COGNITIVE AND LOCOMOTOR STRATEGIES OF ARBOREAL LOCOMOTION IN NON-HUMAN APES AND HUMANS

by

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A thesis submitted to the
University of Birmingham
for the degree of
Doctor of Philosophy

School of Biosciences
College of Life and Environmental Sciences
University of Birmingham
February 2016

Abstract

All non-human great apes (NHAs) are endangered and understanding their behavioural ecology is vital for captive conservation efforts. Furthermore, as our closest living relatives, research into NHA behaviour and evolution can provide insight into our own origins. All non-human great apes are large (from 35 kg [adult female bonobo] to 200 kg [adult male gorilla]) and forage arboreally. The demands of the arboreal environment are complex and pose problems for large bodied apes. Arboreal supports are: dynamic and arranged randomly in relation to each other and to resources; resources are often situated at the end of compliant and weak branches; and supports that make up a travel route are broken by gaps between tree crowns. Therefore, arboreal travel for a large bodied ape is energetically demanding and risky due to the possibility of falling, and careful selection of supports is essential for safe and efficient locomotion. Selecting supports in a travel route would require an individual to possess some knowledge of the functional properties of supports and how supports may deform under an individuals' body weight. Similar cognitive processes have been observed in NHAs when selecting suitable tools, however, this has not been tested for in terms of arboreal support selection. This thesis investigates whether bonobos (*Pan pansicus*) select supports based on knowledge of their functional properties and which ecological factors influence decision making in human (*Homo sapiens*) tree climbers.

The influence of the functional properties of vertical ropes on support selection was tested in naturalistically housed bonobos (*Pan paniscus*). Two ropes were placed to either side of a food goal 2 m from the ground, the ropes differed such that one provided easy access to the goal and the other required more demanding postures. It was found that they selected ropes based on their distance from the goal and their flexibility, and that individual body specifications, such as hand preference and limb reach were also important. Human rope climbers were tested in a similar way, and the ropes differed in their distance, flexibility, and connectivity (ropes were tied back to an additional lateral rope which had to be untied before climbing). The human rope climbers performed well in the distance trail, however, the nature of the experimental apparatus meant that the additional level of manipulation required in the connectivity trial was not perceived before action for the majority of participants.

The ecological factors influencing decision making during arboreal locomotion were tested in human tree climbers in a natural canopy, using a novel combination of qualitative (the participants own words) and quantitative (observations of their behaviour) data. Participants were asked to collect four goals hung in the periphery of the tree canopy a total of three times each, their locomotor repertoires and support use were recorded along with electromyography of six muscles important in climbing (three in the hind limb, three in the fore limb). Post climb interviews revealed that the participants fell into two groups who considered risk avoidance and ease/efficiency the main factors influencing their decision making whilst climbing. The risk participants took longer to complete a climb, but saved time after their first climb. The ease and efficiency participants used bipedalism more than the risk group, and had a higher average EMG for their *vastus lateralis* (in their hind limb). However, there were no other significant differences between the two groups. It was concluded that speed is compensated for when risk is considered more important than ease and efficiency, however, repeated use of the same environment can decrease travel time due to an increased confidence in and memory of routes and supports.

In conclusion, this study demonstrates that the demands of the arboreal environment require knowledge of the functional properties of supports and that memory of routes may increase efficiency of arboreal locomotion.

For Granny and Benjamin, for inspiring me every day.

Acknowledgements

I would first like to thank Dr Jackie Chappell and Dr Susannah Thorpe for their continued support and supervision throughout my studies. I am eternally grateful for your guidance and inspiration over the last four years, and I look forward to many more years working alongside you both. I would also like to thank Emily Saunders for sharing this journey with me, picking me up and never failing in your friendship. I hope one day to repay you in kind a hundred times over, you truly are a wonderful friend.

Thank you to Twycross Zoo for granting permission for the observational studies of the bonobos and siamangs. Special thanks to Zak Showell and Charlotte MacDonald for your expertise and help in coordinating the data collection. Also thank you to Simon Childs and Tony Dobbs for your hard work and help in implementing the enclosure modifications, your essential knowledge of ape husbandry and for allowing me to volunteer as a member of your team in my spare time. And special thanks to Amber Cocks for your friendship, support, and interest throughout.

Thank you James Ashley and Naomi Mountford for your help coordinating participants in the rock climbing study. Thank you Chloe Walters for your student project on the bonobo social networks, on which the dominance rank used in my analysis was based. Thank you to Fran Childs and Maria Ntolopoulou for joining us on the cold, wet, and long March days for the human tree climbing study, you were indispensable!

Thank you to Red Point Climbing Centre, Birmingham, for hosting the rock climbing study, and special thanks to Philip and Paula Minal for your help in recruiting volunteers and organising the data collection, and thank you to James Hughes for your patience in setting and re-setting the climbing wall between each trial and for supervising the safety of the climbing participants. Thank you to King Edward VI High School for Girls for the hire of your gymnasium. Thank you to Canopy Access Ltd. for providing the safety equipment and to Ian Geddes for supervising the human tree climbing study. Finally thank you to my participants, the tree climbers, the gymnasts, and the rock climbers, and the bonobos and siamangs of Twycross Zoo.

This research was funded by the Natural Environment Research Council.

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CHAPTER ONE

GENERAL INTRODUCTION

"Structure, function and behaviour are interdependent, and the success of an organism can be marred by imperfections at any one of these three levels; but whatever the underlying cause, the fate of an organism is finally decided by its behavioural responses to its natural environment."

J. R. Napier & P. H. Napier

A handbook of living primates 1976

Chapter contents

In this thesis I investigate broadly, the concept that the complexities faced by large bodied primates moving around an arboreal environment requires simple decision making processes that could form the precursors necessary for the development of more complex behaviours such as tool use. First by exploring decision making at the individual support level, by breaking down support selection within an arboreal route to investigate individual functional properties of supports within a route. This represents a novel and naturalistic way to investigate non-human ape decision making and explores what knowledge about the physical environment non-human apes may possess. Much the same as in tool selection studies in which tools are selected based on their length or rigidity, non-human ape ability to select arboreal supports based on functional properties such as distance to a goal or flexibility are investigated. These experiments are then applied to humans performing similar climbing tasks (selecting and climbing vertical ropes), this is to investigate potential differences or similarities in the decision making process of non-human apes and humans. Furthermore, to extend the discussion to the evolutionary origins of behavioural or cognitive processes it is important to compare phylogenetically distinct, but related, species such as non-human apes and humans. Finally, by looking at decision making at the whole route level in a natural canopy environment the overriding ecological factors influencing whole route selection is explored. Observations of wild non-human ape arboreal behaviour suggests that due to the complexity of the canopy environment large bodied apes travelling arboreally are faced with a trade-off between risk avoidance and efficiency (Remis 1995, Hunt 2004, Thorpe et al. 2007, Myatt and Thorpe 2011), however, the ecological factors influencing decision making have not been directly tested before. By investigating how individual functional properties of supports (such as distance to a goal) and whole-environment ecological factors (such as risk avoidance) influence decision making in both non-human apes and humans I aim to provide a well-rounded view of how the canopy environment may have selected for various cognitive processes (such as body-schema and some knowledge of physical properties of the environment).

1.1 Understanding ape ecology

All non-human great apes are threatened in the wild and are suffering decreasing populations due to the destruction of natural habitats, poaching, hunting for bush meat, and civil wars (Walsh et al. 2003, Singleton et al. 2004, Hockings and Humle 2007, Reinartz et al. 2008). Bornean orangutans (*Pongo pygmaeus sp.*), Eastern gorillas (*Gorilla beringei*), chimpanzees (*Pan troglodytes sp.*), and bonobos (*Pan paniscus*) are listed as endangered, and Sumatran orangutans (*Pongo abelii*) and Western Lowland gorillas (*Gorilla gorilla gorilla*) are critically endangered (IUCN 2015). Captive breeding and the reintroduction of individuals to protected areas is becoming increasingly important for conservation (Mallinson 1995, Goossens 2005). An understanding of ape ecology is vital for both *ex situ* and *in situ* conservation programmes.

