within a local environment (Wainwright, 1991). Therefore, field studies must incorporate detailed data on the local environments of primates, as this is key in determining the performance and overall fitness of a species.

1.7 Kinematics of locomotion

The classification of locomotor behaviours is based on the biomechanics of a behaviour (Thorpe & Crompton, 2005). For example, flexed-elbow vertical climbing involves the activation of different muscle groups and variation in limb orientation and hand posture compared to extended-elbow vertical climbing (Hirasaki et al., 2000; Isler, 2002; Isler, 2005; Neufuss et al., 2017). Similarly, torso-orthograde (vertical) suspension is distinct from torso-pronograde (horizontal) suspension. However, the way in which different species engage in the same locomotor behaviour (even on the same support) can be considerably distinct. In quantifying an animals performance (efficiency and effectiveness of a behaviour), biomechanics is an approach that can be used to look at how morphological design influence the movements and efficiency within a locomotor behaviour. Biomechanics is the study of the motion, function and structure of a biological organism and can be split into several subfields. Most existing primate locomotor literature focuses on two specific fields: kinematics and kinetics. Kinematics is the study of the geometric motions without considering the forces behind the motions whereas kinetics concentrates predominantly on these forces. These fields of study can shed light on how morphological form is expressed in specific characteristics of a locomotor behaviour, revealing more about the form-function interface of a specific trait, or set of traits.

Kinetic analysis focuses mostly on topics such as muscle activation patterns, ground reaction forces and energy expenditure (e.g. Demes et al., 1994; Patel, 2010; Hanna et al., 2015; Granatosky, Tripp & Schmitt, 2016; Goh et al., 2017; Larson, 2018). However, most kinetic analysis benefits from a laboratory setting because of the necessity for sophisticated technology (Stevens, Ratsimbazafy & Ralainasolo, 2010).

Kinematic analysis, however, is less restricted and can be conducted using video footage, making it applicable for general use in various settings (e.g. Reghem et al., 2013; Hirasaki, Kumakura & Matano, 2000; Pontzer, Raichlen & Rodman, 2014; Finestone et al., 2018). Research into the kinematics of primate locomotion has covered topics such as spatio-temporal gait parameters (e.g. Youlatos & Gasc, 2010; Wei et al., 2016; Granatosky, Schmitt & Hanna, 2019), velocity (e.g. Kimura, 1992) and joint kinematics (e.g. Larson et al., 2001; Nakano, Kirasaki & Kumakura, 2006). Gait parameters, including stride length (step distance), duty factor (length of time in contact with support) and limb sequences, provide insight into the biomechanical efficiency, stability and degree of adaptation towards certain environments (or supports). Conversely, joint and segment kinematics is often used to explore whether mobility influences the efficiency of locomotion (Schmidt, Voges & Fischer, 2002; Orr, 2017). Kinematics of locomotion is evidently important in understanding how primates address the biomechanical challenges of moving in the trees.

Most of what is known at present about primate locomotor kinematics has come from captive settings (Larson et al., 2001; Schmitt, 2003; Stevens, Ratsimbazafy & Ralainasolo, 2010). In fact, there are very few studies that have documented the biomechanics of wild apes (Neufuss et al, 2018), which means that it is still not known how morphology and habitat influence the distinct ways in which *Pongo, Pan* and *Gorilla* engage in locomotor behaviours. In a comparison of the kinematics of great apes during vertical climbing, it was found that they were all distinct in their gait (Isler, 2002; Isler & Thorpe, 2002; Isler, 2005). When climbing a flexible rope, the African apes exhibited smaller excursion values (joint extension) for both the shoulder and elbow joints than orangutans. However, hindlimb joints displayed dissimilar patterns, as bonobos showed a more extended hip and flexed knee than gorilla (specifically the male gorilla) and resembled maximum values instead, of orangutan (Isler, 2002). For gorillas, the maximum elbow angle between the adult male and adult female was very similar, yet for all other joints, there were significant differences, likely as a result of body size and mass (Isler, 2005). Interspecific variation in biomechanic performance has also been documented during bipedal walking. In a study of African apes' bipedal walking in captive environments, it was found that gorillas exhibited similar maximum hip and knee extension, but less flexion at the knee and dorsiflexion of the ankle compared to chimpanzees (Saunders, 2017). Similar to *Pan*, but opposite to *Pongo,* gorillas do not employ straight stiff hindlimbs during bipedal walking. Hip and hindlimb excursion angles were sensitive to support orientation and diameter and differed between arboreal and terrestrial substrates. Whilst most bipedal kinematic studies have reached conclusions based on terrestrial substrates (Schmid, Schmidt & Piaget, 1994), this highlights the importance of arboreal substrates on the mechanisms that define and constrain not only bipedal walking, but all locomotor behaviours (Nyakatura, Fisher & Schmidt, 2008; Schoonaert et al., 2016; Dunmah et al., 2018). However, primates have not evolved to locomote on the structures within captive environments, which means that locomotor kinematic investigations need to be conducted in wild environments (Dunham et al., 2018). Habitat is considerably influential in driving *how* a species goes about performing a locomotor behaviour relative to their anatomical adaptations.

It therefore seems appropriate that the next step, after quantifying the positional behaviour repertoire of great apes in the wild, is to direct focus towards locomotor biomechanics in natural habitats. It would not be possible to reconstruct the trajectory of locomotor adaptations or understand what shapes the variation in expressed behaviours without an integrated approach which encompasses biomechanics alongside morphology, ecology and behaviour (Fleagle & Liberman, 2015).

1.8 Evolution of great ape locomotion

The great apes have previously been documented to exhibit a variety of locomotor behaviours (Tuttle & Watts, 1985; Sugardjito & Van Hooff, 1986; Cant, 1987; Hunt, 1991; Doran, 1993; Remis, 1995; Thorpe & Crompton, 2005; Manduell, Morrogh-Bernard & Thorpe, 2011). These behaviours have evolved because of a combination of environmental pressures, morphological adaptations and social structures. However, the fossil record for ancestral *Pongo, Gorilla* and *Pan* is fragmented and sparse. Whilst some of these fossils have been assigned as close relatives of extant apes such as *Sivapithecus*, which has been attributed to be the closest ancestor of orangutans because of facial and palatal similarities (Pilbeam, 1982) and *Sahelanthropus* which has been assigned as the last common ancestor of *Pan* and *Homo* (Brunet et al., 2002), many other fossils are difficult to assign because of their fragmented nature. The interpretation of evolutionary relationships of early crown hominoid such as *Dryopithecus* (Begun, 1994) and *Proconsul* (Le Gros Clark & Leakey, 1951) (and many more) is still debated because they present mosaic features and/or they are considerably fragmented. This makes understanding the evolution of hominoid locomotion considerably complex.

What we do have, is a relatively more complete hominin fossil record. As more fossil evidence is being discovered and biomechanical analyses of extant ape locomotion is developing our knowledge of the form-function interface, it is possible that we can use these to develop our understanding of the ancestral form which preadapted extant ape locomotor behaviours. The evolution of bipedal locomotion, in particular, has received much attention and has been heavily debated within palaeoanthropological literature for over a century. All apes are capable of (and will occasionally engage in bouts of) bipedal walking (Tuttle & Watts, 1985; Hunt, 1991; Doran, 1996; Thorpe & Crompton, 2005; Thorpe, McClymont & Crompton, 2014), but we still don’t know what was the preadaptive condition to human-like obligate bipedalism. It is generally accepted that the trajectory of characteristically human bipedality from the last common ancestor occurred in a step wise fashion rather than a direct linear sequence of speciation events (Crompton, Vereecke & Thorpe, 2008; Harcourt-Smith, 2010; Hunt, 2016). To reconstruct the locomotor capacity of extinct hominoid and understand the evolutionary stages that stimulated anatomical adaptations, there are two main approaches that are traditionally used. The ‘fossil-first’, otherwise known as bottom/ground up, approach starts with descriptive analyses of morphological characteristics of the fossil record that are subsequently used to infer corresponding functional capabilities (DeSilva & McNutt, 2018; Kozma et al., 2018). The ‘function-first’, or top-down, approach instead emphasises the use of extant nonhuman primates as referential models by assessing locomotor performance alongside anatomical constraints to hypothesise the preadaptive condition of the last common ancestor (LCA) (Hunt, 1994; Richmond, Begun & Strait, 2001; Crompton, Sellers & Thorpe, 2010; Pilbeam & Lieberman, 2017; Kozma et al., 2018). Both approaches are not mutually exclusive, but instead can be used together to more accurately infer the behaviours of extinct taxa. Combining what is known about performance profiles during locomotor behaviours of great apes with morphological analyses of skeletal remains can offer crucial information on the constraints of the musculoskeletal architecture and how a species overcomes external pressures by adapting their behaviour. By developing our understanding of how the great apes move in their natural environments, we can use them as referential models for the evolution of bipedal locomotion.

Several models have been put forward which offer different perspectives on how early hominins may have transitioned to bipedal walking. The brachiation model, often referred to as the 'hylobatian model', hypothesised that the extended hip and knee joints during terrestrial bipedalism and the habitual suspensory locomotion without ricochet performed by gibbons makes them suitable models for how bipedalism evolved (Keith, 1923). Conversely, the vertical climbing model posited that the muscular effort and limb excursion angles during vertical climbing are more parsimonious with bipedality than quadrupedal walking (using chimpanzees as referential models) (Prost, 1980; Fleagle et al., 1981). However, the knuckle-walking hypothesis remains as one of the prevailing models for the acquisition of bipedalism. This hypothesis suggests that bipedalism was a transition from quadrupedal knuckle-walking (as seen in extant gorillas and chimpanzees) because of the presence of knuckle-walking traits in the hands and wrists of several hominin species (Washburn, 1967). However, biomechanical analysis of quadrupedal walking has since shown that whilst the African apes do exhibit some similarities in this locomotor behaviour, there are significant interspecific kinematic distinctions (Inouye & Shea, 2004; Kivell & Schmitt, 2009; Tarrega-Saunders et al., 2021). It has therefore been suggested that knuckle-walking is either a shared inheritance of behavioural flexibility or evidence of independent evolution as a response to environmental pressures (Thorpe, McClymont & Crompton, 2014; Tarrega-Saunders et al., 2021). Instead, more fossil evidence suggests that the last common ancestor of great apes would have been orthograde in arboreal environments (Crompton, Vereecke & Thorpe, 2008; Crompton, Sellers & Thorpe, 2010). Anatomical characteristics associated with orthograde have been identified in early crown hominoids including *Pierolapithecus* (13ma) (Moyà-Solà et al., 2004) and *Morotopithecus* (16-20ma) (Maclatchy et al., 2000). For early hominins, palaeoenvironment evidence suggests that they would have inhabited woodlands and so may have developed bipedalism in an arboreal setting (WoldeGabriel et al., 2001). Evidence for both bipedality and arboreality have been documented in more recent fossils such as *Orrorin* (6ma) (Senut et al., 2001) and *Ardipithecus* (Haile-Selassie, 2001; Lovejoy et al., 2009). Extant non-human great apes have also been documented to engage in occasional bouts of arboreal bipedal walking and orthograde suspension (Hunt, 1991; Remis, 1995; Doran, 1996; Thorpe & Crompton, 2005), which further supports the idea that arboreal orthograde postures could have been a precursor to bipedal walking on the ground. However, whilst it is difficult to base a whole model on one or two extant species and an incomplete fossil record, it must also be acknowledged that using phylogenetically distinct primate species that possibly possess completely distinct biomechanical mechanisms during locomotion complicates the ability to determine conclusions. This thesis aims to develop our understanding of how the great apes move in arboreal environments from an ecomorphological perspective (by integrating morphology, environment and behaviour), to provide more evidence which can be used in understanding how locomotor repertoires may have evolved.

1.9 Western lowland gorilla feeding ecology

Gorillas remain relatively understudied in terms of their arboreal locomotor in the wild. They are the largest apes that exploit arboreal environments and are among the most sexually dimorphic of the extant primates (Taylor, 1997). Much of the research on western lowland gorillas has focused on diet and nutritional needs, resource availability and ranging patterns (Jones & Sabater Pi, 1971; Calvert, 1985; Remis, 1997; Nowell & Fletcher, 2008; Masi, Cipolletta & Robbins, 2009) and the variation in these behaviours as a result of body size. This may affect their feeding strategies, social dynamics and energetic demands. As body weight increases, so does the metabolic rate, but the energy required per unit body weight decreases; this means that smaller gorillas have a higher energetic and nutritional requirement than larger gorillas (McNab, 1978; Jungers, 1984). Furthermore, relative to body size, females experience higher nutritional requirements as a result of reproduction. Gestation and lactation, in addition to travelling with dependent infants is incredibly metabolically costly, so they require a higher intake of calories (Nowell & Fletcher, 2008). Adolescents also have to intake a considerable number of calories to account for their growth. These differences have been documented in age-sex variations in time spend feeding, with the silverback feeding less than adult females and adolescents (Masi, Cipolletta & Robbins, 2009). However, this is also driven by the quality of food types and the social dynamics within a gorilla troop. Dominant silverback gorillas have been observed to chase females away from feeding sites that are abundant in high-quality fruits (Remis, 1995). When highly sought after nutritional resources are less abundant, lower-ranking gorillas may be more likely to compensate for this by altering their behaviour patterns and diet.

The average annual home range for western lowland gorillas is around 15km^2, but they will often use a core area within their home range of approximately 4km^2 (Seiler & Robbins, 2020). The distribution of resources between the forest canopy, the forest floor, and the swamps provides the gorillas with different habitats and environments to feed in, many of which fluctuate seasonally. This has an impact on the gorillas’ daily travel distances, which vary (depending on the site) from 0.8km a day, to 7.6km in a single day (Remis, 1995; Cipolletta, 2004; Seiler & Robbins, 2020), with an average of 2km per day. Where resources are less abundant, the gorillas engage in longer travel distances which increase the cost of foraging and energy for locomotion. This is of particular importance for travel between sites of fruit availability, in the canopy, as fruiting trees are not always within the same area. Arboreal nutritional resources such as fruits and leaves are an important aspect of their diet, which means that so is tree-climbing in order for them to access them (Remis, 1994; Nishihara, 1995). Fruit is one of the main motivations for western lowland gorillas to leave the terrestrial environment for the trees. However, fruit is not the only resource that influences behavioural patterns as western lowland gorillas also exploit nutritional resources in swamps which fluctuate seasonally. Within the lowland forests of Central Africa, there are complex networks of lagoons, swamps and floodplains because of the low altitude and proximity to the coast. The ecological niche of a swamp (defined as permanently inundated areas surrounded by *terra firma* (Doran-Sheehy et al., 2004; Head et al., 2011)) is considerably different to the forest floor and are characterised by unique conditions and challenges. However, they offer a variety of different nutritional resources (Fay et al., 1989; Head et al., 2011; Oelze et al., 2014; Seiler and Robbins, 2020; Robbins et al., 2022). In a study on the influence of swamp resource availability, Seiler and Robbins (2020) found that as the density of nonfruit resources and swamps in area increased, daily travel distance decreased. The movement patterns of western lowland gorillas are dictated, as for all primates, by the availability of resources. As the acquisition of nutritional resources is the key motivator for western lowland gorillas to access arboreal environments, in order to develop our understanding of this species, we need to understand how they go about accessing food when in the trees and how they find solutions to the challenges of feeding in arboreal environments.

1.10 The Loango National Park

The Loango Ape Project began in 2005, when the habituation of gorilla troops began (Boesch et al., 2007; Head et al., 2011). The site is located in the North of the Loango National Park, Gabon (2°04′S and 9°33′E) and is situated on a strip of land between the Atlantic Ocean to the West and a large lagoon to the East (Head et al., 2011).

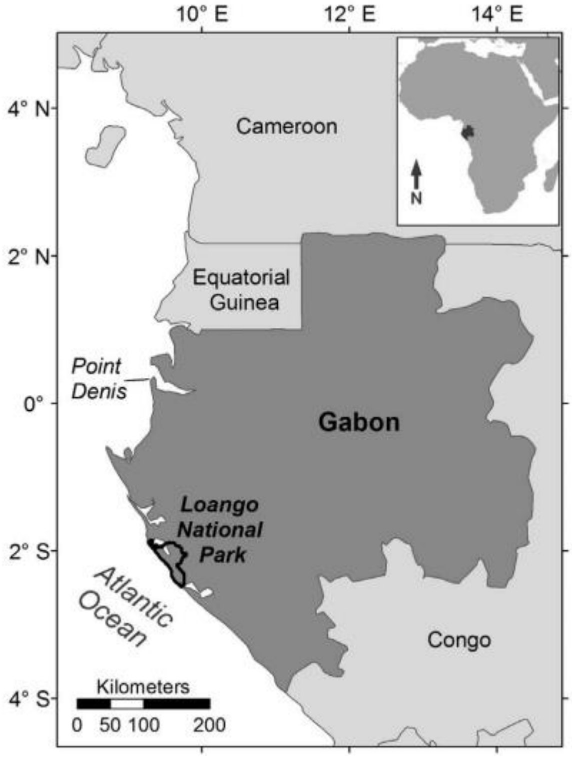

Figure 1.4: Location of Loango National Park in Gabon, taken from Harris et al (2012).

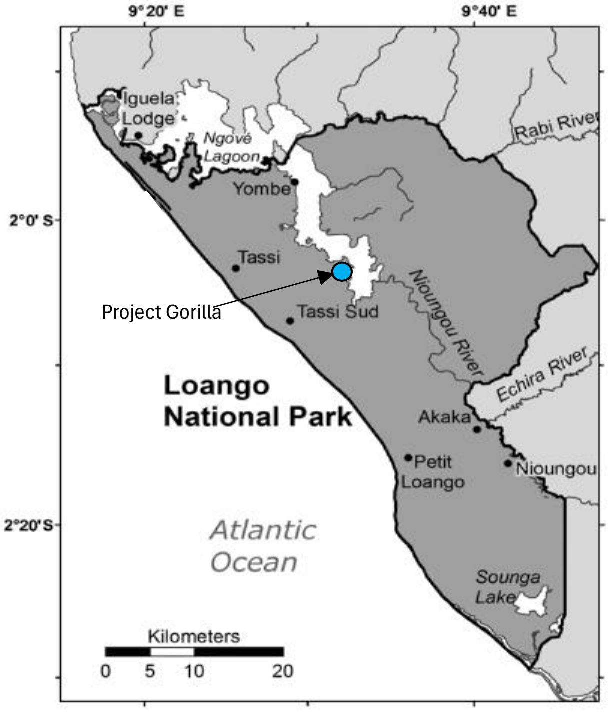

Figure 1.5: Location of Loango National Park in Gabon, showing the position of the lagoon and research site, adapted from Harris et al (2012).

The Loango National Park in Gabon is characterised by a differing array of habitat types, from coastal forests, savannahs, mangroves, vast areas of swamps and primary forests (Head et al., 2011; Harris et al., 2012). Loango differs from other forests in Africa (and even other forests in Gabon) inhabited by great apes because of its coastal location, variation in seasonal fruiting patters (Head et al., 2011) and the density of herbaceous vegetation, which is low in Loango (Furuichi, Inagaki & Angoue-Oyono, 1997; Morgan, 2000). As most data on the Loango National Park has been documented from the perspective of great apes and large mammals (for example diet, ranging patterns and forest use), our understanding of the overall phenology, forest structure and ecology of the Loango is not fully known.

Given its coastal location, the terrain in the Loango National Park is mostly flat, with very little fluctuation in topography (Rabanal et al., 2010). The forests are dominated by mature trees, which reach heights of up to 50 meters in places. The canopy is relatively closed, which restricts sunlight to the forest floor, so there is few saplings and shrubs (Furuichi, Inagaki & Angoue-Oyono, 1997). There is not much secondary forest, and the understorey of the forest is mostly very open (Head et al., 2011). Lianas, up to 50cm in diameter, suspend from mature trees, creating intertwined networks. These networks also reach the forest floor, where they form large bundles of lianas which are impenetrable in places. Whilst some areas of dense foliage are found in places at the forest floor, the forest floor is mostly characterised by vast areas of flat open space. Elephants and other large mammals create pathways throughout the forest, which has formed a system of large, open trails.

Swamps make up a larger proportion of the Loango National Park compared to other African forest habitats occupied by great apes (although the exact figure of swamp versus terrestrial land has not been quantified) (Boesch et al., 2007; Oelze et al., 2014). The size and depth of swamps fluctuate seasonally and during periods of high rainfall, the swamps span lengths of up to 200 meters and unknown depths. Within the swamps, large trees are less abundant because of waterlogged, low-oxygen soil conditions and low essential nutrient availability (Lugo, Brown & Brinson, 1990; Aber, Pavri & Aber, 2012; Butt et al., 2021). As a result, this creates large gaps in the forest canopy. Swamp plants and vegetation therefore survive as they receive sunlight within these vast gaps in the forest canopy. Fallen trees create natural pathways across the swamps in some areas, but at the periphery of the swamps and lagoon, mangroves are often located, offering refuge from the waterlogged floor. The mangroves in the Loango National Park create intertwined and often dense pathways (Nowak, 2013) which can reach lengths of 400 meters, especially at the periphery of the lagoon. During the dry season, the mangrove roots are exposed, but during the rainy season, the mangrove roots are submerged underwater.

Figure 1.6: Photograph showing the proximity of the lagoon to the forests inhabited by the gorillas.

Figure 1.7: Images showing some of the mature trees found in the Loango National Park. On the left is a *Ficus aurea* which reaches heights of 40 meters. On the right is *Piptadeniastrum africanum,* which has large buttress roots at the base, and can reach a total circumference of over 10 meters at the forest floor.

Figure 1.8: Images showing the vast open space on forest floor and presence of sporadic large mature trees. Photograph a. is an area of inland forest and shows a large pathway (lighter section through the middle) made by the habitual use of elephants and other large mammals. Photograph b. shows a typical forest floor located near the lagoon, where there is more green foliage on the floor.

Figure 1.9: Photograph showing a network of large and small lianas suspending from the trees and reaching the forest floor.

Figure 1.10: Images of the swamps and mangroves located in the Loango National Park. Photograph a. is of a large, mostly landlocked swamp and shows the border of the forest, on *terra firma,* made up by large mature trees. There are few young trees within the swamp, but mostly the vegetation is characterised by swamp grass and plants. Photograph b. shows a swamp which feeds directly into the lagoon and the presence of long mangroves roots descending into the mud and water. Photograph c. shows a dense mangrove forest which separates the swamp and the lagoon.

1.11 Thesis aims

Western lowland gorillas are the largest extant apes that exploit arboreal environments, but they possess postcranial morphologies towards terrestrial quadrupedal walking (Gebo, 1996; Tuttle, 1967). It is often assumed that the African apes have retained adaptations towards vertical climbing and suspension (Hunt, 2016), but whether these influence the way in which gorillas access and move around in the canopy is not understood. The primary aim of this thesis is to expand our understanding of the arboreal locomotor behaviours of wild western lowland gorillas and examine whether body size influences the strategies used to move in complex arboreal environments. Building upon previous work by Remis (1995), by integrating standardised descriptions of locomotor behaviours (Hunt et al., 1996; Thorpe & Crompton, 2005) and detailed information on the heights and supports that western lowland gorillas use, we can answer some of the big questions in gorilla locomotor ecology. It is still not fully understood how arboreal gorillas are, so one of the key research aims is to determine how much time the gorillas spend in the trees and whether there is an age-sex or body size variation in the degree of arboreality. Furthermore, given their large size, how do western lowland gorillas feed in the trees, especially on resources that are located in the periphery of tree crowns? Do the gorillas avoid risky locomotor behaviours when accessing nutritional resources to reduce the risk of falling and injuring themselves? Is it possible to understand which arboreal behaviours are energetically demanding because of their adaptations towards terrestrial quadrupedal walking and body size, and is this reflected in the amount of time they engage in energetically demanding behaviours? Are the gorillas restricted to using only large supports that can bear their weight and is there a relationship between the size of supports used and body size? Alternatively, do the gorillas compensate for their size by using multiple supports, similar to the strategies used by orangutans when moving on small supports in the trees? By answering these questions, we can gain a deeper insight into how this species interacts with their natural environment. This will shed light on the relationship between their anatomical form and behavioural repertoire and reveal more about the selective pressures that shaped their development and adaptation.

Moreover, this thesis also aims to improve our knowledge of great ape ecomorphology by comparing the arboreal locomotor behaviours of western lowland gorillas, to Sumatran orangutans (Thorpe & Crompton, 2006) and new, unpublished data for chimpanzees (Pettifer & Thorpe, Unpublished data). Great apes vary in size, habitat, anatomy and the degree of sexual dimorphism, but it is still not known whether species or body size shapes their arboreal behaviours. Therefore, one of the primary aims of this comparative study is to reveal whether there is a relationship between arboreal locomotor ecology with either or both body size and species. We know how *Pongo, Gorilla* and *Pan* differ in their postcranial morphology, but are these anatomical differences associated with diverse locomotor strategies (or is it even possible to determine)? For example, orangutans possess adaptations towards suspensory locomotion, but do they engage in this behaviour much more than the African apes? Do adaptations for terrestrial quadrupedal walking in chimpanzees and gorillas limit their ability to move in complex arboreal environments to feed on arboreal resources when compared to orangutans? The great apes also differ in the habitats that they occupy, but to what extent do their arboreal habitats differ? Is this reflected in the way in which they move in the trees, or is it even possible to isolate habitat as a potential contributing factor? Although great apes exhibit intraspecific sexual dimorphism, can we study the role of body size for great apes combined? How do larger apes move and feed in the canopy compared to smaller apes, for example, do they use different locomotor behaviours or different supports because of their size? By studying the arboreal locomotor ecology of species-related groups and body-size related groups, it may be possible to determine how evolutionary adaptations because of selective pressures contribute to how the great apes tend to survival and ecological roles in varied environments.

It is notable that the next step in understanding how great apes move in their natural habitat is to explore the kinematics of locomotion. However, there have been very few studies that have investigated the joint and segment angles of wild great apes because of difficulties in obtaining quality video footage and the time required to manually code the images. As technology is becoming more advanced, the use of machine learning tools has revolutionised how locomotor kinematics can be studied, but it is not known whether these tools are ready to be used in wild settings. The final aim of this thesis is to test some of the leading and novel tools in pose estimation to determine their applicability and to discuss the implication for machine learning in the future of great ape biomechanics. Are new state-of-the-art machine learning tools easily accessible and user friendly? Whilst they are often successful in captive environments, are they ready to be applied to wild type environments given the complexities of great ape natural habitats? If not, what are the next steps in wild ape biomechanics, and how can develop computational frameworks to be effective in the wild? What can we do with biomechanic data produced by machine learning tools and how does this improve our understanding of the form-function interface of a species?

There are many unanswered questions regarding great ape locomotor ecology and biomechanics, but this thesis aims to answer some of these questions. It might be possible to use potential new findings to develop our understanding of hominoid evolution and use great apes as referential models for the evolution of hominin bipedalism. Furthermore, understanding how great apes use their natural habitats will be beneficial for developing conservation strategies and how we can integrate new data to encourage wild-type behaviours in captive great apes.

1.11.1 Chapter outline

In Chapter Two, I detail the results of a twelve-month field study in the Loango National Park, Gabon, where I documented the positional behaviour of wild western lowland gorillas. I discuss the ways in which the gorillas move in the trees and the effect that body size had on the strategies used to access, move around and deal with discontinuity in the canopy. I integrate these data in Chapter Three with locomotor ecology data for wild Sumatran orangutans and new unpublished data for wild chimpanzees. I discuss the arboreal locomotion of these great apes and investigate whether the apes exhibit any shared characteristics in their arboreal behaviours and further explore whether body size and/or species drives the variation in their locomotor repertoires. Chapter Four focuses on the musculoskeletal biomechanics of locomotion as I investigate whether state-of-the-art machine learning technology is accurate enough to be applied within kinematic studies of wild apes by using video footage taken of wild gorillas. Finally, in Chapter Five, I summarise the results of these studies and discuss the next steps in developing our understanding of great apes in their natural habitats and the importance of studying apes within the ecomorphology framework.

CHAPTER TWO

THE LOCOMOTOR ECOLOGY OF WILD WESTERN LOWLAND GORILLAS: HOW DOES THE LARGEST APE EXPLOIT COMPLEX ARBOREAL ENVIRONMENTS?

2.1 Abstract

Western lowland gorillas are the largest and most sexually dimorphic ape that habitually navigate arboreal environments. Their size, robust musculature and specialised adaptations towards terrestrial locomotion makes them interesting models for understanding how great apes are able to exploit complex arboreal habitats. This paper offers a comprehensive analysis of the arboreal locomotor ecology of western lowland gorillas by integrating biology, ecology and morphology. A group of fully habituated wild western lowland gorillas were followed for twelve months in the Loango National Park, Gabon. Statistical analysis applying regression modelling and Akaike's Information Criterion was used to identify the relationship between locomotor behaviours, height, contextual behaviour and support use. Walking and vertical climbing dominated the gorillas' arboreal locomotor repertoire, but gap-crossing behaviours made up a considerably larger proportion of their locomotor repertoire than expected. The size of supports used was an influential factor in the variation of arboreal locomotion by gorillas of different body size. The silverback used large supports more than smaller gorillas, and small supports less. Overall, the gorillas employed strategies to mitigate the risk of falling in their use of various supports which allow for robust hand grips and their flexibility in using biomechanically distinct locomotor behaviours when accessing arboreal resources. Despite their large size, they exhibited considerable adaptability in their locomotor repertoire, suggesting that their adaptations for terrestrial quadrupedal walking do not limit their use of arboreal environments. Instead, their morphology and behavioural flexibility perhaps enhances their ability to exploit diverse habitats, contributing to their ecological and evolutionary success.

2.2 Introduction

Gorillas are the largest and most sexually dimorphic ape that habitually exploits arboreal environments to feed on fruits and foliage. Nevertheless, it is not yet understood how, with large bodies weighing substantially more than the almost exclusively arboreal orangutan, they are able to move around complex arboreal environments.

Western lowland gorillas (*Gorilla gorilla gorilla*) inhabit dense tropical rainforests in central Africa, which are dominated by swamps, mangroves and lowland forests (Yamagiwa, Angoue-Ovono & Kasisi, 1995; Caldecott & Kapos, 2005). The highest layer in the canopy can reach heights of up to 50 meters and is typified by sporadic emergent trees. The main canopy, conversely, is highly concentrated with intertwined foliage and branches which offer lots of travel routes but is highly dense in places which can be challenging to penetrate and is limited in visibility (Harris et al., 2012). Below the canopy, the understorey is characterised by vertical supports. This includes tree trunks and suspending lianas which offer lots of vertical pathways to the canopy from the ground (Cant, 1992). These highly complex environments pose many challenges for the gorillas as both access to arboreal environments from the ground and movement within the trees requires an understanding of the properties of arboreal supports which can deflect or break under their weight and the ability to adapt locomotor behaviours accordingly (Grand, 1972; Povinelli & Cant, 1995; Brownlow et al., 2001; Van Casteren et al., 2012). Understanding how they find solutions to the problems of travelling and feeding in trees, whilst mitigating the risk of falling, requires an integration of their ecology, morphology, and behaviour; an approach encapsulated in the ecomorphology framework (Bock & Wahlert, 1965; Karr & James, 1975; Wainwright, 1991; Soligo &

Smaers, 2016). This study aims to reveal how western lowland gorillas interact with their natural environment by identifying the strategies they use to access different heights and move around the canopy, and whether these are associated with body size, hand posture and postcranial morphology. Given their large size, it might be expected that the gorillas will compensate for their size by using larger, more stable supports and take less risks when acquiring food in the periphery of tree crowns where supports are smaller and unpredictable.

Western lowland gorillas also exhibit the largest degree of sexual dimorphism. Silverback males weigh up to 170kg and females weigh up to 70kg, compared to 90kg for adult male orangutans and 40kg for female orangutans (Rodman, 1984; Knott, 1998; Doran & McNeilage, 1998; Zihlman & McFarland, 2000). However, very little data exists on their positional behaviour (locomotion and posture). Using broad classifications of locomotion and posture alongside data on activity, diet, locomotion and support use, Remis (1994) found that the gorillas spent most of their arboreal time quadrupedally climbing and walking, then descending to the ground to travel between feeding sites. Observations of prolonged bouts of suspensory locomotion or gap-crossing between trees were rare. This, however, was based on a relatively small dataset (approximately 25 hours of observations) of semi-habituated gorillas, with most (80%) of observations taking place during the rainy season. These factors were noted to impact the interpretation of results (Remis, 1994; Remis, 1995). Furthermore, limited data meant that it was not possible to quantify the variation in locomotor repertoires based on body size differences.

In contrast to the sparse data available for gorillas, the locomotion of orangutans in complex arboreal environments has been well studied (Cant, 1987; Thorpe & Crompton, 2005; Thorpe, Holder & Crompton, 2009; Manduell, Harrison & Thorpe, 2012) and has benefitted from the development of detailed and uniform classifications of positional behaviour (Hunt et al., 1996; Thorpe & Crompton, 2005). Their locomotor repertoire is dominated by suspensory behaviours and is shaped by ecological factors such as branch diameter, type of supports and number of supports used (Thorpe & Crompton, 2005). Height in the canopy and contextual behaviour were also found to be highly influential in determining their locomotor strategies (Thorpe & Crompton, 2006). However, gorillas, unlike orangutans, routinely exploit terrestrial environments and thus must find solutions to arboreal challenges despite conflicting demands on their musculoskeletal system for terrestrial behaviours (Remis, 1995; Doran, 1996), in additional to their much larger size. Several studies on the biomechanics and energetic costs involved in their arboreal movement have shown that gorillas exhibit high energetic costs when accessing and negotiating arboreal habitats (although based on captive gorillas) (Tuttle et al., 1972; Isler, 2002; Kozma, 2020), but they are able to adapt their gait when walking and vertical climbing on different sized arboreal supports as a strategy to minimise energy expenditure (Isler & Thorpe, 2003; Pontzer & Wrangham, 2004; Schoonaert et al, 2016; Neufuss et al, 2018; Finestone et al., 2018; Tarrega-Saunders et al., 2021). However, in order to ascertain whether gorillas’ large size and conflicting demands for terrestrial locomotion force them to operate at the high end of their physiological and anatomical capacity during arboreal activity, further data is needed on their locomotor ecology.

One of the biggest biomechanical challenges for gorillas is how they transition from the ground to the canopy, and how they move between different levels when in the canopy. Vertical climbing (ascent and descent) is metabolically costly for gorillas since the mechanical work and muscular effort required to generate force against gravity increases with body weight (Pontzer & Wrangham, 2004; Isler, 2005; Hanna & Schmitt, 2011). However, the energetic cost of vertical climbing is also influenced by the size of supports used (Isler, 2002; Isler & Thorpe, 2005; Neufuss et al., 2018) and the number of limbs used to support mass. Small supports are less mechanically challenging to climb than larger supports (Isler, 2002; Neufuss et al., 2018) because forearms can reach higher, and there is less requirement for full-body muscle engagement. However, in wild habitats, small supports are also riskier. For horizontal travel within the canopy on smaller supports, suspensory locomotion is less metabolically challenging than walking, particularly for larger individuals (Cartmill & Milton, 1977). When forelimbs are fully extended at the shoulder, elbow and wrist joints, and the whole weight of an individual is underneath a support, the individual has effectively already 'fallen-off' the support, so they are stable and there is less requirement for constant muscle activity (Thorpe, Holder & Crompton, 2009). Horizontal travel on large supports, however, is more similar to the characteristics of terrestrial environments. Orangutans tend to use quadrupedal walking on large tree boughs where possible but are able to rely heavily on suspensory locomotion for posture and movement on thinner supports at the periphery of tree crowns (Thorpe & Crompton 2005;2006). Whether gorillas are able to resort to suspension in the same way as orangutans or are more restricted to larger supports is a key component of their ability to exploit arboreal resources.

Another biomechanical challenge that is accompanied by considerable risk for gorillas is gap-crossing, which requires moving across empty space within, or between trees (Graham & Socha, 2020). Compared to walking and climbing, gap-crossing requires a considerable number of skills. Walking on top of a support requires balance and appropriate weight distribution (Schmitt, 1999) and vertical climbing needs high levels of force production and coordination (Schoonaert, D'Aoû t & Aerts, 2006; Hanna et al., 2017). Gap-crossing, however, requires an accurate judgement of distances, an understanding of physical properties such as branch compliance, the ability to reach and grasp supports accurately and the musculoskeletal mechanisms to deal with support instability (Cartmill & Milton, 1977; Fleagle et al., 1981; Susman, 1984; Larson & Stern, 2006; Graham & Socha, 2020). In addition, gap-crossing can be highly energetically demanding as compliant supports increase muscular effort and metabolic cost (Schmitt, 1999; Graham & Socha, 2020). Orangutans are highly competent at gap-crossing not only as a result of physiological adaptations, but also in their cognitive and physical ability to manipulate branches and lianas to 'sway', 'ride' and bridge between supports (Thorpe & Crompton, 2006). In fact, gap-crossing using compliant supports is significantly less costly for orangutans than jumping or descending and reascending a tree, as they use branch flexibility to their advantage by utilising energy stored in the supports during travel (Thorpe, Holder & Crompton, 2007, 2009). It might be expected that gorillas will be exposed to greater risks when gap-crossing, given their size and that they spend less time in the trees and perhaps have less familiarity with the properties of supports. On the other hand, considering the energetic cost of vertical climbing, gorillas may instead exhibit a preference towards gap-crossing as a strategy to avoid descending and re-ascending trees (Hunt, 1991).

