A multifactorial approach to improving captive primate welfare and enclosure usage

Thesis submitted in accordance with the requirements of the University of Liverpool
for the degree of Doctor in Philosophy by
Colleen Goh
June 2016

Table of Contents

List of Figures

List of tables

Acknowledgements

Firstly, I thank my parents (Austin & Rosy) for providing endless moral, emotional (and financial!) support throughout my PhD. I would not have been the person I am today if not for them. I would also like to thank my Grandma for her prayers and who always cheered me on from halfway around the world. I thank Mary, not only for her professional help and expertise, but also for her moral and emotional support day to day. We have shared many good (and stinky) memories in the dissection room. She has let me get away with household chores when I am too busy and kept me well fed! My hamsters Chicken Pie and Chicken Nugget, whose silliness have made my final year of writing up a very cheerful one!

I am grateful for my supervisors Robin and Karl. Without Robin, I would not even have embarked on this PhD. Robin has provided support both inside and outside my PhD. He was always brimming with new ideas, which has been helped great deal in guiding me throughout my PhD. Also it is thanks to Robin that my writing skills have greatly improved! We have also shared quite a few fond memories outside the lab. I would like to thank Karl who has been extremely patient, putting up with my endless questions about modelling and Matlab. Karl was also very quick in responding to my questions despite how busy he was, which I truly appreciate. Learning 3D computer modelling was a steep learning curve for me, and without Karl I very much doubt that I would have been able to do it. I have many fond memories, both inside and outside the lab, of my fellow colleagues Michael, Kris, Russ, Sarita, Dave, Juliet, Ali, Sophie, Abby, Lyn and Miral that I am grateful of.

I thank Amanda, who I know would be there to listen to me from halfway around the world over our regular skype sessions. Emma, who has been there for me from the first day I came over to the UK and I am glad to say we are good friends now. Kugan and Chris, who have been excellent badminton training and eating buddies! Xiuling, who has kept in contact with me daily despite time and geographical differences!

I am grateful for Twycross Zoo, which I have worked closely throughout my PhD. Zak, Manuela and the primate keepers have been so helpful, it has been such a pleasant journey working with Twycross Zoo. I would also like to thank Howletts Wild Animal Park and Lorna, for enabling me to carry out my research there. I thank Tony, whom I am grateful for offering his expertise and advice! I thank my collaborators Susannah, Emily, Nardie, Ian and Shelly. Susannah has been a great help professionally. Emily, who started her PhD the same time as I did and on the same species of primate, is now a friend of mine. Nardie who was always very eager to help, especially with drawings! Ian has been very supportive and helpful, he went above and beyond and collected videos of wild gorillas in a way that was more suitable for me. Shelly who also provided me with videos of wild gorillas was always eager to help.

Finally, I have obtained funding from 1) the Primate Society of Great Britain Captive Care Working Party and Research Working party, 2) PRACTICE scheme from University of Liveprool and 3) Postgraduate Award from University of Liverpool. I am extremely grateful for my funders, without which I would not have been able to carry out most of the research projects for this PhD.

Abstract

Title: A multifactorial approach to improving captive primate welfare and enclosure usage

Author: Colleen Goh

This thesis examines factors affecting the welfare of captive primates from a multi-factorial perspective: positional and non-positional behaviour, anatomical adaptations and enclosure usage. Past studies have shown that the provision of naturalistic environments for primates reduces stereotypical behaviours, decreases inactivity (Honess and Marin 2005; Zaragoza et al. 2011), and encourages species-typical positional behaviour repertoires (Jensvold et al. 2001). This suggests that encouraging species-typical behaviour improves captive primate welfare. It was found that reduced occurrence of stereotypical behaviour was associated with enrichment encouraging tool-use, a high fibre diet, and increased social behaviour. Compared to wild gorillas, captive gorillas adopted similar feeding and resting postures but performed substantially less vertical climbing, likely arising from differences in habitat structure and food distribution. It was found that the genus *Gorilla* has a strong preference for <20cm diameter and vertical/angled supports, but equally, gorillas have to some extent retained locomotor plasticity as suggested by Myatt et al. (2011) and Neufuss et al. (2014). Thus, from construction of a 3D musculoskeletal model of a hindlimb, it was found that bipedalism was associated with higher moment arms and torque around the hip, knee and ankle (except for extensor torque), than vertical climbing. This indicates that in terms of moment arms and torque, the ability to walk bipedally is not restricted by musculoskeletal adaptations to vertical climbing. It was also found that the gorilla foot had interossei that attached to distal phalanges, which may be important for fine flexion movements for grasping/manipulation of objects. These findings stress the importance of taking into account locomotor restrictions and plasticity when encouraging species-typical behaviour, which has not previously been emphasized. Further, accurate quantification of support availability and preference for enclosure design and positional behaviour studies has not been achieved before. Thus a novel method of studying enclosure usage was developed, via construction and analysis of a computer-aided design model of an enclosure. Besides successful accurate quantification of support preference and availability, the model permitted identification of specific favoured supports/areas and behaviour trends.

Chapter 1: Introduction

1.1 Background information

This thesis looks at the welfare of captive primates from a multi-factorial perspective and will deal with their positional behaviour, non-positional behaviour, anatomical adaptations and enclosure usage. But first, I would introduce the history of captive primate welfare and the current issues and methods in captive animal welfare, before delving into the rationale of this thesis.

Captive primate welfare has been studied since the 1940s, initially focussed on physical (Kennard and Willner 1941) and mental (Hebb 1947) disease in laboratory chimpanzees. In the 1960s, researchers started to study the stereotypical behaviour in captive monkeys and link that to enclosure size (Draper and Bernstein 1963) and compared the behaviour of captive populations of monkeys with wild counterparts to draw conclusions about stereotypical behaviour (Mason 1960; Mason and Green 1962). Nutrition also became a subject of importance for captive care (Moreland 1968). In the 1970s more research was carried out on abnormal behaviour of captive monkeys (Erwin et al. 1973). Only in the 1980s did captive primate welfare studies become substantially more common in monkeys and nonhuman apes (McGrew 1981; Clarke et al. 1982; Mallinson 1982; Maple 1982; Rails and Ballou 1982; Pond and Rush 1983; Glatston et al. 1984; Mallinson 1984; Moran and Sorensen 1984; Quick 1984; Akers and Schildkraut 1985; Gould and Bres 1986; Hosey and Druck 1987; Maple and Finlay 1987; Bloomsmith et al. 1988; Bryant et al. 1988; Novak and Suomi 1988; Poole 1988; Segal 1989; Snowdon and Savage 1989). Studies focussed on creating captive environments that mimic the wild (McGrew 1981; Clarke et al. 1982; Quick 1984; Maple and Finlay 1987; Poole 1988; Segal 1989) and issues related to management in captivity such as infant rearing (Maple 1982), influence of visitors (Glatston et al. 1984; Moran and Sorensen 1984; Hosey and Druck 1987), reproduction (Mallinson 1982; Maple 1983; Mallinson 1984), psychological well-being (Erwin et al. 1973; Bryant et al. 1988; Novak and Suomi 1988; Segal 1989; Snowdon and Savage 1989) and housing/physical enrichment

(Clarke et al. 1982; Maple 1982; Maple and Finlay 1987; Bryant et al. 1988). Also, regurgitation and reingestion in nonhuman apes (Akers and Schildkraut 1985; Gould and Bres 1986; Maple and Finlay 1987) and enclosure space usage as an indicator of welfare (Hosey and Druck 1987; Maple and Finlay 1987) started to become subjects of importance. One of the first comprehensive studies of enclosure space usage as a measure of enclosure appropriateness was carried out (Maple and Finlay 1987). In the 1990s, a comprehensive review on regurgitation and reingestion in captive gorillas was published (Lukas 1998). Numerous studies on captive primate welfare were carried out over the 1990s – 2010s on various aspects of captive primate welfare (Veasey et al. 1996; Jensvold et al. 2001; Melfi and Feistner 2002; Young 2003; Blaney and Walls 2004; Hill 2004; Honess and Marin 2005; Hosey 2005; Mallapur et al. 2005b; Mallapur et al. 2005a; Garner 2006; Mason et al. 2006; Croney and Newberry 2007; Olsson and Westlund 2007; Price and Stoinski 2007; Carrasco et al. 2009; Hill 2009; Ross et al. 2009; Ross et al. 2010; Fabregas et al. 2011; Ross et al. 2011a; Ross et al. 2011b).

Traditional observation methods always remain a valid way to record animal behaviour and for examining captive animal welfare. However modern advances ensure there is an array of technical methodologies at a researcher's disposal. Recent studies have employed epidemological approaches for elephants (Meehan et al. 2016) and utilised urinary cortisol levels to examine high plucking in bonobo (Brand et al. 2016). A combination of traditional observation and examination of fecal glucocorticoid metabolites is likely to provide a more well-rounded picture of stress levels and causal factors (Clark et al. 2011). Even traditional methods have been updated, whereby in a study on chimpanzees and gorillas observers recorded their exact locations using a map interface on a tablet (Ross and Shender 2016).

A trend in recent captive studies, especially for primates, have examined how visitor numbers and interactions affect behaviour of captive animals. The results of these studies are mixed, even for the same species, and strongly suggest that individual differences and varying enclosure design play a greater part than visitor numbers. For example Bonnie et al. (2016) found that visitor numbers had a limited effect on gorillas and chimpanzees held at Lincoln Park Zoo. However Collins and Marples (2016) noted that negative responses to visitors in gorillas lessened after the birth of a baby.

The plight of captive animals has often been in the news in recent times. The story of Marius, the Danish giraffe, surplus to requirement, killed and dissected in public was probably the first time that most people had been aware of this issue (see eg Eriksen (2014)). As Asa (2016) discusses, controlling captive populations comes down to primarily separation of individuals, euthanasia or contraception. There are no easy options: separation causes stress in all but solitary species; contraception disrupts normal social behaviour; euthanasia is often viewed as morally wrong.

Many people are querying the ethics of keeping large bodied and/or highly intelligent animals in captivity. For example, Sea World in America has come under repeated backlashes for maintaining orca populations, especially since the release of Blackfish (Cowperthwaite 2013), a documentary movie on Tilikum, a male orca, captured from the wild and involved in the deaths of three people. The negative publicity finally resulted in Sea World announcing an end to it's orca breeding programme in March 2016 (see eg. BBC (2016)).

The keeping of great apes in captivity has been challenged by repeated attempts in multiple countries for great apes to be granted human rights and some have been partially successful. For example, an orangutan has been granted basic human rights in Argentina (see eg. BBC (2014a)), however, attempts to give human rights to chimpanzees in America have been unsuccessful (see eg. BBC (2014b). These cases do show that perception of non-human animals is changing and it is quite possible that long term people will be as unaccepting of captive great apes as they are orca.

Of course it is not just zoos and wildlife parks that hold captive animals. The greatest proportion of captive animals are animals farmed for human consumption, with over a billion a year slaughtered in the UK (Viva! 2014) and this area is the focus of many studies (Heath et al. 2016).

This thesis provides contributions to the field of captive gorilla welfare (Chapters 2-4), and contributes to the improvement of current methods of the study of captive animal welfare (Chapter 5). The importance of creating naturalistic enclosures, that attempt to mimic the wild, to increase captive primate welfare has been well-established (Bayne et al. 1991; Jensvold et al. 2001; Honess and Marin 2005; Hosey 2005; Mason et al. 2006; Coe et al. 2009; Ross et al. 2009; Fabregas et al. 2011; Zaragoza et al. 2011). However, some have debated that there are problems with using wild behaviour as a benchmark to measure welfare (Veasey et al. 1996). Nonetheless, past studies have shown that the provision of naturalistic environments for primates reduces stereotypical behaviours and decreases inactivity (Honess and Marin 2005; Zaragoza et al. 2011), and encourages species-typical positional behaviour repertoires (Jensvold et al. 2001). This suggests that encouraging species-typical behaviour improves captive primate welfare. Therefore in this thesis, I use wild behaviour only as a guideline, given that captive animals have different needs and are exposed to different challenges that their wild counterparts. Species-typical behaviour refers to behaviour profiles and repertoires that are performed by the species' wild counterparts as reported in the literature by researchers that have conducted studies in the wild, and thus may vary at each study site.

Species-typical behaviour can be classified into positional (locomotion or posture) and non-positional behaviour (feeding, travelling, inactivity etc.). Positional behaviour is carried out in the context of non-positional behaviour: for example, sitting might occur during feeding. If a species' locomotor potential (the ability to perform a range of locomotor modes based on musculoskeletal adaptations) can be adequately expressed by providing suitable support types, distribution or availability in an enclosure, this promotes health and wellbeing. This is because locomotor capabilities are based on musculoskeletal adaptations and body size, and thus restrict, to a certain extent, those habitats in which these animals can live or to which they can adapt (Fleagle and Mittermeier 1980; Crompton 1984; Youlatos 2004). On the other hand, from Venkataraman et al. (2013a); Venkataraman et al.

(2013b), it was found that animals can be plastic in their musculature to adapt to their habitat. Thus it would be useful to find out how plastic or restricted a species' locomotor abilities are, to ensure that the species could be provided with suitable support types/distribution/availability in an enclosure. Subsequently the primate will be likely to travel more and hence be more active. Thus positional behaviour, and non-positional behaviour and the study of species' musculoskeletal adaptations are closely linked to each other.

The many studies on enclosure usage mentioned above however do not consider the locomotor potential and plasticity of the species. In this thesis, I show the importance of locomotor potential and plasticity in enclosure design and hence welfare. I emphasize the importance examining captive primate welfare using a holistic, multi-factorial approach - not just behaviour and activity levels (Chapter 2), but also enclosure usage (Chapters 3 and 5) and positional behaviour and support usage preferences (Chapters 3-5). Furthermore, previous studies all relied on traditional observation methods. Here the novel use of a 3D computer model to aid enclosure usage and behavioural studies, will be shown to have potentially exciting applications and implications for captive care of primates and the evolution of enclosure usage and behavioural study methodologies.

To better understand how to design an enclosure successfully, a zoo would need to adapt conditions with the aim of providing suitable support types/distribution/availability in an enclosure. Information on patterns of enclosure and support usage in relation to positional and non-positional behaviour types would be necessary for this. This information will aid in zoo enclosure design and subsequently help in improving the welfare of their primates. For example, it is essential for zoos to ensure that an enclosure has sufficient types of a certain resource (eg. supports for primate to feed on, enrichment that provides mental stimulation, or places for retreat) to prevent over or underutilisation, and maintain and improve the welfare of their primates (Ross et al. 2009).

This thesis therefore aims to find out how to improve the welfare of one of the great apes, namely the western lowland gorilla, (*Gorilla gorilla gorilla*), in terms of:

1) encouraging species-typical behaviour profile and reducing stereotypical behaviour (Chapter 2),
2) encouraging species-typical positional behaviour repertoire and support usage preference (Chapter 3),
3) finding out how and if any musculoskeletal adaptations restrict gorilla locomotor capabilities, and what supports gorillas are adapted to using (Chapter 4) and
4) developing a novel method of studying enclosure and support usage and quantifying support availability and preference (Chapter 5).

Numerous aspects of captive western lowland gorilla welfare have been examined. A number of studies on visitor effects have shown that large crowds are associated with higher stress levels and hence the importance of providing 'nets' or opportunities for hiding (Blaney and Walls 2004; Wells 2005; Davey 2007; Kuhar 2008). Studies on sensory enrichment (Wells et al. 2006; Wells et al. 2007) have also been carried out to test the effects of olfactory and auditory cues on welfare. Recently, physical enrichment studies that suggest space-use and enclosure design as welfare indicators have become a subject of interest (Stoinski et al. 2001; Coe et al. 2009; Ross et al. 2009; Ross et al. 2010; Ross et al. 2011b; Zaragoza et al. 2011). Feeding enrichment studies (Rooney and Sleeman 1998; Ryan et al. 2012) have shown that different feeding devices and methods such as bags/rags/browse/boomer balls have differing effects on behaviour. Positive reinforcement training although criticised by some (Hutchins et al. 1978), have yielded positive results in captive gorillas such as reduced keeper-directed aggression (Leeds et al. 2016) stereotypical behaviour and aggression and increased affiliation and play (Carrasco et al. 2009). Given the numerous studies on captive gorilla welfare, and hence improvements, the welfare of captive gorillas are hence considered to be good. However it remains a subject of debate as to whether certain stereotypical behaviours, or the absence of certain species-typical behaviours exert a negative impact on welfare and whether wild animal behaviour profiles should be used as a benchmark for captive animal behaviour profiles (Daven 2007;(Veasey et al. 1996; Hosey 2005).

Stereotypical behaviour has been defined as repetitive, unvarying and without any obvious function (CAHSJ 1965; Fox 1965; Odberg 1978; Mason et al. 2006). More recently it has been suggested that 'unvarying' should be omitted from the definition as behaviours such as over-grooming in itself are variable (Mills and Luescher 2006). However, 'function' was still a challenge to determine, as sometimes repetitive behaviours do have beneficial functions (Mason and Latham 2004). Therefore, the definition of stereotypical behaviour has been modified to refer to repetitive behaviour stimulated by frustration, recurrent efforts to cope and/or brain dysfunction (Mason et al. 2006). This enables stereotypical behaviour to stem from some biological causation and the inclusion of functional behaviours. Causes of stereotypical behaviour can be classified into 'frustration-induced' (direct trigger from captive environment) or 'malfunction-induced' (brain processes affected by prolonged stress in captivity, or a past, rearing experience) (Mason et al. 2006). Frustration-induced stereotypical behaviours thus directly reflect the underlying problem ie. physical discomfort or distress. Malfunction-induced stereotypical behaviour is more complex in the sense that the underlying problem may not be directly reflected by the behaviour. For example, infant primates that have been separated from their mothers prematurely display eye-poking (Mason 2006). Over time, stereotypical behaviour may become independent of its stimulus (Levy 1944). In terms of captive animal welfare, stereotypical behaviours are often used as indicators, leading to the rise of ethical concerns about the conditions (space, isolation, insufficient stimulation, fear) of which the animals are being kept in (Foley Jr 1934; Meyer-Holzapfel 1968; Clubb and Mason 2002; Mason et al. 2006).

Whether or not stereotypical behaviours are classified as abnormal or normal is another subject of contention. This is because stereotypical behaviours can share aspects of being both 'normal' and 'abnormal', depending on the definition of 'abnormal' (Mason 1991). 'Abnormal' can be defined as either being statistically different from a population (Fraser and Broom 1990) or as being functionless/harmful to the animal (McMahon and McMahom 1983). With the first definition, one can treat a stereotypical behaviour seen in captivity as not 'abnormal' if the particular behaviour ie. regurgitation and reingestion is prevalent in the reference population ie. captive gorillas. Most researchers tend to use wild populations as a benchmark, thus classifying stereotypical behaviours seen in captivity but not in the wild as 'abnormal'. With the second definition, one has to determine if a stereotypical behaviour is detrimental to health before it can be classified as 'abnormal'. In many cases in zoos, unless self-harming, it is difficult to conclude if a particular stereotypical behaviour is actually harmful to the animal ie. thumb-sucking, rocking, pacing. In fact, some stereotypical behaviours are a coping mechanism for a particular problem (Koolhaas et al. 1999; Pomerantz et al. 2012) and are therefore beneficial in that situation.

In this thesis I focus on one particular stereotypical behaviour, namely regurgitation and reingestion (R&R). R&R is the voluntary movement of food/fluid from the stomach/oesophagus to mouth/hands/substrate followed by ingestion of the same food/fluid (Gould and Bres 1986; Lukas 1998). Whether R&R should be classified asAs R&R is so common in captive apes, some researchers refer to R&R as a 'normal' behaviour (Gould and Bres 1986). However, R&R can be seen as 'abnormal' on two levels. Firstly, R&R is not seen in wild gorilla populations. Secondly, although R&R has yet to be associated directly with health problems, it has become apparent that stomach acid is regurgitated during R&R, similar to the human renumination syndrome that is associated with oesophagael problems, ulcers and pulmonary aspiration (Hill 2009). Hence many researchers continue to class R&R as 'abnormal' (Miller and Tobey 2012; Bergl et al. 2014; Kranendonk and Schippers 2014). Occurrence of R&R has been linked to stress and boredom (Yerkes 1943; Loeffler 1982), social factors (Miller and Tobey 2012; Leeds et al. 2016), and insufficient time spent on feeding and dietary composition (Morgan et al. 1993; Lukas et al. 1999; Cassella et al. 2012; Bergl et al. 2014; Lukas et al. 2014). The last two factors are closely linked, as an increase in fibre content would inevitable lead to more time spent on feeding. With this in mind, researchers have tried to tackle R&R in various ways, with differing levels of success. Provision of naturalistic enclosures (Goerke et al. 1987; Kranendonk and Schippers 2014), auditory stimuli (Robbins and Margulis 2014), positive reinforcement training (Leeds et a. 2016), alteration of space availability (Kranendonk and Schippers 2014; Herrelko et al. 2015), change of environments (Bowen 1980; Clarke et al. 1982), alteration of diet composition (ie. increase of fibre) (Morgan et al. 1993; Lukas et al. 1999; Cassella et al. 2012; Bergl et al. 2014; Lukas et al. 2014) and/or feeding enrichment (Ryan et al. 2012) are common routes to reducing R&R.

Although captive gorilla welfare has been studied substantially, and is therefore generally considered to be good, as mentioned earlier, there are still many unanswered questions with regards to causes of R&R and other abnormal stereotypical behaviours. Furthermore, despite the enormous amount of studies on captive gorilla welfare, up to 68% of western gorillas in zoos and breeding centres are known to exhibit “abnormal repetitive behaviours” (Garner 2006), with 65% displaying R&R (Gould & Bres 1986). With regards to availability of wild data for comparison, western lowland gorilla positional behaviour (Remis 1994; Remis 1995; Remis 1998; Goldsmith 1999; Remis 1999) and non-positional behaviour (Masi et al. 2009) have been studied in the wild, allowing for comparison with captive data. Another reason for picking western lowland gorillas is that they are known to live in complex three-dimensional environments. Wild western gorillas forage at heights of sometimes more than 30m (Remis 1995). Further, they defend territory while dealing with loss of members or transfers during encounters with other gorilla groups (Fossey 1983; Gatti et al. 2004; Robbins et al. 2004). This high level of environmental complexity is difficult to represent fully in a captive environment. Also, the influence of habitat structure on wild gorilla positional behaviour has been documented (Remis 1998), where levels of arboreality are strongly affected by habitat structure and fruit consumption. Captive environments, where habitat structure differ strongly from that of the wild, in terms of support types, distribution and materials, coupled with space limitations, likely represent extremes of possible environmental adaptation. The less complex environments of captive animals may be linked to health problems (Hosey 2005). Finally, it has been shown that captive gorillas have a preference for structures such as trees and rocks, and spaces near vertical structures (Stoinski et al. 2001; Hosey 2005), or doors, barriers and corners (Ross et al. 2011b), thus increasing the chances of displaying support preferences. Therefore the western lowland gorilla is a suitable candidate for studying how enclosure and support usage in captive environments impact their behaviour and welfare.

While examining the positional behaviour repertoire and support preference of captive and wild gorillas, it is a challenge to draw conclusions with certainty about how much of the ‘preference’ displayed stemmed from environmental bias (eg. support availability) or from musculoskeletal adaptations. This difficulty has been observed in other studies on positional behaviour and support usage in the wild or in captivity, where it is difficult to accurately account for support availability/distribution (Crompton 1980; Cannon and Leighton 1994; Britt 1996; Warren 1997; Thorpe and Crompton 2006; Blanchard et al. 2015). To quantify how plastic or restricted their locomotor abilities were, based on musculoskeletal adaptations, a 3D musculoskeletal model of a gorilla hindlimb was built to examine the moment arms and torque generating capacity of muscles around the hip/knee/ankle, and flexion/extension capabilities of muscles around the foot, important for grasping supports (Chapter 4).

To accurately quantify support availability and preference, I created an easy-to-build 3D model of a siamang enclosure (Chapter 5). Siamangs, the largest species of gibbon (Aldrich-Blake and Chivers 1973; Chivers et al. 1975), were chosen for a number of reasons. Firstly they are arboreal (Chivers 1977), known to use certain pathways repeatedly, namely “arboreal highways” (Fleagle 1976) indicating support preferences. Secondly their positional behaviour has only been studied once in the wild (Fleagle 1976) and never in captivity. Therefore this study would be valuable in not only providing a standardized method for zoos or researchers interested in studying enclosure and support usage patterns but would also be the first study of captive siamang positional behaviour. Finally siamangs were chosen for this instead of gorillas as they locomote more rapidly, allowing sufficient positional data to be collected within the time available.

Chapter 2: Tackling Stereotypical Behaviour in Captive Western Lowland Gorillas

2.1 Introduction

Wild western lowland gorillas (*Gorilla gorilla gorilla*) live in complex three-dimensional environments that require them to forage at heights of sometimes more than 30m (Remis 1995), to range for ~1105m (Tutin 1996), cope with seasonal changes in diet (Masi et al. 2009) and defend territory while dealing with loss of members or transfers during encounters with other gorilla groups (Fossey 1983; Gatti et al. 2004; Robbins et al. 2004). This level of environmental complexity is difficult to represent fully in a captive environment. The less complex environments of captive animals may be linked to health problems, such as obesity (due to inactivity and/or possibly diet (Pontzer et al. 2012)), and aberrant behaviours including regurgitation and reingestion (R&R) of food (Hosey 2005). As many as 68% of western gorillas (*Gorilla gorilla*) in zoos and breeding centres are estimated to exhibit "abnormal repetitive behaviours" (Mason et al. 2006), R&R being one such commonly displayed abnormal repetitive behaviour (Akers and Schildkraut 1985; Gould and Bres 1986; Lukas 1998; Hill 2009). R&R refers to the voluntary retrograde movement of food and/or drink from the oesophagus or stomach to the mouth, hands or substrate and subsequent consumption of the regurgitant (Gould and Bres 1986; Lukas 1998). Some abnormal repetitive behaviours can be addressed to a certain extent by environmental enrichment, which aims to provide environments of greater physical, temporal and social complexity which affords animals more of the behavioural opportunities found in the wild (Honess and Marin 2005). Environmental enrichment therefore encompasses feeding enrichment, and can potentially reduce stress levels/frustrations by offering more opportunities to engage in preferred behaviours such as feeding, or more control in terms of opportunities for retreat (Mason et al. 2006).

Past studies have shown that the provision of naturalistic environments reduces stereotypical behaviours, has a positive influence on social behaviour (Stoinski et al. 2001) and decreases inactivity (Honess and Marin 2005; Zaragoza et al. 2011). In a study of western gorillas and orang-utans, provision of complex play facilities was observed to be qualitatively associated with more activity, social behaviour and species-typical behaviour and a quantitative reduction in aggression (by 100% in orang-utans; >50% in male gorillas) and abnormal behaviours (R&R reduced by 100% in gorillas) (Maple and Finlay 1987). This is not only beneficial to animal health, but is more likely to create a more positive experience for visitors, allowing them to appreciate and learn more about natural behaviour and habitat (Stoinski et al. 2001; Hosey 2005). As a result, the value of captive conservation can be increased (Honess and Marin 2005).

The objectives of this study were to 1) compare behavioural profiles between zoos and individuals and with data gathered in the wild, in order to tease out factors that might contribute to aberrant and self-directed behaviours in captive lowland gorillas; 2) to identify which forms of feeding enrichment increase frequency of normal behavioural patterns; 3) where possible, to propose simple changes to enclosure furniture and feeding enrichment which may help encourage naturalistic behaviour. This study compared the behavioural effects of different forms of environmental enrichment used by two different zoos (Zoo A and Zoo B) to find out what forms of enrichment are likely to encourage species-typical behaviour. Since activity budgets of the same species can differ dramatically between captive habitats because of the available enclosure furniture (Hosey 2005) it was essential to study conditions in more than one zoo to get a more accurate representation of the species' general behaviour repertoire. Therefore, given time and funding available, two zoos were chosen for this study. In addition, the data from this study was compared with wild data from the literature (Remis 1994; Goldsmith 1999; Masi et al. 2009) to find out how captive behavioural profiles differed from the wild. To aid in teasing out factors that contribute to abnormal repetitive behaviours, behaviour profiles were examined before and after changes in diet and social environment in Zoo A.

I hypothesized that 1) the different forms of enrichment (within each zoo) ie. tool-use based enrichment will increase activity levels relative to non tool-use based enrichment like a scatter feed, and 2) a social-group structure which includes juveniles and blackbacks would increase social behaviour and hence activity levels. Similarly, I hypothesized that 3) captive gorillas would show substantially less activity and engage in less ingestion than their wild counterparts due to the less complex environments in captivity. Lastly I hypothesized that 4) abnormal repetitive and aberrant behaviours in Zoo A would decrease significantly after changes in diet were carried out and the group's social dynamics changed in with the development of the infant.

2.2 Materials and methods

2.2.1 Study sites and subjects

For the first part of the study observations took place at Zoo A (March 2013), as shown in Figure 2. 1, and at Zoo B (May 2013), as shown in Figure 2. 2., for three weeks each, as funding permitted. "Zoo A" and "Zoo B" were used to preserve anonymity as requested by one of the zoos. The second part of the study was conducted 24 months later at Zoo A (February 2015) after some changes were implemented in the interim period, for three weeks. At Zoo A, all three adult females and one adult male in the enclosure were studied. At Zoo B two adult males and two adult females from one enclosure; and two juveniles from a different enclosure had to be chosen due to restrictions in group configurations in the enclosures. All subjects were physically healthy without injuries. Details of each adult gorilla's age, sex and rearing history are in Table 2. 1.

Zoo A's indoor enclosure is made from concrete walls with two points of access to the outdoor enclosure. The gorillas spent most of their time indoors during the time of the study, but had access to the outdoor enclosure at all times. The indoor enclosure had multiple small platforms along the walls at differing levels, and a large tree trunk in the middle with medium sized platforms around it (Figure 2. 1).

Different sized ropes were placed across the whole indoor enclosure. The bedrooms were connected to the indoor enclosure with three access points.

The individual gorillas at Zoo A were fed four to five times a day. They are separated in their bed areas for their morning and afternoon feed, to allow individual diet requirements to be addressed and observations on each individual's behaviour and health status. The other feeding times consisted of scatter feeds either in the outside enclosure or the bed areas. Where possible, food was displayed high off the ground, on branches, browse holders or shelves to encourage higher activity levels. The scatter feeds allowed the animals to perform natural foraging behaviours for a prolonged time period. Food items are mainly given in large pieces to allow the animals to manipulate and process the food themselves. The diet for the gorillas consisted of a range of different brassica, vegetables, greens, pellets and small amounts of fruits. Browse was also given on a daily basis. The exact composition of food items was adapted according to the season. Drinking water was always available through water dispensers in the indoor and outdoor enclosure. Enrichment was given on a regular basis and varied between food based and non-food enrichment devices. Large amounts of wood wool allowed the animals to perform nest building behaviours and to make themselves comfortable sleeping areas. Regular training sessions with each individual were carried out by the keepers to train for general husbandry behaviours and veterinary examinations. All training session are completely voluntary for the animals, using positive reinforcement techniques.

Zoo B's enclosure was made up of a wire mesh. The gorillas had access to both indoor and outdoor enclosures. During the time of this study they spent most of their time in the outdoor enclosure. The outdoor enclosure consisted of a long metal platform in the middle connected to a slide, medium sized metal platforms and smaller wooden platforms hanging from the roof scattered around the enclosure (Figure 2. 2), and honey pots built in around the side of the enclosure.

At Zoo B, the daily diets consists of a large range of food items and drinks: 45 base food items (basic fruit and vegetables), over 30 different types of exotic fruit, over 12 types of browse, over 20 other food items e.g. dried fruits, nuts and natural yoghurt, and very small quantities of leaf eater and primate pellets. Drinks offered include herbal teas, and sugar free fruit juices. All food is fed in their natural state, to encourage natural feeding behaviours and to maintain nutritional values. The diet is adapted according to season, to incorporate the fruits and vegetables that are in season. In the summer, when this study was carried out, browse is plentiful and the gorillas receive leafy browse daily. They adopt a semi flexible feeding routine, with 5 to 8 feeds a day. For the first and last feed of everyday, to maintain a level of routine and structure the gorillas are encouraged to come into their bedrooms for a short period of time to allow the keepers to visually observe each individual and tailor the diets accordingly to meet their individual needs. The daily feed is given using a wide range of methods such as roof feeds and scatter feeds. Keepers have access to both indoor and outdoor roofs of the cages. Food items in different sizes (whole or finely chopped) are used so that some remains on top of the cage while some fall to the ground. At the end of each day the gorillas are kept in the indoor enclosure.

Figure 2. 1 Zoo A indoor (top) and outdoor (bottom) enclosures.

Figure 2. 2 Zoo B enclosure consisting of long metal platforms with slide (left), medium sized platforms (top right) and small wooden hanging platforms (bottom right).

Table 2. 1 Life histories of gorillas

Name of individual	Zoo	Hand reared by humans	Age at time of Study 1	Remarks
ASB	A	No	21	Silverback
AF1	A	No	19	Adult female
AF2	A	No	40	Adult female
AF3	A	Yes	28	Adult female
BSB	B	No	26	Silverback
BBB	B	No	10	Blackback
BF1	B	No	33	Adult female
BF2	B	Yes	26	Adult female

2.2.3 Sampling method and variables recorded

For all parts of the study two hour focal instantaneous sampling at one minute intervals were used on each focal subject (Altmann 1974). Instantaneous sampling involves recording a behavioural event at fixed intervals. Thus in this study a behavioural event was recorded every one minute. 29 focal samples were carried out at Zoo A in the first part of the study and 24 samples in the second. Focal sampling refers to observing one subject at a time for each sample. Twenty five samples were collected from the adults and 12 samples from the juveniles in Zoo B. Behavioural profiles were measured by calculating the frequency of each behavioural event (defined below in Table 2. 2). A behavioural event was recorded at every focal interval. When the gorilla under observation was not in full view at the focal interval, the event was recorded as Out-of-sight (OOS). Individuals were classed by age and sex. Food-based enrichment methods (defined below in Table 2. 3) already in use were recorded for each day of data collection. As both zoos used different enrichment methods, the effects on behaviour were examined separately for each zoo.

Table 2. 2 Definitions of behaviours observed

Behaviour	**Definition**
Self-directed behaviours[1] (SB)	Actions done to self such as scratching, autogrooming, often regarded as induced by stress[1]
ARBs[2] and aberrant behaviours (AAB)	Regurgitation and reingestion (R&R), thumb- sucking, rocking, self-biting
Solitary Play (SP)	Activities carried out alone such as swinging, jumping and object handling
Social affiliative behaviours[3] (SAB)	Non-aggressive activities with more than one individual, such as play, chasing, nursing, grooming or engaging in body contact
Agonistic Behaviours[3] (AB)	Aggressive behaviours such as hitting surfaces, bluff charges, chest beating displays, chasing, physical fighting, submission and fleeing
Sexual displays (SD)	Presentation of genitals, masturbation and sexual intercourse
Ingestion[3] (IN)	All food gathering and intake activities, fruit and non-fruit
Travel[4] (T)	Any physical displacement that takes place eg. walking, climbing, running, with or without carrying objects

Inactivity[4] (IY)	Sleeping, reclining with eyes opened or closed, being stationary when not feeding or socializing
Interaction with visitors[5] (IV)	Any behaviour directed at visitor(s) including observer
Nesting[4] (N)	The act of gathering branches/hay to create a structure to rest on and constructing the nest

[1]Castles and Whiten (1998), [2]Garner (2006), [3]Modified from Kuhar (2008), [4]Modified from Blaney and Walls (2004), [5] Hosey and Druck (1987)

Table 2. 3 Definitions of food-based enrichment methods used

Enrichment	**Definition**
Jumbo bales	Bundles of hay tightly bound together
Log feeders	Hanging logs with holes where food such as jam is placed into
Browse	Tree branches/ twigs scattered around the enclosure
Kongs	Rubber barrels with treats/apples/muesli stuffed inside
Honey pots	Pots with holes in which honey is placed for gorillas to use sticks to extract food from
Hessian parcels	Sacks with food inside
Rooftop feed	Food thrown from enclosure roof down into the enclosure
Scatter feed	Keeper scatters food randomly around the enclosure
Pellet/oat balls	Primate food compressed into balls
Frozen fruits	Frozen fruits such as apples
Puzzle feeders	An apparatus with holes where food inside can only be reached by manipulation eg sticking fingers through holes
Syringe drinks	Keeper uses a syringe to squirt drinks directly into the gorillas’ mouths
Yoghurt spread	Yoghurt is spread around the enclosure

2.2.4 Changes made at Zoo A

During the interim period, three log feeders were added, and an infant male (2 months old during the first study) became increasingly independent and engaged in social behaviour with all group members. Diet was modified (in August 2014 and January 2015) with the help of software Zootrition, using standards produced by European Association of Zoos and Aquaria (EAZA) great ape taxon advisory group (TAG), to consist of less fruit (-11.5%) and pellet (-31.3%), and more greens (33.3%), root vegetables (1.6%) and brassicas (33.3%). Ideally only one change should be made at a time. However as funding for the second part of the study was only available two years later, these changes had already taken place.

2.2.5 Statistical analysis

SPSS version 22 was used for all data analyses. Pearson's chi-square tests (exact two-tailed) were used to test for significant relationships between variables. Pearson's Chi-square test of independence is used to test if unpaired observations on two variables are independent of each other. To obtain the chi-square statistic:

$$\mathbf{X^2 = \Sigma[(O-E)^2/E]}$$

where O = observed frequency and E = expected frequency. A chi-square table for testing the relationship between the two variables needs be to built to calculate E. For example, observed frequencies of each locomotor mode are plugged into rows and observed frequencies of each behaviour type plugged into columns. To calculate the expected frequency for each cell, the row total in which the cell is found, is multiplied by the column total in which the cell is found, and divided by the grand total. Chi-square test of independence was chosen as variables were categorical, and loglinear modelling, which was used to test multivariate relationships (in Chapter 3), is commonly interpreted with chi-square tests (Thorpe and Crompton 2005). Also, previous behaviour studies on primates have used chi-square to test for significant relationships between variables (Nash et al. 1999; Gursky 2000). As my sample size was considered small and observations were not completely independent of each other, I only considered tests where the Pearson's chi-square statistic yielded a strict p-value ($P \leq 0.01$) to constitute significant relationships. The standardized residual (SR), an estimate of an error divided by its variance, was used to indicate the strength and direction of association between two variables. If an SR value was more than two, or less than minus two, an association was held to exist at the 95% confidence level (Tabachnick and Fidell 1996). Therefore if an SR is more than two, or less than minus two, this event occurred significantly more than expected. Behavioural modes that were similar in terms of context were conflated. Social behaviours included any behaviours that involved interaction with another individual hence affiliative behaviours were clumped with agonistic behaviours. This was to ensure sufficient numbers were present in categories (Table 2. 4 below), as cross-tabulations cannot be calculated when any cell has an expected count of zero, or more than 20% of cells have an expected count of less than 5. When more than one method of enrichment was used in a day, the types of enrichment that were used were recorded as one variable, to record the overall effect of the array of enrichments used in a day for simplification as some enrichments were given simultaneously. For example, if honey pots and browse were used together on one day, and honey pots alone on another day, “honey pots and browse” would be one variable-state and “honey pots” would be a separate variable-state.

Table 2. 4 Conflated behavioural modes

Social	Social affiliative behaviours (SAB) Agonistic Behaviours (AB) Sexual displays (SD) Interaction with visitors (IV)
Ingestion	Ingestion (IN)
Inactivity	Inactivity (IY)
Travel	Travel (T)
Stereotypical behaviour	Self-directed behaviours (SB) ARBs and aberrant behaviours (AAB)
Others	Solitary play (SP) Nesting (N)

2.3 Results

Unless otherwise stated, all results were from adult gorillas as most of the analyses focussed on adults due to juveniles not exhibiting any ARBs and collection of data from adults only at Zoo A. Only significant SR values (greater or less than two/minus two), meaning that one variable occurred significantly more or less than expected, are given.

2.3.1 Description and comparison of behaviour profiles at Zoo A and B in first part of study

Figure 2. 3 Behaviour profiles of gorillas at Zoo A and Zoo B in first part of study. Top shows raw percentages, bottom shows percentages of mean of individual means, with standard error bars. Percentages are shown at the top of each bar.

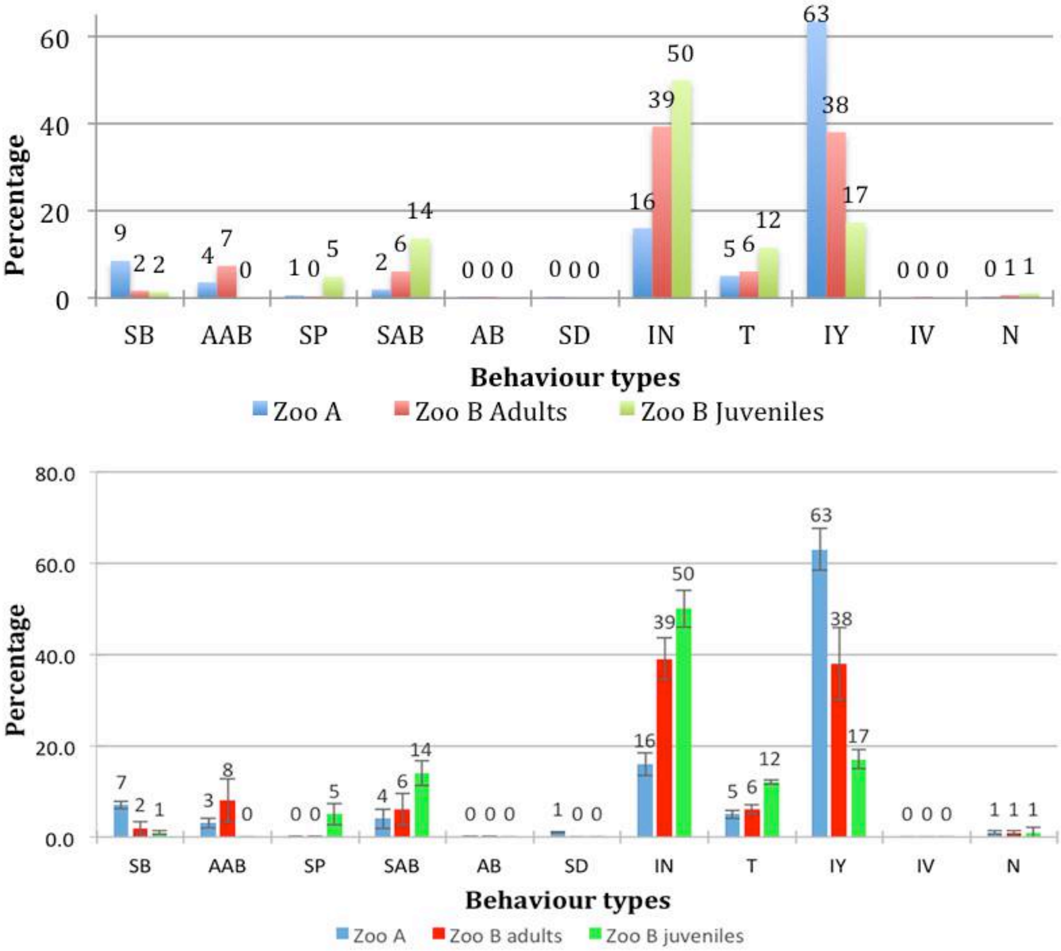


Table 2. 5 Frequency and percentage of each behaviour type at Zoo B, with adults and juveniles combined.

Behaviour	Frequency	Percent
SB	55	2
AAB	184	6
SP	53	2
SAB	272	8
AB	3	0
SD	1	0
IN	1,415	42
T	254	8
IY	1,093	33
IV	3	0
N	27	1
Total	3,360	100

From Figure 2. 3, there were no substantial differences in the behaviour profile between the two methods of generating a behaviour profile. Therefore any statistical tests here were carried out directly on the raw data.

At Zoo A, a total of 3507 events were recorded from 29 samples, of which 512 were out of sight (OOS). According to Figure 2. 3, the most common behaviours were gorillas were inactivity (63%), ingestion (16%) and self-directed behaviours (9%).

At Zoo B, a total of 4479 events were recorded from 37 samples, out of which 1092 were OOS. Of the 893 behavioural events, from 12 samples, recorded for juveniles, the most common behaviours were ingestion (50%), inactivity (17%), social-affiliative behaviours (14%) and travel (12%) (Figure 2. 3). No AAB behaviour was recorded. The most common behaviours in the adults (2489 behavioural events from 25 samples) were ingestion (39%), inactivity (38%), and AAB (7%) (Figure 2. 3). Combining adults and juveniles, ingestion (42%), inactivity (33%), travel (8%) and social affiliative behaviour (8%) formed the most common behaviours (Table 2. 5).

Table 2. 6 Differences in behaviour between Zoo A and Zoo B adults based on SR values. SR refers to standard residual. SRs that are more than or less than two are highlighted in grey.

	Stereotypical behaviour	Others	Social	Ingestion	Travel	Inactivity
Zoo A SR	2.2	0.1	-5.1	-11.2	-1	8.7
Zoo B SR	-2.4	-0.1	5.6	12.4	1.1	-9.6

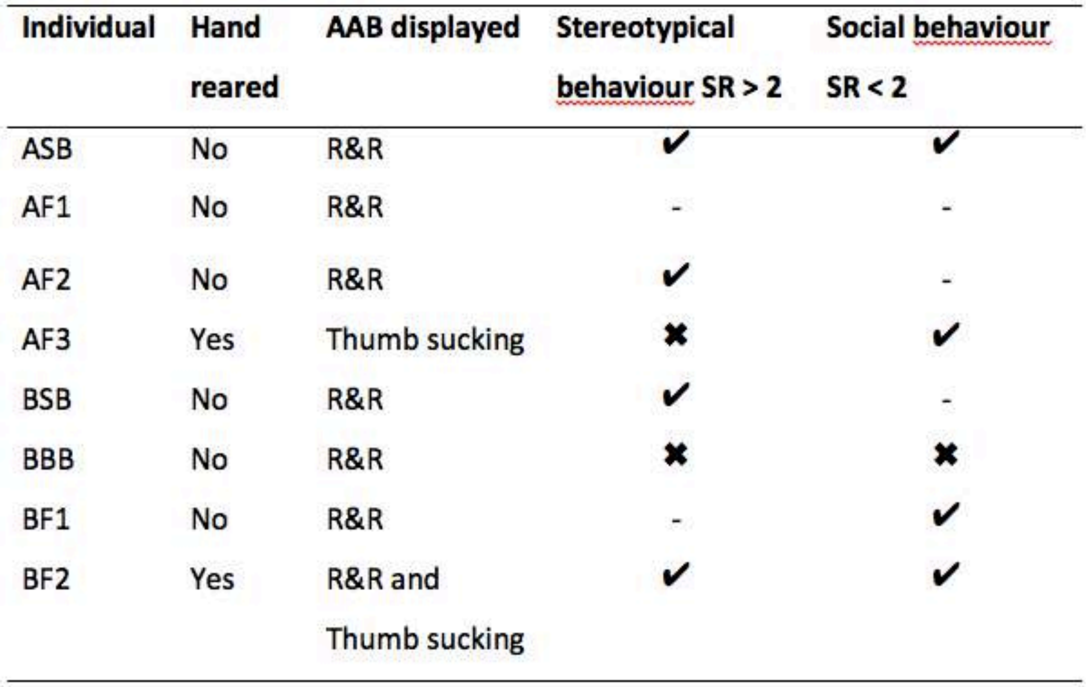
According to Table 2. 6, more observations of ingestion (SR 12.4) and social behaviour (SR 5.6), and less of inactivity (SR -9.6) and AAB (SR = -2.4) were observed at Zoo B than Zoo A (χ^2 = 519.380, df = 5, n = 5477, *P* = 0.000).

Table 2. 7 Differences in behaviour between Zoo B adults and juveniles based on SR values. SR refers to standard residual. SRs that are more than or less than two are highlighted in grey.

	Stereotypical behaviour	Others	Social	Ingestion	Travel	Inactivity
Adult SR	3.8	-3.8	-3.5	-2.1	-2.7	4.8
Juvenile SR	-6.3	6.3	5.8	3.6	4.4	-7.9

Differences (Table 2. 7) were observed between adult and juvenile behaviour (χ^2 = 283.455, df = 5, n = 3358, *P* = 0.000): juveniles travelled (SR 4.4), socialized (SR 5.8) and ingested (SR 3.6) more than adults, and displayed less stereotypical behaviour (SR -6.3), whereas adults were more inactive (SR 4.8).

Table 2. 8 Type of AAB displayed by each individual in Zoo A and Zoo B, and whether stereotypical and social behaviours occurred significantly more or less than expected (SR >2 or <-2). SR refers to standard residual. A tick indicates the trend named in the top row is true, a cross indicates the trend is false. For example for AF3 SR < 2 for stereotypical behaviour and SR < 2 for social behaviour. A dash refers to SR between -2 and 2.



Individual	Hand reared	AAB displayed	Stereotypical behaviour SR > 2	Social behaviour SR < 2
ASB	No	R&R	✔	✔
AF1	No	R&R	-	-
AF2	No	R&R	✔	-
AF3	Yes	Thumb sucking	✖	✔
BSB	No	R&R	✔	-
BBB	No	R&R	✖	✖
BF1	No	R&R	-	✔
BF2	Yes	R&R and Thumb sucking	✔	✔

According to Table 2. 8, at Zoo A, more than expected stereotypical behaviours were seen in the silverback (SR = 2.4) and AF2 (SR = 2.4), less in AF3 (SR = -4.8); less social behaviour was seen in the silverback (SR = -3.4) and AF3 (SR = -4.0) (χ^2 =239.111, df = 12, n = 3004, *P* = 0.000). At Zoo B, the silverback (SR = 6.4) and hand reared adult female (BF2) (SR = 9.0) displayed stereotypical behaviours more than expected, less in the blackback (BBB; SR = -7.2) and remaining adult female (BF1) (SR = -7.0). Social behaviour occurred less than expected in the hand reared BF2 (SR = -5.5) and BF1 (SR = -5.0), and more in BBB (SR = 10.1) (χ^2 = 565.603, df = 12, n = 2489, *P* = 0.000) (Table 2. 8).

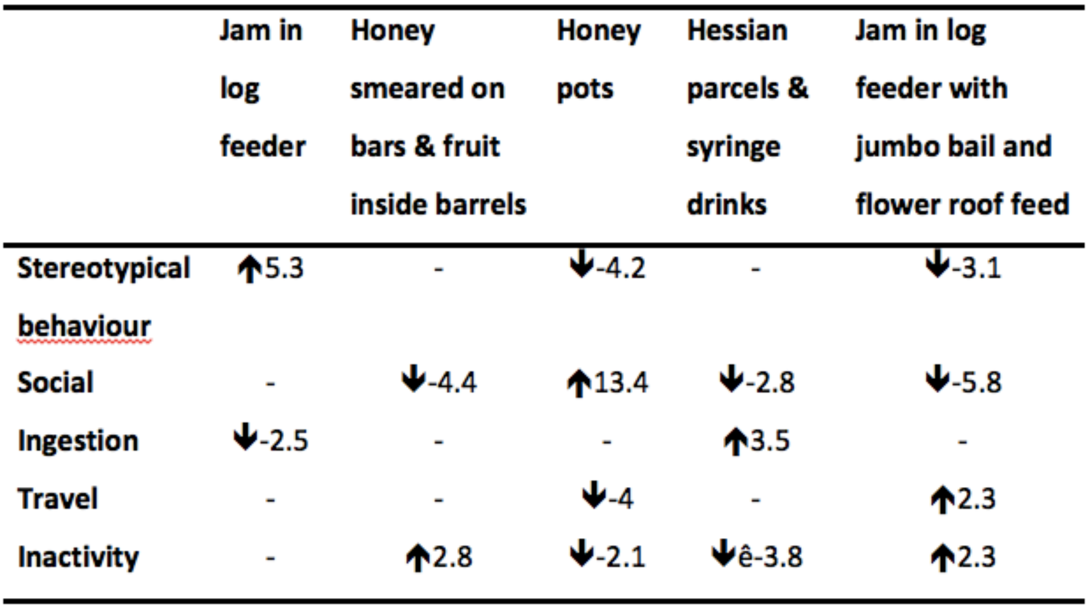
2.3.2 Identification of forms of enrichment that encourage species-typical behaviour

Zoo A (during Part 1 of study)

A statistically significant relationship exists between enrichment type and behaviour (χ^2 = 108.728, df = 16, n = 1699, *P* = 0.000). Stereotypical behaviour (for definition refer to Table 2) occurred less than expected (SR -4.4) when “browse” enrichment or “yoghurt spread” were used, but more than expected when kongs were used (SR 3.6). Travel occurred more often than expected (SR 2.4) when “pellet/oat balls” were used. Social behaviour occurred more than expected (SR 2.7) when “browse” was used.

Zoo B

Table 2. 9 Crosstabs between conflated behaviour and enrichment types. Numbers represent standard residual (SR) values of each type of enrichment associated with behaviour types. Up arrows depict a particular behaviour occurring more than expected for a specific enrichment type, down arrows less than expected.



	Jam in log feeder	**Honey smeared on bars & fruit inside barrels**	**Honey pots**	**Hessian parcels & syringe drinks**	**Jam in log feeder with jumbo bail and flower roof feed**
Stereotypical behaviour	↑5.3	-	↓-4.2	-	↓-3.1
Social	-	↓-4.4	↑13.4	↓-2.8	↓-5.8
Ingestion	↓-2.5	-	-	↑3.5	-
Travel	-	-	↓-4	-	↑2.3
Inactivity	-	↑2.8	↓-2.1	↓ê-3.8	↑2.3

The relationship between enrichment and behaviour (χ^2 =92.611, df = 20, n = 1991, *P* = 0.000) at Zoo B was examined next (Table 2. 9). Inactivity occurred more than expected when “honey was smeared on bars and when fruit was placed inside barrels”, and when the combination of “jam in a log feeder with jumbo bail and flower roof feed” was used. Inactivity occurred less than expected when “honey pots” or “hessian parcels and syringe drinks” were used. Social behaviour occurred more than expected when “honey pots” were used but less when “honey was smeared on bars and fruit was placed inside barrels” or when “hessian parcels and syringe drinks” or “jam in log-feeders with jumbo bale and roof-feed with flowers” were used. Stereotypical behaviour occurred less than expected when “honey pots” or when “jam in log-feeders with jumbo bale and roof feed with flowers” were used, but more when “log feeders” were used alone.

2.3.3 Behaviour profile at Zoo A in second part of study

A total of 2909 events were recorded from 24 samples, out of which 716 were Out-of-sight. 47.6% of the time was spent on inactivity, 12.4% on ingestion, 5.4% on stereotypical behaviour and 3.6% on social behaviour. As in the first part of the study, all AAB was regurgitation and reingestion in ASB, AF1 and AF2. In AF3, all AAB involved thumb sucking.

2.3.4. Differences in behaviour profiles at Zoo A between first and second part of study

Table 2. 10 Standard residual (SR) values of each individual associated with increase in social behaviour, decrease in R&R or increase in thumb sucking in second part of study.

Increase in social	Decrease in R&R	Increase in thumb sucking
AF2 (SR=2.9)	Silverback (SR=-3.9) AF1 (SR=-3.1) AF2 (SR=-5.2)	AF3 (SR=3.3)

Compared to the first part to the study, there was a significantly less-than-expected incidence of R&R in all parent reared individuals (see Table 2. 10) that were observed to have engaged in this abnormal behaviour – the silverback and two adult females (ASB: $\chi^2 = 37.445$, df = 4, p = 0, N = 1290; AF1: $\chi^2 = 24.018$, N = 1161, df = 4, p = 0; AF2 χ^2 =71.610, df = 4, p = 0, N = 1211). Abnormal behaviour (thumb sucking) in AF3, that was hand reared, however increased (see Table 2. 10, SR = 3.3, χ^2 = 40.344, df = 4, p = 0). There was a significant overall increase in social behaviour (SR = 3.5, χ^2 = 65.953, df = 4, p = 0, N = 5212), and specifically in AF2 (see Table 2. 10). However the hand reared female (AF3) showed less social behaviour than expected relative to her parent reared counterparts (SR = -2.8, χ^2 =81.619, df = 4, n = 2116, *P* = 0.000).

2.3.5 Behavioural comparison between hand reared and parent reared individuals for both zoos during both parts of study

In both zoos, and in both parts of the study, the individuals that were hand reared exhibited less social behaviour than expected (Zoo A Part 1: SR = -4.0, χ^2 = 100.465, df = 4, n = 3004, *P* = 0.000; Zoo A Part 2: SR = -2.8, χ^2 = 81.619, df = 4, n = 2116, *P* = 0.000; Zoo B: SR = -6.2, χ^2 = 113.382, df = 4, n = 1864, *P* = 0.000).

2.4 Discussion

2.4.1 Differential frequencies in activity between captivity and wild may explain R&R expression in captivity

In the first part of the study at Zoo A, “inactivity” and “self-directed” behaviours are among the three most frequent behaviours, making up 76% of the gorillas’ behavioural profile. This suggests that physical enrichment did not promote sufficient cognitive stimulation and physical activity. This 63% of “inactivity” recorded is substantially greater (more than three times) than the 21.0% recorded in the wild (Masi et al. 2009). At Zoo B, according to Table 2. 11, overall the gorillas spent a closer amount of time “inactive” (33%) to values in the wild (21%) (Masi et al. 2009), but exhibited less “travel” (8% vs 12%) and “ingestion” (42% vs 67%), and more “social affiliative behaviour” (8% vs 0.5%) (Masi et al. 2009). Of course one should not expect captive gorillas to display identical behaviour profiles to those of the wild due to different needs that are being met or restrictions in captivity (Veasey et al. 1996). However zoos can use deviations from wild behavioural profiles as an indicator for welfare when looking at stereotypical behaviours that are known to be harmful eg. R&R (Veasey et al. 1996).

Table 2. 11 Comparison of behaviour types between Zoo B gorillas and wild gorillas. Values are percentages. SB = Social affiliative behaviour; IN = Ingestion; T = Travel; IY = Inactivity.