*1.1.1 The importance of the captive environmen*t

The challenge of any zoological collection is to conserve and elicit naturalistic behaviours and educate the general public about conservation and animal behaviour whilst providing the best standard of welfare for the animals in their care. Exhibiting animals that display wild-type behaviours is also key to financial success and customer enjoyment, people want to see and be close to animals behaving naturally (Hosey 2005, Fernandez et al. 2009). While knowledge of wild-type ecology is vital for successful breeding and reintroduction programmes (Baker 2002, Grundmann 2006, Beck et al. 2007, Beck 2010), it also informs welfare and captive care policies (Maple 2007) important for conservation and education. For example, understanding wild-type locomotor repertoires can inform enclosure design that will elicit natural behaviours and activity levels. For instance, wild orangutans are predominantly arboreal and exhibit complicated positional behaviours on thin flexible branches (Thorpe et al. 2009, Myatt and Thorpe 2011), therefore in captivity they require high structures and flexible supports that mimic the complexity of the forest canopy.

The study of captive, naturalistically housed populations offers a controlled environment in which researchers are able to investigate and observe in detail behaviours that are hard to capture or rare in the wild. For example, introducing novel objects into wild populations could be restricted; however Jordan (1982) and Torigoe (1985) were able to report comprehensive repertoires of manipulations of novel objects in captive populations of non-human primates across multiple species. Furthermore, handedness is often influenced by the task and context for which it was recorded (Fagot and Vauclair 1991, McGrew and Marchant 1997) and controlling for these is difficult in the wild. However, providing captive populations with a standardised bimanual feeding task (the tube task) enabled an accurate comparison across different populations and species' for the same task (see Hopkins 1995, Hopkins et al. 2003). Additionally, poor visibility in wild habitats could obscure the detail of subtle behaviours such as the biomechanics and function of different manual grips. However, captive populations enable these minute and precise behaviours to be observed more clearly (Jones-Engel and Bard 1996, Crast et al. 2009, Pouydebat et al. 2011). The captive environment also enables researchers to study the influence of ecological or functional factors of the environment or objects in isolation of other potential influences. For example, when investigating how other apes select tools researchers provided a choice of different tools that differed in one functional property only, such as length or rigidity (Mulcahy et al. 2005, Manrique et al. 2010), and could therefore determine how non-human apes understand these individual properties.

1.1.2 Ecology and evolution

As our closest living relatives, the study of extant non-human great ape (NHA) ecology is key to understanding our own origins (Williams et al. 2010). Behaviours shared by humans and other great apes can shed light on how a common ancestor may have behaved and can reveal the environmental factors that were important in the selection of great ape (including human) behavioural and anatomical adaptations (for example Russon et al. 1996, Parker and McKinney 1999, Schmitt 2003, Preuschoft 2004).

Modern humans are intelligent, terrestrial bipeds, and the origins of these two defining features have been explored through the study of our closest living relatives. The evolution of human bipedalism has been a contentious debate, with a division of thought between theories for a knuckle walking ancestor (Gebo 1992, 1996, Richmond et al. 2001) and an arboreal bipedal ancestor (Thorpe et al. 2007). The theory for a knuckle walking ancestor argues that shared morphological characteristics between African apes and humans (and fossil relatives) suggests our ancestors were adapted to knuckle-walking before bipedalism evolved (Richmond et al. 2001). Gebo (1992) similarly suggests that because humans and African apes share a similar pattern of heel strike (plantigrady) during locomotion which is not evident in non-great ape primates, our ancestors’ passed through a knuckle-walking phase before bipedalism evolved. However, the origin of bipedalism from knuckle-walking has been refuted, for example Preuschoft (2004) suggests that the body plan of an arboreal primate (such as hind-limb dominance, grasping hands and feet, distribution of mass throughout the limbs etc.) are also pre-adaptations to bipedalism and that all other apes are facultative bipeds and therefore it is likely that human terrestrial bipedalism evolved from arboreal bipedalism. Furthermore Kivell and Schmitt (2009) demonstrated that not all African apes share features of the hand and wrist thought to indicate knuckle-walking and that these features are also present in nonknucklewalking species, and therefore, when seen in our common ancestors suggest an adaptation to arboreality rather than terrestrial knuckle-walking. The theory for the origin of bipedalism from an arboreal bipedal ancestor argues that bipedalism evolved in the canopy environment because our hominin ancestors occupied a forested environment (for example Kovarovic and Andrews 2007) and retained adaptations for arboreal locomotion (such as long grasping forelimbs [Ward et al. 1999]). This is also widely supported by behavioural observations of extant NHAs (Hunt 1992, Schmitt 2003, Stanford 2006, Thorpe et al. 2007). Similarly, observations of behaviour and cognitive abilities have informed theories for the evolution of human intelligence (Russon et al. 1996, Parker and McKinney 1999). Whilst the intelligence (as demonstrated by complex technologies and problem solving skills, the use of language and communication, and the cultural transmission of knowledge etc.) of modern humans is unparalleled in other species, including other great apes (Rogers and Kaplan, 2012), the cognitive abilities of our closest living relatives indicate that complex cognition was an adaptation shared by our common ancestor. For example, non-human great apes can use tools and tool-sets (Shumaker et al. 2011 for a review), and there is some evidence to suggest they can plan for future events (Mulcahy et al. 2006, Osvath and Osvath 2008, Martin-Ordas et al. 2010). Furthermore, NHAs often live in complicated social systems (such as large multi-male multi-female groups) which require complex cognition to cope with the demands of predicting and reacting accordingly to the behaviour of conspecifics and maintaining numerous relationships (Whiten and Byrne 1997). Studies of culture and the ability to transmit cultural behaviours socially (such as different methods of tool use to extract a food resource) in NHAs also indicate that aspects of human cognition thought to be unique are shared by our closest living relatives (Whiten et al. 1999, Hohmann and Fruth 2003, van Schaik et al. 2003, Herrmann et al. 2007, van Schaik and Burkart 2011).

1.2 Demands of the arboreal environment

The rainforest canopy is a complex and demanding environment. It is three-dimensional and supports for locomotion are compliant and occur randomly in relation to one another and resources such as ripe fruit. Resources often lie at the end of thin flexible branches termed the terminal branch niche (Grand 1972, Cant 1992). Also, supports within and between neighbouring canopies are discontinuous, often requiring complex patterns of behaviour to cross large gaps in travel routes (Thorpe et al. 2007). Therefore, unpredictability, compliance, and discontinuity pose considerable problems for safe and energetically efficient arboreal travel.

1.2.1 The influence of body size

The demands of the functional environment are less important for small bodied primates. For example, more weight bearing supports are available to smaller species. Gebo and Chapman (1995) demonstrated that smaller primates (*Cercopithecidae sp*.) used small supports more often than larger species, and that these supports were more abundant in the environment. Although Madden et al. (2010) demonstrated that canopy connectivity is a fundamental factor influencing foraging behaviour for very small primates such as tamarins (400-500 g), they are able to use single and weak branches and therefore they have a greater number of functional supports available to them. However, the demands of arboreal travel become increasingly problematic for large bodied great apes (Cant 1992). The largest non-human great ape is the gorilla (adult males > 200 kg, Jungers 1985), yet members of these species' still forage arboreally (Remis 1995, 1999). Orangutans are the largest predominantly arboreal NHA and adults are 36 kg – 79 kg (females and males respectively, Smith and Jungers 1997). For species of this size compliance and support discontinuity are considerably problematic. For large bodied arboreal primates locomotion on thin and compliant supports is energetically demanding due to the loss of potential energy because of support deformation (Alexander 1991, Demes et al. 1995). On rigid supports, or during terrestrial locomotion elastic energy is stored in tendons and ligaments as these are first compressed (as the foot makes contact with the support) and released like a spring during push-off with the limb at the start of the next step (Alexander 1991). However, on compliant supports energy is wasted because the support deforms absorbing potential energy during the push-off phase (Alexander 1991, Demes et al. 1995). Further to this, Thorpe et al. (2007) demonstrated that detouring gaps in the canopy by climbing down and back up into the neighbouring tree crown comes at a substantial energetic cost (compared to crossing the gap directly using tree-sway behaviours).