Our understanding of the influence of body size and sexual dimorphism for gorillas in arboreal environments is still not understood. Broad hypotheses suggest that as body size increases, so should the size of supports used (Fleagle & Mittermeier, 1980; Cant, 1992), and that the location of larger individuals will be closer to the core of trees compared to smaller individuals, who might spend more time at the periphery of trees, where supports are smaller and more unpredictable (Remis, 1995). It is also predicted that larger individuals should engage in more suspension and bridging than smaller individuals when using the same size support (Cartmill & Milton, 1977; Fleagle & Mittermeier, 1980) but less leaping (or acrobatic) behaviours (Garber & Easley, 1984; Fleagle, 1985; Cant, 1992). Based on what is currently known about western lowland gorills, female gorillas have been documented to perform scrambling behaviours and bipedal walking marginally more than males, but adult males used suspensory locomotion twice as often as females (Remis, 1995). There were very little differences in acrobatic behaviours (including tree-swaying, leaping and bridging) between males and females, but they were not used often. The adult male gorillas did spend more time closer to tree cores, and used small supports less than adult females, which allign with body size predictions (Remis, 1995). However, this now needs revisiting to investigate these hypotheses for habituated gorillas.

What may also influence a variation in their arboreal locomotion is age-sex differences. Young gorillas will often engage in more play and social behaviours, which might influence the way in which they exploit arboreal environments (Doran, 1997; Lewis, 2005). Furthermore, the role of adult females in reproduction and infant nurturing sets them apart from adult males and adolescent gorillas. Infant gorillas are not completely dependent, but they rely on their mothers for transport until around the age of four

(Nowell & Fletcher, 2007), and research into the biomechanics of infant carrying of other great apes has shown that the metabolic cost of infant carrying increases as infant weight increases, which impacts the efficiency of locomotion and perhaps their available choices when moving in unstable environments (Schradin & Anzenberger, 2001; Anvari et al., 2014; Goto, Yamade & Nakano, 2022). However, it remains unknown whether or not females have to alter their locomotor behaviours when carrying infants and if this is reflected in their locomotor repertoire.

Finally, hand postures are also of particular interest within the arboreal environment as primates are only able to perform a behaviour if they are physically able to hold or grasp supports. Gorillas have the highest thumb-forefinger index of the other great apes; these hand proportions are more similar to humans than other apes (Schultz 1930; Almécija, Smaers & Jungers, 2015; Schmitt, Zeininger & Granatosky, 2016). Gorillas, therefore, may have to adjust their behaviour in arboreal environments to compensate for their hand morphology. Although the biomechanics of hand postures in quadrupedal walking has received much attention from a morphological perspective, there is a notable gap in our understanding of arboreal hand postures for wild western lowland gorillas (Kivell & Schmitt, 2009; Neufuss et al., 2017; Tarrega-Saunders et al., 2021). Knuckle-walking dominates the hand postures used during terrestrial quadrupedalism of mountain gorillas (Thompson, et al., 2018). However, in arboreal settings, palmigrady has been observed as a common hand posture, which is likely a strategy to increase contact area and adjust for stability when moving on top of compliant or smaller supports (Hunt, 1992; Kivell & Schmitt, 2009; Finestone et al., 2018; Tarrega-Saunders et al., 2021). There is currently very little data on the hand postures of gorillas when engaging in tensile locomotion. In a study of hand postures during vertical climbing by mountain gorillas, Neufuss et al., (2017) noted that grip type depended upon the size of the support. This indicates a potential relationship between support type, locomotion and hand postures which prompts further investigation of the mechanisms used by western lowland gorillas to move in arboreal environments.

The aim of the present study is to identify the ecological, morphological and behavioural aspects that shape the arboreal locomotor ecology of western lowland gorillas. In order to investigate whether their adaptations towards terrestrial quadrupedal walking and the huge variation in body size influences the exploitation of arboreal environments, there are five overarching questions that will be addressed: i) what strategies are used to access different heights in the canopy, ii) what strategies are used to move around when in the trees and deal with discontinuity, iii) is risk mitigated for by using specific supports, especially at higher heights, iv) is hand morphology a driving force towards the use of particular supports, v) are there differences in the arboreal locomotion between gorillas of different body size and age-sex classes?

2.3 Methods

2.3.1 Location

The field study took place between July 2021 and July 2022 at the Loango Gorilla Project of the Max Planck Institute of Evolutionary Anthropology in the Loango National Park, Ogooue-Maritime, Gabon (2°04′S, 9°33′E). The study site is on a long strip of land bordered to the west by the Atlantic Ocean and is mostly primary forest and lowland swamps fed by the lagoon (Head et al., 2011). There is a long rainy season typically between October to April, which is often interrupted by a short dry season from December to January (Head et al., 2011). The annual temperature in Loango ranged between 18-28° (Hagemann et al., 2019; Klein et al., 2021).

2.3.2 Subjects

The study group was a family of nine western lowland gorillas including a silverback, three adult females, a blackback, a subadult, a juvenile and three dependant infants (Table 2.1). Habituation of the group began in 2011, with the group being sufficiently habituated for routine data collection by 2015. In this study, data was not collected on infant individuals under the age of two because of their dependency on travelling with their mothers (Nowell & Fletcher, 2007; LaRocque, 2009).

Table 2.1: Sex, age and estimated body weight of the seven gorillas which made up the study subjects of this research.

Individual	Sex	Age[1]	Estimated body weight[2]	Notes
Kamaya	Male	30-35	~170kg	Silverback, dominant male
Tonda	Female	25	80kg	Adult female, gave birth to infant 25.03.22 (carried by mother) and mother of Ogwely
Ambia	Female	25	75kg	Adult female, mother of Waka and dependant infant Malumbi (born August 26, 2020), who was carried often but not exclusively
Mokebo	Female	30	70kg	Adult female, mother of Orema and dependant infant Etc (carried by mother) who was born on May 23, 2021, and died 26.06.22
Waka	Male	11	75kg	Blackback, offspring of Ambia
Orema	Male	9	35kg	Subadult, son of Mokebo, independent
Ogwely	Male	5	30kg	Juvenile son of Tonda, independent

[1] Age from beginning of the study. Exact age of Orema and Ogwely are known, but for other individuals, age estimation is based on body size descriptions in Breuer et al., 2009 and knowledge of gorilla size and age.

[2] Body weight estimated using comparisons of known weight and size of captive gorillas. The variation in weight of adult females was determined based on the variation in their absolute size.

2.3.3 Data collection protocols

Focal individuals were chosen at random each morning and were followed for the duration of one day. First contact was made after 7:00, once the group was located, between 7:05 and 12:00 (n = 263 days) with few occasions where contact was not made for the duration of the day. The gorillas were followed until 16:30. If the focal animal moved out of sight for more than two hours, another individual was selected at random and observed for the remainder of the day (n = 5 days). The gorillas would frequently traverse mangrove thickets and swamps that were not suitable for the research team to follow. In this case, the contact would be paused until the focal animal was seen again. When high in the canopy and positioned in areas of dense vegetation, identification of the focal individual and other behavioural and ecological data would also often be difficult to observe so partial observations were recorded such as height-only or locomotor data without information on support use. Considerable self-training and regular testing was performed to maintain accuracy in estimating support properties and height. This was done by measuring landmarks at different distances and documenting their absolute distance with a laser rangefinder. To accurately determine support size at different distances (as a support further away gives the impression of being smaller), training was done by estimating the size of branches at varied lengths horizontally (for example, placed on the ground 10 or 20 meters away), and subsequently measured. This was then repeated for supports that varied in diameter.

Instantaneous data was collected on the one-minute mark (Altman, 1974; Doran, 1992; Thorpe & Crompton, 2005). Every minute, locomotor behaviour, height and hand posture were documented, as well as support properties for each weight-bearing limb (Table 2.2).

Table 2.2: List of locomotor ecology variables collected in the field using one-minute instantaneous sampling.

1.	Date
2.	Time
3.	Individual: Kamaya; Tonda; Ambia; Mokebo; Waka; Ogwely; Orema
4.	Weather: wet, when raining and dry when not raining (recorded for each data point)
5.	Locomotor mode and submode: 15 modes with 57 subsequent submodes[1]. Modes: Quadrupedal walk, tripedal walk, bipedal walk, vertical climb, vertical descent, torso-orthograde suspension, torso-pronograde suspension, forelimb-hindlimb swing, bridge, leap, drop, sway and ride.
6.	Height (meters): 0-2; 2-5; 5-10; 10-15; 15-20; 20-25; 25-30; >30 (defined as height from ground directly below the focal individual)
7.	Support type: tree trunk; branch; liana; liana/branch (combination of tree branch and liana); branch bundles (clusters of small branches intertwined and used in bunches)
8.	Support diameter: 0-4cm; 4-10cm; 10-20cm; 20-40cm; 40+cm (recorded for each weight bearing limb)
9.	Support orientation: horizontal (0° +/- 20°); angled ~45° (and supports between >20° of horizontal and <20° of vertical); vertical (90° +/- 20°); U-shaped; mixed orientations (for each weight bearing limb)
10.	Number of limbs in contact with supports: 1,2,3 or 4 for each weight bearing component; defined as a limb or body part that is bearing more weight than the limb itself (Hunt et al., 1996)
11.	Number of supports: 1; 2-4; >4 (Thorpe & Crompton, 2005)
12.	Behavioural context: travelling; feeding (actively seeking, accessing, processing and consuming food); other (resting; grooming; grooming other; travelling; affiliative (Pereira & Altmann, 1985); playing; agonistic threaten; agonistic attack (Harcourt, 1979); sexual (Stoinski, Perdue & Legg, 2009); avoid (Pereira & Altmann, 1985); autoplay; chest beat; nest building; vigilant (Kutsukake, 2007); breastfeeding; human watch (where focus is on researchers- often as an intense stare that lasts several seconds))
13.	Hand position: for tensile postures, power grip (all five digits and the entire palm in contact with the support); diagonal power grip (small supports rest diagonally across the fingers and palm); diagonal finger hook grip (the thumb and palm is not used, but instead supports will rest on the phalanges) (Napier,1960). For compressive postures: knuckle; fist; palm; wrist; forearm (Thompson et al., 2018)

[1] Submodes defined in Appendix A.1.

2.3.4 Data analysis

The aim of the statistical analysis was to explore whether there were relationships among locomotor behaviours, height, support use and hand postures, and to ascertain whether these varied based on body size. A methodological data exploration protocol was established to address the complexities in the data set. This approach involved appropriate grouping of variables and descriptive analysis using bivariate standardised cell residuals to examine two-way relationships. Subsequently, statistical techniques were used to expose underlying patterns in the data.

In order to enhance model interpretability and avoid issues of overfitting and zero-inflation (as a consequence of too many combinations of variables), variables were conflated (see Table 2.3). Locomotor behaviours were grouped based on biomechanical similarities, for example the exploitation of specific muscle groups or the loading of specific anatomical structures depending on the orientation and contact of specific limbs and the external forces acting on a body part influencing motion. To test the body size hypotheses, individuals were combined into appropriate body size groups based on body weight estimations. Height was also conflated for statistical analysis into three arboreal categories that represent the different layers in the forest: <10, 10-20 and >20 meters. Although there is variation because of the maturity and species of trees, these categories represented the general layout of the forest. It was found that the canopy typically began to develop at heights of around 10 meters and at heights above 20 meters, the canopy was less dense and sparser; these categories were therefore determined to be ecologically meaningful. For each weight bearing limb, data was collected for the support type, diameter and orientation that it contacted. This resulted in a number of combinations too large to include in a multivariate analysis, so the data was combined. Support diameter was grouped into five categories (Table 2.3): small, medium, large, branch bundles and mixed sizes. Support orientation was grouped into five categories: vertical, angled, horizontal, U-shaped and mixed orientations. Behaviour was split into travelling and feeding, with other behaviours removed because of the small number of observations (n=21). Feeding was defined as actively seeking, accessing and consuming food.

Table 2.3: Description of conflated categories for locomotion, body size, arboreal height and support parameters used within the modelling process.

	Conflated variables	Description
Locomotion	Walking	Quadrupedal walk; Tripedal walk; Bipedal walk
	Vertical climbing	Vertical climb; Vertical descent
	Suspension	Torso-orthograde suspensory; Torso-pronograde suspensory; Forelimb/Hindlimb swing
	Gap crossing	Bridge; Leap; Drop; Sway; Ride
Body size	170kg	Adult male (silverback)
	~70kg	Adult females; blackback
	<40kg	Subadult; juvenile (hereafter known as adolescents)
Height (meters)	< 10	Low
	10-20	Mid-height
	> 20	High
Support diameter	Small	All supports ≤10cm
	Medium	All supports 10-20cm
	Large	All supports >20cm
	Mixed	Mixture of size
	Bundles	All supports are branch bundles
Support orientation	Vertical	Vertical: 90° [+/-20°]
	Angled	Between >20° of horizontal and <20° of vertical
	Horizontal	Horizontal: 0° [+/-20°]
	U-shaped	U-shaped lianas
	Mixed	Combination of different orientations
Behaviour	Travelling	Travelling is the primary behaviour used to move between feeding sites.
	Feeding	Specific movement patterns while actively seeking, accessing, and consuming food.

Figure 2.1: Screen captures of mid-bout locomotion showing differences in locomotor behaviour : a) Ogwely quadrupedal walking, within the conflated locomotion category of walking; b) Tonda hand-assisted flexed bipedal walking, also within the locomotor category walking; c) Ogwely engaging in a bimanual pull-up, within the category vertical climb; d) Kamaya using a forelimb-swing, a torso-orthograde suspensory locomotion, within the locomotion category of suspension.

2.3.5 Statistical analysis

Statistical analysis was conducted in R version 4.3.1. (2023) with the following packages: *lme4* (version 1.1-34, Bates et al., 2014) for fitting Generalised Linear Mixed Models and *AICcmodavg* (version 2.3-2, Mazerolle, 2023) for model selection using AIC. Graphs were produced using the *ggplot2* package (v3.3.3; Wickham & Wickham, 2016).

Observations were transformed into count data to represent the frequency of occurrences. As such, generalized linear modelling (GLM) was chosen to be the most appropriate model for data analysis using the Poisson log link function, the most suitable method for count data. A Poisson distribution ($[g(\mu) = \log(\mu)]$ where $g(\mu)$ is the link function and μ is the mean of the Poisson distribution) was used as response variables in all models (Nelder & Wedderburn, 1972; Zuur et al., 2009). These models provided a suitable framework for examining the occurrences of events, such as combinations of locomotor ecology variables. The rate parameter, or lambda (λ), was used in the models to represent the expected number of events for a given combination of predictor variables.

For the fitted Poisson GLM models, the Akaike's Information Criterion (AIC) was used to identify which model interactions best represented the data (Bozdogan, 1987; Aho et al., 2014; Van Andel et al., 2015). In order to deal with overfitting, the AIC uses the measure of parsimony by adding penalties for additional predictor variables within models of higher complexity, so that models with more variables are not preferred over models with fewer variables (Aho, Derryberry & Peterson, 2014). Backwards stepwise regression was performed on the models using AIC as the selection criteria to determine which variables contributed significantly to the fit of the data. This process eliminated variables that did not increase the fit of the model, leaving only interactions and main effects that played a substantial role in the observed patterns in the data.

To test for potential heterogeneity, several generalised linear mixed models (GLMM) with random effects were performed with individual specified as a random effect to assess whether individual variance should be accounted for in the final models (Zhu &

Zhang, 2006; Bolker et al., 2009). However, there was not a significant improvement in the models' fit to the data when accounting for potential unobserved variability due to individual identity. Any benefit gained from the inclusion of individual variation was offset by model complexity meaning that the GLM's provides a better balance between model fit and complexity. The Poisson regression models provided statistical estimates of the expected counts of particular variables and interactions in order to make comparisons between different groups (Tables 2.6 and 2.7). To avoid problems of multicollinearity, separate models were performed differentiating between variables that display high correlation: this ensured that associations between variables were not influenced by the effects of collinearity, improving the interpretability of results (Dormann et al., 2013).

Diagnostic tests were performed to ensure that the models satisfied assumptions of Poisson GLM analysis. This included systematic examination of linearity, independence, homoscedasticity and zero-inflation. Zero inflation is a common issue in ecological datasets where an excess number of zeros is observed compared with an expected count distribution. This occurs as a result of rare events that are documented in small frequencies which are included in models with other ecological variables that occur in large frequencies. The GLM final models were tested for zero-inflation using the *Performance* package (version 0.10.4, Lüdecke et al., 2021) and the models revealed a maximum ratio of 1.52 (observed zeros: predicted zeros) indicating a suitable amount of observed zeros (Gurmu, 1991; Deng & Paul, 2005).

Post-hoc analysis was conducted to assess the strength of variables within the models using standardised cell residuals (SCRs) of multiway contingency tables. These identified discrepancies between observed and expected values which exceed expectations, revealing underlying correlations within a significant interaction (Beasley & Schumacker, 1995). SCRs of absolute values above 2.0 and below -2.0 contribute to the overall statistical significance (Haberman, 1973). SCRs above 2.0 suggests that an interaction was documented more than predicted whereas below -2.0, the interaction occurred less than predicted by the model. These are discussed alongside the absolute frequencies of observations to assess the relationships between variables.

2.3.6 Limitations

GLM models using AIC as the selection criteria are valuable tools in model selection. However, model selection is not straightforward and there is no universal method for selecting the ‘best’ model (Brewer, Butler & Cooksley, 2016; Burnham & Anderson, 2004). In ecological literature, the most appropriate approach for AIC use within stepwise regression involves an integration of balanced statistical metrics and an understanding of the biological relevance of a model. The aim was to strike a balance between model complexity and capturing underlying patterns in the data. The silverback was a single individual within the largest body size category, so conclusions based on body size should be interpreted with caution.

2.4 Results

Overall, 944 hours of data, and 56,635 instantaneous positional behaviour observations were collected (Table 2.4). Of these, the focal gorilla was visible for 35,951 observations (599 hours). Height only observations (when the focal location was known, but not visible) accounted for 193 hours. The silverback was visible the most, whereas the blackback (Waka) was visible the least. When in the trees, the silverback was the least active (engaged in the least amount of locomotion), whereas the youngest induvial was the most active.

Table 2.4: Total focal time, amount of time spent arboreally and quantity of time observed spent engaging in locomotion for each individual subject.

Individual	Age-sex class	Total focal time (hours)	Total observations (n)	Out of sight (% of total observations)	Height only (n)	Total visible observations (n)[1]	Time spent arboreal (%)[2]	Locomotion (% of total positional behaviour)	Arboreal locomotion (% of all arboreal positional behaviour)[3]	Arboreal locomotor observations (n)
Kamaya	Silverback	118	7094	1109 (15.6)	1252	4733	19.5	16.3	7.7	90
Tonda	Adult female	136	8142	2954 (36.3)	1707	3481	37.6	17.7	9.6	187
Ambia	Adult female	145	8687	3134 (36.1)	1663	3890	35.4	19.3	10.5	206
Mokebo	Adult female	144	8667	3296 (38.0)	1953	3418	26.2	24.1	12.1	170
Waka	Blackback	122	7308	3685 (50.4)	1249	2374	35.4	23.2	11.7	150
Orema	Adolescent	140	8380	3109 (37.1)	1933	3338	37.7	22.3	11.8	235
Ogwely	Adolescent	139	8357	3397 (40.6)	1846	3114	40.9	27.0	14.8	300
Total		944	56635	20684 (36.5)	11603	24348	32.8	20.9	11.3	1338

[1] Whilst height-only observations represent occasions where the height of the gorilla was known, but the focal was completely out of sight, 'visible' observations account for when the gorilla was visible in some way (either their whole body, or body part).

[2] Time spent arboreal accounts for all observations, including locomotion, posture and height-only.

[3] Arboreal locomotion denotes how much time each individual gorilla engaged in locomotion when off the ground (when they were visible). For example, when off the ground, the youngest gorilla, Ogwely, moved the most.

Overall, arboreal locomotion of the gorillas was dominated by walking (42%). Of these walking behaviours, quadrupedal walking was used the most, accounting for 67%, and bipedalism made up 31% (Table 2.5). Vertical climbing accounted for 35% of all arboreal locomotion. Suspension, which was almost exclusively torso-orthograde, occurred in slightly higher frequencies than gap-crossing (13% vs 10% respectively). Twenty percent of all gap-crossing behaviours were oscillatory, which included 'ride' and 'tree-sway'.

Table 2.5: Percentage of arboreal locomotor modes for all individuals and each age-sex category.

Locomotor mode	**All individuals**	Silverback	Females + Blackback	Adolescents
Quadrupedal walk	**28.1**	20.0	31.7	24.7
Tripedal walk	**0.7**	0.0	1.1	0.2
Bipedal walk	**13.4**	14.4	13.0	13.6
Vertical climb	**15.7**	18.9	15.0	16.1
Vertical descent	**19.4**	26.7	20.5	16.8
Torso- orthograde suspension	**12.2**	7.8	11.1	14.4
Torso- pronograde suspension	**0.6**	1.1	0.1	1.1
Forelimb- hindlimb swing	**0.1**	0.0	0	0.4
Bridge	**3.1**	0.0	2.8	3.9
Leap	**1.7**	2.2	0.7	3.0
Drop	**3.1**	5.6	2.2	3.9
Sway	**0.2**	0.0	0.4	0.0
Ride	**1.6**	3.3	1.3	1.9
Number of arboreal locomotor observations =	*1338*	*90*	*713*	*535*

2.4.1 Arboreal locomotion

The initial model that examined the interaction between locomotion, height, behaviour and body size tested whether there were any significant relationships between the locomotor behaviours, contextual behaviours and heights used by the gorillas, and whether these varied between body size groups. The modelling process removed all three-way interactions but retained all possible two-way interactions.

Table 2.6: Poisson GLM model results for the interaction between locomotion, body size, height and behaviour.

Model	Model variables	Retained interactions[1]	Deviance (*df*)	*p*- value	Residual deviance (*df*)[2]
1	Locomotion	Locomotion: body size	23.86(6)	<.001	67.71
	Body size	Locomotion: height	28.74(6)	<.001	(68)
	Height	Locomotion: behaviour	83.90(4)	<.001	
	Behaviour	Body size: height	19.32(4)	<.001	
		Body size: behaviour	26.20(4)	.016	
		Height: behaviour	35.33(4)	.042	

[1] All main effects retained in the model.

[2] Residual deviance and *df* for final model.

Overall, the gorillas moved in the trees at heights of less than 10 meters 58% of the time. They used these lower heights 1.5 times more than heights between 10-20 meters and almost 6 times more than heights above 20 meters. Locomotion below 20 meters was dominated by walking and vertical climbing (Table 2.7). SCRs for the relationship between locomotion and height revealed that the gorillas walked at heights above 20 meters more than predicted by the model (SCR=3.5) but used vertical climbing at these heights less than the expected amount (SCR=-3.1). The gorillas engaged in suspension 14% of the time and gap-crossing 8% of the time. Both suspension and gap-crossing was observed the most at heights less than 10 meters.

When moving in the trees, the gorillas travelled 5 times more than they engaged in feeding (actively searching and acquiring food). When feeding, the gorillas walked t 72% of the time, in frequencies much more than predicted by the model (SCR=6.1), whereas vertical climbing and suspension when feeding was observed in much lower frequencies than predicted (SCR=-4.5) (Table 2.7). When travelling, walking and vertical climbing each accounted for 38-40% of locomotion, but whilst walking occurred less than expected (SCR=-2.7), vertical climbing was used in frequencies more than expected (SCR=2).

TABLE 2.7: Contingency table for the interactions between locomotion and height, and locomotion and behaviour. Figures represent the row % and (column %) for each interaction. E.g., the gorillas engaged in walking 41.1% of the time when moving at heights of less than 10 meters, but when walking, 54.3% of the time there were observed at heights of less than 10 meters. White cells signify that the SCR of the interaction was within the predicted range by the model. Coloured cells indicate whether the interaction fell below or above the predicted range (see key).

		Locomotion				
		Walking	Vertical climbing	Suspension	Gap-crossing	Total
Height (meters)	<10	41.1(54.3)	🟦 39.3(62.3)	13.0(56.1)	6.6(55.1)	57.5
	10-20	42.0(32.6)	35.6(33.2)	14.6(37.0)	7.8(38.2)	33.8
	>20	🟦 65.5(13.1)	🟧 18.6(4.5)	10.6(6.9)	5.3(6.7)	8.7
	Total	43.5	36.3	13.3	6.9	100
Behaviour	Travelling	🟧 37.9(73.1)	🟦 40.0(92.3)	14.4(90.4)	7.6(92.0)	83.7
	Feeding	🟦 71.6(26.9)	🟧 17.2(7.7)	🟧 7.8(9.4)	3.4(8.0)	16.3
	Total	43.4	36.3	13.3	7.0	100

🟦 SCR= **> +2**
🟧 SCR= **< -2**

As height increased, so did the amount of time that the gorillas spent feeding, but frequencies did not deviate from predictions based on SCRs. The gorillas used locomotion during feeding 12% of the time below 10 meters, 19% of the time at heights 10-20 meters, but 35% of the time above 20 meters. The modelling process removed the interaction between height, behaviour and locomotion; this suggests that the locomotor behaviours used at different heights were not dependent upon whether the gorillas were travelling or feeding.

2.4.2 Body size

The large degree of sexual dimorphism was reflected in the variation of frequency of locomotor behaviours, contextual behaviours and heights used by different body size gorillas. The silverback engaged mostly in vertical climbing (accounting for 46% of his locomotion), whereas the females and blackback used walking the most (also accounting for 46% of their locomotion), but only the female and blackback results was more than expected (SCR=2.3) (Figure 2.2). The adolescents used walking and vertical climbing in similar relative proportions to the adult females and blackback, but with slightly lower frequencies. They did, however, engage in suspension and gap-crossing more than the larger body size categories, in frequencies higher than predicted (SCR=2.4 and 2.8 respectively). Whilst the silverback exhibited a slightly higher propensity to engage in gap-crossing than the females and blackback, the females and blackback used suspension more than the silverback.

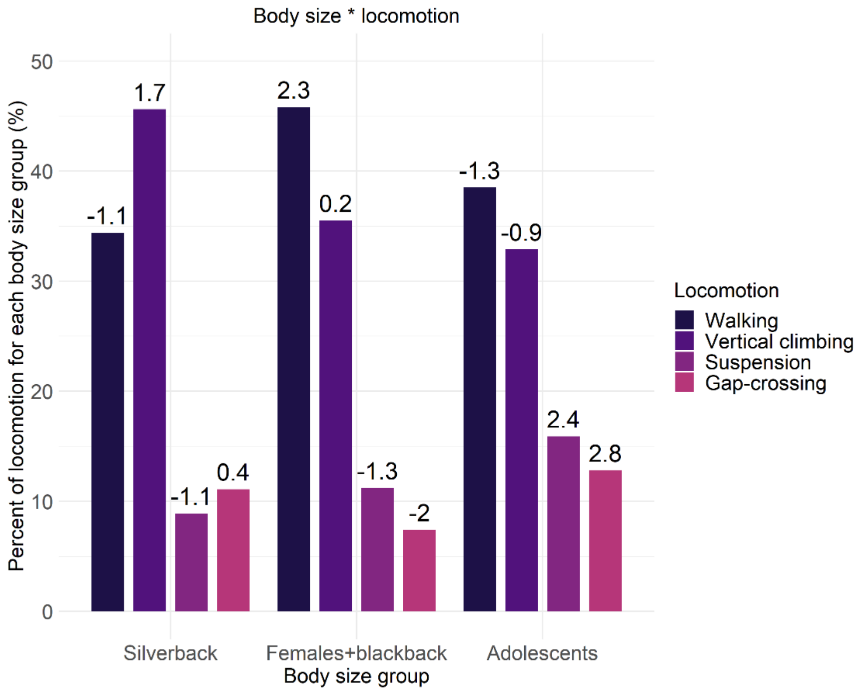

Figure 2.2: Model interaction between body size and locomotion, showing the locomotor behaviours used by each body size group. Values above the bars represent the SCRs.

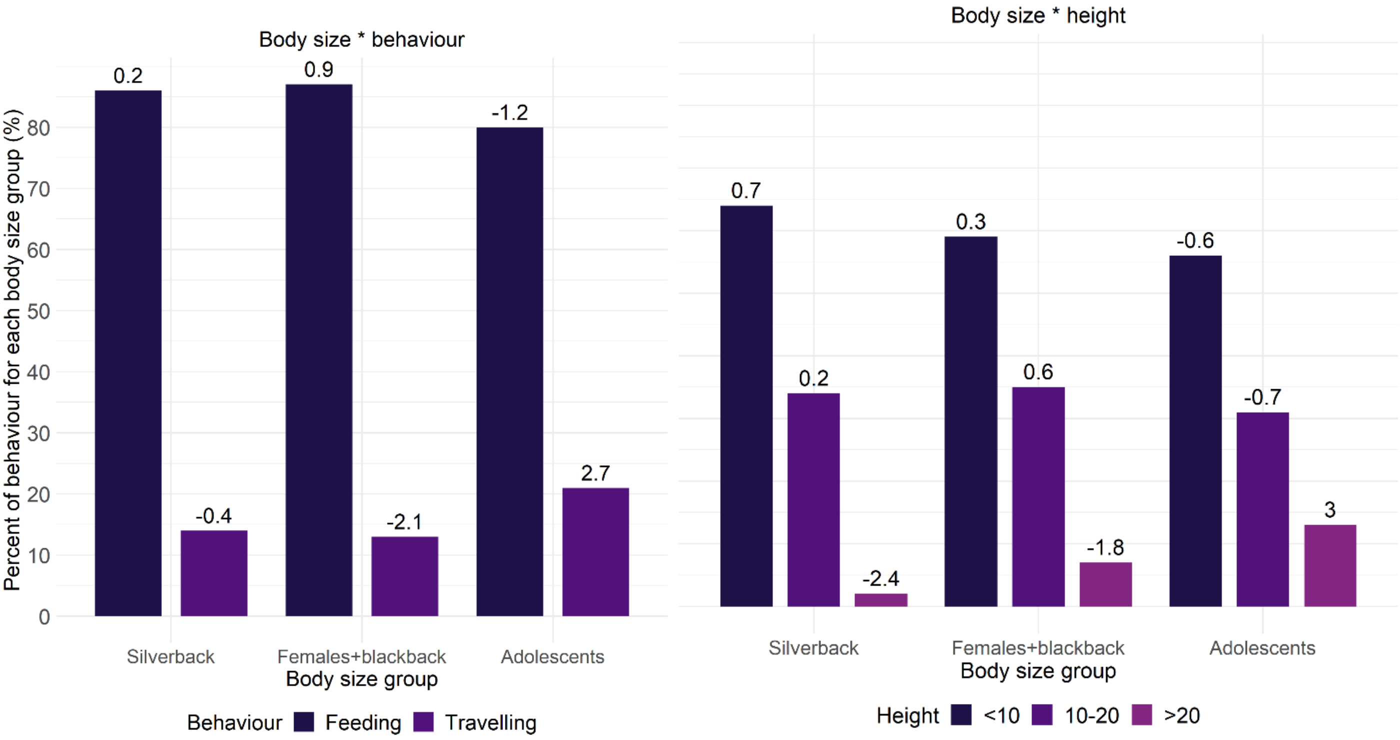

Figure 2.3: Model interactions showing the contextual behaviours and heights used by each body size group. Values above the bars represent the SCRs.

Gorillas of all body size categories spent the most amount of time locomoting below 10 meters (56-63%), followed by mid-heights (31-34%), all within the predicted SCR range. The silverback spent the least amount of time moving at heights above 20 meters, accounting for only 2%, which was a frequency much smaller than predicted by the model (SCR=-2.4). The females spent more time at this height (7%) and in frequencies as expected, but the adolescents used these heights much more than predicted (13%, SCR=3.0).

The silverback, females and blackback moved in the trees whilst feeding 13-14% of the time, but whilst this fell within the predicted range for the silverback (SCR=-0.4), it was much less than predicted for the females and blackback (SCR=-2.1) (Figure 2.3). The adolescents used locomotion while feeding 20% of the time, more than expected (SCR=2.7). Travelling for all body size groups did not deviate from the expected range based on SCRs.

2.4.3 Arboreal support use

Statistical Model 2 in Table 2.8 tested whether the supports that the gorillas used differed according to locomotor behaviour and if larger individuals compensated for their size by using different supports to smaller individuals. Locomotor behaviour was significantly associated with variation in support type, support diameter and support orientation. The removal of all interactions between body size and other variables except for diameter indicates that body size was accompanied by variation in the size of supports used, but not the type of supports, support orientation or the number of supports used.

Table 2.8: Poisson GLM model results for the interactions between locomotion and body size with support properties (Model 2), number of supports (Model 3) and hand posture (Model 4).

Model	Model variables	Retained interactions[1]	Removed interactions[2]	Deviance (*df*)	*p*-value	Residual deviance (*df*)[3]
2	Locomotion	Body size: diameter		22.28(8)	<.001	318.1
	Body size	Locomotion: diameter		157.87(12)	<.001	(644)
	Diameter[4]	Locomotion: support type		83.55(6)	<.001	
	Orientation[4]	Locomotion: orientation		774.78(9)	<.001	
	Support type	Diameter: support type		128.4(8)	<.001	
		Diameter: orientation		202.8(12)	<.001	
		Orientation: support type		62.68(6)	<.001	
			Body size: locomotion	16.99(6)	.01	
			Body size: orientation	8.43(6)	.21	
			Body size: support type	1.66(4)	.79	
3	Body size	Body size: locomotion		16.99(6)	<.001	83.52
	No. of supports	Body size: height		9.60(4)	.048	(72)
	Locomotion	Locomotion: height		26.51(6)	<.001	
	Height	No. supports: locomotion		59.79(6)	<.001	
		No. supports: height		11.84(4)	.019	
			No. supports: body size	3.25(4)	.516	
4	Body size	Body size: diameter		15.87(8)	.04	140.37
	Locomotion	Locomotion: diameter		143.75(12)	<.001	(324)
	Diameter	Locomotion: hand posture		538.31(18)	<.001	
	Hand posture	Diameter: hand posture		575.15(24)	<.001	
			Body size: hand posture	23.66(12)	.02	
			Body size: locomotion	11.39(6)	.07	

[1] All main effects retained for all models.

[2] Three-way interactions were included, but subsequently removed from all models.

[3] Residual deviance and *df* for final model.

[4] Diameter and orientation refer to support diameter and support orientation.

When moving arboreally, the gorillas used small supports (<10cm) more than one third of the time (Table 2.9). Large supports (>20cm) were the second most frequently used support size accounting for 27% and medium supports (10-20cm) were used 21% of the time. When walking, the gorillas used all support sizes in frequencies as expected, with a slight preference for small supports than larger supports. When engaging in vertical climbing, large supports were used much more than expected (SCR=4), but small supports were used much less than predicted (SCR=-3.5). Suspension and gap-crossing saw a very large preference towards small supports, accounting for more than 60% for each locomotor behaviour, and in frequencies much more than expected

(SCR=4.6 and 4.1). Conversely, for both suspension and gap-crossing, large supports were used less than 8% of the time, much less than expected (SCR=-4.7 and -3.8).

Table 2.9: Contingency table for the interaction between locomotion, and support size. Figures represent the row % and (column %) for each interaction. White cells signify that the SCR of the interaction was within the predicted range by the model. Coloured cells indicate whether the interaction fell below or above the predicted range (see key).

	Support diameter				
Locomotion	Small	Medium	Large	Mixed	Total
Walking	34.5(35.9)	20.7(37.3)	27.9(39.3)	16.9(45.2)	38.5
Vertical climbing	🟧 26.1(29.3)	24.8(48.3)	🟦 37.9(57.6)	11.3(32.6)	41.6
Suspension	🟦 65.6(18.1)	15.6(7.5)	🟧 2.1(0.8)	16.7(11.9)	10.2
Gap-crossing	🟦 63.0(16.7)	15.2(7.0)	🟧 6.5(2.3)	15.2(10.4)	9.8
Total	37.0	21.4	27.3	14.3	100

🟦 SCR= **> +2**
🟧 SCR= **< -2**

Body size was significantly associated with the support diameter variable, suggesting that the variation in size between the silverback, females and adolescents is linked to differences in the size of supports used, but not orientation, number of supports or hand position. Figure 2.4 illustrates the percentiles and SCRs for the interaction between body size and support diameter. The silverback used small supports the least, but large supports the most, whereas the adolescents used small supports the most and large supports the least. The silverback, females and blackback used supports of all sizes in frequencies as expected. Conversely, the adolescents used small supports more than expected (SCR=2.3), accounting for more than 40% of all supports, but used large supports less than expected (SCR=-2.1).