	Zoo B	**Wild**[1]
SAB	8	0.5
IN	42	67
T	8	12
IY	33	21

[1] Values from Masi et al. (2009)

2.4.2 Differential frequencies of ingestion and social behaviour between zoos associated with R&R

Significantly more “social affiliative behaviour” and “ingestion”, but less “inactivity” and “AAB” occurred at Zoo B compared to Zoo A in the first part of the study. It has been shown in gorillas that infant males play more than infant females (Maestripieri and Ross 2004), and that males were a preferred playing partner for either sex (Brown 1988). In other nonhuman primates, males (adults, juveniles and infants) tended to play more than females (Loy 1979; Brown 1988; Mendoza-Granados and Sommer 1995; Spijkerman et al. 1996). Therefore it is highly likely that the difference in “social affiliative behaviour” frequency can be mostly explained by the presence of an additional adult male at Zoo B; Zoo B had a black-back and a silverback, whereas Zoo A only had a silverback. The black-back male was responsible for 72% of the “social affiliative behaviour” recorded among the adults at Zoo B and if the silverback was included, 94% of “social affiliative behaviour” involved one or both males. Conversely the silverback at Zoo A accounted for only 5% of the “social affiliative behaviour” in his group in the first part of the study. These trends suggest that encouraging social behaviour and ingestion may lead to a decrease in AAB.

2.4.3 Social structure in captive gorillas influences amount of mental stimulation and subsequently affects R&R frequency

In the second part of the study at Zoo A, there was significantly more “social affiliative behaviour” as compared to the first. Although not quantified in this study, the infant male in the second part of the study was observed by Goh to have become more independent and to have engaged in increased “social affiliative behaviour” with all members of the group as compared to the first part of the study. It is also known that infant males play significantly more than infant females (Maestripieri and Ross 2004). This could have contributed to the significantly more “social affiliative behaviour” seen in the second of the study in Zoo A as compared to the first part of the study. Therefore, similarly to the blackback in Zoo B, the infant male engaging in more social behaviour, may have contributed to a decrease in R&R in Zoo A in the second part of the study. As with previous studies (Honess and Marin 2005; Hosey 2005; Carrasco et al. 2009), it was found that even in adults increased “social affiliative behaviour” is associated with reduced “inactivity”, i.e. increasing physical and/or mental stimulation may help to decrease “inactivity”, “AAB” and “self-directed behaviours”. The average group size of wild western lowland gorillas is ~8 (Parnell 2002), typically composed of a silverback, three adult females, and possibly blackblacks, with 32% of the group made up of infants/juveniles (Parnell 2002), and play is carried out more often between male-and-female or male-and-male, but seldom between female-and-female (Brown 1988). Group size and group composition are essential factors in creating opportunities for social learning, cognitive ability development and socialising, for captive nonhuman primates (Croney and Newberry 2007; Olsson and Westlund 2007) and hence are closely linked to animal welfare and the display of stereotypical behaviour (Olsson and Westlund 2007). Thus zoos should attempt to house lowland gorillas in a family group consisting not just of a silverback male and adult females with infant(s), but also juveniles and black-back male(s) to create a social environment more similar to that in the wild. However caution must be taken when using group size and compositions of the wild as a benchmark for captivity as the animals have different needs (eg. food resource availability is seldom a concern for captive animals), and often housing primates in too dense a setting can cause adversely high levels of aggression (Price and Stoinski 2007). Therefore with constant monitoring of the behaviour of captive animals, along with using wild data as guidelines, zoos can be flexible in order to find an appropriate group size and composition specific to the needs of the group.

2.4.4 Differential frequencies of ingestion and social behaviour between adults and juveniles likely explain R&R at Zoo B

Looking next at differences in juvenile and adult behaviour profiles in Zoo B, juveniles engaged in “travel”, “social affiliative behaviour” and “ingestion” significantly more than expected as compared to adults, whereas adults were substantially more “inactive” (38%) than juveniles (17%). The amount of time spent on “ingestion” by juveniles (50%) was also closer to that of wild gorillas (67%) (Masi et al. 2009) whereas that of the adults (39%) was substantially less. It must be noted that percentages from Masi et al. (2009) were calculated from both adult and juveniles, thus being a very conservative benchmark for zoos to aim for in juveniles but high for adults as juvenile primates tend to spend more time feeding than adults (Pereira and Fairbanks 1993). Although in this study juveniles were held in a different enclosure from the adults that were studied, the dimensions and structures of the enclosures, and feeding enrichment provided were similar. As no “AAB” (R&R or thumb sucking) was recorded in the juveniles, it is therefore likely that the lack of mental stimulation in the adults, in this case in the form of social activity, and lack of ingestion time that led to the display of “AAB” in the adults at Zoo B.

2.4.5 Dietary fibre levels highly likely to be associated with R&R in Zoo A gorillas

R&R significantly decreased in the second part of the study. Unfortunately it is impossible to tell for sure if this decrease in R&R was because of the infant encouraging social behaviour and/or the change in diet. In order to tease out these differences, one would need to control the study by making sure only one change occurs at a time. However in agreement with previous studies (Morgan et al. 1993; Lukas 1998; Hill 2004; Cassella et al. 2012), a decrease in fruit intake (low-fibre) and the increase in brassiccas, greens, fruit and vegetables (all high-fibre), have let do decrease in R&R. Therefore it is likely that the change in diet here has contributed to a decrease in R&R. “Stereotypical behaviours”, which includes “AAB” and “self-directed behaviours”, occurred significantly less often when “browse” enrichment was used. Browse is high in fibre, reinforcing a link between dietary composition and behaviour. Studies of wild lowland gorillas (Remis 1994; Remis 1995; Remis 1998; Goldsmith 1999; Remis 1999) indicate that their behaviour and diet are influenced by seasonality. During wet seasons, the gorillas travel more and have a diet consisting more of fruit and termites, while in dry seasons diet consisted more of leaves and woody vegetation (Remis 1995; Goldsmith 1999). This finding is consistent with Remis (1999)’s demonstration that dietary fibre quantity varies with seasons. On the other hand, captive gorillas are too often fed with fruits and domestic vegetables low in fibre (Schmidt et al. 2005) and this deficiency has led to a number of problems, from health issues, to apparent ‘fibre cravings’ causing stress in captive gorillas (Schulman et al. 1995; Masi 2011). However as browse also takes longer to consume, resulting in more time spent feeding (Gould and Bres 1986) it cannot be said for sure that the decrease in R&R here was associated specifically with a high-fibre diet or an increase in feeding time. More specific studies on feeding need to be carried out. Nonetheless it important to take into consideration the influence of seasonality on the behaviour and dietary composition of wild gorillas and the possible effects of lack of this source of variation in captivity. Having less fruit and a high-fibre diet would require zoos to obtain a substantially larger volume of foodstuffs, which may not be practical in terms of storage space and cost. Also, as mentioned before, as wild and captive animals face different challenges, having an identical diet to that of wild gorillas may not be advisable. However, if gorillas are only adapted to a wild diet (with seasonality etc.), meaning that by providing a diet that is different can cause health problems, then zoos should attempt, as far as possible to provide a diet similar to, or at least analogous to that in the wild to encourage normal behaviour profiles, within the practical boundaries of costs and storage space for food. A balance must be found between practicality and animal welfare before this issue can be resolved.

2.4.6 Tool-use based enrichment reduces AAB

Only Zoo B provided tool-use based enrichment methods: “honey pots” and ‘”log-feeders”. At Zoo B, “honey pots” and “hessian parcels and syringe drinks” promoted less “inactivity”, while “honey smeared on bars and fruit inside barrels” and “jam in log feeders with jumbo bail and flower roof feed” promoted “inactivity”. Usage of “honey pots” was associated with an increase in “social behavior” and a decrease in “stereotypical behavior”. As “stereotypical behavior” probably results from lack of activity, mental stimulation and/or stress, the increase in “social behavior” and decrease in inactivity is likely to be a factor contributing to reduction in abnormal or aberrant behaviours. Unfortunately, some other forms of enrichment, such as “honey smeared on bars and fruit inside barrels” and “jam in log feeders with jumbo bail and flower roof feed”, seemed to have the opposite effect. “Honey pots” provide an intense form of mental stimulation involving tool-use. It is known that wild gorillas although not considered as extractive foragers, are capable of different types of tool-use (Breuer et al. 2005; Wittiger and Sunderland-Groves 2007; Kinani and Zimmerman 2015), and recently have exhibited tool use for food acquisition (Kinani and Zimmerman 2015). Furthermore, captive gorillas engage in similar tool-use patterns to those used when eating from “honey pots” where food is provided as a reward (Zaragoza et al. 2011). Young (2003) notes that in addition to the effects of general mental stimulation, specifically encouraging food acquisition processes similar to those in the wild is important for encouraging natural behaviour. Thus for lowland gorillas that are known to practice extractive foraging, honey pots could readily be seen to mimic this natural food acquisition technique. Naturalistic behaviours have been known to decrease inactivity and stress levels (Honess and Marin 2005), which therefore could lead to a more relaxed environment that encourages social behaviour. Further, it is known that increasing foraging time tends to reduce AAB (Hill 2004) and the usage of tools in honey pots also lengthens the foraging time.

Although “log feeders” also require tool-use, they were filled in the morning, at least an hour before observations commenced, and gorillas were rarely observed using them. “Honey pots” however, were filled during observation periods. Hence it seems likely that “log feeders” were used first thing in the morning, immediately after filling, before observations could commence, so that any enrichment effect may have ‘worn off’ before observations began.

Hill (2009) and Lukas (1998) suggest that a lack of “goal-directed” species-specific foraging behaviour in captivity could result in AAB, and that increasing the complexity of feeding environments could lead to decreased AAB, by ensuring more time is spent foraging and feeding. Hill (2004) managed to reduce R&R in two individual western lowland gorillas by incorporating enrichment tailored to increase feeding time. Furthermore, Bloomsmith and colleagues (1988) found that increasing foraging time decreased AAB in chimpanzees. Here tool use enrichment may provide a form of complex feeding/foraging environment, enhancing mental stimulation and increasing time spent on ingestion. Thus it would be valuable to collect time-specific data on enrichment with regards to behaviour, to further examine how quickly the gorillas engage in enrichment-focused activity after an enrichment has been installed, and for how long the gorillas engage in the enrichment-focused activity. This would give some form of indication of how effective different types of enrichment are and how each influences behaviour. Further, research is needed on other primate species that use tools in the wild to better understand if and how tool-use alleviates AAB.

2.4.7 Different types of AAB stem from different reasons

Life history of each gorilla needs to be considered when studying abnormal behaviour in captive gorillas. Although wild gorillas are not predominantly social (only 0.5% in the wild according to Masi et al. (2009)), “social behaviour” was consistently less common than expected in hand-reared individuals in both zoos, and in Zoo A even after the changes, indicating that the hand-reared individuals were exceedingly unsocial for a captive setting, consistent with previous studies on captive gorillas (Meder 1989). The hand-reared individual in Zoo A did not display any “R&R”, unlike the parent-reared individuals, but displayed “thumb sucking” instead, a behaviour not seen in the parent-reared individuals. This pattern was somewhat similar in Zoo B as although the hand-reared individual displayed both

"R&R" and "thumb sucking", the parent-reared individuals did not display "thumb sucking". After the changes in Zoo A, "R&R" decreased only in parent-reared individuals, but in the hand-reared individual, "thumb sucking" increased, indicating that abnormal behaviour in the parent-reared individuals (R&R) stemmed from different reasons from that of the hand reared-individual (thumb sucking). Perhaps the hand-reared female was more stressed from the increased forced sociality of the infant and thus displayed more "thumb sucking". Thumb sucking is common in hand-reared chimpanzees, and was shown to stem from different stimuli than stereotyped repetitive movements like rocking (Berkson et al. 1963; Berkson and Mason 1964). It is known that AABs are dependent on multiple variables like rearing, development and immediate stimuli (Davenport and Menzel 1963). Thumb sucking in this study seemed to be triggered mainly from social reasons, and is likely to be an idiosyncratic behaviour developed from a socially deprived childhood (Mason 1991; Olsson and Westlund 2007). "R&R" in Zoo A seemed to be associated with levels of fibre, ingestion time, social activity and mental stimulation. Thus this study provides more basis for the importance of taking a multifaceted and customized approach to tackling AAB, sometimes even tailored to specific individuals, as there is no one cure to all AAB.

2.5 Conclusions

Hypothesis One, that behaviour profiles and activity levels would increase with tool-use based enrichment, is therefore supported by the data from this study, as honey pots had a positive effect on the gorillas.

In agreement with Hypothesis Two, which suggests that family groups that include juveniels and blackback(s) would lead to more social interaction and hence activity, is also supported by data from this study, as shown by the blackback male (Zoo B) and the infant male (Zoo A) having a significant influence on behaviour profiles, by contributing to differing frequencies in social behaviour and inactivity.

Hypothesis Three, that captive gorillas would show substantially more inactivity and engage in less ingestion than their wild counterparts due to the less complex environments in captivity, is supported by data from this study as there were higher amounts of ingestion and less inactivity in wild gorillas as compared to the study groups. This can be attributed to diet composition and environmental complexity, leading to ingestion and inactivity time differences.

Hypothesis Four, that abnormal repetitive and aberrant behaivours in Zoo A would decrease significantly after changes in diet and social environment, is supported for R&R in the parent-reared individuals in Zoo A, but not for thumb sucking in the hand-reared individual. This study lends further evidence to the potential of dietary fibre quantity influencing displays of R&R.

Chapter 3: The role of habitat structure in the locomotor repertoire of captive and wild gorillas

3.1 Introduction

The majority of studies of wild gorilla positional behaviour have been on one subspecies of eastern gorillas - the mountain gorillas (*Gorilla beringei beringei*) (Schaller and Emlen Jr 1963; Schaller 1963; Tuttle and Watts 1985; Doran 1996) while there are none on the eastern lowland gorilla (*G. b. graueri*). The positional behaviour of western lowland gorillas (*Gorilla gorilla gorilla*) has only been studied once in the wild (Remis 1994; Remis 1995; Remis 1998; Remis 1999), while that of the Cross River gorilla (*G. g. diehli*) has never been studied. This is a result of a lack of habituated groups of western lowland gorillas and the fact that mountain gorillas have been habituated since the 1970s (Fossey 1983).

Both gorilla species are adapted for knuckle-walking and vertical climbing (Tuttle and Watts 1985; Remis 1998). For example the transverse dorsal ridges at the bases of the metacarpal heads are prominently developed to reduce effects of compressive stress during knuckle walking and maintain the integrity of metacarpophalangeal joints during load-bearing (Tuttle and Watts 1985). Gorillas also have wide ventrally oriented iliac blades, the width of which provides leverage for bulky gluteal muscles (extensors of the hip joint) necessary for vertical climbing (Tuttle and Watts 1985). However the loss of contrahentes in the hand and its transformation to an aponeurosis, in both mountain and lowland gorillas, indicates an arboreal ancestor as this transformation is regarded as associated with increased grasping ability and suspensory behaviour (Jouffroy and Lessertisseur 1959). This modification enables constant passive force to be generated to counter the strong tensile forces on the metacarpophalangeal joints during suspension (Jouffroy and Lessertisseur 1959). It has been suggested that that vertical climbing was pre-adaptive for terrestrial knuckle-walking, as both require extended elbows with flexed hips and knees (Thorpe et al. 2007).

Western lowland gorillas travel arboreally between trees (Remis 1995; Doran 1996), and can be found at heights of more than 30m (Remis 1995). The study site of Remis's studies (Remis 1994; Remis 1995; Remis 1998; Remis 1999) was Bai Houkou, Central African Republic, which consisted of lowland rainforest. It must be noted that Remis' studies (Remis 1994; Remis 1995; Remis 1998; Remis 1999) were carried out on semi-habituated lowland gorillas and observations could thus have been biased towards arboreal sightings, as visibility was poor on the forest floor and gorillas that were arboreal were less likely to be aware of/disturbed by the presence of the researcher. Schaller and Emlen Jr (1963) observed that mountain gorillas in Virunga National Park, Congo, that consists of montane tropical forest, sit frequently during feeding, rarely climb trees, and climb using big supports (Schaller 1963). When climbing on supports with diameters of greater than 20cm, the hallux is not opposed, but when the support is less than 10cm in diameter the hallux is opposed and the heel positioned away from the support (Sarmiento 1994). Both western lowland and mountain gorillas display sexual differences in their use of the arboreal environment. Males spend less time arboreally than females and females prefer to feed on the periphery of tree crowns (smaller, variously angled supports) whereas males tend to feed in the core (Remis 1999; Inouye 2003). Little is known about eastern lowland gorilla positional behaviour. They were originally documented as terrestrial folivores (Casimir 1975), similar to mountain gorillas (Schaller 1963). More recently they have been viewed as intermediates, in terms of dietary fruit consumption, between mountain and western lowland gorillas (Yamagiwa et al. 1992; Yamagiwa et al. 1994), however they are considered more similar to western lowland gorillas (Yamagiwa et al. 1996).

Comparing western lowland and mountain gorillas, there are differences in levels of arboreality, diet composition, arboreal feeding postures and locomotor repertoires. Lowland gorillas use more suspension and bipedalism than mountain gorillas (Tuttle and Watts 1985), and are more arboreal; male lowland gorillas climb almost twice as frequently as male mountain gorillas (Doran 1996). Mountain gorillas are mainly folivorous while lowland gorillas are frugivorous (Nishihara 1995; Remis 1998).

There are also anatomical differences between western lowland and mountain gorillas that indicate mountain gorillas are more adapted for terrestriality than lowland gorillas. Mountain gorillas have broader hands, less divergent halluces and shorter forelimbs than lowland gorillas (Straus 1930; Schultz 1934), and always possesses a fibularis tertius, whereas only 30% of lowland gorillas have this muscle (Straus 1930). The fibularis tertius helps in eversion of the foot and hence has been seen as an adaptation to terrestriality (Smith 1882). Mountain gorillas have greater medial humeral torsion than lowland gorillas probably due to increased pronation for terrestrial knuckle walking (Inouye 2003).

The influence of habitat structure on wild gorilla positional behaviour has been documented (Remis 1998), where levels of arboreality are strongly affected by habitat structure and fruit consumption. As mentioned before, previous studies on mountain gorillas indicate that they are rarely arboreal (Schaller and Emlen Jr 1963; Schaller 1963; Tuttle and Watts 1985). Working in the Karisoke Research Station (Rwanda) Tuttle and Watts (1985) observed that mountain gorillas are arboreal only 3% of their time. However the forest canopy at Karisoke is low, with most trees only up to 7m tall, and there are few sources of fruits available (Fossey 1983), hence little incentive to climb. It has further been suggested that the different levels of arboreality between mountain and lowland gorillas are largely habitat-related (Inouye 2003). Recently it has been shown that where more fruiting trees are present, and forest is generally denser and taller (eg. Bwindi, Uganda), mountain gorillas are more arboreal and engage in vertical climbing (Ian Redmond pers. comm.). Likewise the more arboreal lowland gorillas live in forests with trees up to 40m or more in height with abundant fruit (Remis 1998). Evidently, habitat structure and food distribution plays a substantial role in levels of arboreality and positional behaviour repertoires in both mountain and lowland gorillas. This agrees with other studies of primates (Warren 1997; Dagosto and Yamashita 1998; McGraw 1998; Manduell et al. 2012) where habitat structure is known to influence locomotor repertoires.

Captive environments, where habitat structure differ strongly from that of the wild, in terms of support types, distribution and materials, coupled with space limitations, likely represent extremes of possible environmental adaptation. As such, they are an effective tool in understanding the locomotor potential of a species. Also equally important, captive care requires that the departure of such environments from those in nature should be minimized, so at least analogous stimuli exist in which a species' locomotor potential can be adequately expressed, to promote health and wellbeing. This is because locomotor capabilities are based on musculoskeletal adaptations and body size, and thus restrict, to a certain extent, those habitats in which these animals can live or to which they can adapt to (Fleagle and Mittermeier 1980; Crompton 1984; Youlatos 2004).

The importance of creating naturalistic enclosures to increase captive animal welfare has been well-studied (Bayne et al. 1991; Jensvold et al. 2001; Honess and Marin 2005; Hosey 2005; Mason et al. 2006; Coe et al. 2009; Ross et al. 2009; Fabregas et al. 2011; Zaragoza et al. 2011). Past studies have shown that the provision of naturalistic environments for primates reduces stereotypical behaviours, decreases inactivity (Honess and Marin 2005; Zaragoza et al. 2011) and encourages species-typical positional behaviour repertoires (Jensvold et al. 2001). Previous studies on captive apes show that horizontal and vertical space-use is influenced by the physical environment. Space is used selectively (Ross et al. 2009; Ross et al. 2011b), and captive apes have a preference for structures such as trees and rocks, and spaces near vertical structures (Stoinski et al. 2001; Hosey 2005), or doors, barriers and corners (Ross et al. 2011b). Sufficient space is also required for natural and rapid locomotor behavior (Honess and Marin 2005). Thus, by determining how the structures/sizes of the enclosure influence locomotor/postural behaviour and support usage, zoos can work towards 'exhibit-naturalism' (Stoinski et al. 2001) by applying strategies to help animals behave in a more naturalistic manner. As a result, the value of captive conservation can be increased (Honess and Marin 2005). This is not only beneficial to the health of the animals but also creates a more positive experience for the visitors by allowing them to appreciate and learn more about subjects' natural behaviour and habitat (Stoinski et al. 2001; Hosey 2005).

The primary part of this study was carried out on western lowland gorillas in two zoos to compare levels of environmental enrichment and their effectiveness. The secondary part of this study was carried out on videos of wild western lowland gorillas, eastern lowland gorillas and mountain gorillas. The captive data collected in this study was compared with studies of wild western lowland gorilla locomotion from the literature (Remis 1994; Remis 1995; Remis 1998; Goldsmith 1999; Remis 1999) and from a wild dataset based on videos collected by Ian Redmond and Shelly Masi (details on sites and collection method can be found in the methods below).

Therefore, the primary objectives of this study were to 1) investigate if western lowland gorillas have sufficient locomotor plasticity to accommodate the extreme departure of habitat structure from the natural environment in captivity, and 2) use this information to make recommendations on how zoos can alter their enclosures to encourage natural positional behaviour and support usage. If the positional behaviour profiles and support usage differs between captivity and the wild, this suggests that habitat structure influences gorilla positional behaviour and support usage. Subsequently this means that gorillas have sufficient locomotor plasticity to accommodate the differences in environment. To examine how habitat structure influences positional behaviour and support usage, firstly positional behaviour profiles between the zoos and between captive and wild data were compared; secondly vertical space and support usage at both zoos in relation to behaviour/posture/locomotion were compared. The secondary objective of this study was to find out what differences and similarities exist between each gorilla subspecies. This was done by comparing profiles of arboreal positional behaviour and support usage between species in the wild dataset.

3.2 Methods

3.2.1 Data collection and study sites

For the captive dataset, data was collected by two observers, observer 1 (CG) collected data from Zoo A (Figure 3. 1) for two months and at Zoo B (Figure 3. 2) for one month, observer 2 (ES) collected data from Zoo B for one month. Observer 1 used two hour focal instantaneous sampling at one minute intervals on each focal subject, and observer 2 used 20 minute focal instantaneous sampling at one minute intervals (Altmann 1974). When examining locomotion, data from observer 2 was combined with observer 1's data to ensure sufficient locomotor data was present to carry out statistical tests. To ensure reliability between observers, data was collected simultaneously at Zoo A for a total of four hours and statistical tests were run to ensure that all locomotor data collected showed no significant difference between the two observers. All work was conducted with ethics permission from both zoos and the University of Liverpool and the University of Birmingham. In total there were 106 hours of observation at Zoo A, and 129 hours and 40 minutes at Zoo B. Out-of-sight (OOS) events were defined as instances when the gorilla being observed was not in the observer's view at the focal instant, or when the gorilla was too far away to record accurate postural or locomotor data or sight of the gorilla was partially blocked. All three adult females and one adult male were studied at Zoo A. Two adult males, two adult females and two juveniles were studied at Zoo B.

Zoo A's indoor enclosure is made from concrete walls with two points of access to the outdoor enclosure. The gorillas spent most of their time indoors during the time of the study. The indoor enclosure had multiple small platforms along the walls at differing levels, and a large tree trunk in the middle with medium sized platforms around it (Figure 3. 1). The bedrooms were connected to the indoor enclosure with three access points. For more information on husbandry please refer to Chapter 2, Section 2.2.1.

Zoo B’s enclosure was made up of a wire mesh. The gorillas had access to both indoor and outdoor enclosures. During the time of this study they spent most of their time in the outdoor enclosure. The outdoor enclosure consisted of a long metal platform in the middle connected to a slide, medium sized metal platforms and smaller wooden platforms hanging from the roof scattered around the enclosure (Figure 3. 2), and honey pots built in around the side of the enclosure. For more information on husbandry please refer to Chapter 2, Section 2.2.1.

Figure 3. 1 Zoo A indoor (top) and outdoor (bottom) enclosure.

Figure 3. 2 Zoo B enclosure consisting of long metal platforms (left), medium sized platforms (top right) and small hanging wooden platforms (bottom right).

For the wild dataset, Ian Redmond (IR) and Shelly Masi (SM) collected videos of wild gorillas opportunistically. Data was transcribed by MB and CG from 259 minutes (898 clips) of videos of wild western lowland gorillas (Bai Hokou and Mongambe, Dzanga-Ndoki National Park, Central African Republic, provided by SM; and Mondika, Republic of the Congo, provided by IR), 78 minutes (191 clips) of eastern lowland gorillas (Kahuzi-Biega, Democratic Republic of Congo, provided by IR) and 82 minutes (185 clips) of mountain gorillas (Bwindi, Uganda, provided by IR). Videos from SM consisted only of arboreal sightings of western lowland gorillas. All other videos were from a mix of terrestrial and arboreal contexts. Transcription of videos was done by all-occurrence sampling (Altmann 1974) of all adult and adolescent individuals in order to obtain sufficient data for analysis.

3.2.2 Variables recorded

For the captive dataset, behavioural profile (and context) was measured by tabulating the frequency of each behavioural event (defined in Table 3. 1), in relation to the corresponding locomotor and postural modes in Table 3. 2 and Table 3. 3 (Remis 1998; Thorpe and Crompton 2006) and utilization of enclosure furniture (eg. vertical space and size/orientation/compliance of support), as elaborated in Table 3. 4. The distribution of locomotor-enhancing enrichment (platforms, hanging hoses, ladders, hammocks, tyres, cargo nets, artificial vines, slopes and ropes) in each enclosure were used to interpret the data on locomotor activity. Locomotor and postural modes were divided into broad modes (in bold in Table 3. 2 and Table 3. 3), which were themselves divided into kinetically and mechanically distinct submodes. Modes involving forelimb compression were defined as one where pushing forces were applied from a top-down direction on to the support where the forelimb contacts the support below shoulder level and includes “pressing” actions involving the palm (opened) or elbow. Forelimb suspension referred to pulling forces on supports; if a forelimb contacted support below shoulder level but the wrist was above elbow, grasping vertical supports using fingers and palm was recorded as forelimb suspension and not compression. Where hybrid positional modes were used, such as sitting combined with lying, bipedal stand with forelimb compression/tripedal stand, the body part that bore the most weight was recorded first. This could be observed in various ways: by the amount of support deformation, by the extent of rebound when weight was removed, by body position and by position of cheiridia (hands and feet) and limbs. Sizes, orientations and compliance of supports were recorded, with definitions as in Table 3. 4 (Thorpe and Crompton 2005; Thorpe and Crompton 2006). Individuals were classed by age and sex (Thorpe and Crompton 2006). The ground was not included as a support in statistical analysis, as including the ground would bias the distribution of supports used to large, stiff, horizontal supports and here I am interested in support variety. Therefore any reference made to supports here excludes the ground. Adults and juveniles were in some tests combined to ensure sufficient numbers for statistical analysis, however elsewhere all tests were on adults only. This is because the statistical tests used require a large enough sample for it to be valid. Both loglinear and Chi-square tests require there to be no sampling zeros or low expected cell counts; no more than 20% of expected counts should be under 5, with no expected counts under one (Tabachnick and Fidell 1989). Compliant supports were conflated with inelastic but flexible supports (C&I) to test for significance between support compliance and locomotion. Angled supports were conflated with vertical supports to ensure sufficient data for statistical analysis when testing for significance between support orientation and locomotion. Small, medium and large supports were conflated into one category (≥4cm) to ensure sufficient data for statistical analysis. The support used for each limb was recorded. But only Forelimb support 1 was included in the analysis as chi-square tests showed that the size, compliance and orientation of Forelimb support 2, Hindlimb support 1 and Hindlimb support 2 were all significantly more similar to Forelimb support 1 than expected (see how to calculate expected values in Chapter 2, Section 2.2.5). Therefore any support discussed refers to a forelimb support.

Table 3. 1 Behaviours observed for during study period

Behaviour	**Definition**
Self-directed behaviours[1] (SB)	Actions done to self such as scratching, autogrooming, often regarded as induced by stress[1]
ARBs[2] and aberrant behaviours (AAB)	Regurgitation and reingestion (R&R), thumb- sucking, rocking, self-biting
Solitary Play (SP)	Activities carried out alone such as swinging, jumping and object handling
Social affiliative behaviours[3] (SAB)	Non-aggressive activities with more than one individual, such as play, chasing, nursing, grooming or engaging in body contact
Agonistic Behaviours[3] (AB)	Aggressive behaviours such as hitting surfaces, bluff charges, chest beating displays, chasing, physical fighting, submission and fleeing
Sexual displays (SD)	Presentation of genitals, masturbation and sexual intercourse
Ingestion[3] (IN)	All food gathering and intake activities, fruit and non-fruit
Travel[4] (T)	Any physical displacement that takes place eg. walking, climbing, running, with or without carrying objects
Inactivity[4] (IY)	Sleeping, reclining with eyes opened or closed, being stationary when not feeding or socializing

Interaction with visitors[5] (IV)	Any behaviour directed at visitor(s) including observer
Nesting[4] (N)	The act of gathering branches/hay to create a structure to rest on and constructing the nest

Table 3. 2 Postural modes modified from Thorpe and Crompton (2006)

Sit	P1a-1f[1] Combines sit-in, sit-out, chair-sit, foot-prop sit, ischium-sit
Sit with forelimb suspend	P1g
Sit with forelimb compression	As in "sit" but with forelimb(s) in compression
Sit with forelimb suspend and forelimb compression	As in P1g but with other forelimb in compression and suspension
Sit with knuckles	As in "sit" but with knuckles in contact with substrate (level to substrate ischium is on)
Sit with 1 knuckle	As in "sit with knuckles" but with knuckles from one forelimb in contact with substrate only
Sit with knuckle and forelimb suspend	As in "sit with 1 knuckle" but with other forelimb in suspension
Sit with knuckle and forelimb compression	As in "sit with 1 knuckle" but with other forelimb in compression
Sit with 1 wrist	As in "sit" but with wrist from one forelimb in contact with substrate (level to substrate ischium is on) bearing some weight
Sit with knuckle and wrist	As in "sit with 1 knuckle" but with one wrist in contact with substrate level to that of ischium
Sit with hindlimb compression	As in "sit" but with hindlimb(s) in compression
Sit with forelimb suspend and	As in "sit with forelimb suspend" but with

hindlimb compression	hindlimb(s) in compression
Sit with knuckle and hindlimb compression	As in "sit with 1 knuckle" with hindlimb(s) in compression
Sit with forelimb and hindlimb suspend	As in "sit" but with forelimb(s) and hindlimb(s) in suspension
Squat	P2
Squat with knuckles	As in P2 but with knuckles from both forelimbs in contact with substrate (level to substrate hindlimbs are in contact with) supporting some weight
Squat with 1 knuckle	Same as "squat with knuckles" but with knuckles from 1 forelimb only
Squat with 1 wrist	As in P2 but with one wrist (in contact with substrate level to that of hindlimbs) bearing some weight
Squat with knuckle and wrist	As in "squat with 1 knuckle" but with wrist from other forelimb (in contact with substrate level to that of hindlimbs) bearing some weight
Squat with 1 elbow	As in P2 but with elbow from one forelimb (in contact with substrate level with that of hindlimbs) bearing some weight
Squat with forelimb suspend	As in P2 but with forelimbs(s) in suspension
Squat with forelimb compression	As in P2 but with forelimb(s) in compression
Squat with knuckle and forelimb suspend	As in "squat with 1 knuckle" but with other forelimb in suspension
Squat with knuckle and forelimb compression	As in "squat with 1 knuckle" but with other forelimb in compression
Quadrupedal stand with knuckles	As in P4a but forelimbs contact substrate with knuckles only
Quadrupedal stand with wrists	As in P4a but forelimbs contact substrate

	with wrists
Quadrupedal stand with knuckle and wrist	As in P4a but with wrist from one forelimb in contact with substrate
Quadrupedal stand with knuckle and palm	As in P4a but with one forelimb palmigrade
Quadrupedal forelimb crouch	As in P4c2, with knuckles bearing weight
Quadrupedal forelimb crouch with 1 elbow	As in P4c2 but with elbow from one forelimb bearing significant weight
Quadrupedal forelimb crouch with elbow and wrist	As in P4c2 but with wrist from one forelimb and elbow from other forelimb bearing weight
Tripedal stand with knuckles	As in P4b but with knuckles in contact with substrate
Tripedal stand with wrist	As in P4b but with wrist in contact with substrate
Tripedal stand with knuckle and elbow	As in “tripedal stand with knuckles” but with elbow from other forelimb (in contact with substrate level to that of hindlimbs) bearing some weight
Tripedal stand with forelimb compression	As in “tripedal stand with knuckles” but with other forelimb in compression bearing some weight
Bipedal stand	P5a
Bipedal stand with forelimb suspend	P5c
Bipedal stand with forelimb compression	As in P5a but with forelimb(s) in compression bearing some weight
Lateral lie	P13c
Lateral lie with elbow	As in P13c but with one elbow providing some support on substrate level to that of the body

Lateral lie with knuckle and elbow	As in “lateral lie with elbow” but with knuckle from remaining forelimb providing some support on substrate level to that of the body
Lateral lie with forelimb suspend	As in P13c but with forelimb(s) in suspension
Lateral lie with hindlimb suspend	As in P13c but with hindlimb(s) in suspension
Lateral lie with fore- and hindlimb suspend	As in P13c but with suspended fore- and hindlimb(s)
Prone lie	Lying on belly
Prone lie with elbows	As in “prone lie” with elbows supporting weight
Prone lie with 1 elbow	As in “prone lie with elbows” but with 1 elbow only
Prone lie with elbow and forelimb suspend	As in “prone lie with 1 elbow” but with other forelimb in suspension
Supine lie	P13a
Supine lie with forelimb suspend	As in P13a but with forelimb(s) in suspension
Supine lie with hindlimb suspend	As in P13a but with hindlimb(s) in suspension
Supine lie with forelimb and hindlimb suspend	As in P13a with suspended fore- and hindlimb(s)
Pronograde bridge	P14
Forelimb suspend with hindlimb compression	Forelimb(s) in suspension with most weight borne by forelimbs and hindlimb(s) in compression
Bimanual forelimb suspend	As in P8b

Table 3. 3 Locomotor modes modified from Thorpe and Crompton (2006)

Quadrupedal walk with knuckles	As in L1a[1] but with knuckles from both forelimbs in contact with substrate
Quadrupedal walk with knuckle and wrist	As in L1a but with knuckles from one forelimb and wrist from one forelimb in contact with

	substrate
Pronograde scramble	L1c
Quadrupedal run with knuckles	L5
Bipedal walk	L3b
Bipedal walk with forelimb compression and suspension	As in L3b but with one forelimb in compression and one forelimb in suspension, same as hand-assisted bipedal walk
Bipedal scramble with forelimb compression and suspension	Similar to hand-assisted bipedal scramble, hindlimbs use oddly angled supports with forelimbs either in suspension or compression or both
Bipedal run	L7
Bipedal walk with forelimb compression	As in L3b but with forelimb(s) in compression
Bipedal walk with forelimb suspension	As in L3b but with forelimb(s) in suspension
Tripedal walk with knuckles	As in L2b but with knuckles from forelimb in contact with substrate
Bipedal squat walk	As in L3b but with hindlimbs fully flexed
Bipedal squat walk with knuckle	As in “bipedal squat walk” but with knuckles from one/both forelimbs (in contact with substrate level to that of hindlimbs) bearing significant weight
Vertical climb	L8a
Vertical scramble	L8c
Bimanual pull-up	As in L8f but with forelimbs grasping one/two supports in any orientation
Bipedal climb	Using only hindlimbs to progress upwards on typically horizontal supports
Ladder climb	L8b
Sideways vertical climb	As in L8i but upwards

Pulse climb	As in L8e but hindlimbs grasp supports of any orientation and forelimbs can grasp more than one support
Rump-first vertical descent Bipedal rump-first descent with forelimb support Firepole slide	L8g1 Only hindlimbs move downwards first (used as brakes) and carry most of body weight, with one forelimb bearing some weight above L8l but sometimes hindlimbs or forelimbs may use other supports as brakes on the way down
Head-first scramble descent	L8h2
Upward vertical bridge	L11c
Flexed forelimb and hindlimb swing	As in “forelimb-hindlimb swing” but with all limbs highly flexed

Table 3. 4 Height, support size and orientation (Thorpe and Crompton 2005; Thorpe and Crompton 2006)

Diameter	<4cm; 4-10cm; >10-20cm; >20cm
Orientation	Vertical ≤20°; angled 20-45°; horizontal >45-90°
Type	Flexible but inelastic eg. ropes[1]; stiff; compliant eg. hoses[2]
Height	≤100cm; >100-200cm; >200-300cm; >300cm

Table 3. 5. Conflated postural modes

Sit	All sits and squats
Pronograde	Quadrupedal stand with knuckles/wrists/palms/elbows /knuckle and wrist/knuckle and palm, quadrupedal forelimb crouch/crouch with 1 elbow/elbow and wrist, pronograde forelimb compression, ipsilateral bipedal stand, tripedal stand with knuckles/wrist/knuckle and elbow, tripedal stand with forelimb

	compression/palm/forelimb suspension/hindlimb compression, pronograde bridge, body hang, tripedal stand with forelimb compression
Bipedalism	Bipedal stand, bipedal stand with forelimb suspend/forelimb compression, monostand with forelimb and hindlimb compression
Lie	All lies
Others	Forelimb suspend with hindlimb compression, bimanual forelimb suspend

Table 3. 6 Conflated locomotor modes

Pronograde	Quadrupedal walk or run with knuckles/knuckle and wrist/palms, pronograde scramble, tripedal walk with knuckles
Bipedalism	Bipedal walk or run, bipedal walk or run with forelimb compression w/o suspension/forelimb suspension, bipedal scramble with forelimb compression and suspension, bipedal squat walk w/o knuckle, orthograde transfer
Vertical climb	Bipedal/ladder/sideways climb, vertical climb/scramble, bimanual pull-up, unimanual pull-up, upward vertical bridge
Vertical descent	Rump-first vertical descent, bipedal rump-first descent with forelimb support, firepole slide, ladder/bipedal descent, arrested drop, bimanual suspensory drop, head-first scramble descent
Others	Forward/side roll, pronograde/bipedal leap, crawl, flexed fore- and hindlimb swing, forelimb/stationary forelimb swing, bimanual forelimb swing upwards, brachiate, orthograde transfer downwards

Table 3. 7 Conflated behaviours

Social	SAB, AB, SD, IV
Ingestion	IN
Inactivity	IY
Travel	T
Others	SB, AAB, SP, N

For the wild dataset, the same locomotor and positional modes were recorded according to Table 3. 2 and Table 3. 3. However for conflated postural modes, ‘other’ posture was substituted with ‘orthograde’ posture. An event was defined as a single locomotor/posture mode without any support usage or positional behaviour change. If the locomotor/posture mode remained the same but a support use changed, a new event was recorded only if this was coupled with 0.5m of displacement of the body. For each event, support usage was recorded as:

- Total number of initial supports
- Total number of initial supports for the forelimb & hindlimb individually
- Initial support orientation of the forelimb/s, hindlimb/s, ischium & back (vertical/horizontal/both)
- Initial support diameter of the forelimb/s, hindlimb/s, ischium & back (<20cm/>20cm/ both)

3.2.3 Statistical analysis

SPSS was used for all data analyses. Pearson’s Chi-square test of independence were used to test for significant bivariate relationships. For details on why Chi-square test was chosen please refer to Chapter 2, Section 2.2.5. Only Chi-square tests that yielded a p value of ≤0.01 were considered significant. The standardized residual (SR), an estimate of the error (deviation from the observed and true values) divided by its variance, was used to indicate the strength and direction of association between two variables. If a SR was more than two, or less than minus two, an association was held to exist at the 95% confidence level. Where possible, multivariate relationships were analysed [using loglinear analysis following Thorpe and Crompton (2005) and Crompton et al. (2010)], as it is important to consider the effects of multiple variables on each other simultaneously. To find the interactions that best explained the data, multiple loglinear tests were run with variable states (ie support diameter) classified differently (ie <4cm or ≥4cm) to find which combinations best explained the data. The aim is for the highest 'goodness of fit' possible, with a fit of 1 explaining all the data. Within each significant model, significant expressions are themselves ranked by the value of the standardised Chi-square. While loglinear modelling tells us which variable combinations best explain the dataset, the effect of one variable on another was further explored using chi-square testing as described above. Both loglinear and Chi-square tests require there to be no sampling zeros or low expected cell counts; no more than 20% of expected counts should be under 5, with no expected counts under one (Tabachnick and Fidell 1989). Behavioural, postural and locomotor modes that were similar in terms of context and kinesiology (mechanics and physiology) were clumped, as required, for statistical analysis (see Table 3. 5, Table 3. 6 and Table 3. 7).

3.3 Results

Here 'arboreal' equates to above ground (no limb or body part is in contact with the ground), since although arboreal is commonly taken to mean 'in the trees' the zoos had broadly analogous structures such as ropes/platforms/hanging hoses. All given standardized residuals (SR) were significant, meaning that one variable occurred significantly more or less than expected. Unless otherwise stated, all results are for adult gorillas. Unfortunately there was often insufficient locomotor data to test for significant differences between the zoos, but where possible statistical testing has been carried out.

3.3.1 Comparison of profiles of locomotion and posture between both zoos

At Zoo A a total of 6416 events were collected: 4873 postural, 350 locomotor and 1193 OOS (out of sight). The gorillas spent 63.2%, 16.2% and 5.3% of their time respectively in ’inactivity’, ’feeding’ and ’travel ’ (Figure 3. 3). At Zoo B, a total of 7818 events were recorded from adults and juveniles: 750 locomotion (includes observer 1 and observer 2’s data), 5976 postural and 1092 OOS. The adult gorillas spent 51.0%, 34.7% and 6.0% of their time respectively in ‘inactivity’, ‘feeding’ and ’travel ’ (see Figure 3. 4).

Figure 3. 3 Percentages of conflated behaviour modes displayed at Zoo A.

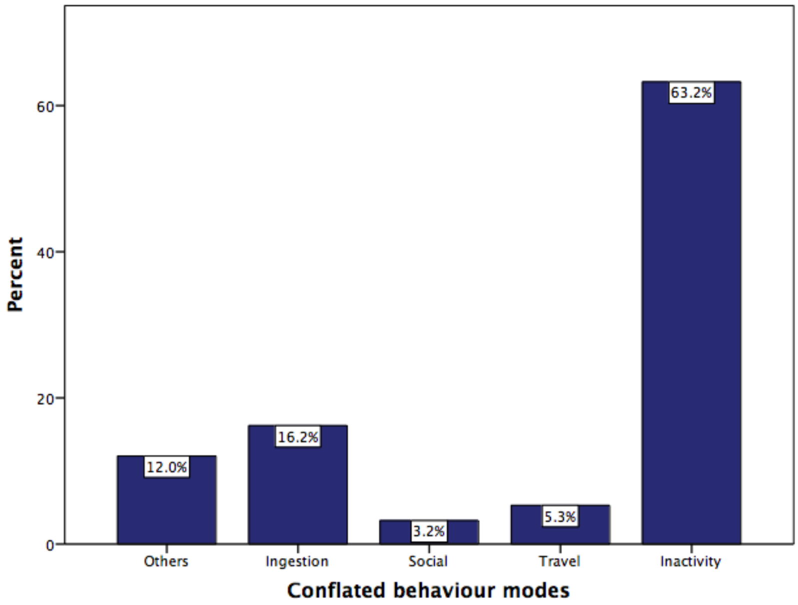
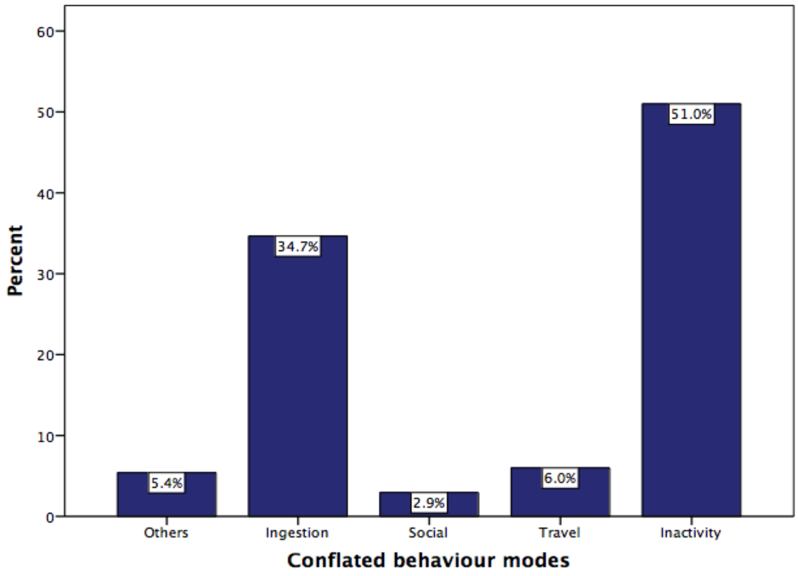


Figure 3. 4 Percentages of conflated behaviour modes displayed at Zoo B.



’Sit ’ (43.6%), ’lie ’ (33.0%), and ’pronograde ’ (8.0%) dominated the postural modes at Zoo A (Figure 3. 5). At Zoo B, according to Figure 3. 6, ’sit ’ (45.5%) was the most common, followed by ’pronograde’ (18.7%) and ’lie ’ (25.5%). Comparing the two zoos, significantly more ’bipedalism’ (SR 2.3) and ’pronograde’ (SR 10.1) postures, and less ’lie ’ (SR -6.4) occurred at Zoo B (χ^2 = 307.113, df = 4, P = 0.000 N= 11 208).

Figure 3. 5 Percentages of conflated postures displayed at Zoo A.

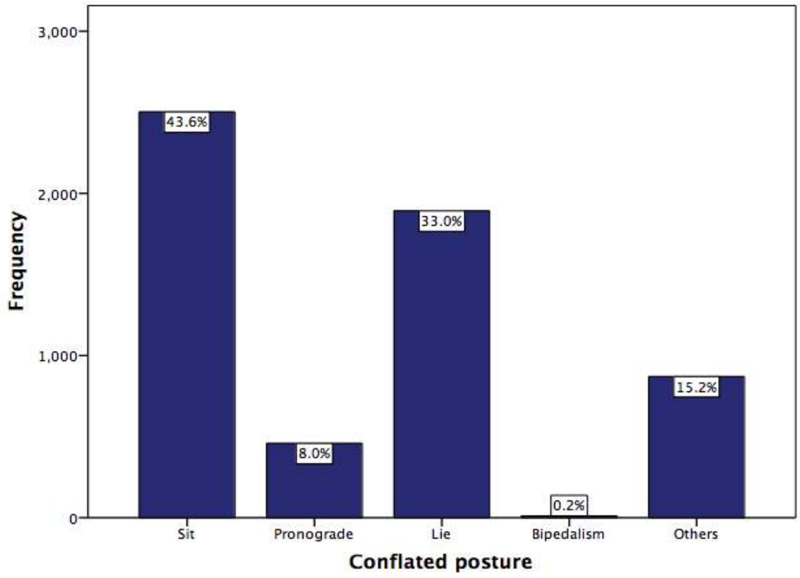
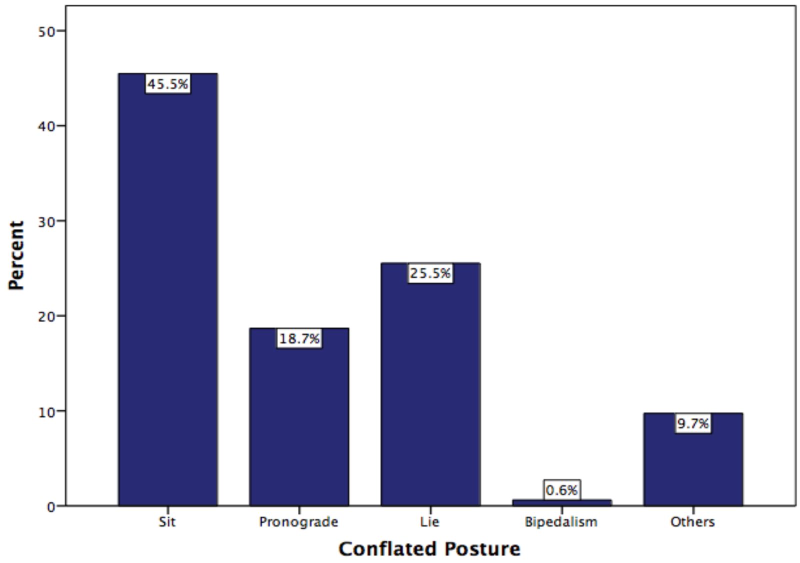


Figure 3. 6 Percentages of conflated postures displayed at Zoo B.



At Zoo A, ’sit ’ (SR 5.3), ’pronograde ’ (SR 17.0) and ’bipedal’ (SR 3.1) postures occurred more than expected during ’ingestion ’, while ’lie ’ (SR 7.8) occurred more than expected during ’inactivity ’ (χ^2 = 784.175, df = 15, N = 4835, p = 0.000). At Zoo B, similarly ’lie ’ (SR 13.7) occurred more than expected during ’inactivity’ however only ’pronograde ’ (SR 14.2) postures occurred more during ’ingestion’, and ’bipedalism’ (SR 2.1) more during ’social’ behaviour (χ^2 = 911.328, df = 16, P = 0.000 N=5275).

At Zoo A, according to Figure 3. 7, ’pronograde’ locomotion (inclusive of quadrupedal and tripedal walk/run/scramble) was most common (86.9%), followed by ’vertical climb’ (5.5%) then ’bipedalism’ (3.8%). Looking at Figure 3. 8, similarly at Zoo B, the most common locomotor modes were ’pronograde’ (88.3%), ’vertical climb’ (4.2%) and ’bipedalism’ (3.8%).

Figure 3. 7 Percentages of conflated locomotor modes displayed at Zoo A.

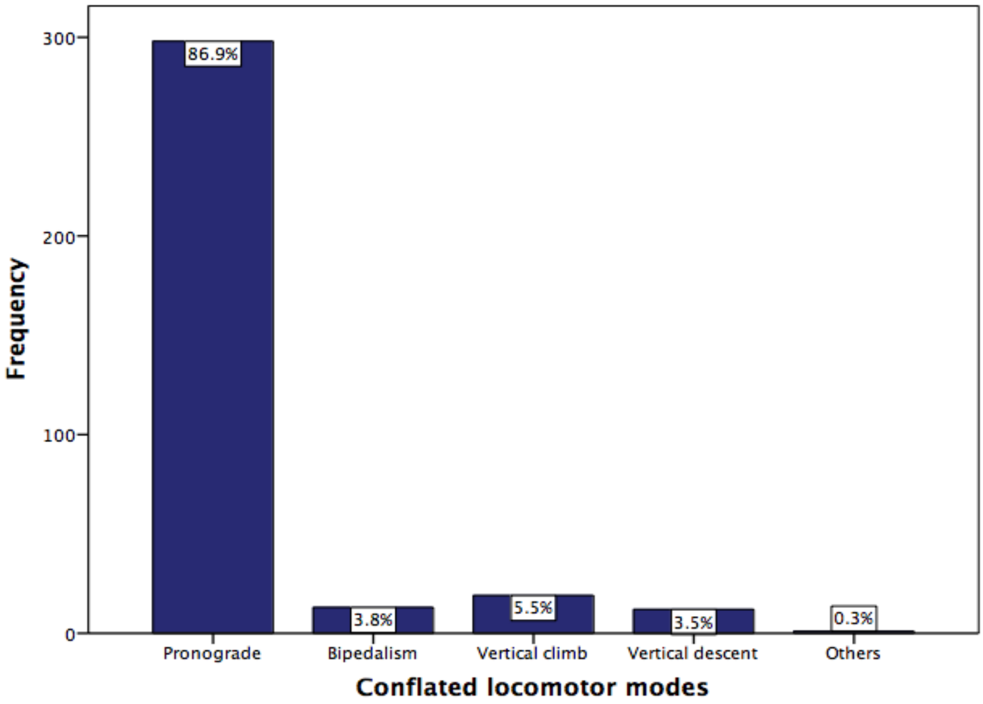
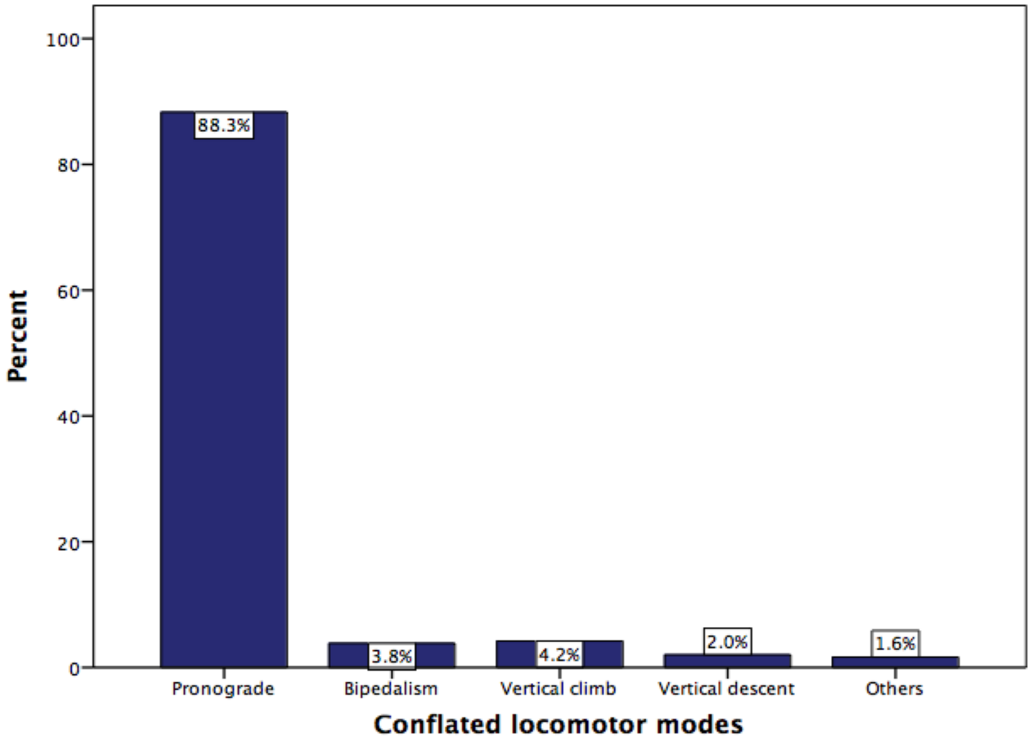


Figure 3. 8 Percentages of conflated locomotor modes displayed at Zoo B.



3.3.2 Vertical space usage in relation to behaviour/posture/locomotion

At Zoo A, 67.1%, of the time was spent below 1m, followed by 16.2% above 3m (Figure 3. 9). The male was found less often than expected above 1m (SR -16.9) but females more often (SR 9.6; χ^2 = 679.203, df = 1, P = 0.000, N = 6416). Vertical space usage at Zoo B was similar in that the gorillas, according to Figure 3. 10. In both zoos (Zoo A: χ^2 = 679.203, df = 1, N =6416, p = 0.000; Zoo B: χ^2 = 136.730, df = 1, N =6360, p = 0.000), males were observed most often below 1m (Zoo A: 15.1; Zoo B: SR 4.9), and less above 1m (Zoo A: -16.9; Zoo B: SR -7.1), whereas females more often than expected above 1m (Zoo A: 9.6; Zoo B: SR 6.5) and less below 1m (Zoo A: -8.6; Zoo B: SR -4.5). Comparing vertical space usage between zoos, gorillas at Zoo B were more frequently than expected below 1m (SR 3.0) and less above 3m (SR -7.0), and vice-versa at Zoo A (χ^2 = 120.990, df = 3, P = 0.000, N = 11166). It should be noted that differences in height between enclosures may account for some of the differences seen here. However as height categories used were identical, and the difference in height between enclosures was small ~1m, a direct comparison should be acceptable for the purposes of this study.