1.2.2 The risk avoidance / energy efficiency trade off

Therefore, arboreal locomotion is energetically demanding, and balancing energetic expenditure and intake is essential for survival; however, avoiding falling from the canopy is potentially more important. For example, chimpanzees are adapted to arboreal locomotion and postures such as vertical climbing and arm-hanging (Hunt 1991), nevertheless they are predominantly terrestrial knuckle walkers (Doran 1996), and adopt a torso-pronograde posture on the ground using all four limbs in postural support. Pontzer and Wrangham (2004) demonstrated that chimpanzees retain these anatomical adaptations to arboreal travel despite the fact that they reduce the energetic efficiency of their more frequently used terrestrial locomotion. They concluded that rather than reducing energetic expense during infrequent bouts of arboreal locomotion these adaptations reduce the risk of falling during arboreal travel and that this is the more important selective factor. A risk “debt” cannot exist; if a great ape falls from the canopy it could be fatal. This becomes increasingly important for large species because the risk of bone fracture is greater (Jurmain 1997, Carter et al. 2008) and the risk of fatality from bone trauma is high in apes (Bulstrode 1990, Jurmain 1997). Therefore, as compliance increases and the weight bearing properties of supports decrease with larger body size, there exists a trade-off between energy efficient travel and risk avoidance. The ability to plan routes and select suitable supports is therefore, vital to safe and efficient arboreal travel.

1.3 Cognitive solutions to the risk avoidance / energy efficiency trade-off

1.3.1 Selection of supports

Selecting suitable supports in an arboreal route may require the individual to possess some understanding of where they are in space and some knowledge of the functional properties of supports, and thus how their movements will impact on their environment. For instance, although Chevalier-Skolnikoff et al. (1982) reported that wild orangutans tested branches before using them in locomotion (by applying some of their body weight to the new support whilst still maintaining weight bearing contact with other supports), selecting supports in a travel route by trial and error would not always be safe, efficient, or possible. If the next branch in a travel path occurs across a gap in the canopy testing it before use would be impossible; therefore, it is likely that NHAs possess some knowledge of the mechanical properties of canopy supports to overcome problems of discontinuity. Furthermore, testing every support before use would be time consuming and would restrict necessarily fast paced locomotion. However, chimpanzees are able to use rapid arboreal locomotion when hunting (particularly the ‘chaser’ in a hunting party, Boesch 2002) or when escaping aggression from conspecifics (specifically during behaviours such as ‘chase’ or ‘flee’, Nishida et al. 1999) without the need to test supports as they go and do not regularly fall due to misjudging supports. Therefore, it is likely they possess some ability to predict how supports will respond to loading and can select these successfully and rapidly when required to do so.

It has been shown that NHAs possess some knowledge of the functional properties of tools and can select tools based on properties such as length, rigidity, and connectivity (Tomasello and Call 1997, Povinelli 2000, Mulcahy et al. 2005, Herrmann et al. 2008, Manrique et al 2010). For example, Mulcahy et al. (2005) demonstrated that gorillas and orangutans were able to select a tool of the correct length to reach an out-of-reach food reward. The apes were given a choice of two straight wooden tools of differing lengths (one which would reach the reward, one which would not) which they could use to move a grape towards themselves. The apes selected the tool of the correct length, and were more likely to refuse to use tools that were presented to them but not of the appropriate length. Herrmann et al. (2008) demonstrated that four species of NHAs (orangutans, gorillas, bonobos, and chimpanzees) were able to select the correct tool based on its connectivity with a food reward with no previous exposure to the problem. Apes were given a choice of two pieces of cloth which differed in their contact with a piece of banana as the food reward. One piece of cloth enabled the ape to pull the reward towards them, the other was either not in contact with the banana, or ripped so that it would not bring the food reward towards the ape if it was pulled. The authors also used canes and ropes in a similar arrangement, so that selection of one would result in the apes being able to pull a reward towards them. The findings demonstrated that the NHAs were able to select tools with more complex functional properties with minimal experience of the problem. Similarly, Manrique et al. (2010) demonstrated that NHAs were able to select the correct tool to reach an out-of-reach food reward based on its rigidity or flexibility depending on the task requirements and could do so with only minimal visual inspection of the tool prior to selection. A similar knowledge of functional properties of supports for locomotion in the canopy environment could be employed during selection of supports in arboreal travel. As discussed, non-human ape and human ancestors evolved in the canopy environment therefore, the ability to select a support based on its functional properties could have formed the cognitive precursors to more complex abilities required for tool use.

1.3.2 Individual body specifications

To be able to predict how a support will behave when body weight is applied may also require flexible cognitive processes that are specific to an individual's body size or limb reach and individual limb preferences. All primates (including NHAs) possess simple motor planning abilities (such as the end-state comfort effect; Weiss et al. 2007, Chapman et al. 2010) and body schema (a sense of self in space that is updated continuously during movements; Holmes and Spence 2004, Iriki et al 1996, Maravita and Iriki 2004). The end-state comfort effect is a simple motor planning process by which an individual is able to select an awkward or uncomfortable grasping position prior to a hand action that results in a preferred final position (Weiss et al. 2007, Chapman et al. 2010). Weiss et al. (2007) demonstrated that cotton-top tamarins (*Saguinus oedipus*) adopted unusual grasping positions when presented with a cup containing a marshmallow suspended in various orientations. Chapman et al. (2010) went on to demonstrate that six species of lemurs also exhibited end-state comfort effect in a food extraction task. Lemurs were provided a stemmed cup placed inverted or up-right on a board. In the up-right position lemurs grasped the stem of the cup in a thumb-up position, in the inverted condition lemurs grasped it in a thumb-down position so that they could end the movement in a thumb-up position when they had transported the cup to access the food reward. Holmes and Spence (2004) demonstrated the existence of body schema in the form of an internal representation of the body (such as limb reach, height, and weight) and the peripersonal space (the space around the body) in human and non-human primates. Body schema can be used to explain how an individual understands (through internal processing of visual, somatosensory, and auditory inputs) that an object is within reach. It has also been demonstrated that when humans and non-human primates use tools that body schema are extended to include the length, shape, or reach of the tool (Maravita and Iriki 2004, Iriki et al. 1996).

In this way selecting supports based on individual reach and limb preference is also important. For example, use of a preferred limb has been associated with increased efficiency in humans (Goble and Brown 2008, Janssen et al 2011, Hughes et al. 2011) and primates including NHAs (*Cebus apella*, Fragaszy and Mitchell 1990; *Gorilla gorilla berengei*, Byrne and Byrne 1991; *Saguinus oedipus*, King 1995; *Macaca nemestrina*, Rigamonti et al. 1998; *Pan troglodytes*, Hopkins et al. 2002). Evidence for species level limb preference (which is the majority of the population preferring the same hand for the majority of tasks) is inconclusive for NHAs (Hopkins 2006, Cashmore et al. 2008). However, it has been demonstrated more consistently at the individual level, in which individuals have a preference for either the left or the right hand for different behaviours (Hopkins et al. 1993, Hopkins and de Waal 1995, Ingmanson 1998, Ingmanson 2005, Chapelain and Hogervorst 2009, Chapelain et al. 2011). Thus, it is likely it was the ability to specialise and not the direction of that specialisation (either left or right) that was important in evolutionary selection (Corballis 1989). Therefore it is likely that a sense of self in space – including individual anatomical specifics (such as handedness and length of limbs or reach) – combined with knowledge of the mechanical properties of available supports, underlies an ability to select supports in arboreal routes. It is suggested that the evolution of cognition in non-human primates was successive, and that simple processes such as motor planning could form the cognitive scaffold for more complex cognition such as that which is required for tool use (Johnson-Frey 2004, Vaesen 2012). Therefore, it is possible that the seemingly simple processes involved in support selection in an arboreal environment formed the precursors to more complex cognition.