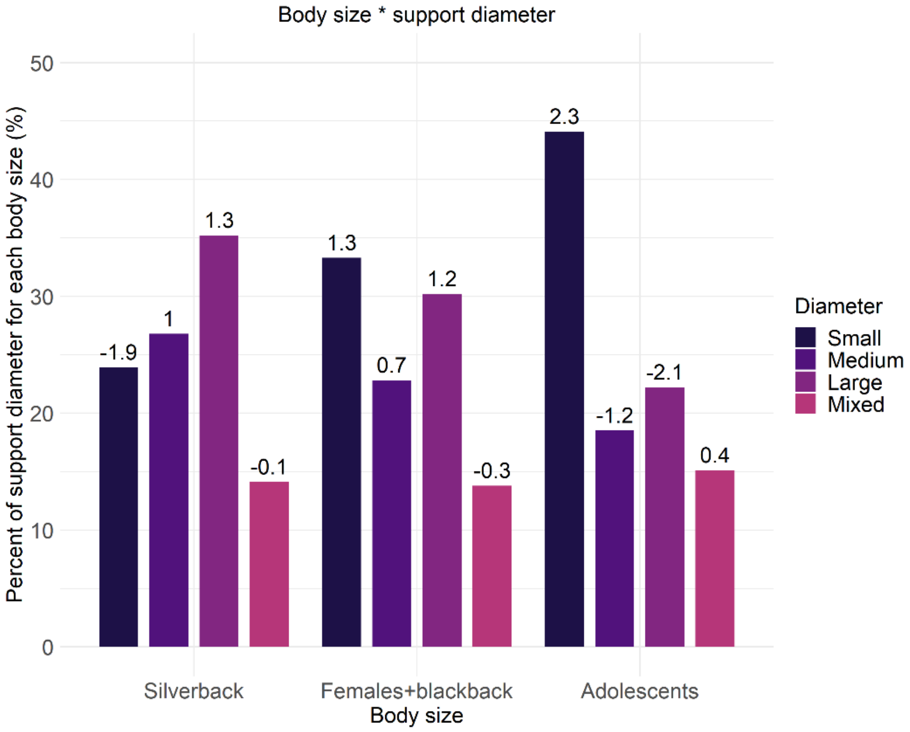

Figure 2.4: Model interaction between body size category and support diameter.

The gorillas used tree branches 78% of the time when moving arboreally, 3.5 times more than any other support type. Branch bundles were the second most frequently used support type, accounting for 9%, followed by lianas which were used 7% of the time (Table 2.10). Tree trunks were the least frequent support type, accounting for only 1.6% of all supports. When walking, the gorillas used branch bundles more than expected (SCR=2.1), but lianas much less than expected (SCR=-4.2). Conversely, when engaging in vertical climbing, branch bundles were only used 4.5% of the time, much less than predicted (SCR=-4.6), but lianas were used more (SCR=5.6). When engaging in suspension, the gorillas used all support types within the expected range with the exception of liana/branch combinations, which accounted for 12% of all suspension (SCR=4.5). The gorillas crossed gaps on all support types except for tree trunks, but all support types fell within the expected frequencies for this locomotor behaviour.

Table 2.10: Contingency table for the interaction between locomotion and support type. Figures represent the row % and (column %) for each interaction. White cells signify that the SCR of the interaction was within the predicted range by the model. Coloured cells indicate whether the interaction fell below or above the predicted range (see key).

	Support type					
Locomotion	Liana	Liana/ branch	Branch	Trunk	Bundles	Total
Walking	🟧 2.7(15.8)	3.2(30.0)	80.9(43.8)	1.6(42.9)	🟦 11.7(55.0)	42.2
Vertical climbing	🟦 14.3(70.5)	3.0(23.3)	75.7(34.2)	🟦 2.6(57.1)	🟧 4.5(17.5)	35.1
Suspension	4.0(7.4)	🟦 12.1(35.0)	71.1(11.8)	🟧 0	12.7(18.3)	12.9
Gap-crossing	4.6(6.3)	5.3(11.7)	81.7(10.3)	0	8.4(9.2)	9.8
Total	7.1	4.5	77.9	1.6	9.0	100

🟦 SCR= **> +2**
🟧 SCR= **< -2**

Table 2.11 shows the percentages and SCRs for the interaction between locomotion and support orientation. When walking, the gorillas predominantly used horizontal supports, in frequencies higher than expected (SCR=10), but vertical supports much less than expected (SCR=12). They also used multiple supports of mixed orientations more than expected (SCR=2.9). Vertical climbing was not restricted to vertical supports, but they were used considerably more than all other orientations (SCR=13.6). Unlike walking and vertical climbing, suspensory locomotion and gap-crossing saw a more varied use of different support orientations. The gorillas used suspension to travel in approximately equal amounts on horizontal, angled and vertical supports, but U-shaped lianas (U-shape supports were exclusively lianas) were used much more than expected (SCR=4.6), along with angled supports (SCR=3.7). When gap-crossing, the gorillas used mostly vertical supports, but all supports were used in frequencies as predicted.

Table 2.11: Contingency table for interaction between locomotion and support orientation. Figures represent the row % and (column %) for each interaction. White cells signify that the SCR of the interaction was within the predicted range by the model. Coloured cells indicate whether the interaction fell below or above the predicted range (see key).

	Support Orientation					
Locomotion	Horizontal	Angled	Vertical	U-shaped	Mixed	Total
Walking	55.8(75.6)	16.1(51.1)	1.4(1.5)	1.9(27.6)	24.8(52.9)	39.2
Vertical climbing	4.7(6.0)	5.2(15.6)	77.6(79.5)	1.9(10.3)	11.7(24.1)	37.4
Suspension	23.9(10.4)	21.7(22.2)	26.8(9.5)	9.4(44.8)	18.1(13.4)	13.2
Gap-crossing	25.0(7.9)	15.0(11.1)	37.0(9.5)	5.0(17.2)	18.0(9.6)	9.5
Total	29.5	12.6	36.5	2.7	18.8	100

🟦 SCR= **> +2**
🟧 SCR= **< -2**

2.4.4 Number of supports

Model 3 tested whether the gorillas of different body size groups used more supports when engaging in different locomotor behaviours or at different heights (Table 2.8). Body size was not associated with number of supports but instead the gorillas used different amounts of supports when moving in different locomotor behaviours and at different heights. Overall, the gorillas used a single support more than multiple supports, accounting for 66% of observations (Table 2.12). Single supports were used much less than predicted when the gorillas were walking (SCR=-2.). However, when climbing vertically, the gorillas used a single support more than predicted (SCR=3.0), but more than one support less than predicted (SCR=-2.7 and -3.8). When using suspension, the gorillas used >4 supports more than predicted (SCR=3.7), however, when crossing gaps, the number of supports used did not deviate from expected frequencies.

Single and 2-4 supports were used by the gorillas at all heights within the expected frequencies predicted by the models. However, at lower heights, the gorillas used >4 supports less than predicted by the model (SCR=-2.4) and at mid-heights and high heights, they used >4 supports more than predicted (SCR=2.1 and 3.6). The interaction between number of supports, locomotion and height was removed from the modelling process, which suggests that height did not influence the number of supports used for each locomotor behaviour.

Table 2.12: Contingency table for the interactions between number of supports with locomotion and height. Figures represent the row % and (column %) for each interaction. White cells signify that the SCR of the interaction was within the predicted range by the model. Coloured cells indicate whether the interaction fell below or above the predicted range (see key).

		No. of supports			
		1	2-4	>4	Total
Locomotion	Walking	🟧 58.2(35.6)	🟦 31.3(50.0)	10.4(51.2)	40.5
	Vertical climbing	🟦 78.6(47.9)	🟧 18.7(29.8)	🟧 2.7(13.4)	40.5
	Suspension	62.1(10.9)	19.8(9.1)	🟦 18.1(25.6)	11.7
	Gap-crossing	50.7(5.6)	38.4(11.1)	11.0(9.8)	7.4
	Total	66.3	25.4	8.3	100
Height (meters)	<10	68.0(64.3)	25.7(63.3)	🟧 6.4(42.4)	62.0
	10-20	63.4(30.3)	24.3(30.2)	🟦 12.3(41.3)	31.3
	>20	53.0(5.4)	24.2(6.5)	🟦 22.7(16.3)	6.7
	Total	65.6	25.1	9.3	100

🟦 SCR= **> +2**
🟧 SCR= **< -2**

2.4.5 Hand posture and grip

Model 4 tested whether the gorillas altered their hand posture for specific locomotor behaviours and whether hand posture varied for different body size groups (Table 2.13). Hand posture was not associated with body size, but instead, was associated with locomotion and support diameter. During tensile locomotor behaviours, on small supports, the gorillas used a diagonal power grip considerably more than expected (SCR=7.8), but power grips much less (SCR=-11.2). Similarly on branch bundles, the gorillas used diagonal power grips more than predicted (SCR=4.5). When using medium and large supports, power grips were used much more than expected (SCR=2.5 and 13.2).

When the gorillas engaged in compressive, above-branch locomotion, they contacted supports using knuckle-down, fist-down and palm-down postures. As support diameter increased, the frequency of knuckle and fist use increased. On small supports, the gorillas used knuckles less than expected (SCR=-2.5), but palms much more (SCR=2.4). Hand posture deviated the least on medium supports and exhibited the least amount of variation. On large supports, the gorillas used palms less than expected (SCR=-4.2) but knuckles more than expected (SCR=5), accounting for more than 60% of locomotion on large supports. When moving on branch bundles, the gorillas used knuckle postures much less (SCR=-2.5), but palm contact much more than predicted (SCR=2.1).

Table 2.13: Contingency table for the interaction between support size and hand posture split by tensile and compressive locomotion. Figures represent the row % and (column %) for each interaction. White cells signify that the SCR of the interaction was within the predicted range by the model. Coloured cells indicate whether the interaction fell below or above the predicted range (see key).

		Support size				
	Hand posture	Small	Medium	Large	Bundles	Total
Tensile locomotion	Diagonal power grip	64.3(93.8)	18.5(55.4)	0.6(1.4)	16.6(97.2)	60.6
	Diagonal finger grip	86.7(3.0)	0	0	13.3(1.8)	1.4
	Power grip	3.5(3.2)	23.7(44.6)	72.6(98.6)	0.2(0.9)	38.0
	Total	41.5	20.2	28.0	10.3	100
Compressive locomotion	Knuckle	21.4(18.4)	33.3(23.3)	44.0(40.7)	1.2(4.2)	25.2
	Fist	15.6(5.1)	34.4(9.2)	46.9(16.5)	3.1(4.2)	9.6
	Palm	34.6(76.5)	37.3(67.5)	18.0(42.9)	10.1(91.7)	65.2
	Total	29.4	36.0	27.3	7.2	100

🟦 SCR= **> +2**
🟧 SCR= **< -2**

2.5 Discussion

Gorillas are the largest apes that exploit arboreal environments to access nutritional resources. However, they also possess postcranial adaptations towards terrestrial quadrupedalism (as outlined in Chapter One), which have been shaped by natural selection to better suit the biomechanical demands of travelling on the ground in their local environments (Tuttle, 1967; Larson & Stern, 1987; Gebo, 1996). It was not previously understood how, given their size and morphology, they address the ecological challenges of accessing, moving around and dealing with discontinuity in the canopy.

This study has revealed that despite the complexities of the arboreal environment and their large size, gorillas are able to effectively negotiate arboreal habitats by employing strategies to mitigate risks and achieve the goal of travelling and feeding safely in the trees. The results indicate that locomotion, height, behavioural context and body size interact to shape the arboreal locomotor repertoire of wild western lowland gorillas. Whilst support properties, or the number of supports used when moving arboreally was associated with locomotor behaviour, the only support property associated with body size was the variation in use of different diameter supports. Despite the very large variation in size between the silverback, adult females and adolescents, they did not vary in the number of supports, type of supports or orientation of supports they used. The different body size groups also did not vary in the hand postures used when moving arboreally; instead, hand posture was associated with locomotor behaviour, and the size of supports used.

2.5.1 How does body size affect the gorillas' ability to access the forest canopy?

One of the biggest biomechanical challenges for gorillas is how they transition from the ground to the canopy, and how they move between different levels in the canopy. Body size appears to have impacted the gorilla's access to arboreal resources, since the silverback in this study spent far less time arboreally than the other age-sex categories (19.5% vs 26.2-40.9%). Hunt (1992) observed chimpanzees preferentially entering trees by walking on angled supports until the support became too steep and thenmoving onto vertical supports. The gorillas spent 58% of their time at less than 10 meters, but locomotion in this height bracket was dominated by both walking and vertical climbing. . Overall, the silverback exhibited greater levels of vertical climbing than walking, whereas the females and blackback showed the opposite pattern, which may indicate that the females and blackback were small enough to access the canopy in a similar way to chimpanzees, but the silverback had to climb. At low heights, the understorey is characterised by large tree trunks, young trees and descending lianas which offer numerous natural vertical pathways into the canopy (Cant, 1992).

Chimpanzees showed a preference for small supports and tended to only climb on large supports when smaller supports were not available (Hunt, 1992). Gorillas are more than twice the weight of chimpanzees, so small supports may represent a bigger challenge. In this study , when ascending at lower heights, the gorillas mostly used large supports (38%), although they also used small and medium sized supports relatively often (25-26%). This somewhat supports the classic prediction that larger primate species will engage in the same locomotor behaviour as smaller species but on a larger support (Cartmill & Milton, 1977). Large supports are more stable than smaller supports during vertical climbing, as they will sway less under the weight and movement of the animal (Isler, 2002). However, when using small and medium sized supports to climb to the canopy, gorillas can use ‘flexed-elbow’ vertical climbing and use more stable hand positions compared to climbing on large tree trunks, where they use ‘extended-elbow’ climbing and the hands cannot grasp the support well. This suggests that the gorillas were adaptable in their approach to moving between different heights to achieve the end goral of reaching food sources in the trees.

Surprisingly, the high degree of sexual dimorphism in gorillas was not reflected in the strategies used to move between different heights in the trees in this study. All age-sex classes engaged in vertical climbing on the same type and number of supports. It might have been expected that the silverback would mitigate the risk of snapping a support or falling by using multiple supports, similar to the way in which orangutans use bundles of small supports (Thorpe & Crompton, 2005). Orangutans are able to mitigate this risk by grasping multiple supports with their limbs in different directions, but the gorillas have shorter fingers (Tuttle, 1969) which means they can hold fewer branches.as well as a larger body mass, which likely precludes multiple support use as a safety mechanism and more weight to be constantly negotiating between different supports. The gorillas of all body sizes used compliant lianas in similar frequencies to each other. Compliant lianas are a crucial support type for orangutans, particularly for vertical climbing (Cant, 1987; Thorpe & Crompton, 2005) because even thin lianas are extremely strong when force is applied along their line of action. Although they are much more abundant in the Bornean and Sumatran forests (Manduell et al, Harrison & Thorpe, 2012), they are also found in the lowland forests of central Africa. Western lowland gorillas have rarely been documented to use lianas; Remis documented the gorillas in the Central African Republic to use lianas only 1% of the time (Remis,1995).

However, the gorillas in this study used lianas 14% of the time when vertical climbing (and 7% overall) which suggests that they may be an important mechanism for offsetting the impact of large size when changing height in the forest canopy.

The only difference identified by the models in the strategies used to access and move between different heights in the canopy by gorillas of different body size was in the size of supports used during vertical descent. The silverback used large supports for descent more than smaller individuals, who descended on small supports. Cant (1992) proposed that negotiating larger vertical supports is one of the biggest challenges in arboreal environments, but for the silverback gorilla, descending a large support was less metabolically expensive than descending a small support since his longer limbs, larger hands and greater upper body strength allowed him to make use of ‘fire-pole’ slide and ‘bear-hugging’ motions compared to smaller individuals(Tuttle, 1969, Fannin et al., 2023). Descending on small supports, however, is metabolically more expensive for the silverback, as the forelimbs have to support his whole weight whilst the hindlimbs simultaneously contacted the support which was likely displacing underneath to break the fall (Isler, 2002; Neufuss et al., 2017). If the silverback gorilla spends less time moving away from tree cores (Remis, 1995), then he may always be close to a large support to descend.

Overall, vertical climbing is energetically costly and large primates will experience higher metabolic costs because of the mechanical work and muscular effort in opposing gravity relative to their size (Fleagle, 1980; Pontzer & Wrangham, 2004; Isler, 2005; Hanna & Schmitt, 2011; Hanna et al., 2017). However, this is not always reflected in intraspecific body size differences in the frequency of vertical climbing in the great apes

(Doran, 1996). Whilst male and female chimpanzees have been documented to engage in similar amounts of vertical climbing, male bonobos climbed vertically more than females (Doran & Hunt, 1994; Doran, 1996), male western lowland gorillas vertical climbed more than females (Remis, 1995), female mountain gorillas climbed more than males(Doran, 1996) and female orangutans only marginally climbed less than males (Thorpe & Crompton, 2005). Gorillas have to access arboreal resources, but because they are highly dimorphic, it would be expected that there would be a difference in the techniques used to move between different heights. However, the difference was contrary to predictions, but in line with previous studies (Remis, 1995), as the silverback engaged in vertical climbing more than any other locomotor behaviour (45% of his arboreal repertoire), and overall, more frequently than smaller age-sex classes (32-35%). There are several possible reasons for this. Remis (1995) documented that the silverback remained close to the tree core, whereas smaller gorillas ventured further into the periphery of the tree crown. This might be because his size has constrained the ability to travel horizontally, or that he is more selective in the supports used when in the canopy compared to the females, blackback and adolescents who are less restricted in the size and type of supports: this might mean that he has to access resources by travelling vertically on stable supports which is why he engages in this behaviour so often. It might also reflect social structure. Hunt (1994) noted that body size differences between chimpanzees might be confused for social rank, and that it would be difficult to determine which of these factors drives the variation in a behaviour (Ghiglieri, 1985). The dominant silverback gorilla might travel between different heights and in doing so, this chases the females and adolescents out into the peripheries (as observed in this study and by Remis, 1995) (Maryanski-Turner, 1986).

2.5.2 How does body size affect how gorillas move around the canopy?

The primary challenge of horizontal travel is addressing small branches which taper towards the periphery of tree crowns (Chatani, 2003). In order to access resources, primates require the ability to move away from the tree core, where supports are larger and more abundant, into the periphery where supports are narrow, sparse and unpredictable (Napier, 1967; Cant, 1992). Whilst smaller primates can travel horizontally through the canopy by leaping between, or running on top of supports (Ripley, 1967; Schmitt et al., 2006), large primates have to be more cautious. The two main locomotor strategies used by great apes to move around the canopy are walking and suspension (Hunt, 1992; Remis, 1995; Thorpe & Crompton, 2005). Suspension is considered to be less risky than walking on top of small supports (which are abundant in tree canopies) because the individual's weight is already loading the support. Therefore it was expected that the gorillas would rely strongly on suspension when travelling on small supports, and that the silverback would engage in suspension more than smaller individuals (Cartmill & Milton 1977). However, the silverback, females and blackback only engaged in suspension 20% of the time, whereas the adolescents used suspension 30% of the time; the rest of the time was spent walking.

Gorillas possess more adaptations towards walking than they do for suspension (Schultz, 1963; Gebo, 1992). These adaptations are perhaps transferable in arboreal environments when quadrupedal walking on large horizontal supports (which are somewhat similar to the conditions on the ground), allowing the gorillas to use knuckle and fist-walking hand postures like they do terrestrially (Thompson et al., 2018). However, when walking on small supports, the gorillas walked quadrupedally only half the time, and the other half, they adopted hand-assisted bipedal walking postures.

During orthograde walking, the centre of mass is higher which increases the energy expenditure (Isler et al., 2006; Pontzer, Raichlen & Rodman, 2014), but holding supports with the hands increases stability. This strategy is also used by orangutans (Thorpe & Crompton, 2005) and humans (Johannsen et al., 2017) when walking on flexible supports. When quadrupedal walking on small supports, the gorillas adopted strategies similar to patterns observed for chimpanzees (Hunt, 1991). As support diameter decreased, the gorillas (and chimpanzees) switched from knuckle-walking to palm-walking. Using a palm grip, rather than knuckle, allows the thumb to grip onto the other side of the support, so if it begins to oscillate or rotate, the gorillas can adjust their stability, to create ‘frictional resistance’ to avoid toppling to the side (Preuschoft, 2002:184). This is a strategy seen in many other primates as a single small support is accompanied by the risk of slipping, or rotating off (Preuschoft, 2002). Previous studies that have examined the biomechanics of arboreal quadrupedal walking have noted that the African apes demonstrate considerably flexibility in their walking locomotion by adopting flexed-knee and flexed-elbow postures and longer contact times on branches to prevent a support from swaying (Larson et al., 2001; Pontzer et al., 2014; Finestone et al., 2018; Granatosky et al., 2019; Tarrega-Saunders et al., 2021). However, little was known about the hand postures used in wild environments during quadrupedal walking. This presents new evidence to suggest that altering gait parameters and joint angles to stabilise flexible-branch walking is also considerably aided by robust hand grips.

The hand morphology of gorillas has been selected for to facilitate efficient terrestrial knuckle-walking (Tuttle, 1967; Zihlman, Mcfarland & Underwood, 2011; Matarazzo, 2013**)**. However, although the gorillas’ manual adaptations for terrestrial walking may have compromised their adaptations to suspension (Bardo et al., 2017), their hand morphology does have clear benefits for arboreal locomotion. Gorillas did not lose complete mobility in the wrist joint, nor did they lose carpal and phalangeal curvature or their large flexor sheath ridges which allow for more robust flexor muscles to assist in gripping supports (Susman, 1979; Sarmiento, 1988). These morphologies allow them to robustly grasp small supports when climbing vertically and when engaging in above-head suspensory locomotion. However, the models revealed that suspensory locomotion was very strongly associated with the use of small supports (66% of supports used). Gorillas possess the highest thumb-forefinger index (Schultz 1930) which means that they are capable of opposing their thumbs, but their relatively short digits compared to the orangutans (which have the lowest thumb-forefinger index) mean that they are restricted in the size of supports they can suspend from. In fact, the gorillas used small supports when engaging in suspension twice as often as the orangutans documented by Thorpe and Crompton (2005).

The silverback engaged in horizontal travel the least out of the gorillas (43% versus 57% for the females, blackback and adolescents), which suggests that he may have been restricted in his capacity to move in the periphery of trees because of his much larger size relative to the supports available. The adolescents, who were much smaller in size, fed the most out of the age-sex classes when locomoting arboreally, probably because they could be less cautious in their access to, and movement around the periphery of tree crowns (however, it should be noted that locomotor behaviours do not capture most feeding events which occurred mostly using stationary postures). The silverback fed the least when locomoting. Instead, he would often arrive at a feeding site and remain stationary, while using his longer arms and increased strength to reach branches nearby and pull them towards him (Remis, 1999). Remis (1999) also observed that that when fruiting trees had low abundance, the silverback opted to remain on the ground rather than access and travel around in the canopy to acquire resources which may not yield much nutritional benefit. One of the key aspects of the optimal foraging theory is that primates will forage for food sources which offer the highest energy return relative to both the risk and the effort and calories expended in accessing and obtaining food (Martin, 1983; Schoener, 1987; Garber, 1987). Although arboreal resources such as fruits and leaves are rich in nutrients (Williamson et al., 1990; Remis, 1997; Remis et al., 2001; Masi, Cipolletta & Robbins, 2009), the risks involved and energetic costs of moving on small supports is perhaps not always outweighed by the calorie intake of resources when in the canopy for the large-bodied silverback gorilla. This might be why the silverback spent the most amount of time on the ground and travelled horizontally to feed less than smaller gorillas. Furthermore, although adult male gorillas have a high nutritional requirement, females (relative to body size) experience a higher nutritional requirement because of reproduction, as gestation, lactation and travelling with dependant infants is metabolically costly (Nowell & Fletcher, 2008) and adolescents require a high intake of calories to support the physiological demands during growth. Therefore, they must meet these demands by effectively foraging and feeding on high-calorific food in the tree canopy, and they are able to do so on small supports because of their smaller size compared to adult males.

Whilst feeding was one of the primary motivations for adult males and females to travel in and around tree canopies, the arboreal locomotion of adolescents is also shaped by their developmental needs. Adolescents are not dependant on their mothers, but their development is shaped by independent exploration and play behaviours with other adolescents in the trees (locomotion during playing accounted for 4% of the adolescents' arboreal repertoire) (Brown, 1988; Lewis, 2005). Adolescent gorillas are also more agile and experience less risk of severe injury from falling (Cartmill & Milton, 1977; Preuschoft, Schönwasser, & Witzel., 2016), so they are able to move around the canopy to test their arboreal abilities and boundaries with less risk of injury. The adolescents' increased tendency to engage in horizontal travel, particularly through suspension in the tree canopies might be attributed to their stage of maturation. Although their much smaller size may permit them to travel on small supports with less risk, these age-based maturation factors likely also influences the way in which they move in the canopy.

Whether the gorillas have a preferred locomotor strategy to move around the canopy, or a preferred support that they use (or a combination of both) is difficult to determine, but the gorillas in this study were able to use small supports when presented with them in the canopy. However, when using small supports to move around the canopy, 40% of the time, they used multiple small supports. When walking, especially at heights of more than 20 meters, where supports are sparser and more unpredictable, the gorillas used multiple small branches and clusters of small, intertwined branches. At heights above 20 meters, the gorillas fed more than lower heights, so to reduce the chance of falling when foraging, processing and eating food which requires freeing up a forelimb, the gorillas walked on multiple supports. At mid-heights, where the gorillas used suspension to travel to feeding sites, the gorillas also used multiple supports, by using lianas in combination with tree branches as well as small branch bundles. At these heights, which represent the lower and main canopy, the canopy is abundant with intertwined branches and lateral branches which create routes in horizontal directions

(Fleagle, 1985; Cant, 1987; Cant, 1992). The main canopy is the densest with vegetation and foliage, so suspension below branches is less energetically demanding and (presumably) mentally exhausting than manoeuvring above and between tangled branches using walking behaviours. Furthermore, when using multiple supports to distribute their weight, the gorillas are more secure. This strategy is also seen in orangutans, which frequently grasp bundles of supports when moving in the trees (Thorpe & Crompton,2005).

2.5.3 How does body size influence how gorillas cross gaps in the canopy?

In contrast to terrestrial environments, arboreal habitats comprise of varying degrees of continuity. Crossing gaps, like horizontal travel, is another ecological challenge that must be addressed for a species to be successful when exploiting arboreal environments (Pontzer & Wrangham, 2004; Halsey, Coward & Thorpe, 2016). Gap-crossing is considerably risky, because the supports used when leaving one side of a gap may differ in size and compliance to supports on the other side. When crossing gaps, the gorillas in this study used small supports considerably more than larger supports and used multiple supports of various orientations. The risks involved in gap-crossing may have been mitigated for by using multiple supports.

The gorillas gap-crossed more than expected accounting for 10% of their locomotor repertoire. The smallest age-sex class, the adolescents, engaged in gap-crossing the most, accounting for 13% of their overall repertoire, followed by the silverback (11%) and the females and blackback (7%). However, the expectation that larger body size would be accompanied by more bridging (Cartmill & Milton 1977; Fleagle & Mittermeier, 1980), but less leaping (Fleagle, 1985; Cant, 1992) was not support here. Instead, the silverback was not observed to bridge gaps (this made up a third of smaller gorillas' gap-crossing behaviour) and leaped across gaps twice as often as smaller individuals. The silverback also engaged in oscillation of branches ('riding' and 'swaying') as a gap-crossing behaviour more than smaller individuals. However, whilst the adolescents were observed to occasionally leap to a nearby support to avoid wasp nests in the canopy and flee from more dominant individuals, the silverback was observed to leap when small supports would collapse under his weight. Furthermore, whilst the smaller individuals oscillated branches to move from place to place and engaged in controlled 'riding' at different heights (similarly to orangutans), the silverback was observed to ride branches to the forest floor. This might be because it was more energy efficient to use his body weight to travel to the ground, or because the supports that he would use may not have been able to withstand his weight. The silverback engaged in gap-crossing almost exclusively at heights of less than 10 meters compared to smaller gorillas, who crossed gaps at mid-heights, in the main canopy. At higher heights, falling has bigger consequences, especially for larger apes who have a higher chance of fatality because the kinetic energy that the body has to dissipate upon impact increases (Cartmill & Milton, 1977; Preuschoft, Schönwasser, & Witzel., 2016). Even though a gap is smaller for a silverback than smaller gorillas because of his longer reach, the silverback may have crossed gaps less frequently than smaller gorillas because he was constrained by either his size and/or the supports available to cross these gaps.

Although the silverback used lower heights the most when crossing gaps, the females seemed to be the most cautious in their gap-crossing behaviours out of all the age-sex classes, as they used bridging more than larger individuals. Bridging a gap allows gorillas to slowly transfer onto small supports and test their capacity to bear their weight, so it is safer and less dynamic than leaping, which is characterised by a period of free-flight (Fleagle & Mittermeier, 1980), and oscillation (‘ride’ and ‘sway’), which requires compliant supports to bend, or sway to move an individuals’ location (Hunt et al., 1996; Thorpe & Crompton, 2005; Thorpe, Holder & Crompton, 2007). The adult females in this study were all parous and travelled with dependant infants. Travelling with infants affects the mother’s stability during locomotion because the location of an infant when carried will determine where the centre of mass is (Ross, 2001). It is also inherently risky, as supporting an infant with one forelimb reduces the amount of contact with arboreal supports. It is therefore possible that the inherent parental investment of time and energy in maximising infant survival chances and their reproductive success (Parker, 1999; Robbins, Robbins & Fawcett, 2007; Lee, 2012; Van Noordwijk et al., 2012; Lee, 2012) might reflect their cautiousness when moving in the trees, and their use of more stable gap-crossing behaviours. Adult female orangutans have also been observed to be more cautious when moving in the trees than adult males and adolescents (Thorpe & Crompton, 2005). This suggests that the reproductive status of female apes may influence the way in which they view and attend to risks when moving in complex arboreal environments compared to their male counterparts.

It was not previously understood how often, and how gorillas cross gaps in the canopy (Remis, 1995). The overall tendency for adolescents to engage in gap-crossing more frequently than mature gorillas, even at heights of more than 20 meters, implies that crossing gaps using small supports is within the limit for these smaller gorillas. However, the silverback, who crossed gaps because the supports were not able to bear his weight, was likely more restricted in the supports that he used.

2.6 Conclusion

Gorillas are the largest apes to habitually exploits arboreal environments. Although they possess musculoskeletal adaptations towards terrestrial locomotion, they also need to be able to meet the needs of arboreal locomotion to access arboreal resources. There were clear associations between locomotion, height, behaviour, and support use, which suggest that gorillas have developed strategies towards exploiting different heights and a variety of supports. Overall, the locomotor repertoire of the gorillas is associated with the structure of the forest, supporting the notion that there is a strong link between an environment and expressed behaviour.

Gorillas exhibit the largest degree of sexual dimorphism out of all the great apes. However, although body size was associated with variation in locomotor behaviours, the manner of association was contrary to classic predictions. Larger individuals did not use suspension or bridging more than smaller individuals, nor did they use leaping and vertical climbing less. Instead, what was associated with body size, was a variation in the size of supports used. As predicted, larger gorillas tended to use larger supports than smaller gorillas, suggesting that large individuals must compensate for their size by selecting appropriate supports which can bear their weight. This may have affected their ability to move out into tree canopies where supports are mostly small and unpredictable, which was shown in the silverback’s lower propensity to engage in horizontal travel in the tree canopy.

Whilst this study has indicated that body size and age-sex variation may indeed shape the arboreal repertoire of gorillas, it is difficult to determine to what extent it influences their ability to travel and feed in the trees. We need to gather more data on the locomotor ecology of wild western lowland gorillas, especially silverback individuals, to delve further into the intricacies between anatomical adaptations, biological roles, body size variation, habitat structure and locomotor behaviours (all of which are encompassed within the ecomorphology framework (Karr & James, 1975)). However, in order to understand the ecomorphology of a species, and the role of body size in arboreal environments, focus should be directed towards comparing the locomotor ecology of all great apes This comparative approach will help to unravel the intricate array of ecological, biological and morphological factors that influence how the largest arboreal primates (*Pan, Gorilla* and *Pongo*) travel and feed in the trees. This is of particular interest because the African apes and orangutans inhabit distinct ecological niches, and no previous studies have discussed these variances in detail despite the potential implications that this has on their evolutionary adaptations, survival strategies, and interactions with their local environments.

CHAPTER THREE

THE ECOMORPHOLOGY OF GREAT APES: A COMPARATIVE STUDY OF THE ARBOREAL LOCOMOTION OF WILD CHIMPANZEES (*PAN TROGLODYTES*), WESTERN LOWLAND GORILLAS (*GORILLA GORILLA GORILLA*) AND SUMATRAN ORANGUTANS (*PONGO PYGMAEUS ABELII*).

3.1 Abstract

Chimpanzees, gorillas and orangutans differ in their biology, morphology and the habitats that they occupy. They also exhibit considerable body size variation; the silverback gorilla weighs approximately 170kg, which is around four times the weight of female chimpanzees and five times the weight of adolescent gorillas and orangutans. However, in complex arboreal environments, they must solve the same ecological challenges of accessing, moving around and dealing with gaps in the canopy. This study examined whether species and/or body size were driving forces in shaping how great apes move in the trees. Backwards elimination log-linear modelling was used to identify the relationship between locomotion, height and support use, accounting for both body size and species. It was found that the variation in arboreal locomotor behaviours was best explained as a reflection of their postcranial morphology and adaptations towards specific behaviours, rather than their body size. The orangutans engaged mostly in suspension, whereas the chimpanzees used vertical climbing the most, and the gorillas engaged mostly in walking. The apes exhibited interspecific variation in the supports that they used, but although this may reflect adaptations, the size and type of supports used were also linked to potential habitat differences and the strategies exploited to mitigate the risk of falling. Body size did not influence the arboreal locomotion in the ways that were expected; instead, the results exhibited patterns that were opposite to classic predictions. Larger apes used relatively metabolically expensive and risky locomotion more than smaller apes. Whilst larger apes overall used larger supports, all apes used the same supports for each locomotor behaviour, implying that there are shared characteristics in the size and type of supports used for all apes regardless of their size. Overall, the results suggest that evolutionary selective pressures have shaped the locomotor behaviours used in complex arboreal environments to reduce energy expenditure. However, the variation

in support use reflects many aspects, including their morphology, ecological niche, degree of arboreality and strategies to mitigate the risk of falling.

3.2 Introduction

Despite being phylogenetically close and sharing a myriad of anatomical features, non-human great apes (*Gorilla, Pan* and *Pongo*) have been documented to exhibit distinct positional behaviour repertoires (Hunt, 1991; Remis, 1995; Doran, 1996; Doran & Hunt, 1996; Remis, 1998; Thorpe & Crompton, 2005, Chapter Two). Their positional behaviour shapes the way in which they acquire nutritional resources, compete for mates, escape predators, and maintain social relationships. Positional behaviour therefore plays a crucial role in the survival and reproductive success of great apes. However, it is also influenced by their morphology and ecology. Morphological and physiological construction determine how they physically interact with their local environment, and environmental pressures and habitat structures drive how they address ecological needs within a particular niche.

It is not possible to understand what shapes the overall locomotor repertoire of great apes and what differentiates each species without a full understanding of the complexities within each environment (Wainwright, 1991). Orangutans inhabit highly dense, tall rainforest canopies which differ considerably to the high-altitude montane forests of mountain gorillas and lowland swampy forests occupied by western lowland gorillas and chimpanzees (Hunt, 1992; Doran, 1996; Remis, 1995; Thorpe & Crompton, 2005; Neufuss et al., 2017). What distinguishes the orangutans from other great apes, however, is that they are almost exclusively arboreal and rarely descend to the ground

(Sugardjito & Van Hooff, 1986; Cant, 1987; Thorpe & Crompton, 2005; Morrogh-Bernard et al., 2009). For the African apes, terrestrial travel makes up a large proportion of their locomotor repertoire (Hunt, 1992; Doran, 1992; Remis, 1995; D' Aout et al., 2004; Thorpe & Crompton, 2005; Chapter Two). Arboreal environments are more complex to navigate than terrestrial environments as they are characterised by discontinuity and a variety of supports that differ in size and compliance. Whilst overall, orangutans may experience higher energetic costs and nutritional stress than the African apes because they spend less time on the ground, all great apes encounter high energetic demands when in the trees (Vogel et al., 2017; Takeshita et al., 2019). This dictates that travel routes must be carefully selected. If a feeding site, or destination, can be reached by a travel route using locomotor behaviours and supports that are less energetically demanding, then this will reduce overall energy expenditure. This will then conserve energy for other highly energetically demanding behaviours. This is vital for great apes that depend on arboreal environments to acquire resources. However, the extent to which differing habitat challenges are reflected in strategies to conserve energy and shape expressed locomotor behaviours remains unclear.