Figure 3. 9 Percentages of vertical positions used at Zoo A. Vertical positions 1 = <1m, 2= 1-2m, 3 = 2-3m, 4 = >3m

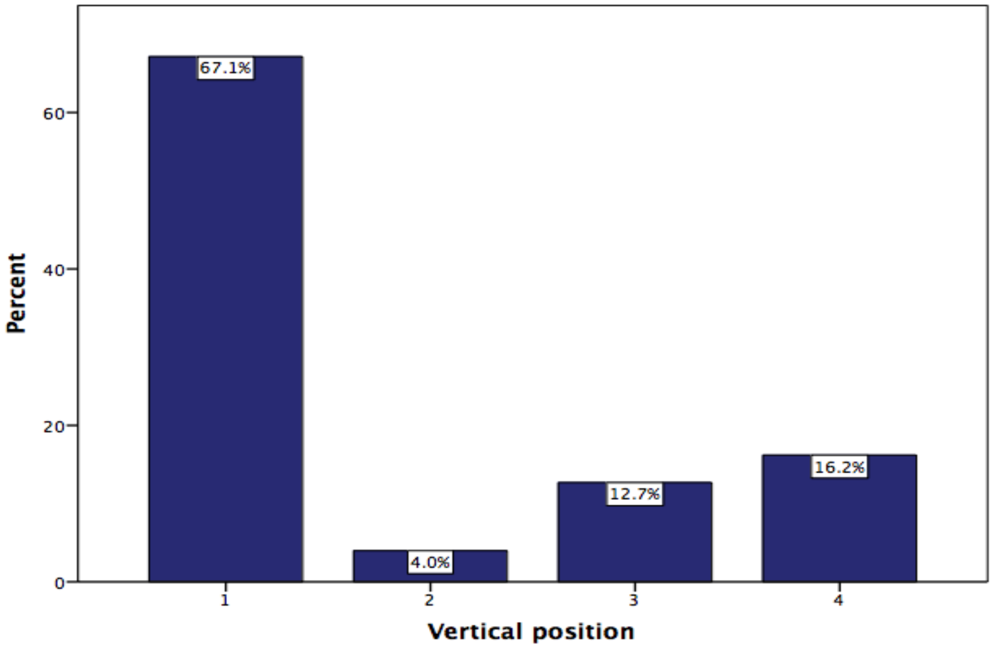
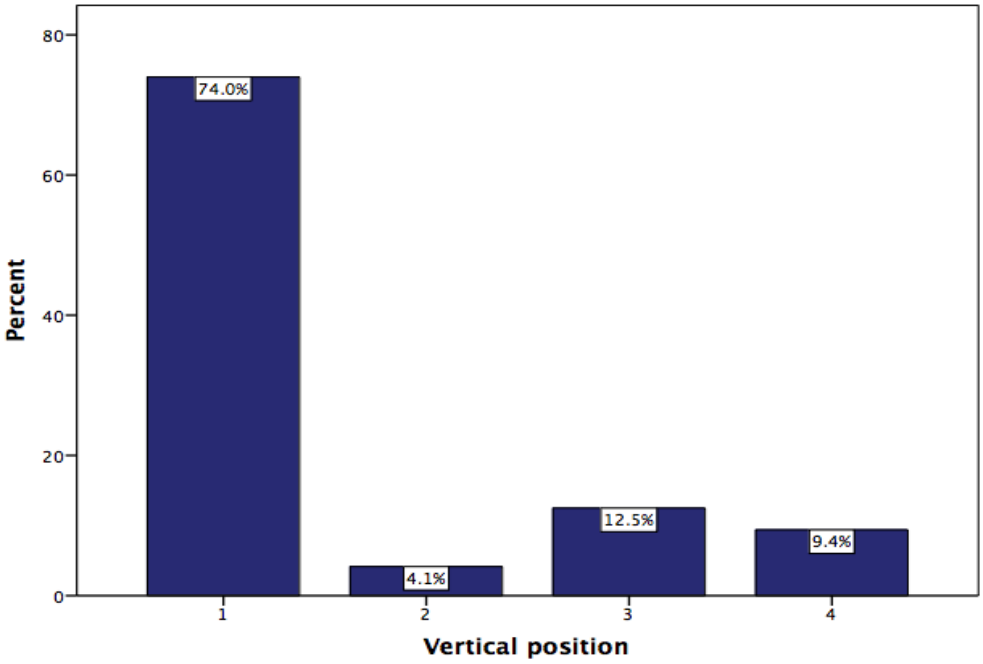


Figure 3. 10 Percentages of vertical positions used at Zoo B. Vertical positions 1 = <1m, 2= 1-2m, 3 = 2-3m, 4 = >3m



With regards to vertical space usage and behaviour, similar trends were found at both zoos. At Zoo A, ingestion occurred more often than expected below 1m (SR 7.1) and less at both 2-3m (SR -3.9) and at above 3m (SR -9.4), while inactivity occurred more often than expected above 3m (SR 7.4; χ^2 =324.403, df = 12, P = 0.000, N = 4975). At Zoo B, ingestion occurred more often than expected at heights below 1m (SR 3.1) and less at 1-2m (SR -2.2), 2-3m (SR -4.3) and above 3m (SR -2.4), while inactivity more often than expected above 3m (SR 4.8; χ^2 = 316.425, df = 12, P = 0.000, N = 5708).

Examining vertical space usage and posture, sit occurred more often than expected below 1m (SR 9.4) and between 1-2m (SR 4.9) at Zoo A, and pronograde more below 1m (SR 7.5) but less at 1-2m (SR -4.1), at 2-3m (SR -6.4) and at above 3m (SR -7.1). Conversely 'lie' occurred less often than expected below 1m (SR -14.8) and 1-2m (-3.3) but more at 2-3m (SR 11.0) and above 3m (SR 20.8; χ^2 =1340.936, df = 12, P = 0.000, N = 4926). At Zoo B, sit postures were exhibited more often than expected from 1-2m (SR 5.5), and pronograde postures more often below 1m (SR 6.7) and less often at 1-2m (SR -3.8), at 2-3m (SR -6.6) and above 3m (SR -8.1). Lie was seen less often than expected (SR -4.0) below 1m and at 1-2m (SR -4.4) but more often at 2-3m (SR 4.0) and above 3m (SR 9.8; χ^2 = 361.314, df = 12, P = 0.000, N = 5284).

Next, the relationship between vertical space usage and locomotion was examined. For both Zoo A and Zoo B, pronograde locomotion (93.4% and 92.8% respectively) was the most common locomotor mode terrestrially (below 1m). Arboreal locomotion was more evenly distributed among the locomotor modes at both zoos (Figure 3. 11 and Figure 3. 12), and this was especially so at Zoo A (Figure 3. 11). At Zoo A 'pronograde' (34.2%) was the most commonly used locomotion arboreally, followed by 'vertical climb' and 'descent' (26.3% each) then 'bipedalism' (10.5%). Similarly at Zoo B, 'pronograde' (65.6%) dominated arboreal locomotion, followed by 'vertical climbing' (15.6%), 'vertical descent' (7.8%) and 'bipedalism' (6.7%).

Figure 3. 11 Percentages of arboreal (above 1m) locomotor modes at Zoo A

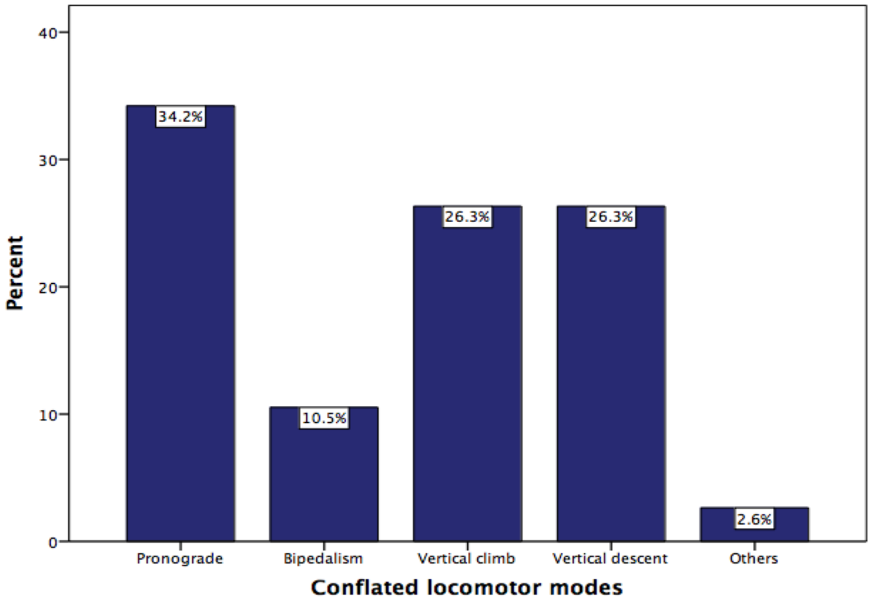
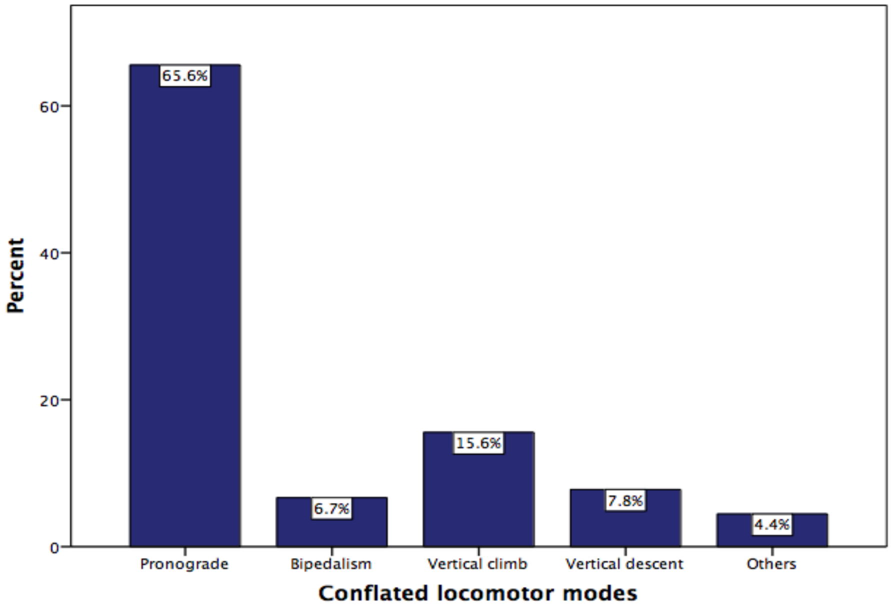


Figure 3. 12 Percentages of arboreal (above 1m) locomotor modes at Zoo B



'Bipedal' locomotion occurred most below 1m (69.2%) and above 3m (15.4%) at Zoo A. At Zoo B, most 'bipedalism' occurred below 1m, and the rest were evenly distributed at 1-2m and 2-3m (14.3% for both). No 'bipedalism' occurred above 3m at Zoo B. Combining the adults from both zoos with the juveniles from Zoo B, 'pronograde' locomotion was found less often than expected (χ^2 =104.011, df = 4, P = 0.000, N = 728) arboreally (SR -3.3), whereas 'other' locomotor modes were found more arboreally (SR 3.8).

Table 3. 8 Model 1: Posture-Behaviour-Arboreality at Zoo A, at P = 0.464

Expression	Chi-square	df	Sig.
Posture*arboreality	55.949	1	0
Posture*behaviour	49.802	1	0
Arboreality *behaviour	6.724	1	0.01

Table 3. 9 Model 2: Posture-Behaviour-Arboreality at Zoo B, at P = 0.356

Expression	Chi-square	df	Sig.
Posture*behaviour	100.747	1	0
Posture*arboreality	171.953	1	0
Arboreality *behaviour	39.488	1	0

Using loglinear analysis, the relationship between posture ('sit' and 'pronograde'), behaviour ('inactivity' and 'ingestion'), and arboreality (terrestrial, ≤1 m and arboreal, >1 m) was significant in both Zoo A (P = 0.464; see Table 3. 8, Model 1) and Zoo B (P = 0.356; see Table 3. 9, Model 2).

For Zoo A, in the most significant expression between posture and arboreality, 'sit' occured more often than expected arboreally (SR 2.3) while 'pronograde' more terrestrially (SR 2.6; χ^2 = 46.830, df = 1, P = 0.000, N = 2101). In the second most significant expression between posture and behaviour (χ^2 = 60.919, df = 1, P = 0.000, N = 2101), 'sit' was used less (SR -2.5) often than expected during 'ingestion' whereas 'pronograde' was used more (SR 6.1) often than expected during 'ingestion' but less (SR -4.0) during 'inactivity'. In the third most significant expression, between arboreality and behaviour, 'ingestion' occurred less often than expected arboreally (SR -2.8; χ^2 = 13.055, df = 1, P = 0.000, N = 21010).

For Zoo B, although the order of the first two significant expressions differ, the patterns found within each significant expression were similar to that in Zoo A. In the most significant expression between posture and behaviour (χ^2 = 207.258, df =

1 , P = 0.000, N = 3191), 'sit' was used less (SR -5.5) often that expected during 'ingestion', but more (SR 5.4) during 'inactivity'. On the other hand, 'pronograde' was used more (SR 8.7) often than expected during 'ingestion' but less (SR -8.5) during 'inactivity'. In the second most significant expression, posture and arboreality, 'sit' occured more often than expected arboreally (SR 5.3) while 'pronograde' more often terrestrially (SR 4.5; χ^2 =123.743, df = 1, P = 0.000, N = 3191). In the third most significant expression, between arboreality and behaviour, 'ingestion' occurred less often than expected arboreally (SR -5.5) but more often terrestrially (SR 3.0). On the contrary, 'inactivity' occurred more often than expected arboreally (SR 5.4) but less terrestrially (SR -2.9; χ^2 = 77.662, df = 1, P = 0.000, N = 3191).

3.3.3 Support usage in bipedal locomotion and posture

Differences in support usage between bipedal locomotion and posture exist. Looking first at support compliance, according to Table 3. 10, bipedal locomotion occurred mostly either on 'inelastic but flexible' or 'compliant' supports for 'forelimb 1', 'forelimb 2' in Zoo A and for all four limbs in Zoo B. On the other hand, bipedal posture occurred mostly on 'stiff' supports for 'forelimb 1' and 'forelimb 2' in Zoo A and all four limbs in Zoo B.

Next support size was examined, and according to Table 3. 10, '<4cm' or '4-10cm' supports were used mostly in bipedal locomotion for 'forelimb 1' and 'forelimb 2' in both zoos. However for bipedal posture mainly '>10cm' or '>20cm' supports were used for 'forelimb 1' and 'forelimb 2' in Zoo A, and for 'forelimb 1', 'forelimb 2' and 'hindlimb 1' in Zoo B.

Support orientation was mostly 'horizontal' for both bipedal locomotion and posture, except for 'hindlimb 1' and 'hindlimb 2' in bipedal posture.

Table 3. 10 Support usage in bipedal locomotion and posture. ‘I’ refers to inelastic but flexible, ‘S’ to stiff, ‘C’ to compliant, ‘H’ to horizontal, ‘A’ to angled. ‘F1’ refers to forelimb 1, ‘F2’ to forelimb 2, ‘H1’ to hindlimb 1, ‘H2’ to hindlimb 2.

		Zoo A		Zoo B	
		Locomotion (N = 2)	Posture (N = 6)	Locomotion (N = 8)	Posture (N = 8)
Compliance	F1	I (100%)	S (66.7%)	I (62.5 %)	S (83.3%)
	F2	I (100%)	S, C (50% each)	I, C and S (33.3% each)	S (100%)
	H1	S (100%)	I (100%)	C (50%)	S (75%)
	H2	S (100%)	I (100%)	I (66.7%)	S (75%)
Size	F1	<4cm (100%)	>20cm (83.3%)	<4cm (50%)	>20cm (66.7%)
	F2	<4cm (100%)	>10cm (50%)	<10cm (33.3%)	>20cm (100%)
	H1	>20cm (100%)	<4cm (100%)	4-10cm (50%)	10-20cm (62.5%)
	H2	>20cm (100%)	<4cm (100%)	<4cm, 4-10cm, >20cm (33.3% each)	4-10cm (50%)
Orientation	F1	H (100%)	H (66.7%)	H (50%)	H (83.3%)
	F2	H (100%)	H (100%)	H (83.3%)	H (100%)
	H1	H (100%)	A (100%)	H (100%)	H (100%)
	H2	H (100%)	A (100%)	H (100%)	H (100%)

3.3.4 Support usage in relation to vertical space usage and behaviour

Table 3. 11 Model 3: Arboreality-Support size-Behaviour, at P = 0.765

Expression	Chi-square	df	Sig.
Arboreality*support size	9.252	1	0.002
Behaviour*support size	7.114	1	0.008

Looking next at arboreality, support size and behaviour, only a significant relationship was found in Zoo B (P = 0.765; see Table 3. 11, Model 3). The most significant expression was between arboreality (terrestrial, ≤1 m and arboreal, >1 m) and support size (<4cm and ≥4cm). ≥4cm supports were used more often than expected terrestrially (SR 2.3; χ^2 = 11.076, df = 1, P = 0.001, N = 357). The second most significant expression was between behaviour and support size (χ^2 = 6.698, df = 1, P = 0.010, N = 240) however no SR values were significant.

Table 3. 12 Model 4: Zoo-Behaviour-Support orientation, at P = 0.896

Expression	Chi-square	df	Sig.
Zoo*support orientation	58.770	1	0
Zoo*behaviour	19.733	1	0

There was a significant relationship between zoo, behaviour ('ingestion' and 'inactivity') and support orientation ('horizontal' and 'angled or vertical') (Table 3. 12). The first most significant expression was between zoo and support orientation (χ^2 = 86.623, df = 1, P = 0.000, N = 1149). At Zoo A, 'horizontal' supports were used less (SR -2.7) often than expected, but 'angled or vertical' supports were used more (SR 4.4). On the other hand, at Zoo B, 'horizontal' supports were used more (SR 4.0) often than expected, but 'angled and vertical' supports were used less (SR -6.6). The second most significant expression was between zoo and behaviour (χ^2 = 422.019, df = 1, P = 0, N = 9102). At Zoo A, 'inactivity' occurred more (SR 8.5) often than expected whereas 'ingestion' occurred less often (SR -12.6). On the contrary, at Zoo B, 'inactivity' occurred less often than expected (SR -7.7), and 'ingestion' occurred more often (SR 11.5).

3.3.5 Wild gorilla positional behaviour profile

Table 3. 13 shows how many events of positional behaviour were collected from each species. A total of 781 events were collected, with western lowland gorilla being the majority (547 events).

Table 3. 13 Frequencies of positional behaviour events collected from each species

	Frequency	**Percent**
Eastern lowland gorilla	89	10.7
Western lowland gorilla	600	71.9
Mountain gorilla	145	17.4
Total	834	100.0

Figure 3. 13 details the frequencies of various postures used by each gorilla species. For western lowland gorillas, 'sit' (65%) was the most common arboreal posture, followed by 'pronograde' (14%) and 'orthograde' (12%) postures. For eastern lowland gorillas, 'sit' (74%) was the most common posture, followed by 'pronograde', 'lie' and 'bipedal stand' (all 7% each). Lastly for mountain gorillas, 'sit' (60%) was the most common posture, followed by 'bipedal stand' (15%). Comparing the postures between species, mountain gorillas displayed 'bipedal stand' (SR 2.1) and 'lie' (SR 2.1) significantly more than expected compared to the other species ($\chi^2 = 30.679$, df = 8, P = 0.000, N = 837).

Figure 3. 14 shows the frequencies of each locomotor mode used by each gorilla species. For western lowland gorilla, 'vertical descent' (36%) was the top arboreal locomotor mode and 'vertical climb' (33%) was the second. Similarly for eastern lowland gorilla, 'vertical descent' (50%) was the most common locomotor mode followed by 'vertical climb' (20%). For mountain gorilla, 'vertical climb' (32%) was the most common locomotor mode and 'bipedal' (27%) was the next. For all species, 'pronograde' was the least common locomotor mode aside from 'others'.

Figure 3. 13 Frequencies of arboreal posture used by each subspecies of gorilla. ‘+’ refers to significantly more, ‘-‘ to significantly less than expected.

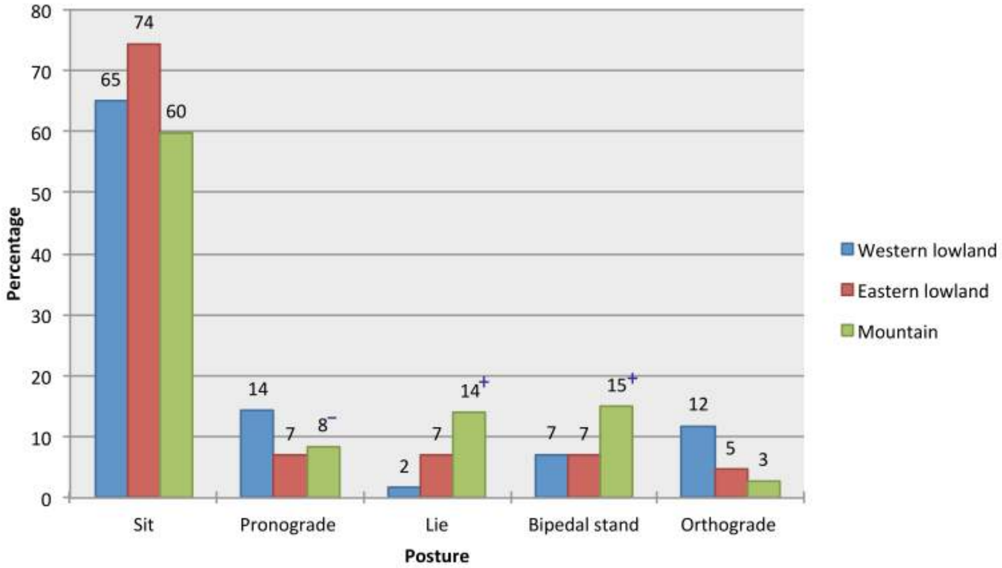
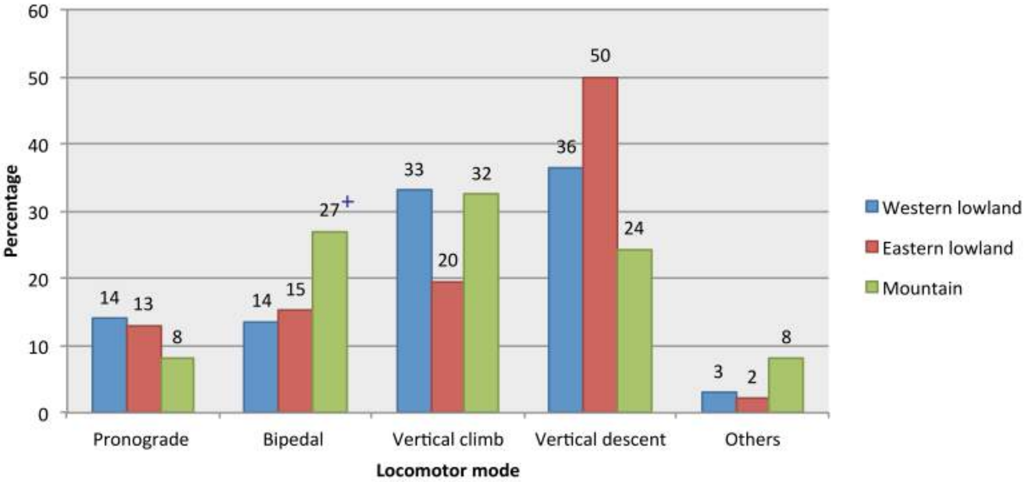


Figure 3. 14 Frequencies of arboreal locomotor modes used by each subspecies of gorilla. ‘+’ refers to significantly more often than expected.



3.3.6 Wild and captive gorilla support usage

Looking next at support orientation, as shown in Figure 3. 15, in all species, ‘vertical’ supports were used most commonly (western lowland 52%; eastern lowland 56%; mountain 49%) and ‘both’ supports were used the least in the wild dataset. In Zoo A, 85% of the forelimb supports were ‘horizontal’, while the rest were ‘angled’ or ‘vertical’. In Zoo B, 92.1% of the forelimb supports used were ‘horizontal’, while the rest were ‘angled’ or ‘vertical’.

Looking next at support diameter, as shown in Figure 3. 16, ‘<20cm’ diameter supports were used most commonly for all species (western lowland 67%; eastern lowland 72%; mountain 64%) in the wild dataset. Again, ‘both’ supports were used the least in all species. In Zoo A, 88% of forelimb supports were ‘<20cm’, while the rest were ‘>20cm’. In Zoo B, 70% of forelimb supports were ‘<20cm’, while the rest were ‘>20cm’. In captivity, when the data from both zoos were combined, males used supports of ‘>20cm’ more often than females (SR 2.6; χ^2 = 13.319, df = 3, P = 0.004, N = 367). Also in wild western lowland gorillas, males used ‘>20cm’ supports more often than females (SR 2.4; χ^2 = 14.804, df = 4, P = 0.005, N = 431). There were no significant sexual differences in support diameter for mountain gorillas (χ^2 = 4.287, df = 4, P = 0.368, N = 144). Due to the small sample size of eastern lowland gorillas, sexual differences in support diameter preferences could not be computed.

No significant differences were found between species for initial forelimb support orientation (χ^2 = 4.203, df = 6, P = 0.649, N = 781) or initial forelimb support diameter (χ^2 =3.278, df = 6, P = 0.773, N = 781) in the wild dataset.

Figure 3. 15 Frequencies of initial forelimb support orientation used by each gorilla subspecies.

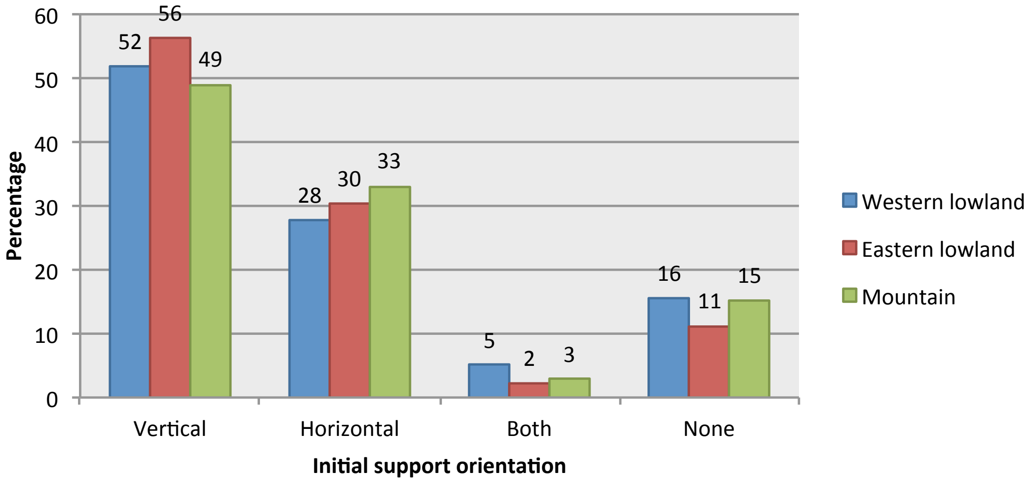
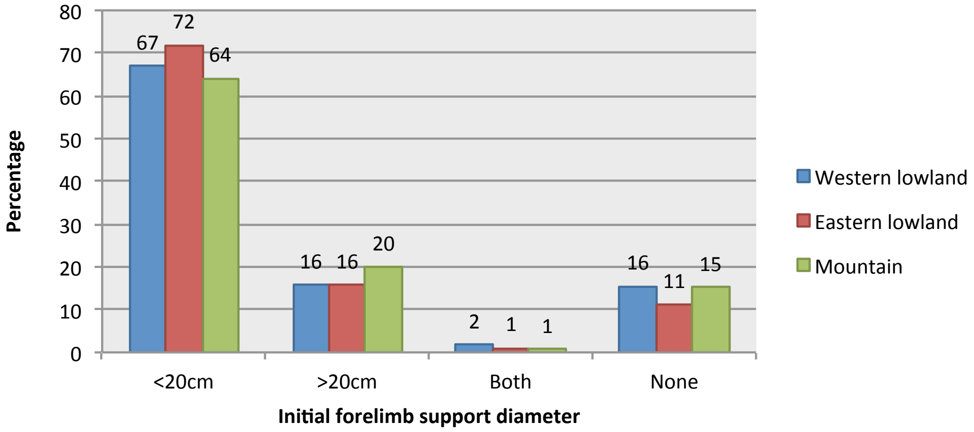


Figure 3. 16 Frequencies of initial forelimb support diameter used by each gorilla subspecies.



In wild western lowland gorillas, use of ‘<20cm’ diameter initial forelimb supports was more often than expected (SR 4.8) used along with ‘<20cm’ diameter initial hindlimb supports. Similarly use of ‘>20cm’ diameter initial forelimb supports was more often than expected (SR 10.6) used along with ‘>20cm’ diameter initial hindlimb supports (χ^2 =255.24, df = 2, P = 0.000, N = 517).

3.3.7 Support diameter and positional behaviour in wild and captive western lowland gorillas

The relationship between initial forelimb support diameter and positional behaviour was significant (χ^2 =121.70, df = 8, P = 0.000, N = 446) in wild western lowland gorillas. ‘Sit’ posture (SR -3.9) and ‘bipedalism’ locomotion (SR -2.4) occurred significantly less often than expected on ‘>20cm’ supports, whereas ‘pronograde’ posture occurred more (SR 8.4) on ‘>20cm’ supports and less (SR -4.1) on ‘<20cm’ supports (Table 3. 14). Just looking at ‘vertical climb’ and ‘vertical descent’, although there was no significant relationship with initial forelimb support diameter, majority of the supports used were <20cm (79% and 77% respectively). At Zoo A, 89% of ‘vertical climb’ occurred on ‘<20cm’ supports. Similarly at Zoo B, 93% of ‘vertical climb’ occurred on ‘<20cm’ supports.

Table 3. 14 Chi-square test examining the relationship between positional behaviour and initial forelimb support diameter in wild western lowland gorillas. SR refers to standard residual. If SR = >2 (shaded orange) or <-2 (shaded blue), the relationship between the two variables is significant.

	Positional mode		**<20cm**	**>20cm**	**Total**
Posture	**Sit**	Count	120	5	125
		SR	1.9	-3.9	
	Pronograde	Count	14	36	50
		SR	-4.1	8.4	
	Bipedalism	Count	21	2	23
		SR	0.6	-1.2	
	Orthograde	Count	33	4	37
		SR	0.6	-1.2	
Locomotion	**Pronograde**	Count	19	8	27
		SR	-0.6	1.2	
	Bipedalism	Count	30	0	30
		SR	1.2	-2.4	
	Vertical climb	Count	54	14	68
		SR	-0.1	0.2	
	Vertical descent	Count	61	18	79
		SR	-0.3	0.7	
	Others	Count	7	0	7
		SR	0.6	-1.2	
	Total	Count	359	87	446

3.4 Discussion

3.4.1 Comparison of arboreal locomotor behaviour profile between captive and wild datasets

It is likely that some of these differences occurred because of differences in habitat structure. One of the biggest differences between the captive and wild dataset was ‘pronograde locomotion’ being substantially more common in the captive dataset (Zoo B 66%; Zoo A 34%) than in the wild dataset (14%). One explanation for this difference is that in both zoos, there were multiple metal platforms (>20cm diameter) found arboreally. These large supports encourage ‘pronograde locomotion’ as it would be analogous to locomoting terrestrially, where the ‘ground’ as a support is of a large diameter.

Another difference was that ‘bipedal’ locomotion (Zoo B 7%; Zoo A 11%) occurred substantially less in the captive dataset than in the wild dataset (27% for ‘bipedal’). This difference is likely to be a result of food resource distribution. In the wild, food, especially fruits, is generally found near the periphery of trees, where supports are small (Thorpe et al. 2007). Thus the animal would be required to spread its body weight on multiple small branches and bipedal locomotion (bipedal walk/scramble) enables that (Thorpe and Crompton 2005). In captivity however most food sources are found ‘terrestrially’, and if the food sources are located ‘arboreally’ the gorilla does not need to travel far in an environment that is as complex and dense as in the wild to access the food sources. Furthermore, in the wild often the food sources (fruits) are surrounded by only small supports in close proximity, whereas in captivity there is a mix of large and small supports arboreally, reducing the need to spread their weight and hence use ‘bipedal’ or ‘others’ locomotion.

Lastly ‘vertical climb’ (Zoo B 16%; Zoo A 26%) and ‘vertical descent’ (Zoo B 26%; Zoo A 8%) were less common in captivity than in the wild dataset (‘vertical climb’ 33%; ‘vertical descent’ 36%). Again this can be attributed to food resource distribution, where in the wild food resources are found in patches, where each fruiting tree represents a patch. The wild gorillas would travel terrestrially between food patches, then climb up the tree to reach the fruits (Remis 1995), thus ‘vertical climb’ and ‘vertical descent’ are an essential part of their locomotion. However in captivity food resources are often evenly distributed around the enclosure, and mostly terrestrially, thus reducing the need to travel terrestrially to a food patch and then climbing up to the food resource. Hence there is little incentive for the gorilla to use ‘vertical climb’ or ‘vertical descent’ in captivity. Therefore to encourage more vertical climbing and less pronograde arboreal locomotion in captivity, the keepers could place food arboreally and in patches (where there are no long metal platforms), perhaps in a logfeeder or in a kong tied to the ceiling/platform to mimic the environment in the wild.

These findings suggest that the habitat structure in captivity departs sufficiently to elicit changes in positional behaviour profiles, and that gorillas possess locomotor plasticity to adapt to these changes.

3.4.2 Gorillas in both zoos adopt terrestrial feeding postures similar to that of the wild

Remis (1998) showed that the most common terrestrial feeding posture adopted in wild lowland gorillas is ‘sit’, followed by ‘quadrupedal stand’ (the major component of ‘pronograde’ postures here). For both multivariate analysis (see loglinear models 1 and 2 where only ‘pronograde’ and ‘sit’ were examined) and bivariate analysis (all conflated postures examined), ‘pronograde’ postures were observed significantly more often below 1m and were used more with ‘ingestion’ at both zoos. Although ‘sit’ occurred less often than expected with ‘ingestion’ and below 1m in the loglinear analysis, in the chi-square analysis ‘sit’ and ‘pronograde’ postures occurred significantly more during ingestion at Zoo A and ‘pronograde’ postures more at Zoo B. Thus gorillas in both zoos are adopting terrestrial feeding postures similar to that of the wild, indicating that the physical and feeding enrichments provided does provide similar terrestrial habitat structures, in terms of terrestrial food distribution, to that of the wild.

3.4.3.Vertical space usage was somewhat similar to that of wild

At both Zoo A and Zoo B, ‘lie’ happened significantly more often at heights over 1m and ‘inactivity’ occurred significantly more often above 3m, indicating that the gorillas prefer to rest over 1m. Further in the loglinear model 2, ‘inactivity’ occurs more often than expected over 1m in Zoo B. It is known that wild western lowland gorillas nest arboreally (Remis 1998) therefore it is likely that the gorillas were displaying similar nesting-related behaviours to those in the wild. These results are in line with the prediction by Tuttle and Watts (1985) that gorillas would retain arboreal features to access trees, perhaps for resting, indicating that the enclosures here provide sufficient arboreal resting sites for the gorillas.

In both zoos more than 20% of the time was spent above 1m, indicating that the gorillas spent a similar time arboreally as those in the wild (at least 20%) (Remis 1998). As the gorillas studied by Remis were semi-habituated, she notes that her observations may have been biased towards arboreal sightings. At both zoos, males were more terrestrial than females. This disparity can be explained by body size differences between males and females. Arboreality is inversely related to size (Tuttle and Watts 1985), thus explaining why smaller bodied females, spend more time arboreally compared to larger bodied males. This could be because with increasing body size more energy is required to climb and descend (Remis 1998). It is known that in mountain gorillas and eastern lowland gorillas males spend less time arboreally than females (Tuttle and Watts 1985; Doran 1996; Inouye 2003).

3.4.4 Differences in vertical space usage between zoos

The gorillas at Zoo B were found significantly often more than expected below 1m and less above 3m when compared with those in Zoo A, indicating that the gorillas in Zoo B were more terrestrial than that of Zoo A. This could partially be a result of Zoo B subjects consisting of two adult males, and only one adult male for Zoo A, as males were found to be more terrestrial than females. Another possible explanation could be habitat structure differences. In Zoo B there were bars just below the ceiling (~3m high) to assist the gorillas in travelling arboreally, however because of the close proximity of these bars to the ceiling, this prevented adult gorillas from standing/sitting comfortably on the bars, thus resulting in less time spent between heights of 3-4m. This likely also explains why no bipedalism occurred above 3m at Zoo B. Therefore enclosures should bear in mind to provide sufficient space arboreally between support structures, to ensure that the gorillas can utilise the space.

3.4.5 Zoos provide similar support size distribution to that of the wild

Looking at Model 3, which examined the relationship between arboreality, support size and behaviour, bigger supports, were used more below 1m. Further at Zoo B, the majority of forelimb supports were ‘<20cm’ arboreally. In the wild dataset, which consists of only arboreal observations, 67% of initial forelimb support usage occurred on small supports. Although no significant relationship was seen for support diameter and arboreality, in Zoo A the majority of the forelimb supports used arboreally were ‘<20cm’. Therefore it is likely that the support size distribution in Zoo B, and possibly in Zoo A, is similar to habitat structure in the wild, where smaller branches are found higher, and larger supports such as tree trunks and boughs are found close to the ground (Remis 1998). Zoos, in general, should attempt to provide a habitat structure where larger supports are found closer to the ground, and increase the number of smaller supports as height increases.

3.4.6 Differences in support availability influence support preference between wild and captive environments, but not between wild sites

Model 4 examined the relationship between zoo, behaviour and support orientation and shows that at Zoo B more ‘horizontal’ but less ‘angled or vertical’ supports were used. Conversely at Zoo A more ‘angled or vertical’ but less ‘horizontal’ supports were used. This pattern is likely due to Zoo B’s enclosure being composed of a wire mesh (see Figure 3. 2), and Zoo A’s enclosure being composed of solid walls (see Figure 3. 1). This inevitably increases the number and availability of horizontal supports at Zoo B as compared to Zoo A, strongly influencing the support choice of the gorillas. There was no significant expression between behaviour and support orientation. This indicates that the difference in behaviour between the zoos (more ‘ingestion’ and less ‘inactivity’ at Zoo B but more ‘inactivity’ and less ‘ingestion’ at Zoo A) is not associated with differences in support availability. Other factors, such as differences in feeding enrichment/social group structure that were discussed in Chapter 2 may have been likely to have caused this difference in behaviour. However the difference in support choice between the zoos indicates that support usage during ‘ingestion’ and ‘inactivity’ is affected by support availability.

For the wild dataset, support orientation and diameter preference is similar across all three species. This shows that despite the differences in species and study sites, this suggests that the gorilla genus is more adapted to using ‘vertical’ and ‘<20cm’ diameter supports arboreally.

Therefore support orientation usage was different between captive and wild gorillas as majority of the supports used in the wild dataset in western lowland gorillas were ‘vertical’, unlike Zoo A and Zoo B, where the majority of supports used were ‘horizontal’. Although not quantified, this difference is likely to be caused by a higher availability of vertical supports in the wild. These findings suggest that support availability in captivity departs sufficiently from that of the wild to elicit a difference in support choice between captive and wild. Coupled with the difference in support orientation choice between the two zoos, this indicates that gorillas are not restricted in terms of support choice, but are able to adapt to different habitat structure by using different supports. Therefore by providing a higher proportion of ‘vertical’ supports arboreally in their enclosures for gorillas, it is likely that zoos will be able to encourage more species-typical arboreal behaviour by, as it has been shown in this study that support preferences of gorillas are influenced by support availability.

3.4.7 Support use in bipedalism

Bipedal locomotion occurred more on ‘4cm’, ‘4-10cm’, ‘compliant’ and ‘inelastic but flexible’ supports at both zoos (except for hindlimb supports at Zoo A). This is interesting as wild lowland gorillas (Remis 1998) and orangutans (Thorpe et al. 2007) use assisted bipedalism arboreally to access periphery of tree crowns, where supports are small and flexible. That even captive gorillas prefer to engage in assisted bipedalism in a similar manner, despite differences in habitat structure between zoos and between zoo and wild environments, suggests that lowland gorillas are adapted to engage in assisted bipedalism on such supports. In addition, arboreal bipedal locomotion in the wild dataset occurred less on the relatively larger, ‘>20cm’ supports. This lends some support to the hypothesis that bipedalism has arboreal origins; where hand-assisted bipedalism was used to access fruit at the periphery of tree crowns, and is considered by some (Thorpe et al. 2007; Crompton et al. 2008) to be pre-adaptive to terrestrial bipedalism. No bipedal locomotion at either zoo happened in the context of foraging as they were all recorded as travel, although there is nothing to say the goal was not to access food. Furthermore, 46.7% of bipedal posture happened in the context of 'ingestion'. More detailed data on arboreal assisted bipedalism, and the support types during assisted bipedalism need to be collected to understand the context(s) of which bipedalism is used for and before a link can be safely drawn between support type, ingestion and assisted bipedalism. Only then can it be said that gorillas are adapted to use assisted bipedalism to access periphery of tree crowns.

That most bipedal postures in both zoos occurred on 'stiff', '10-20cm' and '>20cm' supports, unlike in bipedal locomotion, which occurred on '4cm', '4-10cm', 'compliant' and 'inelastic but flexible' supports in the zoos and less on '>20cm' supports in the wild dataset, this indicates that despite differences in habitat structure and support availability, stronger, bigger supports are nonetheless required for posture. Hence it is likely that stability is more essential in posture than in locomotion. One explanation for this could be that gorilla locomotion, particularly hand-assisted bipedalism where forelimbs are sprawled out for balance, is often slow. In human bipedal walking slow speeds reduce vertical ground reaction forces and increase dynamic stability (Dingwell et al. 2000; Masani et al. 2002). Slow walking speeds in nonhuman primates involve less propulsion, as compared to leaping/running (Franz et al. 2005), hence the substrate is exposed to less force and pressure. In contrast, posture requires the gorilla to be relatively static, hence a large amount of weight and pressure is put onto the support for a longer time, and this is especially so for large animals like gorillas. In addition, small supports are easier to grip quickly, and this is important if the gorilla is moving and needs to transfer weight from one support to another quickly. Hence during enclosure design, zoos can assign specific arboreal structures where food is placed, and make sure that there are some 'large, stiff and horizontal' supports in the immediate proximity with mostly 'small, flexible and angled' supports slightly further away to ensure that gorillas can safely use the latter for locomoting and the initial for feeding arboreally.

3.4.8 Between species comparison of arboreal positional behaviour in wild dataset

In general all three gorilla species show similar postural and locomotor profiles. Differences arose from mountain gorilla, where ‘bipedal stand’ and ‘bipedal’ locomotion occurred more often than expected while ‘pronograde’ posture occurred less. This is surprising as mountain gorillas have been suggested to be adapted to be more terrestrial than lowland gorillas with shorter arms and less divergent big toes (Straus 1930; Schultz 1934; Tuttle and Watts 1985; Remis 1998), and hence would be more adapted to ‘terrestrial’ postures, such as quadrupedal stand, and locomotion, such as knuckle-walking, instead of bipedalism. In fact, mountain gorillas climb trees of up to 40m (observed in the video footage at Bwindi). This study therefore provides evidence that mountain gorillas, although adapted for terrestriality, are not compromised or restricted in terms of arboreal locomotor capacity.

3.4.9 Sexual differences in support size usage

Both in captivity and in the wild, western lowland gorilla males used ‘20cm’ supports more than females. Also in Remis (1995), male gorillas were found on larger substrates than females. Therefore the gorillas in captivity showed similar sexual differences in support diameter usage patterns to the wild. However no significant sexual differences in support diameter for mountain gorillas. This could be linked to body size, where the difference in weight of males in females in western lowland gorillas is 98kg (Jungers and Susman 1984), while that of mountain gorillas is substantially less, 61kg (Jungers and Susman 1984). Hence the great difference in body size between males and females in western lowland gorillas was likely sufficient to elicit support diameter usage differences, and less so in mountain gorillas. Another explanation could be that the sample size of mountain gorillas was too small in this study, to show any sexual difference in support diameter preference.

3.5 Conclusion

Positional behaviour and support usage profiles can serve as an indicator of how physical enrichment can be tailored to create an environment similar to that of the wild. While there were some similarities between wild and captive gorillas: 1) terrestrial feeding postures, 2) nesting-related behaviours, 3) support size usage, 4) vertical space usage, 5) support usage in bipedal locomotion, and 6) sexual differences in support size usage, the captive environment departed sufficiently from that of the wild to elicit some differences in positional behaviour and support usage profiles. Nonetheless support usage remained consistent in all three sites in the wild despite differing habitat structures, indicating that gorillas do have a strong preference for vertical and <20cm supports. Thus the following recommendations, based on the differences between captive and wild datasets, are made for gorilla enclosure design:

1. Place food arboreally and in patches (where there are no long metal platforms), ie. in a logfeeder/kong tied to the ceiling/platform to encourage more vertical climbing and arboreal pronograde locomotion in captivity.
2. Provide sufficient space arboreally between support structures, to increase use of 3-4m space at Zoo B.
3. Provide more horizontal supports that are found closer to the ground, and increase the number of vertical supports as height increases, to encourage similar arboreal support orientation usage as in the wild
4. Assign specific arboreal structures for food to be placed, and make sure that there are some ‘large, stiff and horizontal’ supports in the immediate proximity, but mostly ‘small, flexible and angled’ supports slightly further away, to facilitate safe use of the latter for bipedal locomotion and the initial for bipedal postures during feeding.

Therefore this study emphasizes the importance of taking into account locomotor plasticity of gorillas during enclosure design and when using positional behaviour and support usage as a welfare indicator. Although gorillas can accommodate some habitat structure differences, zoos must strive to ensure that captive habitat structures do not differ to an extent that is outside the range of the locomotor plasticity in gorillas. Given that the trends observed were all considered to be very significant in terms of P value, I believe that they would largely be reproducible if identical methods were used. However in the future a bigger sample size would be ideal, as this would allow statistical tests to be done on locomotion, and a reduced need for clumping data.

Chapter 4: 3D Musculoskeletal Model of a Western Lowland Gorilla Hindlimb

4.1 Introduction

This chapter uses a 3D musculoskeletal model of a gorilla hindlimb to obtain moment arm (MA) and torque data from muscles around the hip, knee, ankle and foot joints. The data here will be used in three ways. First, it will cover a comparison between the data obtained from this study Payne et al. (2006) using the experimental tendon travel method. Second, it will be used to interpret and understand kinematic data for vertical climbing and bipedal walking. Third, the individual data from the foot joints will be studied in detail to find out more about the functions of intrinsic muscles in the foot with regard to grasping supports. Many primates are adapted to a specialised mode of locomotion eg. orang-utans and gibbons are suspensory (Rose 1988; Tuttle and Cortright 1988; Hunt 1991), gorillas and chimpanzees are terrestrial knuckle-walkers and vertical climbers (Hunt 1991; Gebo 1996; Remis 1998), and humans are terrestrial bipeds (Crompton et al. 2008). Thus one would expect these species to have unique musculoskeletal adaptations to its predominant locomotor mode eg. long curved phalanges in orang-utans for double-locking mechanism (Rose 1988). However more recently, research (Thorpe and Crompton 2006; Manduell et al. 2012) has shown that for some species, although adapted to a predominant locomotor mode, are not restricted in terms of locomotor capacity, and are capable of a large range of locomotor modes. For example, Thorpe and Crompton (2006) found that orang-utans, besides suspension, are capable of many other locomotor and postural modes, and Manduell et al. (2012) observed that orang-utans alter the frequencies of these many locomotor/postural modes according to their environment. Even more striking, mountain gorillas, which have been described in the literature for years as an almost strictly terrestrial species (Schaller 1963; Fossey 1983; Inouye 2003), have now been revealed that they climb and forage at up to 40m at Bwindi (Redmond pers. comm.). Previous studies (Schaller 1963; Fossey 1983; Doran

1996a; Doran 1996; Tuttle 2003) on mountain gorillas were carried out at sites that had minimal sources of food arboreally, hence there was no incentive for gorillas to climb, however it has been shown that in other sites (such as Bwindi), where food is available arboreally, the gorillas engage in arboreal positional behaviour. Venkataraman et al. (2013b) has shown that hunter-gatherer populations in Malaysia that climb trees frequently to obtain food have muscular adaptations (longer fascicle lengths) that permit dorsiflexion of the ankle to similar extents of chimpanzees. Therefore this is an example of adaptation versus phenotypic plasticity whereby although a certain species may be adapted to a particular locomotor mode, this does not mean that they are restricted in terms of locomotor capacity. Hence when drawing functional interpretions of apparent musculoskeletal adaptations it is important to bear in mind locomotor plasticity.

A musculoskeletal system can be considered as an interconnected arrangement made of bones linked by ligaments and balanced by muscle-tendon tensions. Muscle torque is a quantitative measure of the ability of a muscle-tendon unit to rotate a bone about a joint centre. Muscle moment arm (MA) refers to the shortest perpendicular distance from the joint centre to the muscle-tendon unit line of action/force, and can be calculated using equation 1 below (Payne et al. 2006), where dL refers to length change of tendon and dθ refers to angle change about the joint. From equation 2 it can be gathered that muscle torque is affected by MA and the contractile force generated by the muscle fibres.

$$\text{Moment Arm} = dL/d\theta \qquad (1)$$

$$\text{Moment or torque} = \text{Contractile Force} \times \text{Moment Arm} \qquad (2)$$

In other words, moment arms convert muscle force to muscle torque, muscle contractile (or shortening) velocity to joint angular velocity and muscle excursion to joint excursion. Moment arms, and hence torque will vary with joint angles. Since joint angles can change moment arms, it has led others (Payne et al. 2006; Michilsens et al. 2010; Fujiwara and Hutchinson 2012) to suggest that animals will favour and/or be optimised for specific postures or range of joint angles during their habitual locomotor activities. Michilsens et al. (2010) found that siamangs brachiate at angles at which elbow moment arms are the highest. Fujiwara and Hutchinson (2012) found that relative elbow moment arms reliably indicate different locomotor systems in terrestrial quadrupeds. Payne et al. (2006) has attributed high moment arms at flexed positions to maintenance of flexed postures during arboreal quadrupedalism and climbing. However the relationship between muscle moment arm and muscle function (and hence locomotion capabilities) is more complex. For example higher moment arms correlate to slower angular velocity (Channon et al. 2010), small fibre lengths are can produce high angular velocity with small moment arms (Lieber and Friden 2001). Further, Hutchinson et al. (2014) has shown that ostriches do not use joint angles that coincide with optimal moment arms. Hutchinson et al. (2014) suggests that dynamic contractile properties of muscles or tendons, and Daley and Usherwood (2010) suggests stability, as part of trade offs with energetic costs, play an important role in determining locomotor capabilities. Nonetheless, while there are good theoretical reasons that moment arms matter, evidence is currently mixed. Quantification of moment arms and torque therefore remains an important aspect of understanding biomechanics and how animals might be adapted to different locomotor tasks/functions.

There are multiple methods of obtaining moment arm data. An et al. (1984) provide good descriptions of various methods of obtaining moment arms and torques and their advantages/disadvantages, which will be discussed briefly here. The first few methods discussed here are based on geometric measurement, which involves locating tendon and muscle paths about a joint via the joint coordinate system, which are then used to calculate orientations and MAs. These include (An et al. 1984) the bi-planar x-ray method (requires prior knowledge of constraints experienced by tendons and muscles about the joint for selecting proper locations for metal markers), the direct digitization method (An et al. 1984) (similar to bi-planar x-ray method, but uses 3D digitizer instead, and requires more extensive dissection for exposure), and the serial cross-sectioning method (An et al. 1984). The next method is based on direct load measurement, where a load transducer is used at the distal segment to measure the forces resulting from applying a load at the proximal segment of muscles and tendons, and moment arms can be determined from simple equilibrium equations (An et al. 1984). However this requires very sensitive load transducers. In vivo, one can use magnetic resonance imaging (MRI) to calculate moment arms as the subject voluntarily moves the joint (Rugg et al. 1990; Spoor and Van Leeuwen 1992). This method involves manually measuring the distance between the line of action of a muscle/tendon to an estimated joint centre. However this method has proven to be less reliable than the tendon travel method (Spoor and Van Leeuwen 1992).

The tendon travel method (or tendon and joint displacement method as in An et al. (1984)), was first used in (Landsmeer 1961)is a common method used in non-human apes (Marzke et al. 1999; Thorpe et al. 1999; Payne et al. 2006; Channon et al. 2010), thus it will be discussed in more detail. This method requires an electrogoniometer and electropotentiometer to measure joint angle and tendon excursion respectively (Payne et al. 2006; Channon et al. 2010). According to Payne et al. (2006), the tendon travel method involves calculating MA from the derivative of distance the tendon has moved with respect to the joint angle. The muscle of interest is tied around its belly with a string. The string has a coloured label and is thread through a hook at the insertion, with a weight hanging off the end to keep the string taut. The distance moved by the coloured label as the joint is flexed/extended would then be the distance the tendon as moved. The slope of tendon excursion and joint angle curve represents the MA. Advantages of this method are that prior knowledge of the joint centre of rotation is not needed and multiple joint configurations can be studied (An et al. 1984). It is also a practical method for cadavers, where ethical considerations make it impractical to experiment on living apes. This method has been adapted for use on live, sedated macaques (Graham and Scott 2003) but this is a highly invasive procedure that results in the euthanisation of the animal after the experiment. Limitations of this method can be inferred from the description of this method here and in Payne et al. (2006), which involves simplifying muscles to 2-dimensional straight line approximations, the inability to account for muscle paths accurately, maintaining the camera at a perfectly orthogonal position to rotation, ensuring that the limb movement is limited only to one plane (ie. only flexion-extension without any abduction-adduction or long-axis rotation). This makes it difficult to produce repeatable results across cadavers unless the experiment is tightly controlled as in (Young et al. 1993; Michilsens et al. 2010).

More recently, researchers have been using 3D musculoskeletal models to study biomechanics in humans (Hatze 1977; Delp et al. 1990; Delp et al. 1999; Modenese et al. 2011). This type of 3D musculoskeletal modelling allows moment arm data to be generated, as shown by models built for multiple animal species such as ostrich (Hutchinson et al. 2014), alligator (Bates and Schachner 2012), chimpanzee (O'Neill et al. 2013), macaque (Chan and Moran 2006), cats (Burkholder and Richard Nichols 2004) and horses (Brown et al. 2003). This method involves building a model based on digital models of skeletal material, then using muscular data collected from dissection or the literature to create the model. Unless the tendon travel method is done under extremely strict conditions as in (Young et al. 1993), there are many advantages of the 3D computer model method. These include being able to limit the motion about each joint to a singular axis (thus reducing error), being able to account for complex three dimensionality muscle paths (thus increasing accuracy) and the convenience of having a reference when interpreting results. Also, one can change the origin/insertion sites and see the effect this has on moment arms (Delp et al. 1990). Furthermore, if the area of origin/insertion is relatively big and/or irregular, it is difficult to estimate the exact location of the centroid of the origin, but with this method, error can be checked for more efficiently. It has been shown that moment arm data generated using this method is not particularly sensitive to small changes in the point chosen (O'Neill et al. 2013) and that in vivo the centre of force application, which varies with motor unit recruitment, is more representative of the true origin of the muscle (Monti et al. 2001). Therefore the potential applications for this method are high. Nonetheless, a limitation with this method will be discussed here. This limitation was imposed by the researcher, and hence not a limitation of the modelling method per se. Therefore considering the advantages of the 3D model method and given that only access to a cadaver was possible, and as mentioned before it is impractical to conduct such experiments on live apes, the 3D musculoskeletal model method would have provided the most accurate results in this situation and was chosen.

The moment arm data predicted from a 3D musculoskeletal model can be used simultaneously with kinematic data, to better understand the animal's locomotor abilities; for example to test the hypothesis that an animal will use a certain range of joint angles during locomotion/posture that maximizes moment arm and or torque (Payne et al. 2006; Michilsens et al. 2010; Bates and Schachner 2012; Hutchinson et al. 2014). To achieve this it is first necessary to identify the forms of locomotion that are and are not integral to a species. In the wild, western lowland gorillas (Remis 1998) utilize vertical climbing as 40% (females) and 42% (group males) of their arboreal locomotion making vertical climbing an integral part of locomotion for this species. On the other hand, bipedal locomotion only amounted to 4.2% (females) and 2.6% (group males) of arboreal locomotion (Remis 1998). Thus the following locomotor modes were chosen for this study: bipedalism and vertical climbing. Kinematic data, namely joint angles from the literature was used in this study (Isler 2005; Watson et al. 2009), to find out the range of joint angles and corresponding MAs for each locomotor mode. I hypothesize that 1) joint angle ranges used for climbing will coincide with angles that correspond to higher MAs in the model than that of bipedalism as in western lowland gorillas, vertical climbing forms a much higher proportion than bipedalism of their arboreal locomotion. The implication of this is that gorillas have musculoskeletal adaptations that allow relatively higher moment arms for climbing than for bipedalism. However, orthogrady has proven to be a crown hominoid feature (Crompton et al. 2008) and there have been growing evidence of using orthogrady, particularly hand-assisted bipedalism, to negotiate fine branches to obtain fruit (Thorpe et al. 2007). Hence if the moment arms predicted for joint angles used during bipedalism versus vertical climbing do not differ substantially, this may lend support to gorillas retaining some adaptations to orthogrady/bipedalism. A third possibility, which cannot be tested using a single model, is that moment arms within tetrapod limbs in general are not optimised for habitual kinematics (Hutchinson et al. 2005; Bates and Schachner

2012; Bates et al. 2012a; Bates et al. 2012b; Maidment et al. 2014), or that the mixed mechanical demands of multiple locomotor and postural activities (e.g. sitting, standing, bipedal/quadrupedal walking, bipedal/quadrupedal running, climbing, suspension, brachiation etc.) mean that adaptive signals for individual activities are highly diluted, even when animals show a high preference for single locomotor habits. Testing these possibilities, however, is beyond the scope of this work.