1.3.3 The role of the arboreal environment in the evolution of cognition in primates

One of the most important factors defining non-human great ape biology and behaviour is their adaptation to, and use of, the arboreal environment (in terms of: morphology, Fleagle 1999, Preuschoft 2002, 2004, Payne et al. 2006a, 2006b; behaviour, Pontzer and Wrangham 2004, Thorpe and Crompton 2005, Thorpe et al. 2007, Myatt and Thorpe 2011; and cognition: Chevalier-Skolnikoff et al. 1982, Povinelli and Cant 1995, Hunt 2004). For example, NHAs have long forelimbs, a short torso, and relatively short hind limbs which are important for locomotion in the forest canopy (Preuschoft 2002, 2004). Kimura (1992) demonstrated that arboreal primates are hind limb dominant compared to quadrupedal terrestrial species (which means they produce greater forces in their hind limbs), an adaptation that was important in the evolution of bipedalism (Preuschoft 2004). Furthermore, NHA limb morphology also enables the greatest range of motion which is associated with locomotion in a complex three-dimensional arboreal environment (Payne et al. 2006a, 2006b). Similarly, observations of orangutan (the largest arboreal ape) positional behaviour indicate that flexible locomotor and postural repertoires enable safe and efficient use of compliant and discontinuous supports typical of the canopy environment (Thorpe and Crompton 2005, Thorpe et al. 2007, Myatt and Thorpe 2011).

Lastly, it has been suggested that complex cognition, such as that which is required for tool use, evolved as a response to the ecological demands faced by large bodied apes in an arboreal environment (Chevalier-Skolnikoff et al. 1982, Povinelli and Cant 1995, Hunt 2004). Chevalier-Skolnikoff et al. (1982) demonstrated that wild orangutans employ complex problem solving skills in negotiating the arboreal environment, and suggested that the demands of locomotion were most important in selecting for their higher cognitive abilities. Furthermore, Povinelli and Cant (1995) suggested that self-awareness as seen in NHAs (demonstrated by the mirror recognition test) most likely evolved in a large bodied arboreal NHA ancestor as an adaptation to cope with the demands of negotiating weak supports. They further suggested that other theories for the evolution of complex cognitive abilities, such as the demands of increasingly complex social systems (Byrne and Whiten 1988) could not explain the phenomenon self-awareness in NHAs. Although there exists a debate as to whether the mirror test demonstrates self-awareness (see Gallup et al. 2002 for a review), the suitability of this test is not of importance here. Regardless of the methods by which self-awareness was inferred, what is plausible is that the demands of the arboreal environment could select for some understanding of how an individuals' own body will impact on available supports. The evolution of other cognitive processes such as memory and route planning (Milton 1981, discussed in this Chapter, Section 1.4) have been attributed to the demands of foraging in the arboreal environment. Therefore, it is clear that the complex demands faced by NHAs in the forest canopy pose very specific problems that require flexible cognitive abilities that enable careful selection of supports and route planning.

1.4 Routes and planning

Selecting suitable supports in an arboreal route is therefore necessary (due to the physical demands of the environment as discussed in Section 1.2) and there is evidence to suggest that non-human apes possess the cognitive requirements to do so (as discussed in Section 1.3). Despite this very little is known about arboreal route planning in NHAs, or about how the functional environment influences their decision making in support selection and use during arboreal travel.

1.4.1 Spatial memory and route planning in non-human great apes

Although van Schaik et al. (2013) demonstrated that male orangutans long-call in the direction of their intended travel suggesting they at least plan their overall direction of travel in advance (although the causal relationship between the direction of travel and the direction of the long-call is difficult to separate), most previous studies of route planning have tested NHAs for spatial memory in a terrestrial environment (Menzel 1973, MacDonald 1994, Gibeault and MacDonald 2000). In these studies NHAs were shown food sites or given access to enclosures with known baited food sites and tested for memory of the locations of the food rewards. MacDonald and Agnes (1999) used similar methods but included food sites at different heights in an enclosure, but did not quantify support use or route planning in terms of support availability. These studies have shown that NHAs have good spatial memory and can choose the shortest routes or those that visit preferred food items efficiently (Menzel 1973, MacDonald and Agnes 1999, Gibeault and MacDonald 2000).

1.4.2 Spatial memory and route planning in other primates

Similar studies have revealed that other primates also possess spatial memory and select efficient (the shortest or near shortest) routes between goals (*Cercopithecus ascanius whitesidei*, MacDonald and Wilkie 1990; *Cercopithecus aethiops*, Cramer and Gallistel 1997), although evidence of multi-step route planning (for instance planning ahead of action to visit two or more resource sites in a single route) has been contested (Janson and Byrne 2007, Janson 2014). Some studies of other primates have looked more closely at routes and planning in a natural arboreal environment (Valero and Byrne 2007, Di Fore and Suarez 2007, Asensio et al. 2011) and the ecological factors that may select for cognitive functions such as memory (Milton 1981). These studies have revealed that other primates (*Hylobates lar*, Asensio et al. 2011; *Ateles geoffroyi yucatanensis*, Valero and Byrne 2007) change their direction of travel once they have depleted a resource (such as a fruiting tree) and that the straight-line travel paths are goal directed towards the next (out-of-sight) resource. It is likely that primates remember travel routes that follow recognisable land-marks such as ridgetops rather than remember the specific location of numerous different resource sites because this would require remembering thousands of individual and distinct sites (Di Fore and Suarez 2007).

1.4.3 Routes and decision making

Therefore, NHAs and other primates possess spatial memory and can select efficient routes to resources. The term ‘planning’ encompasses a broad spectrum of behaviours that require different cognitive and processing abilities (Chappell et al. 2012). Simple processes such as motor planning evolved early in the primate lineage (Chapman et al. 2010), whereas the existence of more complex cognitive processes such as episodic memory, even in NHAs, is still debated (Suddendorf and Corballis 2007). Despite this, there is evidence to suggest NHAs can plan in advance of action (Mulcahy et al. 2006, Osvath and Osvath 2008, Martin-Ordas et al. 2010) or at least possess the ability to plan for current needs (Dufour and Sterck 2008, Tecwyn et al. 2013).

Thus, it is likely that NHAs plan routes or use known pathways in arboreal travel, however, evidence for this is lacking in the literature, not necessarily because the phenomenon doesn't exist but because the research hasn't been done yet. Furthermore, the little that is known about route planning and spatial memory in NHAs is largely based on terrestrial tasks in which straight-line distances to resource sites has been used as a proxy for efficiency (Menzel 1973, MacDonald 1994, Gibeault and MacDonald 2000). In a terrestrial task locomotion is not constrained or influenced by the functional properties of supports, routes of travel are not restricted by discontinuity and support availability, and individuals are not faced with the potentially fatal risk of falling. These demands would be important in individual decision making and support selection *within* a route, on a smaller scale. However, the potential ecological influences on support selection within arboreal routes have not been directly tested in NHAs.

1.5 Thesis objectives and structure

As has been shown the arboreal environment is demanding, especially for large bodied non-human great apes. However, it is likely that these demands (such as patchily distributed and seasonal resources, discontinuity and compliance of supports, and the risk avoidance/energy efficiency trade-off) selected for cognitive abilities (such as simple motor planning, a sense of self in space and knowledge of individual anatomical specialisations, and the ability to plan ahead of action) to cope with these demands. However, there are clear gaps in the literature involving two important questions: do NHAs select supports within a route based on a knowledge of the functional properties of the supports, and to what extent is this decision making influenced by individual anatomy, such as limb reach or preference? Finally, which ecological factors are important in decision making in the canopy environment? These research questions form the basis of this thesis.

First, the influence of demanding suspensory postures on hand preference is explored in captive bonobos (*Pan paniscus*) in a symmetrical test environment (Chapter Two). By removing the complexity of the arboreal environment the influence of individual anatomical specifications on support choice can be investigated, for example, limb preference can be tested in a symmetrical test environment which is not possible in a natural canopy where available supports occur randomly to the left and right of resources.

Chapter Three explores the influence of simple functional properties of supports (such as distance from a food goal and flexibility) on the selection of ropes to use to access a hard-to-reach food goal in bonobos. This chapter also explores the effect of individual anatomical specifications such as limb reach and hand preference on support choice. Testing for a knowledge of functional properties of supports (such as distance from a goal and flexibility) is important because these factors define the physical properties of the canopy environment and pose specific problems for arboreal locomotion. Furthermore, there is evidence that NHAs use a similar knowledge of functional properties in tool selection and use, but it is likely that the demands of the arboreal environment selected for these abilities before complex cognition and tool use evolved. The captive environment provides the ideal setting in which the individual functional properties of supports (such as ropes for climbing) can be manipulated and controlled by the researcher. Using rope supports in this way enables the testing of these individual properties in isolation, for example, by providing a choice of two ropes that differ only in their distance from a food goal.