Previous studies of the locomotor ecology of great apes have mostly focused on a single species (e.g. Susman, 1984; Sugardjito & Van Hooff, 1986; Hunt, 1992; Doran, 1992; Remis, 1995; Thorpe & Crompton, 2005) or genus (Doran, 1993a; Remis, 1998; Manduell et al., 2013). However, whilst single-species studies have shed light on specific adaptations and expressed behaviours within a particular environment, comparative studies of great apes can reveal a broader perspective on the great apes' capacity to adapt. This means that it is possible to identify the similarities and differences in how great apes have adapted to optimise their environments and whether shared morphological or environmental traits are also expressed as shared behaviours. Until now, comparative studies (see Tuttle & Watts, 1985; Hunt, 1991; Doran, 1993a; Thorpe, Crompton & Alexander, 2007) have not been able to discuss the intricate relationships between the apes' locomotor repertoires because of differences in methodologies. However, inter-specific comparisons have partially addressed some of the big questions in locomotor ecology, which will be built upon in this paper (Tuttle & Watts, 1985; Hunt, 1991; Doran, 1996).

In a comparison of the positional behaviour of non-human apes and *Papio anubis (olive baboons)*, Hunt (1991) identified differences in locomotor behaviours among the different genera. It was found that the Asian apes (*Pongo* and *Hylobates*) were distinct from the African apes and *Papio,* in their much higher propensity to engage in suspensory locomotion. Hunt only briefly mentioned the locomotor behaviour of mountain gorillas (*Gorilla beringei beringei*), documented by Tuttle and Watts (1985), because of limited data on their positional behaviour and concluded simply that they are primarily terrestrial knuckle-walkers. The locomotor behaviour of western lowland gorillas (*Gorilla gorilla gorilla*) was not quantified until 1995 by Remis, so it was not known whether this species presented more similarities to their Eastern counterparts, or to the chimpanzees with which they are sympatric. Hunt also suggested that the locomotion of orangutans appeared to be broadly similar to chimpanzees, based on orangutan data collected by MacKinnon, (1974) and Cant (1987). This idea was based largely on the frequency of vertical climbing (although it was not clear from Hunt (1991) whether vertical climbing of orangutans and chimpanzees was kinematically distinct and/or whether the manner of vertical climbing was dependent on support size, as data on support use was not available at the time). In contrast, Doran suggested that chimpanzees (*Pan troglodytes*) in lowland forests were similar to western lowland gorillas in their frequency of vertical climbing (Doran, 1996). However, Doran's comparison was restricted to the African apes. Furthermore, before Hunt et al (1996) presented a set of standardised descriptions for primate positional behaviour, postural and locomotor classifications were broad and lacked uniformity. This meant that previous comparative studies were limited in their discussion of biomechanically distinct behaviours that are important to understand the ecomorphology of great apes (as there are now more than 57 distinct locomotor behaviours that have been identified for the great apes (Hunt et al., 1996; Thorpe & Crompton, 2005)). Thus, whilst the morphological differences between the great apes have been well documented (see e.g. Corruccini & McHenry, 1979; Susman; 1979; Shea, 1985; Schwartz, 1988; Leigh et al., 2003), there remains a gap in our understanding of how these translate into differences in their locomotor behaviours, the way in which they deal with risk and how they employ strategies to reduce energetic costs in arboreal environments.

Great apes exhibit considerable variation in body size. Adult male gorillas weigh around 170kg, which is more than twice the weight of female gorillas and adult male orangutans, and more than four times the weight of female and male chimpanzees (Grether & Yerkes, 1940; Rodman, 1984; Uehara & Nishida, 1987; Knott, 1998; Doran & McNeilage, 1998; Zihlman & McFarland, 2000). Such extreme variation in body size might be expected to impact their energy expenditure and risk when travelling arboreally (e.g. Sugardjito & van Hooff, 1986; Hunt, 1992; Leigh & Shea, 1995; Remis, 1995; Doran, 1993a; Doran, 1993b; Doran, 1996; Remis, 1998; Thorpe & Crompton, 2005). The classic body size predictions state that larger individuals will spend more time at lower heights and use above-head suspensory locomotion more than smaller individuals because of the mechanical and energetic advantages and risks involved compared to above-branch locomotion (especially on smaller supports) (Cartmill & Milton 1977; Fleagle et al., 1981; Susman, 1984; Tuttle & Watts, 1985; Cant, 1987; Remis, 1995). However, these classic body size predictions are not supported for all species. Doran (1996) found that whilst intraspecific body size differences were not apparent for chimpanzee locomotion, bonobos (*Pan* paniscus) exhibited sex-based variation in the locomotor behaviours that they used, even though they exhibit the least amount of sexual dimorphism. Remis (1995) also suggested that for western lowland gorillas, there were no significant body size differences in their locomotor behaviour (although in Chapter Two, I dispute this and instead show that there are variations in locomotion based on body size). Given that chimpanzees and western lowland gorillas exhibit a larger degree of sexual dimorphism than bonobos, and as a species are larger in size, it is likely that the documented sex-differences of bonobos were a representation of limited sample sizes or influenced by social constraints (Remis, 1995; Doran; 1996).

Another classic body size prediction for primates is that larger individuals will use larger supports more than smaller individuals (Catmill & Milton, 1977; Cant, 1992). Intra-specific studies have supported this for western lowland gorillas (Remis, 1995; Chapter Two), which display the largest degree of sexual dimorphism, but it is not known if this is true for great apes collectively . The supports used by great apes might instead reflect interspecific habitat differences (because of support availability) or morphological variation (for example, the hands of the great apes are diverse in size and dimensions). One of the biggest challenges in arboreal environments is dealing with support fragility, as using small flexible branches increases the risk of branch breakage and falling from height. Male orangutans, although twice the weight of female orangutans, are more similar in body size to adult female gorillas and blackbacks (approximately 70-80kg), whereas female orangutans weigh around 40kg, which is within the range of both male and female chimpanzees (Grether & Yerkes, 1940; Rodman, 1984; Uehara & Nishida, 1987; Knott, 1998; Doran & McNeilage, 1998; Zihlman & McFarland, 2000). In order to fully understand the relationship between great apes, support use and the performance of arboreal locomotor behaviours, focus needs to be directed towards examining both body size and species. This multifaceted approach may also shed light on whether larger individuals operate at the high end of their capabilities and whether they have to compensate for their size when moving in the trees compared to smaller individuals.

For all arboreal apes, locomoting in arboreal environments can be split into three main ecological challenges: access to different heights in the trees, movement around the canopy, and addressing discontinuity in trees. The strategies used by great apes to address these challenges may be biomechanically distinct because of morphological adaptations towards specific behaviours. However, the degree of adaptation, or efficiency, for a specific locomotor behaviour is not directly linked to the time spent performing it, but it is also dependent upon the properties of supports used (Cant, 1992; Isler, 2002). Primates will only achieve ecological and evolutionary success if they are physically able to hold the supports that are available in arboreal environments. For example, as is typical for most tropical forests, tree peripheries are characterised by supports that are less continuous, smaller and more compliant. Orangutans have been documented to have a good understanding of branch compliance and have shown that they can exploit small supports to their advantage to ‘sway’ and ‘ride’ gaps, a gap-crossing strategy used to conserve energy (Thorpe, Crompton & Alexander, 2007).

However, whether the use of similar arboreal supports is accompanied by similar strategies to access different heights and move around in the canopy is not yet understood. Only by isolating preferences towards particular supports among species or great apes of different body sizes that perform a common behaviour, can the function and capability of certain behaviours be determined (Kay & Cartmill, 1977). Now that more data is available on the supports used by chimpanzees, orangutans and gorillas, a more in-depth analysis can be directed towards understanding the complex interplay of variables that play a role in shaping great apes' arboreal repertoires.

The aim of this study is to build upon previous comparative studies of great apes by incorporating comprehensive data on their locomotor ecology collected during three separate studies into a single analysis. This will be the first to compare specifically the arboreal locomotor behaviour of chimpanzees (Pettifer & Thorpe, Unpublished data), western lowland gorillas (Chapter Two) and Sumatran orangutans (*Pongo pygmaeus abelii)* (Thorpe & Crompton, 2005). The focus of this study is to compare specifically their arboreal locomotor repertoire. By comparing the arboreal behaviours of the great apes, they can be used as referential models to gain insight into the evolutionary history of locomotion. The evolutionary history of great apes is still not fully understood, but using the fossil record alongside data for how extant species move in their natural habitats, we can help to answer some of the big questions about the evolution of locomotion. Whilst orangutans have been used as models for arboreal orthograde hypothesis for bipedal evolution (Thorpe, Holder & Crompton, 2007; Crompton, Vereecke & Thorpe, 2008), the African apes have been central to the knuckle-walking model (Washburn, 1967). However, if we can identify to what extent/if the great apes share an arboreal repertoire and how postcranial adaptations may influence their locomotion, this will help us to construct more accurate models of how locomotion has evolved over time.

The first objective of the study is to examine one of the biggest questions in great ape ecomorphology: how do different great ape species address the three challenges of accessing, moving around, and dealing with gaps in the canopy? Chimpanzees, gorillas and orangutans are all distinct in their postcranial musculoskeletal morphologies, so by determining what locomotor behaviours they use will help our understanding of the form-function interface and the energy expenditure of arboreal locomotion. The second objective is to ask this same question for body-size-related groups. This will, in turn, reveal whether there is a threshold for individuals of a particular size/species for performing particular locomotor behaviours. The third aim is to understand how, and to what extent, environmental factors shape the arboreal repertoire of great apes. By understanding the interplay between locomotion and support use, more can be understood about the capabilities of great apes and elucidate to a potential collective limit to their behaviours in arboreal environments. This may also indicate whether great apes, some of which spend a considerable amount of time in terrestrial environments, alter their behaviour in arboreal contexts to mitigate the risk of falling.

3.3 Methods

Western lowland gorilla (hereafter gorilla) locomotor ecology data was collected in the Loango National Park, Gabon from July 2021 to July 2022 (Chapter Two). Data for orangutans, presented in Thorpe and Crompton (2005 and 2006) was collected in the Gunung Leuser National Park from December 1998 to December 1999 and chimpanzee data was taken by Pettifer in Taï National Park between February and December 2018 (Pettifer & Thorpe, Unpublished data).

Study subjects were all fully habituated. The gorilla study group was a family troop made up of one silverback, three parous adult females each with a dependant infant younger than one year, a single blackback and two adolescents. Orangutan subjects were two adult males, three adult females (one of which travelled with a dependant infant), two subadult males and three juveniles (Thorpe & Crompton, 2005). Chimpanzee observations were made from three independent groups which lived in separate areas of the forest. Chimpanzee data was also collected as part of a study on the effects of aging on the positional behaviour of this species; as a result, all subjects are mature individuals and above the age of 19 (Table 3.1).

Table 3.1: Observations, study subjects and site details for the gorilla, chimpanzee and orangutan datasets used in the comparative analysis.

	Western lowland gorilla (*Gorilla gorilla gorilla*)	Chimpanzee (*Pan troglodytes*)	Sumatran Orangutan (*Pongo pygmaeus abelii*)
	King et al., (submitted manuscript)	Pettifer & Thorpe (Unpublished data)	Thorpe and Crompton (2005 and 2006)
Number of locomotor observations[1]	5066 (1338)	3496 (439)	2811 (2811)
Study date	July 2021- July 2022	February 2018- December 2018	December 1998- December 1999
Study subjects	Adult ♂ x1 Adult ♀ x3 Blackback x1 Adolescents ♂ x2	Adult ♂ x7 Adult ♀ x18	Adult ♂ x2 Adult ♀ x3 Subadult ♂ x2 Adolescents ♀ x1 / ♂ x2
Study site	Loango National Park, Gabon	Taï National Park, Côte d'Ivoire	Gunung Leuser National Park, Sumatra, Indonesia
Habitat type	Tropical lowland forest, swamps and wetlands.	Tropical primary forest, secondary forest and disused oil palm plantations.	Lowland and highland tropical forests.

[1] Overall locomotor observations; parentheses indicate arboreal locomotion, which are the focus of this study.

3.3.1 Body size categorisation

Table 3.2 shows the body size groups for all study subjects, combined into groups based on similarities in body weight. The silverback gorilla was the largest individual by more than 100kg, constituting the largest body size group. Since this category included but a single individual, caution was taken in interpreting the results. The adult female gorillas and blackback gorilla were similar in their body weight to adult male orangutans, between approximately 70-80kg. Collectively these made up the second largest body size group. Weighing between 40-50kg were the adult female orangutans, subadult male orangutans and all chimpanzee subjects. The smallest body size group comprised adolescent gorilla and orangutan subjects, which weighed less than 40kg.

Table 3.2: Interspecific body size groups conflated by estimated weight categories.

Body size category (BSC)	Weight category	Species		Sex	Individuals (n)	Approximate weight (kg)[1]	Arboreal locomotor observations
BSC 1	170kg	Gorilla	Silverback	♂	1	170	90
BSC 2	70-80kg	Gorilla	Adult female	♀	3	70-80	1073
		Gorilla	Blackback	♂	1	70	
		Orangutan	Adult male	♂	2	80	
BSC 3	40-50kg	Orangutan	Subadult male	♂	2	50	1582
		Orangutan	Adult female	♀	3	40	
		Chimpanzee	Adult female	♀	7	50	
		Chimpanzee	Adult male	♂	18	40	
BSC 4	<40kg	Orangutan	Adolescent	♂	2	35	1842
		Orangutan	Adolescent	♀	1	30	
		Gorilla	Adolescent	♂	2	30-35	

[1] Estimated weight described for orangutans (Rodman, 1984; Knott, 1998), chimpanzees (Grether & Yerkes, 1940; Uehara & Nishida, 1987; Doran & McNeilage, 1998) and gorillas (Doran & McNeilage, 1998; Zihlman & McFarland, 2000).

3.3.2 Comparability of datasets

Arboreal locomotor data was collected throughout each study using one-minute instantaneous sampling. All three studies quantified biomechanically distinct locomotor behaviours based on the standardised descriptions presented by Hunt et al. (1996) and further developed by Thorpe and Crompton (2005). This means that there was very little ambiguity in the way in which complex locomotor behaviours were identified. Height was documented in each study using 5-meter intervals from the ground. Researchers were self-trained in height estimation and used regular monitoring to ensure the reliability of arboreal height. The identification of contextual behaviour for each study included travelling (actively moving from one place to another as the primary context) and feeding (foraging, processing or eating food). Other contextual behaviours were documented for chimpanzees, gorillas and orangutans including social interactions, aggression and avoid (n=52) (Table 3.3). However, because of the potential variation in the classification of contextual behaviour, it was not included in the modelling process.

For arboreal supports, the orientation and diameter of a support was documented using uniform categories within all datasets (Table 3.3). This includes how orientation was categorised (horizontal, angled and vertical) and the categories for the size of a support (0-4cm, 4-10cm etc..). Each researcher, including myself, Pettifer (Pettifer & Thorpe, Unpublished data) and Thorpe (Thorpe & Crompton, 2005) underwent rigorous self-training to accurately identify these parameters which reduced the potential for interobserver error. However, there was some variability in data collection. Support properties were documented for gorillas and orangutans using an identical protocol. For each weight-bearing limb, the number, size, type and orientation of supports was identified and recorded. This also provided an overall number of weight-bearing limbs during locomotion. Chimpanzee data, however, was collected using an alternative approach. Data was collected on the size, orientation and type of support for only the primary weight-bearing support. This meant that chimpanzee data was not comparable to data for gorillas and orangutans and so was removed from the modelling process.

3.3.3 Conflation of datasets

In order to ensure a sufficient sample size within each subset, each variable was conflated to reduce the number of combinations, as shown in Table 3.3. The 57 locomotor submodes were combined to reflect four categories that represent different ecological challenges: accessing different heights (vertical climbing), moving around the canopy (suspension and walking) and gap-crossing. Height was grouped into three levels, below 10 meters, 10-20 meters and above 20 meters. Because of the variation in forest ecology between the different study sites, these categories do not directly reflect different forest structures or canopy levels. Instead, these height groups were chosen as they align with the data published by Thorpe and Crompton (2005) and are convenient for data analysis. Categorising height into groups with different intervals (e.g. 0-10 and 10-15 meters) will introduce errors that will complicate the comparative analysis.

The total number of combinations for the diameter and type of supports was too large to be meaningful as there were combinations which had relatively very few observations. Therefore, these variables (for orangutans and gorillas only) were grouped. Support diameter was conflated into seven categories, which include single-size groups (all supports are a particular diameter) and mixed-size groups (a variation in sizes) (Table 3.3). Single and mixed supports were also documented for the type of supports used.

Table 3.3: Locomotor ecology variables and conflated variables used in the modelling process.

	Variable	Description	Conflated variables used in the modelling process
	Individual	Chimpanzee x25, Orangutan x10, Gorilla x7	
	Age-sex class	Adult male, adult female, adolescent male, adolescent female (blackback for Gorilla data)	
	Locomotion[1]	Quadrupedal walk, tripedal walk, bipedal walk Vertical climb, vertical descent Torso-orthograde suspension, torso-pronograde suspension, forelimb-hindlimb swing Bridge, leap, drop, sway, ride, roll	Walking Vertical climbing Suspension Gap-crossing
	Height (meters)	0-5, 5-10 10-15, 15-20 20-25, 25-30, 30-35, 35-40, 40+	<10 10-20 >20
	No. weight- bearing limbs *	1,2,3,4,4+	
	Behavioural context *	Feeding (inclusive of foraging, processing, and eating), Travelling, Affiliative and social, aggression (asserting dominance, displays of threat, physical and vocal aggression) and avoid (moving away from other individuals or engaging in submissive behaviours)	
Chimpanzee: primary weight-bearing limb **Orangutan and gorilla:** for each weight-bearing limb	**Support diameter (cm)**	0-4, 4-10, 10-20, 20-40, 40+	0-4 + 4-10 10-20, >20 Mix <20 Mix >10 Branch bundles[3]
	Support orientation *	Horizontal, angled, vertical, U-shaped	
	Support type	Tree trunk, compliant liana, branch, terminal branch bundles[3], buttress	Branch bundles[3] Branch Liana Liana Mix (liana + branch) Trunk mix (trunk + other type)
	Number of supports	1,2,3,4,4+	1; 2-4; >4

[*] Variables not included in the analysis: number of weight-bearing limbs, behavioural context and support orientation.

[1] Locomotor modes (10) and submodes (57) are defined in Appendix A.

[2] Description of support use documented for each species. Only orangutan and gorilla support data was used in the data analysis.

[3] Branch bundles are defined as clusters of small branches intertwined and used in bunches.

3.3.4 Statistical analysis

Statistical analysis was conducted in R version 4.3.1 (2023) with the following packages: *lme4* (version 1.1-34, Bates et al., 2014) for fitting Generalised Linear Mixed Models and *AICcmodavg* (version 2.3-2, Mazerolle, 2023) for model selection using the Akaike Information Criterion (AIC). Graphs were produced using the *ggplot2* package (v3.3.3; Wickham, 2016). The aim of the statistical analysis was to explore potential relationships between variables and to identify whether body size and species were influential in shaping the arboreal locomotor repertoire of great apes.

Generalized linear modelling (GLM) was chosen as the most appropriate data analysis method using the Poisson log link function (the most suitable model family for counts of observations). A Poisson distribution ([$g(\mu) = \log(\mu)$] where $g(\mu)$ is the link function and μ is the mean of the Poisson distribution) (Nelder & Wedderburn, 1972; Zurr et al., 2009). The response variable is the frequency of observations, which means that the models predict how often certain events, or outcomes occur.

To avoid problems of multicollinearity, separate models were performed for variables that display high correlation (for example, number of supports exhibited collinearity with support type where ‘branch bundles’ exclusively fall into the category of >4 supports). This ensured that associations between variables were not influenced by the effects of collinearity, improving the interpretability of results (Dormann et al., 2013). Backwards stepwise regression was performed on the models using the Akaike Information Criterion (AIC) as the selection criteria to determine the most parsimonious model which best explains the data (Bozdogan, 1987; Aho et al., 2014; Van Andel et al., 2015).

This process eliminated variables that did not increase the fit of the model, leaving only interactions and main effects that played a substantial role in the observed patterns in the data.

In order to test potential unobserved covariance between body size and species, several generalised linear mixed effect (GLMER) models were performed. This involved including individual as a random effect in the models to test for variance due to individual differences. It was found that all models failed to converge. Examination of the optimisation process revealed that the models were not computationally feasible because body size category 1 (BSC1) contained only a single species and individual (the silverback gorilla). Poisson GLM models, therefore, were the most appropriate modelling procedure.

Body size models and species models were performed separately and were not directly comparable, but each model independently revealed the relationship with other locomotor ecology variables. Diagnostic tests were performed to ensure that all models satisfied assumptions of Poisson GLM analysis. This included systematic examination of linearity, independence, homoscedasticity and zero-inflation. The models were tested for zero-inflation using the *Performance* package (version 0.10.4, Lüdecke et al., 2021) and the models indicated a suitable number of observed zeros, satisfying assumptions (Gurmu, 1991; Deng & Paul, 2005).

Post-hoc analysis was conducted to assess the strength of effects of variables within the models using standardised cell residuals (SCRs) of multiway contingency tables.

These identified discrepancies between observed and expected values which exceed expectations and revealed underlying relationships within a significant interaction identified in the modelling process (Beasley & Schumacker, 1995). SCRs of absolute values above 2.0 and below -2.0 contribute to the overall statistical significance (Haberman, 1973).

3.4 Results

Locomotor observations for the orangutans were 100% arboreal (n=2792), compared to 12.5% for the chimpanzees (n=434) and 26.4% for the gorillas (n=1338) (Figure 3.1). The orangutans engaged in 49 biomechanically distinct locomotor submodes, whereas the gorillas used 48 and the chimpanzees used 27; descriptions and frequencies of these are presented in Appendix A.1 and A.2.

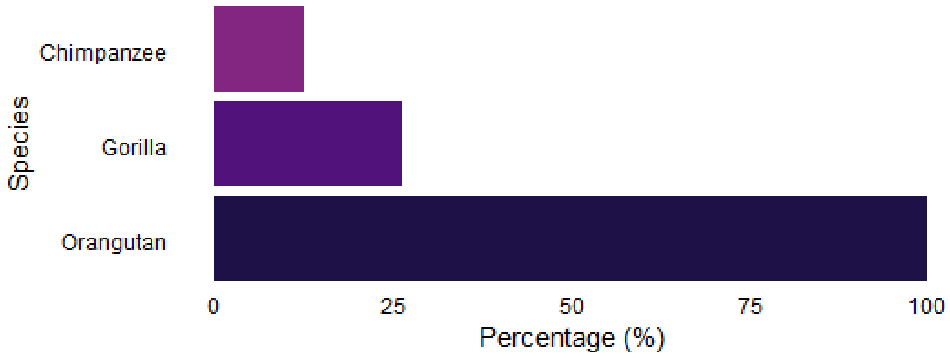

Figure 3.1: Chart showing the percentage of locomotion which took place arboreally for each species.

Table 3.4 shows the percentage of locomotor behaviours, by mode, for each species. The African apes engaged in arboreal walking more than the orangutans, but the gorillas' walking repertoire included considerably more bipedal walking than the orangutans and chimpanzees. The chimpanzees used vertical ascent and descent more than the orangutans and gorillas. Conversely, the orangutans engaged in much more suspension than the African apes and used both torso-orthograde and torso-pronograde suspensory postures. Torso-orthograde suspension almost exclusively made up the suspensory repertoire of the African apes. The variation in frequency of gap-crossing behaviours was dependent upon whether they were oscillatory (‘ride’ and ‘sway’) or non-oscillatory behaviours such as bridging, leaping and dropping. The chimpanzees used oscillatory gap-crossing more than non-oscillatory, whereas the gorillas and orangutans used both.

Table 3.4: Percentage of arboreal locomotor modes for each species.

	Gorilla %	Orangutan %	Chimpanzee %
Quadrupedal walk	28.1	17.5	29.7
Tripedal walk	0.7	0.1	0.5
Bipedal walk	13.4	7.3	1.4
Vertical climb	15.7	16.1	34.1
Vertical descent	19.4	9.4	21.4
Torso-orthograde suspension	12.2	36.1	8.5
Torso- pronograde suspension	0.6	3.7	0.0
Forelimb- hindlimb swing	0.1	0.3	0.0
Bridge	3.1	2.9	0.7
Leap	1.7	0.0	0.5
Drop	3.1	0.6	0.0
Sway	0.2	5.6	1.8
Ride	1.6	0.5	1.4
Number of arboreal locomotor observations =	1338	2792	434

Definitions for each locomotor submode are given in Appendix A.1. Frequency of submodes are given in Appendix A.2.

3.4.1 Basic models: locomotion and height with species and body size

Two basic models, one which included body size as a predictor variable, and the other which has species a predictor variable, examined the relationship alongside locomotion and height as predictor variables. The response variable for both models was the frequency of observations. Table 3.5 shows all of the interaction terms, and whether they were retained or removed from each model. Post-hoc analysis using standardised cell residuals (SCRs) focuses only on the highest-order interactions retained in the models. The interaction between species, locomotion and height was removed from the modelling process which suggests that the variation in height was accompanied by similar locomotor behaviours for the gorillas, chimpanzees, and orangutans. However, species was accompanied by variation in locomotion, and variation in height independently. In the body size model, the highest-order retained interaction was the three-way interaction between body size, locomotion, and height.

Table 3.5: Basic poisson GLM model results for the interactions between locomotion and height with species and body size.

	Interactions	df	Deviance	*p*-value
Species	Species * Locomotion * Height			
	Species*Locomotion	6	607.81	**<.001**
	Species*Height	6	1613.05	**<.001**
	Locomotion*Height	6	90.14	**.002**
	Removed interactions:			
	Species*Locomotion*Height	12	19.51	.294
Body size	Body size * Locomotion * Height			
	Body size*Locomotion*Height	18	39.22	**<.001**
	Body size*Locomotion	9	117.61	**<.001**
	Body size*Height	6	209.54	**<.001**
	Locomotion*Height	6	196.48	**.001**

*Species * locomotion*

The orangutans, gorillas and chimpanzees each exhibited distinct locomotor repertoires (Figure 3.2). The African apes walked and climbed vertically more than twice as often as suspension. However, the orangutans engaged in suspension more than other locomotor behaviours. The gorillas and orangutans engaged in gap-crossing in similar frequencies, twice as often as the chimpanzees.

The SCRs indicate that the chimpanzees used vertical climbing in frequencies more than predicted by the model (SCR=9) whereas gorillas walked more than predicted (SCR=7.7). The African apes however, both engaged in suspension less than predicted. The orangutans walked and vertically climbed much less than predicted (SCR=-5.4) but used suspension more than predicted (SCR=10.8).

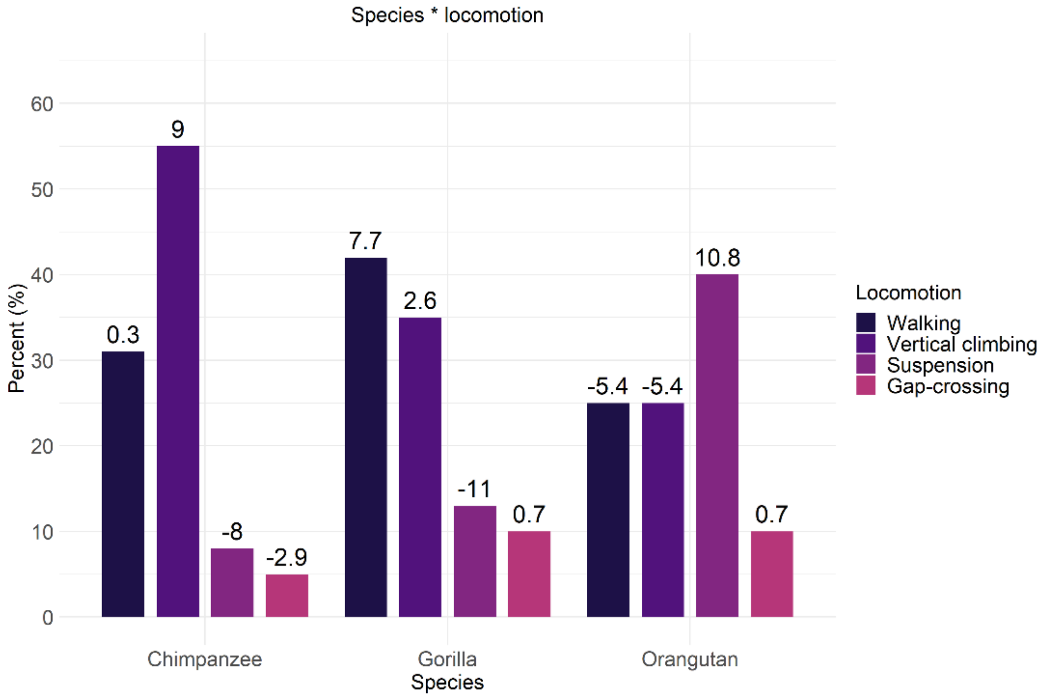

Figure 3.2: Model interaction between species and locomotion. Values above the bars are standardised cell residuals.

*Species * height*

Each species exhibited variation in the heights used. The African apes locomoted when off the ground predominantly at heights of less than 10 meters. However, the chimpanzees used heights above 20 meters more than the gorillas. The orangutans locomoted mostly at heights of 10-20 meters, followed by heights of above 20 meters, and only used heights of less than 10 meters 9% of the time. The SCRs show that the African apes used heights of above 10 meters less than predicted by the model (see Figure 3.3), but lower heights more than predicted (SCR= 14.8 for chimpanzees and 21.2 for gorillas). This was contrary for orangutans, who used heights of less than 10 meters less than predicted (SCR= -20.5) but heights above 10 meters more than predicted.

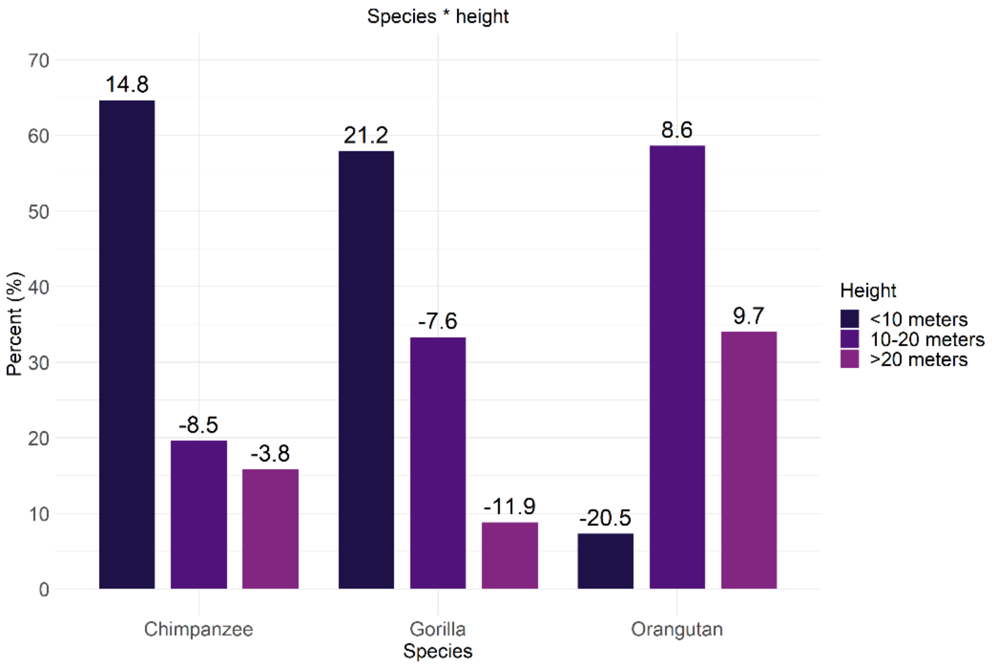

Figure 3.3: Model interaction between species and height. Values above the bars are standardised cell residuals.

*Body size * locomotion * height*

Body size was associated with variation in locomotor behaviours at different heights, as shown in Table 3.6. The general trends showed that overall, larger apes (BSC1+2) spent less time at heights of more than 20 meters than smaller apes (BSC3+4): at these heights, larger apes engaged in walking the most (exclusively for BSC1) and smaller apes walked and used suspension in similar frequencies. Larger apes engaged in vertical climbing the most at heights of less than 10 meters, but smaller apes used vertical climbing the most at heights 10-20 meters. The largest group engaged in gap-crossing the most at heights of less than 10 meters, but all other groups gap-crossed the most at heights 10-20 meters, and the smallest group gap-crossed more than all larger apes at heights of more than 20 meters.

The SCRs show that large apes (BSC1+2) engaged in walking more than predicted by the models at heights less than 10 meters. All apes, except for BSC4, engaged in walking more than predicted at heights of more than 20 meters (SCR=2.1, 2.8 and 2.4 respectively for BSC1,2 and 3). At heights of more than 20 meters, BSC4 used suspension and gap-crossing more than predicted (SCR=2.5 and 2.1). At mid-heights, larger apes engaged in suspension less than predicted (SCR=-2.3 and -2.5) but smaller apes engaged in suspension more than predicted (SCR=4.7 and 4.2).

Table 3.6: Contingency table for the interaction between body size, locomotion, and height. Figures represent the row % and (column %) for each interaction within the body size group E.g., for BSC1, this group walked at heights of less than 10 meters 74.2% of the time, and 40.4% of locomotion at this height category was walking. White cells signify that the SCR of the interaction was within the predicted range by the model. Coloured cells indicate whether the interaction fell below or above the predicted range (see key).

	Body size group		*Height (meters)*			
		Locomotion	<10	10-20	>20	Total
BSC1	Silverback gorilla	Walking	🟦 74.2(40.4)	19.4(19.4)	🟦 6.5(100)	34.5
		Vertical climbing	61.0(43.9)	🟦 39.0(51.6)	0	45.6
		Suspension	🟧 37.5(5.3)	🟧 62.5(16.1)	0	8.9
		Gap-crossing	🟦 60.0(10.5)	40.0(12.9)	0	11.1
		Total	63.3	34.4	2.2	100
BSC2	Female gorilla Blackback gorilla Male orangutan	Walking	🟦 45.6(44.9)	34.3(33.9)	🟦 20.1(39.5)	39.4
		Vertical climbing	45.8(35.8)	40.8(32.0)	🟧 13.4(20.9)	31.3
		Suspension	🟧 21.9(11.2)	🟧 44.3(22.7)	33.8(34.4)	20.4
		Gap-crossing	36.8(8.1)	51.6(11.4)	🟧 11.6(5.1)	8.9
		Total	40.1	39.9	20.0	100
BSC3	Subadult male orangutan Female orangutan Male and female chimpanzee	Walking	26.7(26.4)	🟧 35.7(19.9)	🟦 37.6(37.0)	26.1
		Vertical climbing	🟦 36.8(47.0)	42.8(30.8)	20.5(26.0)	33.8
		Suspension	🟧 16.6(19.9)	🟦 56.7(38.4)	26.7(32.0)	31.8
		Gap-crossing	21.5(6.7)	🟦 62.3(10.9)	🟧 16.2(5.0)	8.2
		Total	26.5	47.0	26.6	100
BSC4	Adolescent orangutan Adolescent gorilla	Walking	26.6(30.4)	🟧 46.4(25.3)	33.0(35.3)	29.0
		Vertical climbing	25.5(36.6)	52.8(27.8)	🟧 21.6(22.4)	28.1
		Suspension	🟧 12.0(2.01)	🟦 58.9(36.2)	🟦 29.0(35.1)	32.8
		Gap-crossing	24.7(12.8)	55.9(10.7)	🟦 19.4(7.3)	10.2
		Total	19.6	53.3	27.1	100

🟦	SCR= > +2
🟧	SCR= < -2

3.4.2 Support use models: type, diameter, and no. of supports with species and body size

Separate models for body size and species analysed support use. Three models for body size and species included the interactions between locomotion with support variables: type, diameter and number of supports. Models were separated like this because of multicollinearity between support use variables. Species and body size were limited to just orangutan and gorilla data, as differences in the methods used to collect data for chimpanzees meant that they could not be included in the analysis.

Table 3.7 shows the interaction terms between variables in each model, and whether they were retained or removed during the analysis process. Species was associated with variation in locomotion and number of supports, support type and support diameter. Conversely, body size was only associated with variation in locomotion and number of supports. The two-way interactions between body size with support type and support diameter, however, suggest that there is an association between body size and these support variables, but the variation was not also dependent on locomotor behaviour.