In this study the MA data generated by a 3D computer model will be compared to the experimental tendon travel data (Payne et al. 2006). Payne's data mainly showed linear trends in moment arms, similar to other studies that have used the tendon travel method (Thorpe et al. 1999; Smith et al. 2007; Williams et al. 2008). Recent studies (Bates and Schachner 2012; O'Neill et al. 2013; Hutchinson et al. 2014) have shown that MAs generated from the tendon travel method differ from the computer modelling method. In O'Neill et al. (2013) which compared moment arms in chimpanzees generated from computer modelling with the tendon travel method in Thorpe et al. (1999), their data showed nonlinear trends of moment arms as opposed to straight lines or constants from the Thorpe et al. (1999) data. In addition, there was a difference in magnitude for the gluteus maximus proprius and gracilis. In Hutchinson et al. (2014), a study on ostrich hindlimb, there was a difference in not just direction and magnitude and also function for multiple muscles including flexor digitorium longus and extensor digitorium longus with tendon travel method. In Bates and Schachner (2012), also on ostrich hindlimb, data was compared to the tendon travel data from (Smith et al. 2007) and differences in magnitude with hip extensors and opposite trends in iliofibularis, a knee extensor, were found. Looking at previous studies on the tendon travel method, the most challenging things were to account for muscle paths and ensure that the joint was moved only in a single plane to achieve nonlinear moment arms, only possible under extremely strict conditions to minimize human error. To solve the problem of linearity of data collected from the tendon travel method, splines (Spoor et al. 1990; Channon et al. 2010) and higher order polynomials (Murray et al. 1995; Michilsens et al. 2010) were used to derive moment arm data, which provided an improvement in terms of non-linear curves. In fact, most of the data collected from the tendon travel method and computer modelling method was similar in the Murray et al. (1995) study. Michilsens et al. (2010) ensured that the data collected was reliable by carrying out repeatability tests. In a study (Young et al. 1993) on cats where the experiment tightly controlled motion, so that in two axes motion was limited, allowing only movement in one axis at a time ie. flexion/extension, thus increasing accuracy, Young et al. (1993) generated results that were more similar to those from a computer model (Burkholder and Richard Nichols 2004). Therefore I hypothesize that 2) results from the model would be non linear and vary in magnitude from Payne et al. (2006), especially for muscles that are more challenging (relative to the tendon travel method in Payne et al. (2006)) to move in a single plane (lateral or medial to the joint) or to account for muscle paths (irregularly shaped, restricted by retinaculum) as these problems will be taken into account through via points and wrapping surfaces in the 3D model. Non linear moment arms are what one would expect and therefore more likely to be accurate ie. typically a flexor will be pushed towards a joint during flexion and pulled away from the joint during extension, hence producing a curved moment arm trend.

Lastly, how moment arms, around the foot joints, differ during grasping of different sized vertical supports (4-30cm) are examined. This information is potentially important for understanding why certain support sizes are preferred over others. In the wild, western lowland gorillas prefer to climb vertical supports that are <20cm in diameter (chapter 3). Although moment arms typically peak close a neutral position (i.e. at zero flexion-extension angle in the 3D model presented here) and hence smaller supports that involves more flexion (Daniel 1999) will elicit lower moment arms than bigger supports, I hypothesize that 3) the flexor moment arm for some digits will not decrease significantly during flexion, thus allowing moment arms and therefore torques to remain high for grasping small supports. Also the functions of the interroseous muscles and lumbricals in gorilla feet are poorly studied due to the difficult nature of obtaining dissection data from these small muscles, with data from Ochiltree (1912) representing the only published work to date. The moment arms generated for the intrinsic muscles, namely the lumbricals and the interossei, in this study therefore provide the first quantitative measure of their function. Most studies of other apes suggest that interossei function as abductors or adductors (Straus 1949; Vereecke et al. 2005), and more specifically, only a couple of studies on other apes such as gibbons and bonobos in Vereecke et al. (2005) and orangutans in Rose (1988) have suggested that the dorsal interossei may act as flexors because of their relatively plantar position. Only one study (Ochiltree 1912) mentions the possibility of the dorsal interossei in gorilla acting as a flexor. Given that the interossei are found either medial or lateral to joints, their function is likely to change between extensor and flexor as the joint angle varies. Thus it is an objective of this study to quantify how effective these interossei are as flexors or extensors, and how their function varies between flexor/extensor and between the digits. I hypothesize that 4) the interossei will be effective flexors/extensors especially in digits 1 and 2 which are important for grasping small objects.

4.2 Methods

Table 4. 1 Abbreviations of muscles in alphabetical order.

Word/phrase	Abbreviation
Extensor digitorium brevis	EDB
Extensor digitorium longus	EDL
Extensor hallucis brevis	EHB
Extensor hallucis longus	EHL
Flexor digitorum brevis	FDB
Flexor digitorum brevis superficialis	FDBS
Flexor digitorum longus	FDL
Flexor digiti minimi	FDM
Flexor digitorum profundus	FDP
Flexor hallucis brevis	FHB
Flexor hallucis longus	FHL

4.2.1 Dissection and subject data

The right thigh, left crus and left foot of one adult female gorilla were dissected to determine muscle origins and insertions. Different sides were dissected because the right foot was previously dissected by another researcher and the left thigh was damaged. For each muscle, tendon, and muscle tendon unit, mass (using an Adam Equipment PGW 2502i lab balance electronic scale accurate to 0.01g) and length (using a ruler) was measured. Where origins/insertions could reasonably be approximated to a point, the location of the point was recorded descriptively in relation to bony markers and measured (using a ruler) how proximal/distal/medial/lateral it was to a these markers. Where the origins/insertions were of a bigger area, the same method that was used to measure a 'point' origin or insertion was used, but for the borders of the area instead. For example, an origin could be recorded as "on the anterior surface of the tibia, 3cm distal to the most proximal point on the lateral condyle of the tibia, then medially for 2cm and distally for 5cm". Where the origins/insertions were long, the start and end point of the origin/insertion would be recorded. For example, an origin could be recorded as "starting 5cm from the most proximal point of the femur, along the medial border, for 10cm distally". Photographs were also taken of each origin and insertion at multiple angles for record and to aid in interpreting the data. As the gorilla used for creating the bones of the model was different to the one that was dissected, the measurements taken were used as a guide along with photographs to link dissection data to the choice of origin/insertion sites for the model. Abbreviations used for muscles are given in Table 4. 1.

Fibre lengths for each muscle were taken five times and the average was calculated. Pennation angle was also measured using a protractor using the method described in Payne et al. (2006) where the muscle was cut along the long axis of the tendon to expose the orientation of the muscle fibres relative to the long axis of the tendon. PCSA was calculated using the same formula as in Payne et al. (2006) and Thorpe et al. (1999), which is PCSA = $m/\rho l$ where m is muscle belly mass in grams, ρ is muscle density [(1.06 g cm^{-3}, Mendez and Keys (1960)] and l is muscle fibre length. Photographs were taken for each muscle after separation from other muscles while still attached, and after removal, for a visual record.

The gorilla was provided by Twycross Zoo, euthanased on 5th October 2011 at 46 years, 8 months old after suffering from age related pathologies, and weighed 72kg at time of death. She was kept in a freezer after necropsy was carried out. Her tibia was 30.7cm long (from most proximal point of medial condyle to most distal point of medial malleolus) and fibula was 28.5cm long (from most proximal point of lateral condyle to most distal point of lateral malleolus). All length measurements were made directly on the bones by a measuring tape, accurate to 0.01m, after muscles were removed.

4.2.2 Building the 3D musculoskeletal model

A sub-adult male western lowland gorilla weighing 152kg at time of death was CT scanned (Computerized axial tomography scan) at the University of Liverpool Small Animal Hospital using a Siemens Volume Zoom (4 slice) scanner. Ideally, anatomical dissection and 3D computer model construction would be carried on the same specimen. However, a single gorilla specimen available for this study was not suitable for modelling due to skeletal damage and partial dissection carried out by other researcher. Therefore, I used qualitative information collected during dissection of the damaged specimen [supported by reference to Diogo et al. (2010)] to map muscle origins, insertions and 3D paths on to the model constructed from the CT scan of the sub-adult male gorilla to take into account the difference in size owing to sexual dimorphism. Using the same anatomical markers as before for measurement, her tibia was 22.6cm and her fibula 20.9cm long. Its left hindlimb skeleton was segmented using AMIRA 5.4.3. Segmenting involved thresholding then going through each slice at a time and colouring each bone differently to digitize the virtual bones. The segments are shown in Table 4. 2. After segmentation and surface meshing to produce 3D polygonal meshes, the virtual bones were exported into MeshLab in .stl (stereolithography) format where they were separated into segments, and any remaining triangles that belonged to non-skeletal tissues were removed before the stl models were converted to .OBJ files. The .OBJ files were imported into Autodesk Maya 2015 SP2, where the segments' centre of masses

(CoM) and joints were assigned coordinates. CoM positions were estimated by eye as this positional information was required to build the GaitSym model (see below) but does not influence moment arm or muscle function calculations in any way (Bates and Schachner 2012; Bates et al. 2012a; Bates et al. 2012b; Maidment et al. 2014; Bates et al. 2015). Joint centres were initially estimated by qualitatively fitting spheres to the proximal/distal ends of limbs bones in Maya as in a number of previous studies (Bates and Schachner 2012; Bates et al. 2012a; Bates et al. 2012b; Sellers et al. 2013). The initial joint centre position derived from each sphere was checked by flexing and extending the joints around the estimated joint centre in Maya to qualitatively ensure that an appropriate range of motion was possible at each joint. The bones were then rotated about these joint centres into a 'neutral position' where the hip is flexed 90° and knee and ankle are fully extended. A neutral position refers to joint angles being 0°±0.001 for hip, knee, ankle and 0°±0.05 for foot joints on all three rotational axes (i.e. flexion-extension, abduction-adduction, and long-axis rotation), based on our reconstructed joint centres (Table 4. 2) shows the neutral position and how the hip, knee and ankle joints are directly above each other ie. in the same y plane and z plane). The difference being the foot joints had to be aligned according to a single plane as the digits were splayed out (for example the MTP joints would all be in the same z plane, but in different positions in the y plane), whereas the hip, knee and ankle joints were aligned in two planes. The model was set up so that hip flexion-extension was horizontal, parallel to the global z-axis, the adduction-abduction axis was aligned to the global x-axis, and the femoral long-axis rotation axis parallel to the global y-axis in the initial neutral posture (refer to Figure 4. 1A and 4. 1B for neutral position and axes orientations). During motion, or when posture is statically altered, our joint axes rotate following the scheme outlined in (Wu et al. 2002). Specifically, the flexion-extension axes were fixed to the joint's proximal segment, while long axis rotation axes were fixed to the joint's distal body. Abduction-adduction axes move accordingly to remain orthogonal to the flexion-extension and long axis rotation axes depending on the rotations involved. Specifically the abduction-adduction axis is rotating by rotation about the flexion-extension axis but is not affected by rotation about the long-axis rotation axis. The bones in this neutral position were then exported into GaitSym 2013a (www.animalsimulation.org), an open source forwards dynamic modelling software package (Sellers and Manning 2007). An .xml file (Extensible Markup Language file) was created for Gaitsym to read, which had all the information of each muscle (origin, insertion, fibre length, tendon length, PCSA, via point coordinates), the coordinates of each joint centre and the position (i.e. CoM; see above) and orientation of each body were specified. The data collected from dissection and the photographs were used to help specify the positions, or co-ordinates, of muscle origins, insertions and 3D paths. Figure 4. 1C illustrates where some of the major muscle groups (gluteals, quadriceps, adductors and triceps surae) that have been mapped onto the skeleton for easier visualisation of origins, insertions and muscle paths used. Muscles that were deepest were first written into the .xml file, followed by those that were more superficial. Where the muscle was fan shaped (e.g. gluteals) multiple muscle tendon paths that converged onto a single line of action were used. This meant multiple origin sites were determined where there were obvious and strong attachments (did not come off easily with the scalpel), or if the muscle was strongly attached to a large area, origins were spread out as evenly as possible, meaning that the origins were placed in a way such that the muscle paths from each origin were of similar distances from each other. Figure 4. 2 shows the muscle origins and muscle paths of the gluteus maximus, a fan-shaped muscle with strong attachments, to illustrate the approach. PCSAs for muscles that had more than one muscle path were divided equally among each muscle-tendon path so as to avoid over-representation of muscle PCSA. For example, if a muscle had two origins and hence two separate muscle codes in the .xml file, the PCSA, which was calculated based on the mass of the entire muscle, including both origins, would be divided by two for each code in the .xml file. Each muscle path was checked as the joint was flexed and extended to ensure that the muscle did not pass through bones or other muscles and ‘via points’ were added into the muscle code in the .xml file whenever necessary to increase accuracy of muscle paths. ‘Via points’ provide constraints to the muscle paths equivalent to those that would be present *in vivo* from bones shape, other muscle-tendon units and reticulae, absence of which constraints would produce data that are biologically less meaningful or accurate because the path of the muscle would not be representative as joint angle changed.

Table 4. 2 Segments of the model and the bones each segment consists of.

Segments	**Bone(s) included**
Trunk	Pelvis
Left Thigh	Femur
Left Crus	Tibia, fibula
Left Rearfoot and midfoot	Calcaneus, talus, navicular, cuboid, medial cuneiform, middle cuneiform, lateral cuneiform
First metatarsal	First metatarsal
First proximal phalanx	First proximal phalanx
First distal phalanx	First distal phalanx
Second metatarsal	Second metatarsal
Second proximal phalanx	Second proximal phalanx
Second middle phalanx	Second middle phalanx
Second distal phalanx	Second distal phalanx
Third metatarsal	Third metatarsal
Third proximal phalanx	Third proximal phalanx
Third middle phalanx	Third middle phalanx
Third distal phalanx	Third distal phalanx
Fourth metatarsal	Fourth metatarsal
Fourth proximal phalanx	Fourth proximal phalanx
Fourth middle phalanx (not captured in CT)	Fourth middle phalanx
Fourth distal phalanx	Fourth distal phalanx
Fifth metatarsal	Fifth metatarsal
Fifth proximal phalanx	Fifth proximal phalanx
Fifth middle phalanx	Fifth middle phalanx
Fifth distal phalanx (not captured in CT)	Fifth distal phalanx

Figure 4. 1 (A) Anterior and (B) lateral (right) views of hindlimb at neutral position. (C) depicts where the major muscle groupsare found. Muscle paths are red, joints (and their orientations) are blue. Note that the hip joint is directly above the knee joint. Axes are indicated by ‘X’, ‘Y’ and ‘Z’.

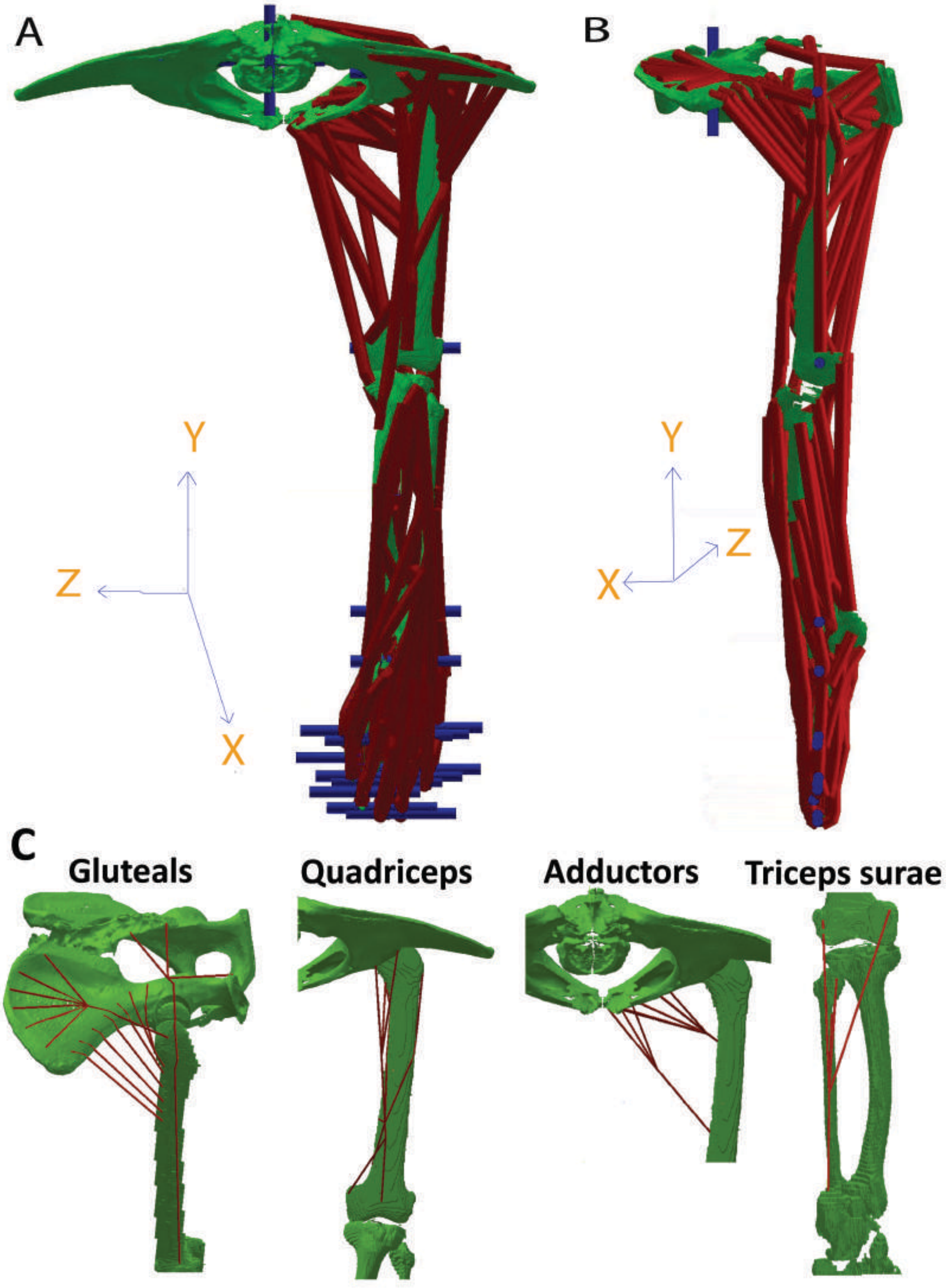
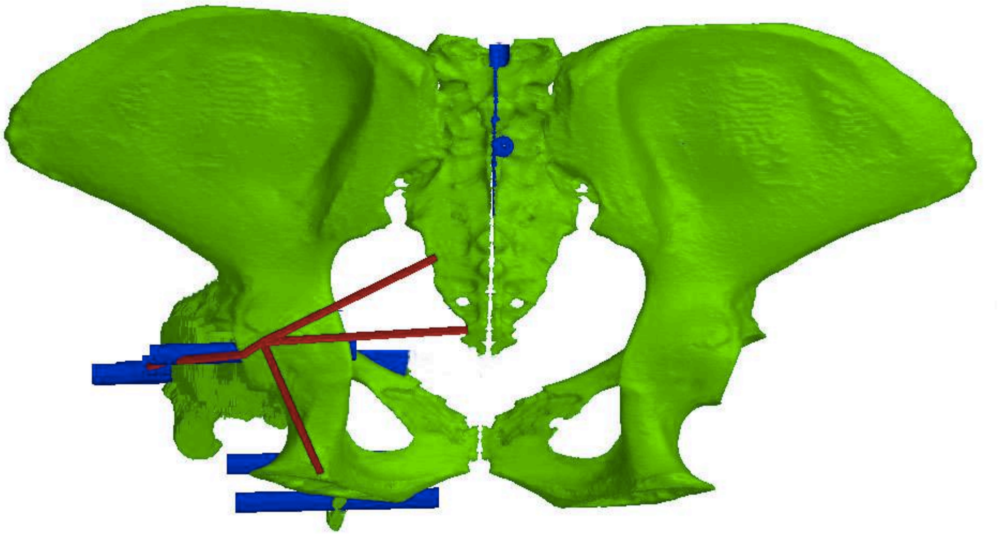


Figure 4. 2 Gluteus maximus sites of origin and muscle paths. Note there are three origins, which have been chosen because of the strong attachment to pelvis at these sites.



4.2.3 Collecting moment arm data

Each joint (hip, knee, ankle and all foot joints where it was possible) was flexed and extended in GaitSym, muscle lengths and joint angles being output continuously as data streams at each step- increment in the simulation. Moment arms for each muscle was calculated from muscle length changes and joint angle rotations using a custom written Matlab script as in previous studies (Bates and Schachner 2012; Bates et al. 2012a; Bates et al. 2012b; Maidment et al. 2014). If a muscle had more than one belly, the average moment arms would be taken. The moment arm for each muscle was summed, before dividing the summed value by the summed maximum moment arms possible about the joint to create a normalised summed moment arm. Figure 4. 3 shows how each the hip, knee and ankle were flexed. The foot joints are illustrated in more detail in Table 4. 3. The hip, being a ball and socket joint, was abducted/adducted at 0, 20 and 50°, and adducted at 20° (Figure 4. 4), and moment arms collected from each abduction/adduction posture. Studies have shown that the ankle joint is a multiaxial joint and not strictly a hinge joint (Siegler et al. 1988; Lundberg et al. 1989; Leardini et al. 1999). In this case the ankle was treated as a multiaxial joint (see Figure 4. 4; flexion-extension along x-axis and abduction-adduction along z-axis), as some abduction, of up to 10°, occurs during climbing in western lowland gorillas (DeSilva 2008) and thus moment arms were collected when the ankle was abducted to 0, 10 and 20°.

Figure 4. 3 (A) Hip, (B) knee and (C) ankle in flexion. Black arrows show direction of flexion.

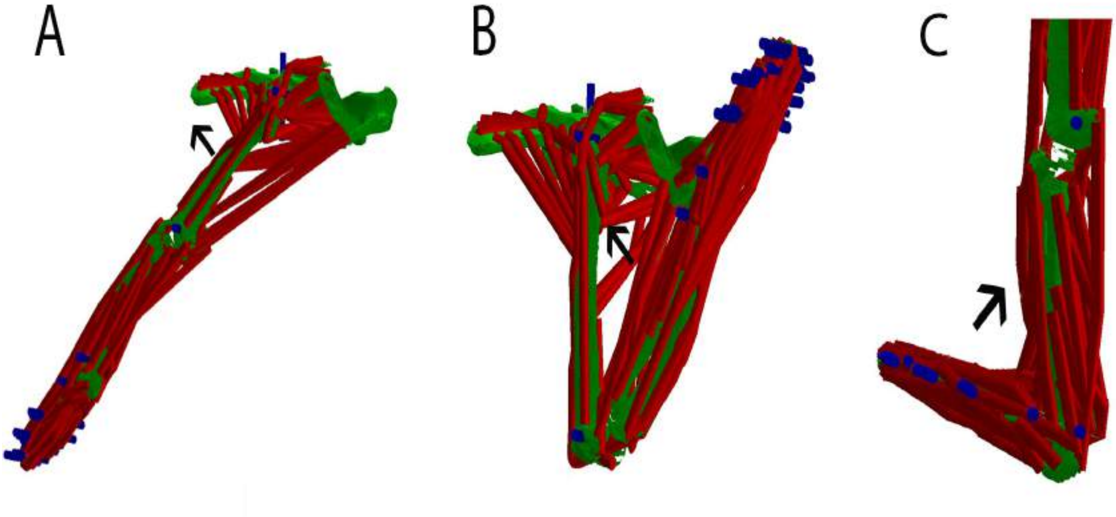


Figure 4. 4 From top left to right, hip at (A) 0°, (B) 20°, (C) 50° and (D) -20° abduction. Black arrow to the left shows direction of adduction, black arrows to the right show direction of abduction. Axis depicted in the bottom left corner is for an anterior view. Bottom (E) shows the two joint axis used in the ankle, flexion-extension (left) and abduction-adduction (right).

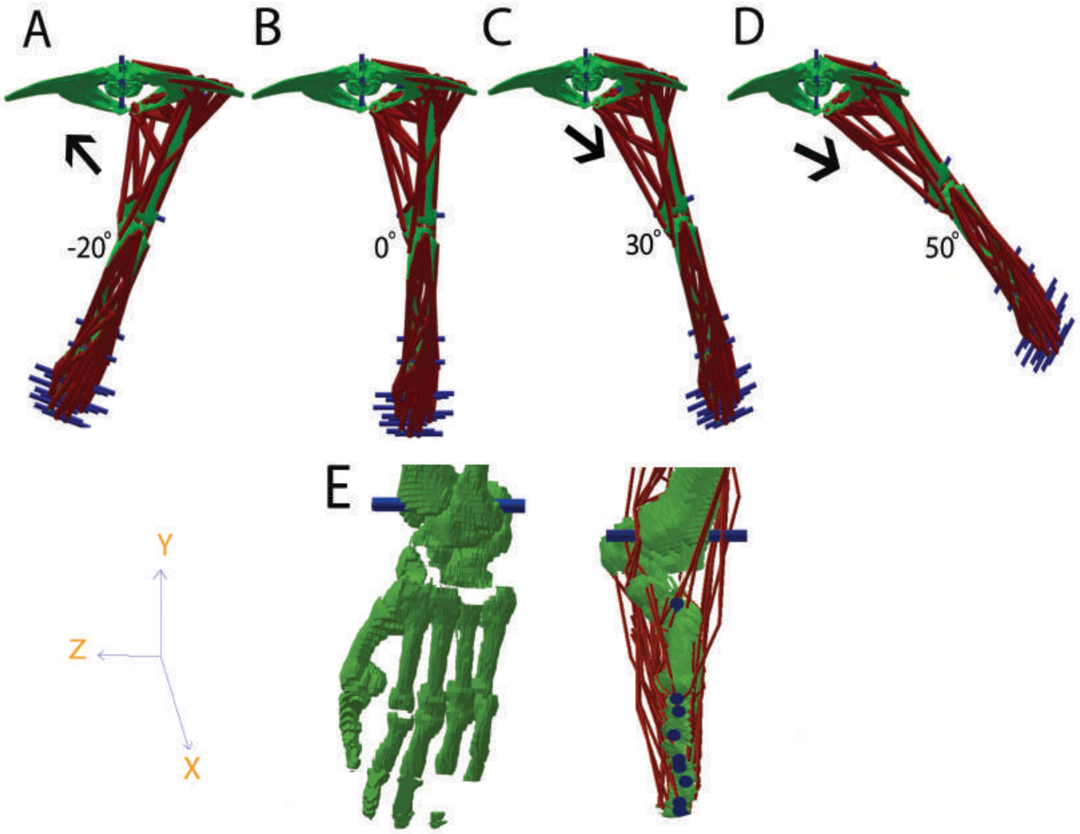


Table 4. 3 Foot joints and the corresponding segments involved.

Joint Name	**Segments involved**
Tarsometatarsal	‘Rearfoot and midfoot’, and ‘metatarsal’
Metatarsophalangeal	‘Metatarsal’ and ‘proximal phalanx’
Proximal interphalangeal	‘Proximal phalanx’ and ‘middle phalanx’
Distal interphalangeal	‘Middle phalanx’ and ‘distal phalanx’

In order to examine the effects of modifying origins/insertions on moment arms generated, a sensitivity analysis of the gastrocnemius lateral and medial head around the knee, and gluteus minimus medial head 3 and rectus femoris around the hip were carried out. The gastrocnemius was chosen as the origin of both heads were extremely close the knee joint, causing function to change from flexor to extensor at extreme postures of flexion. Thus the origins were moved superiorly by 0.01m, and moment arms were collected to examine the effects of the altered positions of the origins had on function. Rectus femoris was chosen as the origin was very close and inferior to the hip joint, causing function to change from flexor to extensor at extreme postures of flexion. Thus the origin was moved superiorly by 0.005m and 0.01m, and moment arms were collected to examine the effects of the altered positions of the origins had on function. Gluteus minimus medial head 3 was chosen as a benchmark for sensitivity analysis of muscles that were unlikely to change function at extreme postures as its origin and insertion were not in close proximity to the hip joint. The insertion was moved superiorly and inferiorly by 0.01m each, and moment arms were collected to examine the effects of the altered positions of the origins had on moment arms.

4.2.4. Collecting torque data

Torque, defined as the tendency of a force to rotate an object about an axis (Serway and Jewett 2004), is directly proportional to the moment arm and force applied. Therefore the formula for calculating torque at maximum isometric force is τ = PCSA x MA x 300 000 where PCSA is in m^2, MA is moment arm in m, τ is torque in Nm and 300 000 is the force per unit area (or maximum isometric stress) at maximum isometric contraction (Nm^{-2}). A broad range of values for maximum isometric stress is available in the literature (e.g. 100,000 – 1, 000, 000 Nm^{-2}) reflecting the highly variable contractile properties of vertebrate muscle, both within muscle groups and between individual species (Medler 2002). Values between 200,000-400,000 Nm^{-2} (Pierrynowski 1995; Zheng et al. 1998; Alexander 2003; Umberger et al. 2003; Westneat 2003) are widely reported for a range of species and muscles and as such 300 000 Nm^{-2} is commonly used as an average value in modeling studies (Hutchinson 2004; Bates et al. 2010b; Sellers et al. 2013). Torque was calculated for the hip, knee and ankle joints using the 3D model.

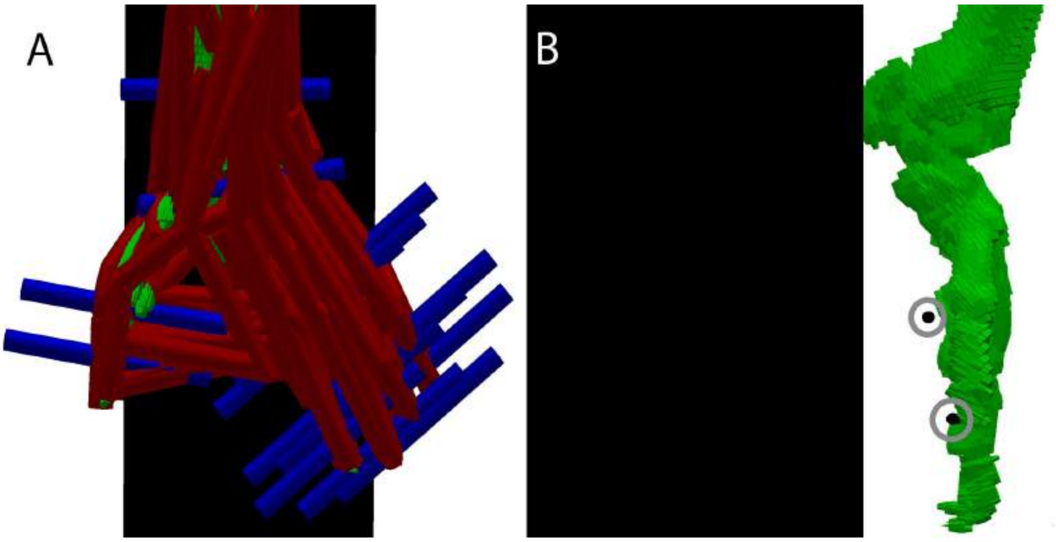
4.2.5 Incorporating kinematic and joint angle data into our moment arm and torque graphs

Watson et al. (2009) found that during bipedalism, gorillas extend their hips between 95° to 170°, their knees between 100° to 170°, and dorsiflex their ankles between 70° to 150°. Isler (2005) found that during climbing, when gorillas abduct their hips up to 54°, their hips are flexed at 54°, and when their hips are extended at 132°, their hips are adducted at 18°. Isler (2005) also found their knees to extend from 44° to 130° during climbing. DeSilva (2008) found that gorillas can abduct their ankles up to 10°, and dorsiflex their ankles up to 61° during climbing. These are all intersegmental angles and are therefore directly comparable to our data and are used herein to find out what moment arm values these angles coincide with in our data.

4.2.6 Collecting moment arm data with varying support sizes

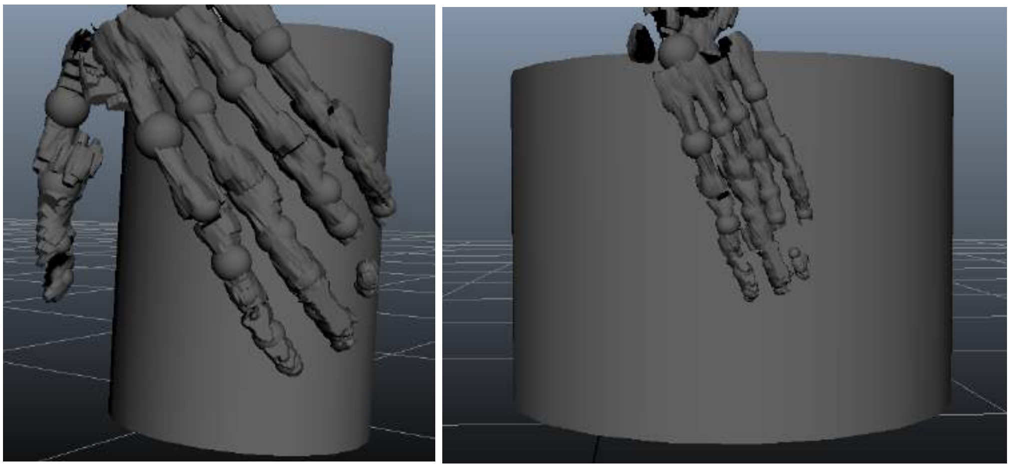
For metatarsal 1 and digit 1, a large vertical support cylinder 'geom' (25cm diameter) and small vertical support cylinder geom (12cm) were put into the hindlimb model in GaitSym (Figure 4. 5). A Geom is an element that is defined in the .xml file, just like a body/muscle/joint is. Therefore it has a specified position, and in our case this is just superficial to head of metatarsal 1 and head of distal phalanx 1. Geoms can generate multiple contacts with intersecting Geoms, generating an output log file that contains information for each contact. The ankle was abducted at 10°, as in climbing. Tarsometatarsal 1 and digit 1 joints were then simultaneously flexed/extended until the support cylinder came into contact with the geoms attached to the heads of metatarsal and distal phalanx 1. The output log file can be opened in Excel and specifies the time in which contact was made during the simulation and hence the corresponding joint angles can be found.

Figure 4. 5 (A) Anterior view of foot with small support geom and (B) medial view of foot with large support geom and geoms circled in grey attached to metatarsal 1 head and distal phalanx 1 head. Geoms are in black.



For metatarsals 2-5 and digits 2-5, Maya was used to determine the joint angle at contact for each joint between foot and support. Support cylinders of 4cm, 10cm, 20cm and 30cm in diameter were created in Maya (see Figure 4. 6). Metatarsals 2-5 and digits 2-5 were grouped together and rotated by a magnitude of 0, 35, 25 and 30 (for 4cm, 10cm, 20cm and 30cm supports respectively) along the x-axis about the tarsometatarsal 2 joint centre to account for abduction of the phalanges when grasping a support, as efficient grasping of a support requires tilting the tarsometatarsal 2-5 joints away from the midline, to ensure maximum contact between foot and support and hence stability. For each digit, the metatarsal was grouped with the phalanges, then rotated manually about the tarsometatarsal joint until the metatarsal head was in contact with the support. After which, the proximal phalanx was grouped with the middle and distal phalanges and rotated manually about the metatarsophalangeal joint until the proximal phalanx head contacted the support. This was repeated for the middle and distal phalanges of each digit. Angle of contact with support of each joint was then calculated in Excel by using trigonometry. Coordinates of the joint centres of the proximal and distal joint would provide lengths of the adjacent and opposite side of a triangle, from which the joint angle could be calculated from the inverse tangent of these sides. Once the contact joint angles were collected, they were then plotted on the moment arm graphs.

Figure 4. 6 Anterior view of foot with 10cm(left) and 30cm(right) support cylinders.



4.2.7 Comparison with Payne's data

PlotDigitizer was used to digitize the graphs from Payne et al. (2006), as Payne and colleagues did not have the raw data and exact numbers could not taken directly from the paper. In PlotDigitizer, a screen shot of the graph was taken and opened in PlotDigitizer, then the maximum and minimum points of the x and y axis were selected to calibrate the scale of the graph. After which, the points along the graph were clicked on, generating an output file that would contain the coordinates of these points. This output file was opened in Excel and then combined with our data that was already in Excel.

4.3 Results

4.3.1 Hypothesis 1

Joint angle ranges used for climbing will coincide with angles that correspond to higher hip moment arms than that of bipedalism as in western lowland gorillas, as vertical climbing forms a much higher proportion of their arboreal locomotion.

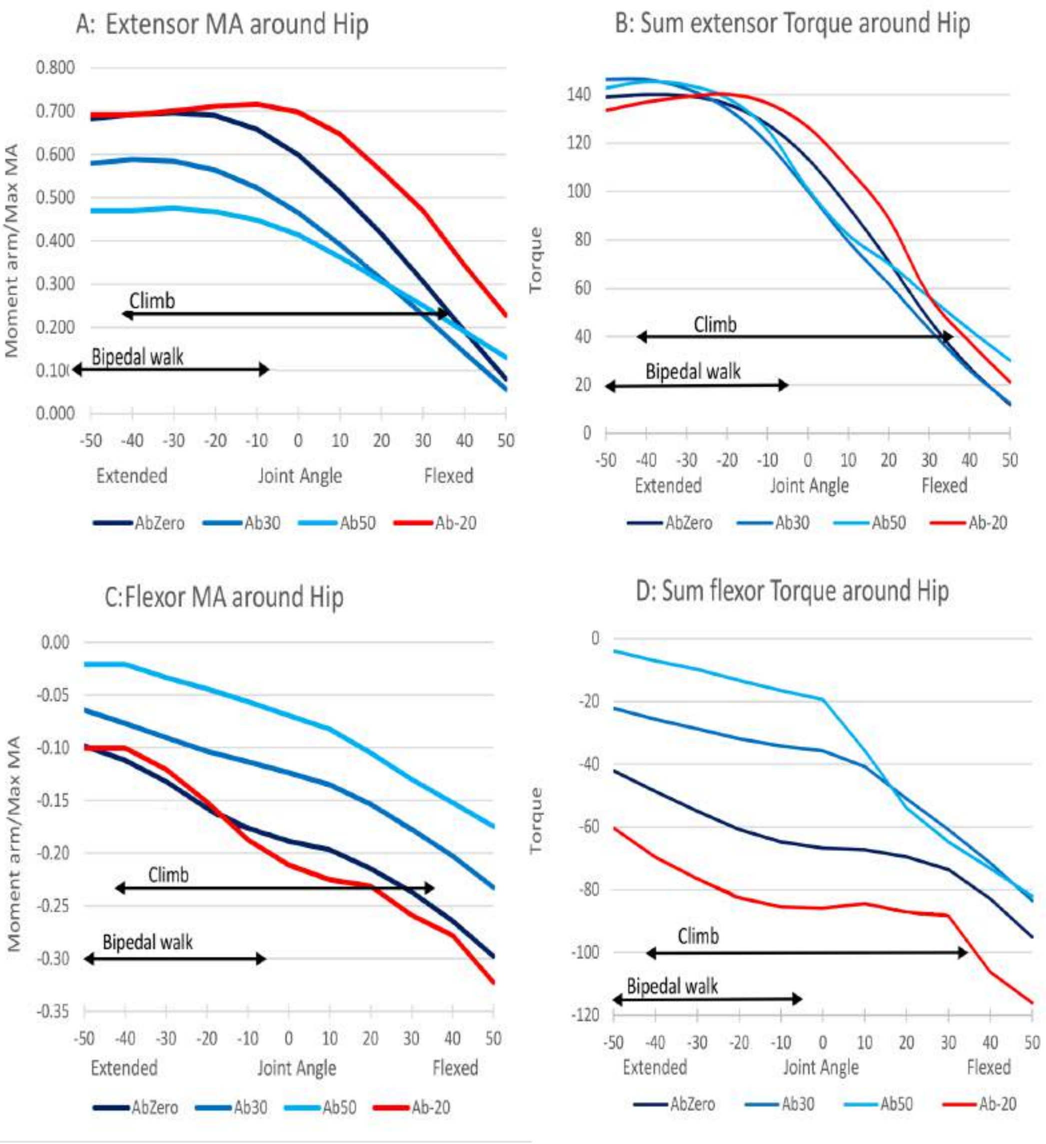
Data on the sum extensor and flexor moment arm and torque around the hip at several hip abduction angles is presented, and where possible bipedal walking and climbing kinematics are applied to the interpretation of the moment arm values

(Figure 4. 7). During climbing maximum hip flexion occurs at maximum abduction, and maximum extension occurs at minimum abduction (Isler 2005). Bipedal walking kinematics are taken from Watson et al. (2009), however no abduction angles are available for gorilla bipedalism in the literature and thus data from chimpanzee was used as a proxy, where abduction occurs up to 15° (DeSilva 2008).

Overall, extensor moment arm and torque decrease as the hip flexes, and the flexor moment arm and torque decreases as the hip extends. Differences between extensor moment arm and torque tend to occur at highly extended (-50°) or flexed positions (50°) (see Figure 4. 7A and B), respectively. At extended position (-50°), moment arm is higher by 45%, but torque is lower by 3.6%, when the hip is abducted at 0°, as compared to when the hip is abducted at 50°. This difference is most likely attributable to muscles medial to the hip joint. For example, when hip abduction is 0°, the summed extensor moment arm by the adductors (adductor brevis, adductor longus and adductor magnus) is at least 0.08m greater than when the hip is abducted at 50°. However this difference is not observed with torque, as shown by the similar torque values at extended position (-50°). This is a result of gluteus maximus that has a substantially higher torque (34.5Nm) and gluteus medius changing from flexor at 0° abduction to extensor at 50° abduction with 27Nm torque, despite most of the other hip muscles having lower torque when hip is abducted at 50° as compared to at 0°. At flexed position (50°), torque at 50° hip abduction is 100% higher than at 0° abduction. This is a result of gluteus medius having a high extensor torque (23.5Nm) when hip is at 50° abduction, and being a flexor instead of an extensor at 0° hip abduction. With regard to flexor moment and torque, these are consistently lower when hip is abducted at 50° than 0°. This is probably attributable in this case to muscles lateral to the hip joint. For example, when hip is abducted at 0°, gluteus minimus has a maximum flexor moment arm that is at least 0.03m more, and maximum torque 15Nm more, than when hip is abducted at 50°. Further, gluteus medius is flexor when hip is abducted a 0°, but changes to an extensor when hip is abducted at 50°.

Looking next at the flexion-extension kinematics for climbing, although when the hip is abducted at 50°, the extensor moment arm is relatively low at maximum flexion (50°), torque is relatively high (see Figure 4. 7A and B). Compared to climbing, bipedal walk coincides with relatively high values of extensor moment arm when the hip is abducted at 0° and at 20° (see Figure 4. 7A). In contrast, bipedal walking range coincides with lower flexor moment arm and torque when the hip is abducted at 0° and at 20° (see Figure 4. 7C and D). Flexor moment arm at maximum extension is relatively high (~-0.1m) when the hip is abducted at 0° and at -20° when compared to the rest (see Figure 4. 7C, ~-0.06m for when the hip is abducted 30°; ~-0.04m for when hip is abducted at 50°).

Figure 4. 7 A-D, Moment arm (in metres) and torque (Nm) at varying abduction angles around the hip. MA refers to moment arm. Extensor MA is positive, flexor MA is negative. Flexed joint angles are positive, extended are negative, 0° refers to neutral position. AbZero refers to hip abducted at 0°, Ab30 at 30°, Ab50 at 50° and Ab-20 at 20°. Black arrows depict ranges of joint angles used for bipedal walking and climbing. Range of hip extension in bipedal walking is -5° to -80° (Watson et al. 2009). Range of hip extension in climbing is 36° to -42° (Isler 2005).



Below data on the sum extensor and flexor moment arm and torques around the knee is presented, and where possible, known bipedal walking and climbing kinematics were applied to the moment arm values (Figure 4. 8). During climbing, and during bipedal walking, the knee is flexed from 50 to 136°**,** and from 10 to 80°**,** respectively. Both moment arms and torque follow similar trends. Extensor moment arms and torque are consistently higher than flexor moment arms. Extensor moment arms and torque decrease as the knee is flexed. Flexor moment arms decrease as the knee is flexed, and Figure 4. 9 shows that this is attributable to the gastrocnemius and popliteus becoming extensors at highly flexed postures of the knee. Thus climbing, which involves more flexed postures, corresponds with lower summed flexor and extensor moment arm and torque values than does bipedal walking, consistent with the trends observed in majority of individual muscles. Conversely, bipedal walking exclusively coincides with higher moment arm and torque values during a majority of the knee range motion. It must be noted that as the patella was modelled to be attached to the femur (no translation allowed), this might skew the moment arms slightly during knee flexion to be shorter than in reality as the patella would have been able move inferiorly or superiorly and hence away from the joint.

Figure 4. 8 Moment arm (in metres) and torque (Nm) around the knee. MA refers to moment arm. Extensor MA is positive, flexor is negative. 0° refers to neutral position, 140° refers to fully flexed knee. Black arrows depict ranges of joint angles used for bipedal walking and climbing. Range of knee extension in bipedal walking is 50° to 136° (Watson et al. 2009), and in climbing is 10° to 80° (Isler 2005).

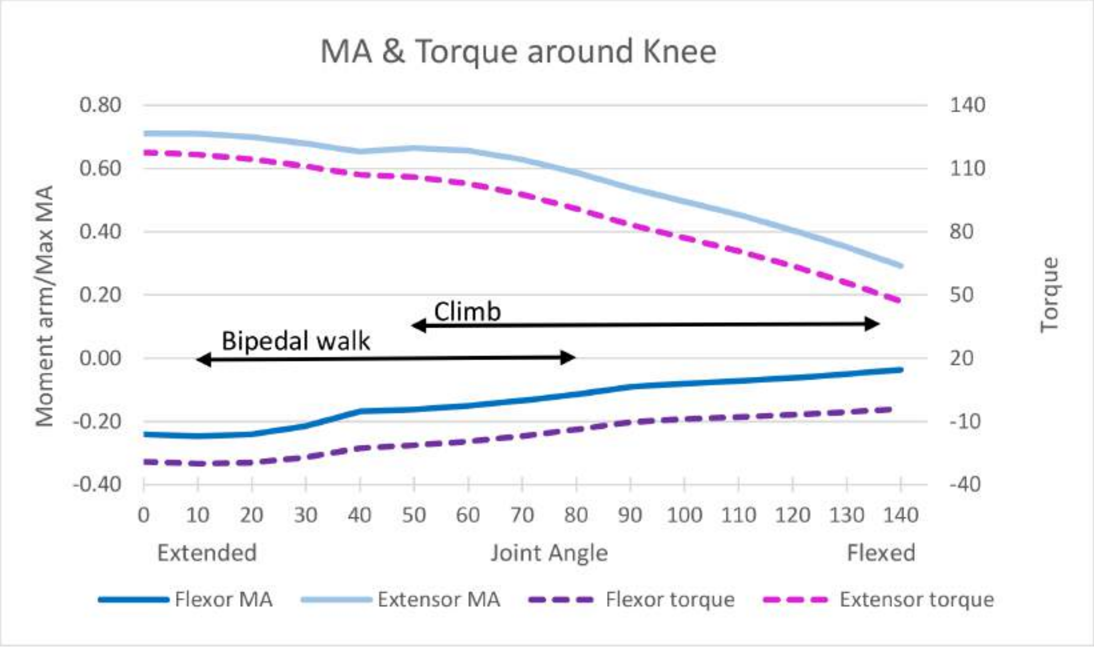
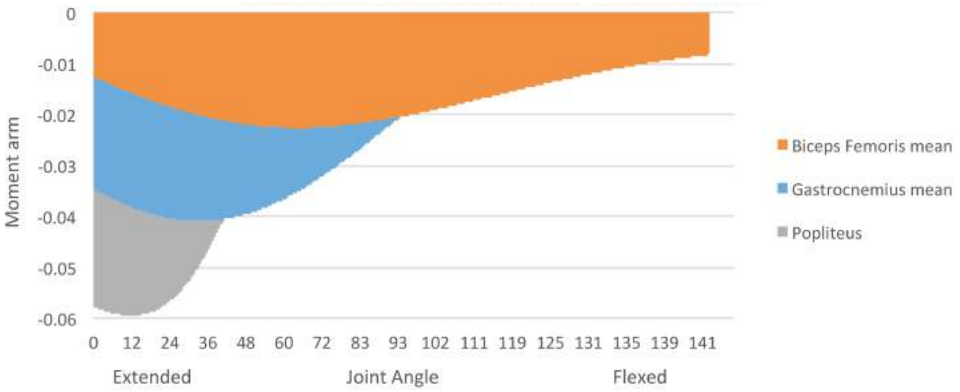


Figure 4. 9 Magnitude of individual flexor muscles' moment arm (MA – in metres) around knee. 0° refers to extended position, 140 to flexed position. "Mean" of biceps femoris and gastrocnemius indicates that the average MA was taken between muscle heads.

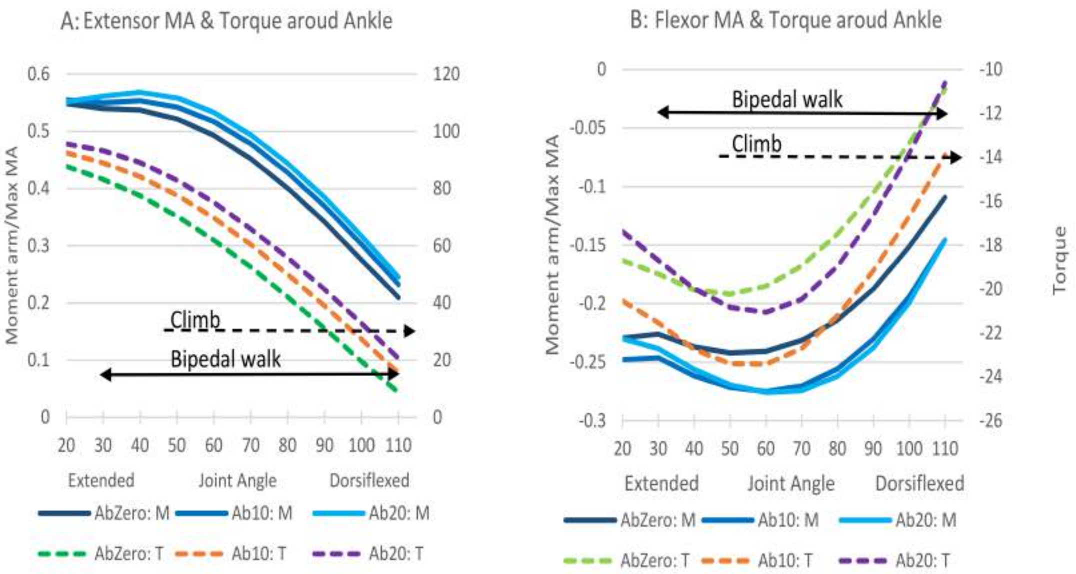


Finally, data on the sum extensor and flexor moment arm and torque around the ankle at different hip abduction angles is presented, and, where possible, data on bipedal walking and climbing kinematics is applied to interpretation of the moment arm values (Figure 4. 10). In climbing the ankle is abducted up to 10° and can be dorsiflexed by as much as 119° (DeSilva 2008). Bipedal walking involves dorsiflexion of 30° to 110° (Watson et al. 2009).

Torque (which takes into account PCSA) and moment arms follow similar trends. Climbing and bipedal walking use similar ranges of moment arm and torque values. Summed extensor and flexor moment arms and torque decrease as the ankle is dorsiflexed. The summed extensor moment arm peaks at ~40°, and torque peaks at a more extended position (~10°). Flexor moment arm and torque peak at relatively similar positions (50° for torque and 60° for moment arm). Little difference exists between 0° and 10° of abduction in extensor moment arms and torque through the range of joint angles tested here. For summed extensor moment arm and torque, overall values for when ankle is abducted at 0° is the lowest, followed by at 10° and at 20°. For summed flexor moment arm, from 30-100°, values for when ankle is abducted at 0° are the lowest, followed by 10° and 20° which have similar values. On the other hand, summed flexor torque is lowest when the ankle is abducted at 0°, followed by 20° then 10°. This is a result of tibialis anterior having a higher torque (2.8Nm) when ankle is abducted at 10° than at 20°. Extended joint angles, in bipedal walking (30° to 40°) corresponds with the high extensor moment arm (Figure 4. 10A), and as the ankle is dorsiflexed from this degree of extension (~60°), this corresponds also with high flexor moment arm and torque, as flexor moment arm and torque increases as dorsiflexion increases from 40° to 60° (Figure 4. 10B).

Figure 4. 10 A-B, Sum extensor (A) and flexor (B) moment arm (MA – in metres) and torque (Nm) at different abduction angles around the ankle. MA refers to moment arm, T torque; ankle is dorsiflexed as joint angle increases. AbZero refers to ankle abducted at 0°, Ab10 at 10°, Ab20 at 20°. Black arrows depict ranges of joint angles used for bipedal walking and climbing. Range of ankle dorsiflexion in bipedal walking is 30° to 110° (Watson et al. 2009), and in climbing the ankle is abducted up to 10° and can be dorsiflexed by as much as 110°(DeSilva 2008). Dotted black arrow

used for climbing as only maximum dorsiflexion angle is known, unlike in bipedal walking where the exact range is known.



4.3.2 Hypothesis 2

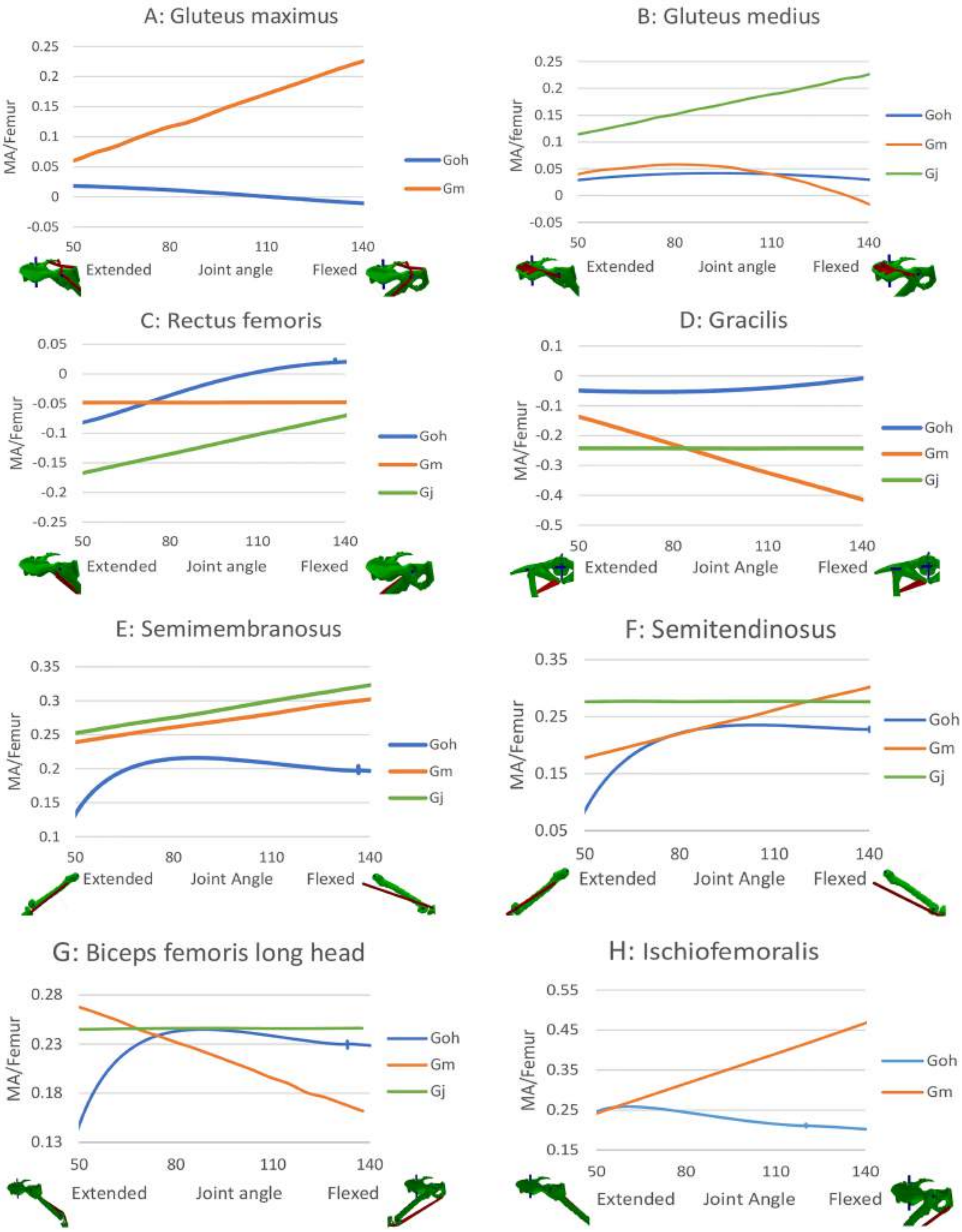
Results from the model would be non linear and vary in magnitude from Payne et al. (2006), especially for muscles that are more challenging to for motion in a single plane (lateral or medial to the joint) or account for muscle paths (irregularly shaped, restricted by retinaculum) as these problems will be taken into account through via points and wrapping surfaces in the 3D model.

Firstly the muscle moment arms around the hip (Figure 4. 11) are reported. There were substantial differences between data generated from the model and that of Payne et al. (2006). The most striking difference was that while moment arm-joint angle relationships from the model were all non-linear, all of Payne et al. (2006)’s muscles except gluteus medius showed linear relationships or constant values across the joint angles tested (Figure 4. 11A, C-H). The most substantial differences were for muscles with broad and irregularly-shaped attachments. For example, the gluteus maximus (Figure 4. 11A) and gluteus medius (Figure 4. 11B) where not only was the trend in the opposite direction, the difference in magnitude was close to 2 times in both muscles.

The other muscles that showed significant differences were muscles that were not directly above or below the hip joint. Gracilis muscle from the model came out as a much weaker flexor than Payne et al. (2006)’s (four times less). Biceps femoris long head and ischiofemoralis showed opposite trends.

The moment arm values of rectus femoris in Payne had a similar overall trend to the model, but differed in magnitude. Furthermore, the rectus femoris in the model changed functions from flexor to extensor as hip was flexed, in contrast to Payne et al. (2006)’s, which remained as flexors.

Figure 4. 11 A-F, Moment arms (in centimetres) around hip for Gluteus maximus, Gluteus medius, Rectus femoris, Gracilis, Semimembranosus, Semitendinosus, Biceps femoris long head and Ischiofemoralis. Goh refers to subject from this study. According to Payne et al. (2006), Gm refers to eastern, Gj to western lowland gorilla. MA/femur refers to moment arm divided by femur length to account for differences in body size. Joint angle at 0° refers to extended position, 120° to flexed position. Flexor moment is negative, extensor is positive.