Chapter Four considers the role of social learning and dominance in support selection tested in a group setting. For example, the bonobos were tested in their social groups, meaning that individuals had the opportunity to observe and potentially socially learn which support to use to access a food reward. Therefore it is important to consider the influence of testing in a social setting on support selection and access of a food reward.

Bonobos are one of our closest living relatives and therefore are suitable subjects for answering questions about the origin of human behaviour and adaptations (Wrangham and Pilbeam 2002). Furthermore, they are an important model species for this study because they travel and forage arboreally (Susman et al. 1980, de Waal and Lanting 1997), and more frequently than their (and our other) closest relatives *Pan troglodytes* (Doran 1993). Bonobos also possess the cognitive abilities to use tools (Jordan 1982, Gold 2002), but do not do so habitually in the wild (Ingmanson 1996). This suggests that this ability may serve a different function in the wild, such as, for coping with complex relationships or play (Ingmanson 1996, Gruber et al. 2010) or for coping with the demands of arboreal travel (Chevalier-Skolnikoff et al. 1982, Povinelli and Cant 1995), or may have served a different function in the past and is maintained in modern populations.

Chapter Five explores rope selection based on simple functional properties such as distance to a goal, flexibility, and connectivity in human rope climbers. Testing humans in a similar setting (such as in a symmetrical controlled environment) provides an important comparison to the bonobo experiments in Chapters Two – Four. By demonstrating that the study of modern human behaviour can further our understanding of non-human ape behavioural ecology because we can ask human participants to perform specific tasks (such as untying a flag) rather than designing a test environment which we hope will reveal behaviours of interest in NHAs. Furthermore, testing a spectrum of apes (including humans) enables more justifiable observations of behavioural responses to the different functional properties of supports being tested.

Finally, the ecological factors influencing decision making in human tree climbers is explored with a novel combination of qualitative (participants own words) and quantitative (observations of their behaviour) data (Chapter Six). Testing humans climbing in a natural canopy is important because two defining features of modern humans (intelligence and bipedalism) evolved in this environment (for example, Chevalier-Skolnikoff et al. 1982, Thorpe et al. 2007). Furthermore, human participants can verbally explain the ecological factors influencing their decision making during climbing which can only be inferred in NHAs from observations of their behaviour. Therefore, we can investigate important questions such as: is there a risk avoidance/energy efficiency trade off? And, what are the most important ecological factors influencing decision making during arboreal locomotion?

CHAPTER TWO

ARBOREAL POSTURES ELICIT HAND PREFERENCE WHEN ACCESSING A HARD-TO-REACH FOOD GOAL IN CAPTIVE BONOBOS (*PAN PANISCUS*)

Abstract

Complex arboreal, and in particular, suspensory postures may elicit a preference for the strongest limb to be used in postural support in large bodied primates. However, it has been suggested that for chimpanzees fishing for ants in arboreal postures it is ambilaterality rather than a preference for a particular hand that was selected for (Marchant and McGrew 2007). We recorded hand preference of captive bonobos manipulating a food goal during terrestrial and arboreal postures in a symmetrical environment. When accessing the food goal in the arboreal position the bonobos adopted demanding and predominantly suspensory postures. There was no population level preference for manipulating the goal with either hand in either the terrestrial or arboreal positions. However, four out of seven individuals demonstrated a significant preference when manipulating the goal (two were left handed, two were right handed) in the arboreal position compared to one individual in the terrestrial position. This suggests that in a symmetrical arboreal environment individuals are able to use their preferred or strongest limb for postural support, resulting in a bias for the opposite hand for manipulation. However, the hand that is preferred for postural support differs between individuals. More data is needed for different environments and species to fully understand the influence of the demand of arboreal postural support and environmental complexity on hand preference.

Chapter contents

2.1 Introduction

Laterality of hand use is the preference for using one hand over the other for the majority of the time or for particular tasks (Harris 1974). In humans it is well documented that a preference for one hand (the dominant hand) is associated with enhanced motor performance such as strength, speed, and accuracy (Goble and Brown 2008, Janssen et al. 2011, Hughes et al. 2011). Evidence for enhanced performance for the preferred hand also exists for other primates (*Cebus apella*, Fragaszy and Mitchell 1990; *Gorilla gorilla berengei*, Byrne and Byrne 1991; *Saguinus oedipus*, King 1995; *Macaca nemestrina*, Rigamonti et al. 1998; *Pan troglodytes*, Hopkins et al. 2002). However, most studies of laterality of hand use in non-human primates (hereafter NHP) have been concerned with determining the origin of right handedness in humans (see Cashmore et al. 2008). This ignores the important role of laterality of hand use in NHP in providing key information regarding the relationship between behaviour and brain function (MacNeilage 1993) and the behavioural ecology of NHP.

Since individuals (NHP) vary in whether the left or right hand is preferred, it is the ability to specialise and not the direction (which hand is preferred) that is important in evolution (Corballis 1989). The ability to specialise with either hand results in neurological benefits for the individual such as increased neural capacity (Vallortigara and Rogers 2005). Furthermore, it has been shown that strongly lateralised wild chimpanzees (that use only one hand but either the left or the right during a tool use activity) benefit from increased foraging success compared to ambilateral individuals using both hands indiscriminately (McGrew and Marchant 1999). Therefore it is likely that individual handedness to either side can play an important role in increasing evolutionary fitness.

Studies of NHP handedness are often focussed on terrestrial foraging behaviours (e.g. Llorente et al. 2009, Hopkins et al. 2011) or tool use (e.g. O'Malley and McGrew 2006, Marchant and McGrew 2007). However, locomotion is one of the most demanding physical behaviours a primate performs and morphological and anatomical asymmetries in paired limbs for foraging must also be influenced by the demands of the locomotion and postures required to access the food source (Hopkins 2006). Nevertheless, few studies have addressed the specific influence of energetically demanding postures and locomotion (such as suspensory postures where a significant proportion of the body weight is borne by one forelimb) on handedness (Morcillo et al. 2006, Hopkins 2008, Peters and Rogers 2008). These studies indicate that a complex interaction between handedness and the type of locomotion or posture exists. Morcillo et al. (2006) found a right bias for the leading limb in common, non-demanding locomotor behaviours (such as walking) but a left bias for some demanding locomotor and postural behaviours (such as descending and hanging) in chimpanzees. Peters and Rogers (2008) found a right bias for leading limb in gap crossing locomotion in wild orangutans, and individual hand preference for feeding behaviours. Furthermore, there is some evidence to suggest that such behavioural asymmetries result in morphological asymmetries of forelimb bones (Sarringhaus et al. 2005, Hopkins 2008). Similarly, Carlson et al. (2006) suggested that degree of arboreality, rather than individual locomotor repertoires plays an important role in long bone morphology in chimpanzees. It has also been suggested that maintaining balance or body weight are important factors influencing direction and strength of laterality (Hopkins 1993, Hopkins et al. 1993, Vleeschouwer et al. 1995). Therefore, postural and locomotor behaviour, and the degree to which a forelimb provides postural support or contributes to balance (McGrew and Marchant 1997a) should be included in any study that seeks to interpret laterality within an ecological context. Despite this most studies that include posture or locomotion have concentrated on non-demanding postures or on those that are important for understanding human evolution, such as the differences between quadrupedal and bipedal standing (Hopkins 1993, Westergaard et al. 1998, Braccini et al. 2010).

Among the primates, the role of positional behaviour in hand preference is particularly crucial for the large-bodied great apes. The arboreal positional behavioural repertoires' of great apes (excluding humans) includes demanding suspensory postures (Doran 1996, Thorpe et al. 2005). Although *Pan spp*. and *Gorilla spp*. are habitual terrestrial quadrupeds they still need to move frequently and proficiently in the forest canopy (Remis 1995, Doran 1996). Therefore, arboreal suspensory postures may be of particular importance in the study of laterality of hand use because at least one forelimb is required to support the majority of the body's weight (Hunt 1996). Some studies have considered how handedness may influence arboreal postures or *vice versa* (Morcillo et al. 2006, Rogers and Kaplan 1996, Marchant and McGrew 2007, Vleeshouwer et al. 1995). Other studies have included arboreality but found little evidence for its influence on laterality (Harrison and Nystrom 2008, Fletcher and Weghorst 2005, Marchant and McGrew 1996). However, in these studies arboreality was generally defined in terms of height from the ground or support type (for example, on or off the ground) and did not specify if demanding suspensory postures were used. Marchant and McGrew (2007) included the proportion of body weight borne by the limb not being used for manipulation (e.g. providing "major" support) but found no evidence that these postures elicited laterality for foraging behaviours in a complex, natural canopy environment. Therefore the influence of energetically demanding postures (such as forelimb suspension) on handedness is currently unclear.