Table 3.7: Poisson GLM model results for interactions between type, diameter and number of supports with species and body size for orangutans and gorillas.

	Interactions	df	Deviance	*p*-value
Species	Species * Locomotion * No. of supports			
	Species*Locomotion*No. of supports	6	50.4	**<.001**
	Species*No. of supports	2	259.5	**<.001**
	Species*Locomotion	3	295.2	**<.001**
	Locomotion*No. of supports	6	135.5	**<.001**
	Species * Locomotion * Support type			
	Species*Locomotion*Support type	12	81.6	**<.001**
	Species*Support type	5	300.1	**<.001**
	Species*Locomotion	3	317.2	**<.001**
	Locomotion*Support type	15	250.2	**.034**
	Species * Locomotion * Support diameter			
	Species*Locomotion*Support diameter	21	98.4	**<.001**
	Species*Support diameter	7	264.5	**<.001**
	Species*Locomotion	3	313.8	**<.001**
	Support diameter*Locomotion	21	377.1	**.003**
Body size	Body size * Locomotion * No. supports			
	Body size*Locomotion*No. supports	18	47.1	**.002**
	Body size*No. of supports	6	76.31	**<.001**
	Body size *Locomotion	9	106.1	**<.001**
	Locomotion*No. of supports	6	158.1	**.002**
	Body size * Locomotion * Support type			
	Body size *Support type	12	100.6	**<.001**
	Body size*Locomotion	9	131.4	**<.001**
	Locomotion*Support type	15	278.8	**<.001**
	Removed interactions:			
	Body size*Locomotion*Support type	36	68.3	.264
	Body size * Locomotion * Support diameter			
	Body size*Support diameter	21	159.4	**<.001**
	Body size*Locomotion	9	114.3	**<.001**
	Support diameter*Locomotion	21	454.3	**<.001**
	Removed interactions:			
	Body size*Locomotion*Support diameter	54	101.9	.035

*Species * locomotion * number of supports*

The number of supports used during different locomotor behaviours was distinct between the gorillas and orangutans (Table 3.8). For all locomotor behaviours, the gorillas used a single support the most, and >4 supports the least. Conversely, whilst the orangutans exhibited a similar pattern when walking and vertical climbing, they showed more variation in the number of supports used during suspension and gap-crossing. The orangutans engaged in suspension the most on a single support, followed by >4 supports, whereas they gap-crossed mostly using >4 supports. When walking, the gorillas use 2-4 supports and >4 supports more than predicted by the model (SCR=6 and 3.3 respectively), whereas the orangutans used >4 supports less than predicted (SCR=-4.9). The gorillas and orangutans both used >4 supports less than expected when engaging in vertical climbing, but the gorillas used a single support more than expected (SCR=7.5). When gap-crossing, the number of supports used by the gorillas fell within the frequencies predicted by the model, but the orangutans used a single support less than predicted (SCR=-5.7) but >4 supports more than expected (SCR=6.1).

Table 3.8: Contingency table for the interaction between species, locomotion, and number of supports. Figures represent the row % and (column %) for each interaction. White cells signify that the SCR of the interaction was within the predicted range by the model. Coloured cells indicate whether the interaction fell below or above the predicted range (see key).

		No. of supports			
	Locomotion	1	2-4	>4	Total
Gorilla	Walking	58.2(33.9)	31.3(51.2)	10.4(50.0)	39.4
	Vertical climbing	78.6(45.7)	18.7(30.5)	2.7(13.1)	39.3
	Suspension	62.1(10.4)	19.8(9.3)	18.1(25.0)	11.4
	Gap-crossing	68.3(10.0)	21.8(8.9)	9.9(11.9)	9.9
	Total	67.6	24.1	8.2	100
Orangutan	Walking	43.8(27.6)	34.7(30.1)	21.6(19.8)	26.1
	Vertical climbing	45.8(28.8)	33.8(29.1)	20.4(18.6)	26.0
	Suspension	42.3(40.0)	24.7(32.1)	30.1(45.4)	39.2
	Gap-crossing	17.0(3.6)	30.1(8.7)	52.9(6.2)	8.7
	Total	41.4	30.1	28.5	100

🟦 SCR= > +2
🟧 SCR= < -2

*Body size * locomotion * number of supports*

Body size was associated with variation in locomotor behaviours and the number of supports used, as shown in Table 3.9. The general trends showed that overall, all body size categories walked and vertically climbed mostly on a single support and engaged in these behaviours the least on >4 supports. The largest body size group used >4 supports exclusively during walking, whereas smaller apes used >4 supports the most during suspension and gap-crossing. The smaller apes (BSC3+4) gap-crossed mostly using >4 supports, but larger apes (BSC1+2) gap-crossed the most on a single support.

The SCRs showed that when vertical climbing, BSC1,2 and 4 used a single support more than predicted by the models (SCR=2.6,4.6 and 2.0), but used >4 supports less than predicted (SCR=-2.9, -4.9, -3.3). BSC3+4 used a single support less than predicted when gap-crossing (SCR=-3.6 and -3.1), but >4 supports more than predicted (SCR=4.9 and 5.4).

Table 3.9: Contingency table for the interaction between body size, locomotion, and number of supports. Figures represent the row % and (column %) for each interaction. White cells signify that the SCR of the interaction was within the predicted range by the model. Coloured cells indicate whether the interaction fell below or above the predicted range (see key).

	Body size group		*No. supports*			
BSC1	Silverback gorilla	*Locomotion*	1	2-4	>4	Total
		Walking	45.8(21.2)	37.5(50.0)	16.7(100)	32.4
		Vertical climbing	🟦 78.9(57.7)	21.1(44.4)	🟧 0	51.4
		Suspension	83.3(9.6)	16.7(5.6)	0	8.1
		Gap-crossing	100(11.5)	0	0	8.1
		Total	70.3	24.3	5.4	100
BSC2	Female gorilla Blackback gorilla Male orangutan	Walking	56.7(35.5)	30.0(43.0)	🟧 13.4(29.1)	36.3
		Vertical climbing	🟦 68.4(40.2)	22.9(30.8)	🟧 8.7(17.7)	34.1
		Suspension	47.2(17.3)	🟧 19.4(16.4)	🟦 33.3(42.6)	21.3
		Gap-crossing	48.6(6.9)	30.0(9.8)	21.4(10.6)	8.3
		Total	58.0	25.3	16.7	100
BSC3	Subadult male orangutan Female orangutan Male and female chimpanzee	Walking	46.7(29.2)	34.2(27.0)	19.2(18.6)	25.7
		Vertical climbing	49.6(31.3)	32.2(25.7)	18.2(17.8)	25.9
		Suspension	🟧 36.1(35.0)	32.1(39.1)	🟦 31.8(47.8)	39.7
		Gap-crossing	🟧 21.0(4.4)	30.9(8.1)	🟦 48.1(15.8)	8.7
		Total	41.0	32.5	26.4	100
BSC4	Adolescent orangutan Adolescent gorilla	Walking	46.2(27.9)	🟦 35.0(37.3)	18.8(23.1)	29.3
		Vertical climbing	🟦 55.8(33.6)	29.1(30.9)	🟧 15.0(18.4)	29.2
		Suspension	49.5(32.2)	🟧 19.9(22.8)	🟦 30.6(40.7)	31.6
		Gap-crossing	🟧 31.3(6.3)	25.3(9.0)	🟦 43.3(17.9)	9.8
		Total	48.6	27.6	23.8	100

🟦	SCR= > +2
🟧	SCR= < -2

*Species * locomotion * support diameter*

The diameter of supports used during different locomotor behaviours was distinct between the gorillas and orangutans (Table 3.10). The gorillas walked slightly more on supports >20cm than other support types, whereas the orangutans walked mostly on 10-20cm supports and branch bundles. The gorillas also used >20cm supports during vertical climbing, compared to the orangutans, who climbed vertically mostly using 4-10cm supports and bundles. The gorillas engaged in vertical climbing and gap-crossing on 4-10cm supports, whereas the orangutans, again, used branch bundles.

The SCRs indicated that the gorillas used supports smaller than 10cm less than predicted by the model during walking and vertical climbing. However, both species used 0-4cm supports more than predicted when gap-crossing (SCR= 2.2 for orangutans and 3.4 for gorillas). The largest supports (>20cm) were used more than predicted during walking and vertical climbing for the gorillas (SCR=4.8 and 11.7), however, both species used these supports less than predicted during suspension and gap-crossing.

Table 3.10: Contingency table for the interaction between species, locomotion, and support diameter. Figures represent the row % and (column %) for each interaction. White cells signify that the SCR of the interaction was within the predicted range by the model. Coloured cells indicate whether the interaction fell below or above the predicted range (see key).

🟦 SCR= > +2
🟧 SCR= < -2

		Support diameter (cm)							
	Locomotion	0-4	4-10	10-20	>20	Mix <20	Mix >10	Bundles	Total %
Gorilla	Walking	🟧 6.3(31.8)	🟧 15.4(31.9)	17.5(37.3)	🟦 22.2(38.5)	🟦 19.4(47.7)	🟦 3.7(59.3)	🟧 15.4(55.0)	40.3
	Vertical climbing	🟧 5.1(24.7)	🟧 16.3(32.4)	🟦 23.5(48.3)	🟦 35.0(58.3)	13.6(32.2)	1.5(22.2)	🟧 5.1(17.5)	38.8
	Suspension	13.6(18.8)	🟦 34.7(19.8)	12.7(7.5)	🟧 1.7(0.8)	18.6(12.6)	0	18.6(18.3)	11.1
	Gap-crossing	🟦 20.4(24.7)	🟦 32.0(15.9)	13.6(7.0)	🟧 5.8(2.4)	12.6(7.5)	🟦 4.9(18.5)	🟧 10.7(9.2)	9.8
	Total %	8.0	19.5	18.9	23.3	16.4	2.5	11.3	100
Orangutan	Walking	9.1(22.5)	🟧 16.6(18.8)	🟦 20.1(36.3)	16.3(46.7)	14.9(30.5)	0.8(41.7)	22.2(19.9)	26.2
	Vertical climbing	9.7(23.4)	23.9(26.4)	15.0(26.4)	14.2(39.5)	15.2(30.2)	0.7(33.3)	21.3(18.6)	25.5
	Suspension	11.3(41.8)	🟦 27.8(47.3)	13.5(26.6)	🟧 3.2(13.8)	🟧 10.2(31.2)	🟧 0.3(25.0)	🟦 33.7(45.3)	39.3
	Gap-crossing	🟦 14.6(12.3)	19.5(7.5)	🟧 1.0(0.6)	🟧 0	11.7(8.1)	0	🟦 53.2(16.2)	8.9
	Total %	10.6	23.1	14.5	9.1	12.8	0.5	29.3	100
Chimpanzee	Total %	23.6	26.0	21.2	29.1	-	-	-	100

Chimpanzee support diameter (for primary weight-bearing support) is also documented.

*Body size * support diameter*

Although not associated with specific locomotor behaviours, each body size category exhibited variation in the size of supports used, as shown in Table 3.11. BSC1 used the largest supports (>20cm) more than smaller apes, and BSC4 used them the least. Conversely, larger apes (BSC1+2) used the smallest supports (<4cm) less than smaller apes (BSC3+4). Supports that were 4-10cm were used the most by BSC2, but the least by BSC1.

The SCRs showed that larger apes used the largest supports more than predicted (SCR= 4.2 for BSC1 and 3.6 for BSC2), and BSC4 used them less than predicted by the model (SCR=-2.0). The smallest body size group used the smallest support size more than predicted (SCR=4.5): whilst BSC2 used supports 0-4cm less than predicted (SCR=-4.9), BSC1 and 3 used supports 4-10cm less than predicted (SCR= -2.6 and -2.1 respectively).

Table 3.11: Contingency table for the interaction between body size and support diameter. Figures represent the row % and (column %) for each interaction. White cells signify that the SCR of the interaction was within the predicted range by the model. Coloured cells indicate whether the interaction fell below or above the predicted range (see key).

🟦 SCR= > +2
🟧 SCR= < -2

	Support diameter (cm)							
Body size	0-4	4-10	10-20	>20	Mix <20	Mix >10	Bundles	Total %
BSC1	7.8(1.8)	7.8(0.8)	24.7(3.6)	31.2(5.3)	18.2(3.0)	2.6(5.1)	7.8(0.7)	2.3
BSC2	4.6(12.0)	24.9(29.0)	17.8(28.6)	18.0(33.9)	13.5(24.7)	2.4(53.8)	18.8(20.2)	25.5
BSC3	9.0(24.6)	18.7(23.2)	16.7(28.6)	12.2(24.5)	15.3(29.8)	0.9(20.5)	27.3(31.2)	27.2
BSC4	13.5(61.6)	22.8(47.0)	13.8(39.3)	10.9(36.3)	13.2(42.6)	0.5(20.5)	25.2(47.8)	45.0
Total %	9.9	21.9	15.9	13.5	13.9	1.2	23.7	100

*Species * locomotion * support type*

Table 3.12 shows the percentage of time that the gorillas and orangutans spent using different support types for each locomotor behaviour. During all locomotor behaviours, both species used tree branches the most, with the exception of gap-crossing by orangutans, where branch bundles were used the most. When vertical climbing, after tree branches, the gorillas used lianas the most, whereas the orangutans used both branch bundles and lianas. The gorillas used tree trunks (in combination with other support types) mostly when walking and vertical climbing, but not when engaging in suspension; conversely, the orangutans used tree trunks rarely when walking, but in similar frequencies for other locomotor behaviours. Branch bundles were used mostly when walking for the gorillas, but the orangutans used bundles mostly when engaging in suspension.

When walking, the gorillas used tree branches more than predicted by the models (SCR=5.6), but lianas less than predicted (SCR=-5.8). The orangutans used liana/branch combinations and trunks less than predicted when walking (SCR= -2.3 and -3.2). Both species used lianas more than predicted when vertical climbing (SCR=2.3 for gorillas and 8.0 for orangutans), but the gorillas vertically climbed less than predicted using branch bundles (SCR=-8.0). Whilst the gorillas used liana/branch combinations more than predicted during suspension (SCR=6.1), the orangutans used branch bundles more than predicted (SCR=7.6). Gap-crossing was used by gorillas less than predicted on branch bundles (SCR= -3.2), whereas the orangutans used tress branches and lianas less than predicted to cross gaps (SCR= -5.3 and -3.2 respectively).

Table 3.12: Contingency table for the interaction between species and support diameter. Figures represent the row % and (column %) for each interaction. White cells signify that the SCR of the interaction was within the predicted range by the model. Coloured cells indicate whether the interaction fell below or above the predicted range (see key).

		Support type					
	Locomotion	Branch	Bundles	Liana	Liana and branch	Trunk Mix	Total
Gorilla	Walking	🟦 80.9(43.8)	11.7(55.0)	🟧 2.7(15.8)	3.2(30.0)	1.6(40.9)	42.1
	Vertical climbing	🟦 75.7(34.2)	🟧 4.5(17.5)	🟦 14.3(70.5)	3.0(23.3)	2.6(54.5)	35.1
	Suspension	71.1(11.8)	12.7(18.3)	🟧 4.0(7.4)	🟦 12.1(35.0)	0	12.9
	Gap-crossing	🟦 81.1(10.3)	🟧 8.4(9.2)	4.6(6.3)	5.3(11.7)	0.8(4.5)	9.9
	Total	77.8	9.0	7.1	4.5	1.6	100
Orangutan	Walking	67.4(33.1)	21.7(19.9)	8.8(18.0)	🟧 1.8(15.9)	🟧 0.2(2.0)	26.3
	Vertical climbing	🟧 52.1(25.1)	20.7(18.6)	🟦 21.3(43.0)	3.0(26.1)	3.0(35.3)	25.8
	Suspension	🟧 49.5(36.3)	🟦 33.1(45.3)	11.9(36.7)	3.9(52.2)	1.5(27.5)	39.2
	Gap-crossing	🟧 33.0(5.4)	🟦 52.9(16.2)	🟧 3.4(2.3)	1.9(5.8)	🟦 8.7(35.3)	8.8
	Total	53.4	28.7	12.8	2.9	2.2	100
Chimpanzee	*Total*	41.0	0.5	10.4	-	48.1	100

🟦 SCR= > +2
🟧 SCR= < -2

*Body size * support type*

Although not associated with specific locomotor behaviours, each body size category exhibited variation in the type of supports used. All body size categories used branches more than any other support type and tree trunks the least. The larger apes (BSC1+2) used branches more than smaller apes (BSC3+4), but branch bundles and lianas less than smaller apes. The SCRs showed that BSC1 and 2 used branch bundles in frequencies less than predicted by the models (SCR=-3.1 and -3.4), whereas BSC3 used them more than predicted (SCR= 3.3). Lianas were used within the expected frequencies for both BSC1 and BSC4, but BSC2 used them less than predicted (SCR=-4.0) and BSC3 used then more than predicted (SCR= 2.4). Liana and branch combinations and tree trunks were used within the expected range for all body size categories.

Table 3.13: Contingency table for the interaction between body size and support diameter. Figures represent the row % and (column %) for each interaction. White cells signify that the SCR of the interaction was within the predicted range by the model. Coloured cells indicate whether the interaction fell below or above the predicted range (see key).

	Support type					
Body size	Branch	Bundles	Liana	Liana and branch	Trunk Mix	Total %
BSC1	77.8(3.0)	6.7(0.7)	5.6(1.3)	6.7(4.6)	3.3(4.2)	2.4
BSC2	71.2(31.7)	15.8(20.2)	7.5(19.4)	3.4(26.9)	2.1(29.2)	27.6
BSC3	53.1(21.7)	26.7(31.2)	13.3(31.5)	4.3(30.8)	2.7(34.7)	25.4
BSC4	60.9(43.7)	23.2(47.8)	11.5(47.9)	3.0(37.7)	1.4(31.9)	44.6
Total %	62.2	21.6	10.7	3.5	1.9	100

🟦 SCR= > +2
🟧 SCR= < -2

3.5 Discussion

Chimpanzees, gorillas and orangutans differ in their biology, morphology and the habitats that they occupy. They also exhibit considerable body size variation; the silverback gorilla weighed approximately 170kg, which is around four times the weight of female chimpanzees and five times the weight of adolescent gorillas and orangutans. However, in complex arboreal environments, they have to solve the same ecological challenges of accessing, moving around and dealing with gaps in the canopy. Determining whether species-related diversity and/or body size-related diversity drives the variation in their arboreal locomotor ecology is an effective approach to understanding the relationship between morphology, ecology and expressed behaviour in complex environments. The arboreal locomotor repertoire of chimpanzees, gorillas and orangutans encompasses not only the locomotor behaviours that they engage in, but also the supports that they use, the heights that they occupy in the trees, and the strategies exploited to reduce energy expenditure and mitigate the risk of falling. In this study, it was found that body size and species were influential in driving an overall variation in locomotor behaviours, but it was body size that shaped the variation in locomotor behaviours at different heights in the canopy. Whilst body size influenced the overall size and type of supports used, all the apes used the same supports for each locomotor behaviour. However, the gorillas and orangutans used different supports when engaging in the same locomotor behaviour, such as walking or vertical climbing (chimpanzee data was not included in support use models).

Body size as a confounding factor that shapes the arboreal repertoire of great apes has been broadly discussed in the literature, in the contexts of the size of supports used, the biomechanics of locomotion, and the energetic demands of certain behaviours (Avis, 1962; Cartmill, 1974a; Cartmill & Milton, 1977; Fleagle, 1980; Fleagle & Mittermeier, 1980; Hunt, 1991; Cant, 1992; Remis, 1995). The body weight of great apes imposes constraints on their arboreal behaviours, affecting the energy expenditure of different locomotor behaviours and a species' ability to use supports that vary in size and compliancy (Hunt, 1994). Energy expenditure is the most essential aspect that shapes the use of arboreal environments for great apes (Steudel, 1994); it would be ineffective if apes, which rely on arboreal resources, have the morphological mechanisms to move in the trees, but do not have the energy to do so (Harvey & Clutton-Brock, 1981). Larger primates have a lower basal metabolic energy rate, but the total energetic cost of locomotion is high because of the scaling of body surface area and muscle power (Warren & Crompton, 1998; Pontzer et al., 2014; Pontzer, 2015). However, relative to their body size, large primates often exhibit more efficient muscle leverage allowing them to move with less energy per kilogram of body weight (McNab, 1978; Jungers, 1984). It was found here that larger-boded great apes did not engage in arboreal locomotion that is typically less metabolically demanding. In addition to energetic expenditure, both experience and an overall reduction in activity also likely play a significant role in the cost of locomotion for primates (Leonard & Robertson, 1997; Pontzer & Wrangham, 2004; Pontzer, 2015). The larger great apes might not have engaged in less metabolically expensive locomotor behaviours than smaller apes because they may instead have developed more efficient movement patterns or learned the most effective routes when travelling in the trees to minimise energy expenditure to offset the cost of locomotion because of their size. Furthermore, it might also be that the larger-bodied apes were able to allocate energy for high-demanding arboreal behaviours because the benefit of accessing highly nutritious resources might outweigh the cost of getting to them. This is one of the key aspects of the optimal foraging theory, that primates will forage for food sources which offer the highest energy return relative to the effort and calories expended in accessing and obtaining food (Martin, 1983; Schoener, 1987; Garber, 1987). This in turn, might influence the way that energy is expended in the trees of apes of different body sizes.

The expectation that large body size would be accompanied by more suspension and bridging (Cartmill & Milton, 1977; Fleagle & Mittermeier, 1980) but less vertical climbing and leaping (Garber & Easley, 1984; Fleagle, 1985; Cant, 1992) was not supported in this study. Instead, larger great apes used suspension and briging much less than smaller apes. The variation in suspension was particularly distinct, accounting for 33% of the arboreal repertoire for the smallest apes (adolescent gorillas and orangutans), 31% for BSC3 (subadult orangutan and chimpanzees), 20% for BSC2 (female gorillas, male orangutan and blackback gorilla), but only 9% for the largest body size group (silverback gorilla). This contradicts the classic theory, which implies that suspension is less- risky for large apes because they have essentially already ‘fallen-off’ the support (Cartmill & Milton, 1977), and that relative to the diameter of the support, larger primates will be forced to hang below the support rather than balance on top of it (Napier, 1967; Cartmill, 1974a; 1985; Gebo, 1996). Furthermore, when crossing gaps in the canopy, smaller apes used bridging more than larger apes, whereas larger apes leaped more than smaller individuals; these patterns again contradict general predictions (Napier, 1967; Gebo, 1987; Demes & Günther, 1989). Leaping is highly energetically demanding. As a result, leaping primates possess specialisations towards this behaviour (such as highly abducted and externally rotated thighs and strong, elastic hindlimb musculature) (Napier & Walker, 1967; Demes, Fleagle & Jungers, 1999; Crompton et al., 2010). However, although great apes are less specialised in their morphology to allow for rare behaviours such as leaping, it is considerably more energetically taxing for larger apes because they have less muscle force per unit mass (Demes et al., 1995). Conversely, bridging is more stable and less metabolically taxing than leaping, as there is no period of free-flight produced by hindlimb propulsion (Hunt et al., 1996), but the larger apes used this to cross gaps much less than smaller apes. Finally, contradicting body size predictions, vertical climbing accounted for 46% of the arboreal repertoire of the largest body size group, compared to only 28% for the smallest group. Climbing is energetically less expensive for smaller apes than larger-boidied apes because of the metabolic cost and muscle excertion relative to their size (Cartmill, 1972; Cartmill & Milton, 1977). Body size is clearly associated with variation in locomotor behaviours which suggests that the requirement to access resources drives them to use behaviours that are risky and challenging.

Great apes of different sizes and weight must have the physical capacity and energy to engage in different locomotor behaviours, especially if the behaviours are vital for survival. However, they must also have the ability to exploit different arboreal habitats, such as different heights in the canopy. Nutritional resources are often located higher in the canopy, so this capability must also be selected for, for small and large apes. However, as height increases, so does the consequences of falling from height, especially for larger apes who have a higher chance of fatality because the kinetic energy that the body has to dissipate upon impact increases (Cartmill & Milton, 1977; Preuschoft, Schönwasser & Witzel, 2016). At higher elevations in the trees, larger apes must find a compromise between stability and security on unpredictable supports, and the most energetically efficient locomotion. As it was found that energetics may have been outweighed by the requirement to access nutritional resources, this then raises the question as to how apes of different body size deal with risk, and whether risk is also outweighed by the requirement to achieve the goal of feeding. Alongside energetics, risk sensitivity is something that all arboreal primates must address. There is a balance between accessing highly nutritious food in the trees and the risks that are involved in achieving this goal, especially for larger apes when moving on supports that are small and unpredictable. Whilst overall, larger apes spent less time at heights above 20 meters, when they used these heights, they engaged mostly in walking. Smaller apes used suspension as often as walking at these heights and crossed gaps more than larger apes. The characteristic unpredictability and sparsity of supports above 20 meters is not as much of a challenge for smaller apes, and this is supported in their strategies to navigate around higher levels in the canopy.

Whilst locomotion is directly related to energetics, and height may be associated with variation in risk, the supports used by apes of different sizes can perhaps help to minimise energy expenditure and reduce risks. The prediction that smaller individuals will tend to use smaller supports more than larger individuals was supported here (Avis, 1962; Cartmill, 1974b; Cartmill & Milton, 1977; Fleagle, 1980; Hunt, 1991; Cant, 1992; Remis, 1995; Larson, 2018). Larger apes used large supports (>20 cm) three times more often than smaller apes, whereas smaller apes used small supports (4-10cm) almost three times more than larger apes. A support is only “large” or “stable” relative to their body size (Avis, 1962), so this variation in size does not mean that apes use *absolutely* larger supports, but instead, all apes effectively used supports that were large-enough and stable-enough. However, despite this overall trend in support size, the apes used supports of similar size when using the same locomotor behaviours. When engaging in walking, the apes used medium supports (10-20cm) most often, but when using vertical climbing, they used small supports and when engaging in suspension and gap-crossing, small supports were used most often. The variation in locomotor behaviours between apes of different sizes in this study was not driven by supports of various sizes, nor was the size of supports used in the trees the reason for apes of different body size to engage in different locomotor behaviours. It has been hypothesised that, especially for locomotor behaviours that require enhanced stability like suspension, that larger apes would use larger supports than smaller apes (Cartmill & Milton, 1977; Cartmill, 1985). Apes of different sizes instead exhibited a shared capacity to engage in the same locomotor behaviours on the same sized supports. This was also true for the type of supports used; larger apes showed an overall stronger preference for branches, whereas smaller apes used lianas and branch bundles (clusters of small branches) more, but these did not vary for each locomotor behaviour. This suggests that different modes of arboreal locomotion are likely characterised by the use of specific supports, and that larger apes are not constrained in their ability to locomote because of the supports, or limited in their use of supports because of the locomotion required. Throughout evolution, as a consequence of selective pressures, larger apes have undergone natural selection which favoured a larger body size within their ecological niche (Shea, 1983; Pickford, 1986). However, they would have still needed to maintain the ability to exploit smaller, compliant supports in order to access food resources in the trees, ensuring their evolutionary success.

Whilst the variation in energy expenditure of different body size groups was not expressed as expected in their arboreal locomotor strategies, the strategies used to conserve energy was instead perhaps a reflection of species-specific morphological adaptations. Energy consumption during locomotion is known to vary not only with body size, but also with species (see e.g. Wheately, 1982; Warren & Crompton, 1998; Snodgrass, Leonard & Rovertson, 2007; Pontzer et al., 2010; Raichlen, Gordon & Sechrest, 2011). The biggest difference between gorillas, chimpanzees and orangutans is that orangutans are almost exclusively arboreal: in fact, when on the ground, they are described as clumsy in their locomotion (MacKinnon, 1974). Whilst the African apes spend a considerable amount of their time travelling and feeding terrestrially (Hunt, 1992; Doran, 1992; Remis, 1995; D’ Aout et al., 2004; Thorpe & Crompton, 2005; Chapter Two), orangutans have to address all of the challenges of travelling and feeding in the trees without coming to the ground. Orangutans therefore experience consistent high energetic and nutritional demands (acquiring essential nutrients to supports their energetic requirements) (Mitani, 1989; Thorpe, Holder & Crompton, 2009; Pontzer et al., 2010; Vogel et al., 2017). The African apes, which regularly travel between the ground and the canopy will experience significant energetic repercussions because of the energetic demands of accessing and negotiating arboreal environments (although the amount of energy used when in arboreal environments is still not fully known (Elton, Foley & Ulijaszek, 1998)) when they possess only retained adaptations towards arboreal locomotion (Pontzer & Wrangham, 2004; Kozma, 2020). Interspecific comparisons of locomotor behaviour revealed a strong correlation between morphological adaptations towards a certain behaviour, and the frequency that this behaviour occurred. Unlike body size, species also influenced a variation in the number, type and size of supports within each locomotor behaviour which means that the strategies used by gorillas, chimpanzees and orangutans to address ecological challenges in different environments were linked to the supports being used.

The most prominent behaviour that distinguished the orangutans from the African apes was, unsurprisingly, the frequency of suspensory locomotion. Suspension accounted for 9% and 13% of the arboreal repertoires for chimpanzees and gorillas, compared to 40% for orangutans. Orangutans are adept at above-head suspension which is facilitated by postcranial musculoskeletal features such as a cranially-orientated glenoid fossa to allow for increased abducted forelimb mobility (Cant, 1987), relatively long forelimbs which provide a mechanical advantage to generate propulsion (Keith, 1923) and long, curved metacarpals and phalanges that provide larger muscular attachments which increase grasping strength (Napier, 1960; Tuttle, 1969; Susman, 1979). These musculoskeletal adaptations towards suspension are not as prominent for the African apes as they have been ‘traded’ for morphological adaptations towards terrestrial walking; selective pressure would have been exerted in favour of chimpanzees and gorillas becoming better able to exploit their most ‘local’ environment, the ground. However, this trade off towards postcranial adaptations for quadrupedal walking, such as long forelimbs relative to hindlimbs (Schultz, 1937; Fannin et al., 2023), a laterally orientated glenoid fossa (Hawkes & Wallis, 1916) and short, robust hands (Tuttle, 1967; Susman, 1979), has lead to the variation in the way in which they address the habitat challenge for which orangutans use suspension.

Whilst the orangutans used suspension to move around when in the canopy, the African apes used above-branch walking to solve the same problem: a variation which perhaos reflects their postcranial adaptations. Walking accounted for 25% of the orangutans' arboreal repertoire, compared to 31% and 42% for chimpanzees and gorillas respectively. Despite aboreal walking being more complex and energetically demanding than terrestrial walking, chimpanzees and gorillas have shown that they can effectively adapt their biomechanics and gait when walking arboreally to account for variation in support properties (Finestone et al., 2018; Tarrega-Saunders et al., 2021). Therefore, the adaptations towards terrestrial walking are likely transferable in arboreal environments and shape the way in which they move around in the canopy. However, when walking arboreally, the gorillas adopted bipedal postures 32% of the time, compared to 29% for the orangutans and only 4% for the chimpanzees (although Hunt (1991) noted chimpanzee bipedality to be higher in Mahale). Orthograde postures dominated the locomotor repertoire of orangutans (Thorpe & Crompton, 2005) and they also have the ability to fully extend (straighten) their legs (Susman, 1974). However, gorillas are mostly pronograde walkers (see Chapter Two), and lack the mechanisms to straighten their legs during bipedal postures (Redmond, 1995). This suggests that despite a variation in postcranial adaptations towards either pronograde or orthograde postures, orthograde postures in the trees are a shared behaviour of the great apes.

From the perspective of evolutionary history, this provides more evidence for the arboreal orthograde model (Crompton, Vereecke & Thorpe, 2008; Crompton, Sellers & Thorpe, 2010) as a more suitable precursor to bipedalism rather than the knuckle-walking model (Washburn, 1967). Whilst features associated with arboreal orthogrady have been documented for several hominin and crown hominoid fossils (Maclatchy et al., 2000; Senut et al., 2001; Haile-Selassie, 2001; Moyà-Solà et al., 2004; Lovejoy et al., 2009), the next step in understanding this behaviour was to understand arboreal orthogrady in extant species (Thorpe, McClymont & Crompton, 2014). Bipedalism is an important behaviour for chimpanzees and gorillas when foraging in the trees (Hunt, 1994; Chapter Two) and for orangutans to access the terminal branch niche where supports are compliant and thin (Thorpe, Holder & Crompton, 2007; Crompton, Sellers & Thorpe, 2010). Given that we now know that all the apes, including the large-bodied gorillas (which are generally the model species for the knuckle-walking hypothesis) engage in orthograde behaviours in the trees, this suggests that that orthograde postures are not exclusive to certain species of apes. The evolutionary shift towards bipedalism on the ground may indeed have transitioned from an orthograde posture in the trees (Thorpe, Holder & Crompton, 2007; Crompton, Sellers & Thorpe, 2010; Thorpe, McClymont & Crompton, 2014). This provides new evidence for the arboreal origins of human bipedalism (Keith, 1903; Thorpe, Holder & Crompton, 2007; Crompton, Sellers & Thorpe, 2010; Thorpe, McClymont & Crompton, 2014).

The reason that the gorillas engaged in such high frequencies of arboreal bipedality is instead perhaps linked to the type of supports that they were using and the strategies to mitigate the risk of falling. When the orangutans encountered extra small (0-4cm) and small supports (4-10cm) in the canopy, they used suspension twice as often as walking, whereas the gorillas used walking almost twice as often as suspension. Orangutans deal with small supports by using a mixture of orthograde and pronograde postures and a slow, irregular gait which reduces the flexion of supports (Thorpe, Crompton & Alexander, 2007; Thorpe, Crompton & Alexander, 2009; Thorpe & Crompton, 2005; Manduell et al., 2012). They also have more mobile joints which allow them to use more small supports within their sphere of reach (Hunt, 1991; Thorpe & Crompton, 2005) than the gorillas. This has perhaps been selected for to increase their efficiency in the trees considering they spend almost all their time arboreally. Small supports, therefore, are riskier for gorillas because of their relative size and hand morphology (Tuttle, 1969; Neufuss et al., 2017). However, when walking on them, they used bipedal postures (see also Chapter Two). Walking bipedally frees up the hands to hold supports above and to the side to aid balance and stability, which also mitigates the risk of falling because of branch breakage (Vereecke, D'Août & Aerts, 2006; O’Higgins & Elton, 2007; Crompton, Vereecke & Thorpe, 2008). If a small support were to snap under the weight of an individual, they could grasp supports with their hands to prevent them from falling. Supports larger then 20cm are less likely to break under the weight of great apes, so when encountering these supports in the canopy, both the gorillas and orangutans walked on them considerably more often than suspending underneath them. However, rather than species-specific anatomical traits which shape this shared behaviour, this instead reflects the mechanics inherent to suspension. Below-branch locomotion is only secure when the weight of the individual is supported by a robust hand grip (often accompanied by an opposed thumb) (Napier, 1960). Although orangutans have longer fingers compared to the relatively shorter fingers of gorillas (Susman, 1979; Almécija, Smaers & Jungers, 2015), supports larger than 20cm will be more challenging to travel underneath because they require greater grip strength. This highlights that postcranial morphology does not determine whether small supports *can* be used, but instead, that alternative strategies might be adopted which are associated with the relative morphologies of a species.