Next the muscle moment arms around the knee (Figure 4. 12) are reported. All muscles show similar overall values with Payne et al. (2006)'s data except semitendinosus, nemius lateral and medial head, and vastus lateralis. However values from the model change in curvilinear manner over the range of joint motion versus the linear trends in Payne. Semitendinosus in Payne shows similar trend and linearity, but varies considerably in magnitude to the model data presented here. For the gastrocnemius lateral and medial heads, and semimembranosus their functions change between flexor and extensor, and this is not present in Payne et al. (2006)'s data. The gastrocnemius lateral and medial heads acting as an extensor is a result of the close proximity of these muscle origins to the knee joint, resulting in the muscle line of actions to cross inferior to the joint (see schematic drawing of muscle in Figure 4. 14). Vastus lateralis and biceps femoris long head in Payne et al. (2006) has opposite trend to that of the model (Figure 4. 12G).

Lastly, muscles moment arms around the ankle (Figure 4. 13) are reported. Similar magnitudes were found for FHL, tibialis anterior and triceps surae between the model and Payne et al. (2006)'s data. There were differences in terms of direction of trend (triceps surae, tibialis anterior, EDL, and FHL) and linearity where muscles from the model all show parabolas and Payne's are either a straight line or a constant.

Figure 4. 12 A-G, Moment arms (in centimetres) around knee for Biceps femoris (short head), Biceps femoris (long head), Gastrocnemius (medial head), Gastrocnemius (lateral head), Semimembranosus, Semitendinosus, and Vastus lateralis. Goh refers to subject in this study. According to Payne et al. (2006), Gm refers to eastern, Gj to western lowland gorilla. MA/femur refers to moment arm divided by femur length to account for differences in body size. Joint angle at 0° refers to extended position, 140° to flexed position. Flexor moment is negative, extensor is positive.

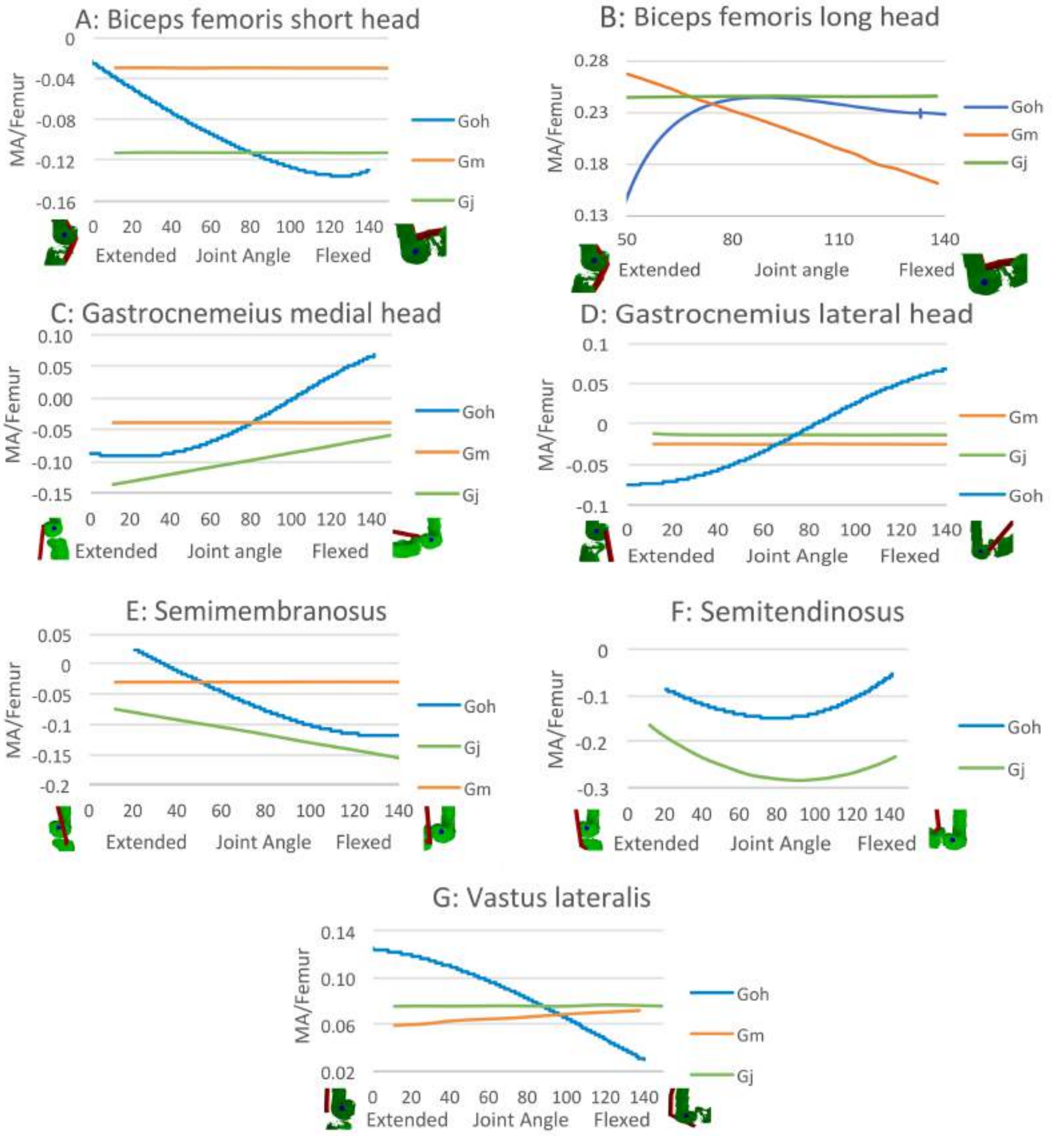
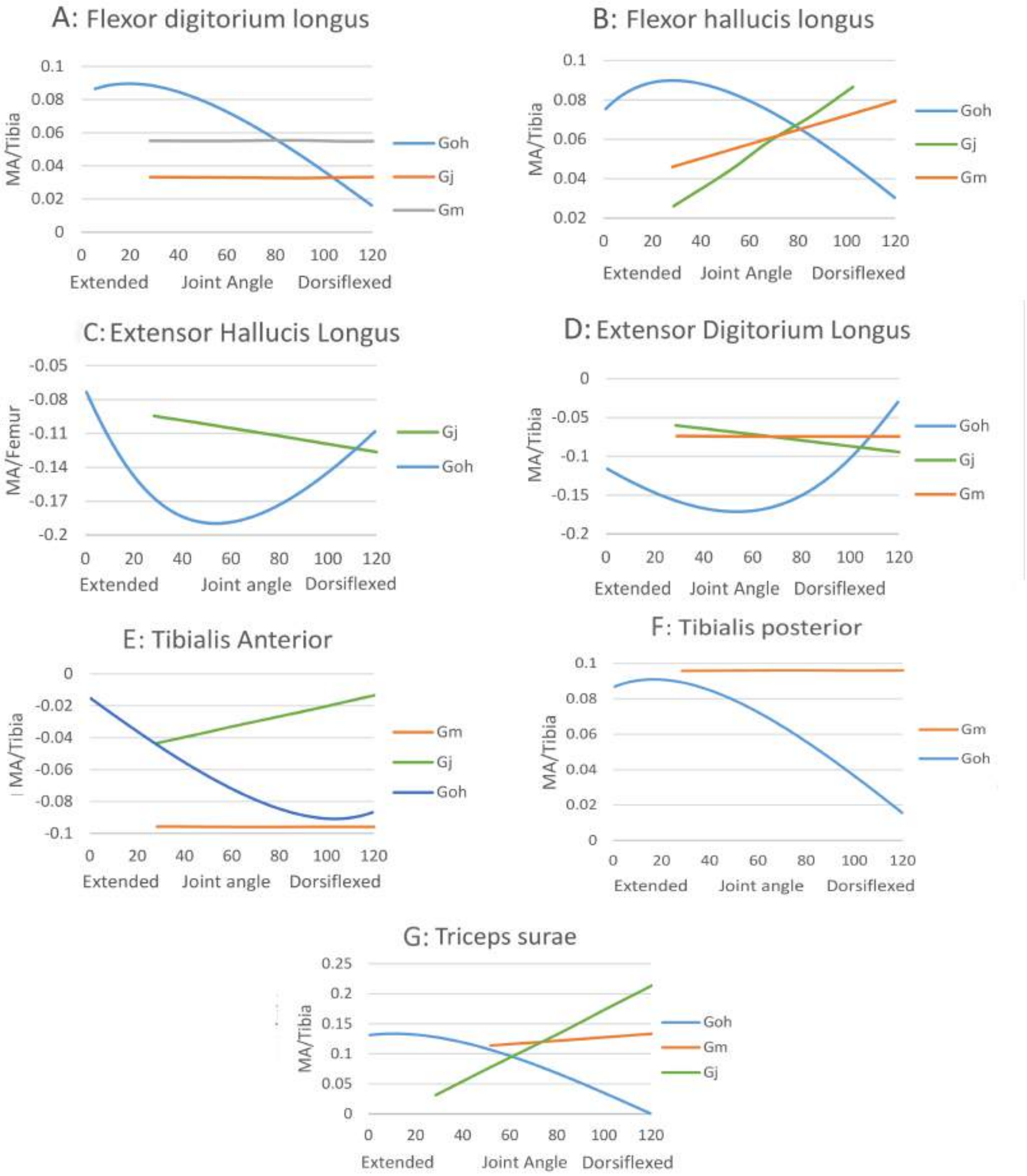


Figure 4. 13 A-G, Moment arms (in centimetres) around ankle for Flexor digitorum longus, Flexor hallucis longus, Extensor hallucis longus, Extensor digitorum longus, Tibialis anterior, Tibialis posterior and Triceps surae. Goh refers to subject in this study. According to Payne et al. (2006), Gm refers to eastern, Gj refers to western lowland gorilla. MA/femur refers to moment arm divided by tibia length to account for differences in body size. Joint angle at 0° refers to extended position, 150° to dorsiflexed position. Flexor moment is negative, extensor is positive.



A: Flexor digitorum longus

B: Flexor hallucis longus

C: Extensor Hallucis Longus

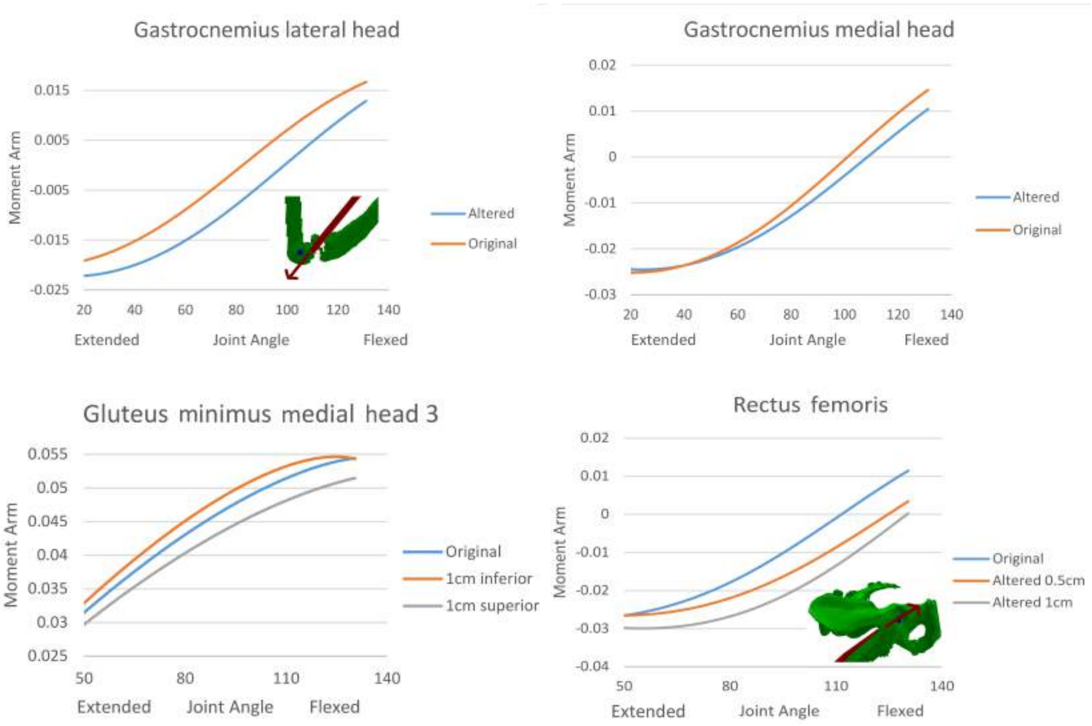
D: Extensor Digitorum Longus

E: Tibialis Anterior

F: Tibialis posterior

G: Triceps surae

Figure 4. 14 Sensitivity analysis for gastrocnemius lateral and medial head around the knee (top), and gluteus minimus medial head 3 and rectus femoris around the hip joint (bottom).



Altering the position of muscle origins for the gastrocnemius lateral and medial heads, rectus femoris, and location of the insertion of gluteus minimus medial head produced relatively modest changes to moment arms (Figure 4. 14), similar in terms of magnitude to muscles tested in (O'Neill et al. 2013). All three muscles retained similar shaped curves. This indicates that the output of this model is not overly sensitive to changes in structure or origins/insertions of muscles and hence the moment arms generated can be considered as accurate. The gastrocnemius and rectus femoris muscles change sign (signifying a switch from flexor to extensor moment) at highly flexed postures (approximately 90° for gastrocnemius and 100° for rectus femoris in our initial model; Figure 4. 14), owing to the close proximity of these muscle origins to the knee and hip joints, respectively. Altering the origins has caused the sign-change to occur at slightly more flexed positions (>100° for gastrocnemius and 120° for rectus femoris; Figure 4. 14). For gluteus minumus medial head 3, altering the insertion by 1cm superiorly and inferiorly caused the moment arms generated to be slightly higher and lower, respectively (Figure 4. 14) reflecting the increased/decrease distance from the hip joint centre.

4.3.3 Hypothesis 3

Flexor moment arm for some digits will not decrease significantly during flexion, thus allowing moment arms to remain high for grasping supports.

For interphalangeal 1 and tarsometatarsal 1 joints, there is minimal difference in the joint angle of contact and corresponding moment arms between large and small supports (Figure 4. 15 and Figure 4. 16). For digits 2 to 5, the contact angle becomes more flexed from digit 2 to 5 for all joints (Figure 4. 15, Figure 4. 17 and Figures S4. 1-3). This trend is most evident for the smallest support (4cm) and decreases as the support size increases (from 10cm to 20 to 30cm). See graphs for digits 4 and 5, where joint angles of contact are all positive (flexed), whereas in digit 3 the joint angles of contact are positive for 4cm and 10cm supports, negative for 20cm and 30cm supports. Overall, the flexor moment arm decreases as the joint is flexed, thus the contact joint angles of the smaller supports (4cm and 10cm) tended to coincide with smaller moment arm values.

The opposite to the overall trend of decreasing flexor moment arm as the joint is flexed is observed in three joints, namely interphalangeal 1 (Figure 4. 16B), metatarsophalangeal 2 (Figure 4. 17A) and proximal interphalangeal 3 (Figure S4. 1B) joints. At interphalangeal 1 joint, joint flexor moment peaks at 50° flexion, as not only does FHL have its highest moment arm at this position, but the transverse head of adductor hallucis brevis also acts as a flexor. Metatarsophalangeal 2 joint has plantar interosseous 2, FHL and flexor digitorum superficialis brevis moment arm that increase as flexion increases. Proximal interphalangeal 3 joint (Figure S4. 1B) has a flexor moment arm that peaks at 40° as the moment arm of FHL, FDL and FDP increases and dorsal interosseous 3 changes from extensor to flexor function as flexion increases. Distal interphalangeal 3 and metatarsophalangeal 5 joints have flexor moment arms that remain high throughout, as the flexor moment arm of FHL and FDL respectively remains high throughout. In fact, FDL moment arm peaks at 30° flexion at metatarsophalangeal 5 joint. Metatarsophalangeal 1 joint also has flexor moment arms that remain high throughout. At flexed positions, this was a result of FHL and FHB moment arms remaining high. At extended positions, although FHL and FHB decreased in moment arms, flexor moment arm manages to remain high due to contribution from adductor hallucis brevis transverse head, EHL and EHB.

Next, a comparison between flexor to extensor moment arms was carried out to determine the importance of flexion about each joint. Tarsometatarsal 1 to 5 joints (Figure 4. 15A-E), and metatarsophalangeal and interphalangeal joints around digits 1 (Figure 4. 16), 3 (Figure S4. 1A and B), 4 (Figure S4. 2) and 5 (Figure S4. 3) all have higher flexor than extensor moment arms. At metatarsophalangeal 1 joint (Figure 4. 16A), there is 0.5X higher maximum flexor moment arm and at interphalangeal 1 joint (Figure 4. 16B), there is 0.5X higher maximum flexor moment arm than maximum extensor moment arm. 0.027

Finally, how flexor moment arms varied mediolaterally across the foot was investigated. Most joints in digits 3 to 5 have higher flexor moment arms than the corresponding joints of digit 2. For example, tarsometatarsal 4 (Figure 4. 15D), tarsometatarsal 5 (Figure 4. 15E), all metatarsophalangeal 3 to 5 (Figure S4. 1A, S2A and S3), proximal interphalangeal 3 (Figure S4. 1B) and proximal interphalangeal 4 (Figure S4. 2B) joints. Within the metartasophalangeal 2 to 5 joints (Figure 4. 17A, S1A, S2A and S3), maximum flexor moment arm increases mediolaterally (from digit 2 to 5).

4.3.4 Hypothesis 4

Interossei will be effective flexors/extensors especially in digits 1 and 2, which are important for grasping objects.

Here the intrinsic muscles of the foot are taken to include the interrosei and the lumbricals. Digit 2 seems to have higher contribution of intrinsic muscles as flexors as compared to digits 3 to 5 (see Table 4. 4). At 30° flexion, digit 2 has three intrinsic muscles working as flexors at the its metatarsophalangeal joint, as opposed to only one or two in the other digits, and has the highest percentage contribution of intrinsic muscles to net flexor moments flexors. Exceptionally, the proximal interphalangeal joint of digit 4 shows a high percentage of contribution from the intrinsic muscles to flexor moment probably because of the small contribution of the long flexors (FHL, FDL, FDP), thus skewing the percentage contribution of the intrinsic muscles.

Table 4. 4 Intrinsic muscles that contribute as flexors and % contribution at 30° flexion.

Joint\Digit	2	3	4	5
Metatarso-phalangeal	Plantar interosseous 2, Lumbrical 2 & Dorsal interosseous 2 27%	Lumbrical 3 12%	Plantar interosseous 4 11%	Plantar interosseous 5 calcaneus head, 19%
Proximal inter-phalangeal	Plantar interosseous 2 23%	Dorsal interosseous 4 7%	Plantar interosseous 4 40%	-
Distal inter-phalangeal	Plantar interosseous 2 34%	Dorsal interosseous 4 2%	-	-

The plantar interosseous in digit 2 remains as a flexor mostly throughout all joint angles shown (Figure 4. 17), whereas for digits 3, 4 and 5 their corresponding interossei act as both flexors and extensors depending on the joint angle. For example, around metatarsophalangeal 3 to 5 joints (Figure S4. 1A, S2A and S3), the plantar interossei change from flexors to extensor as the joints are flexed. Lumbrical to digit 5 also follows the same trend around metatarsophalangeal 5 joint (Figure S4. 3).

The dorsal interossei do not follow a particular trend, but rather changes from flexor to extensor, or extensor to flexor as joint is flexed, or remains as completely a flexor or extensor. At metatarsophalangeal 2 joint (Figure 4. 17A), the dorsal interosseous changes from extensor to flexor as joint is flexed. At proximal interphalangeal 3 (Figure S4. 1B) and metatarsophalangeal 4 (Figure S4. 2A) joints, the dorsal interossei change from flexors to extensors as the joints are flexed. At metatarsophalangeal 3 (Figure S4. 1A) and proximal interphalangeal 4 (Figure S4. 2B) joints they remain as extensors, whereas at distal interphalangeal 3 joint (Figure S4. 1C) they remain as flexors.

From Figure 4. 17, it can be observed that the interossei in this study act upon tarsometatarsal, metatarsophalangeal and interphalangeal joints. Figure 4. 18 illustrates the position of interossei in the model, which crosses over tarsometatarsal, metatarsophalangeal and interphalangeal joints.

Figure 4. 15 A – E (continued on next page), Graphs showing muscle contribution to moment arms (MA – in metres) around tarsometatarsal joints. MA refers to moment arm. Y-axis: flexor moment is negative, extensor moment positive. X-axis: Negative angle refers to extended position, positive value refers to flexed position, and zero refers to neutral position. Ranges of joint angles used by the joint, from neutral position (0°) until the digit is in contact with the support, are represented by the arrows.

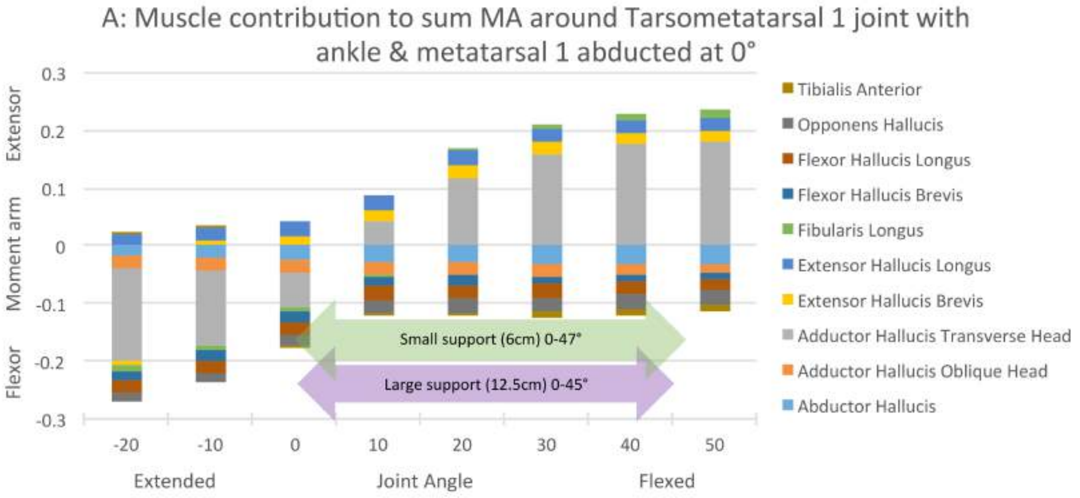
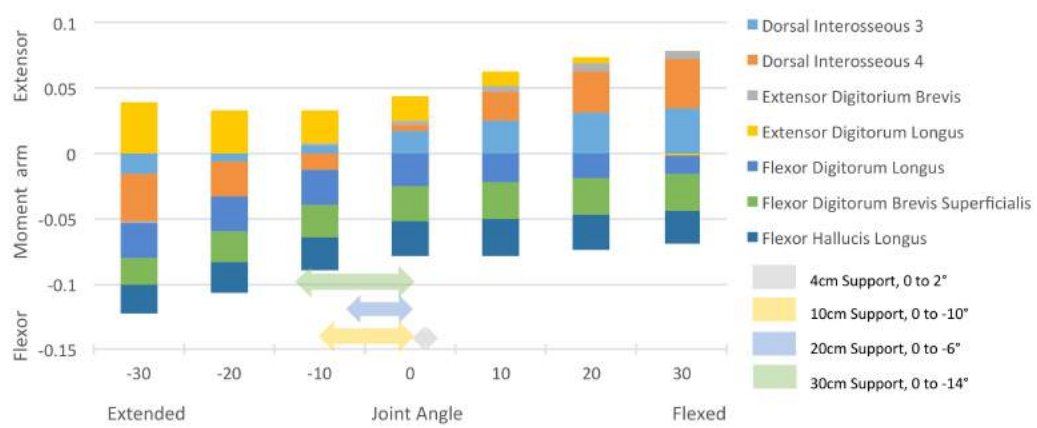
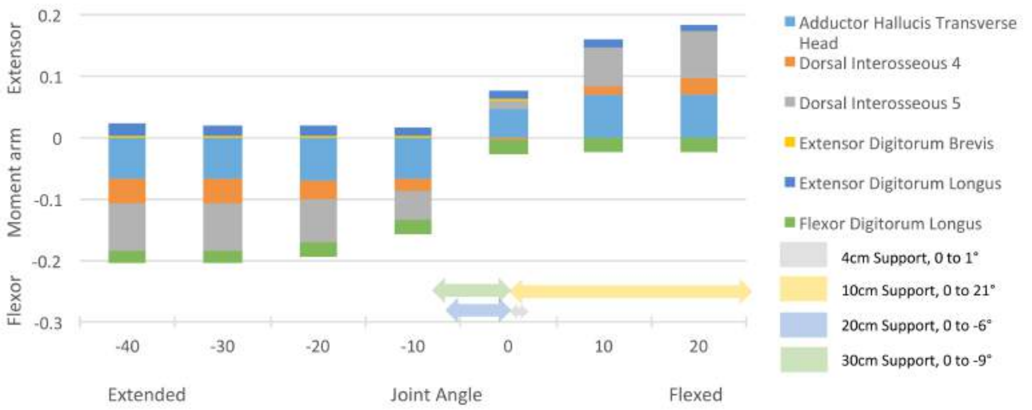


Figure 4. 15 A – E (continued), Graphs showing muscle contribution to moment arms (MA – in metres) around tarsometatarsal joints.


C: Muscle contribution to sum MA around Tarsometatarsal 3 joint


D: Muscle contribution to sum MA around Tarsometatarsal 4 joint

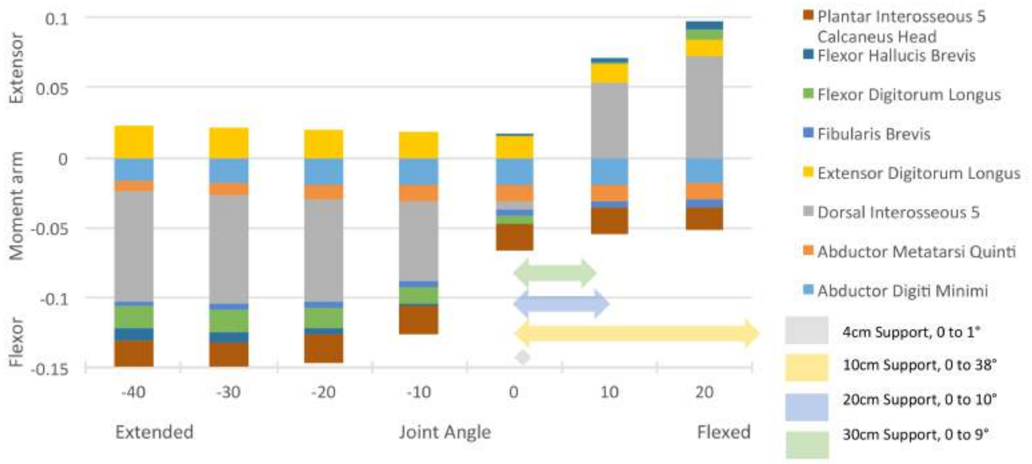

E: Muscle contribution to sum MA around Tarsometatarsal 5 joint

Figure 4. 16 A-B, Graphs showing muscle contribution portion to moment arms (MA – in metres) around tarsometatarsal 1 and interphalangeal 1 joints. Y-axis: flexor moment is negative, extensor moment positive. X-axis: Negative angle refers to extended position, positive value refers to flexed position, and zero refers to neutral position. Ranges of joint angles used by the joint, from neutral position (0°) until the digit is in contact with the support, are represented by the arrows.

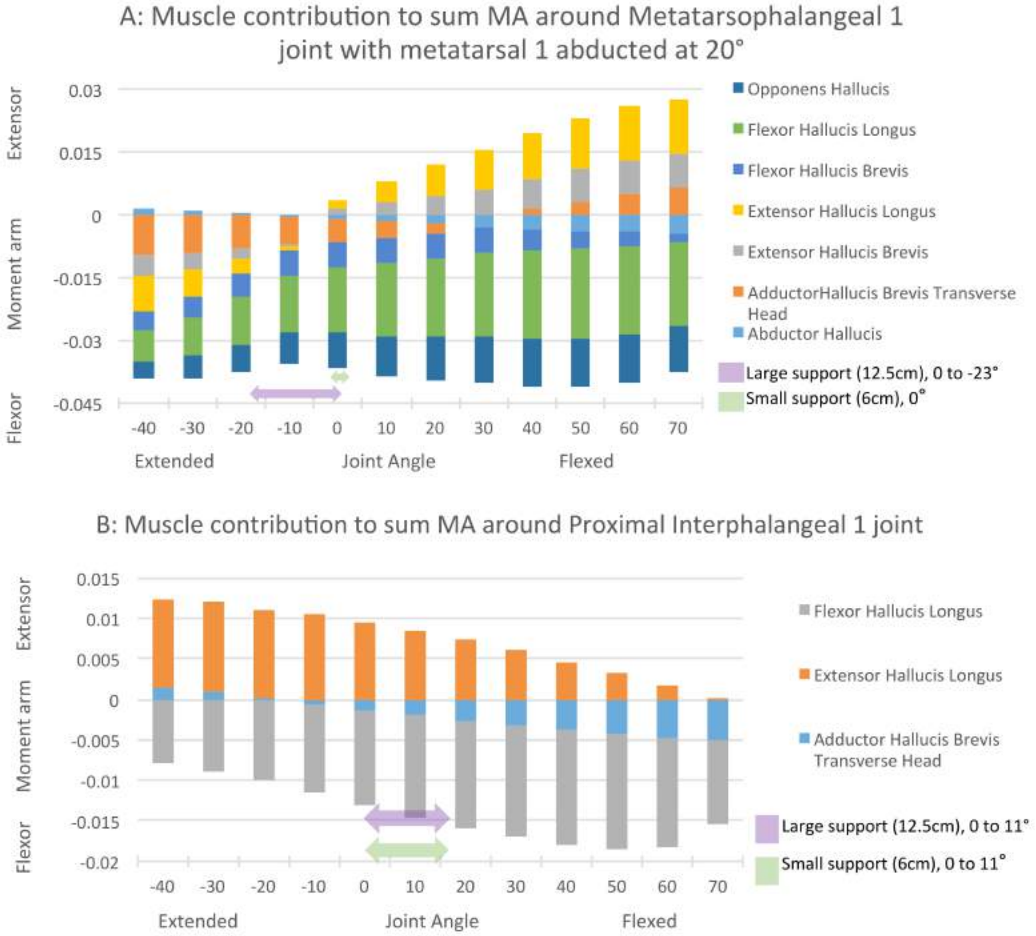
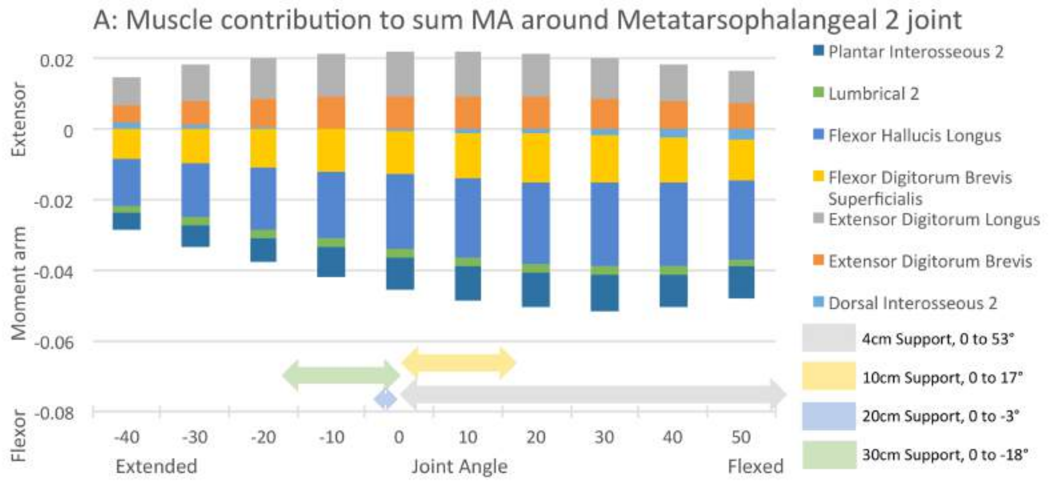
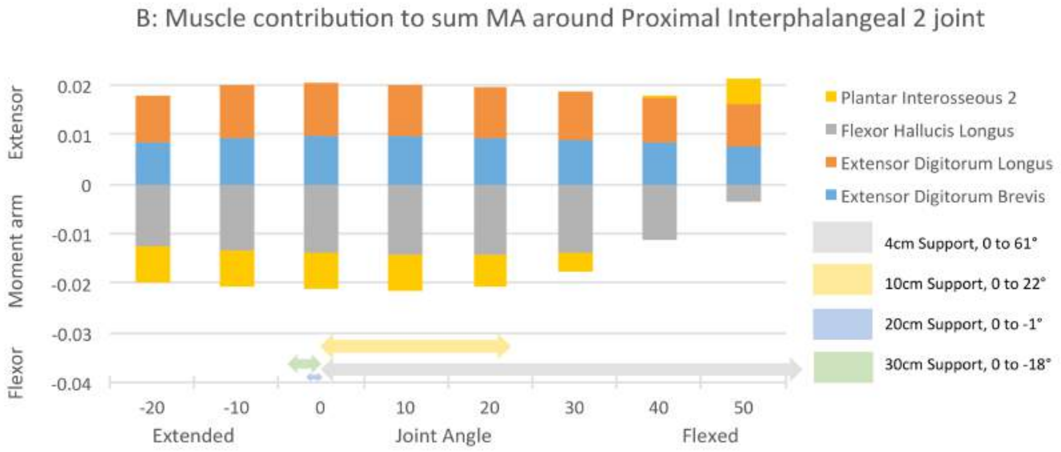


Figure 4. 17 A-C, Graphs showing muscle contribution portion to moment arms (MA – in metres) around tarsometatarsal 2 and interphalangeal 2 joints. Y-axis: flexor moment is negative, extensor moment positive. X-axis: Negative angle refers to extended position, positive value refers to flexed position, and zero refers to neutral position. Ranges of joint angles used by the joint, from neutral position (0°) until the digit is in contact with the support, are represented by the arrows.


A: Muscle contribution to sum MA around Metatarsophalangeal 2 joint


B: Muscle contribution to sum MA around Proximal Interphalangeal 2 joint

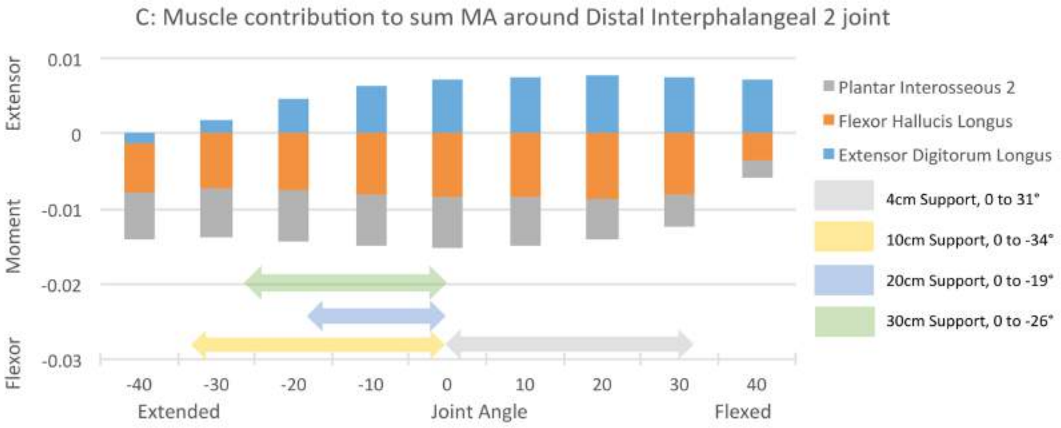

C: Muscle contribution to sum MA around Distal Interphalangeal 2 joint

Figure 4. 18 Dorsal (left) and plantar (right) interossei as seen in the model. Muscles are red.

4.4 Discussion

4.4.1 Hypothesis 1

Joint angle ranges used for climbing will coincide with angles that correspond to higher hip moment arms than that of bipedalism as in western lowland gorillas, as vertical climbing forms a much higher proportion of their arboreal locomotion.

Firstly, I would like to point out that in the model, I assumed maximum isometric contraction at all postures, which is a simplification for calculating muscle force. This is because muscle force would depend on velocity of contraction and whether the muscle is lengthening or shortening at that point in time. Looking at a previous study (Hutchinson et al. 2014) which compared calculated torque using the same assumption of maximum isometric contraction at all postures, versus incorporating length-tension properties, their results show that difference is mainly in magnitude, with trends remaining similar. This implies that when interpreting the torque results here, the magnitudes are likely to be overestimated, but patterns should generally be accurate and here I focus mainly on drawing conclusions from the patterns.

Around the hip, although the summed extensor moment arm when abducted at 50° is relatively low at maximum flexion (50°), the torque is relatively high (Figure 4. 7A and B). This is a result of gluteus medius being a good extensor at 50° and/ or the presence of large muscles (ie. gluteus medius) which could generate power and facilitate the forelimbs in pushing the body upward during climbing. That the summed flexor moment arm when hip is abducted at 0° at maximum extension is relatively high (~-0.1m) compared to the rest (~-0.06m when hip is abducted at 30°; ~-0.04m when hip is abducted at 50°) (Figure 4. 7C), would enable the gorilla to flex its hip easily from an extended position, whilst also keeping its body close to the support the during climbing (provided it keeps its knees flexed simultaneously with the hip). It has been shown (Isler 2005) that great apes keep their bodies close to the substrate during climbing, as it is safer and energetically more efficient to keep the body's centre of mass closer to the support during vertical climbing (Cartmill and Milton 1977; DeSilva 2008; Venkataraman et al. 2013b). As a result, the moment arm between the body's centre of mass and the support is decreased, reducing the torque and in turn the muscle forces needed in counteracting downward force (Cartmill and Milton 1977; DeSilva 2008; Venkataraman et al. 2013b).

Still looking at the hip muscles, compared to climbing, bipedal walk coincides with relatively high values of extensor moment arm and torque (Figure 4. 7). Bipedal walking involves more extended angles (-5° to -80°, see Figure 4. 7 and Watson et al. (2009)) than it does flexed angles, and the ability to extend the hip is important for efficient bipedal walking (Crompton et al. 2008). The results from the 3D model indicate that geometric arrangement of hip extensors in the gorilla are more mechanically effective for bipedal walking, and possibly even for bipedal postures used during displays/feeding, contradicting the suggestion of Payne et al. (2006) of an adaptation to maintain high moment arms at flexed postures around the hip (see above). Extensor moment arm (and torque) from the model peaks at extended postures (-20° to -40°) (Figure 4. 7A), and not at flexed postures like in Payne et al. (2006), Additionally, the adductors are important extensors when hip is abducted at 0°, which would assist extension during bipedal walking where hip is abduction angles are relatively low. Furthermore, the biped walking range coincides with lower flexor moment arm and torque than climbing. This difference suggests that flexion is less important than extension bipedal walking. This is expected, as bipedal walking involves more extended angles [-5° to -80°, see Figure 4. 7 and Watson et al. (2009)] than it does flexed angles, and the ability to extend the hip is important for efficient bipedal walking (Crompton et al. 2008). *Therefore the first hypothesis, that hip joint angle ranges used for climbing will coincide with angles that correspond to higher hip MAs than that of bipedalism as in western lowland gorillas, as vertical climbing forms a much higher proportion of their arboreal locomotion, only holds true for the hip flexors.* With regards to extensors, data from the model suggests that gorillas may have retained some abilities to extend the hip which facilitates orthogrady. However, from a strictly biomechanical perspective it could be argued that this could simply be a result based on geometric inevitability as climbing utilises a larger range of joint angles, and especially flexed angles, which would result in lower moment arms (see patterns of extensor moment arm versus joint angles in a wide range of vertebrates in (Brown et al. 2003; Bates and Schachner 2012; Bates et al. 2012a; Bates et al. 2012b; O'Neill et al. 2013; Hutchinson et al. 2014; Maidment et al. 2014; Bates et al. 2015). Typically in all tetrapods as the hip is flexed, the extensors will be pulled towards the joint, hence decreasing the distance between the muscle line of action and the joint. However from an ecomorphological and adaptive perspective the result is the same, as a capacity for effective bipedalism is the result. Further moment arm data around the hip in other ape species would be valuable in this respect**.**

The knee flexor moment arm and torque increase as knee is extended, which is unexpected, contrary to patterns observed in other joints, where extension often pulls the flexors towards the joint, in turn decreasing the moment arms and hence torque. This trend can be explained by the gastrocnemius and popliteus losing their flexor function at flexed positions as shown in Figure 4. 9. This is a result of the position of their origins, which were very close (within 0.01m) to the functional axis of the joint, making them lose their flexor function at flexed postures (gastrocnemius: >90°, popliteus: > 40°) (see schematic drawing in Figure 4. 14). To illustrate further importance of extension at the knee, extensor moment arm and torque is consistently higher than flexor moment arm. Furthermore, (Zihlman et al. 2011) has shown that gorillas have larger knee extensors than flexors, for propulsion and stability, lending more evidence to the importance of knee extension in gorilla locomotion. All of this would aid in mechanically efficient bipedal walking, which involves mainly extended postures [10 to 80°, see Figure 4. 8 and Watson et al. (2009)] and in extending the knee during climbing. Extensor moment arm and torque decrease as the knee is flexed as expected, as flexing the joint would tend to pull the extensors nearer to the joint. For both extensor and flexor moment arm and torque, bipedal walking coincides with higher values of moment arm and torque than climbing. Therefore this suggests that not only is the knee capable of efficient and powerful extension, but that the knee is more efficient in bipedal walking than climbing. *<u>Subsequently the first hypothesis, that knee joint angle ranges used for climbing will coincide with angles that correspond to higher knee moment arms than that of bipedalism as in western lowland gorillas, as</u>*

vertical climbing forms a much higher proportion of their arboreal locomotion, is not supported by data from the model. Few possibilities exist as to why this is so, firstly it is likely that because climbing involves more flexed angles than bipedalism, and flexed angles result in lower moment arms for extensors (as the muscles are pulled towards the joint) and flexors (as the muscles are pushed inwards and towards the joint). Secondly, it is also possible that other variables such as stability or agility are more important than energetic efficiency and power for climbing. Thirdly, perhaps the gorilla has retained ancestral traits for orthogrady, but again more interspecies comparison needs to be carried out before this can be certain.

At the ankle, extensor and flexor moment arm and torque trends decrease as ankle is dorsiflexed. This is expected as the muscles that dorsiflex the foot will be driven/pushed closer to the joint centre, and the muscles that plantarflex the foot will be pulled towards/flattened against the joint, with increasing dorsiflexion. That there is minimal difference in extensor moment arms and torque between the ankle abducted at 10° or at 0° (Figure 4. 10A), and that for flexor moment arm and torque, values are higher when ankle is abducted at 10° than when at 0° or 20° (Figure 4. 10B), would suggest that ankle abduction during climbing does not compromise efficiency and power of the extensors and in fact increases the efficiency and power of flexors around the ankle. As the relatively high extensor moment arm occurs at a relatively extended posture (40°) (Figure 4. 10A), and the peak flexor moment arm and torque occurs at a less extended posture (60°) (Figure 4. 10B), this enables the extensors of the stance leg to effectively extend the ankle during bipedal walking (just before maximum extension at 30°) to propel the swing leg forward, and the flexors at 60° to be effective in dorsiflexing the foot during swing phase. At maximum dorsiflexion for climbing (119°) and bipedalism (110°), bipedalism coincides with higher extensor and flexion moment arms and torque than climbing. This indicates that the kinematics of bipedalism coincides more with optimal extensor moment arms than with torque, and also coincide with optimal values of both flexor moment arm and torque. Therefore, *the first hypothesis, that joint angle ranges used for climbing will coincide with angles that correspond to higher MAs than that of bipedalism as in western lowland gorillas, as vertical climbing forms a* *much higher proportion of their arboreal locomotion, does not hold true.* This suggests that the ankle is not more adapted to one locomotor mode more than the other, in terms of muscle moment arms. This can arise if the joint angles utilized between locomotor modes do not differ substantially (in this case only for 8° at maximum dorsiflexion).

From the broadly similar trends seen in the results here for the hip, knee and ankle, it can also be concluded that torque and moment arms are mostly equally suggestive of mechanical optimisation for bipedal walking. This result is driven by geometric constraints that favour higher moment arms (and subsequently torques) in the more extended postures typically used in upright bipedal walking. Only in the case of ankle extensors did torque diverge from the trend seen in moment arms, with torque appearing less optimal or predictive of bipedal walking.

4.4.1 Hypothesis 2

Results from the model would be non linear, unlike the data of Payne et al. (2006), and muscles that are irregularly shaped, restricted by retinaculum, and/or lateral or medial to the joint would elicit different moment arms because of the different methodologies.

Substantial differences were found with Payne's moment arm data. Firstly, moment arms predicted by the model were neither straight lines nor constants, like most of Payne's, but instead were always curvilinear. Highly curvilinear trends for moment arm versus joint angle curves are found wherever the methodological approach incorporates broadly realistic constraints on 3D muscle paths, as seen in earlier computational (Pigeon et al. 1996; Delp et al. 1999; Hutchinson et al. 2005; Ogihara et al. 2009; Bates et al. 2012b; O'Neill et al. 2013; Hutchinson et al. 2014; Maidment et al. 2014) and experimental studies (Young et al. 1992; Graham and Scott 2003; Ackland et al. 2008; Michilsens et al. 2010). These discrepancies can be explained by the differences in method used to collect moment arms; the specific tendon travel method approach used by Payne et al. (2006) frequently yields linear relationships for a range of muscles in a variety of taxa (Thorpe et al. 1999; Smith et al. 2007; Channon et al. 2010). This is a product of the fact that in this version of the method muscles were substituted with strings that were attached to a load, hence when the joint is flexed/extended, the string would remain taut and in the case of a flexor, would be gradually lifted away from the joint as the joint is flexed, producing a linear graph. However in reality, this does not happen as the muscle will become loose and get pushed towards the joint. Also any retinacula between origin and insertion were not accounted for in the tendon travel method. In the computer model here, such constraints on muscle paths were accounted for to a degree through the use of via points and wrapping surfaces. These constraints may also account for the large differences in magnitude of some muscles - see hip: all muscles except biceps femoris long head (Figure 4. 11); knee: gastrocnemius medial and lateral heads, semitendinosus and vastus lateralis (Figure 4. 12C, D, F and G); ankle: FDL, EHL, EDl and tibialis posterior (Figure 4. 13A, C, D and F).

Muscle shape also appears to have contributed to differences in our results relative to those from Payne et al. (2006). As shown here, gluteus maximus and gluteus medius (Figure 4. 11A and B), are both wide and irregularly shaped, and are therefore, inherently difficult to represent accurately using a single straight line, as in Payne et al. (2006). The complexity of muscles is important when studying muscle function as shown by Ackland et al. (2008) which demonstrated that sub-regions within the same muscle could have different functions. In the 3D model here, I was able to represent distinct regions with their own muscle path, with customised non-linear behaviour specified by via points and/or wrapping surfaces. Related to this, differences between our data and that of Payne et al. (2006) were more modest for long and thin muscles. Muscles that were thin and long, (knee: biceps femoris long and short heads, gastrocnemius medial head; ankle: tibialis anterior, FHL and triceps surae) showed broadly similar values in magnitude (Figure 4. 12A-C and E and 13B, E and G respectively). Also with rectus femoris, semimembranosus and semitendinosus around the hip, similar trend direction was found at flexed positions (Figure 4. 11C, E and F).

Given their relative origins and insertions, some limb muscles would be expected to change their function as the limb is flexed and extended (Arnold and Delp 2000;

Ackland et al. 2008; Williams et al. 2008; Channon et al. 2010; Michilsens et al. 2010; O'Neill et al. 2013; Hutchinson et al. 2014). For example, changes in function were found for semimembranosus at the knee (Figures 4. 12) as joint angle was varied. However, these expected effects are not seen in the data of Payne et al. (2006) and are difficult to explain in ways other than experimental error (e.g. human error when flexing/extending the limb in an experimental set up) or bony protuberances that were not accounted for ie. patella. It is unlikely that other methodological approaches and simplifications, such as maintaining all non-active joints in the neutral posture, are responsible for differences in the results as these were standardised between our model and the experimental approach of Payne et al. (2006b).

Payne et al. (2006) suggested that the increased moment arms at flexed positions found in muscles such as gluteus maximus, gluteus medius, gracilis, semimembranosus and semitendinosus around the hip (see Figure 4. 11A, B and D-F) to an adaptation to vertical climbing and arboreal quadrupedalism as these locomotor modes require the maintenance of flexed postures. However the results in this study contradicts this suggestion by Payne et al. (2006), as the moment arms of gluteus maximus, gluteus medius and gracilis in the model did not increase in flexed postures (see Figure 4. 11A, B and D). To my knowledge, no other study of muscle moment arms in terrestrial tetrapods has found whole-scale stabilization or increases in extensor (anti-gravity) muscle moments and torques in flexed limb postures. The tendency for the moment arms of hip extensors such as gluteus maximus, gluteus medius, semimembranosus and semitendinosus to decrease with increasing flexion appears to be a fundamental geometric constraint, as these muscles will be pulled towards the joint as the hip is flexed, thus decreasing the distance from the muscles’ lines of action to the joint centre and hence the moment arms (see Figure 4. 11A, B, E and F). This pattern is also observed in O'Neill et al. (2013), where hip extensors such as gluteus maximus proprius, semimembranosus and semitendinosus decrease in moment arms as hip is flexed, and similarly in human studies (Hoy et al. 1990; Visser et al. 1990) had decreasing moment arm with increasing knee flexion. This is theoretically not possible unless there is a bony protrusion/soft tissue that pushes the muscle away as the knee is flexed. In this study and other studies (Visser et al. 1990; Spoor and Van Leeuwen 1992; Krevolin et al. 2004), similar knee extensors are pulled towards the joint as the knee is flexed, causing moment arm to decrease with increasing flexion. This gives more reason to attribute the increased moment arms of hip extensors at flexed postures to error. In the absence of a clear anatomical mechanism responsible for maintaining or increasing extensor moment arms at flexed postures I suggest that the 3D model here, with its increased anatomical detail, provides more accurate qualitative and quantitative representation of muscle moment arms in the gorilla.

The most accurate way of accounting for muscles that are irregularly shaped and that have complicated muscle paths would be to use MRI images, which would enable entire muscles to be separated and digitized accurately, then superimposed onto the bone mesh. For example, Arnold and Delp (2000) used MRI to guide origin and insertion locations of muscles onto the skeletal model.

Therefore the second hypothesis, that results from the model would be non linear, unlike Payne's data and muscles that are irregularly shaped, restricted by retinaculum, and/or lateral or medial to the joint would elicit different MAs because of the different methodologies is supported.

4.4.3 Hypothesis 3

Flexor moment arm for some digits will not decrease significantly during flexion, thus allowing moment arm to remain high for grasping small supports.

That the joint angles of contact become more flexed between digits 2 to 5 may be understandable in terms of an observed mediolateral decrease in displacement between the ankle joint and the distal tips of the phalanges (when grasping a support). For example the distance from the distal tip of digit 2 to the ankle joint is larger than the distance from the distal tip of digit 5 to the ankle joint as digit 5 is flexed more than digit 2 around the support during grasping. It is noteworthy that there are higher maximum flexor moment arms than extensor moment arms for digits 1, 3, 4 and 5 (Figure 4. 16 and S4. 1-3), and that the maximum flexor moments increase mediolaterally (from digit 2 to 5). Further, tarsometatarsal 5 joint has several flexors attaching to it, such as the plantar interosseous, flexor hallucis brevis, fibularis brevis, abductor metatarsi quinti and abductor digiti minimi (Figure 4. 16E), giving tarsometarsal 5 higher maximum flexor moment arm than tarsometatarsal 2 to 4 joints (Figure 4. 16B-C). The FDL moment arm also peaks at 30° flexion, at metatarsophalangeal 5 joint (Figure S4. 3). These findings suggest that the capacity to generate flexor moments increases mediolaterally between the digits, which follows the same trend in contact joint angles (increasingly flexed contact joint angles mediolaterally between digits 2 to 5 as mentioned before) and hence provide powerful grasping ability. *Thus the third hypothesis that the flexor MA for some digits will not decrease significantly during flexion, thus allowing MA to remain high for grasping small supports is supported by data from the model as shown in metatarsophalangeal joint 5.*

An overall trend for flexor moment arms to decrease as flexion increases (Figure 4. 15, 16B and C, S1A and S2), and a preference for smaller supports (<20cm) for vertical climbing in wild gorillas (Chapter 3 page 89 in this thesis), would suggest that moment arms are not an important determinant of support size preference as smaller supports are associated with more flexed positions and hence lower flexor moment arm. That some joints show opposite trends, such as proximal interphalangeal 1 and 3 (Figure 4. 16B and S1B), and metatarsophalangeal 2 (Figure 4. 17A) joints, could be a result of placing viapoints slightly further from or nearer relative to the joint axis as even a difference in millimetres will alter the data. For example, if FDL had a via point just above the metatarsophalangeal 2 joint that was slightly higher than its equivalent via point above the metatarsophalangeal 3 joint, this would cause the muscle line of action across metatarsophalangeal 2 joint to be lifted higher or more superficially when flexed, as compared to in metatarsophalangeal 3 joint.

The importance of flexion for digit 1 is shown by higher flexor than extensor moment arms at metatarsophalangeal 1 and interphalangeal 1 joints (Figure 4. 16), and by the maintenance of higher flexor moment arms throughout joint flexion/extension at metatarsophalangeal 1 joint, aided presumably by adductor hallucis brevis. It is possible that this arrangement enables effective flexion and hence grasping of supports. *Thus the third hypothesis that the flexor moment arm for some digits will not decrease significantly during flexion, thus allowing moment arm to remain high for grasping small supports is supported by data from the model, as shown in metatarsophalangeal 1 joint.*

4.4.4. Hypothesis 4

Interossei will be effective flexors/extensors especially in digits 1 and 2 which are important for grasping small objects

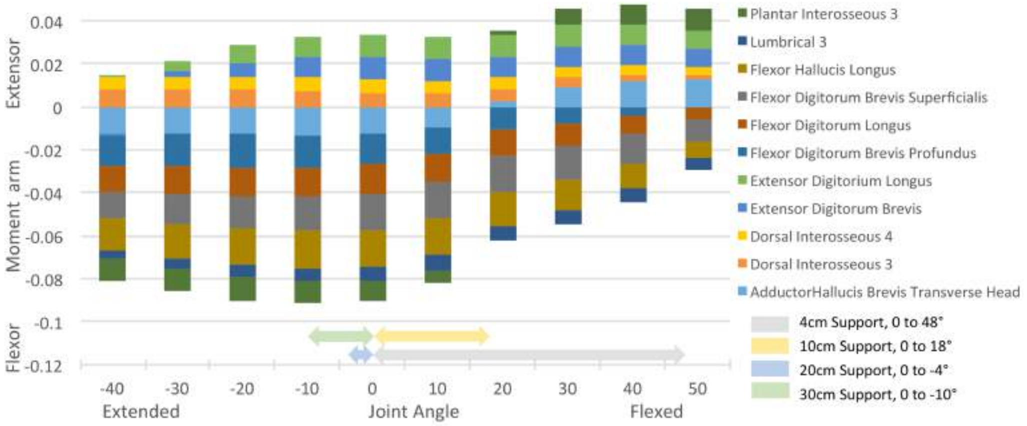
As the intrinsic muscles contribute more effectively as flexors for digit 2, and less so for digits 3, 4 and 5 (Table 4. 4), digit 2 should be more capable than digits 3-5 for small flexor movements. Coupled with the strong flexors of digit 1 mentioned earlier, this would enable a gorilla to pick up small objects like food with their feet. Such behaviour was often observed at the zoo where gorillas would pick up multiple pieces of food with their feet and travel with their feet still grasping the food, before settling down to eat. *Thus the fourth hypothesis that the interossei will be effective flexors/extensors especially in digits 1 and 2, which are important for grasping small objects is supported by data from the model.*

There are two interesting points regarding the interossei of which to take note. Firstly, the effectiveness of the interossei, both plantar and dorsal, as flexors will be discussed. Secondly, how the interossei can act upon tarsometatarsal joints, metatarsophalangeal joints and interphalangeal joints. The first point is to be expected as although the main functions of the interossei in humans are to abduct and adduct the digits at the metatarsophalangeal joints (Straus 1949; Vereecke et al. 2005), in other apes such as the gibbon and bonobo (Vereecke et al. 2005), and orangutan (Rose 1988), both the dorsal and plantar interossei act as flexors at metatarsophalangeal joints. Also following Vereecke et al. (2005), the dorsal interossei seem to be in close proximity to the plantar interossei and not as dorsally placed as in humans (Vereecke et al. 2005). There have also been previous studies which indicate, although indirectly, that the plantar and dorsal interossei of gorillas can act as flexors. A study *on Gorilla beringei* (Straus 1949) states that the fibres of flexor digiti minimi brevis blend with those of the plantar interosseous, and that the fibres of short extensor muscles blend with the fibres of the second dorsal interosseous. It is known (Ochiltree 1912) that dorsal interossei start off in a plantar position during foetal development in humans, then migrate dorsally as the metatarsals separate. This migration is most advanced in humans and less so in dogs, dasyurids and leopards. Therefore it is possible that the particular gorilla studied here has retained a more primitive/plantar form of the dorsal interossei, consistent with those of other non-human ape species, allowing them to act as flexors or extensors depending on joint angle. The second point was unexpected as the literature (Straus 1949; Vereecke et al. 2005) indicates that the interossei only act upon metatarsophalangeal and tarsometatarsal joints, not the interphalangeal joints as in digits 2, 3 and 4 in this study (Figure 4. 17B and C, S1B and C, and S2B respectively). Having the interossei act as flexors/extensors across the interphalangeal joints would enable small flexion movements to occur distally, which would aid in tasks such as food manipulation/carrying of food while travelling. This case might be an anatomical anomaly or simply individual variation as this has not been documented previously. More subjects would need to be dissected to find out if this is indeed an anomaly or if a significant percentage of lowland gorillas possess this adaptation.