Individuals may have a preferred hand for manipulatory behaviours (such as food processing) or a preferred limb for energetically demanding postural support. In the case of an individual expressing a preferred limb for postural support it could be argued that during arboreal suspensory postures where one limb must be used to maintain a significant proportion of body weight a hand bias for the opposite hand for manipulatory behaviours may be induced. Vleescouwer et al. (1995) tested the influence of different postures with increasing demand for stability, from sit through quadrupedal stand to bipedal stand to suspension ("hanging on bars") in captive bonobos. They found that all five subjects demonstrated a left-hand bias while moving from sitting to quadrupedal standing to bipedal standing. They also found increased individual laterality in an arboreal suspensory posture ("hanging on bars") and concluded that unstable postures challenge balance and therefore induce lateralisation for stability. Furthermore, Hook and Rogers (2002) suggested that limb preference during leaping and landing (which are energetically demanding behaviours) in marmosets was due to asymmetry of limb strength e.g. the preference for leading with a particular limb in leaping and landing was due to having a greater strength in the preferred limb. There is evidence to suggest that when one limb (of a pair) is preferentially used for demanding postures asymmetric loading leads to asymmetry of muscle and bone morphology (Sarringhaus et al. 2005, Hopkins 2008). Over time, muscle strength builds in response to repetitive loading which can result in asymmetric morphology (Shaw and Stock 2009) and potentially the ability to produce or withstand greater forces.

Alternatively however, arboreal postures could induce ambipreference because fatigue in the weight-bearing limb might result in an increased number of hand changes within a single bout of a positional behaviour (Marchant and McGrew 2007). Marchant and McGrew (2007) reported the influence of different arboreal postures on hand use in wild chimpanzees during an ant fishing task. They found just over half of their subjects were ambilateral and that the frequency of hand changes for the tool using hand and the proportion that the non-dominant hand was used for postural support were positively correlated. They were responding to the suggested theory that chimpanzees were forced to use either the left or the right hand (ambilateral) because of the random position of ant holes in relation to locations in the trees that permitted sitting or standing for the chimpanzees (Nishida 1977).

It is clear that systematic data for arboreal suspensory postures are lacking in studies of primate laterality. Without this it is difficult to predict if arboreality does induce laterality or ambilaterality which is important in further understanding the link between NHP ecology and behaviour. Therefore, the aim of this study was to investigate the influence of suspensory (arboreal) and compressive (terrestrial) postures on hand preference for manipulating a food goal. Furthermore, testing arboreal postures recorded in a symmetrical environment removes the influence of support availability and complexity associated with a rainforest canopy and could reveal the direct influence of demanding postures on laterality. The two competing hypotheses are:

- The stability hypothesis argues that individual laterality is increased in arboreal postures where a forelimb is used for postural support due to increased demand for stability and limb strength (as suggested by Vleeschouwer et al. 1995 and Peters and Rogers 2008).

- The fatigue hypothesis argues that laterality is reduced (individuals are ambilateral) in arboreal postures where a forelimb is used for postural support because of an increase in change of hands due to fatigue (as found by Marchant and McGrew 2007).

Bonobos represent a useful model species for this study as they forage both terrestrially and arboreally (Susman et al. 1980, de Waal and Lanting 1997) and use suspensory postures

(Susman et al. 1980, Susman 1984, Doran 1993). Yet few studies have tested the influence of arboreal postures on laterality in bonobos (Vleeschouwer et al. 1995, Harrison and Nystrom 2008).

2.2 Methods

All data were collected by NKIH from subjects housed at a zoo in the UK. At the beginning of the study the zoo housed 11 bonobos in two family groups that have adjacent but separate indoor enclosures and a single outdoor enclosure that each group accessed on alternate days. See Table 2.1 for study subjects.

Table 2.1 Details of study subjects

Individual	Sex	Age group	Age at start of study
AdfE	Female	Adult	23 years
AdfA	Female	Adult	17 years
AdfB	Female	Adult	36 years
AdfC	Female	Adult	14 years
AdfD	Female	Adolescent	8 years
InmB	Male	Infant	3 years
InfA	Female	Infant	3 years

The indoor enclosures were approximately 167m^2 furnished with vertical, angled, and horizontal poles, connected with various ropes and flattened hose pipes. Each enclosure also had 3 separate off-show bed areas that the bonobos had access to throughout the day, except when these areas were being cleaned. The four viewing windows (where the arboreal food goal and ropes were positioned) were 1.5 m x 2 m.

2.2.1 Experimental procedure

The three testing conditions were: ‘no goal’; ‘terrestrial’; and ‘arboreal’. The arboreal testing period ran from July 2013 to September 2013, and the terrestrial and no goal testing period ran from December 2014 to January 2015. Hand use and positional behaviour were recorded (Table 2). Food goals were used in the terrestrial and arboreal testing conditions. These were mesh cages constructed of metal containing a hollow plastic ball with one small opening inside. Food could be placed inside the plastic ball so that the bonobos had to pluck or poke the food reward out. One food goal was spherical (mesh 150 mm^2 – 50 mm^2) and measured 0.4 m diameter, and the other was a cube (mesh size 50 mm^2) measuring 0.16 m across.

In the terrestrial experiments two food goals were placed in the enclosure at 1-1.2 m from the ground suspended from a central horizontal pole so that the bonobos could access it from the ground (when sitting or standing). For the arboreal experiments one food goal was placed 2 m from the ground above a viewing window, with ropes placed on both sides to allow the bonobos to access the food goal. See Figure A2.1 (appendix) for examples of goal use in the different experiments. A second food goal was placed elsewhere in the enclosure to reduce aggressive competition for the main goal, however all arboreal data were collected from the central goal above the viewing window.

In both the terrestrial and arboreal testing conditions interactions with the food goals were videoed (Sanyo Xacti CG10 camera, 30 frames per second) from a central viewing position for 30 minutes from the time the subjects were given access to the enclosure, and videos were analysed at a later date. The food reward was usually depleted within the first 15 minutes of each session after which interaction with the goal decreased substantially (with an average of 46 interactions in the first 15 minutes per individual and an average of 28 in the last 15 minutes). Videos were replayed once at normal speed for each subject that interacted with the food goals so that continuous focal data were collected for each individual for each session (Altmann 1974).

In the no goal testing period hand preference was recorded live for ground foraging behaviours (hand-to-mouth feeding and manipulation of food item). Continuous focal data were collected for each individual for 15 minutes in each session.

Table 2.2 details the contextual behaviours for which hand preference was recorded, the action of the hands, and the associated postures from the arboreal testing condition. Goal manipulations (recorded in the arboreal and terrestrial conditions) were touch (touch outer metal cage), power manipulation (hold inner plastic ball in a power grip), and precision manipulation (poke or pluck food out of the opening in the inner plastic ball). Precision manipulations could be unimanual (the dominant hand plucks food out of the opening in the inner plastic ball) or bimanual (the non-dominant hand holds the inner plastic ball while the dominant hand plucks food from the opening). Handedness was recorded in bouts (with duration in seconds). A new bout started when the role of either hand changed (McGrew and Marchant 2001); when the subject altered their posture; or when the subject had been still for 10 seconds or more (Hopkins 1995). The role of each hand was recorded as either: dominant (the hand the action was performed with); non-dominant (second hand in bimanual manipulation); both hands used equally; rest; postural support; or other. Arboreal posture was recorded as either: forelimb suspend combination, in which body weight was borne by at least one forelimb in combination with balance or support from hind-limbs in suspension or compression; unimanual forelimb suspend, in which body weight was borne by one forelimb only; and other, which included rare and brief postures such as hind-limb suspend or leap from the ground.