Further comparison of support types during suspension showed that gorillas and orangutans used different types of supports. After branches, which were the most common support type for both species, the orangutans used branch bundles (clusters of small branches) and lianas more than the gorillas, whereas the gorillas used lianas in combination with branches more than the orangutans. Lianas are able to support a considerable amount of weight (Cant et al., 1990), but they are flexible when they are not loaded in the direction parallel to the fibres of the liana (Thorpe, Holder & Crompton, 2009). Whilst orangutans can employ unique strategies to deal with branch compliance (Thorpe, Crompton & Alexander, 2007; Thorpe, Holder & Crompton, 2009; Myatt and Thorpe, 2011; Van Casteren et al., 2013; Chappell et al., 2015), the gorillas had to compensate for the flexibility of lianas during suspension by also using branches. To reduce the energy expenditure of travelling on lianas that oscillate, the gorillas used tree branches in combination to reduce the flexibility of them, making suspension less energetically costly. The Sumatran forests are more abundant with lianas than the African forests occupied by gorillas and chimpanzees (Cant, 1987; Williamson, 1989; Caldecott & Kapos, 2005; Manduell et al., 2012). Whilst the variation in support types used during suspension may reflect differences in locomotor behaviour at a species level, they could also reflect differences in forest structure and support availability, and the selective pressures to be able to use different arboreal supports. Over time, these selective pressures have been continuously changing due to the effects of climate and environmental change. However, the forests in Africa and Asia were impacted differently by climate change and periods of glaciation which would have led to evertransforming forest environments. The African forests experienced greater susceptible to environmental changes than the Asian forests, leading to the contraction of habitats into small refugia (Maley, 1996; Elton, 2008; Malhi et al., 2013). This reduced the populations' ability to adapt to shifting environmental pressures, contributing to decreasing species diversity and speciation as populations adapted to new ecological niches (Condit, Hubbell & Foster, 1996; Chapman et al., 1999). Conversely, the Asian forests (particualy in the Southeast) were impacted much less by glacial periods and climate fluctuation, meaning that the forests and other environments were more stable and continuous (Hassel-Finnegan et al., 2013). This stability would have favoured higher species richmenss and diversity. Orangutans which inhabit highly diverse forests may have experienced more ecological specialisation whereas the African apes which inhabit fragmented and variable forests may have faced more constraints. This may have led to differences in the evolution and adaptive strategies of great apes, which today are reflected in distinct strategies in the locomotor behaviours and supports used to move in the trees. Although suspensory adaptations were perhaps compromised because of the multiple selective pressures on their anatomy to facilitate terrestrial walking which was necessary in their local environment, the African apes still possess retained adaptations for climbing and suspension which facilitate access to arboreal environments to acquire resources (Pontzer & Wrangham, 2004). Although not as prevalent as for the orangutans, these include an opposable hallux (Aiello & Dean, 1990), mobile glenohumeral joints, strong forelimb and shoulder musculature (Myatt et al., 2012; Thompson, Rubinstein & Larson, 2018), curved metacarpals and phalanges, and strong forelimb flexor muscles (Sarmiento, 1988; Tuttle, 1969). However, whether these retained traits, which are costly to terrestrial locomotion, make vertical climbing for African apes more efficient is not fully understood. In a study of the relative energetics of chimpanzee locomotion, it was found that terrestrial travel was ten-times more energetically costly than vertical climbing (Pontzer & Wrangham, 2004), meaning that minimising energetic cost is perhaps not the driving force behind these retained adaptations. Instead, Pontzer and Wrangham (2004) suggest that mitigating the risk of falling was the primary reason for the retention of these arboreal adaptations. Opposable halluces and powerful forelimb muscles for example, allow for a better grasp of arboreal supports, reducing the chance of apes falling from the trees. The chimpanzees' arboreal repertoire was 55% vertical climbing compared to 35% for gorillas and 25% for orangutans. Vertical climbing may be less energetically costly than terrestrial locomotion for the great apes, but how it compares to other arboreal locomotion has not yet been determined: in fact, not enough is known about the energetic costs of arboreal activities to accurately compare the variation in energetics between locomotor behaviours (Elton, Foley & Ulijaszek, 1998). Given that vertical climbing was used the most by larger apes (in the body size models), but also the most by chimpanzees, this suggests that there is not a clear association between vertical climbing with either morphology or size. The variation in frequency of vertical climbing between the chimpanzees, orangutans and gorillas, might instead be correlated with the energetics of other arboreal locomotor behaviours. Hunt (1991) hypothesised that given the high metabolic cost and muscle exertion associated with vertical climbing, it is more energy efficient to cross gaps arboreally than descend and reascend to similar heights. The orangutans and gorillas engaged in less vertical climbing but crossed gaps in the trees twice as often as chimpanzees. Gap-crossing is inherently risky, and gaps are associated with small supports. Gap-crossing was observed in all apes 57% of the time at canopy heights between 10-20 meters. Chimpanzees do not expend considerable amounts of energy when engaging in vertical climbing (Pontzer & Wrangham, 2004), so returning to the ground, even from the main canopy, might outweigh the risk of using small supports to cross gaps.

Unlike suspensory locomotion and gap-crossing, which are typified by small supports, vertical climbing is possible on supports of various types and sizes. Whilst the size and type of supports did not vary for each locomotor behaviour (including vertical climbing) when accounting for variation in body size, it was found that there were interspecific differences in supports used when vertical climbing. Large, single supports were used during vertical climbing more than smaller supports by the gorillas, whereas the orangutans used multiple, small supports, often lianas. Ascending large vertical supports, which often lack horizontal branches, requires more muscular strength to propel the body upwards and increased compressive grip strength to avoid slipping down, often using extended-elbow forelimb positions (Cant, 1987; Isler, 2005; Nakano, Hirasaki & Kumakura, 2006; Neufuss et al., 2018). This is maybe more challenging for orangutans than gorillas, and likely reflects their adaptations towards suspension, such as a large range of motion of the shoulder joint which allows for increased levels of forearm abduction to reach higher, and long curved hands optimised for grasping smaller supports, but restrict hand contact on larger supports (Tuttle., 1967; Oxnard, 1967; Susman, 1979; Isler, 2005). Gorillas, on the other hand, exhibit a lesser degree of shoulder abduction which restricts their above-head reach when vertical climbing, and possess shorter digits (more similar to human hands), which allow for full hand-contact on large supports. Gorillas may therefore be distinct in their use of large supports when vertical climbing, which perhaps is motivated by their larger size and robust musculature. It has been documented that even large-bodied apes prefer to climb on small-diameter supports in the wild because of the mechanical advantage of flexed-elbow climbing because an individual can grip the support with just one hand (Cant, 1987; Hunt, 1992; Doran; 1993; Isler, 2005; Hanna & Schmitt, 2011). However, gorillas' use of large vertical supports could reflect a preference over small supports, or could instead reflect the availability of supports. The African apes spent the most amount of time locomoting at heights below 10 meters (compared to 10-20 meters for the orangutans), and for all apes at these heights, vertical climbing was the most dominant locomotor behaviour. What characterises the understory and facilitates the transition from the ground into the trees in all forests, is large tree trunks, which offer a direct vertical pathways to the canopy. Within the canopy, however, tree trunks are obscured by dense foliage, and lateral branches which make vertical climbing tree cores more compliacted, so routes further towards the periphery on lianas, or smaller branches may be simpler to navigate. If gorillas use larger vertical supports during vertical climbing, but orangutans use small, multiple supports and lianas, this may reflects their degree of arboreality. However, it might also reflect the variation in forest structure. The tropical forests in Asia are generally more species-rich and denser than those in Africa because they were impacted less by fluctuating climates (Maley, 1996; Elton, 2008). The forest canopies inhabited by orangutans are therefore more abundant with arboreal pathways, which might explain why the supports used differs between orangutans and gorillas; however, to fully understand this, we need to integrate more data on support availability.

One of the shared traits of all forests is that gaps in the canopy are typically characterised by small or sparse supports and this presents a complex arboreal challenge for all apes. The relationship between gap-crossing and body size was completely contrary to predictions based on energetics and risk factors, but interspecific variation in gap-crossing was mostly contingent on whether the chimpanzees, gorillas and orangutans engaged in oscillatory (‘ride’ and ‘sway’) gap-crossing or not. The chimpanzees used oscillatory locomotion the most, accounting for 74% of their gap-crossing locomotion, compared to 64% for orangutans and only 19%

for gorillas. Riding and swaying differ to leaping and bridging as they are a sequence of postures which result in locomotion because of movement of the support, rather than movement of the body (Van Casteren et al., 2013; Saunders, 2017). Oscillation of branches may often reduce the energetic cost of crossing a gap when compared to leaping or descending to the ground and reascending (Thorpe, Crompton & Alexander, 2007) and it relies on smaller, compliant branches or lianas. Orangutans are known for their ability to sway branches, which seems to have been selected for to allow them to move between different heights and trees without using considerable amounts of energy (Cant, 1987; Thorpe, Crompton & Alexander, 2007; Thorpe, Holder & Crompton., 2009; Manduell, Morrogh-Bernard & Thorpe, 2011; Van Casteren et al., 2013). Orangutans also live in forests that are typically more abundant and denser with foliage which may offer ample routes and available supports to be able to ride and sway on branches compared to the more fragmented forests inhabited by gorillas and chimpanzees. However, it was not previously known how the African apes' use of tree swaying or riding branches compared to that of the orangutans, and the direction of travel for which oscillation is employed. The orangutans ride and sway branches to move around in the trees, but the African apes might instead use it as a strategy to descend to the ground. Although they gap-crossed the least, when the chimpanzees did engage in gap-crossing, they use the least metabolically expensive strategy because an alternative approach to arrive at the other side of a gap is to descent and reascend by vertical climbing, which for them is not energetically demanding. This represents a potential trade-off between locomotor behaviours in order to address the challenge of gap-crossing in the most energetically efficient way with minimal risks.

Gap-crossing represents only a small percentage of the apes' arboreal repertoires, but the strategies used to address this challenge can shed light on the capabilities of a species, and the balance between energy efficiency and risk. This is of particular interest for non-oscillatory gap-crossing, which encompasses biomechanically distinct locomotor behaviours in different species. The orangutans used bridging to cross gaps four times more than using dropping behaviours and leaped only once, whereas the gorillas bridged and dropped 31% of the time when crossing gaps and leaped across gaps 18% of the time (non-oscillatory locomotion of chimpanzees only accounted for 5 observations). Bridging differs to leaping and dropping in that it is often characterised by a slow transfer across supports, so the weight-bearing capacity of supports is tested during the crossing (Hunt et al., 1996; Graham & Socha, 2020). Therefore, it is perhaps less risky, but not necessarily energy efficient if all four limbs are muscularly engaged (92% of observations for gorillas and 76% for orangutans) to contact supports and adjust for balance. Dropping and leaping are notable in sharing a period of free-flight, but dropping does not require muscular propulsion like leaping does, but instead is a downwards body movement as a result of gravity (Hunt et al., 1996; Chatani, 2003). Leaping was adopted primarily by primates as a mechanism to avoid predators through repeated changes of direction, but it is considerably expensive, especially on compliant supports that absorb much of the energy during take-off (Demes et al., 1995; Crompton & Sellers, 2007; Crompton et al., 2010; Gebo, 2011). Although leaping is not a strategy for extant gorillas to avoid predators, they still are able to perform this behaviour because of the retained adaptations associated with safety in arboreal environments; the use of leaping by gorillas was observed on many occasions as a strategy to quickly retreat after encountering wasp nests, and also to quickly move from a support that was breaking underneath their weight (see Chapter Two). Gorillas are large in size and weight, which makes gap-crossing on small supports particularly risky. It is difficult to determine the reason for their lack of caution when leaping and dropping to cross gaps. One theory may be that when moving in and between trees, they select the shortest, fastest travel route over the safest route because although they do not have highly specialised morphology for these behaviours, they still have the capacity to do so. It might, alternatively, be that gorillas are highly capable of complex behaviours. Body size is this study was not linked to decreased energy expenditure (as shown in the body size models), so perhaps now it is time to direct focus towards understanding more about what supports are available. Whilst we have a good understanding of the evolutionary changes of tropical forests because of climate change and how this led to intercontinental variability in species and population biodiversity (Maley, 1996; Elton, 2008), we know very little about whether this relates directly to the availability of structures for primates to travel on. This will enhance our understanding of whether arboreal behaviours of great apes reflect necessity or preference and the influence of the environment on how apes of different body sizes move in the trees.

3.5.1 Limitations

Now that more data was available, it was possible to examine the influence of body size and species on the locomotor ecology of great apes. However, the inherent limitations of the dataset used in this comparison suggest that some caution should be taken when interpreting the results. A potential issue given that the data was collected by three separate researchers, is inter-observer reliability. Whilst locomotor behaviours were documented based on standardised descriptions (Hunt et al., 1996; Thorpe & Crompton, 2005), the identification of height and support properties within each study required significant self-training and regular testing by the researcher, but may have been recorded differently by the three researchers. As the datasets varied in homogeneity, data was removed (for example, chimpanzee support use) or combined and grouped (for example, height was categorised into three groups) when appropriate (see Methods).

As a consequence of body size aggregation based on body weight, BSC1 included a single individual (the silverback gorilla) and BSC3 included all subjects of the same species (chimpanzees). Although attempts were made in the modelling process to identify potential influence of individual preference which might have affected the model outcome, it was not possible to determine because of the increased complexity. Furthermore, the gorilla dataset (Chapter Two) included one adult male (because of the demographics of a single family group), and whilst the gorilla and orangutan data (Thorpe & Crompton, 2005) included adolescent individuals, the chimpanzee subjects (Pettifer & Thorpe, Unpublished data) were all mature and over the age of 19 as the study focused on the aging process.

Comparisons with other species-specific positional behaviour studies were conducted to assess whether the subjects in this study were representative of the species. The chimpanzee data used in this study was cross-referenced with Hunt's (1992) locomotor data of chimpanzees in Mahale. Whilst the Mahale chimpanzees bipedally walked slightly more and brachiated more than Taï chimpanzees (this study), the Taï chimpanzees engaged in more vertically climbing; this might be reflected in the chimpanzees' (in this study) high propensity to engage in vertical climbing. However, arboreal transfer and quadrupedal walking, in addition to the size of supports used were consistent for both studies. Comparative studies of *Pan* have documented the variation in locomotor behaviours between chimpanzees and bonobos (Susman et al., 1980;

Hunt, 1991; Doran, 1993a; Doran, 1996; Doran & Hunt, 1996; Videan & McGrew, 2001). Further data using the standardised descriptions presented by Hunt et al (1996) and comprehensive habitat information is required for bonobos, following the work by Susman et al (1980) and Doran (1993), in order to understand the overall positional behaviour of the *Pan* genus.

The locomotor ecology data for the western lowland gorillas in this study (see Chapter Two) revealed some similarities to the locomotor behaviour presented by Remis (1995). Variations in the two studies, in the frequency of locomotor behaviours, can be explained by discrepancies between the two data collection methodologies and varying levels of habituation of study subjects (see Chapter Two). The western lowland gorillas, however, are not representative of the genus *Gorilla*. Tuttle and Watts (1985) documented the positional behaviour of mountain gorillas and found that arboreality was approximately 4.5% and arboreal height was mostly below 10m. Given what is now known about western lowland gorillas (Remis, 1995; Remis, 1998; King et al., Chapter Two), this variation is considered to be a reflection of resource distribution in contrasting habitats. Hunt (1991) suggested that the positional behaviour of Western lowland gorillas diverges in the direction of other great apes rather than mountain gorillas because of the considerable variation in their arboreal behaviour. More data is required, building upon that presented by Tuttle and Watts (1985) in order to fully understand the locomotor ecology of the *Gorilla* genus.

Manduell et al (2013) compared the Sumatran orangutan data used in this study (Thorpe & Crompton, 2005) to locomotor ecology data for Bornean orangutans (*Pongo pygmaeus)*. The habitat and ecology were compared between two peat-swamp forests, one in Borneo and one in Sumatra, and the dry-lowland forest in Sumatra and it was found that the forests varied in the size, canopy height, tree density and liana density (Whitten & Damanik, 2012; Manduell et al., 2013). These include two extremes: Ketambe (Sumatra) consists of a tall, pristine dry forest which has a sparse understory and a continuous upper canopy, whereas the Sabangau (Borneo) forest includes areas at different stages of regeneration and so is highly dense in the understory, but the canopy is discontinuous. Whilst the locomotor behaviours used were similar between the orangutans at different sites, the habitat differences were accompanied by variation in support properties. One of the main differences was that the orangutans in Sumatra demonstrated a strong preference for liana use which was not observed in the disturbed peat-swamp forests in Borneo and that Sumatran peat-swamp orangutans used more compliant supports. Habitat had a stronger influence on their locomotor ecology than species.

3.6 Conclusion

The variation in arboreal locomotor behaviours of the great apes was perhaps best explained as a reflection of their postcranial morphology and adaptations towards specific behaviours. As a consequence of natural selection favouring locomotion that is habitually used within their local environment, chimpanzees, gorillas, and orangutans each exploited locomotor behaviours that were likely less metabolically demanding relative to their overall size and morphology. This is, however, except for the gorillas' gap-crossing behaviours, which included energetically costly and risky locomotion, perhaps as a strategy to select the shortest, fastest travel route. Interspecifically, the apes also exhibited a variation in the supports that they used, but whilst this may also have been a consequence of their adaptive advantage, the size and type of supports used may also reflect habitat differences (given the variation in forest structure between Asia and Africa) and strategies to mitigate the risk of falling. Body size did not shape the arboreal repertoire of the great apes as predicted and was only influential in shaping the way in which apes of different sizes locomoted at different heights. Overall, larger apes used different supports to smaller apes, but regardless of size, all apes used the same supports for each locomotor behaviour.

This study has highlighted the importance of adopting an ecomorphological approach when studying great apes, as morphology, habitat and behaviour are evidently interlinked. Although we still need more quantitative data for great apes in their natural habitats, we can start to build upon this new knowledge by investigating how the apes perform these locomotor behaviours. The orangutans, chimpanzees and gorillas all exhibited a multi-locomotor repertoire and demonstrated the ability to engage in different locomotor behaviours. In order to look at how morphology and habitat shapes the performance of these behaviours, we can integrate a biomechanic approach. This will be the next step in understanding the ecomorphology of great apes.

CHAPTER FOUR

MACHINE LEARNING AND LOCOMOTOR KINEMATICS OF WILD WESTERN LOWLAND GORILLAS: A COMPARISON OF POSE ESTIMATION FRAMEWORKS.

4.1 Abstract

Artificial intelligence is changing the way in which great apes can be studied. Machine learning frameworks that use trained deep neural networks to identify behaviours of wild apes from video footage have yielded some success. Pose estimation is one particularly challenging aspect and in certain situations it can work well however it has not been tested using great ape footage taken directly during fieldwork and the purpose of this chapter is to evaluate the effectiveness of current tools on such data. Two architecturally distinct tools were assessed to determine their proficiency in accurately identifying 16 anatomical landmarks of habituated wild western lowland gorillas (*Gorilla gorilla gorilla*) for potential use in kinematic analysis. Whilst OpenApePose is pre-trained on a dataset of >70,000 great ape images and is therefore able to be used for great ape pose estimation out-of-the-box. DeepLabCut is a general pretrained pose-estimation network that uses transfer learning from manually labelled frames to refine the neural network to detect gorilla-specific landmarks. Overall, OpenApePose produced more similar results to manually labelled landmarks in 2010 randomly selected frames and exhibited a higher degree of consistency in landmark detection to DeepLabCut. DeepLabCut however, located anatomical landmarks more accurately within the range of 50 pixels to the true value. Pose estimation in DeepLabCut was more accurate when footage used in training were analysed compared to novel footage. Overall, however, pose estimation using DeepLabCut and OpenApePose did not meet the expected level of accuracy, particularly for applications in kinematic analysis. Wild environments present considerable challenges in comparison to captive settings due to variation in lighting and dense vegetation. Deep learning-based frameworks are powerful, however, for them to be effective in pose estimation of wild apes, they must be exposed to diverse natural settings. Given the high degree of

accuracy required for kinematic analysis, machine learning requires more development in pose estimation before it can fully replace manual analysis.

4.2 Introduction

The study of animal behaviour is important because it can provide insight into the adaptation of a species, their social dynamics and how they interact with the physical environment. Video footage is a robust, non-intrusive method of data collection for behavioural analysis of captive and wild animals. It allows for complex behaviours such as social interactions, communication, and locomotion to be documented, capturing subtle behaviours that may go unnoticed during real time observations. However, the manual coding of video footage in order to transform images into data for analysis is considerably time consuming. Recent technological advances in deep learning software that use convolutional neural networks (CNNs) to recognise and track objects (Krizhevsky et al., 2012) has revolutionised behavioural identification and tracking. These machine learning techniques used for automated object recognition are becoming an alternative to manual tracking because of their reliability and efficiency (Schofield et al., 2019). Machine learning, using deep learning techniques, is driving the advancement in animal science, and as it continues to evolve, it is accompanied by efficient and accurate methods that provide a deeper understanding of animal behaviour, conservation, ecomorphology and biodiversity. However, whether these approaches can currently be used for kinematic analysis of wild animals in complex environments is yet to be determined.

Deep learning-based methods using CNNs are powerful and versatile, which has led to their success when applied to a diverse range of settings. These frameworks have been used to identify species in camera trap footage (e.g. Norouzzadeh et al., 2018; Tabak et al., 2019) in natural habitats, from marine animal identification in the Norwegian deep sea (Lopez-Vasques et al., 2020), to the detection of endangered gibbons in the tropical rainforest of China (Wang et al., 2022). They have also demonstrated advantages in ecological and wildlife surveys, by automatically counting animals, providing valuable information for the conservation of a species and biodiversity of an ecological niche (e.g. Maire, Alvarez & Hodgson, 2015; Torney et al., 2019; Kellenberger, Tuia & Morris, 2020; Padubidri et al., 2021). Although behaviour classification and monitoring is more complex than animal identification because of the variability of behaviours, automated contextual (e.g. feeding and travelling) and social behaviour detection from video technology has yielded considerable accuracy (e.g. De Chaumont et al., 2019; Alameer et al., 2020; Brandes, Sicks & Berger, 2021; Yin et al., 2024). Machine learning has even been successful in automated face recognition, and the identification and reidentification of individuals by corresponding images of individual traits such as the stripes of zebras (Lahiri et al., 2011), facial characteristics of chimpanzees and gorillas (Loos, 2012; Brust et al., 2017; Guo et al., 2020) and the colour patterns and scars of dwarf minke whales (Konovalov et al., 2018). It has further been hypothesised that artificial intelligence has the potential to be used to study phenotypic evolution, by using trait identification to predict genetic relatedness of primates (Charpentier et al., 2020).

The rate of advancement of machine learning technologies has proved fundamental for many disciplines of animal science. Building on the advancement in software to categorise and identify animal behaviour, automated pose estimation is a specific subdiscipline which specialises in accurately locating and tracking body sections. This requires an additional processing step to detect joints by focusing on skeleton motion rather than overall movement (Fuchs et al., 2023). Deep neural networks in the machine learning algorithm are trained on a dataset of manually annotated images which identify the joint centres for the animal (Schwarz, Schulz & Behnke, 2015; Graving et al., 2019; Nath et al., 2019; Bala et al., 2020). Given that pose estimation software detects the position of multiple anatomical landmarks, it is useful for kinematic analysis. Projects such as OpenPose and equivalent commercial products have shown that obtaining kinematic data from humans, and even obtaining 3D pose data from a single camera, works well particularly in the animation, clinical and sports settings (e.g. Tanaka, 2019; Viswakumar et al., 2019; Kitamura et al., 2022). Kinematics are of particular interest for great apes, our closest living relatives, given that they exhibit a wide range of biomechanically distinct locomotor behaviours, especially in complex arboreal environments (Isler, 2002; Pontzer, Raichlen & Rodman, 2014; Tarrega-Saunders et al., 2021). Studying the kinematics of great ape locomotion can offer valuable insight into the form-function interface of a species, revealing the extent to which morphology shapes their expressed behaviour in the way they move.

Most of the data that is currently available on the kinematics of apes has been produced in captive environments (Isler & Thorpe, 2003; Vereecke, D'Août & Aerts, 2011; Finestone et al., 2018; Kozma et al., 2018; Tarrega-Saunders et al., 2021). In laboratory-based settings, sophisticated technologies such as force plates (Kimura & Yaguramaki, 2008; Vereecke et al., 2011), electromyography (Stern & Larson, 2001) and marker-based motion capture systems (Holowka et al., 2017) produce highly detailed data on the gait parameters, muscle activity, reaction forces and joint excursion and segment angles of captive apes. However, these technologies are not practical in the wild, meaning that data collection is restricted to hand-held *ex tempore* video recording. Kinematic analysis of wild apes is also considerably more challenging because of the complexities involved in obtaining high-quality video footage of unpredictable wild apes in dense tropical forests. Understanding the form-function relationship of a species in their natural habitat relies on wild data, but because of the challenges in data collection, there is very limited data available on the locomotor kinematics of wild great apes. The general approach for extracting kinematics from these sorts of video sources is manual marker tracking, and whilst this is reasonably accurate, it is extremely time consuming (Isler, 2005; Finestone et al., 2018; Mangalam et al., 2018; Kozma et al., 2018). However, now that open-source automated pose estimation software is readily available and user friendly, the discipline of great ape biomechanics is perhaps more accessible and efficient (Fuchs et al., 2023; Wiltshire et al., 2023).

There are several open-source markerless pose estimation frameworks that are theoretically capable of identifying the anatomical landmarks of wild great apes. However, each software package varies in architecture and approach. Deep-learning-based methods for pose estimation are either pre-trained by a large database of open-source images of great apes, such as OpenApePose (OAP) (Desai et al., 2023) and Animal Skeleton-Based Action Recognition (ASBAR) (Fuchs et al., 2023), or pre-trained by a database of all animals, such as DeepLabCut Model Zoo (Kane et al., 2020). Alternatively, frameworks are available, that allow users to use transfer learning to modify a deep neural network to precisely track user-defined features, or body parts, with limited training data; the most widely used and user friendly is DeepLabCut (Mathis et al., 2018). Each software package extracts individual frames and produces an output which includes the coordinates (*x*, *y*) and relative confidence (*p*-value) for each body landmark which can then be used to conduct kinematic analysis, for example joint excursion angles or gait parameters. However, it is not known whether the capabilities of each software are different, and which software is the most accurate in the pose estimation of wild apes. Furthermore, there has been very little application of pose estimation software using a database of captive-based images in identifying and tracking wild great apes in complex natural settings. The aim of this paper is to evaluate the accuracy and user-friendliness of two different deep learning-based pose estimation methods, DeepLabCut and OpenApePose, to determine their suitability for producing data for kinematic analysis of wild western lowland gorilla (*Gorilla gorilla gorilla*).

Gorillas, like other primates, are difficult to track because of their highly mobile joints, and the large ranges of locomotor possibilities (see Chapter Two), which create a huge combination of distinctive body postures (Isler, 2005; Hayden, Park & Zimmermann, 2022). Their extensive range of motion in all planes is three-dimensional, so identifying joint centres, such as the shoulder and hip, especially during tensile (suspensory) postures and locomotion is complex. This is also challenging because of areas of dense, long hair, which obscure joint centres on the body. Their diverse locomotor repertoire (see Chapter Two) and complex anatomy renders them suitable models for testing the accuracy of machine learning tools and can shed light on the limitations of this technology in natural settings.

The first method to be assessed uses one of the leading tools in pose estimation, DeepLabCut, a deep convolutional network that uses pre-trained ResNets which are trained on an object recognition benchmark named ImageNet. (Mathis et al., 2018). DeepLabCut allows users to fine tune the network for a particular task, or in this case, species, by training the software on manually labelled data of annotated body parts. These training frames are then applied to the ResNet, which adapts its weights (or learned parameters), in order to predict specific features (Nath et al., 2019). In recent years, self-training of the algorithm has become easy to use through an intuitive graphical user interface (GUI), which provides a step-by-step guide through the analysis procedure without the need for python coding knowledge or experience with machine learning.

Previous use of DeepLabCut have yielded considerable success in pose estimation (e.g. see Schweihoff et al., 2021; Farahnakian, Heikkonen & Björkman, 2021; Kirkpatrick et al., 2022). It has even been found that the algorithm is capable of producing accurate results with as little as ~200 training frames (Mathis et al., 2018; Forys et al., 2018; Nath et al., 2019). However, little is known about its applicability for videos of wild apes. Wiltshire et al (2022) presented the first application of machine learning using DeepLabCut for pose estimation of wild forest-living chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) from handheld video footage. Despite visually complex environments, which vary in lighting, distance from subjects and foliage coverage, the algorithm was able to identify anatomical landmarks of the apes. Furthermore, it was also determined that pose estimation of 18 anatomical landmarks increased in accuracy when more training frames were used. However, the study of wild chimpanzees and bonobos used multi-animal footage and multi-pose estimation algorithms, and it was noted that the biggest difficulty was in assigning body parts to a particular individual within an assemblage. This study, however, focuses on single-animal footage. Determining whether wild gorilla footage is similar in accuracy to chimpanzees and bonobos (presented by Wiltshire et al., 2022), will be key in determining the success of DeepLabCut as a tool for pose estimation of wild great apes who occupy complex forest environments.

The second method assessed alongside DeepLabCut that uses deep learning in pose estimation, is OpenApePose, an open-source artificial learning model pre-trained for non-human apes (Desai et al., 2023). Architecturally, it differs to DeepLabCut in the use of a HRNet-W48 deep net system, which retains high-resolution throughout the process of pose estimation. OpenApePose is designed specifically for the pose estimation of great apes and is pre-trained on a dataset of 71,868 images of chimpanzees, bonobos, gorillas, orangutans and gibbons (including siamangs) and does not require further training data by the user (Desai et al., 2023). Of this dataset, 12,905 are gorilla images. However, most of these images were taken from zoos and sanctuaries, which differ in complexity to natural ape habitats (Desai et al., 2023). An assessment of OpenApePose using captive footage revealed its accuracy in the identification of 16 landmarks, more accurate than monkey-specific OpenMonkeyPose (Yao et al., 2023) and human-specific ‘COCO’ (Jin et al., 2020) machine learning tools (Desai et al., 2023). It was also found that gorillas were the least difficult to track, which was thought to be a result of the lesser variability of their bodies (Desai et al., 2023), although arguably, they are considerably variable given that they are the most sexually dimorphic ape. However, how OpenApePose compares to user-trained deep learning tools, such as DeepLabCut, that can be trained for wild footage is a key component of this comparative study.

In order to determine the suitability of the OpenApePose and DeepLabCut as tools for pose estimation of wild gorilla footage, their output of coordinates for body landmarks are compared to manually labelled images. Footage of the gorillas engaging in both arboreal locomotion and terrestrial walking are included in the dataset in order to assess whether walking on the ground produces more accurate data than climbing or moving in the trees. Machine learning based tools either focus on pose estimation (Desai et al., 2023; Yao et al., 2023) or behavioural identification of locomotor behaviours (such as determining if the subject is climbing up, climbing down and walking) (Fuchs et al., 2023; Brookes et al., 2024) for wild great apes. However, it is not known if these tools can handle both at the same time, by estimating the body landmarks during different locomotor behaviours. This is further complicated within wild habitats that are characterised by dense foliage which restricts full observation of a gorilla, and the variability of travel direction relative to the camera. Whilst some tools, such as DeepLabCut Model Zoo (Ye et al., 2023) require the animal to be moving perpendicularly to the camera, DeepLabCut user-trained models and OpenApePose may be capable of detecting body landmarks in footage that is more complex, and when gorillas engage in rotation or lateral movement, especially in arboreal habitats.

In addition to determining the accuracy of anatomical landmark identification, this study also discusses the use of these cutting-edge deep learning tools from a practical perspective. Manual labelling is time consuming, yet whether the time invested outweighs potential inaccuracies and computational requirements of deep learning-based methods using CNN's requires more attention. Primate science and disciplines of biomechanics often deal with large datasets, so it is crucial that pose estimation software packages can operate quickly and efficiently using hardware that is available to researchers. Machine learning is revolutionising the way that research is conducted, but whether these tools are ready to be applied to kinematic analysis of wild apes is the leading motivation of this study.

4.3 Methods

4.3.1 Data collection

Video footage of habituated wild gorillas was collected in the Loango National Park, Ogooue-Maritime, Gabon (-2.077374, 9.543998) by a single researcher over a period of 12 months. A total of seven gorillas were recorded: two adolescents, three adult females, one blackback and one silverback. It was not possible to predict when the gorillas would engage in locomotion, so footage was collected *ex tempore*. Videos were documented using a Panasonic HC X 1500 hand-held recording device, with a resolution of 3840:2160 (pixels) and 50 frames per second (fps).

4.3.2 Video footage specification

A criterion was determined to select for appropriate footage for this study. Footage was restricted to only a single animal being in the shot (multi-animal pose estimation is beyond the scope of the current study), and the subject must not be obscured by too much foliage or vegetation for the whole duration of the locomotor bout. Videos were also restricted to a maximum of 60 seconds and included a variety of different locomotor behaviours and environmental conditions.

Given the nature of hand-held footage of wild animals in complex environments, the gorillas were not always framed centrally, and were often partially out-of-frame. This is a frequent occurrence in wild environments, especially for footage documented by wild-based camera traps. However, boundary boxes, or regions of interest (ROI) (Schwarz et al., 2015), were not cropped to frame the subjects in this study. In order to investigate whether automated pose estimation could identify landmarks on partially visible animals in a small portion of the frame, it was crucial that the full frames were retained.

4.3.3 Anatomical landmarks

A total of 16 landmarks were identified (when visible) for all methods following the landmarks pre-determined by OpenApePose, as shown in Figure 4.1. These include nose, right and left eye, head (crown), neck (nape), right and left shoulder (centre of glenohumeral joint), right and left elbow (ulna trochlear notch), right and left wrist (radiocarpal joint), hip (centre point between the two acetabulum's), right and left knee (femorotibial joint), right and left ankle (talocrural joint). These are probably not the exact landmarks that would be selected for a kinematic study but one of the major limitations of OpenApePose is that changing any of the landmarks would require manually labelling all the images. For DeepLabCut, the landmarks can be customised as required.

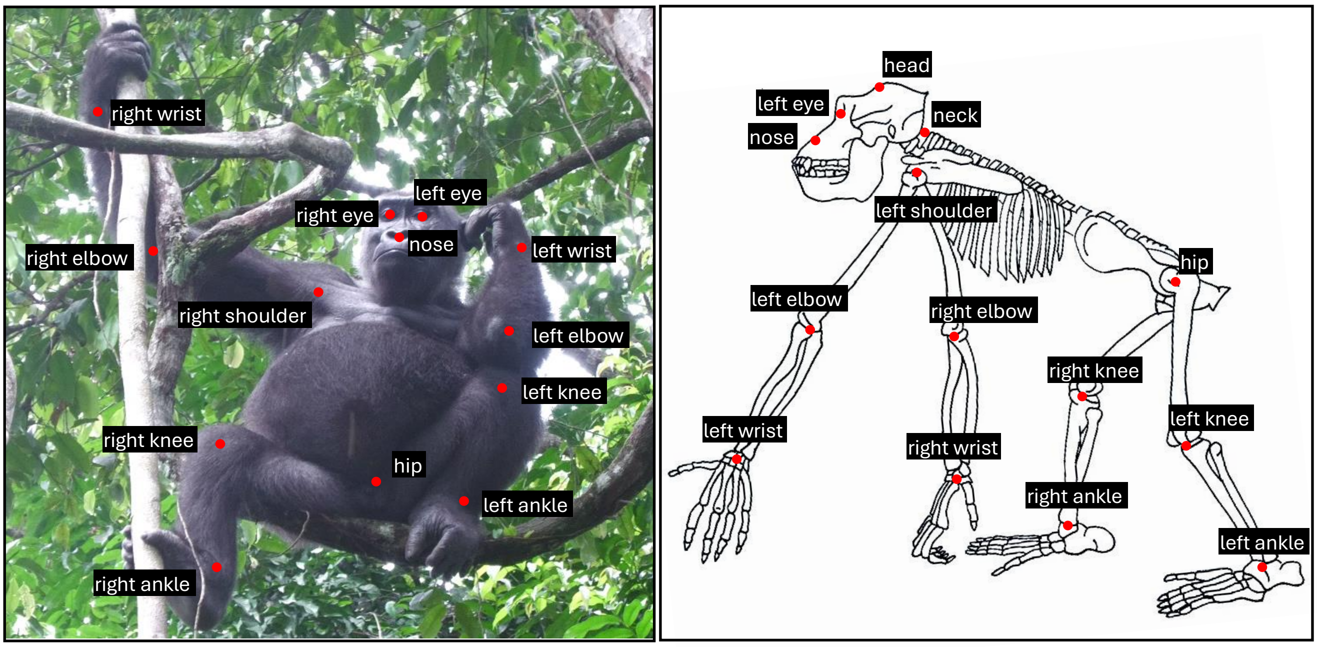

Figure 4.1: Identification of 16 anatomical landmarks (when visible) on a still frame of a gorilla and on a skeletal image.

4.3.4 Model procedures

Overall, 91 videos were used in this study, equating to 23:34 minutes and 70,700 frames. Videos ranged from 6 to 50 seconds, with a mean of 17 seconds (SD=9 seconds). Of the full dataset, 74% were arboreal locomotor bouts and 26% were terrestrial quadrupedal walking.

A total of 480 frames from 24 videos were used to train the neural network in DeepLabCut (Table 4.1). Model 1 assessed the pose estimation within 17 (71%) of the training videos in DeepLabCut. The 510 frames used in the analysis were not frames used in the training process. Model 2 assessed the pose estimation of 67 novel videos (2010 frames: 30fpv) using DeepLabCut, where no frames were included in training. Model 3 examined pose estimation using the OpenApePose software of the same 67 videos and 2010 frames in Model 2. Figure 4.2 shows the steps involved in obtaining a dataset for pose estimation analysis.

Table 4.1: Summary of the methods specifying the number of training frames, testing frames and subset of frames for analysis with manually labelled frames.