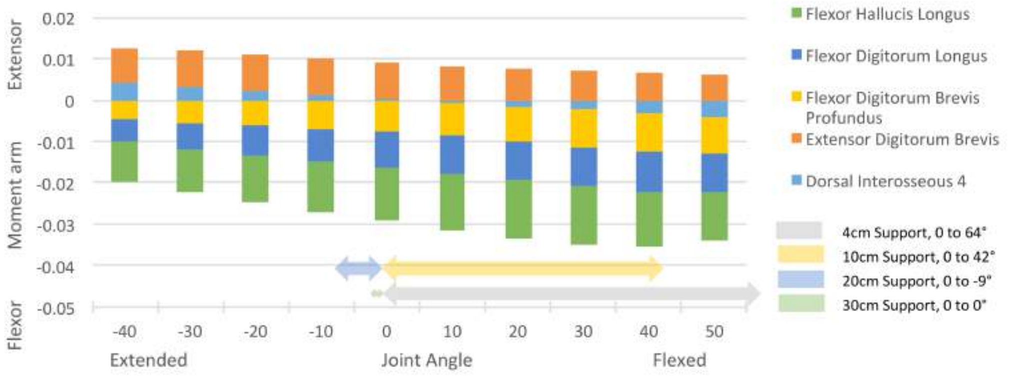
4.6 Appendix

Figure S4. 1 A-C, Graphs showing muscle contribution portion to moment arms (MA – in metres) around tarsometatarsal 3 and interphalangeal 3 joints. Y-axis: flexor moment is negative, extensor moment positive. X-axis: Negative angle refers to extended position, positive value refers to flexed position, and zero refers to neutral position. Ranges of joint angles used by the joint, from neutral position (0°) until the digit is in contact with the support, are represented by the arrows.

A: Muscle contribution to sum MA around Metatarsophalangeal 3 joint



B: Muscle contribution to sum MA around Proximal Interphalangeal 3 joint



C: Muscle contribution to sum MA around Distal Interphalangeal 3 joint

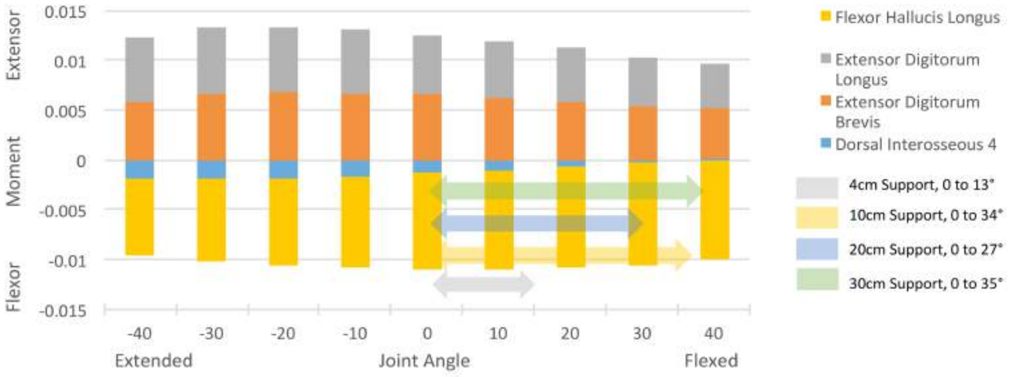


Figure S4. 2 A-B, Graphs showing muscle contribution portion to moment arms (MA – in metres) around tarsometatarsal 4 and proximal interphalangeal 4 joints. Y-axis: flexor moment is negative, extensor moment positive. X-axis: Negative angle refers to extended position, positive value refers to flexed position, and zero refers to neutral position. Ranges of joint angles used by the joint, from neutral position (0°) until the digit is in contact with the support, are represented by the arrows.

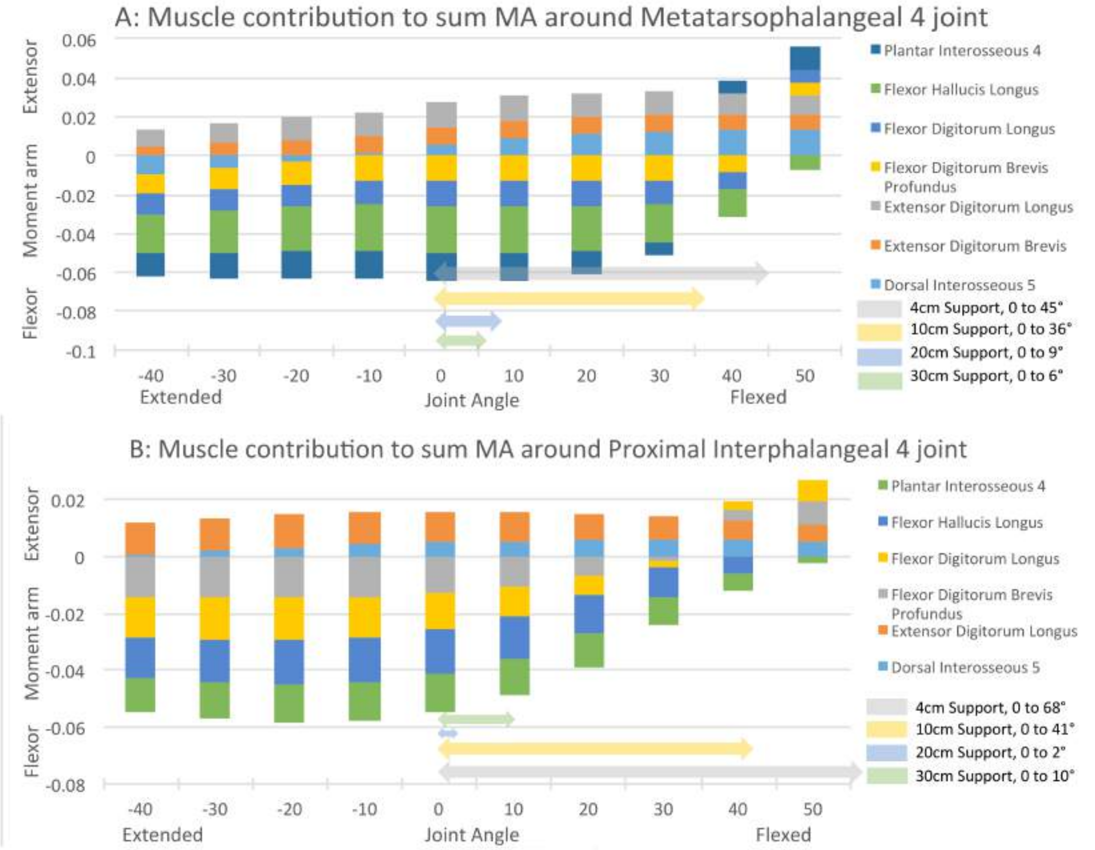
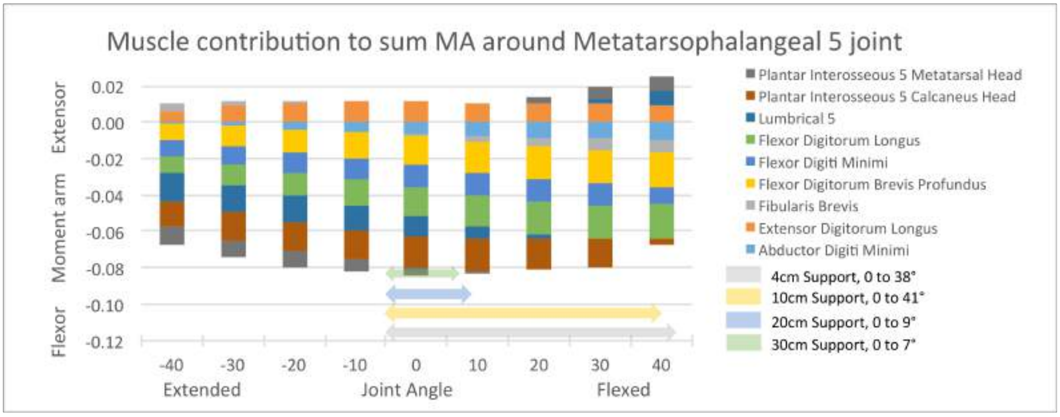


Figure S4. 3 Graph showing muscle contribution portion to moment arms (MA – in metres) around metatarsophalangeal 5 joint. Y-axis: flexor moment is negative, extensor moment positive. X-axis: Negative angle refers to extended position, positive value refers to flexed position, and zero refers to neutral position. Ranges of joint angles used by the joint, from neutral position (0°) until the digit is in contact with the support, are represented by the arrows.



Chapter 5: Using a 3D Computer Model of the Enclosure to Enclosure and Support Usage in Siamangs

5.1 Introduction

This chapter applies a novel method to study enclosure usage trends in terms of behaviour, positional behaviour and support usage in captive siamangs. This method involves building a 3D computer model of the enclosure using computer-aided design (CAD). First, the chapter will cover how the CAD model is validated. Second, the model will be used to identify patterns of enclosure usage. Third, these patterns will be explored and discussed with reference to the model.

Arboreal primates interact with, and locomote within complex 3D environments, but it is difficult to accurately account for support availability/distribution when studying positional behaviour and support usage (Crompton 1980; Cannon and Leighton 1994; Britt 1996; Warren 1997; Thorpe and Crompton 2006; Blanchard et al. 2015). For example, where species use vertical supports more for leaping, this could result from higher availability of vertical supports rather than a behavioural preference/ adaptation. Primates often favour certain routes or feeding/ resting places, and it is important to consider all available structures before drawing conclusions about their behaviour. Unfortunately this problem has not been addressed fully, and no standardized method exists quantifying support availability/distribution. While previous methods (see eg. Cannon and Leighton 1994) include measuring support diameter in quadrats/transects at breast height, or at multiple levels and quantitatively estimate support distribution/ availability, detail is missed and support type arrangement, proximity and density cannot always be obtained. However, 3D-models show detail, display support arrangements, and allow calculation of proximities and densities.

One of the most accurate methods of obtaining a 3D-model is by Lidar (light detection and range) scanning (Bates et al. 2010a). However this is expensive and often impractical in the field. Lidar technology has been used widely in geology (Bates et al. 2008b), palaeontology (Bates et al. 2008a; Bates et al. 2009a; Bates et al. 2009b), engineering (Liu et al. 2010), space travel (Johnson et al. 2002) and forest structure studies (Zimble et al. 2003; Goodwin et al. 2006; Hyde et al. 2006). This study will test the accuracy and reliability of a simple 3D-model of a siamang enclosure, generated by inputting easy-to-take physical measurements into CAD software (SketchUp) and comparing it to 3D-models generated through integrated Lidar scanning and photogrammetry using hardware with accuracies of less than 1mm (Bates et al. 2010a). SketchUp is used mainly in architecture as a cheap alternative to laser scanning and photogrammetry for 3D virtual visualisation of buildings (Hong et al. 2008; Ying et al. 2011; Singh et al. 2013). If the CAD method is proven reliable this method could be used in other captive studies when studying positional behaviour and support usage. This provides a standardized method for quantifying detailed support distribution/ availability, accounting for support type, densities, proximities and arrangements.

Besides examining enclosure usage in terms of positional behaviour and support usage, the study of behaviour trends is equally important in captivity. Previous studies on captive apes show that horizontal and vertical space-use is influenced by the physical environment. Space is used selectively (Ross et al. 2009; Ross et al. 2011b), and captive apes have a preference for structures such as trees and rocks, and spaces near vertical structures (Stoinski et al. 2001; Hosey 2005), or doors, barriers and corners (Ross et al. 2011b). Thus the study of behaviour trends enable zoos to know which areas of the enclosure and supports are favoured by the animals for feeding, resting etc., which will aid in enclosure design.

Siamangs, the largest species of gibbon (Aldrich-Blake and Chivers 1973; Chivers et al. 1975), were chosen for this study as they are arboreal (Chivers 1977), known to use certain pathways repeatedly, namely “arboreal highways” (Fleagle 1976), and their positional behaviour has only been studied once in the wild (Fleagle 1976) and never in captivity. Siamang behaviour (Chivers 1972; Aldrich-Blake and Chivers 1973; Nurcahyo 1999), ecology (Chivers 1972; Raemaekers 1979) and diet (Elder 2009) have been studied in the wild. In captivity, few studies have investigated siamang behaviour patterns (Fox 1972; Fischer and Geissmann 1990). According to Fleagle (1976), the locomotion of siamangs can be categorised broadly into four types: brachiation, climbing, bipedalism and leaping, and are each used to varying extents dependent on behaviour. Postures used during feeding can be categorised into two types: suspension and sitting (Fleagle 1976). As one of the main objectives of this study is methodological, it is not dependent on the species or their locomotor repertoire (as long as the species uses a combination of arboreal and terrestrial supports). Therefore I chose siamangs instead of gorillas as they move more rapidly than gorillas, or any of the other Great Apes, so sufficient data could be collected within the amount of time and funding available. If the CAD method were to be successful, this would be highly beneficial to zoos. This method can be easily transferrable to study behaviour patterns in other species of captive primates and other animals to aid in enclosure design. The model will also be made available online following publication.

Therefore the objectives of this study were to 1) test and compare model generation methodologies to see in what contexts (eg. captivity or wild) which method would be better (in terms of accuracy and feasibility), and if the CAD method is accurate enough to be used to study enclosure usage trends effectively, and 2) find out the patterns of enclosure usage in terms of behaviour, locomotion/posture and support usage of captive siamangs, while considering the influence of habitat structures by quantifying support availability and support preference.

5.2 Materials and methods

5.2.1 Building Lidar model

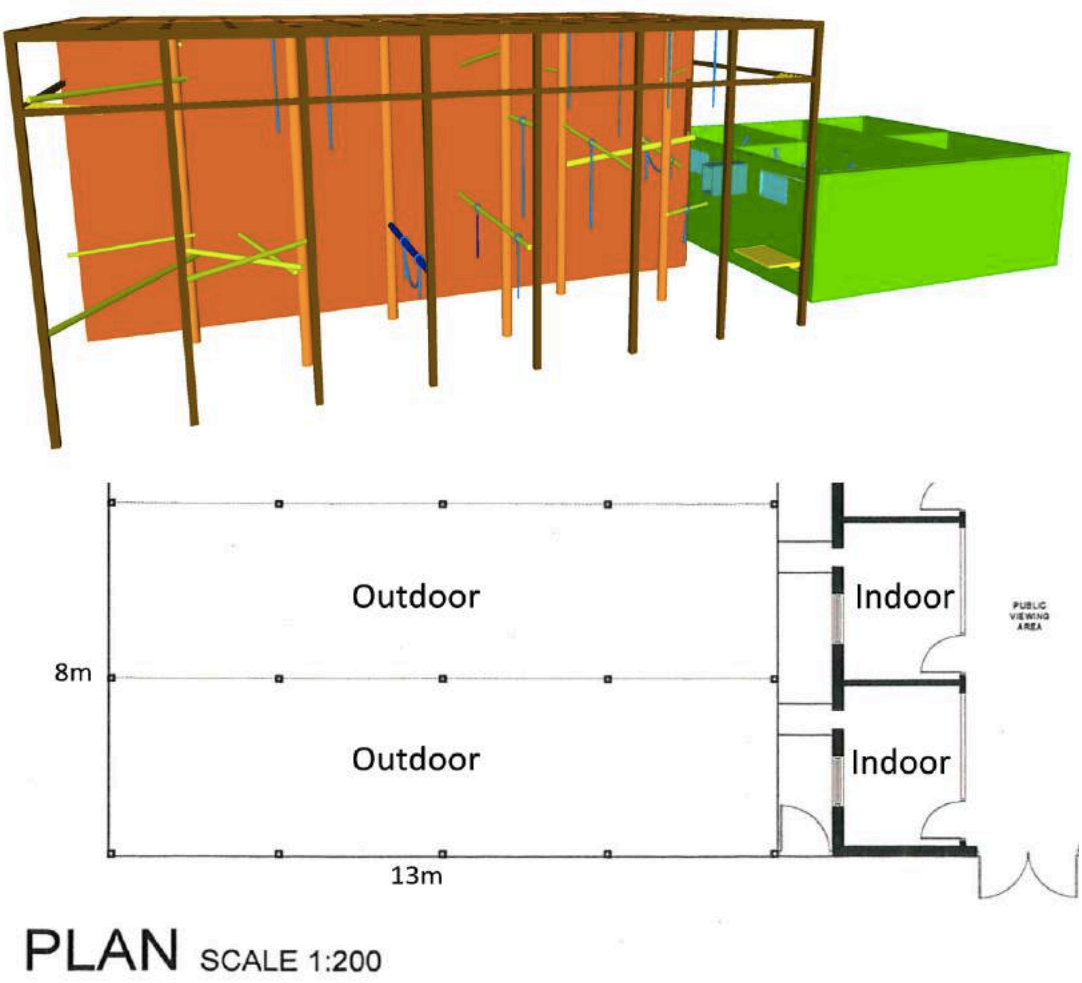
A portable Z+F IMAGER 5010C long range laser-scanner, with an accuracy to one milimetre, was used to digitize the enclosure. Specifically, a series of scans were collected from different scan stations, or locations, to provide full 3D coverage of each enclosure. Scans were then spatially aligned using the automated cloud-to-cloud registration tool in ReCap360 (www.recap.autodesk.com). Aligned point clouds were then imported into Geomagic Studio, where they were cropped that so only points within the enclosure fences were retained. The remaining points were then meshed using Geomagic Studio's surfacing tool. Figure 5. 1 shows the Lidar model.

Figure 5. 1 Lidar model of part of enclosure

5.2.2 Building CAD model

Measurements of diameter, height and angle of structures were taken using a measuring tape on all possible structures in the enclosure. When supports were not within reach because of health and safety reasons, estimation of dimensions by eye was necessary. Architect Michelle Wong created the CAD model by manually building each structure into a model, using these dimensions. Figure 5. 2 shows the CAD model. The siamangs were given access to two indoor enclosures and two outdoor enclosures (see floor plan in Figure 5.2). Each indoor enclosure was connected to each other by a tunnel and to an outdoor enclosure by another tunnel. The outdoor enclosures were also connected to each other by an opening in the wire mesh that separated the two outdoor parts. In this study only behaviour recorded at the outdoor enclosure is examined. The outdoor enclosures had a combined width of 8m, length of 13m and height of 5m. The outdoor enclosures were made from a wire mesh. Wooden corner shelves were found ~4m high and there were multiple large vertical logs and smaller horizontal logs distributed around the enclosure (Figure 5. 2). The animals had access to both indoor and outdoor enclosures at all times, except for feeding and cleaning times.

Figure 5. 2 CAD model of enclosure (top) and floor plan (bottom). Indoor part is represented in green, outdoor part in brown.



5.2.3 Verification of CAD model

As the Lidar model was more accurate (minimal human error, no estimations required) than the CAD model (human error from physical measurements and from estimating), the Lidar model was used to validate the CAD model. All the heights and diameters of supports (total of 10 supports) that were captured in the Lidar model were measured in Meshlab and compared to that in the CAD model. The percentage error for each support was calculated by dividing the difference by the Lidar measurement followed by multiplying by 100 to get a percentage. An average percentage error was then calculated from the percentage errors of each support. If the average percentage error is not large, this means that the CAD model can be used to effectively study and visualise enclosure usage trends, and quantify support density and support preference. Furthermore, finding out where large errors are more likely to occur can help future researchers take precautions when building CAD models.

5.2.4 Husbandry

The Siamangs were fed three times a day (morning, lunch and afternoon) with a range of vegetables, greens, pellets, browse and some fruits. The exact composition of food items varied depending to season. Additionally, small quantities of nuts, dried fruits and seeds were given, often used for enrichment devices or training sessions. The feeding method varied between scatter feeds and hiding and distributing the food in both inside and outside enclosures to encourage natural feeding behaviours and to ensure, that all individuals have access to food. Some food items are chopped in small pieces, whereas others are given in bigger pieces to allow food manipulation and processing by the animals. Water to drink was always available in the indoor and outdoor enclosure through water bottles fixed on the wire mesh. Different enrichment devices were given on a regular basis according to an enrichment rota, which changes between food based, sensory or manipulative enrichment devices. All siamangs were regularly trained by the keepers with a target to train for general husbandry behaviours like for example moving on a scale to do regular weight checks. All training session are completely voluntary for the animals, using positive reinforcement techniques.

5.2.5 Data collection and transcription

Data was collected via videography by Colleen Goh and Mary Blanchard from an adult male (Spike) and female siamang (Tara) that were housed together with their son at a zoo in the UK. Data was collected as events (frequencies) by focal, all-occurrence sampling (Altmann 1974), each focal sample lasting for two minutes. A total of 94 samples were collected over a period of 9 days. Although this may seem like a short amount of time, but the total number of events collected were 713, which was sufficient for the purposes of this methodological study. The dates, times and number of samples are shown in Table 5. 1. The variables collected were name, positional mode, behaviour, height, initial support area, initial support of forelimb and hindlimbs, terminal support area and terminal support of forelimb and hindlimbs. Behaviour was classified into "feed & forage", "travel", "inactivity", "auto-groom", "rocking", "allo-play", "aggression", "repetitive swinging" and "calling". Definitions for each classification can be found in Table 5. 2. Using Hunt et al. (1996) as a guide, positional modes were classified to individual locomotor/postural modes (Table 5. 3). Initial and terminal supports refer to supports used at the beginning and end of each locomotor event. A locomotor event is considered to end when the subject changes support and/or moves by more than 1m. For postural events, only initial supports were recorded as no movement was involved. Description of each locomotor/postural mode can be found in Table 5. 3. To figure out which structures were being used, the video would be paused and the surrounding structures would be used determine exactly which structure(s) was being used. If that could not be ascertained, only the "area" was recorded. The enclosure was divided longitudinally into two halves, C and D (Figure 5. 3). Each half was divided vertically (four levels: a, b, c and d) and horizontally (14 rectangles: CC1-14 for part C and DD1-14 for part D of enclosure) into "areas" as seen in Figure 5. 4. Hence "initial support area" refers to the specified "area" where the subject is found at the beginning of each locomotor/postural mode. Each area and support was assigned a code. Hence the model could display the supports/areas corresponding to certain behaviours/positional modes. Data transcribed was put into an SPSS file.

Table 5. 1 Dates over which data was collected. The time period(s) and number of samples for each day are also shown.

Dates	Times	No. of samples
6 January 2015	1023 - 1105 and 1324 - 1444	38
15 January 2015	1243 - 1359	12
16 January 2015	0947 and 1407	2
17 January 2015	1326 - 1334	4
18 January 2015	1042 - 1114	3
22 January 2015	1459 - 1551	8
23 January 2015	1017 - 1101 and 1322 - 1326	10
24 January 2015	1350 - 1604	14
29 January 2015	1522 - 1535	3

Table 5. 2 Definitions of each behaviour type recorded

Behaviour	Definition
Feed & forage	All food gathering and intake activities, fruit and non-fruit
Travel[1]	Any physical displacement that takes place eg. walking, climbing, running, with or without carrying objects
Inactivity[1]	Sleeping, reclining with eyes opened or closed, being stationary when not feeding or socializing
Auto-groom	Grooming ownself
Rocking	Repetitive forward and backward movement of torso
Allo-Play[2]	Non-aggressive activities with more than one individual, such as play, groom, chase or engaging in body contact
Agression[2]	Aggressive behaviours such as hitting surfaces, bluff charges, chasing, physical fighting, submission and fleeing
Repetitive swinging	Swinging back and forth on a mobile support

[1]Modified from Blaney and Walls (2004), [2]Modified from Kuhar (2008)

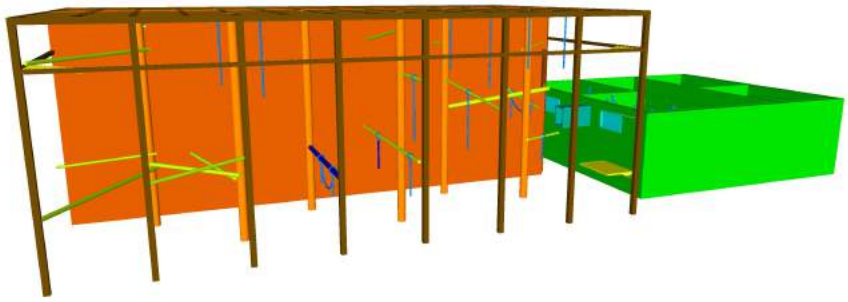
Table 5. 3 Definitions of locomotor and postural modes recorded, modified or taken from Hunt et al. (1996) ie. “L9a” refers to L9a locomotor mode from Hunt et al. (1996).

Locomotor mode	**Definition**
Brachiate	L9a
Unimanual swing across	L9d
Bimanual swing across	Both forelimbs grasp a mobile vertical support to swing across, body remains orthograde
Brachiating richochetal	L9b
Bipedal walk (w/o) assistance	L3a
Bimanual pull-up	L8f
Leap	L12c
Drop	L13c - h
Vertical scramble	L8c
Orthograde transfer	L9f
Shuffle	Similar to L3b, with extreme flexion of hip and knee
Orthograde suspension	L9g
Unimanual swing up	Similar to “unimanual swing across” but upwards
Unimanual swing down	Similar to “unimanual swing across” but downwards
Bipedal squat walk	As in L3b but with hindlimbs fully flexed
Ladder climb	L8b
X Swing	Swinging back and forth on a support, often all four limbs are grasping support simultaneously. Body can be orthograde or pronograde.
Vertical climb	L8a
Bipedal run	L7
Bridge	L11a
Bimanual forelimb swing up	Similar to “bimanual swing across” but upwards
Vertical descend	L8g

Pronograde suspension	L10
Bimanual swing down	Similar to “bimanual swing across” but downwards
Lunge	L11c
Brachiating leap	L9c
Unimanual pull up	Similar to “bimanual pull up” but with one forelimb
Bipedal leap up	Similar to “leap”, with one hindlimb pushing off support, and other hindlimb landing on support
Posture	
Sit	P1 and P2
Orthograde suspension	P8 except P8c and P8d
Bipedal stand (assisted)	P5b - c
Pronograde suspension	P10
Bipedal stand	P5a
Forelimb-suspend/sit-ortho	P8c
Forelimb-suspend/squat-ortho	P8d

Figure 5. 3 Division of enclosure (by wire mesh represented in orange) longitudinally into parts C and D.

Part C of enclosure



Part D of enclosure

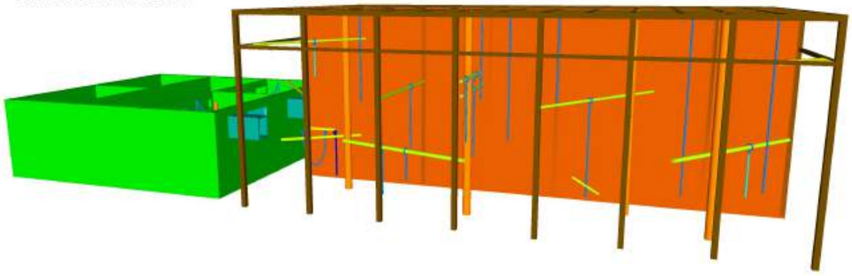
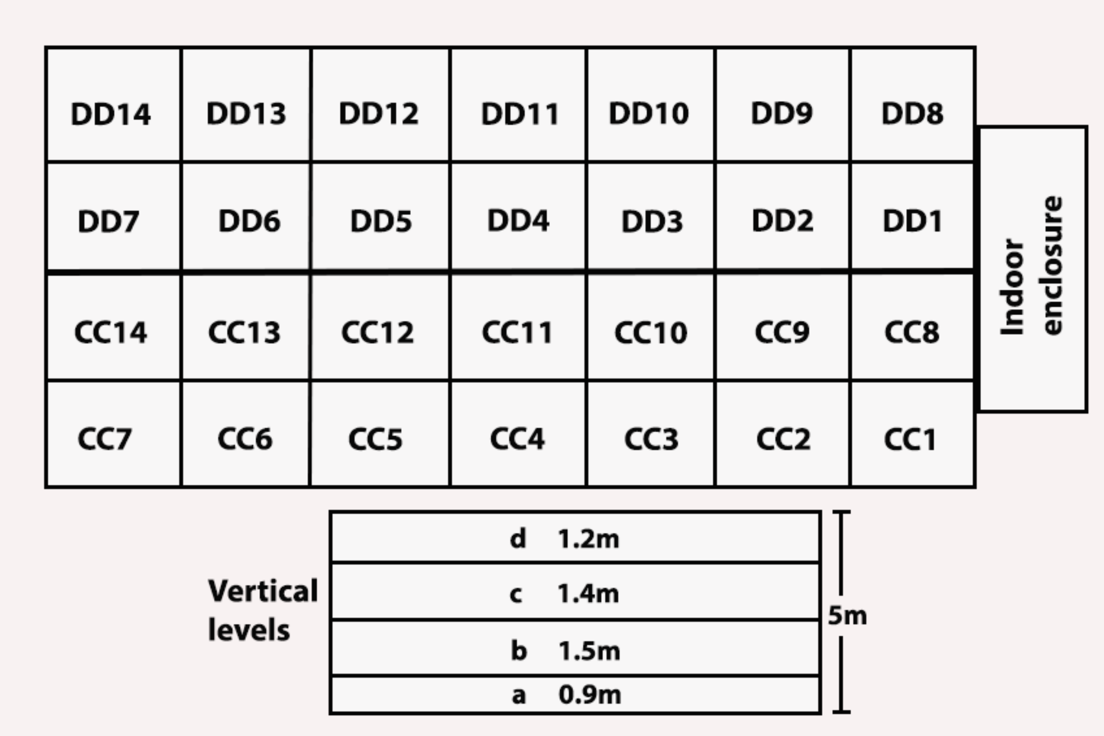


Figure 5. 4 Artificial division of enclosure into horizontal (top) and vertical (bottom) levels. Height of each vertical level is given in metres. Each area is given a horizontal code ie. "CC1" and a vertical code ie "d". "CC1d" therefore refers to the area "CC1" at level "d".



DD14	DD13	DD12	DD11	DD10	DD9	DD8	
DD7	DD6	DD5	DD4	DD3	DD2	DD1	Indoor enclosure
CC14	CC13	CC12	CC11	CC10	CC9	CC8	
CC7	CC6	CC5	CC4	CC3	CC2	CC1	

Vertical levels

d 1.2m
c 1.4m
b 1.5m
a 0.9m

5.2.6 Analysis of enclosure usage areas

The frequency and percentage of use of each area, with corresponding behaviour was calculated using SPSS. A colour map was then created in SketchUp of the enclosure showing the least and most used areas for “travel”, “feed & forage” and “inactivity”.

5.2.7 Analysis of support availability

Support availability for a specified “area” was calculated by the sum of surface areas of each support in the “area”, divided by the volume of the “area”. All calculations were made in metres. For simplification, the surface area of the outside mesh was considered as a single, solid support.

5.2.8 Analysis of support preference

An electivity index (E) is an index from -1 to 1 used to measure the preference of one resource over others. E was used to measure support preference here, as in Ross et al. (2009), for every support in an “area” of interest. Therefore the electivity index in this study takes into account the presence of other supports. A high E indicates a strong support preference. The equation used to calculate E is:

$$E = [W_i – (1/n)] / [W_i + (1/n)]$$

where $Wi = (r_i/p_i)/\Sigma r_i/p_i$, r_i = proportion of time of observed use of support, p_i = proportion of time of expected use of support and n = number of supports in the specified “area”. For example if there are two supports within an “area”, then the proportion of time of expected use of each support would be 0.5.

Electivity indexes were calculated for the most commonly used supports employed in the most common locomotor and postural modes, along with the other supports found in those areas. These electivity indexes were then plotted on the model, which was used to aid in visual identification of patterns/trends of support preference.

5.3 Results

5.3.1 Validation of model

The diameters, relative positions and lengths of all possible accurately measurable supports (ten) that were captured in the LiDAR model were measured and compared directly with the CAD model (see Table 5. 4). It was found that the recorded diameters, positions and lengths of structures based on the CAD model differed from those of the LiDAR model by an average of ±15%. The minimum and maximum percentage differences were 0% and 43.5% respectively, with the maximum percentage error resulting from a support position that had to be estimated, for health and safety reasons. For support positions, percentage error was greater for supports that were higher and had to be estimated by eye (eg D10 horizontal log), as compared to supports that were measured manually (eg D9 horizontal log and D37 ledge). In the case of support diameter, the percentage error was greater for bigger supports (eg D11 horizontal log) than smaller supports (eg D11 and D13 horizontal logs). This unexpected discrepancy could be due to the small sample size. For support length, the longer supports had lower error margins.

Table 5. 4 Comparison of measurements of supports from LiDAR and CAD models.

Position			
Support	**LiDAR**	**SketchUp**	**Error (%)**
D9 horizontal log	1.45m from ground	1.34m from ground	7.6
D10 horizontal log	1.24m from ceiling	0.7m from ceiling	43.5
D11 horizontal log	2.08m from ceiling	1.88m from ceiling	9.6
D12 horizontal log	2.03m from ceiling	1.88m from ceiling	7.4
D13 horizontal log	1.54m from ceiling	1.38m from ceiling	10.4
D37 ledge	1.42m from ground	1.41m from ground	0.70
Diameter			
D10 horizontal log	0.06	0.06	0.0
D11 horizontal log	0.103	0.077	25.2
D13 horizontal log	0.08	0.07	12.5
Length			
D19 vertical rope	0.904	1.18	30.5
D22 vertical rope	1.95	2.2	12.8
D24 vertical rope	1.49	1.69	13.4
D26 vertical rope	1.4	1.09	22.1

5.3.2 Overall enclosure usage

The enclosure was divided vertically and horizontally into “areas” as described in the methods. Thus “support area” is defined as the specified space in which a support is found. “*Initial* support area” therefore refers to the specified space in which a support used at the beginning of a positional mode. “*Terminal* support area” refers to the specified space in which a support is used at the end of a locomotor mode.

A total of 713 events of *initial* and 476 of *terminal* support area usage were collected. The difference in the number of *initial* and *terminal* supports was because postures do not have a *terminal* support. Figure 5. 5 and Figure 5. 6 show which areas were used most (top five) and least (bottom two) in the context of *initial* and *terminal* support use, in parts C and D of enclosure respectively. As seen in Figure 5. 5 and Figure 5. 6, in both *initial* and *terminal* support areas of C and D, the most frequently used areas were near the indoor enclosure and the opening between parts C and D (the opening is obscured in figures). In part C, the distribution of *initial* support areas was different from that of *terminal* support areas (Figure 5. 5). For example, the least used areas (dark blue) were concentrated in the middle of the enclosure for *terminal* supports, but were at either end of the enclosure for *initial* supports. In part D however, the least used *initial* and *terminal* support areas were distributed in a similar pattern, as seen by the overlap in the least used *initial* and *terminal* supports (Figure 5. 6).

Figure 5. 5 Areas of minimum and maximum support usage for *initial* (A) and *terminal* (B) supports in C. Dark red refers to high usage, light and white colours to intermediate usage, and dark blue to low usage. Each area is labelled with its code (eg. CC1d) followed by the frequency of use as a percentage.

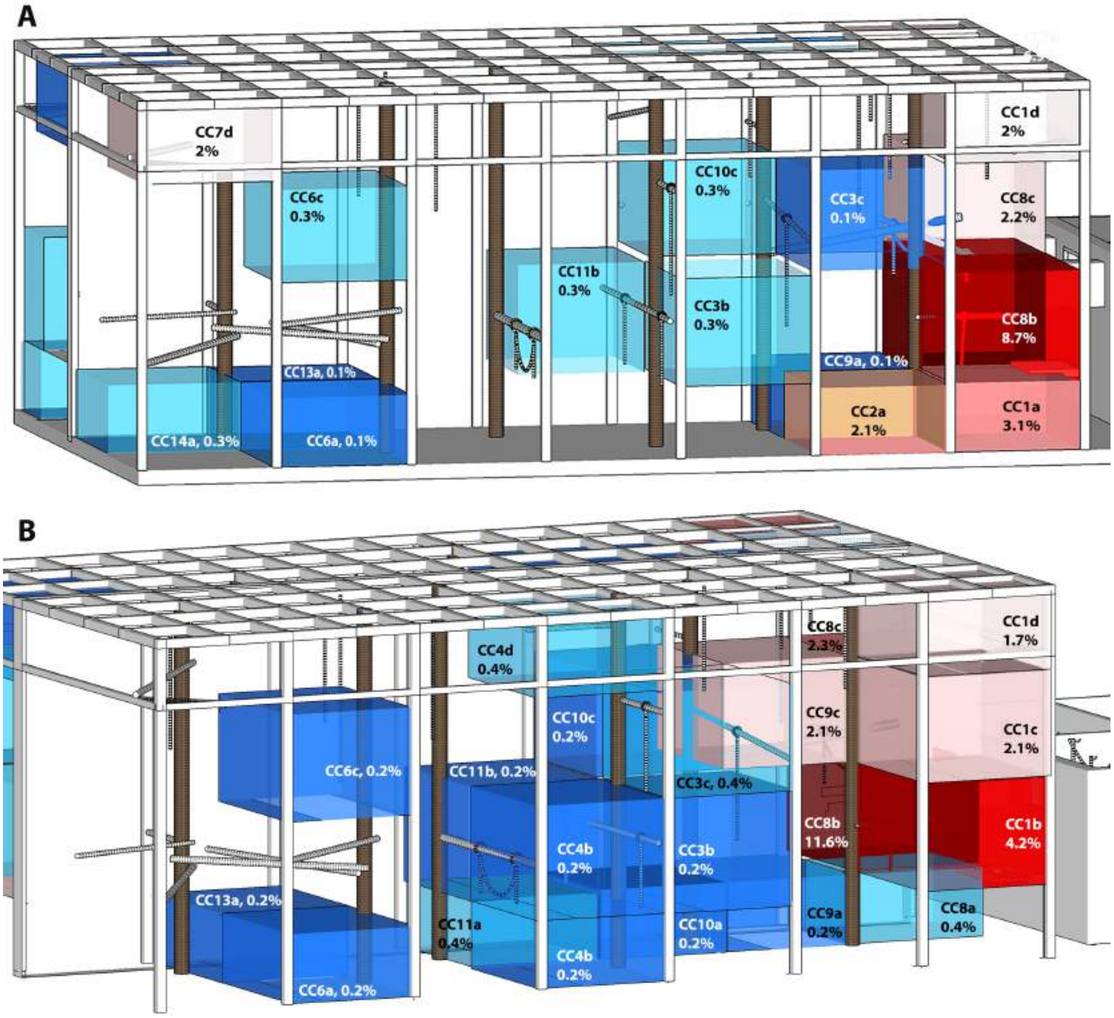
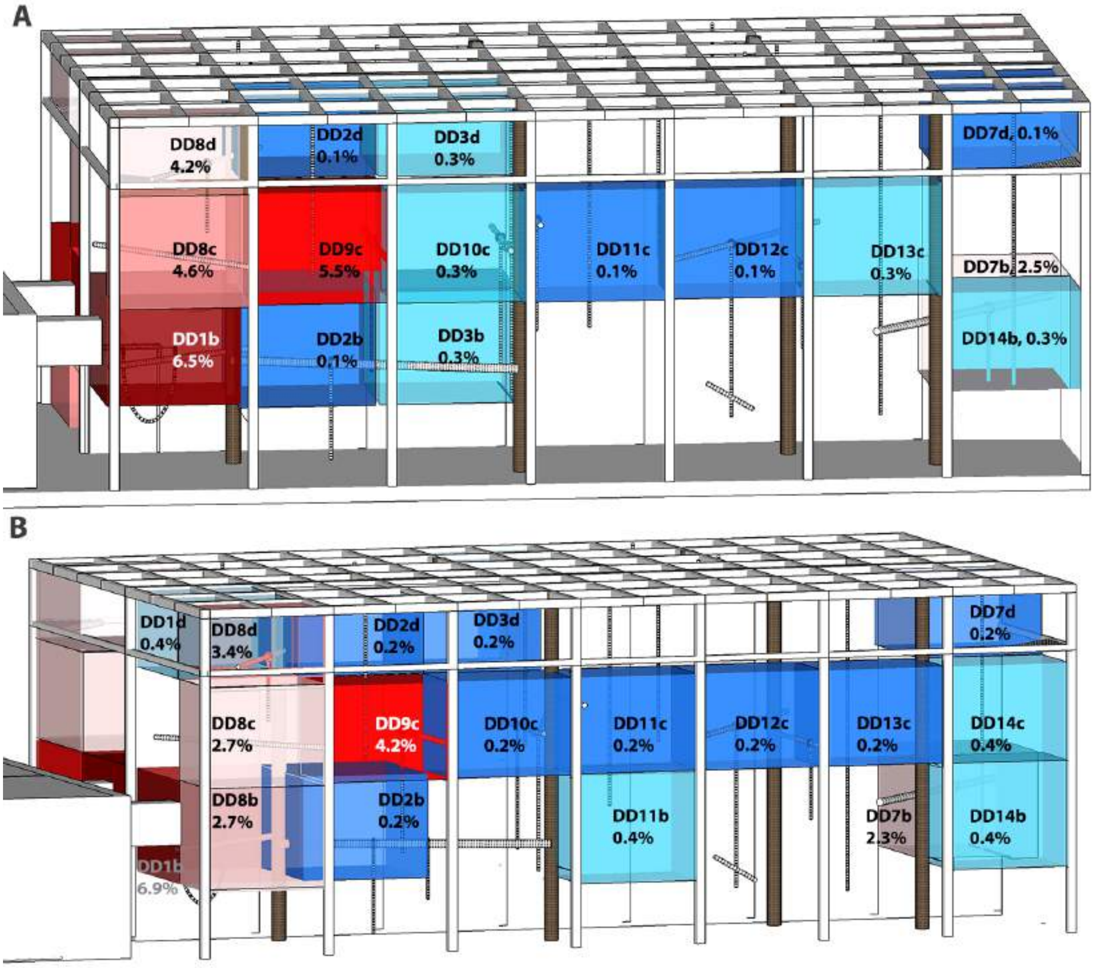
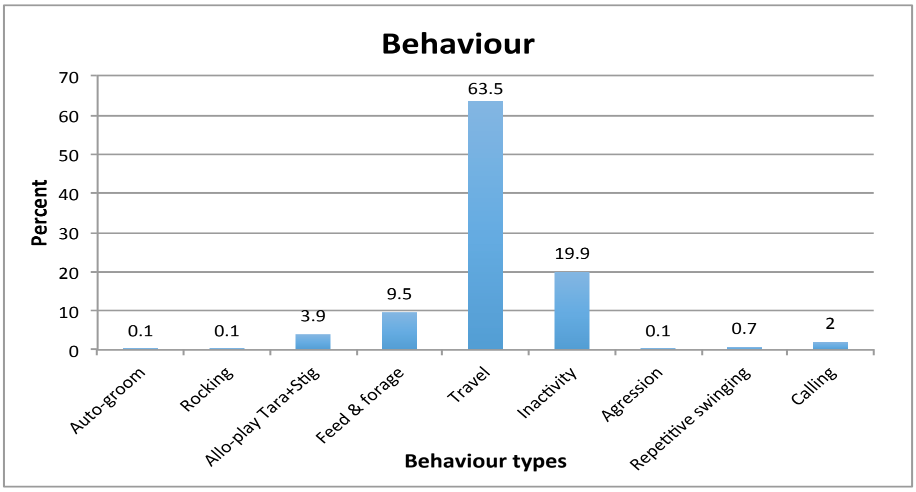


Figure 5. 6 Areas of minimum and maximum support usage for *initial* (A) and *terminal* (B) supports in D. Dark red refers to high usage, light and white colours to intermediate usage, and dark blue to low usage. Each area is labelled with its code (eg. DD1b) followed by the frequency of use as a percentage.



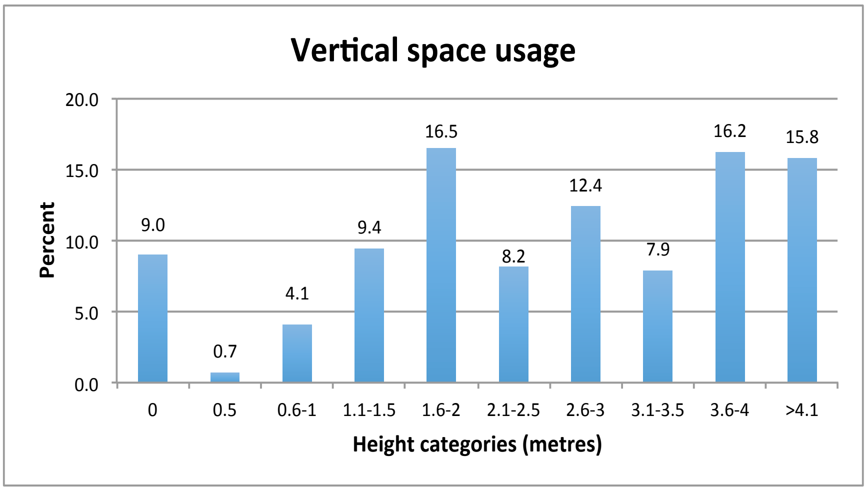
Out of 713 behaviour events, “travel” (63.5%) occurred most, followed by “inactivity” (19.9%) and “feed & forage” (9.5%) (Figure 5. 7). Behaviour was recorded at the start of each positional event.

Figure 5. 7 Percentages of behaviour types displayed. Behaviour was recorded at the start of each positional event.



A total of 713 events of height were collected whereby a height was recorded at the start of each positional event. Figure 5. 8 shows the percentages of each height category used, with “1.6-2m” (16.5%) and “3.6-4m” (16.2%) being the most frequently used height categories, followed by “above 4.1m” (15.8%) and “2.6-3m” (12.4%).

Figure 5. 8 Percentage of each height category used, where height was recorded for each bout of positional behaviour.



Out of 713 events of positional behaviour collected, 484 were locomotion and 229 were posture. 341 bouts were from Tara, 372 from Spike. The most commonly used locomotor modes (Table 5. 5) were “brachiate” (24.7%), “unimanual swing across” (18.7%), “bipedal walk” (8.5%), “bimanual swing across” (7.1%), and “brachiating richochetal” (5.8%). The most commonly used postures (Table 5. 5) were “sit” (66.2%), “orthograde suspension” (23.8%) and “assisted bipedal stand” (3%).

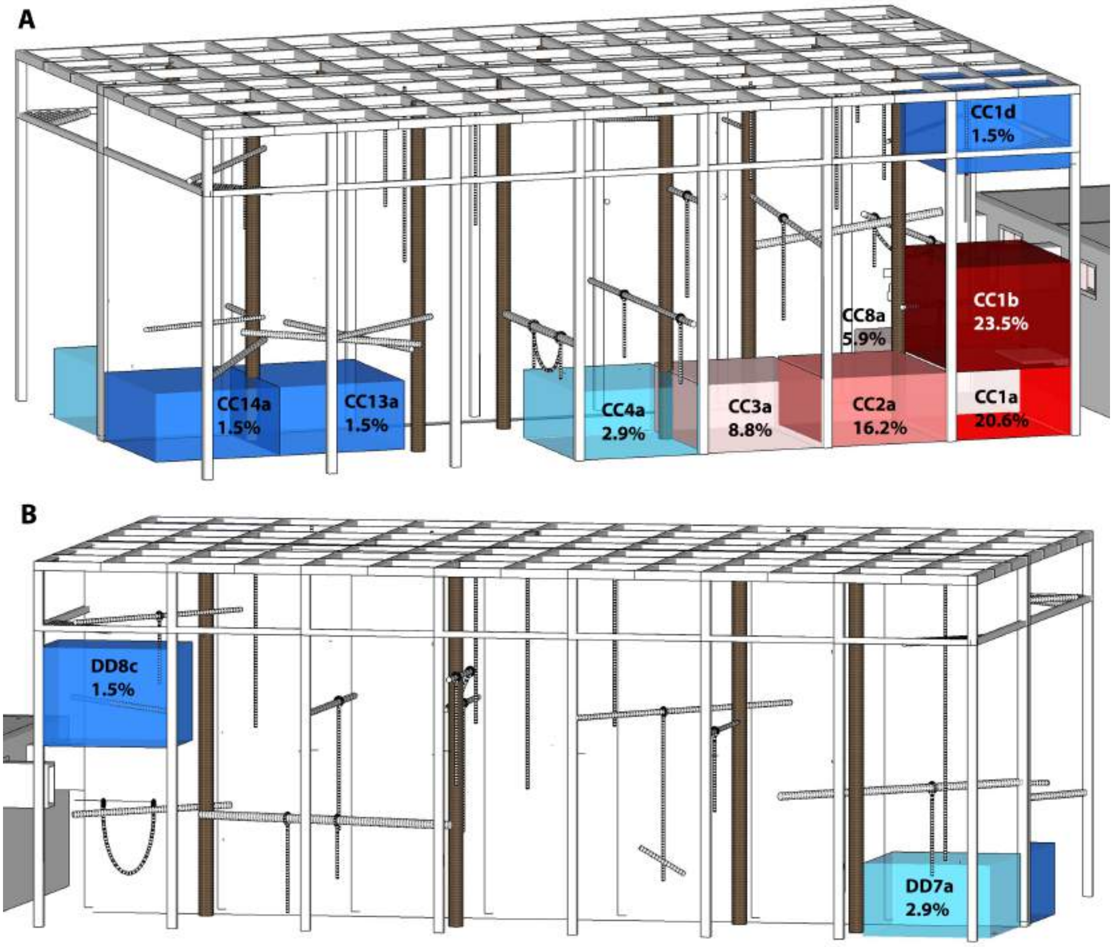
Table 5. 5 Percentage of each positional mode displayed.

Locomotor Mode	%	**Locomotor Mode (continued)**	%
Brachiate	24.7	Pronograde suspension	0.6
Unimanual swing across	18.7	Pull up	0.6
Bipedal walk	8.5	Bimanual swing down	0.6
Bimanual swing across	7.1	Lunge	0.4
Brachiating richochetal	5.8	Brachiating leap	0.4
Bimanual pull-up	4.8	Unimanual pull up	0.2
Leap	3.5	Bipedal leap up	0.2
Drop	3.1		
Vertical scramble	3.1		
Orthograde transfer	2.7		
Shuffle	2.1		
Orthograde suspension	1.9	**Posture**	%
Unimanual swing up	1.9	Sit	66.2
Unimanual swing down	1.5	Orthograde suspension	23.8
Bipedal squat walk	1.2	Assisted bipedal stand	3
Ladder climb	1.2	Pronograde suspension	2.6
X Swing	1	Bipedal stand	2.2
Vertical climb	0.8	Forelimb-suspend/sit - orthograde	1.3
Bi run	0.8	Orthograde suspension	0.4
Bridge	0.8	Forelimb-suspend/squat - orthograde	0.4
Bimanual forelimb swing up	0.8	Sit	66.2
Vertical descend	0.6	Orthograde suspension	23.8

5.3.3 Feeding and foraging

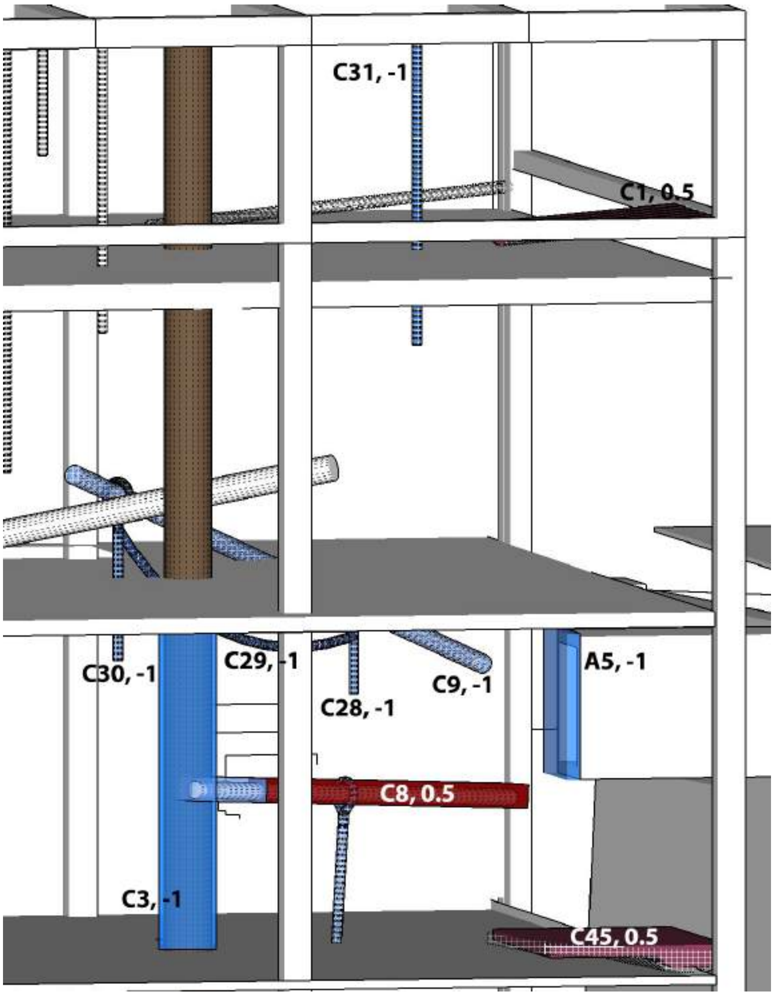
202 instances of support use out of 68 events of “feed & forage” were collected. Figure 5. 9 shows the areas where the siamangs displayed the most (top five frequencies) and least (bottom two frequencies) of “feed & forage” at C and D respectively. Excluding the outside mesh, average support availability of the top five used areas was $0.84m^{-1}$ whereas that of the least five was $0.11m^{-1}$.

Figure 5. 9 Areas used for “feed & forage” at C (A top figure) and D (B bottom figure). Dark red refers to high usage, light and white colours to intermediate usage, and dark blue to low usage. Each area is labelled with its code (eg. CC13a) followed by the frequency of use as a percentage.



With respect to supports used during “feed & forage”, the floor at C was used the most (63.4%) whereas the floor at D was used substantially less (3%). The outside mesh (5.4%), the C45 shelf (21.3%), C8 horizontal log (3%) and C1 corner ledge (1.5%) were also among the most commonly used supports during “feed & forage”. Electivity indexes (a measure of support preference) for these non-ground/outside mesh supports in each corresponding area were calculated. The index is from -1 to 1 and the higher the electivity index, the higher the support preference. It was found that these supports (C45, C8 and C1) all had a high electivity index of 0.5. However all other supports in the areas where these supports (C45, C8 and C1) were found all had a low electivity index of -1. Figure 5. 10 gives the electivity indexes of each support in the areas of interest.

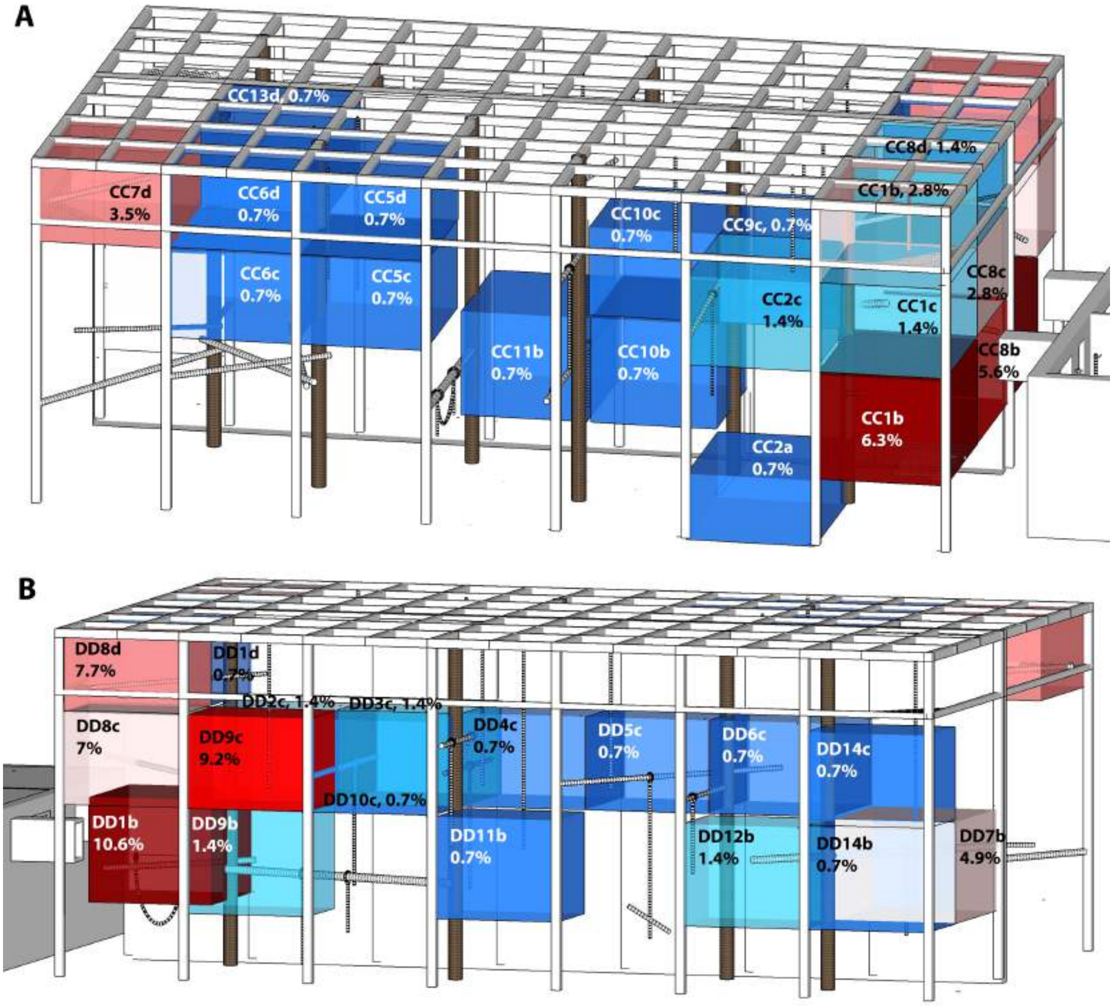
Figure 5. 10 Supports used most (red) and least (blue) during “feed & forage”. Each support is labelled with a support code (eg. C1) followed by electivity index (eg. -1).