Table 2.2. Contextual behaviours and categories of hand action ([1]adapted from McGrew and Marchant 2001, [2] adapted from Hunt et al. 1996)

Contextual behaviour	**Description**
Hand to mouth feeding	Hand transports food to the mouth
Manipulation of food item	Manipulation of food item e.g. tearing or pulling apart
Goal manipulation – touch	Touches outer metal cage of the goal (usually in a power grip)
Goal manipulation – power	Holds inner plastic ball of the goal in a power grip
Goal manipulation – precision[1]	Unimanual – plucks or pokes food out of the hole in the inner plastic ball Bimanual – dominant hand plucks or pokes food out of the hole in the inner plastic ball while the other hand (non-dominant) holds the inner plastic ball in a power grip
Hand action[1]	**Description**
Dominant	Hand is dominant in unimanual or bimanual manipulation tasks, the hand the action is performed with
Non-dominant	Hand is non-dominant during bimanual manipulation task, e.g. supporting the item being manipulated
Both	Both hands are used equally in the same action, e.g. pulling an item
Rest	Hand is not performing any specific task or is not involved in postural support
Postural support	Hand is weight bearing in postural support
Other	Hand is involved in some other action that does not fall into one of the contextual behaviour categories, e.g. grooming

(continued on next page)

Table 2.2 Continued

Arboreal postures[2]	**Description**
Forelimb suspend combination	Body weight is borne by at least one forelimb in suspension, a combination of forelimb-hind limb suspend, or a combination of forelimb suspend hind-limb compression
Unimanual forelimb suspend	Body weight is borne by one forelimb in suspension
Other	Other postures included – hind-limb suspend, hind-limb compression (bipedal stand), and leap or jump

2.2.2 Data analysis

For the three conditions (no goal, terrestrial, and arboreal) a binomial test (two-tailed, p = 0.5) was used to determine individual handedness using counts of left or right hand use (minimum of 6). All analyses were carried out in R version 3.1.0 (2014-04-10), and alpha was set at 0.05. A handedness index score (HI) was also calculated using the formula (R-L)/(R+L), R being the number of right handed bouts and L being the number of left handed bouts as in Hopkins (1999). This indicates the direction and strength of preference from -1 to +1; negative values indicate a left hand preference and positive values indicate a right hand preference.

2.2.3 Correlation of hand changes and proportion of bouts with a dominant hand for posture

If the fatigue hypothesis is correct the rate of change of manipulating hands should be positively correlated with the proportion of bouts in which one hand provides postural support. To test this sequences of bouts of arboreal goal manipulation from all individuals were analysed. Each sequence was made up of a series of behaviours from the point at which the individual first approached the equipment, through any interaction with the food goal, to the moment they returned to the ground. Only sequences that included manipulation of the goal were included. These sequences were therefore equivalent to Marchant and McGrew's (2007) 'sessions'. This method allowed quantification of the number of bouts of manipulation of the food goal and the number of hand changes to be obtained from each sequence. In addition the proportion of bouts of manipulation for which one hand was used in postural support could be obtained. This was calculated by dividing the number of bouts for which the non-dominant hand was used in postural support by the total number of bouts of manipulation in a sequence.

2.3 Results

Over the three different testing periods 2726 bouts of manipulations of the goals or feeding behaviours were collected. The majority arboreal postures included the use of a forelimb as the main weight bearing limb (Figure 2.1). Of these 89.5% were forelimb suspend combination (defined as forelimb suspension or a combination of forelimb-hind limb suspension and forelimb suspend hind-limb compression). All individuals performed in each testing period except one adult female (AdfE) who did not feature in the no goal condition because she was consistently out-of-sight in the off show areas of the enclosure during data collection.

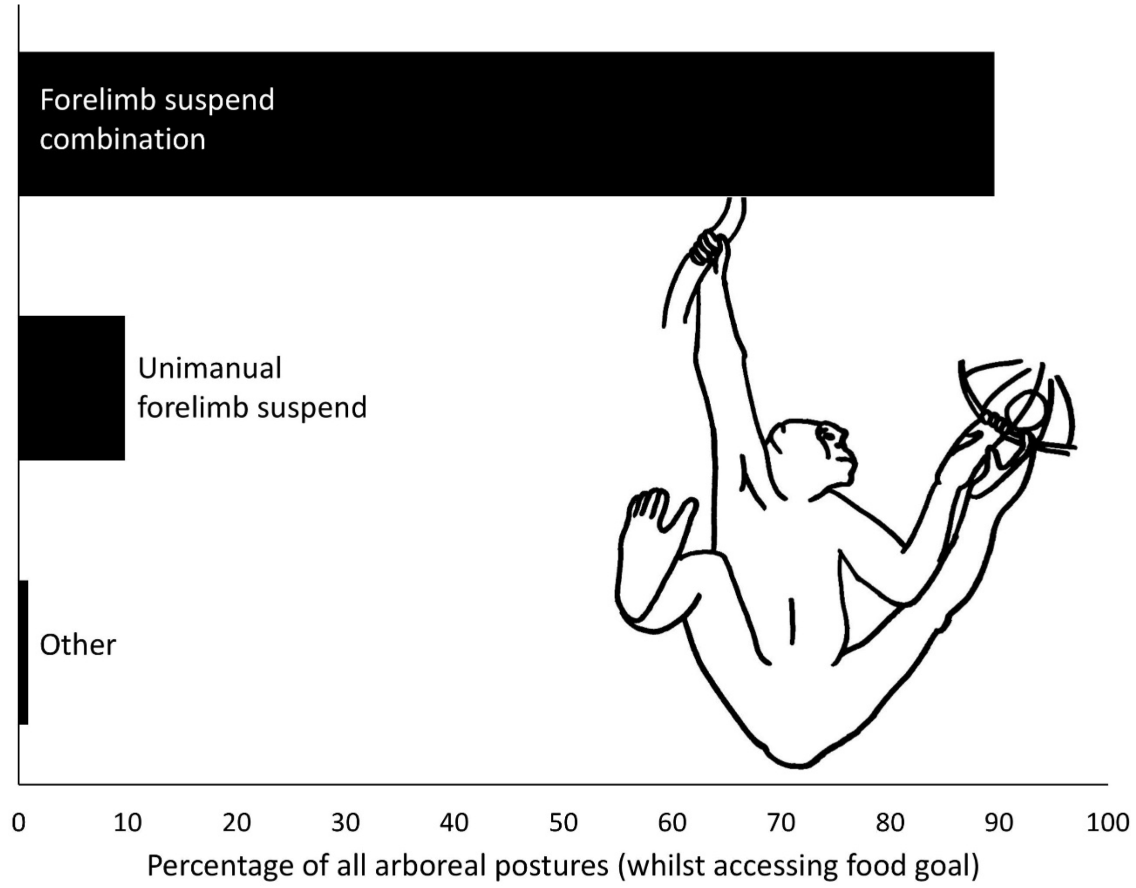

Figure 2.1. Percentage of all arboreal postures (whilst accessing the food goal) and an example of the most common posture (forelimb suspend combination).

Individual laterality is shown in Table 2.3 for each of the testing periods. Two individuals were lateralised in the no goal condition (AdfB was left handed $p < 0.01$; AdfC was right handed $p < 0.005$), and one individual was lateralised in the terrestrial testing condition (AdfD was left handed $p < 0.001$). In contrast four individuals were lateralised in the arboreal testing condition: two were right handed (AdfA and AdfC $p < 0.001$) and two were left handed (AdfD and InmB $p < 0.001$).

Table 2.3. Individual laterality for the three testing periods. HI is handedness index score, calculated according to Hopkins (1999). For binominal tests (B test) p = 0.5, significant scores are shown in bold.