		Training		Testing		Analysis	
Model	Method	# Videos	# Frames	# Videos	# Frames	# Videos	# Frames
1	DeepLabCut- **trained** videos	24	480	24	14,545	17	510
2	DeepLabCut- **novel** videos	24	480	67	52,488	67	2010
3	OpenApePose	0	0	67	52,488	67	2010
	Manual labelling	24	480			**84**	**2520**

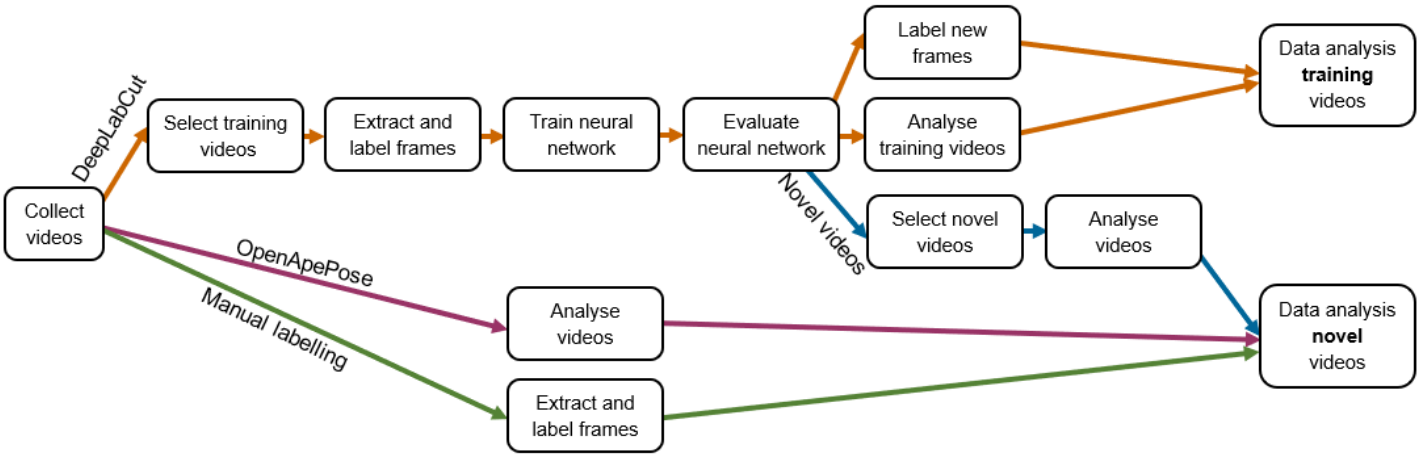

Figure 4.2: Illustration of the process of obtaining a comparable dataset for analysis.

Manual labelling and analysis of videos was done on a high-performance desktop computer equipped with an 8-core, 16-thread AMD Ryzen7 3800X processor with 16GB of DDR4 RAM, offering high-speed data analysis capacities. The desktop computer runs on the Windows 10 operating system.

4.3.5 Manual labelling

A total of 3,000 frames were manually labelled using the DeepLabCut Gui ‘Napari’ plugin (Mathis et al., 2020): 480 to train the neural network in DeepLabCut, 510 for the analysis of trained videos, and 2010 for novel analysis. The training frames were selected at default, to 20 frames per video, using a uniform distribution. The frames used for analysis were selected at the rate of 30 frames per video. Manual labelling was done by a single annotator who has knowledge of gorilla anatomy and locomotion in wild environments. If a body part was not visible, data was not collected. Manual labelling took an approximated time of 130 hours.

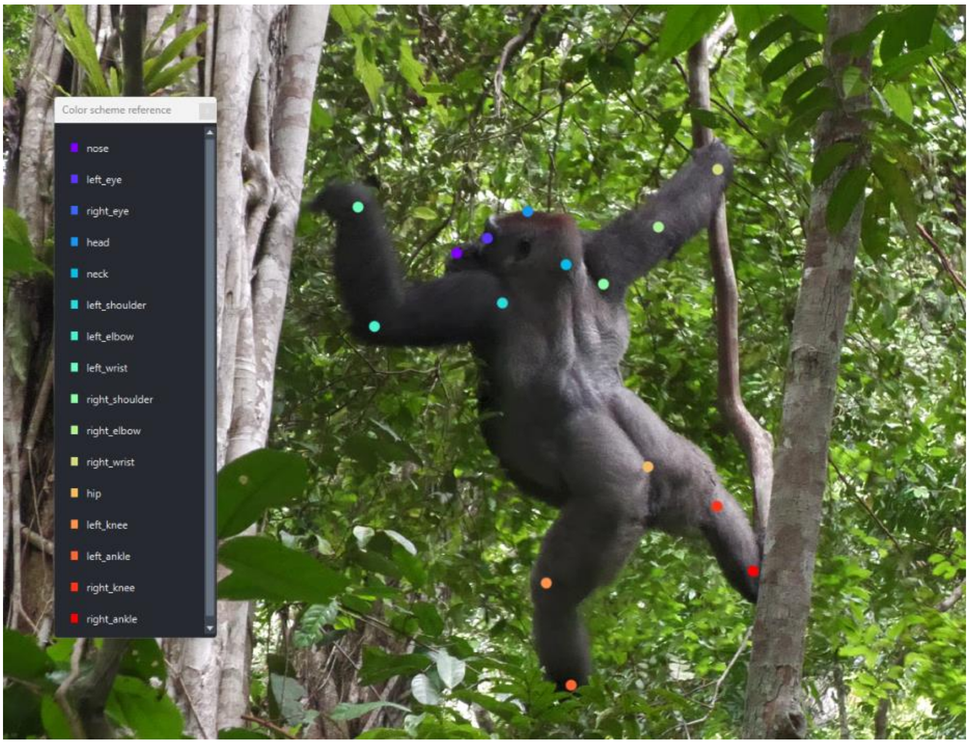

Figure 4.3: Image of the DeepLabCut GUI (Napari) illustrating the manual annotated landmarks.

4.3.6 DeepLabCut: Training a gorilla-specific neural network

The neural network was trained by manually labelling landmark positions (body parts) using the DeepLabCut algorithm and graphical user interface (GUI) (https://github.com/DeepLabCut/DeepLabCut) (Mathis et al., 2018; Nath et al., 2019). The 50-layer ResNet, initially trained to for pose recognition, was transformed by modifying the classification of landmarks specific for the gorillas. This required the configuration of 16 body parts (equivalent to landmarks in OpenApePose for ease of comparison) and their interactions (for example, the left wrist is linked to the left elbow and so on). Twenty frames for 24 video clips were automatically selected using a uniform distribution, equating to 480 total frames/images. The video footage chosen for training encompassed a range of locomotor behaviours (as recommended) (Nath et al., 2019), with variation in proximity to the gorilla and orientation of the gorilla relative to the camera. The model was trained to 100,000 iterations using default parameters for image augmentation and network convergence. The performance of the trained network was evaluated on the training test frames using visual inspection of the output. Training the neural network ready for analysis can be very slow (days to weeks) unless a high performance GPU is available, and may fail if the GPU has insufficient memory available. Analysis of novel footage (footage not included in training) is much quicker and a frame typically took 10s to analyse on a moderate computer. For the 67 novel videos and 17 trained videos that were processed, the total runtime was 150 hours. Coordinate output was to the nearest pixel.

4.3.7 Application of pre-trained OpenApePose software

Pose estimation was performed using the OpenApePose HRNet-W48 PyTorch model ‘MMPose v0.28.0’ (https://github.com/desai-nisarg/OpenApePose) (Desai et al., 2023).

This pre-trained non-human ape software for estimating landmarks is simply fed individual video files and subsequently produced coordinates for all 16 landmarks with an estimated accuracy score (*p*-value) for each body part. This took 984.36 minutes (16.5 hours) of processing time and produced landmark coordinates rounded to the nearest 50th pixel.

4.3.8 Performance analysis

Performance analysis was conducted in R version 4.3.1 (2023). Datasets were combined, and landmark coordinates were standardised to the same reference point (x=0, y=0) and decimal alignment. A total of 2,520 frames were used in the comparison (Table 4.1). If all 16 landmarks were visible, this would equate to 40,320 data points, however, only data where body landmarks were detected were included.

The distance between machine learning tools DeepLabCut and OpenApePose and manual landmarks was evaluated using the mean absolute Euclidean distance, a geometric metric which measures the absolute distance between two vectors (Menger, 1931). Euclidean distance is commonly used in machine learning as a metric for determining distance in multidimensional space because of its computational efficiency and simplicity over metrics such as Manhattan and Minkowski distance (Danielsson, 1980; Yu et al., 2008; Wohlhart & Lepetit, 2015; Behrens et al., 2018). It is also the typical accuracy metric used in commercial marker-based motion capture systems. It was therefore chosen as the most appropriate metric in this analysis. The pairwise formula is as follows, where x and y represent the absolute coordinates:

$$\boldsymbol{Euclidean\ distance} = \sqrt{(\boldsymbol{x_2} - \boldsymbol{x_1})^2 + (\boldsymbol{y_2} - \boldsymbol{y_1})^2}$$

Performance analysis was conducted for landmark coordinates produced by DeepLabCut and Open Ape Pose, for all detections. A further analysis was performed to test the top 5% quintile of *p*-values to assess the relationship between confidence and accuracy between the two models.

4.4 Results

Overall, combining all detections, OpenApePose produced data with the smallest mean absolute Euclidean distance to the human-labelled data, 4% more accurate than DeepLabCut trained videos and 34% more accurate than DeepLabCut pose estimation on novel videos (Table 4.2). All models, overall, exhibited the least difficulty in accurately detecting gorillas' eyes. However, whilst DeepLabCut experienced the most difficulty in identifying the neck in novel videos, the least accurate detection for OpenApePose was the wrist and for DeepLabCut trained videos, this was the hip.

Table 4.2: The mean absolute Euclidean distance (MAED) between the manually labelled data and the data produced by the DeepLabCut and OpenApePose software packages split by anatomical landmark. Percentage is given for each landmark where the Euclidean distance is less than 50 pixels. N signifies the number of detections. Shaded cells indicate which method produced the lowest MAED for each anatomical landmark.

	All detections							
	DeepLabCut novel videos		**OpenApePose**			**DeepLabCut trained videos**		
Anatomical landmark	MAED (SD)	ED = < 50 pixels (%)	MAED (SD)	ED = < 50 pixels (%)	*N*	MAED (SD)	ED = < 50 pixels (%)	*N*
Nose	295 (559)	27.1	142 (260)	12.9	734	44 (340)	50.2	223
Eye	213 (548)	34.5	139 (260)	11.5	617	8 (322)	69.8	189
Head	350 (507)	19.8	138 (326)	15.2	981	103 (171)	32.6	230
Neck	525 (475)	3.9	261 (251)	1.6	913	388 (279)	1.3	238
Shoulder	407 (456)	8.8	231 (270)	26.6	906	354 (327)	10.0	279
Elbow	429 (458)	13.9	351 (289)	9.4	1072	370 (329)	13.5	282
Wrist	481 (482)	7.7	486 (399)	5.5	1063	338 (367)	19.0	300
Hip	428 (485)	2.4	216 (549)	4.3	1197	416 (324)	2.8	324
Knee	374 (447)	10.9	269 (408)	9.9	1045	316 (374)	30.9	320
Ankle	375 (533)	16.9	334 (393)	9.8	1053	331 (388)	18.8	314
Total	**388 (495)**	**15.0**	**256 (341)**	**10.7**	**9581**	**267 (322)**	**24.9**	**2699**

The size of the gorillas, in pixels, varied from ~165,000 to ~1,900,000 pixels, as shown in Figure 4.4. The two still frames show the variation in ROI and visual complexity. In the left image, the gorilla takes up ~3% of the frame and is surrounded by branches and lianas that do not vary extensively in size and shape from the limbs of the gorilla. The left image is also dark, which makes the contrast of the gorilla less clear. In the right image, the gorilla takes up ~20% of the frame and is more visible because of the open, and light-coloured surrounding environment. Additional still frames that show the variation in habitat conditions and focal size are documented in Appendix B.

Figure 4.4: Two frames within the video dataset used in the comparison, showing the variation in ROI (range of interest) because of the distance of the focal individual from the camera.

A detection accuracy of 50 pixels which equated to between 50-200mm. For detections that fell within the distance range of 50 pixels (the smallest range possible for OpenApePose) from the manually labelled landmark, OpenApePose produced the least accurate results, with only 10.7% of detections being within 50 pixels of the true value. Novel video data produced by DeepLabCut was within 50 pixels for 15% of detections, compared to trained videos, which were 24.9% within this range. Overall, the deep learning tools exhibited the most difficulty in detecting the gorillas' hip and neck within 50 pixels of the true value; both the hip and neck were located within the range of 50 pixels only 3% of the time.

Figure 4.5 shows the range between the deep learning-tool pose-estimation output based on mean absolute Euclidean distance, when limited to a maximum distance of 500 pixels. This limit was applied to mitigate potential errors and better assess the performance of the tools. In removing all detections further than 500 pixels in distance, OpenApePose overall exhibited less variability in identification than the DeepLabCut software. However, whilst OpenApePose showed the most variability in the detection of the wrist, and the least variation in the identification of the head, DeepLabCut exhibited the least variation in estimation of the hip, and the most variation in detection of the eye (for novel videos) and the knee (for trained videos).

This suggests that OpenApePose is more consistent in the identification of anatomical landmarks of the gorillas than DeepLabCut (within the threshold of <500 pixels), and overall closer to the true position from the combined Euclidean distance for all detections. However, it was the DeepLabCut software which located anatomical positions more accurately, within the range of 50 pixels to the true position, than OpenApePose.

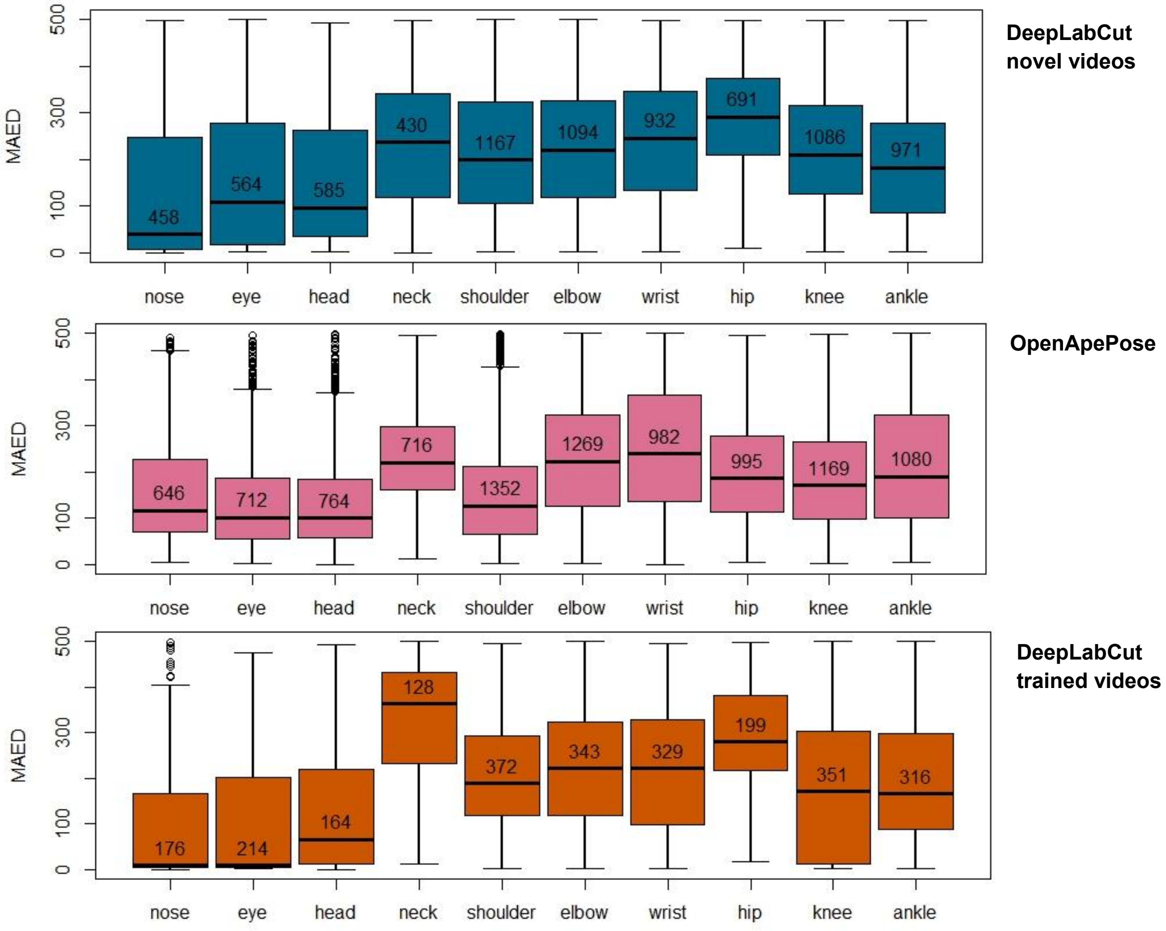

Figure 4.5: Plots showing the performance of each method. MAED is limited to a maximum distance of 500 pixels. Values in the bars represent number of detections.

In order to evaluate the accuracy of confidence levels produced by the OpenApePose and DeepLabCut tools, their likelihood values were compared with corresponding Euclidean distances. The *p*-values given by OpenApePose ranged between 0.02 – 0.97, with a mean of 0.29. Conversely, DeepLabCut produced *p*-values between 0.005 – 0.56 with a mean of 0.04 for novel videos and 0.013 – 0.61 with a mean of 0.15 for trained videos. Within the upper 5% quintile of *p*-values for each model, the Euclidean distance decreased by 48% by DeepLabCut for novel videos, 35% for DeepLabCut trained videos and 47% for OpenApePose (Table 4.4). DeepLabCut had less confidence than OpenApePose, but both tools still exhibited large Euclidean distances from the true values even within the upper quintile.

Table 4.3: The mean absolute Euclidean distances (MAED) for the upper 5% quintile based on p-values for each model. Shaded cells indicates which method produced the lowest MAED for each anatomical landmark.

Anatomical landmark	Upper 5% quintile of p-values								
	DeepLabCut novel videos			**OpenApePose**			**DeepLabCut trained videos**		
	MAED (SD)	*p-value range*	*N*	MAED (SD)	*p-value range*	*N*	MAED (SD)	*p-value range*	*N*
Nose	5 (76)	0.12 - 0.56	88	68 (52)	0.83 - 0.98	79	3 (2)	0.38 – 0.61	3
Eye	6 (95)	0.13 – 0.41	85	78 (51)	0.75- 0.96	65	5 (7)	0.26 – 0.58	25
Head	26 (237)	0.11 – 0.20	51	64 (30)	0.87 - 0.96	82	9 (6)	0.35 – 0.50	17
Neck	414 (469)	0.08 – 0.16	30	194 (60)	0.81 – 0.93	55	414 (157)	0.12 – 0.19	9
Shoulder	192 (221)	0.14 – 0.20	54	105 (126)	0.55 – 0.83	51	285 (128)	0.14 – 0.23	12
Elbow	390 (335)	0.11 – 0.21	63	95 (145)	0.36 – 0.83	77	344 (337)	0.17 – 0.22	11
Wrist	319 (269)	0.06 – 0.18	65	366 (377)	0.21 – 0.67	77	240 (291)	0.16 – 0.23	17
Hip	350 (466)	0.09 – 0.21	67	134 (81)	0.69 – 0.84	81	237 (149)	0.16 – 0.21	9
Knee	132 (210)	0.04 – 0.30	70	135 (113)	0.41 – 0.75	68	173 (155)	0.08 – 0.33	17
Ankle	199 (275)	0.13 – 0.26	69	159 (171)	0.28 – 0.93	67	143 (207)	0.10 – 0.34	17

Total	**203 (265)**	**0.04 – 0.54**	**642**	**137 (121)**	**0.21 – 0.98**	**702**	**175 (144)**	**0.08 – 0.61**	**137**

OpenApePose performed marginally better when the gorillas engaged in terrestrial locomotion compared to arboreal locomotion (Table 4.4). DeepLabCut performed better when the gorillas engaged in arboreal locomotion. One of the issues in arboreal environments is that the support or supports being travelled on obscure part of the gorillas body as show in Figure 4.6. In this still frame, the two software packages were able to identify a body part, but not the correct body part. The values in the image indicate the MAED from the true locations to the landmarks identified by OpenApePose and DeepLabCut and how this relates to the overall size of the frame. The MAED, from 171 to 416 are not too dissimilar to the average values produced by the packages, but this shows what these values look like on a typical (randomly selected) still frame.

Table 4.4: The mean absolute Euclidean distances (MAED) for all anatomical landmarks combined split by arboreal locomotion and terrestrial locomotion.

	All detections				
	DeepLabCut novel videos	**OpenApePose**		**DeepLabCut trained videos**	
	MAED (SD)	MAED (SD)	*N*	MAED (SD)	*N*
Arboreal	331 (487)	292 (314)	6501	274 (348)	2143
Terrestrial	437 (489)	225 (383)	3080	337 (328)	556

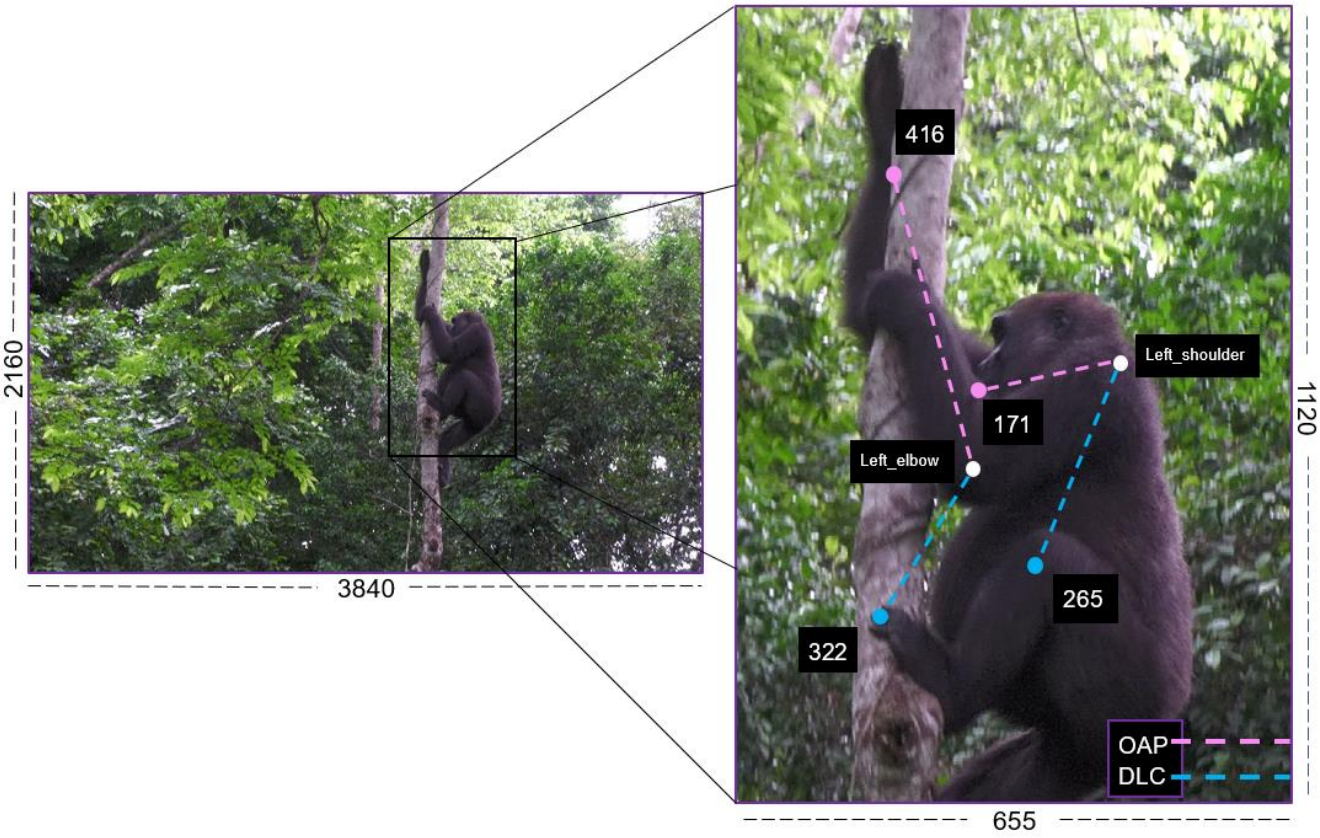

Figure 4.6: Image showing the comparison of OpenApePose and DeepLabCut generated landmarks of the 'left_shoulder' and 'left_elbow' compared to the manual label. Both tools locate a body section, but not the correct one.

4.5 Discussion

4.5.1 Behavioural identification verses pose estimation in wild apes

Computational frameworks are being used more frequently within the disciplines of animal science. For wild great apes, they have been used in behavioural recognition, such as the identification of nut cracking and tree buttress drumming by chimpanzees using both audio and video input (Bain et al., 2021). Other tools, like the ASBAR (Fuchs et al., 2023) and PanAf20K (Brookes et al., 2024) frameworks focus on identifying different locomotor (walking, climbing up, climbing down) and posture (standing, sitting, hanging) behaviours of wild apes (also see Sakib & Burghardt, 2020). Videos and images of wild apes engaging in less common, or difficult to observe behaviours such as vocalisation, tool use, sex or displays of aggression are required in order to train the network to identify these behaviours (Trapanotto et al., 2022; Fuchs et al., 2023; Brookes et al.,2024). Pose estimation is similar in that the software requires exposure to different body poses. However, the accuracy required is considerably different. The identification of behaviours such as grooming, or feeding are relatively distinct in their sequence of actions or movements, and are often contextualised by environmental surroundings, such as peripheral food sources, contact of individuals or facial expressions. Pose estimation, however, requires precise identification of body landmarks simultaneously. Whilst the identification of behaviours of wild apes has yielded much success, it was not understood whether transfer learning architectures yet have the capacity for accurate and consistent pose estimation in natural environments.

This study has tested the applicability of current state-of-the-art machine learning approaches in the tracking and pose estimation of wild gorillas from hand-held single-camera video footage. One of the leading pose-estimation tools, DeepLabCut, was compared to OpenApePose, a new, ape-specific pose-estimation software package. Both tools vary in their architectural design: the ResNet in DeepLabCut is structured to allow for training deep in the neural network, whereas the HRNet, instead, focuses on maintaining high-resolution information when locating landmarks. The DeepLabCut toolbox is versatile and allows users to define body parts within the transfer learning algorithm. Here, three-times the minimum recommended number of frames were used to train the network and the step-by-step guide was followed to assess the CNN, ready for video analysis (Nath et al., 2019). OpenApePose, conversely, is a pre-trained deep net, specifically engineered for pose estimation of non-human great apes (Desai et al., 2023). Both of these machine learning tools have claimed that they are robust, however, they have also noted that they are best suited towards behaviours that can be captured consistently with minimal occlusions to the subject animal (Nath et al., 2019; Mathis et al., 2018; Desai et al., 2023). Whilst the footage chosen included those with the least occlusions, this dataset tests the limits of DeepLabCut and OpenApePose as in such uncontrolled environments, occlusions are inevitable.

4.5.2 User-experience

The Python toolbox and Graphical User Interface in DeepLabCut is referred to as 'user-friendly' and suitable for researchers without extensive programming skills (Nath et al., 2019). It is organised to the intuitive workflow of a single-animal pose estimation project, which includes project creation, followed by extraction and labelling of training frames, network training, refinement and augmentation, and video analysis (Nath et al., 2019). This process was efficient and uncomplicated, with informative step-by-step instructions in publications and on GitHub platforms (Mathis et al., 2018; DeepLabCut, 2023). The Python toolbox can be used to alter specifications within the process, but other than to open the GUI, there is no coding required. The OpenApePose framework, conversely, does not run through a GUI. Instead, it requires a small amount of Python programming to open the ‘MMPose’ interface and manually write the script to perform the video analysis. Demonstration scripts and online guides offer examples which can be manually adapted and used, which makes the process efficient and certainly no harder than running a simple analysis in R (OpenMMLab, 2021; Desai et al., 2023). The biggest challenge using both toolboxes is getting them to work properly with the installed GPU and the need to use some sort of package manager such as Anaconda to get the correct versions of python and the various neural network libraries installed.

Given that the ultimate goal for machine learning frameworks in pose estimation is to make them accessible, these tools still have some way to go to make them truly user friendly. In addition, they require a moderately powerful computer to perform analyse adequately (Mathis et al., 2018; Nath et al., 2019; Desai et al., 2023). In order to obtain a dataset of postures from just 23 minutes of footage in DeepLabCut, >200 hours of computer processing and >150 hours of human-coding was required. OpenApePose was much less demanding as it did not require the manual training, or coding of footage. This highlights the huge investment in time required to train a deep neural network; which, in this case, was not accompanied by increased accuracy.

4.5.3 Pose estimation

It was found that whilst OpenApePose produced, on average, smaller distances between the true values of gorillas' anatomical landmarks, and was more consistent in the detections, DeepLabCut located body parts more accurately within the range of 50 pixels to the true value. Furthermore, whilst an increased likelihood (*p*-values) provided for each landmark corresponded to a marginal increase in accuracy, the variation of these values within, and between the software packages, meant that determining a threshold for which coordinates were sufficiently accurate was difficult to ascertain. Whilst OpenApePose produced likelihood values that were very high, the values given by DeepLabCut were low, and both varied in their range. Overall, however, the coordinates produced by both tools were not accurate, suggesting that challenges remain within the process of pose estimation using these deep learning architectures.

This does not mean that OpenApePose and DeepLabCut are unsuccessful in pose estimation of great apes. It is amazing that they work at all, and given the success of human pose estimation software, it is likely that their performance will rapidly improve. The advances of these machine learning tools have changed the way in which primate posture can be measured and have yielded success in captive and laboratory settings (see e.g. Hayden, Park & Zimmermann, 2022; Marks et al., 2022; Desai et al., 2023; Rotaru et al., 2023). However, captive studies have clear benefits for behavioural and biomechanic studies of great apes, as sophisticated camera set-ups can be used in well-lit areas that have been designed for research that can be replicated (Stevens, Ratsimbazafy & Ralainsolo, 2010). Also, depending on the variables being examined, the enclosure can be arranged so that the subject is more likely to perform the desired behaviour, where the cameras are aligned in order to document this with very little error.

Wild environments are much more complicated. It is likely that the results of this study were not comparable to pose estimation of captive studies because wild environments introduce considerable complexity that is accompanied by potentially substantial errors. The footage used in this study included a wide range of visual complexities. This included variation in the distance between the focal gorilla and the camera, distinct lighting conditions, motion blur, visibility of the focal, and the presence of foliage and trees that complicate the surrounding environment. This likely contributed to the difficulty in pose estimation. Occlusion of anatomical landmarks from foliage or other animals is considered to be one of the main sources of error in pose estimation and this is unavoidable for gorillas in wild environments (Hayden, Park & Zimmermann, 2022). During locomotion, half of the body inevitably conceals the other half, and when engaging in arboreal locomotion such as vertical ascent and descent of tree trunks, trees also make their anatomical landmarks less visible.

The data produced by DeepLabCut increased in accuracy when analysing footage from the same in-domain visual distributions (footage used in training) in comparison to out-of-domain, novel footage. By familiarising the algorithm with specific environmental conditions and possible body postures, the CNN was able to adapt to these parameters and produce more accurate results. Although deep learning tools can learn autonomously, it is crucial that they are introduced to the potential variation in environmental conditions (Norouzzadeh et al., 2018; Nath et al., 2019; Sturman et al., 2020; Bain et al., 2021). Transfer learning is powerful as it does not require considerable amounts of training data (Nath et al., 2019): however, a true figure, or percentage of trained data required for accurate automatic landmark estimation is still unknown. Wiltshire et al (2023) found that the accuracy of pose estimation of wild bonobos and chimpanzees increased when more training frames were used. This highlights the importance of adequately training the deep neural network and suggests that more time invested in generating a larger training dataset would improve the results in this study.

In addition to exposing the CNN architectures to distinct environmental conditions, in order for it to perform detailed recognition of different postures, they must also be trained on a species-specific dataset which includes the range of motion capable by the species. This is challenging for primates, as their range of motion across all planes of motion is vast, and also difficult to accurately depict in 2 dimensional images. The OpenApePose deep net system was trained on a dataset consisting of diverse poses in more than 70,000 images (Desai et al., 2023). Whilst this likely contributed to their success in exhibiting the most consistency in pose estimation of the wild gorillas, if a more diverse dataset that includes images from wild settings were introduced to the architecture, it would be expected that this would greatly improve the results of wild ape studies like this one.

4.5.4 Machine learning and great ape kinematics

Whilst it is the general agreement that kinematic data for wild great apes is more informative than captive data, it is extremely lacking in the literature (DeSilva, 2009; Griffin et al, 2010; Schoonaert et al, 2016; Neufuss et al, 2018; MacLean & Dickerson, 2020). Positional behaviour data for wild great apes over the last few decades has become increasingly prevalent (Hunt, 1991; Remis, 1995; Doran, 2003; Thorpe & Crompton, 2006; Chapter Two), yet biomechanical analyses of these animals is perhaps deficient due to the difficulty in implementing apparatus such as pressure plates, and video cameras, often fundamental in obtaining and quantifying kinematics and kinetics. Furthermore, the data required for kinematic analysis, such as joint excursions, require a considerable degree of accuracy. However, marker-less kinematic analysis from video footage is complex because of the combination of sagittal plane flexion and extension, coronal plane abduction and adduction and axial rotation of joints (Schmid, Schmidt & Piaget, 1994). If a joint centre is not accurately located, this has huge implications for joint excursion angles.

Almost all of the current kinematic analysis of great apes has directed focus towards locomotion true orthogonal to the camera during quadrupedal and bipedal walking (Kozma et al., 2018; Finestone et al., 2018; Tarrega-Saunders et al., 2021) and vertical climbing (Isler, 2002; Schoonaert et al., 2016). This is because when a subject is not locomoting perpendicular to the camera (or more than 10° off perpendicular (Finestone et al., 2018)), it is much more challenging to accurately pinpoint joint centres. This can occur if a primate is rotating around a tree, or if they are walking away from the camera. The results here found that the gorillas’ neck and hip were the most difficult to identify. This can be attributed to size of the hip and neck area, which provide lots of room for variability and error. The hip joint, defined here as the centre point between the left and right acetabulum, may be easy to determine when both hindlimbs are perpendicular to each other, yet in a diagonal gait posture the hip joint shifts more superior and anterior as the whole pelvis moves. This variation in mobility is even more extreme for the shoulder girdle since the scapular is mobile. The glenohumeral joint is much easier to identify when a gorilla is walking quadrupedally than when engaging in tensile locomotion, such as brachiation, as the whole joint can move depending on whether muscles are engaged or not. Whilst human coders, with knowledge of biomechanics and anatomy, can identify these nuances, machine learning tools do not have this specialist-level accuracy, although it is possible to use explicit musculoskeletal models in the motion capture workflow to help overcome some of these issues (Wang et al., 2021).

The most common practice, at current, for quantifying joint excursions and segment orientations is to use video footage that is then manually digitised using software such as Kinovea and ImageJ (Nakano, Hirasaki & Kumakura, 2006; Griffin et al., 2010; Venkataraman, Kraft & Dominy, 2013; Finestone et al, 2018; Thompson et al, 2018; Watson et al, 2009; Sarringhaus, Wuthrich & MacLatchy, 2018). The results here have shown that pose estimation through the use of deep learning tools is not yet capable of specialist-level accuracy. Instead, the manual labelling of anatomical landmarks for kinematic analysis remains the most reliable and robust approach. As machine learning architectures continue to develop, through the augmentation of training datasets, this may soon be possible.

4.6 Conclusion

Advances in artificial intelligence, using deep learning, has changed the way in which primate posture can be measured. However, whilst they are advancing rapidly, they are still not ready to replace manual analysis within the discipline of locomotor kinematics. Analysis of joint excursion angles requires a high level of accuracy which, at current, cannot be achieved by deep learning tools. Pose estimation and kinematic analysis is particularly challenging for gorillas (and other great apes) because of their vast range of body postures, body fur, and probably the most influential factor, the complexity of their natural forest habitats. DeepLabCut and OpenApePose are state-of-the-art frameworks, which have yielded considerable success in ape pose estimation in captive settings. However, they struggle to accurately detect anatomical landmarks of wild gorillas because of lighting conditions, motion blur, foliage and vegetation coverage and occlusions during arboreal locomotion from trees and other arboreal supports. In order to develop these tools, focus should now be directed towards integrating wild images and footage into readily available machine learning tools. By doing this, the deep neural networks can be exposed the variation in natural habitats which will assist in their advancement towards accurate pose estimation of wild apes.