5.3.4 Inactivity

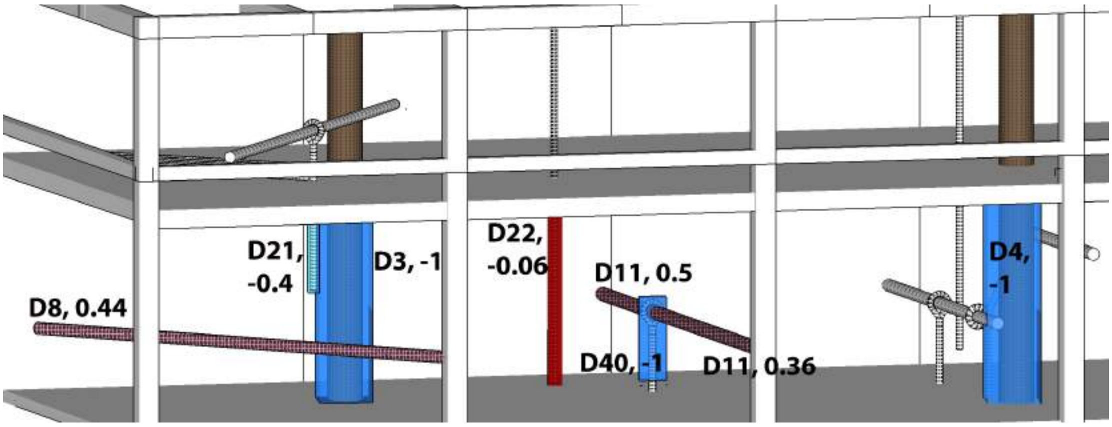
A total of 142 bouts of "inactivity" and 506 bouts of support use during "inactivity" were collected. Figure 5. 11 shows the areas in which the siamangs displayed the top five frequencies and the bottom two frequencies of "inactivity" at C and D respectively. The average support availability of the top five used areas was 1.94m^{-1} whereas that of the least five used areas was 0.95m^{-1}.

Figure 5. 11 Areas used during "inactivity" at C (A top figure) and D (B bottom figure). Dark red indicates to high usage, light and white colours to intermediate usage, and dark blue to low usage. Each area is labelled with its code (eg. CC13d) followed by the frequency of use as a percentage.



With respect to supports used during “inactivity”, besides the outside mesh, which was used the most (20.8%), D11 horizontal log (8.3%), vertical rope D22 (4.9%), and D8 horizontal log (5.3%) were also among the most used. It was found that D11 horizontal log had electivity indexes of 0.36 (at DD9c) and 0.5 (at both DD2c and DD10c). D22 ertical rope had an electivity index of -0.06 and horizontal log D8 had an electivity index of 0.44. The remainder of the supports had lower electivity indexes that ranged from -0.4 to -1. Figure 5. 12 gives the electivity indexes of each support in the areas of interest.

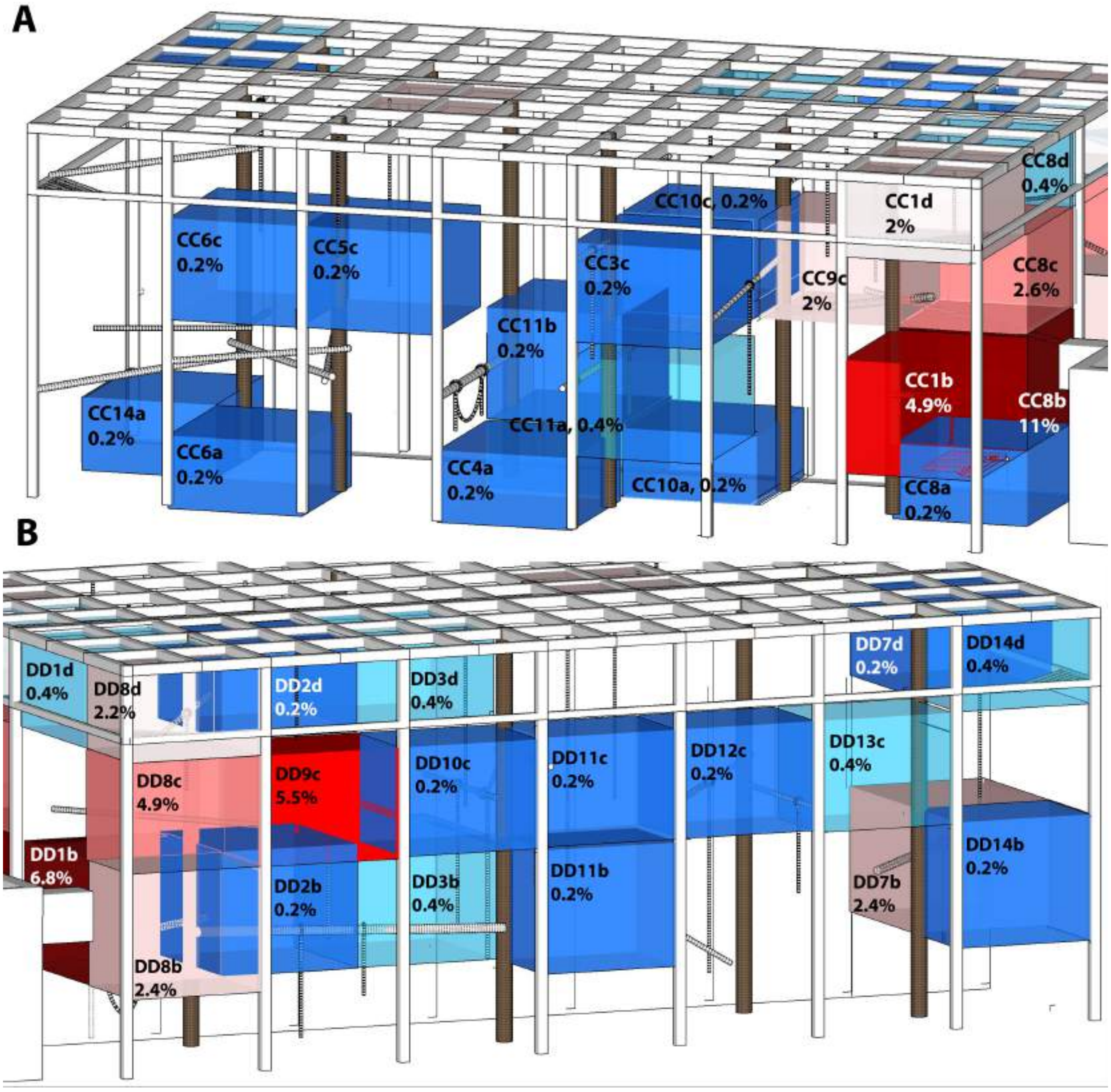
Figure 5. 12 Supports used most (red) and least (blue) during “inactivity”. Each support is labelled with a support code (eg. D4) followed by electivity index (eg. -1).



5.3.5 Travel

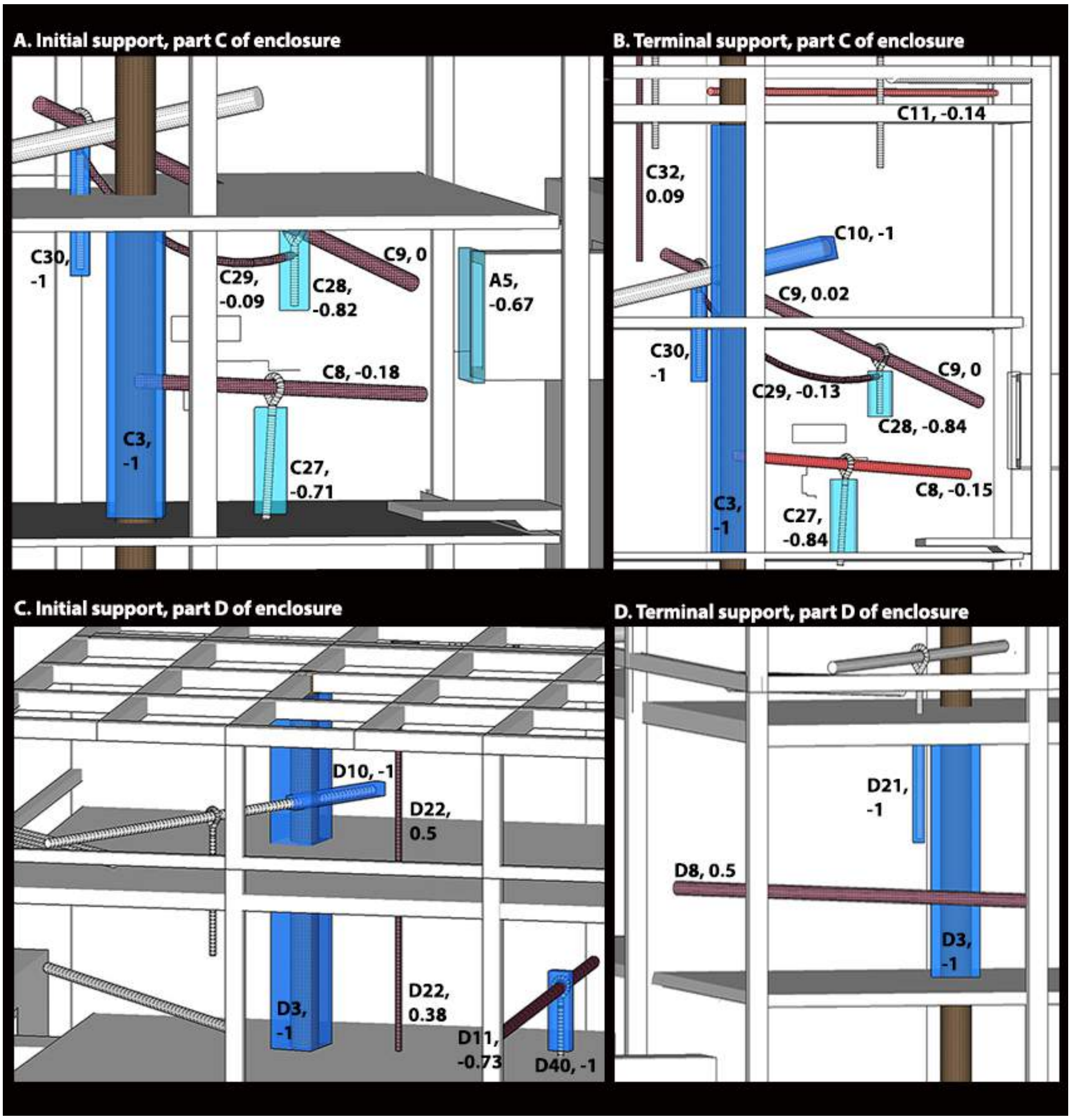
A total of 453 bouts of “travel”, 897 bouts of *initial* support use and 1019 bouts of *terminal* support use were collected. Figure 5. 13 shows the areas in which the siamangs displayed the top five frequencies and the bottom two frequencies of “travel” at C and D. Average support availability for the top five used areas was 1.29m^{-1}, whereas that of the five least used areas was 0.85m^{-1}.

Figure 5. 13 Areas used during “travel” at C (A top figure) and D (B bottom figure). Dark red refers to high usage, light and white colours to intermediate usage, and dark blue to low usage. Each area is labelled with its code (eg. CC1d) followed by the frequency of use as a percentage.



Regarding supports used during “travel”, the outside mesh was used the most as an *initial* support (25.2%) and a *terminal* support (23%). For *initial* supports, vertical rope D22 (5.5%), and C9 (4.8%) and C8 (4%) horizontal logs were among the most used. It was found that support D22 had electivity indexes of 0.38 (at DD9c) and 0.5 (at DD9d). C9 had electivity indexes of 0 (at CC8b) and -0.25 (at CC8c). C8 had an electivity index of -0.18. The remainder of the supports (except C29 horizontal rope (at CC8b), C32 vertical rope, C11 horizontal log and D11 horizontal log) had lower electivity indexes ranging from -0.54 to -1. Figure 5. 14 gives the electivity indexes of each support in the areas of interest for parts C and D of the enclosure respectively. For *terminal* supports, C9 (5.3%) and C8 (4.1%) horizontal logs, and D8 horizontal log (4.4%) were among the most used. It was found that C9 had electivity indexes of 0 (at CC8b) and 0.02 (at CC8c) as seen in Figure 5. 14. C8 had an electivity index of -0.15. D8 had an electivity index of 0.5 at both DD8c and DD1c (Figure 5. 14). The remainder of the supports (except horizontal rope C29 (at CC8b), C32 vertical rope and C11 horizontal log) had lower electivity indexes ranging from -0.84 to -1 (Figure 5. 14).

Figure 5. 14 Supports used most (red) and least (blue) during “travel”. Each support is labelled with the support code (eg. C3) followed by electivity index (eg. -1).

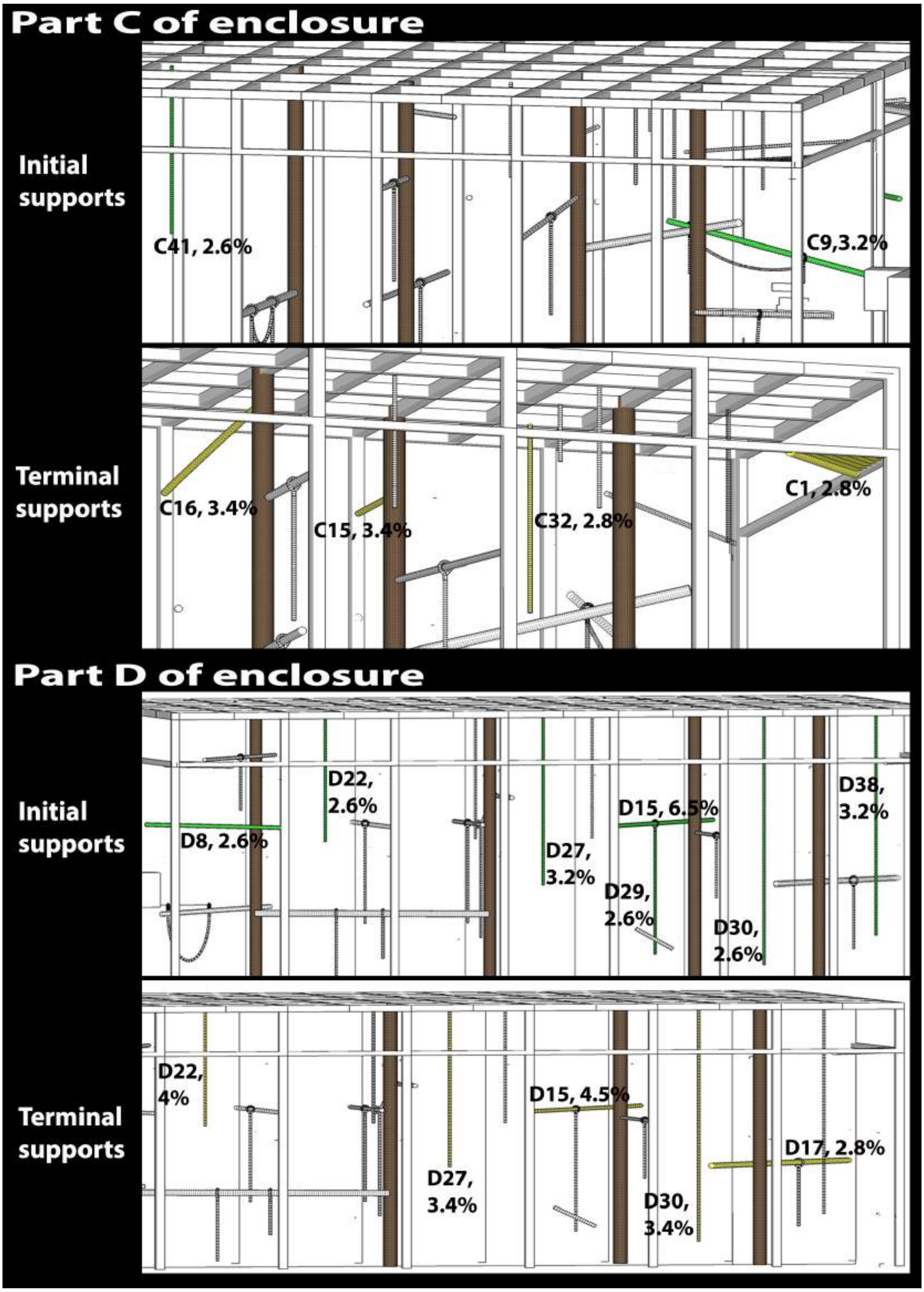


5.3.6 Locomotion

The supports used during five most commonly displayed locomotor modes (“brachiation”, “unimanual swing across”, “bimanual swing across”, “richochetal brachiation” and “bipedal walk”) were examined next (Table 5. 6). The outside mesh and D22 vertical rope were among the most frequently used supports during “brachiation”, “unimanual swing across”, “bimanual swing across” and “richochetal brachiation”. C9 horizontal log and C32 vertical rope were used during all five locomotor modes in differing frequencies as *initial* and/or *terminal* supports.

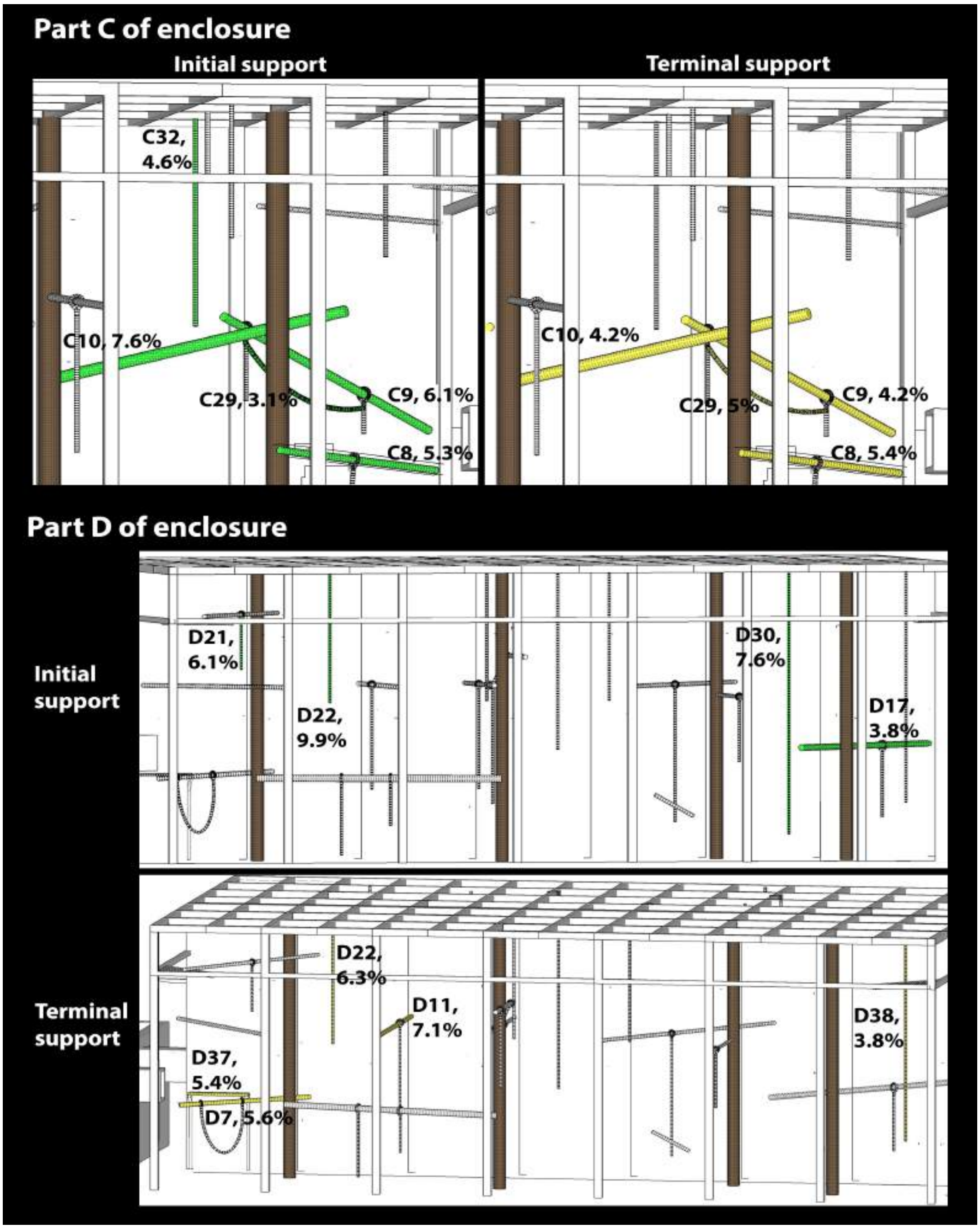
178 instances of support use during “brachiation” were collected. There were a couple of similarities found between *initial* and *terminal* supports used. Firstly, the top two supports (outside mesh and D15 horizontal log) used during “brachiation” were the same (see Table 5. 6). Secondly, *initial* and *terminal* supports were evenly spread out along D (Figure 5. 15). However there were many differences as well. Firstly at C, *initial* supports were found at either end of the enclosure but *terminal* supports were distributed along the half nearer the indoor enclosure (Figure 5. 15). Secondly, only five supports were used as both *initial* and *terminal* supports. Thirdly, there were only two *initial* supports from part C of the enclosure (Table 5. 6 and Figure 5. 15), as compared to four *terminal* supports. Fourthly, overall excess of horizontal to vertical supports increased from 12% in *initial* supports to 16.6% in *terminal* supports. Finally, only three out of the top ten *initial* supports (including the outside mesh as horizontal) were horizontal, as compared to five out of the top ten *terminal* supports (Table 5. 6).

Figure 5. 15 Supports used most during “brachiation”. Each support is labelled with the support code (eg. C1) followed by percentage of use.



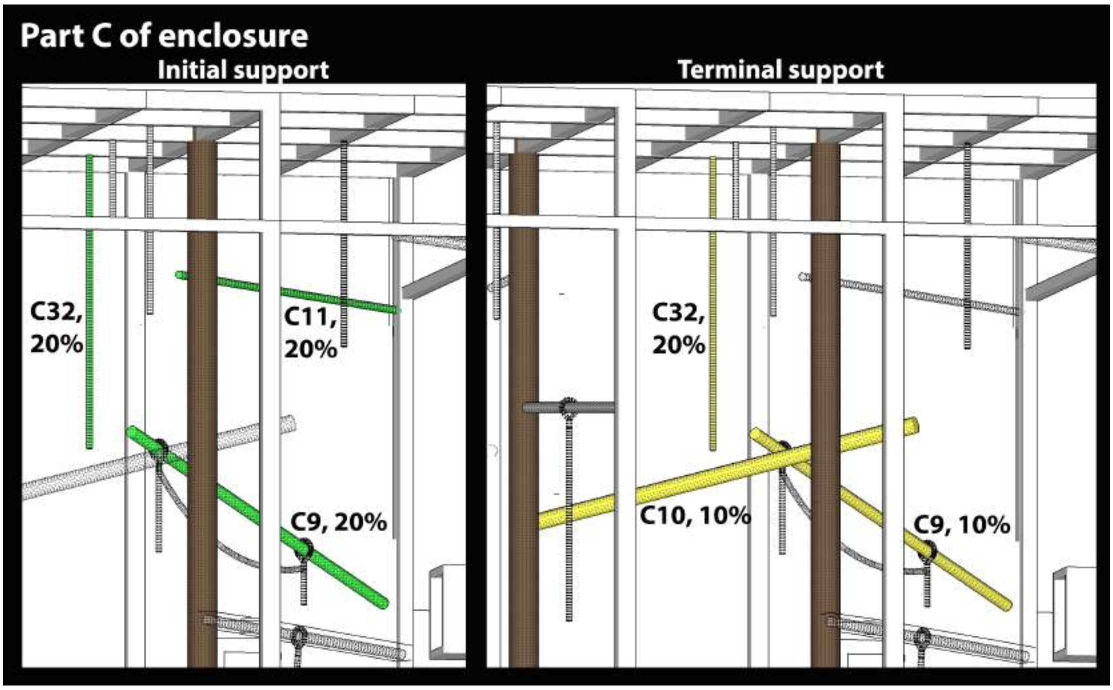
For the 330 instances of support use during “unimanual swing across”, similarities existed between *initial* and *terminal* supports. Firstly, *initial* and *terminal* supports shared five supports. Secondly *initial* and *terminal* supports in part C were concentrated near the opening between C and D (Figure 5. 16). Differences between *initial* and *terminal* supports were also present. Firstly, in part D *terminal* supports were concentrated near the same opening, whereas *initial* supports were found at both ends of the enclosure (Figure 5. 16). Secondly, six out of ten *initial* supports were horizontal, as compared to eight out of ten *terminal* supports (Table 5. 6). Thirdly, for *initial* supports there were 5.8% more vertical supports used than horizontal, whereas for *terminal* supports there were 38.8% more horizontal supports used than vertical.

Figure 5. 16 Supports used most during “unimanual swing across”. Each support is labelled with the support code (eg. C9) followed by percentage of use.



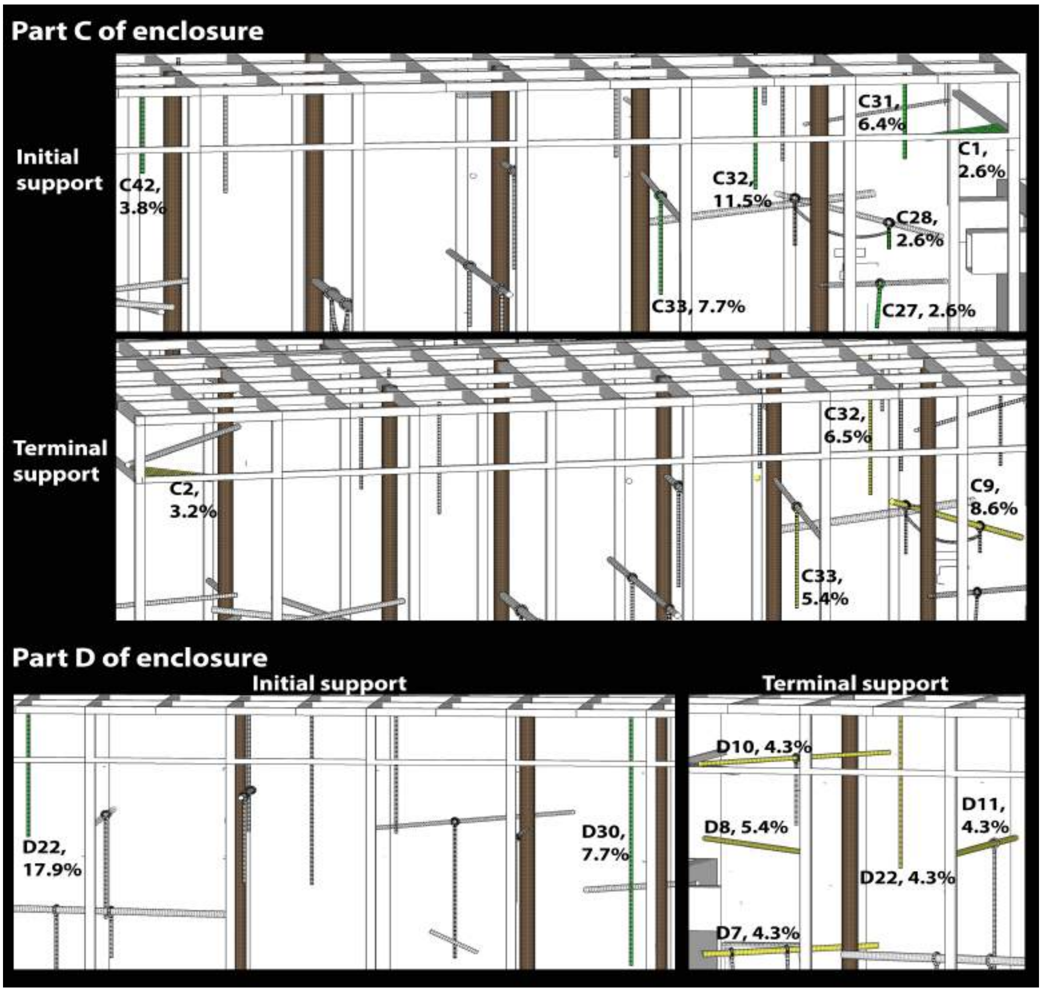
For the 133 instances of support use during "bipedal walk", there were many similarities between *initial* and *terminal* supports (Table 5. 6). Firstly, *initial* and *terminal* supports shared three out of the top four supports. Secondly, the top four supports used were all from part C. Thirdly, *initial* and *terminal* supports were both concentrated near the opening between parts C and D of the enclosure (Figure 5. 17). Fourthly, the only vertical support used (C32 vertical rope) was identical for *initial* and *terminal* support (Table 5. 6). Further, three out of four supports used were horizontal for both *initial* and *terminal* supports (Table 5. 6). Finally for both *initial* and terminal supports, overall, ~65% more horizontal supports were used than vertical supports. The only difference found was that C11 horizontal log was used as an *initial* and not a *terminal* support, whereas horizontal log C10 was used as a *terminal* and not an *initial* support (Table 5. 6).

Figure 5. 17 Supports used most during "bipedal walk". Each support is labelled with the support code (eg. C1) followed by percentage of use.



There were 175 instances of support use during “bimanual swing across”. Similarities existed between the top ten used *initial* and *terminal* supports. *Initial* and *terminal* supports shared four supports (Table 5. 6). In part C, *initial* and *terminal* supports were concentrated near the opening between parts C and D (Figure 5. 18). Differences existed between *initial* and *terminal* supports. Firstly in part D, *terminal* supports were concentrated near the same opening, but *initial* supports were found at both ends of the enclosure (Figure 5. 18). Secondly, two out of the top ten *initial* supports as opposed to seven out of ten *terminal* supports were horizontal. Thirdly, overall 53.6% more vertical than horizontal *initial* supports were used, as opposed to 42% more horizontal than vertical *terminal* supports. Finally, in part C, there were seven out of ten *initial* supports, as opposed to four out of ten *terminal* supports (Table 5. 6).

Figure 5. 18 Supports used most during “bimanual swing across”. Each support is labelled with the support code (eg. C1) followed by percentage of use.



Looking next at 68 instances of support use during “richochetal brachiation”, there was more similarity between the most used *initial* and *terminal* supports in part D than C. Firstly, *initial* and *terminal* supports in part D of the enclosure were distributed evenly along the middle (Figure 5. 19). Secondly, *initial* and *terminal* supports shared three supports (all horizontal logs) (Table 5. 6 and Figure 5. 19). However in part C, *initial* and *terminal* (Table 5. 6 and Figure 5. 19) supports did not share any supports. Further, *initial* supports in C were concentrated near the opening between C and D, whereas *terminal* supports were distributed at either end of the enclosure (Figure 5. 19). Out of the most used supports, six out of eight *initial* supports were horizontal. Also, overall 31.2% more horizontal than vertical *initial* supports were used. However for *terminal* supports, horizontal and vertical supports were used equally.

Figure 5. 19 Supports used most during “richochetal brachiation”. Each support is labelled with the support code (eg. C1) followed by percentage of use.

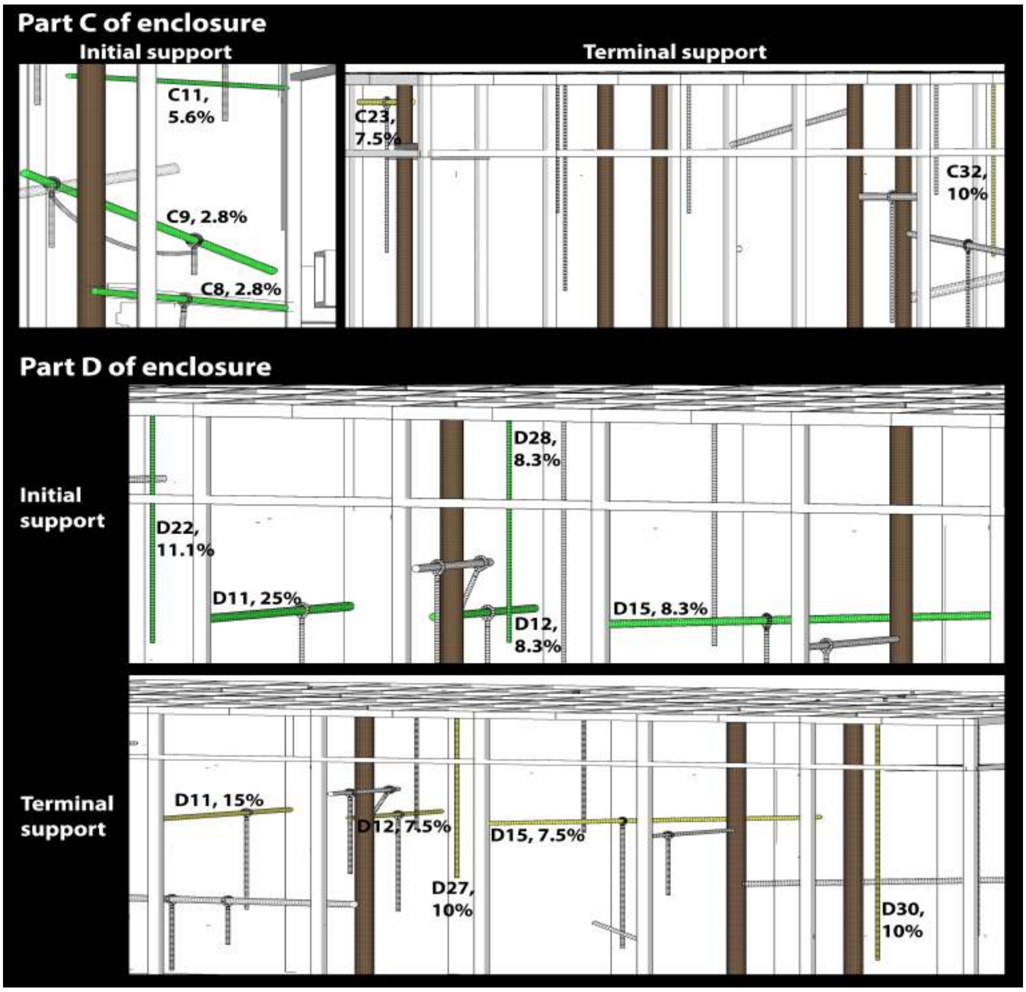


Table 5. 6 Percentages of the most commonly used *initial* and *terminal* supports during the five most frequently displayed locomotor modes.

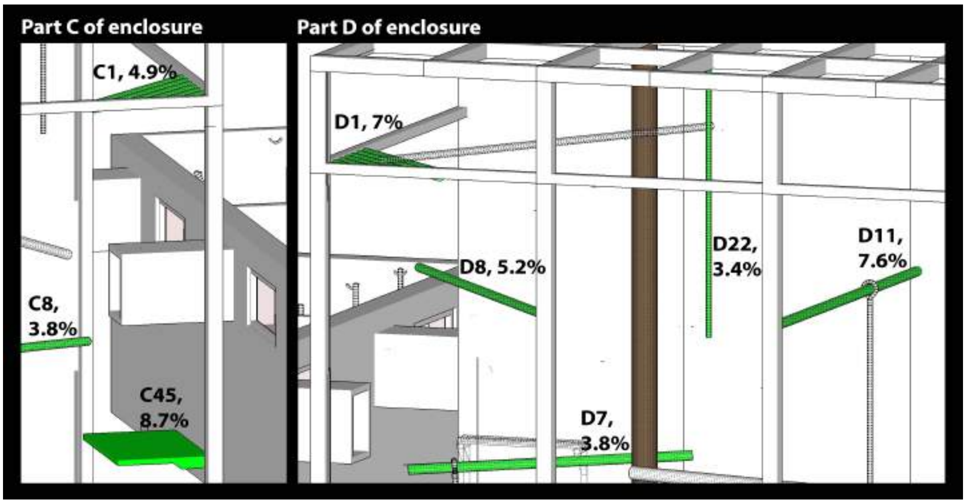
Locomotor mode	***Initial* support**	**%**	***Terminal* support**	**%**
Brachiation	Outside mesh	52.3	Outside mesh	44.1
	D15 horizontal log	6.5	D15 horizontal log	4.5
	C9 horizontal log	3.2	D22 vertical rope	4
	D27 vertical rope	3.2	C15 horizontal log	3.4
	D38 vertical rope	3.2	C16 horizontal log	3.4
	C41 vertical rope	2.6	D27 vertical rope	3.4
	D8 horizontal log	2.6	D30 vertical rope	3.4
	D22 vertical rope	2.6	C1 corner ledge	2.8
	D29 vertical rope	2.6	C32 vertical rope	2.8
	D30 vertical rope	2.6	D17 horizontal log	2.8
Unimanual swing across	Outside mesh	11.5	Outside mesh	16.3
	D22 vertical rope	9.9	D11 horizontal log	7.1
	C10 horizontal log	7.6	D22 vertical rope	6.3
	D30 vertical rope	7.6	C8 horizontal log	5.4
	C9 horizontal log	6.1	D37 Ledge	5.4
	D21 vertical rope	6.1	C29 horizontal rope	5
	C8 horizontal log	5.3	D7 horizontal log	4.6
	C32 vertical rope	4.6	C9 horizontal log	4.2
	D17 horizontal log	3.8	C10 horizontal log	4.2
	C29 horizontal rope	3.1	D38 vertical rope	3.8
Bimanual swing across	Outside mesh	21.8	Outside mesh	23.7
	D22 vertical rope	17.9	C9 horizontal log	8.6
	C32 vertical rope	11.5	C32 vertical rope	6.5
	C33 vertical rope	7.7	C33 vertical rope	5.4
	D30 vertical rope	7.7	D8 horizontal log	5.4
	C31 vertical rope	6.4	D7 horizontal log	4.3
	C42 vertical rope	3.8	D10 horizontal log	4.3
	C1 corner ledge	2.6	D11 horizontal log	4.3

	C27 vertical rope	2.6	D22 vertical rope	4.3
	C28 vertical rope	2.6	C2 corner ledge	3.2
Richochetal brachiation	D11 horizontal log	25	D11 horizontal log	15
	D22 vertical rope	11.1	C32 vertical rope	10
	Outside mesh	11.1	D27 vertical rope	10
	D12 horizontal log	8.3	D30 vertical rope	10
	D15 horizontal log	8.3	C23 horizontal log	7.5
	D28: vertical rope	8.3	D12: horizontal log	7.5
	C11: horizontal log	5.6	D15: horizontal log	7.5
	C8: horizontal log	2.8	Outside mesh	7.5
	C9: horizontal log	2.8		
Bipedal walk	C44 Floor	40	C44 Floor	60
	C9 horizontal log	20	C32 vertical rope	20
	C11 horizontal log	20	C9 horizontal log	10
	C32 vertical rope	20	C10 horizontal log	10

5.3.7 Posture

Apart from the floor, where “sit” occurred the most (19.9%), seven out of the eight most used supports were horizontal. “Sit” was concentrated at the end near the indoor enclosure, in both C and D as shown in Table 5. 7 and Figure 5. 20.

Figure 5. 20 Supports used most during “sit”. Each support is labelled with the support code (eg. C1) followed by percentage of use.



Apart from the outside mesh, where “orthograde suspension” occurred mostly (43.2%), seven out of eight most used supports were vertical, and distributed evenly along both C and D (Table 5. 7 and Figure 5. 21).

Figure 5. 21 Supports used most during “orthograde suspension”. Each support is labelled with the support code (eg. C1) followed by percentage of use.

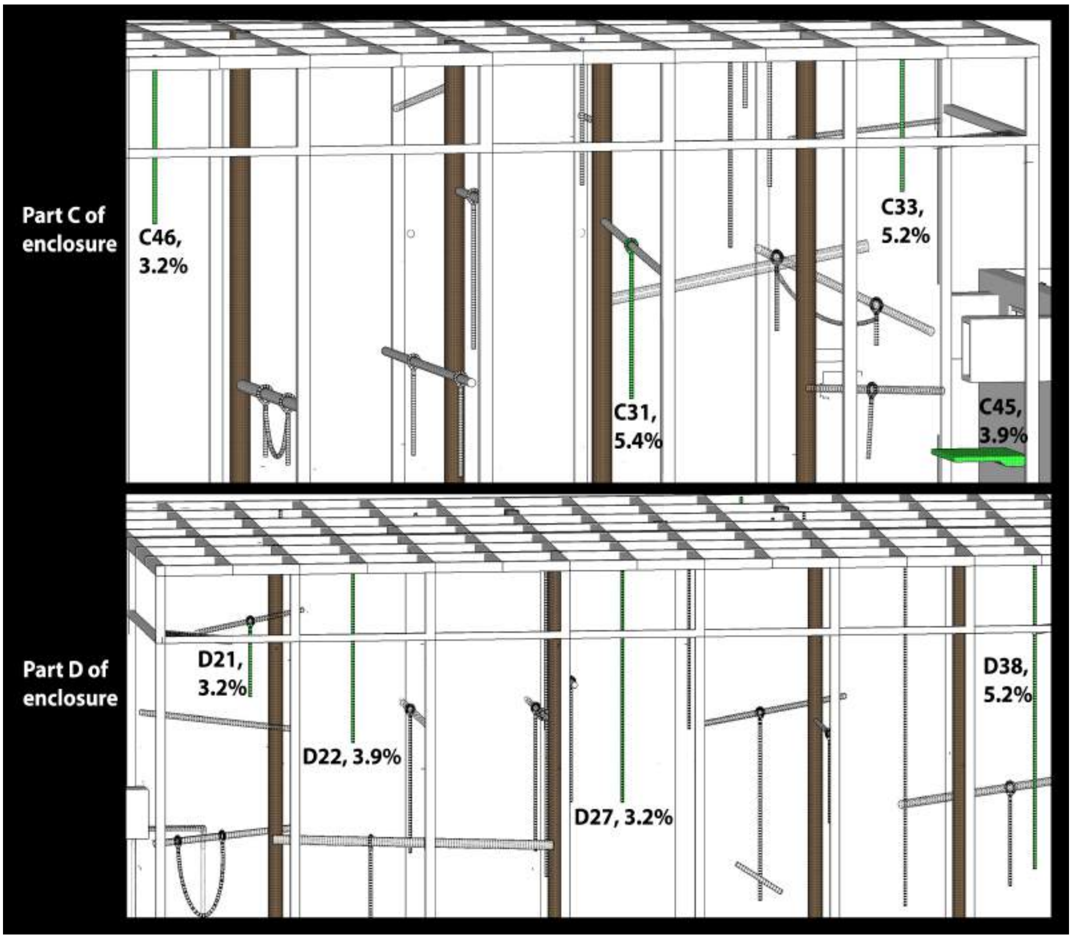


Table 5. 7 Percentages of the most commonly used supports during the two most frequently displayed postural modes: “sit” and “orthograde suspension”.

Sit	%	Orthograde suspension	%
C44 Floor	19.9	Outside mesh	43.2
C45 Shelf	8.7	C33 Rope - vertical	5.2
Outside mesh	8.7	D38 Rope - vertical	5.2
D11 horizontal log	7.6	C31 Rope - vertical	4.5
D1 Corner ledge	7	C10 Log - horizontal	3.9
D8 horizontal log	5.2	D22 Rope - vertical	3.9
C1 Corner ledge	4.9	C45: Shelf	3.9
C8 horizontal log	3.8	C46 Rope - vertical	3.2
D7 horizontal log	3.8	D21 Rope - vertical	3.2
D22 vertical rope	3.4	D27 Rope - vertical	3.2

5.3.7 Summary of key findings

- Overall, in both *initial* and *terminal* support areas of C and D, the most frequently used areas were near the indoor enclosure and the opening between parts C and D
- “Travel” (63.5%) dominated the behaviour profile, followed by “inactivity” (19.9%) and “feed & forage” (9.5%)
- The most commonly used locomotor modes were “brachiate” (24.7%), “unimanual swing across” (18.7%), “bimanual swing across” (7.1%), “brachiating richochetal” (5.8%) and “bipedal walk” (5%)
- The most commonly used postures were “sit” (66.2%), “orthograde suspension” (23.8%) and “assisted bipedal stand” (3%)
- Average support availability of top five “feed & forage” areas was 0.84m^{-1} whereas that of the least five was 0.11m^{-1}
- Average support availability of the top five areas for “inactivity” was 1.94m^{-1} whereas that of the least five was 0.95m^{-1}
- Average support availability for the top five “travel” areas was 1.29m^{-1}, whereas that of the five least was 0.85m^{-1}

- *Initial* and *terminal* supports for "brachiation" were evenly spread out along D but in C, *initial* supports were found at either end of the enclosure and *terminal* supports distributed along the half nearer the indoor enclosure
- *Initial* and *terminal* supports for "richochetal brachiation" in D of the enclosure were distributed evenly along the middle, but in C, *initial* supports were concentrated near the opening between parts C and D, and *terminal* supports were distributed at either end of the enclosure
- *Initial* and *terminal* supports for "bipedal walk" were both concentrated near the opening between parts C and D of the enclosure

5.4 Discussion

5.4.1 Factors influencing enclosure usage for "travel", "feed & forage" and "inactivity"

When interpreting the results, it must be noted that as data was collected as events (does not reflect time spent on the activity), the data here does not represent an activity budget, but rather reflects frequencies of occurrence of each behaviour type. Implications for this include resting behaviours being under-represented and feeding and/or travel behaviours being over-represented in terms of time spent on a behavioural type. However for the purposes of this methodological study, events are sufficient.

Support density played an important role in enclosure usage for "travel", "feed & forage" and "inactivity", as support density was always higher in the most commonly used areas those behaviours. However support density was not the only factor in determining enclosure usage.

That "travel" occurred mostly near the opening, can be explained by other factors besides support density. For example, the intension to travel between parts C and D, and the only way being that opening, is likely to be a contributing factor. To find out whether support density or intention is more important, one would need to provide another opening with a lower support density and see if the siamangs used the other opening equally or more. It should also be noted that in the areas used mostly for "travel", majority of the supports used were horizontal, despite the fact that vertical supports were also available within the areas. This indicates that the provision of horizontal supports is important in encouraging enclosure usage for "travel".

Besides support density, enclosure usage for "inactivity" is also influenced by several factors. "Inactivity" occurred frequently not only near the opening between C and D, but also at CC1b, CC7d and CC8d, where shelves are present. "Inactivity" involves being stationary and was dominated by postures such as sitting or orthograde suspension. These shelves, along with the horizontal logs D11 and D8 serve as large horizontal supports for sitting. Orthograde suspension can occur on both horizontal or vertical supports, and is proven by the use of both vertical (D22 rope) and horizontal (D11 and D8 logs) supports. However as the electivity indexes for the horizontal supports were much higher (D8: 0.44, D11: 0.5 and 0.36) as compared to the vertical supports in the corresponding areas (D21, D3, D22, D40 and D4 were -0.4, -1, -0.06, -1 and -1 respectively), this indicates that horizontal supports are preferred and would likely encourage sitting/orthograde suspension. Therefore besides support density, support orientation and type also play important roles in enclosure usage for "inactivity".

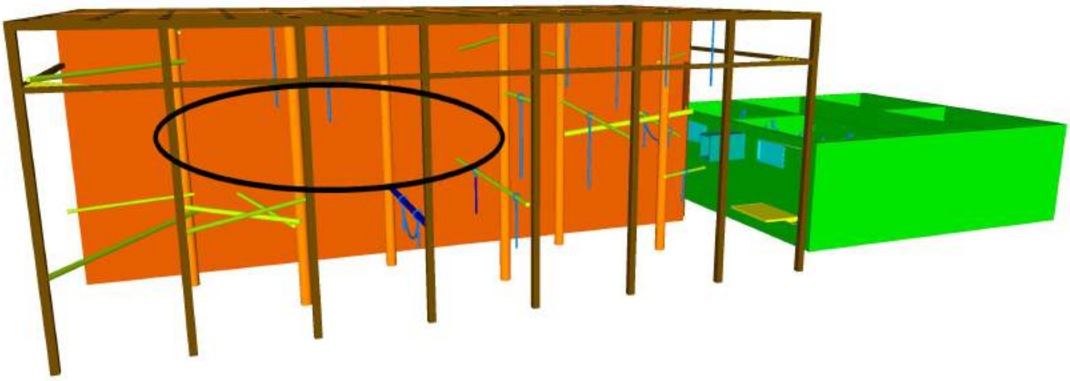
Similarly, "feed & forage" occurred mostly at areas with a higher support density, but not near the opening between C and D, indicating that support density is not the only factor that influences enclosure usage. "Feed & forage" occurred most frequently on C45 shelf, C8 horizontal log and on the ground near C45 shelf. It was observed that the siamangs were often fed near or on C45 shelf, or were eating the grass on the ground in those areas. This likely explains why "feed & forage" occurred near the ground and in those areas near C45 shelf. Within the areas used most commonly for "feed & forage", horizontal supports (C45 shelf and C8 horizontal log) were preferred over vertical supports, as indicated by the higher electivity indexes in horizontal supports. Therefore for "feed & forage", the primary factor that influences enclosure usage for "feed & forage" was where they were fed, and the secondary factors were support density and presence of horizontal supports within the areas that they were fed.

5.4.2 Enclosure usage during “brachiation”, “unimanual swing across”, “bimanual swing across”, “richochetal brachiation” and “bipedal walk”

As mentioned earlier, when interpreting the results, it is important to bear in mind that data here was collected as events (does not reflect distance covered). Hence the data only reflects frequencies of occurrence of each locomotor mode. An implication of this would be that the key locomotor modes for travel would be under-represented. However for the purposes of this methodological study, events are sufficient.

One interesting observation during “brachiation” was the difference in support usage distribution between C and D - initial supports at C were found at either ends of the enclosure and terminal supports were evenly distributed along the half nearer the indoor enclosure, whereas initial and terminal supports were evenly distributed along D. This suggests that in C, “brachiation” often started at either end and finished at the half nearer the indoor enclosure, whereas in D, “brachiation” started and finished throughout the enclosure. This can be explained by the absence of supports (vertical and horizontal) near the middle of C (Figure 5. 22) at the height where most preferred “brachiation” supports were found elsewhere in the enclosure (above ~2.5m). That out of the most frequently used supports during “brachiation”, three out of ten initial supports (including the outside mesh as horizontal) were horizontal, as compared to five out of ten terminal supports, suggests that siamangs prefer landing on horizontal supports after each arm swing. This is backed up by the fact that overall the excess of horizontal supports as compared to vertical supports increased from 12% to 16.6% in terminal supports. This is likely to be attributed to the fact that horizontal supports provide more stability for landing. The use of more vertical supports as initial supports could be a result of transitioning from a different positional mode to” brachiation”, and the less need for stability at the start of “brachiation”. Evenly distributed horizontal logs at the appropriate height should be provided to encourage brachiation throughout the enclosure, as brachiation is a key locomotor mode used by siamangs both in the wild (Fleagle 1976) and in captivity (24.7%; this study).

Figure 5. 22 Part C of enclosure. Black oval indicates where there is an absence of supports.



For “unimanual swing across”, the most frequently used initial and terminal supports were found in similar areas to each other in both C and D. This can be explained by the fact that the distance of a bout of “unimanual swing across” is limited by arm length (if the support is immobile), and by the arm length and support length (if support is mobile). Hence the start and end position of each bout, and subsequently the initial and terminal support, are often found in close proximity to each other. It was observed that the siamangs would frequently “unimanual swing across” C9, C10 and C8 horizontal logs interchangeably or one after the other. This provides an explanation as to why both initial and terminal supports consisted mostly of these supports or supports nearby in C, and why D37 shelf (which is nearby) could have acted as a terminal support after a “unimanual swing” from C9, C8 or C10. Lastly, support orientation likely plays an important role for terminal supports during “unimanual swing across”. This is because out of the most frequently used supports, eight out of ten terminal supports were horizontal as opposed to only six out of ten initial supports being horizontal. Also, overall more vertical *initial* supports were used than horizontal (5.8%), as opposed to more horizontal *terminal* supports used than vertical (38.8%). It is possible that as with “brachiation”, landing on a horizontal support at the end of a bout provides more stability. Therefore to enable “unimanual wing across”, the relative distance between mobile immobile supports needs to be sufficiently close, with a mixture of both horizontal and vertical supports present in close proximity.

The siamangs were observed to use “bipedal walk” often on C9 horizontal log after coming through the opening from D to C. It is therefore likely that the nearby C32 vertical rope and C11 horizontal log were used by the forelimbs for balance and assistance while walking bipedally on C9. A bout of bipedal walk on C9 would then end by the siamang continuing to walk bipedally onto C10 horizontal log or changing positional mode. The popularity of C9 horizontal log and the supports nearby in “bipedal walk” could be explained by the combination of a number of factors: 1) the length of the individual C9 horizontal log and/or the combination with another C10 horizontal log increasing the length available for continuous “bipedal walk”, 2) the position of the logs near the opening giving the siamangs no other choice but to use those supports to get to the rest of C and 3) the presence of nearby supports for forelimb assistance during “bipedal walk”. All these factors need to be considered to encourage safe bipedal walking in the enclosure.

The siamangs often performed “bimanual swing across” by grasping a vertical rope with both hands while using the rope to swing across and land on another support with their feet. Therefore it is understandable that 1) eight out of ten of the most frequently used initial supports were vertical ropes, and seven out of ten terminal supports were horizontal, and 2) overall, 53.6% more vertical *initial* supports were used than horizontal, 42% more horizontal *terminal* supports were used than vertical. D22 vertical rope was used so frequently (17.9%), that all of the most commonly used terminal supports were found in close proximity to D22. A possible reason why D22 was so popular for an initial support in “bimanual swing across” could be the combination of the relatively long length of the rope and the comfortable proximity of four horizontal logs that were not too near or far from the rope (Figure 5. 18). During enclosure design it is important that the relative position of horizontal logs to a vertical rope be considered to allow “bimanual swing across” to be displayed around the enclosure.

For “richochetal brachiation”, the was a difference in support usage distribution between C and D - initial supports in C were found near the opening between C and D, and terminal supports at either end of the enclosure, whereas initial and terminal supports were evenly distributed along D. Similar to “brachiation”, this can be explained again by the absence of supports (vertical and horizontal) near the middle of C (Figure 5. 22) at the height where most preferred “richochetal brachiation” supports occurs (above ~2.5m). However in “richochetal brachiation” initial support orientation was more important, unlike “brachiation” where terminal support orientation was more crucial. Overall, for *initial* supports 31.2% more horizontal supports were used than vertical, however for *terminal* supports, horizontal and vertical supports were used equally. Also out of the most frequently used supports during “richochetal brachiation”, the siamangs used more horizontal initial supports (six out of eight) during “richochetal brachiation”, as opposed to three out of ten in “brachiation”. This difference could be explained by the need for producing a much stronger propulsive force on the initial support to create the flight phase that defines and differentiates “richochetal brachiation” from normal “brachiation”. This propulsive force can be generated from pushing off strong horizontal logs. Thus the provision of evenly distributed horizontal strong supports at the appropriate height can encourage “richochetal brachiation”.

5.4.3 Enclosure usage during “sit” and “orthograde suspension”

“Sit” occurred mainly on horizontal supports such as the floor, logs and shelves. As “sit” is used mostly during “feed & forage” or “inactivity” the need for a stable support where the siamang can be stationary on for a long period of time, can be fulfilled in this case by the floor, a horizontal log or shelf. Thus to encourage feeding at a certain area, shelves could be put in place.

“Orthograde suspension” was displayed evenly along C and D, indicating that there were sufficient suitably placed supports for this positional mode. Most supports were vertical ropes, apart from C45 shelf. As “orthograde suspension” involves hanging from supports with an upright body, the siamangs were often seen grasping the same support with a foot and a hand ipsilaterally, with the other hand and/or foot grasping the outside mesh or another support. Hence the usage of vertical ropes and the outside mesh in "orthograde suspension". A likely explanation for C45 being used for "orthograde suspension" would be that the siamangs were observed to hang from the shelf while reaching down to the grass on the floor to "feed & forage".

5.4.4 Advantages and limitations of the CAD method

As this study has shown, there are many advantages of using the CAD method to study behaviour trends in captive primates. The software is free and easily available, with many free tutorials online. It can be used to artificially split the enclosure into cubes to enable detailed study of enclosure usage. The model allowed the identification of favoured supports in the context of behaviour and positional modes. Further, this method enabled the calculation/quantification of support availability. Finally, this method enabled the determination of which supports were preferred over others by looking at un-used neighbouring supports. This direct comparison with used/unused supports removed the possibility that preferred supports were simply the most common. Hence conclusions can be drawn about what aspects of a support were important to the subject during specific behaviour/positional modes. This information is vital for studies that examine the role of habitat structure in locomotion (Crompton 1980; Crompton 1984; McGraw 1996; Thorpe and Crompton 2006; Manduell et al. 2012; Blanchard et al. 2015) but quantification of used versus unused supports has always been a challenge and most studies resort to estimates of support availability (Crompton 1984; Britt 1996; McGraw 1996; Warren 1997; Manduell et al. 2012; Blanchard et al. 2015). Finally the researcher will have access to their study site's architecture anytime.

As with any method, there are limitations. Firstly, the need for data to be collected by video, leading to a time consuming period of data transcription in addition to the initial data collection. Video is necessary to determine the exact position of the subject in the enclosure, impossible to achieve accurately using traditional pen and paper observations. The CAD model was shown to have an average of 15% error in support height and diameter when compared to the far more accurate LiDAR model. This error could be reduced to some extent by having a rigorous training period to improve accuracy of estimating dimensions by eye. The maximum percentage error arose from the position of supports that were very high and had to be estimated. According to Nilsson (1996), in a forest with an average tree height of 12.5m, heights measured and estimated from the ground were underestimated by 2.1 - 3.7m. This has implications on locomotor studies (Blanchard et al. 2015; Britt 1996; Crompton 1984; Manduell et al. 2012; McGraw 1996; Warren 1997) conducted in the wild that involve estimating and guessing support heights that are relatively much higher (eg. >10m). In the future a longer period of training might be considered to ensure more accurate estimates of height and diameter. Thirdly it would be challenging to replicate this method in the wild. The sheer number of branches and the extreme heights of the trees make it almost impossible to accurately obtain support diameters and numbers and hence manually build a model in SketchUp. This accuracy of support size and number would be needed to identify support usage trends and calculate support density, respectively. One solution for this would be to use a more accurate, but more expensive, portable laser scanner as a laser scanner would be able to accurately capture support sizes and numbers at the top of the canopy, without human error. However in captivity, the CAD method is a very useful tool to examine enclosure usage.

Chapter 6: Conclusions - multifactorial approach to improving captive primate welfare

In this chapter I 1) summarises the findings and conclusions of each chapter, and the implications resulting from Chapters 2 to 5, 2) provide an overall conclusion linking the chapters and 3) provide a one-page executive summary summarising the recommendations for captive care.

6.1 Findings and conclusions of each chapter and their implications

In Chapter 2, I compared behaviour profiles of captive gorillas between two zoos and with those of gorillas in the wild, and examined the effects of various forms of enrichment in order to tease out factors that contribute to differences in behaviour profiles and the display of abnormal repetitive behaviour. Firstly it was found that ***behaviour profiles and activity levels were influenced by different forms of enrichment (tool-use based enrichment was associated with reduced regurgitation and reingestion) as well as social group structure***. Secondly, the ***lack of activity and ingestion in captive gorillas could be attributed to diet composition and environmental complexity***. Thirdly ***regurgitation and reingestion (R&R) in Zoo A decreased significantly after increases in dietary fibre levels and social behaviour in individuals that were parent reared. However, thumb sucking did not decrease for the hand-reared individual***. Therefore this study lends further evidence to the potential of dietary fibre quantity in reducing R&R and the fact that different abnormal repetitive behaviours have different triggers, all of which are important information for zoos whereby they may be able to improve welfare of their gorillas.

Another way of improving captive animal welfare would be to encourage species-typical positional behaviour and support usage (Jensvold et al. 2001; Pruetz and McGrew 2001; Fabregas et al. 2011; Schmidt 2011). Hence in Chapter 3, I compared positional behaviour and support usage preferences between two zoos and that of the wild to find out what factors, in terms of enclosure design/physical enrichment, would be likely to encourage species-typical positional behaviour and support usage preferences. While there were some similarities between wild and captive gorillas, the captive environment departed sufficiently from that of the wild to elicit some differences in positional behaviour and support usage profiles. For example, ***less vertical climbing and more pronograde locomotion occurred in captivity***. With the more pronograde locomotion being used coupled with increased life expectancy this would lead to long-term differential spine and joint loading (relative to other locomotor modes). This could have potential implications like back problems and arthritis. Also ***support orientation usage was mostly horizontal in captivity but vertical in the wild dataset***. Thus, to some extent, gorillas are not restricted in terms of positional behaviour and support usage. However as ***support usage remained consistent in all three sites in the wild despite differing habitat structures, this indicates that gorillas do have a strong preference (likely stemming from musculoskeletal adaptations) for vertical and <20cm supports***. Recommendations, based on the differences between captive and wild datasets, were made for gorilla enclosure design to encourage more species-typical locomotor behaviour and support usage. This study emphasized the importance of taking into account locomotor plasticity of gorillas during enclosure design (Schmidt 2011) and when using positional behaviour and support usage as a welfare indicator. Although gorillas can accommodate some habitat structure differences, zoos must strive to ensure that captive habitat structures do not differ to an extent that is outside the range of the locomotor plasticity in gorillas. This study shows that positional behaviour and support usage profiles can serve as an indicator of how physical enrichment can be tailored to create an environment similar to that of the wild. The combination of suitable feeding enrichment (eg. tool-used based enrichment or arboreal feeding) and preferred supports types would likely lead to more time spent on feeding and activity (Zaragoza et al. 2011). This is especially important given the high levels of inactivity and lack of time spent on feeding compared to that of the wild, as found in chapter 2.

As positional behaviour and support usage preference is not only affected by habitat structure but restricted, to a certain extent, likely by musculoskeletal adaptations as observed in Chapter 3, I investigated how various muscles in the hindlimb of a gorilla function as flexors/extensors. This was achieved by building a 3D computer model of a gorilla hindlimb, which permitted the collection of moment arm data of individual muscles across the hip, knee, ankle and foot joints. Payne et al. (2006) previously collected moment arms in gorillas using the tendon travel method. However recent literature (Young et al. 1992; Michilsens et al. 2010; Hutchinson et al. 2014) has shown that the tendon travel method, if not strictly controlled, was not as accurate and reliable as the 3D modelling method. Thus I compared the 3D modelling method to the tendon travel method in Payne et al. (2006) to find out test how accurate and reliable the moment arms reported in Payne et al. (2006) were. It was found that the ***3D computer model provided more reliable and accurate moment arm data for irregularly shaped muscles and muscles that were not directly above the joint, as compared to the tendon travel method from Payne et al. (2006).*** To find out if moment arms were a good predictor for locomotor optimization, I investigated if the joint angle ranges used during vertical climbing, a key locomotor mode used by wild gorillas (Remis 1998), coincided with higher moment arms that that of bipedal walking, a substantially less common locomotor mode used by wild (Remis 1998), around the hip/knee/ankle. It was found that only for hip flexors did joint angle ranges in climbing coincide with higher moment arms than that of bipedalism. Joint angle ranges in climbing did not coincide with higher moment arms that that of bipedalism for hip extensors, or knee and ankle flexors and extensors. This indicates that ***except for hip flexors, moment arms are not predictive for locomotor optimization in gorillas***. Next I looked at moment arms of muscles about the foot to find out how gorillas were adapted to grasping and if moment arms were predictive for support usage preferences. ***Moment arms around metatarsophalangeal joints 1 and 5 did not decrease during flexion (as one would expect the muscles to get pushed towards the joint), but remained high instead, indicating strong grasping ability of sufficiently small supports that require flexion of first and fifth digits ie. <20cm supports as seen in Chapter 3.*** Finally interossei were also found to be effective flexors, especially over Digit 2. Interestingly, this was the ***first evidence for interossei acting over interphalangeal joints***. All these factors contribute to the ability to carry out fine flexion movements, likely to be important for grasping, as it is known that gorillas are capable of precision grapsing (Christel 1993; Marzke 1997), and manipulating small objects like food. This suggests that when designing gorilla enclosures, smaller supports are needed, as these are the supports to which gorillas are most anatomically adapted to using and indeed use most in the wild (Chapter 3). ***While large trees may look most suitable to the zoo visitor for a large bodied gorilla, the provision of multiple small arboreal supports are more likely to encourage more locomotion and species-typical support usage and positional behaviour.*** Again, this would improve the welfare of the gorilla as activity is encouraged (Schmidt 2011; Zaragoza et al. 2011).

As it was difficult to determine with certainty if support preferences shown in Chapter 3 were a result of a prevalence of certain support types in the environment or a restriction from musculoskeletal adaptations, I developed a method to quantify support density and identify favoured supports while taking into account any influence from neighbouring supports. A 3D computer model of a siamang enclosure was built using SketchUp, and validated with a Lidar scan model. Through the CAD model, it was found that ***"travel", "feed & forage" and "inactivity" occurred mostly in areas with high average support density***. In addition, looking at specific locomotor modes, initial and terminal supports used were affected by support orientation and support distribution. Firstly, ***the siamangs preferred to land on horizontal supports for "brachiation" and "unimanual swing across" for stability, whereas they preferred to initiate "richochetal brachiation" on horizontal supports to generate sufficient propulsive force for the flight phase in "rhichochetal brachiation".*** Secondly, the ***presence of evenly distributed strong, horizontal logs along the length of the enclosure at the appropriate height would likely encourage "brachiation" and "richochetal brachiation".*** Thirdly, ***a long horizontal support with presence of nearby supports for forelimb assistance would be likely to encourage "bipedal walk".*** Therefore the CAD model successfully enabled the study of behaviour trends, the identification of favoured supports (over neighbouring supports) in the context of behaviour and positional modes, and the calculation/quantification of support availability. This information is vital for zoos when it comes to drawing conclusions for enclosure design to encourage specific species-typical behaviour and support usage.

6.2 Overall conclusion

The aim of this thesis was to find out how to improve the welfare of captive western lowland gorillas in terms of encouraging species-typical positional and non-positional behaviour and reducing stereotypical behaviour (Chapters 2 and 3). I did so by using traditional behavioural observation methods (Chapters 2 and 3), which was largely successful in teasing out the factors that were associated with encouraging species typical behaviour (positional and non-positional) and reducing stereotypical behaviour (non-positional). In order to understand why certain trends were seen with regards to positional behaviour and support usage, I adopted modern approaches such as 3D computer modelling to look at what anatomical adaptations underlay the positional behaviour and support usage trends observed (Chapter 4) and digitizing an enclosure which allowed the study of behaviour (positional and non-positional) enclosure usage trends and support usage preferences in such detail that has never been achieved before (Chapter 5).

Therefore the study of positional behaviour and support usage by the combination 1) musculoskeletal studies, and 2) identification of enclosure usage trends (with the aid of a CAD model), complements traditional behaviour studies in improving captive primate welfare. The interweaving threads in this thesis show how and why researchers should always strive to achieve a holistic approach for the study of captive primate welfare as anatomy, habitat structure and behaviour are all interlinked.

6.3 Executive summary

To reduce R&R, a combination of strategies can be employed. Firstly, tool-use based enrichment such as log-feeders and honey-pots can be used. Not only does this increase mental stimulation, anatomically gorilla feet are adapted to small flexion movements and such enrichment would allow them to display such movements. Provision of browse and/or increase in fibre quantity of diet composition is also a common way to reduce R&R. Encouragement of social behaviour (perhaps through keeping gorillas as a family group with juveniles and blackback(s)) is also recommended. However, different stereotypical behaviours stem from different reasons (as seen here between R&R and thumb sucking) and are likely to vary between individuals. Therefore I suggest that various enrichment methods be tested, with time-specific and individual-specific monitoring of behaviour before, during and after enrichment. This is because different types of enrichment are likely to have varying effects on each individual.

More vertical climbing needs to be encouraged in captivity. This can potentially be done by making sure food is available arboreally in patches and by providing a support environment that is similar to that of the wild (ie. small, vertical supports that can be grasped, medium sized (~3m in length) platforms) to encourage species-typical support usage. While large trees may look most suitable to the zoo visitor for a large bodied gorilla, the provision of multiple small arboreal supports are more likely to encourage more locomotion and species-typical support usage and positional behaviour. The combination of suitable feeding enrichment (eg. tool-used based enrichment or arboreal feeding) and preferred supports types would likely lead to more vertical climbing and more time spent on feeding and activity.

Building a SketchUp model of an enclosure can be very useful for studying enclosure usage trends and support usage preferences in detail. Support density can be quantified accurately and I found that to encourage usage of certain areas, perhaps support density in that area needs to be increased. The SketchUp model also provides easy visualisation of favoured areas and supports. I found that feeding areas were associated primarily with where they were fed and large horizontal supports were favoured. In addition, I found that a certain area that was lacking in strong horizontal supports, resulting in the siamangs not being able to use that area for brachiation. Such information is useful for zoos when it comes to drawing conclusions for enclosure design to encourage specific species-typical behaviour and support usage.

References

Ackland DC, Pak P, Richardson M et al. 2008. Moment arms of the muscles crossing the anatomical shoulder. Journal of Anatomy 213(4):383-390.

Akers JS, and Schildkraut DS. 1985. Regurgitation/reingestion and coprophagy in captive gorillas. Zoo Biology 4(2):99-109.

Aldrich-Blake F, and Chivers D. 1973. On the genesis of a group of siamang. American Journal of Physical Anthropology 38(2):631-636.

Alexander RM. 2003. Principles of animal locomotion. Princeton, New Jersey: Princeton University Press.

Altmann J. 1974. Observational Study of Behavior: Sampling Methods. Behaviour 49(3-4):227-266.

An K-N, Takahashi K, Harrigan TP et al. 1984. Determination of Muscle Orientations and Moment Arms. Journal of Biomechanical Engineering 106:280-828.

Arnold AS, and Delp SL. 2000. Rotational moment arms of the medial hamstrings and adductors vary with femoral geometry and limb position: implications for the treatment of internally rotated gait. Journal of Biomechanics 34(4):437-447.

Asa C. 2016. Weighing the options for limiting surplus animals. Zoo biology 35(3):183-186.

Bates K, Falkingham P, Rarity F et al. 2010a. Application of high-resolution laser scanning and photogrammetric techniques to data acquisition, analysis and interpretation in palaeontology. International Archives of Photogrammetry, Remote Sensing and Spatial Information Sciences XXXVIII:68-73.

Bates K, Maidment SC, Schachner ER et al. 2015. Comments and corrections on 3D modeling studies of locomotor muscle moment arms in archosaurs. PeerJ PrePrints.

Bates K, and Schachner E. 2012. Disparity and convergence in bipedal archosaur locomotion. Journal of the Royal Society Interface:rsif20110687.

Bates KT, Benson RBJ, and Falkingham PL. 2012a. The evolution of body size, stance and gait in Allosauroidea (Dinosauria: Theropoda). Paleobiology 38:486-507.

Bates KT, Falkingham PL, Hodgetts D et al. 2009a. Digital imaging and public engagement in palaeontology. Geology Today 25(4):134-139.

Bates KT, Maidment SC, Allen V et al. 2012b. Computational modelling of locomotor muscle moment arms in the basal dinosaur Lesothosaurus diagnosticus: assessing convergence between birds and basal ornithischians. Journal of Anatomy 220(3):212-232.

Bates KT, Manning PL, Hodgetts D et al. 2009b. Estimating mass properties of dinosaurs using laser imaging and 3D computer modelling. PLoS One 4(2):e4532.

Bates KT, Manning PL, Margetts L et al. 2010b. Sensitivity analysis in evolutionary robotic simulations of bipedal dinosaur running. Journal of Vertebrate Paleontology 30(2):458-466.

Bates KT, Manning PL, Vila B et al. 2008a. Three-dimensional modelling and analysis of dinosaur trackways. Palaeontology 51(4):999-1010.

Bates KT, Rarity F, Manning PL et al. 2008b. High-resolution LiDAR and photogrammetric survey of the Fumanya dinosaur tracksites (Catalonia): implications for the conservation and interpretation of geological heritage sites. Journal of the Geological Society 165(1):115-127.

Bayne K, Mainzer H, Dexter S et al. 1991. The reduction of abnormal behaviors in individually housed rhesus monkeys (*Macaca mulatta*) with a foraging/grooming board. American Journal of Primatology 23(1):23-35.

BBC. 2014a. Court in Argentina grant basic rights to orangutan. BBC.

BBC. 2014b. US chimpanzee Tommy 'has no human rights' - court. BBC.

BBC. 2016. SeaWorld to stop breeding orcas following controversy. BBC.

Bergl R, Ball R, Dennis P et al. 2014. Implementing a low-starch biscuit-free diet in zoo gorillas: The impact on behavior. Zoo biology 33(1):63-73.

Berkson G, and Mason WA. 1964. Stereotyped behaviors of chimpanzees: relation to general arousal and alternative activities. Perceptual and Motor Skills 19(2):635-652.

Berkson G, Mason WA, and Saxon SV. 1963. Situation and stimulus effects on stereotyped behaviors of chimpanzees. Journal of Comparative and Physiological Psychology 56(4):786.

Blanchard ML, Furnell S, Sellers WI et al. 2015. Locomotor flexibility in Lepilemur explained by habitat and biomechanics. American journal of physical anthropology 156(1):58-66.

Blaney E, and Walls D. 2004. The influence of a camouflage net barrier on the behaviour, welfare and public perceptions of zoo-housed gorillas. Animal Welfare 13:111-118.

Bloomsmith MA, Alford PL, and L. MT. 1988. Successful feeding enrichment for captive chimpanzees. American Journal of Primatology 16(155-164).

Bonnie KE, Ang MY, and Ross SR. 2016. Effects of crowd size on exhibit use by and behavior of chimpanzees (*Pan troglodytes*) and Western lowland gorillas (*Gorilla gorilla*) at a zoo. Applied Animal Behaviour Science 178:102-110.

Bowen R. 1980. The behaviour of three hand-reared lowland gorillas, Gorilla g. gorilla with emphasis on the response to a change in accommodation. Dodo: Journal of the Jersey Wildlife Preservation Trust.

Brand CM, Boose KJ, Squires EC et al. 2016. Hair plucking, stress, and urinary cortisol among captive bonobos (*Pan paniscus*). Zoo Biology: doi:10.1002/zoo.21320

Breuer T, Ndoundou-Hockemba M, and Fishlock V. 2005. First observation of tool use in wild gorillas. PLoS Biology 3(11):e380.

Britt A. 1996. Environmental influences on the behavioural ecology of the black-and-white ruffed lemur (*Varecia variegata variegata*). PhD Dissertation: University of Liverpool.

Brown NA, Pandy MG, Kawcak CE et al. 2003. Force-and moment-generating capacities of muscles in the distal forelimb of the horse. Journal of Anatomy 203(1):101-113.

Brown SG. 1988. Play behaviour in lowland gorillas: age differences, sex differences, and possible functions. Primates 29(2):219-228.

Bryant C, Rupniak N, and Iversen S. 1988. Effects of different environmental enrichment devices on cage stereotypies and autoaggression in captive cynomolgus monkeys. Journal of Medical Primatology 17(5):257-269.

Burkholder TJ, and Richard Nichols T. 2004. A Three Dimensional Model of the Feline Hindlimb. Journal of morphology 261(1):118-129.

CAHSJ H. 1965. The effects of environmental complexity on the stereotyped behaviour of children. Animal Behaviour 13:1-4.

Cannon CH, and Leighton M. 1994. Comparative locomotor ecology of gibbons and macaques: Selection of canopy elements for crossing gaps. American Journal of Physical Anthropology 93(4):505-524.

Carrasco L, Colell M, Calvo M et al. 2009. Benefits of training/playing therapy in a group of captive lowland gorillas. Animal Welfare 18:9-19.

Cartmill M, and Milton K. 1977. The lorisiform wrist joint and the evolution of "brachiating" adaptations in the hominoidea. American Journal of Physical Anthropology 47(2):249-272.

Casimir MJ. 1975. Feeding ecology and nutrition of an eastern gorilla group in the Mt. Kahuzi region (Republique du Zaire). Folia Primatologica 24(2-3):81-136.

Cassella CM, Mills A, and Lukas KE. 2012. Prevalence of regurgitation and reingestion in orangutans housed in North American zoos and an examination of factors influencing its occurrence in a single group of Bornean orangutans. Zoo biology 31(5):609-620.

Castles DL, and Whiten A. 1998. Post-conflict Behaviour of Wild Olive Baboons. II. Stress and Self-directed Behaviour. Ethology 104(2):148-160.

Chan SS, and Moran DW. 2006. Computational model of a primate arm: from hand position to joint angles, joint torques and muscle forces. Journal of neural engineering 3(4):327.

Channon AJ, Crompton RH, Gunther MM et al. 2010. Muscle moment arms of the gibbon hind limb: implications for hylobatid locomotion. Journal of Anatomy 216:446-642.

Chivers DJ. 1972. THE SIAMANG AND GIBBON IN MALAY PENINSULA. In: Rumbaugh DM, editor. Gibbon and Siamang: S. Karger. p 103-135.

Chivers DJ. 1977. The feeding behaviour of siamang (*Symphalangus syndactylus*). In: Clutton-Brock TH, editor. Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes. London: Academic Press. p 355-382.

Chivers DJ, Raemaekers JJ, and Aldrich-Blake FPG. 1975. Long-Term Observations of Siamang Behaviour. Folia Primatologica 23(1-2):1-49.

Christel M. 1993. Grasping techniques and hand preferences in Hominoidea. In: Preuschoft H, and Chivers D, editors. Hands of Primates. Vienna: Springer. p 91-108.

Clark FE, Fitzpatrick M, Hartley A et al. 2011. Relationship between behavior, adrenal activity, and environment in zoo-housed western lowland gorillas (*Gorilla gorilla gorilla*). Zoo biology 31(3):306-321.

Clarke AS, Juno CJ, and Maple TL. 1982. Behavioral effects of a change in the physical environment: a pilot study of captive chimpanzees. Zoo Biology 1(4):371-380.

Clubb R, and Mason G. 2002. A review of the welfare of zoo elephants in Europe: RSPCA Horsham, UK.

Coe JC, Scott D, and Lukas KE. 2009. Facility Design for Bachelor Gorilla Groups. Zoo Biology 28:144-162.

Collins C, and Marples N. 2016. The effects of zoo visitors on a group of Western lowland gorillas *Gorilla gorilla gorilla* before and after the birth of an infant at Dublin Zoo. International Zoo Yearbook.

Cowperthwaite G. 2013. Blackfish.

Crompton RH. 1980. *Galago* locmotion. Unpublished PhD dissertation: Harvard University.

Crompton RH. 1984. Foraging, Habitat Structure, and Locomotion in Two Species of Galago. In: Cant JGH, editor. Adaptations for foraging in nonhuman primates: contributions to an organismal biology of prosimians, monkeys, and apes. New York: Columbia University Press. p 73-111.

Crompton RH, Vereecke EE, and Thorpe SKS. 2008. Locomotion and posture from the common hominoid ancestor to fully modern hominins, with special reference to the last common panin/hominin ancestor. Journal of Anatomy 212:501-543.

Croney CC, and Newberry RC. 2007. Group size and cognitive processes. Applied Animal Behaviour Science 103(3–4):215-228.

Dagosto M, and Yamashita N. 1998. Effect of habitat structure on positional behavior and support use in three species of lemur. Primates 39(4):459-472.

Daley MA, and Usherwood JR. 2010. Two explanations for the compliant running paradox: reduced work of bouncing viscera and increased stability in uneven terrain. Biology letters:rsbl20100175.

Daniel S. 1999. Compliant walking in primates. Journal of Zoology 248(2):149-160.

Davenport RK, and Menzel EW. 1963. Stereotyped behavior of the infant chimpanzee. Archives of General Psychiatry 8(1):99-104.

Davey G. 2007. Visitors' Effects on the Welfare of Animals in the Zoo: A Review. Journal of Applied Animal Welfare Science 10(2):169-183.

Delp SL, Hess WE, Hungerford DS et al. 1999. Variation of rotation moment arms with hip flexion. Journal of Biomechanics 32(5):493-501.

Delp SL, Loan JP, Hoy MG et al. 1990. An interactive graphics-based model of the lower extremity to study orthopaedic surgical procedures. Biomedical Engineering, IEEE Transactions on 37(8):757-767.

DeSilva JM. 2008. Vertical climbing adaptations in the anthropoid ankle and midfoot: Implications for locomotion in Miocene catarrhines and Plio-Pleistocene hominins: University of Michigan.

Dingwell J, Cusumano J, Sternad D et al. 2000. Slower speeds in patients with diabetic neuropathy lead to improved local dynamic stability of continuous overground walking. Journal of Biomechanics 33(10):1269-1277.

Diogo R, Potau JM, Pastor JF et al. 2010. Photographic and Descriptive Musculoskeletal Atlas of Gorilla: With Notes on the Attachments, Variations, Innervation, Synonymy and Weight of the Muscles: CRC Press.

Doran DM. 1996. Comparative positional behavior of the African Apes. In: McGrew WC, Marchant LF, and Nishida T, editors. Great Ape Societies. Cambridge: Cambridge University Press. p 213-224.

Draper W, and Bernstein I. 1963. Stereotyped behavior and cage size. Perceptual and Motor Skills 16(1):231-234.

Elder AA. 2009. Hylobatid Diets Revisited: The Importance of Body Mass, Fruit Availability, and Interspecific Competition. In: Whittaker D, and Lappan S, editors. The Gibbons: New Perspectives on Small Ape Socioecology and Population Biology. New York: Springer. p 133-159.

Eriksen L. 2014. Marius the giraffe killed at Copenhagen zoo despite worldwide protests. The Guardian. London.

Erwin J, Mitchell G, and Maple T. 1973. Abnormal behavior in non-isolate-reared rhesus monkeys. Psychological Reports 33(2):515-523.

Fabregas MC, Guillen-Salazar F, and Garces-Narro C. 2011. Do naturalistic enclosures provide suitable environments for zoo animals? Zoo Biology 30:1-12.

Fischer JO, and Geissmann T. 1990. Group harmony in gibbons: Comparison between white-handed gibbon (*Hylobates lar*) and siamang (*H. syndactylus*). Primates 31(4):481-494.

Fleagle JG. 1976. Locomotion and Posture of the Malayan Siamang and Implications for Hominoid Evolution. Folia Primatologica 26(4):245-269.

Fleagle JG, and Mittermeier RA. 1980. Locomotor behavior, body size, and comparative ecology of seven Surinam monkeys. American Journal of Physical Anthropology 52(3):301-314.

Foley Jr JP. 1934. First year development of a rhesus monkey (*Macaca mulatta*) reared in isolation. The Pedagogical Seminary and Journal of Genetic Psychology 45(1):39-105.

Fossey D. 1983. Gorillas in the Mist. Boston: Houghton Mifflin Co. 326 p.

Fox GJ. 1972. Some comparisons between siamang and gibbon behaviour. Folia Primatologica 18(1-2):122-139.

Fox M. 1965. Environmental factors influencing stereotyped and allelomimetic behavior in animals. Laboratory Animal Care 15(5):363.

Franz TM, Demes B, and Carlson KJ. 2005. Gait mechanics of lemurid primates on terrestrial and arboreal substrates. Journal of human evolution 48(2):199-217.

Fraser A, and Broom D. 1990. Farm Animal Behaviour and Welfare. Bailliere Tindall: London, England.

Fujiwara S-i, and Hutchinson JR. 2012. Elbow joint adductor moment arm as an indicator of forelimb posture in extinct quadrupedal tetrapods. Proceedings of the Royal Society of London B: Biological Sciences 279(1738):2561-2570.

Garner J. 2006. Implications of recognising mechanistic differences in abnormal repetitive behaviour. In: Mason G, and Rushen J, editors. Stereotypic Behaviour in Captive Animals: Fundamentals and Applications for Welfare. CAB International: Wallingford. p 294-295.

Gatti S, Levréro F, Ménard N et al. 2004. Population and group structure of western lowland gorillas (*Gorilla gorilla gorilla*) at Lokoué, Republic of Congo. American Journal of Primatology 63(3):111-123.

Gebo DL. 1996. Climbing, brachiation, and terrestrial quadrupedalism: Historical precursors of hominid bipedalism. American Journal of Physical Anthropology 101(1):55-92.

Glatston AR, Geilvoet-Soeteman E, Hora-Pecek E et al. 1984. The influence of the zoo environment on social behavior of groups of cotton-topped tamarins, *Saguinus oedipus oedipus*. Zoo Biology 3(3):241-253.

Goerke B, Fleming L, and Creel M. 1987. Behavioral changes of a juvenile gorilla after a transfer to a more naturalistic environment. Zoo Biology 6(4):283-295.

Goldsmith ML. 1999. Ecological Constraints on the Foraging Effort of Western Gorillas (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. International Journal of Primatology 20(1):1-23.

Goodwin NR, Coops NC, and Culvenor DS. 2006. Assessment of forest structure with airborne LiDAR and the effects of platform altitude. Remote Sensing of Environment 103(2):140-152.

Gould E, and Bres M. 1986. Regurgitation and reingestion in captive gorillas: Description and intervention. Zoo Biology 5(3):241-250.

Graham KM, and Scott SH. 2003. Morphometry of *Macaca mulatta* Forelimb. III. Moment Arm of Shoulder and Elbow Muscles. Journal of Morphology 255:301-314.

Gursky S. 2000. Effect of seasonality on the behavior of an insectivorous primate, *Tarsius spectrum*. International Journal of Primatology 21(3):477-495.

Hatze H. 1977. A complete set of control equations for the human musculo-skeletal system. Journal of Biomechanics 10(11):799-805.

Heath C, Main D, Mullan S et al. 2016. Sequential sampling: a novel method in farm animal welfare assessment. animal 10(02):349-356.

Hebb D. 1947. Spontaneous Neurosis in Chimpanzees: Theoretical Relations with Clinical and Experimental Phenomena. Psychosomatic medicine 9(1):3.

Herrelko ES, Buchanan-Smith HM, and Vick SJ. 2015. Perception of available space during chimpanzee introductions: Number of accessible areas is more important than enclosure size. Zoo biology 34(5):397-405.

Hill SP. 2004. Behavioural and physiological investigations of welfare in captive western lowland gorillas *(Gorilla gorilla gorilla*): University of Cambridge, UK.

Hill SP. 2009. Do gorillas regurgitate potentially-injurous stomach acid during 'regurgitation and reingestion?'. Animal Welfare 18(2):123-127.

Honess PE, and Marin CM. 2005. Enrichment and aggression in primates. Neuroscience and Biobehavioral Reviews 30(2006):413-436.

Hong DF, Yang GD, and Wang ZH. 2008. Construction of Virtual Campus Based on ArcScene and SketchUp [J]. Computer Technology and Development 12:014.

Hosey GR. 2005. How does the zoo environment affect the behaviour of captive primates? Applied Animal Behaviour Science 90(2005):107-129.

Hosey GR, and Druck PL. 1987. The influence of zoo visitors on the behaviour of captive primates. Applied Animal Behaviour Science 18(1):19-29.

Hoy MG, Zajac FE, and Gordon ME. 1990. A musculoskeletal model of the human lower extremity: the effect of muscle, tendon, and moment arm on the moment-angle relationship of musculotendon actuators at the hip, knee, and ankle. Journal of Biomechanics 23(2):157-169.

Hunt K. 1991. Positional behavior in the Hominoidea. International Journal of Primatology 12(2):95-118.

Hunt KD, Cant JGH, Gebo DL et al. 1996. Standardised descriptions of primate locomotor postural modes. Primates 37:363-387.

Hutchins M, Hancocks D, and Calip T. 1978. Behavioral engineering in the zoo: a critique. International Zoo News 25(7):18-23.

Hutchinson JR. 2004. Biomechanical modeling and sensitivity analysis of bipedal running ability. I. Extant taxa. Journal of Morphology 262(1):421-440.

Hutchinson JR, Anderson FC, Blemker SS et al. . 2005. Analysis of hindlimb muscle moment arms in *Tyrannosaurus rex* using a three-dimensional musculoskeletal computer model: implications for stance, gait, and speed. Paleobiology 31(04):676-701.

Hutchinson JR, Rankin JW, Rubenson J et al. 2014. Musculoskeletal modeling of an ostrich (*Struthio camelus*) pelvic limb: influence of limb orientation on muscular capacity during locomotion. PeerJ PrePrints.

Hyde P, Dubayah R, Walker W et al. 2006. Mapping forest structure for wildlife habitat analysis using multi-sensor (LiDAR, SAR/InSAR, ETM+, Quickbird) synergy. Remote Sensing of Environment 102(1–2):63-73.

Inouye SE. 2003. Gorilla Biology, A Multidisciplinary Perspective. The Edinburgh Building, Cambridge: Cambridge University Press.

Isler K. 2005. 3D-Kinematics of Vertical Climbing in Hominoids. American Journal of Physical Anthropology 126:66-81.

Jensvold MLA, Sanz CM, Fouts RS et al. 2001. Effect of enclosure size and complexity on the behaviors of captive chimpanzees (*Pan troglodytes*). Journal of Applied Animal Welfare Science 4(1):53-69.

Johnson AE, Klumpp AR, Collier JB et al. 2002. Lidar-based hazard avoidance for safe landing on Mars. Journal of guidance, control, and dynamics 25(6):1091-1099.

Jouffroy Ft, and Lessertisseur J. 1959. Réflexions sur les muscles contracteurs des doigts et des orteils (*contrahentes digitorum*) chez les primates. Annales des Sciences Naturelles, Zoologie. p 211-235.

Jungers W, and Susman R. 1984. Body Size and Skeletal Allometry in African Apes. In: Susman R, editor. The Pygmy Chimpanzee: Springer US. p 131-177.

Kennard MA, and Willner MD. 1941. Tuberculosis and tuberculin tests in subhuman primates. The Yale journal of biology and medicine 13(6):795.

Kinani JF, and Zimmerman D. 2015. Tool use for food acquisition in a wild mountain gorilla (*Gorilla beringei beringei*). American Journal of Primatology 77(3):353-357.

Koolhaas J, Korte S, De Boer S et al. 1999. Coping styles in animals: current status in behavior and stress-physiology. Neuroscience & Biobehavioral Reviews 23(7):925-935.

Kranendonk G, and Schippers EP. 2014. A pilot study on the effects of a change in behavioural management on the behaviour of captive chimpanzees (*Pan troglodytes*). Applied Animal Behaviour Science 160:127-137.

Krevolin JL, Pandy MG, and Pearce JC. 2004. Moment arm of the patellar tendon in the human knee. Journal of Biomechanics 37(5):785-788.

Kuhar CW. 2008. Group differences in captive gorillas' reaction to large crowds. Applied Animal Behaviour Science 110(3):377-385.

Landsmeer J. 1961. Studies in the anatomy of articulation. II. Patterns of movement of bi-muscular, bi-articular systems. Acta Morphologica Neerlando-Scandinavica 3:304-321.

Leardini A, O'Connor JJ, Catani F et al. 1999. A geometric model of the human ankle joint. Journal of Biomechanics 32(6):585-591.

Leeds A, Elsner R, and Lukas K. 2016. The effect of positive reinforcement training on an adult female Western lowland gorilla's (*Gorilla gorilla gorilla*) rate of abnormal and aggressive behavior. Animal Behavior and Cognition 3(2):78-87.

Levy DM. 1944. On the problem of movement restraint: Tics, stereotyped movements, hyperactivity. American Journal of Orthopsychiatry 14(4):644.

Lieber RL, and Friden J. 2001. Clinical Significance of Skeletal Muscle Architecture. Clinical Orthopaedics and Related Research 383:140-151.

Liu W, Chen S-E, Boyajian D et al. 2010. Application of 3D LiDAR scan of a bridge under static load testing. Materials evaluation 68(12):1359-1367.

Loeffler DG. 1982. Regurgitation and reingestion in captive lowland gorillas: Oklahoma City Zoo.

Loy J. 1979. Play and aggression: A study of rhesus monkeys. By Donald Symons. Columbia University Press, New York. 1978. viii + 246 pp., figures, tables, bibliography, index. $20.00 (cloth). American Journal of Physical Anthropology 50(1):140-141.

Lukas K, Bergl R, Ball R et al. 2014. Implementing a low-starch biscuit-free diet in zoo gorillas: The impact on health. Zoo biology 33(1):74-80.

Lukas KE. 1998. A review of nutritional and motivational factors contributing to the performance of regurgitation and reingestion in captive lowland gorillas *(Gorilla gorillas gorilla)*. Applied Animal Behaviour Science 63(3):237-249.

Lukas KE, Hamor G, Bloomsmith MA et al. 1999. Removing milk from captive gorilla diets: The impact on regurgitation and reingestion (R/R) and other behaviors. Zoo Biology 18(6):515-528.

Lundberg A, Svensson O, Nemeth G et al. 1989. The axis of rotation of the ankle joint. Journal of Bone & Joint Surgery, British Volume 71(1):94-99.

Maestripieri D, and Ross SR. 2004. Sex differences in play among western lowland gorilla (*Gorilla gorilla gorilla*) infants: Implications for adult behavior and social structure. American Journal of Physical Anthropology 123(1):52-61.

Maidment SC, Bates KT, Falkingham PL et al. 2014. Locomotion in ornithischian dinosaurs: an assessment using three-dimensional computational modelling. Biological Reviews 89(3):588-617.

Mallapur A, Waran N, and Sinha A. 2005a. Use of Enclosure Space by Captive Lion-Tailed Macaques (*Macaca silenus)* Housed in Indian Zoos. Journal of Applied Animal Welfare Science 8(3):175-185.

Mallapur A, Waran N, and Sinha A. 2005b. Use of enclosure space by captive lion-tailed macaques (*Macaca silenus*) housed in Indian zoos. Journal of Applied Animal Welfare Science 8(3):175-186.

Mallinson JJ. 1982. The establishment of a self-sustaining breeding population of gorillas in captivity with special reference to the work of the anthropoid ape advisory panel of the British Isles and Ireland. American Journal of Primatology 3(S1):105-119.

Mallinson JJ. 1984. The breeding of great apes at the Jersey Wildlife Preservation Trust and a look into the future. Zoo Biology 3(1):1-11.

Manduell KL, Harrison ME, and Thorpe SKS. 2012. Forest Structure and Support Availability Influence Orangutan Locomotion in Sumatra and Borneo. American Journal of Primatology 74(12):1128-1142.

Maple TL. 1982. 14. Orangutan behavior and its management in captivity. The Orang Utan: its biology and conservation 2:257.

Maple TL. 1983. Environmental psychology and great ape reproduction.

Maple TL, and Finlay TW. 1987. Post-occupancy evaluation in the zoo. Applied Animal Behaviour Science 18(1):5-18.

Marzke MW. 1997. Precision grips, hand morphology, and tools. American Journal of Physical Anthropology 102(1):91-110.

Marzke MW, Marzke RF, Linscheid RL et al. . 1999. Chimpanzee thumb muscle cross sections, moment arms and potential torques, and comparisons with humans. American Journal of Physical Anthropology 110(2):163-178.

Masani K, Kouzaki M, and Fukunaga T. 2002. Variability of ground reaction forces during treadmill walking. Journal of Applied Physiology 92(5):1885-1890.

Masi S. 2011. Differences in gorilla nettle-feeding between captivity and the wild: local traditions, species typical behaviors or merely the result of nutritional deficiences? Animal Cognition 14:921-925.

Masi S, Cipolleta C, and Robbins MM. 2009. Western lowland gorillas (*Gorilla gorilla gorilla*) change their activity patterns in response to frugivory. American Journal of Physical Anthropology 71:91-100.

Mason G. 2006. Stereotypic behaviour in captive animals: fundamentals and implications for welfare and beyond. Stereotypic animal behaviour: fundamentals and applications to welfare:325-356.

Mason G, Clubb R, Latham N et al. 2006. Why and how should we use environmental enrichment to tackle stereotypic behaviour? Applied Animal Behaviour Science 102(2007):163-188.

Mason G, and Latham N. 2004. Can't stop, won't stop: is stereotypy a reliable animal welfare indicator? Animal Welfare 13:S57-S70.

Mason WA. 1960. The effects of social restriction on the behavior of rhesus monkeys: I. Free social behavior. Journal of Comparative and Physiological Psychology 53(6):582.

Mason WA. 1991. Effects of social interaction on well-being: development aspects. Laboratory animal science 41(4):323-328.

Mason WA, and Green PC. 1962. The effects of social restriction on the behavior of rhesus monkeys: IV. Responses to a novel environment and to an alien species. Journal of Comparative and Physiological Psychology 55(3):363.

McGraw WS. 1996. Cercopithecid locomotion, support use, and support availability in the Tai Forest, Ivory Coast. American Journal of Physical Anthropology 100(4):507-522.

McGraw WS. 1998. Comparative locomotion and habitat use of six monkeys in the Tai Forest, Ivory Coast. American Journal of Physical Anthropology 105(4):493-510.

McGrew WC. 1981. Social and cognitive capabilities of nonhuman primates: lessons from the wild to captivity.

McMahon FB, and McMahom JW. 1983. Abnormal Behavior: Psychology's View. Homewood, Illinois: Dorsey Press.

Meder A. 1989. Effects of hand-rearing on the behavioral development of infant and juvenile gorillas (*Gorilla g. gorilla*). Developmental Psychobiology 22(4):357-376.

Medler S. 2002. Comparative trends in shortening velocity and force production in skeletal muscles. American Journal of Physiology-Regulatory, Integrative and Comparative Physiology 283(2):R368-R378.

Meehan CL, Mench JA, Carlstead K et al. 2016. Determining connections between the daily lives of zoo elephants and their welfare: an epidemiological approach. PloS one 11(7):e0158124.

Melfi V, and Feistner A. 2002. A comparison of the activity budgets of wild and captive Sulawesi crested black macaques (*Macaca nigra*). Animal Welfare 11(2):213-222.

Mendez J, and Keys A. 1960. Density and composition of mammalian muscle. Metabolism-Clinical and Experimental 9(2):184-188.

Mendoza-Granados D, and Sommer V. 1995. Play in chimpanzees of the Arnhem zoo: self-serving compromises. Primates 36(1):57-68.

Meyer-Holzapfel M. 1968. Abnormal behaviour in zoo animals. Abnormal behavior in animals:476-503.

Michilsens F, Vereecke EE, D'Août K et al. 2010. Muscle moment arms and function of the siamang forelimb during brachiation. Journal of Anatomy 217(5):521-535.

Miller LJ, and Tobey JR. 2012. Regurgitation and reingestion in bonobos (*Pan paniscus*): Relationships between abnormal and social behavior. Applied Animal Behaviour Science 141(1):65-70.

Mills D, and Luescher A. 2006. Veterinary and pharmacological approaches to abnormal repetitive behaviour. Stereotypic animal behaviour: fundamentals and applications to welfare:325-356.

Modenese L, Phillips A, and Bull A. 2011. An open source lower limb model: hip joint validation. Journal of Biomechanics 44(12):2185-2193.

Monti RJ, Roy RR, and Edgerton VR. 2001. Role of motor unit structure in defining function. Muscle & nerve 24(7):848-866.

Moran G, and Sorensen L. 1984. The behavioral researcher and the zoological park. Applied Animal Behaviour Science 13(1):143-155.

Moreland AF. 1968. Nutritional factors in animal care. Canadian Medical Association Journal 98(19):900.

Morgan L, Howell SM, and Fritz J. 1993. Regurgitation and reingestion in a captive chimpanzee (*Pan troglodytes*). Lab animal.

Murray WM, Delp SL, and Buchanan TS. 1995. Variation of muscle moment arms with elbow and forearm position. Journal of Biomechanics 28(5):513-525.

Nash LT, Fritz J, Alford P et al. 1999. Variables influencing the origins of diverse abnormal behaviors in a large sample of captive chimpanzees (*Pan troglodytes*). American Journal of Primatology 48(1):15-29.

Nishihara T. 1995. Feeding ecology of western lowland gorillas in the Nouabale-Ndoki National Park, Congo. Primates 36(2):151-168.

Novak MA, and Suomi SJ. 1988. Psychological well-being of primates in captivity. American Psychologist 43(10):765.

Nurcahyo A. 1999. A Study of the Daily Behavior of Siamang (*Hylobates syndactylus*) in Bukit Barisan National Park. Unpublished Undergraduate Thesis, University of Gadjah Mada, Yogyakarta, Indonesia(In Indonesian).

O'Neill MC, Lee L-F, Larson SG et al. 2013. A three-dimensional musculoskeletal model of the chimpanzee (*Pan troglodytes*) pelvis and hind limb. The Journal of Experimental Biology 216(19):3709-3723.

Ochiltree AB. 1912. Some muscular anomalies in the lower limb. Journal of Anatomy and Physiology 47(Pt 1):31.

Odberg F. 1978. Abnormal behaviours: stereotypies. Proceedings of the first world congress on ethology applied to zootecnics, Madrid. p 475-480.

Ogihara N, Makishima H, Aoi S et al. 2009. Development of an anatomically based whole-body musculoskeletal model of the Japanese macaque (*Macaca fuscata*). American Journal of Physical Anthropology 139(3):323-338.

Olsson IAS, and Westlund K. 2007. More than numbers matter: The effect of social factors on behaviour and welfare of laboratory rodents and non-human primates. Applied Animal Behaviour Science 103(3–4):229-254.

Parnell RJ. 2002. Group size and structure in western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. American Journal of Primatology 56(4):193-206.

Payne R, Crompton RH, Isler K et al. 2006. Morphological analysis of the hindlimb in apes and humans. II. Moment arms. J Anat 208:725-742.

Pereira ME, and Fairbanks LA. 1993. Juvenile Primates: Life History, Development and Behavior, with a New Foreword: University of Chicago Press.

Pierrynowski MR. 1995. Three-dimensional analysis of human movement 215-256 p.

Pigeon P, Yahia L, and Feldman AG. 1996. Moment Arms and Lengths of Human Upper Limb Muscles as Functions of Joint Angles. Journal of Biomechanics 29(10):1365-1370.

Pomerantz O, Paukner A, and Terkel J. 2012. Some stereotypic behaviors in rhesus macaques (*Macaca mulatta*) are correlated with both perseveration and the ability to cope with acute stressors. Behavioural Brain Research 230(1):274-280.

Pond CL, and Rush HG. 1983. Self-aggression in macaques: five case studies. Primates 24(1):127-134.

Pontzer H, Raichlen DA, Wood BM et al. 2012. Hunter-gatherer energetics and human obesity. PLoS One 7(7):e40503.

Poole TB. 1988. Behaviour, housing and welfare of non-human primates. New developments in biosciences: Their implications for laboratory animal science: Springer. p 231-237.

Price EE, and Stoinski TS. 2007. Group size: Determinants in the wild and implications for the captive housing of wild mammals in zoos. Applied Animal Behaviour Science 103(3–4):255-264.

Pruetz JD, and McGrew WC. 2001. What does a chimpanzee need? Using natural behavior to guide the care and management of captive populations. Care and management of captive chimpanzees:17-37.

Quick DLF. 1984. An integrative approach to environmental engineering in zoos. Zoo Biology 3(1):65-77.

Raemaekers J. 1979. Ecology of sympatric Gibbons. Folia Primatologica 31(3):227-245.

Rails K, and Ballou J. 1982. Effects of inbreeding on infant mortality in captive primates. International Journal of Primatology 3(4):491-505.

Remis MJ. 1994. Feeding Ecology and Positional Behavior of Western Lowland Gorillas (*Gorilla Gorilla Gorilla*) in the Central African Republic. New Haven, Connecticut: Yale University.

Remis MJ. 1995. Effects of Body Size and Social Context on the Arboreal Activities of Lowland Gorillas in the Central African Republic. American Journal of Physical Anthropology 97:413-433.

Remis MJ. 1998. The Gorilla Paradox: The Effects of Body size and Habitat on the Positional Behaviour of Gorillas. In: Strasser E. FJ, editor. Primate Locomotion. New York: Plenum Press. p 95-106.

Remis MJ. 1999. Tree Structure and Sex Differences in Arboreality Among Western Lowland Gorillas (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. Primates 40(2):383-396.

Robbins L, and Margulis SW. 2014. The effects of auditory enrichment on gorillas. Zoo biology 33(3):197-203.

Robbins MM, Bermejo M, Cipolletta C et al. 2004. Social structure and life-history patterns in western gorillas (*Gorilla gorilla gorilla*). American Journal of Primatology 64(2):145-159.

Rooney MB, and Sleeman J. 1998. Effects of selected behavioral enrichment devices on behavior of western lowland gorillas (*Gorilla gorilla gorilla*). Journal of Applied Animal Welfare Science 1(4):339-351.

Rose MD. 1988. Orang-utan Biology: Oxford University Press.

Ross S, Wagner K, Schapiro S et al. 2011a. Transfer and Acclimatization Effects on the Behavior of Two Species of African Great Ape (*Pan troglodytes* and *Gorilla gorilla gorilla*) Moved to a Novel and Naturalistic Zoo Environment. International Journal of Primatology 32(1):99-117.

Ross SR, Calcutt S, Schapiro SJ et al. 2011b. Space use selectivity by chimpanzees and gorillas in an indoor–outdoor enclosure. American Journal of Primatology 73(2):197-208.

Ross SR, Schapiro SJ, Hau J et al. 2009. Space use as an indicator of enclosure appropriateness: A novel measure of captive animal welfare. Applied Animal Behaviour Science 121(1):42-50.

Ross SR, and Shender MA. 2016. Daily travel distances of zoo-housed chimpanzees and gorillas: implications for welfare assessments and space requirements. Primates 57(3):395-401.

Ross SR, Wagner KE, Schapiro SJ et al. 2010. Ape behavior in two alternating environments: comparing exhibit and short-term holding areas. American Journal of Primatology 72(11):951-959.

Rugg S, Gregor R, Mandelbaum B et al. . 1990. In vivo moment arm calculations at the ankle using magnetic resonance imaging (MRI). Journal of Biomechanics 23(5):495-501.

Ryan EB, Proudfoot KL, and Fraser D. 2012. The effect of feeding enrichment methods on the behavior of captive Western lowland gorillas. Zoo biology 31(2):235-241.

Sarmiento EE. 1994. Terrestrial Traits in the Hands and Feet of Gorillas. American Museum Novitates 10024(3091):1-56.

Schaller GB, and Emlen Jr JT. 1963. Observations on the ecology and social behavior of the mountain gorilla. African ecology and human evolution:368-383.

Schaller GE. 1963. The mountain gorilla: ecology and behavior.

Schmidt DA, Kerley MS, Porter JH et al. 2005. Structural and nonstructural carbohydrate, fat, and protein composition of commercially available, whole produce. Zoo Biology 24(4):359-373.

Schmidt M. 2011. Locomotion and postural behaviour. Advances in Science and Research 5(1):23-39.

Schulman YF, Farb A, Virmani R et al. 1995. Fibrosing cardiomyopathy in captive western lowland gorillas (*Gorilla gorilla gorilla*) in the United States: a retrospective study. Journal of Zoo and Wildlife Medicine(26):43-51.

Schultz AH. 1934. Some distinguishing characters of the mountain gorilla. Journal of Mammalogy 15(1):51-61.

Segal EF. 1989. Housing, care and psychological wellbeing of captive and laboratory Primates: Noyes Publications.

Sellers W, Margetts L, Bates K et al. 2013. Exploring Diagonal Gait Using a Forward Dynamic Three-Dimensional Chimpanzee Simulation. Folia Primatologica 84(3-5):180-200.

Sellers WI, and Manning PL. 2007. Estimating dinosaur maximum running speeds using evolutionary robotics. Proceedings of the Royal Society of London B: Biological Sciences 274(1626):2711-2716.

Serway RA, and Jewett JW. 2004. Physics for Scientists and Engineers: Thomson-Brooks/Cole.

Siegler S, Chen J, and Schneck CD. 1988. The Three-Dimensional Kinematics and Flexibility Characteristics of the Human Ankle and Subtalar Joints - Part I: Kinematics. Journal of Biomechanical Engineering 110:364-373.

Singh SP, Jain K, and Mandla VR. 2013. Image Based 3D Modeling of Campus (Department of Civil Engineering, IIT Roorkee, Uttarakhand, India) by Using SketchUp. International Journal of Advanced Civil Engineering and Architecture Research 2(1):pp. 65-71.

Smith N, Payne R, Jespers K et al. . 2007. Muscle moment arms of pelvic limb muscles of the ostrich (*Struthio camelus*). Journal of Anatomy 211(3):313-324.

Smith WS. 1882. The functions of the peroneus tertius muscle. Edinburgh Medical Journal 28:632-656.

Snowdon C, and Savage A. 1989. Psychological well-being of captive primates: general considerations and examples from callitrichids.

Spijkerman RP, Dienske H, Van Hooff JA et al. 1996. Differences in variability, interactivity and skills in social play of young chimpanzees living in peer groups and in a large family zoo group. Behaviour 133(9):717-739.

Spoor C, and Van Leeuwen J. 1992. Knee muscle moment arms from MRI and from tendon travel. Journal of Biomechanics 25(2):201-206.

Spoor CW, van Leeuwen JL, Meskers CGM et al. 1990. Estimation of instantaneous moment arms of lower-leg muscles. Journal of Biomechanics 23(12):1247-1259.

Stoinski TS, Hoff MP, and Maple TL. 2001. Habitat Use and Structural Preferences of Captive Western Lowland Gorillas (*Gorilla gorilla gorilla*): Effects of Environmental and Social Variables. International Journal of Primatology 22(3):431-447.

Straus WL. 1930. The foot musculature of the highland gorilla (*Gorilla beringei*). The Quarterly Review of Biology 5(3):261-317.

Straus WL. 1949. The riddle of man's ancestry. The Quarterly review of biology 24(3):200-223.

Tabachnick B, and Fidell L. 1996. Using Multivariate Statistics (3rd ed.). New York: HarperCollins.

Tabachnick BG, and Fidell LS. 1989. Using multivariate statistics. New York: Harper and Row.

Thorpe SKS, and Crompton RH. 2005. Locomotor Ecology of Wild Orangutans (*Pongo pygmaeus abelii*) in the Gunung Leuser Ecosystem, Sumatra, Indonesia: A Multivariate Analysis Using Log-linear Modelling. American Journal of Physical Anthropology 127:58-78.

Thorpe SKS, and Crompton RH. 2006. Orangutan Positional Behavior and the Nature of Arboreal Locomotion in Hominoidea. American Journal of Physical Anthropology 131:384-401.

Thorpe SKS, Crompton RH, Gunther MM et al. 1999. Dimensions and Moment Arms of the Hind- and Forelimb Muscles of Common Chimpanzees. American Journal of Physical Anthropology 110:179-199.

Thorpe SKS, Holder RL, and Crompton RH. 2007. Origin of Human Bipedalism as an Adaptation for Locomotion on Flexible Branches. Science 316:1328-1331.

Tutin CE. 1996. Ranging and social structure of lowland gorillas in the Lopé Reserve, Gabon. Great ape societies:58-70.

Tuttle RH. 2003. Gorilla Biology, A Multidisciplinary Perpective. The Edinburgh Building, Cambridge.: Cambridge University Press.

Tuttle RH, and Cortright GW. 1988. Orang-utan Biology: Oxford University Press.

Tuttle RH, and Watts DP. 1985. The positional behavior and adaptive complexes of *Pan gorilla*. In: Kondo S, editor. Primate morphophysiology, Locomotor Analyses and Human Bipedalism: University of Toyko Press. p 261-288.

Umberger BR, Gerritsen KG, and Martin PE. 2003. A model of human muscle energy expenditure. Computer methods in biomechanics and biomedical engineering 6(2):99-111.

Veasey J, Waran N, and Young R. 1996. On comparing the behaviour of zoo housed animals with wild conspecifics as a welfare indicator. Animal Welfare 5:13-24.

Venkataraman VV, Kraft TS, Desilva JM et al. 2013a. Phenotypic Plasticity of Climbing-Related Traits in the Ankle Joint of Great Apes and Rainforest Hunter-Gatherers. Human Biology 85(1):Article 14.

Venkataraman VV, Kraft TS, and Dominy N. 2013b. Tree climbing and human evolution. PNAS 110(4):1237-1242.

Vereecke EE, D'Aout K, Payne R et al. 2005. Functional analysis of the foot and ankle myology of gibbons and bonobos. Journal of Anatomy 206:453-476.

Visser J, Hoogkamer J, Bobbert M et al. 1990. Length and moment arm of human leg muscles as a function of knee and hip-joint angles. European journal of applied physiology and occupational physiology 61(5-6):453-460.

Viva! 2014. The slaughter of farmed animals in the UK.

Warren RD. 1997. Habitat use and support preference of two free-ranging saltatory lemurs (*Lepilemur edwardsi* and *Avahi occidentalis*). Journal of Zoology 241(2):325-341.

Watson J, Payne R, Chamberlain A et al. 2009. The kinematics of load carrying in humans and great apes: implications for the evolution of human bipedalism. Folia Primatologica 80(5):309-328.

Wells DL. 2005. A note on the influence of visitors on the behaviour and welfare of zoo-housed gorillas. Applied Animal Behaviour Science 93(1–2):13-17.

Wells DL, Coleman D, and Challis MG. 2006. A note on the effect of auditory stimulation on the behaviour and welfare of zoo-housed gorillas. Applied Animal Behaviour Science 100(3):327-332.

Wells DL, Hepper PG, Coleman D et al. 2007. A note on the effect of olfactory stimulation on the behaviour and welfare of zoo-housed gorillas. Applied Animal Behaviour Science 106(1):155-160.

Westneat MW. 2003. A biomechanical model for analysis of muscle force, power output and lower jaw motion in fishes. Journal of Theoretical Biology 223(3):269-281.

Williams SB, Wilson AM, Daynes J et al. 2008. Functional anatomy and muscle moment arms of the thoracic limb of an elite sprinting athlete: the racing greyhound (*Canis familiaris*). Journal of Anatomy 213(4):373-382.

Wittiger L, and Sunderland-Groves JL. 2007. Tool use during display behavior in wild cross river gorillas. American Journal of Primatology 69(11):1307-1311.

Wu G, Siegler S, Allard P et al. 2002. ISB recommendation on definitions of joint coordinate system of various joints for the reporting of human joint motion—part I: ankle, hip, and spine. Journal of Biomechanics 35(4):543-548.

Yamagiwa J, Maruhashi T, Yumoto T et al. 1996. Dietary and ranging overlap in sympatric gorillas and chimpanzees in Kahuzi-Biega National Park, Zaire. Great ape societies. Cambridge University Press, Cambridge:82-98.

Yamagiwa J, Mwanza N, Yumoto T et al. 1992. Travel distances and food habits of eastern lowland gorillas: a comparative analysis. Topics in primatology 2:267-281.

Yamagiwa J, Mwanza N, Yumoto T et al. 1994. Seasonal change in the composition of the diet of eastern lowland gorillas. Primates 35(1):1-14.

Yerkes RM. 1943. Chimpanzees: a laboratory colony.

Ying S, Li L, and Guo R. 2011. Building 3D cadastral system based on 2D survey plans with SketchUp. Geo-spatial Information Science 14(2):129-136.

Youlatos D. 2004. Multivariate analysis of organismal and habitat parameters in two neotropical primate communities. American Journal of Physical Anthropology 123(2):181-194.

Young R, Scott S, and Loeb G. 1993. The distal hindlimb musculature of the cat: multiaxis moment arms at the ankle joint. Experimental Brain Research 96(1):141-151.

Young RJ. 2003. Environmental Enrichment for Captive Animals: Blackwell Publishing.

Young RP, Scott SH, and Loeb GE. 1992. An intrinsic mechanism to stabilize posture-joint-angle-dependent moment arms of the feline ankle muscles. Neuroscience Letters 145:137-140.

Zaragoza F, Ibanez M, Mas B et al. 2011. Influence of environmental enrichment in captive chimpanzees (*Pan troglodytes spp.*) and gorillas (*Gorilla gorilla gorilla*): behavior and faecal cortisol levels. Revista Cientifica XXI(5):447-456.

Zheng N, Fleisig GS, Escamilla RF et al. . 1998. An analytical model of the knee for estimation of internal forces during exercise. Journal of Biomechanics 31(10):963-967.

Zihlman AL, McFarland RK, and Underwood CE. 2011. Functional Anatomy and Adaptation of Male Gorillas (*Gorilla gorilla gorilla*) With Comparison to Male Orangutans (*Pongo pygmaeus*). The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology 294(11):1842-1855.

Zimble DA, Evans DL, Carlson GC et al. 2003. Characterizing vertical forest structure using small-footprint airborne LiDAR. Remote Sensing of Environment 87(2–3):171-182.