CHAPTER FIVE

GENERAL DISCUSSION AND FUTURE DIRECTIONS

5.1 Impact of the covid-19 pandemic on this thesis

The aim of this thesis has always been to study the locomotor ecology of wild western lowland gorillas. However, at the outset, I wanted to look at their overall arboreal strategies, but also delve into the details about specific locomotor behaviours such as arboreal bipedalism. Arboreal bipedalism is a strategy used by many primates in the trees to free-up the hands to forage and hold supports to increase stability. Bipedalism, as a primate locomotor behaviour, has received much attention, so I wanted to investigate whether and/or how the largest apes use this behaviour in the trees. This is important as gorillas can then be used as referential models, which might reveal more about the evolution of human bipedality (given that gorillas are similar in several ways to humans, such as in their hand morphology). Furthermore, I had also planned on conducting biomechanical analysis of gorillas when engaging in locomotion, including gait analysis, joint kinematics, and detailed investigations into hand postures. The aim was to use this data to assist in building 3D musculoskeletal models of this species. Overall, integrating quantitative data on how often gorillas engage in locomotor behaviours, with information on *how* they locomote provides a comprehensive picture of the performance of western lowland gorillas, which was not previously known. As a consequence of the covid-19 pandemic, I experienced considerable delays to my fieldwork. During this time, I conducted a zoo-based study which examined the spatial use and effect of public absence on captive gorillas (this is not included in this thesis because it does not align with the general theme). However, the delay to fieldwork meant that I did not have the time that I had planned to analyse the data and so I had to adapt the objectives of my thesis. Despite the delays, I have provided three detailed chapters which discuss the locomotion of gorillas which offer new insights into their wild behaviours. In this discussion, I present an overview of the results of these studies and suggest how we can take the next steps in understanding wild great ape locomotion and the implications this has for evolution and conservation.

5.2 Summary of thesis aims, main findings and limitations

The primary aim of this thesis was to improve our understanding of western lowland gorilla arboreal locomotion and how it compares to the arboreal locomotor behaviours of other non-human great apes. Of the great apes, orangutans are the most well-studied in terms of their locomotor behaviours (Cant, 1987; Thorpe & Crompton, 2005; Manduell, Morrogh-Bernard & Thorpe, 2011), but there remained a gap in our understanding of how the western lowland gorillas interact with arboreal environments. Gorillas are the largest ape, so moving in the trees is complex, especially because the canopy is typified by branches and lianas that can snap under their weight. This can affect they ways in which they acquire resources, maintain social relationships and deal with inter and intragroup competition. Interspecific comparisons of great apes were limited until now because data was missing for western lowland gorillas (Hunt, 1991; Doran, 1996). Comparing the arboreal locomotor ecology of great apes can reveal whether species-specific traits and body size is reflected in potential diversity in the solutions employed to deal with the complexities of arboreal environments. All great apes rely on arboreal environments, but the strategies used might vary considerably and the aim was to understand exactly how these strategies vary. The final aim of this thesis was to determine how researchers can use machine learning to develop our understanding of how morphology and habitat variation shapes variation in locomotor behaviours of great apes by investigating the accuracy of some of the leading tools in pose estimation to obtain kinematic data under field conditions.

In Chapter Two, I discussed the locomotor ecology of a group of fully habituated wild western lowland gorillas. It was not previously known how often gorillas exploit arboreal environments, or whether their body size influences the way in which they deal with the ecological challenges of accessing, moving in, and dealing with discontinuity in the canopy. The aim of this chapter was to build on previous studies that examine the locomotor ecology of great apes (Hunt, 1992; Remis, 1995; Thorpe & Crompton, 2005) by integrating comprehensive data on support use, heights and contextual behaviour in order to examine potential strategies used by the largest arboreal apes to travel and feed whilst reducing energy expenditure and minimising risk. This involved quantifying the positional behaviour of wild gorillas in the lowland rainforest of Gabon over a period of 12 months and conducting statistical analysis to reveal any patterns in their arboreal behaviour. Although the gorillas were not as arboreal as some previous estimations of 60% (Crompton, Sellers & Thorpe, 2016), they did spend more than a third of their time arboreally. The canopy is fundamental for gorillas to access nutritional resources (Masi, Cipolletta & Robbins, 2009; Robira et al., 2023), but the way in which they move in the trees had previously been mis-represented due to methodological constraints (Remis, 1995). The gorillas did not rely on suspension as much as predicted when negotiating small supports (Cartmill & Milton, 1977), but instead engaged in walking and mitigated the risk of falling by using robust hand grips and bipedal hand-assisted postures. In addition to possessing manual adaptations towards quadrupedal walking, the gorillas seemed to rely on hand grips to increase stability when in the trees (Neufuss et al., 2017). The silverback gorilla engaged in less horizontal travel and used larger supports than smaller gorillas, but he also exhibited risky gap-crossing behaviours. Overall, despite their large size, the gorillas exhibited considerable adaptability, which suggests that they understood the complexities of the arboreal environment and possess cognitive mechanisms to deal with instability and unpredictability.

The western lowland gorillas in this study were a family group of 10 individuals (seven adolescents and adults, and three infants). As is common in studies of a gorilla troop, data on social relationships, reproductive strategies, intergroup competition, and activity patterns is based on a single silverback male dominated group. This is one of the biggest limitations of positional behaviour studies, as adult male locomotion and posture is determined by a single individual. As discussed in Chapter Two, the silverback also constitutes the largest body size group within the modelling process. Therefore, results should be interpreted with caution until more data on the locomotor ecology of this species can be added to what is already known (Remis, 1995).

Western lowland gorillas occupy the lowland swamps which run along the coastline of Gabon, Cameroon and Equatorial Guinea, but they also inhabit forests further inland in these countries as well as the forests in the Republic of Congo. Populations of western lowland gorillas might therefore be subject to slightly different ecological conditions, which might include variations in habitat composition, resource distribution, human conflict/influence (poaching and disease) and varying degrees of habitat loss and degradation (Devos et al., 2008; Bender & Ziegler, 2011). For example, the western lowland gorillas in the Dja Reserve in Cameroon occupy forests with high herb densities, swamps and young secondary forests (Willie et al., 2013), whereas the gorillas in the Lope Reserve in Gabon occupy lowland forests with areas of vast open expanses and hills (Tutin, 19969). This might in turn result in differences in ape density, resource availability, ranging patterns and the use of arboreal environments. The western lowland gorillas studied in this thesis may be representative of the species, but there might also be differences to other populations as a result of slight habitat variation. Furthermore, western lowland gorillas are distinct from cross river gorillas

(*Gorilla gorilla diehli)* taxonomically (Coolidge, 1929; Sarmiento & Oates, 2000) and in the habitats that they occupy. Cross river gorillas inhabit the Cross River watershed on the border between Cameroon and Nigeria, which is typified by semi-deciduous and montane forest (Sarmiento, 2003). Therefore, it would not be appropriate to use western lowland gorillas as a proxy for all western gorillas. More data is required on the positional behaviour of cross river gorillas, the mountain gorilla (*Gorilla beringei beringei*) and the eastern lowland gorilla (*Gorilla beringei graueri*) in order to fully understand the positional behaviour within the genus.

In Chapter Three, I compared the novel data (described in Chapter Two) for western lowland gorillas with arboreal locomotor data for Sumatran orangutans (Thorpe & Crompton, 2005) and chimpanzees (Pettifer & Thorpe, Unpublished data). Interspecific comparisons using the ecomorphology approach is the next step in understanding how species and body size influences how great apes use arboreal environments, but because of different ethograms and limited data for western lowland gorillas, no previous study had compared these three species. The classic predictions that larger apes would engage in less risky or less metabolically demanding locomotion (Cartmill & Milton, 1977; Cant, 1992) was not supported. The great ape populations observed in these studies instead found solutions to the challenges of moving in arboreal environments, which did not fit precisely with previous assumptions based on their body size. The variation in arboreal locomotor behaviours of the great apes also varied interspecifically. Orangutans used orthograde suspension which reflected adaptations towards this behaviour (Thorpe & Crompton, 2005), and the African apes used walking to travel around the canopy. However, each species was not restricted to these locomotor modes, but instead were flexible in how they moved in the trees. Their adaptability allowed them to employ different strategies in order to find solutions to moving on small supports and dealing with discontinuity.

The next logical step after understanding the locomotor ecology of a single species is to compare them to other species who are distinct in phylogeny, morphology and/or the habitats that they occupy. However, further advancing our understanding requires a biomechanical approach. Primates often use similar locomotor behaviours when moving in their natural habitat, but the mechanics of these behaviours will often vary. Speed, muscular engagement, joint mobility, contact durations and positioning of body segments are some of the ways in which a single locomotor behaviour can be executed in a range of ways (D'Aout et al, 2004; Watson et al, 2009; Nakano, Hirasaki & Kumakura, 2006; Venkataraman et al, 2013; Finestone et al, 2018; Sarringhaus, Wuthrich & Maclatchy, 2018). Although great apes use locomotor behaviours in different amounts, when in arboreal environments, they do use similar locomotor behaviours (e.g. suspension, bipedal walking or symmetrical vertical climbing), as described in Chapter Three. By quantifying if and how locomotor behaviours are biomechanically distinct can shed light on the form-function interface of a species, and whether the strategies used to achieve the same goal in different environments is constrained by their musculoskeletal structures. Advancement in kinematic techniques have led to the hope for these frameworks to be used in analysis of wild ape locomotion, as this would revolutionise how great apes in their natural habitats can be studied and our understanding of their ecomorphology. In Chapter Four, I compared two new machine learning frameworks, DeepLabCut (Nath et al., 2019) which was first released in 2019 and OpenApePose (Desai et a., 2023) which was made available only five months ago. Given the high degree of accuracy required for kinematic analysis, it was found that these tools are not yet ready to be applied to footage of wild gorillas engaging in diverse locomotor behaviours. The two pose estimation frameworks are highly advanced, but the next step in developing these tools is to train them on more wild footage.

5.3 Current limitations and future directions in great ape ecomorphology

Ecomorphology has been one of the key themes throughout this thesis, as it integrates the morphology, habitats and expressed behaviours of great apes into a single framework that can be used to understand the complex array of influences on expressed behaviour (Karr & James, 1975). This approach differs to functional morphology in that it focuses specifically on how morphology functions within a specific natural environment (Bock, 1994). The functional morphology of great apes has been studied in controlled, or captive settings (e.g. Isler, 2002; Finestone et al., 2018; MacLean & Dickerson, 2020; Tarrega-Saunders et al., 2021), yet essential to the nature of a biological role, is a comprehensive understanding of the local ecosystem. However, morphology is much easier to quantify than ecology and it is often difficult to define the environment of a species because a single ecosystem can include many habitat types (Elton et al., 2016). For example, the lowland forests occupied by western lowland gorillas encompass swamps, wetlands, thick impenetrable vegetation, and open areas on the forest floor. These represent only the terrestrial habitats: arboreally, habitats vary from dense canopy to sparse areas that are characterised by small unpredictable branches. As a result of this environmental complexity, the consequence of morphological variation is easier to examine when looking at similar species who occupy the same ecological niche (Wainwright, 1991).

In a comparative study of orangutan habitats, it was found that the way in which Bornean and Sumatran orangutans solved the problems associated with arboreal travel reflected the structure of the forest rather than species or intraspecific populations (Manduell, Harrison & Thorpe, 2012; Manduell, 2013). As different supports were used in different environments, this might suggest that habitat structure and the availability of supports is highly influential in how apes move in arboreal environments. However, *Pongo* are more morphologically similar to each other than they are to African apes, and exhibit less intraspecific variation than *Gorilla* and *Pan*, so it is considerably more difficult to conduct comparisons to understand the role of habitats outside of *Pongo.* This is because habitat might not be the only variable influencing behavioural variation. Instead, it could be a consequence of habitat and/or diet, activity patterns, social relationships, group size, intragroup competition, and morphology (Tutin et al., 1991; Doran, 1993a; Galdikas, 1995; Doran, 1996; McGrew, Marchant & Nishida, 1996; Stanford & Nkurunungi, 2003; Robbins et al., 2004). These challenges are also prevalent when examining the influence of morphology on habitat use. Interspecifically, the only sympatric great apes are the chimpanzees and western lowland gorillas in central, west Africa. The chimpanzees in the comparative study discussed in Chapter Three inhabited the forests in the Ivory Coast, so it was challenging to determine whether differences in their expressed behaviours reflected species-specific or habitat-specific traits. Furthermore, as the chimpanzee subjects were all older than 19 years, their behaviour might also have been linked to their older age. However, if differences are observed in the habitat use of sympatric gorillas and chimpanzees, this might instead reflect their social dynamics (Hunt, 1994) or dietary differences (Tutin & Fernandes, 1993; Yamagiwa & Basabose, 2006; Head et al., 2011) rather than their morphology.

Another challenge when interpreting locomotor ecology data is understanding the direction of causation. Great apes might select routes in the canopy in which they can engage in a specific locomotor behaviour, or they might instead select a travel route based on the properties of supports (or both). It was found that orangutans used small supports more frequently than gorillas, which locomoted more on larger supports. However, whether the supports were actively selected for, or a reflection of a preferential locomotor behaviour is difficult to determine. Alternatively, great apes might select the most direct route regardless of metabolic cost (because of morphological adaptations) or the risks involved. In this case, the ecological goal is the driving force in shaping how they move in trees. Furthermore, it might also reflect what supports are available for a great ape to access feeding sites. Gorillas used lianas less than orangutans, but this might be because they are more abundant in the Sumatran forests, rather than a species-specific preference (Manduell, Harrison & Thorpe, 2012). The orangutans used multiple supports (rather than a single support) more than the gorillas, but this might reflect the higher abundance of supports and canopy density in the Asian forests compared to Africa. Evidently, great apes are highly complex in all aspects of their biology and behaviour, which makes them complex to study. In fact, during a recent symposium on primate ecomorphology (see Thorpe, 2016), one of the key discussion points was that although ecomorphology is the best approach to understanding what shapes behaviour, it is inherently challenging to study (Elton et al., 2016; Hunt, 2016; Soligo & Smaers).

Great ape anatomy is well understood but focus now needs to be directed towards integrating a more detailed methodology into the ecomorphological approach. In order to understand the role that each factor plays in shaping arboreal behaviours, it is important to carefully consider the traits being measured (Bock, 1994). This is why the classification of appropriate ecological variables is fundamental. Since the standardised descriptions by Hunt et al., (1996) and Thorpe and Crompton (2006), locomotor and postural classifications have become streamlined. However, now we need to determine a standardised framework for which primate researchers document support use and habitat structures. Whilst some of the forest structures in Borneo and Sumatra have been described in terms of the supports available (Manduell, Harrison & Thorpe, 2012; Manduell, 2013), the forests inhabited by the African apes have not been described in as much detail (Williamson, 1993; Remis, 1999; Nkurunungi et al., 2004; Morgan et al., 2018). This is the first step in making interspecific comparisons more informative as we can only understand variation in what is used if we understand the variation in what is available. Furthermore, the classification for which the size, type, number and orientation of supports used needs to be standardised, as previously, this has led to difficulties within comparative analyses (see also Chapter Three). Finally, as social factors may play a significant role in shaping how great apes interact with their environment, a system needs to be developed in which we can quantify the influence of social dynamics. For example, ranking chimpanzee individuals based on social hierarchy and integrating this into statistical modelling may reveal whether social dynamics play a role (Hunt, 1994; Pettifer & Thorpe, Unpublished data). Diet and distribution of resources is another variable that can be integrated into ethograms which will introduce more information on strategies used to access different resource sites. As discussed in Chapter Three, location of resources is missing from locomotor ecology data which means that it is difficult to interpret the role of acquiring nutritional resources in shaping arboreal behaviours.

This thesis has highlighted that great ape ecomorphology is important when comparing the arboreal locomotor behaviours of great apes, but this approach requires further development in order to further advance our understanding of primate behaviours. These advancements will have greater implications for how we study hominid evolution and how we adapt conservation efforts towards wild apes. If theenvironmental conditions that are highly important for wild apes are better understood, then we can make sure to protect these ecosystems using an evidence-based approach (Junker et al., 2020). As a consequence of climate change and human conflict, the forests inhabited by great apes are becoming more fragmented (Hockings, 2009; Bessone et al., 2021; Carvalho et al., 2021). Conservation attempts will be better equipped to help wild apes if we know how they behave by integrating data on their diet, ranging patterns, social behaviours with comprehensive information on their locomotor ecology (Lonsdorf, 2007; Breuer & Mavinga, 2010; Tranquilli et al., 2012; McLennan, 2013).

5.4 Next steps for great ape locomotor kinematics

Joint and segment mobility is often described as a biomechanically informative as it is able to shed light on the adeptness, or efficiency of a behaviour (Orr, 2017). Furthermore, interspecific studies are even more informative, as they can reveal how the variation in morphology is reflected in variation in locomotor biomechanics (for example, how the variation in orangutan and gorilla morphology influences the way in which they vertical climb on small supports). There are three main approaches that are generally used to measure joint and segment angles of great apes. The most common practice for quantifying joint excursions and segment orientations is to use video footage that is then manually digitalised where angles can then be computed using software such as Kinovea and ImageJ (D’Août et al, 2002; Watson et al, 2008; Nakano et al, 2006; Venkataraman et al, 2013; Finestone et al, 2018; Thompson et al, 2018; Sarringhaus, Wuthrich & Maclatchy, 2018). The least used approach is applying physical markers to pinpoint the articulation location of a joint during *in vivo* analysis (Johnston, 1980). However, this technique is not commonly used because of its invasiveness. The final approach uses markerless techniques which employ machine learning software to automatically locate joint centres (Labuguen et al., 2019; Marks et al., 2020; Hayden, Park & Zimmermann, 2022; Yao et al., 2023; Fuchs et al., 2023). This is considerably more complex because automated software does not have the human precision to locate anatomical landmarks when primates are moving in different planes of motion and obscured by structures.

The next step in developing our understanding of how great apes interact with their environment is to conduct wild studies using new sophisticated techniques to examine locomotor kinematics. Machine learning tools are advancing quickly and will make locomotor analysis highly efficient when they are ready to be used in primate research. In Chapter Four, I discussed that some of the leading machine learning software programmes (DeepLabCut and OpenApePose) are highly advanced, but the only way in which we can progress their applicability in pose estimation of wild apes, is to expose them with more images/footage of wild apes. Their success in captive settings is because they have been built on tens of thousands of images, as this is how deep convolutional networks train the algorithm to recognise anatomical landmarks (Krizhevsky, Sutskever & Hinton, 2012). Therefore, in order to train these tools to be able to differentiate between wild structures and gorilla limbs, as well as accurately identifying where a limb might be located even when out of sight, more focus needs to be directed towards using these programmes and creating an open-access depository of wild images (Desai et al., 2023; Fuchs et al., 2023).

5.5 Extant apes as referential modes for understanding the evolution of hominoid locomotion

Understanding the relationship between ecology and function that are also reflected in morphology allows ecomorphological approaches to be used to reconstruct the behaviours and environments of extinct species (Elton et al., 2016). The ancestral form that evolved to become the locomotor repertoires practiced by extant apes has been heavily debated within palaeoanthropological literature (e.g. Morton, 1922; Keith, 1923; Washburn, 1972; Tuttle, 1975; Prost, 1980; Pilbeam, 1996; Crompton, Vereecke & Thorpe, 2008; White et al., 2015; Böhme et al., 2019). However, it is generally accepted that the trajectory of evolution of locomotion occurred in a step wise fashion rather than a direct linear sequence of speciation events (Crompton, Vereecke & Thorpe, 2008; Harcourt-Smith, 2010; Hunt, 2016).

Extant apes are not living fossils but should be regarded instead as modern species that have experienced phenotypic and genetic accommodation as a response to environmental change (Wrangham & Pilbeam, 2002; Bradley, 2008; Bertossa, 2011; Hunt, 2016; Senut et al., 2018). As is true for all living organisms, it would have been necessary for extinct hominoid taxa to have applied appropriate adaptive responses in their behaviour and musculoskeletal arcitechture to facilitate survival. The concept of behavioural plasticity is defined as an ability to react to internal or external pressures by changing in form, state, movement or rate of activity and cannot be observed from skeletal material alone (West-Eberhard, 2003; Chromiak & Antonio, 2008; Bateson & Gluckman, 2012; Crompton, 2016). Significant and abrupt environmental change, which would require behavioural change would result in increased levels of behavioural plasticity of a population and this is likely to be followed by rapid phenotypic modifications towards the new environmental condition (Antón & Kuzawa, 2017). Whilst behavioural plasticity is an adaptive response to changing environmental pressures, anatomical plasticity also plays a vital role. When exposed to external forces and loads, the musculoskeletal system will undergo changes depending on the condition of the load, such as in compression, tension, torsion or bending (Susman, 1974; Carter, Wong & Orr, 1991; Andriacchi & Alexander, 2000; Rabey et al., 2015). The skeletal system in particular is capable of remodelling and these changes can occur rapidly if the functional loading is repetitive (Schaffler & Burr, 1984; Sarringhaus et al., 2016; Antón & Kuzawa, 2017). The physiological cross-sectional area, tendon lengths, muscle body lengths and pennation angles all define the function of muscles, which are also susceptible to plasticity. Muscles and ligaments differ to bones in that they possess elastic components that allow for energy storage, shock absorption and energy conversion; this has been the focus of many kinetic analyses of extant great apes over the last few decades (Payne et al., 2006; Myatt, Schilling & Thorpe, 2011; Myatt et al., 2012; Rabey et al., 2015). The performance of soft tissues adaptability and flexibility during *in vivo* studies has illuminated the necessity of using extant apes as referential models to be able to quantify their performance, which in turn can be used during reconstructions of fossil taxa (D'Aout et al., 2002; Isler, 2002; Thorpe & Crompton, 2006; Carlson, 2006; Griffin et al., 2010; DeSilva, 2009; Pontzer, Raichlen & Rodman, 2014; Wunderlich & Ischinger, 2017; Kozma et al., 2018; Neufuss et al., 2018; MacLean & Dickerson, 2020). However, the degree to which plasticity and environmental conditions influences the habitual behaviours of extant apes is not yet understood

(Tarrega-Saunders et al., 2021). As this cannot be interpreted from skeletal material alone, extant great ape proxies are crucial in reconstructing an accurate picture of the locomotor profiles of extinct taxa, by accounting for both environmental response and plasticity. This is only achievable by developing our knowledge on great ape ecomorphology alongside locomotor biomechanics. This can reveal extent to which great apes perform within their general capacity, and whether they exhibit plasticity that allows them to perform outside of this threshold within their local environment.

Extant great apes are phylogenetically close, yet do not exhibit homologous locomotor regimes; the variability of locomotor regimes between *Pongo, Pan, Gorilla* and humans raise concerns regarding whether hominid ancestors would have displayed biomechanically similar locomotor modes, or those that are significantly distinct and are not represented by extant genera. Furthermore, the versatility of positional behaviour within a single species demonstrates that it is highly unlikely that extinct hominoids would have occupied a single locomotor profile, but instead a multi-locomotor repertoire. Despite the variation in their arboreal repertoires, it was found that the great apes all shared a propensity to engage in orthograde locomotion in the trees (see Chapter Two and Three). This aligns with fossil evidence which suggests that the last common ancestor of the great apes, and the locomotor behaviour which may have transitioned into terrestrial bipedalism, would have exhibited arboreal orthogrady (Crompton, Vereecke & Thorpe, 2008; Crompton, Sellers & Thorpe, 2010). The African apes do not possess specialised adaptations for orthograde postures (Schultz, 1963; Tuttle, 1967; Gebo, 1992; Zihlman et al., 2011; Matarazzo, 2013. However, the requirement to move in complex tree canopies to feed on arboreal fruits and leaves on small, compliant supports (Chapter Three) was likely a strong selective pressure for the acquisition/ability to engage in arboreal bipedality and suspension for chimpanzees and gorillas. Orangutans engage mostly in suspensory locomotion when in the trees, but they also use bipedalism to move in the terminal branch niche (Thorpe & Crompton, 2005; Thorpe, Holder & Crompton, 2007; Myatt & Thorpe, 2011). This is facilitated by considerable joint mobility and adaptations in their hands compared to the African apes because orangutans are almost exclusively arboreal and require adaptations for tree-life to reduce energetic expenditure. Therefore, regardless of variation in postcranial morphology, great apes, including humans (Johannsen et al., 2017), use orthograde postures when moving in tree canopies. Given that the knuckle walking model for what predated bipedalism is based on the African apes (because of their terrestrial locomotion and adaptations), but they exhibit considerable behavioural plasticity when in the trees in the direction of orthograde postures, this favours the arboreal orthogrady model as a preadaptive condition to bipedalism. Furthermore, biomechanical analysis of quadrupedal walking has also shown that whilst the African apes do exhibit some similarities in their knuckle walking, there are significant interspecific kinematic distinctions (Inouye & Shea, 2004; Kivell & Schmitt, 2009; Tarrega-Saunders et al., 2021). This implies that knuckle-walking is either a shared inheritance of behavioural flexibility or evidence of independent evolution as a response to environmental pressures, but likely not the locomotor condition which transitioned into bipedalism (Tarrega-Saunders et al., 2021). We already know that the great apes differ in their biomechanics when using orthograde locomotion, as for example orangutans use extended-leg bipedalism (Thorpe & Crompton, 2005; Crompton, Sellers & Thorpe, 2010) whereas the African apes employ flexed-leg bipedalism (Crompton, 1998; Hunt, 1991; Chapter Two). This suggests that although great apes likely shared evolutionary pressure to use orthograde postures in the trees, they may have developed distinct biomechanics within these behaviours because of local environmental pressures. This provides new evidence for the evolutionary trajectory of hominoid locomotion, but the next step in developing this understanding is to introduce more data for the great apes and delve further into the form-function interface and behavioural plasticity of great apes as a whole, and on a species level.

5.6 Thesis Conclusion

This thesis has provided new insights into the locomotor ecology of western lowland gorillas in arboreal environments. Gorillas are the largest arboreal apes, but their body size and postcranial morphological adaptations towards terrestrial quadrupedal walking did not seem to constrain the way in which they move in the trees. Instead, they found solutions to the challenges of accessing, moving and dealing with gaps in tree canopies, even when supports were small and unpredictable. A comparison of the arboreal behaviours of gorillas, orangutans and chimpanzees highlighted the importance of adopting an ecomorphological approach. Great apes vary in their habitats, locomotor behaviour, morphology and body size, and although these all contribute towards shaping their arboreal behaviours, in order to understand the influence of each factor, more research is required. These studies have also shed light on the gaps in our knowledge and so I have discussed the ways in which future research should be directed. The advancement of machine learning tools is revolutionising the way in which primate studies can be carried out, but what needs to follow is applying these frameworks to wild type settings. Therefore, by developing our knowledge of great ape ecomorphology and integrating new approaches to explore locomotor biomechanics, this will provide a new framework for which the arboreal behaviours of extinct hominoid can be reconstructed.

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APPENDIX A

LOCOMOTOR SUBMODE DESCRIPTIONS AND PERCENTAGES FOR GORILLAS, ORANGUTANS AND CHIMPANZEES

Appendix A.1 Descriptions of locomotor submodes by Hunt et al., (1996) and developed by Thorpe and Crompton (2005).

Locomotor mode, *submode,* description
Quadrupedal walk
Symmetrical gait walk, regular (usually diagonal sequence, diagonal couplets) gait sequence
Irregular gait walk, scramble, lacking a regular gait
Quadrupedal run symmetrical, fast often with a period of free flight
Quadrupedal run irregular, fast, where footfall patterns follow no regular sequence
Tripedal walk
Tripedal walk, same as quadrupedal, except one limb is not used
Bipedal walk
Extended bipedal walk, hip and knee are extended
Flexed bipedal walk, hip and knee are relatively flexed
Hand assisted extended bipedal walk,* hindlimbs bear more than 50% of body mass in full extension, but one or both forelimbs as used to assist, either in suspension or compression and bear more than their own weight
Hand assisted flexed bipedal walk,* as for ‘hand assisted extended bipedal walk’, but hindlimbs are relatively flexed
Bipedal scramble,* hindlimbs bear majority of body mass but hindlimb kinematics are not characterised by a regular sequence
Hand assisted bipedal scramble,* as for ‘bipedal scramble’, but with hand assistance
Vertical climb
Flexed-elbow vertical climb, propulsion provided by hindlimbs as well as forelimb flexion to pull body upwards
Ladder climb, as for ‘flexed-elbow vertical climb’, but except supports are often relatively horizontal and never a single vertical support
Vertical scramble, upwards progression on multiple often oddly angled supports with no regular gait
Extended-elbow vertical climb, propulsion provided by hindlimbs (mainly through hip extension) with extended elbow forelimbs and some forelimb propulsion
Vertical climb forelimbs only,* vertical ascent where body mass is fully borne by forelimbs
Bimanual pull-up, body is lifted up by forelimbs using elbow flexion and humeral retraction
Inverted flexed-elbow vertical climb,* ascent only on angled (20-45°) supports, whereby body is effectively hanging underneath support, while ascending
Vertical descent
Rump-first symmetrical descent, rump-first symmetrical descent, similar to flexed-elbow vertical climb
Rump-first scramble descent, as for ‘rump-first symmetrical descent’, but with no discernible gait often on multiple supports with odd orientations
Rump-first forelimb only descent,* rump-first descent in which only forelimbs are used to bear weight
Rump-first cascade descent,* as for ‘head-first cascade descent’, but rump-first
Rump-first extended elbow descent,* kinematic reverse of ‘extended-elbow vertical climb’
Fire pole slide, rump-first sliding down vertical or subvertical support, usually larger than 20cm
Head-first scramble descent, head-first on multiple supports with odd orientations and no discernible gait
Head-first cascade descent, as for ‘head-first scramble descent’, except supports are smaller and radically angled

Pronograde slide, head-first quadrupedal descent of smooth branches where the body moves by sliding

Sideways vertical descent, body is at right angle of long axis of support

Cartwheel descent,* descent in which limbs grasp supports in motion which resembles limb sequence of human cartwheels

Torso-orthograde suspensory

Brachiate, classic hand over hand orthograde suspensory locomotion where forelimbs bear more than 50% of body mass with extreme trunk rotation, approaching 180°

Forelimb swing, similar to ‘brachiate’ but with little trunk rotation

Flexed elbow forelimb swing, as for ‘forelimb swing’ but with elbows flexed

Orthograde transfer, often begins with bimanual forelimb-suspension and may contain a lunge, where hands grasp small supports, after which a branch is pulled towards body with hand over hand or hand over foot motion. Weight is gradually transferred

Orthograde clamber, forelimb-suspensory where the hindlimbs assist and all four limbs are propulsors with the body weight borne by abducted forelimbs. Like brachiation but hindlimbs support in different orientations

Arrested drop, swinging from on top to underneath a support.

Torso-pronograde suspensory

Inverted quadrupedal walk, hands and feet used in combination with torso-pronograde and all limbs are in tension

Inverted tripedal walk,* as for ‘inverted quadrupedal walk’ but with only three limbs

Inverted quadrupedal run, as for ‘inverted quadrupedal walk’ but more rapidly

Inverted pronograde scramble, as for ‘inverted quadrupedal walk’, but on irregular angled supports and no discernible gait

Hindlimb swing*, body is held upside-down and animal swings on one or both hindlimbs

Forelimb-hindlimb swing

Cartwheel swing,* sequence of suspensory locomotion on horizontal or negatively inclined supports which resembles sequence of limbs like human cartwheel

Ipsilateral swing,* swinging from ipsilateral fore- and hindlimb. Often as a single swing to join two other modes of locomotion

Bridge

Cautious pronograde bridge, torso-pronograde gap-closing movement where hands reach out to grasp support and cautiously pull body across

Inverted pronograde bridge,* as for ‘cautious pronograde bridge’ but in inverted pronograde suspension

Lunging bridge, feet grasp a support, and a lunge closes the gap, with hands then grasping a distant support.

Supinograde bridge, as for ‘lunging bridge’, except suspensory

Descending bridge, an incomplete leap yielding hindlimb suspension that spans a gap followed by grasping support with forelimbs

Leap

Pronograde leap, torso-pronograde at take-off from either a posture or locomotion

Pumping leap, similar for ‘pronograde leap’ but with several forceful extensions of limbs to initiate branch sway which is used to add length to leap

Vertical cling leap, torso-orthograde clinging posture at take-off on a vertical support with push off mostly hindlimb powered

Bipedal upward leap[1]*,* differs from bipedal hop as hindlimbs push off simultaneously and there is a period of free flight, but progression is upwards and is only single bout rather than repetitive progression. Forelimbs can hold supports for stability but body weight is mostly borne on the hindlimbs

Drop

Unimanual suspensory drop, single forelimb suspension before drop, where body falls after releasing support

Bimanual suspensory drop, as for ‘unimanual suspensory drop’ but from both forelimbs

Bipedal drop, above branch bipedal balanced posture before drop

Quadrupedal drop, as for ‘bipedal drop’ but from quadrupedal posture

Flexed elbow suspensory drop, as for ‘suspensory drop’ but with forelimbs flexed

Forelimb hindlimb suspensory drop, drop from a forelimb and hindlimb suspension posture

Sway, gap-crossing movement used between supports by swaying a support where oscillations of increasing amplitudes using body weight and swayed until the animal can reach the other side of the gap. Also includes the oscillation of vertical branches and lianas

Ride, similar to sway but using supports to descend to lower levels in the trees or the ground

*Submodes described by Thorpe & Crompton (2006)

[1] Newly identified locomotor behaviour for gorillas

Appendix A.2 Frequency of arboreal locomotor submodes for gorillas (Chapter Two), orangutans (Thorpe & Crompton, 2006) and chimpanzees (Pettifer & Thorpe, Unpublished data). Not all species engaged in all submodes.

Locomotor submode	Gorilla *(Gorilla gorilla gorilla)*	Orangutan *(Pongo pygmaeus abelii)*	Chimpanzee *(Pan troglodytes)*
Quadrupedal walk			
Symmetrical gait walk	14.05	8.00	20.96
Irregular gait walk	13.97	9.36	7.74
Quadrupedal run symmetrical	-	-	0.68
Quadrupedal run irregular	0.07	-	-
Tripedal walk			
Tripedal walk	0.67	0.22	0.45
Bipedal walk			
Extended bipedal walk	0.29	1.28	-
Flexed bipedal walk	0.67	0.36	1.36
Hand assisted extended bipedal walk	5.0	2.88	-
Hand assisted flexed bipedal walk	3.74	0.57	-
Bipedal scramble	0.30	0.14	-
Hand assisted bipedal scramble	3.36	2.03	-
Vertical climb			1.13
Flexed-elbow vertical climb	8.52	5.59	25.74
Ladder climb	0.37	0.18	0.23
Vertical scramble	4.41	7.08	4.78
Extended-elbow vertical climb	0.67	1.17	1.82
Vertical climb forelimbs only	-	1.28	-
Bimanual pull-up	1.72	0.18	-
Inverted flexed-elbow vertical climb	-	0.5	-
Vertical descent			0.68
Rump-first symmetrical descent	9.27	1.99	12.98
Rump-first scramble descent	5.08	4.45	5.46
Rump-first forelimb only descent	0.67	0.60	-
Rump-first cascade descent	0.82	0.18	-
Rump-first extended elbow descent	1.27	0.28	-
Fire pole slide	2.09	0.18	0.68
Head-first scramble descent	0.15	0.36	0.91
Head-first cascade descent	0.07	0.07	-
Pronograde slide	-	0.04	0.23
Sideways vertical descent	-	1.07	-
Cartwheel descent	-	0.14	-
Torso-orthograde suspensory			
Brachiate	0.07	6.15	1.88

Forelimb swing	5.16	8.25	-
Flexed elbow forelimb swing	0.07	0.18	-
Orthograde transfer	4.84	6.05	3.87
Orthograde clamber	0.22	14.37	2.50
Arrested drop	1.79	0.85	0.23
Torso-pronograde suspensory			
Inverted quadrupedal walk	0.45	2.28	-
Inverted tripedal walk	-	0.11	-
Inverted quadrupedal run	-	0.04	-
Inverted pronograde scramble	0.15	1.28	-
Hindlimb swing	-	0.14	-
Forelimb-hindlimb swing			
Cartwheel swing	-	0.18	-
Ipsilateral swing	0.15	0.07	-
Bridge			
Cautious pronograde bridge	0.60	2.53	0.23
Inverted pronograde bridge	-	0.11	0.45
Lunging bridge	0.45	0.14	-
Supinograde bridge	1.27	0.04	-
Descending bridge	0.75	0.04	-
Leap			
Pronograde leap	0.60	0.04	0.45
Pumping leap	0.07	-	-
Vertical cling leap	0.30	-	0.23
Bipedal upward leap	0.75	-	-
Drop			0.45
Unimanual suspensory drop	1.49	0.36	-
Bimanual suspensory drop	0.90	0.57	-
Bipedal drop	0.45	-	-
Quadrupedal drop	0.07	-	-
Flexed elbow suspensory drop	0.07	-	-
Forelimb hindlimb suspensory drop	0.15	-	-
Sway	0.22	4.55	1.82
Ride	1.64	0.50	1.36

APPENDIX B

VIDEO FOOTAGE FOR POSE ESTIMATION

Appendix B.1: Image stills from video footage showing the different array of environmental conditions and focal size where the gorilla is not obscured by foliage. All images were used in the comparison of pose estimation frameworks (Chapter Four).

Appendix B.2: Image stills from video footage when the focal gorilla was only partially visible. All images were used in the comparison of pose estimation frameworks (Chapter Four).