Individual	**No goal**		**Terrestrial**		**Arboreal**	
	Count (L/R) *HI*	Laterality B test	Count (L/R) *HI*	Laterality B test	Count (L/R) *HI*	Laterality B test
AdfE	-	-	48/32 *-0.2*	Not lat. p = 0.093	5/1 *-0.667*	Not lat. p = 0.219
AdfA	99/96 *-0.015*	Not lat. p = 0.886	85/85 *0*	Not lat. p = 1	73/124 *0.259*	**Right** **p < 0.001**
AdfB	33/14 *-0.404*	**Left** **p = 0.008**	16/18 *0.059*	Not lat. p = 0.864	58/65 *0.057*	Not lat. p = 0.589
AdfC	28/57 *0.341*	**Right** **p = 0.002**	17/27 *0.227*	Not lat. p = 0.174	3/41 *0.864*	**Right** **p < 0.001**
AdfD	41/34 *-0.093*	Not lat. p = 0.489	90/43 *-0.353*	**Left** **p < 0.001**	115/39 *-0.494*	**Left** **p < 0.001**
InfA	48/45 *-0.032*	Not lat. p = 0.836	129/99 *-0.132*	Not lat. p = 0.055	237/264 *0.054*	Not lat. p = 0.245
InmB	63/70 *0.053*	Not lat. p = 0.603	62/75 *0.095*	Not lat. p = 0.305	167/80 *-0.352*	**Left** **p < 0.001**

2.3.1 Hand changes and proportion of bouts with a dominant hand for posture

Sequences of interaction with the arboreal goal were ranked by the frequency of hand changes, which was then correlated with the proportion of non-dominant hand use for postural support per bout (Figure 2.2). This gave a significant negative correlation of -0.074 (Spearman’s rank-correlation coefficient two-tailed, n = 288, S = 4681, p < 0.005). However,

$R^2 = 0.0055$, which suggests that only 0.6% of the variance in the proportion of bouts with postural support can be explained by variance in frequency of hand changes.

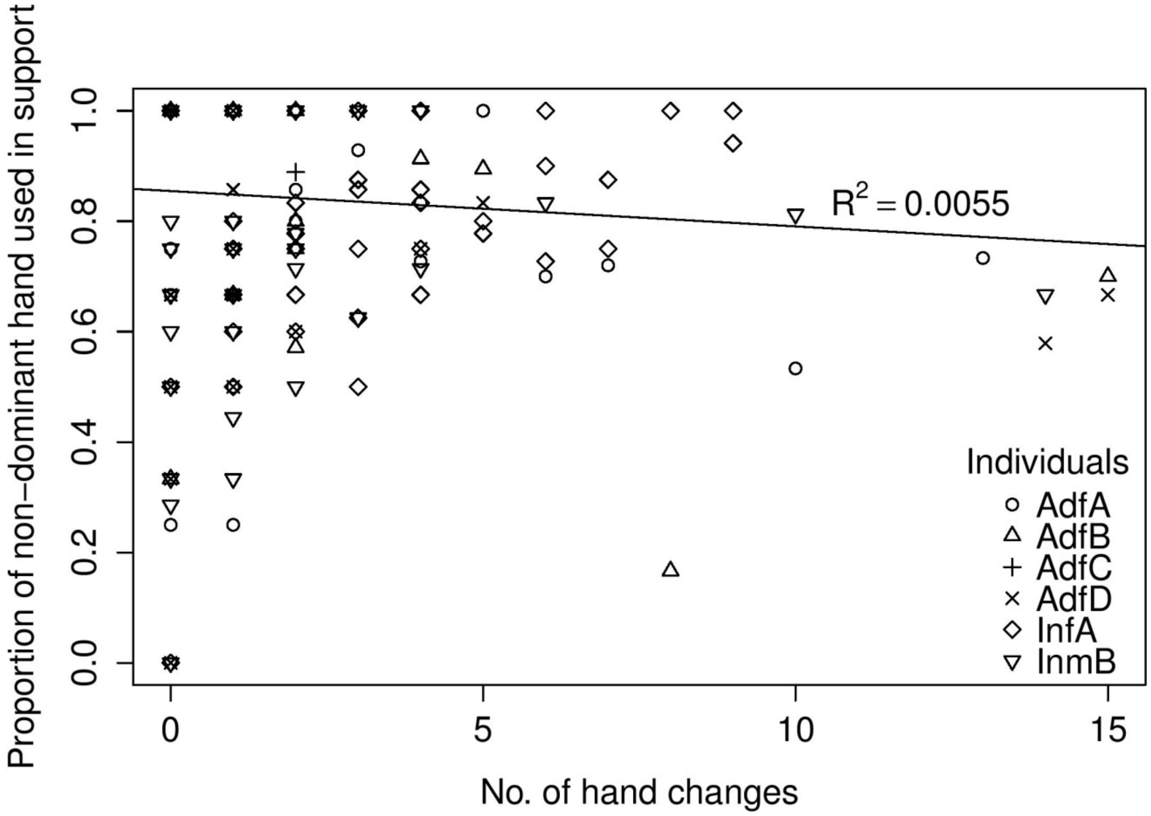

Figure 2.2. The proportion of bouts where the non-dominant hand (the hand not manipulating the goal) was used for support in relation to the number of changes of hand used for manipulating the goal.

2.4 Discussion

Captive bonobos were tested for evidence of hand preference during an arboreal and terrestrial food goal manipulation task. It was found that the majority of individuals had a preferred hand when accessing the goal in the arboreal testing condition, whereas only one individual exhibited a hand preference for manipulating the same goal in the terrestrial testing condition. There was no consistent direction of handedness across individuals (two individuals were left handed and two individuals were right handed). Therefore, the handedness observed during the arboreal testing condition appears to be the expression of individual preference, which could be due to a preference for use the stronger limb to maintain demanding suspensory postures.

Marchant and McGrew (2007) proposed that the rate of change of the manipulating hand should be positively correlated with the proportion of bouts in which the non-dominant hand provides postural support due to fatigue (fatigue hypothesis). However, we found no evidence of support for the fatigue hypothesis. Instead the individuals in this study did not change the hand used for manipulation of the goal more frequently when a hand was required for postural support.

The most frequent arboreal postures recorded in this study were suspension alongside or underneath the food goal. In the majority of cases (89.5%) body weight was borne by a forelimb suspend combination posture in which at least one forelimb was used and a further 9.7% were unimanual suspend (body weight borne by a single forelimb). Marchant and McGrew (2007) recorded arboreal handedness for postures that included a forelimb as the “major support”, however, they did not specify demanding postures such as forelimb suspend.

It is likely that the differences in arboreal laterality seen in this study are due to the more demanding postures recorded, such as suspend.

Marchant and McGrew (2007) suggest that because the locations of the arboreal ant holes used by the chimpanzees are unpredictable and random in comparison to available supports in the trees, the chimpanzees would need to use both hands equally when fishing which would result in ambilaterality. Despite this they do not quantify the location of the ant holes or the available supports relative to selected supports in their analysis, and so this cannot be tested. Furthermore, they do not consider the possibility that lateralised individuals could plan their body position in relation to using their preferred limb. For example if an individual is strongly lateralised for a range of activities they would be likely to predict and select supports that would allow the use of this hand. Similarly, if an individual is not strongly lateralised for manipulatory tasks but has a preferred limb for postural support (for instance because it is stronger) then laterality may be exhibited when demanding postures are required.

To rule out any influence of the location of the food goal in relation to available supports in this study these variables were kept constant, and the goal itself could provide postural support. This would have enabled the bonobos to express their preferred hand for suspensory postures. Therefore, the results of this study more closely follows Vleeschouwer et al.'s (1995) and Peters and Rogers' (2008) suggestion that laterality is more pronounced in postures where one hand is used in postural support due to individuals having a preferred hand for this behaviour (the stability hypothesis).

Current data for population-level laterality of hand use in bonobos is inconclusive (Shafer 1997 and Ingmanson 2005 found group level right handedness; Vleeschouwer et al. 1995 found group level left handedness; Hopkins et al. 1993 and Hopkins and de Waal 1995 found a right and left bias for different behaviours; McGrew and Marchant 1997b, Ingmanson 1998, Harrison and Nystrom 2008, Chapelain and Hogervorst 2009, and Chapelain et al. 2011 found no evidence of group level handedness). However, in most cases individual bias for either the right or the left hand has been found (this study, Hopkins et al. 1993, Hopkins and de Waal 1995, Ingmanson 1998, Ingmanson 2005, Chapelain and Hogervorst 2009, Chapelain et al. 2011). It has been argued that hand preference for either the left or the right hand is dependent upon the complexity of the task for which handedness is recorded (Fagot and Vauclair 1991). The findings of this study suggest that the physical demand of a task (such as maintaining arboreal suspensory postures) also elicits individual handedness.

In conclusion the results of this study do not follow the previous suggestion that ambilaterality during arboreal postures results from fatigue in the limb being used in postural support, as reported for wild chimpanzees for an arboreal ant fishing activity (Marchant and McGrew 2007). The data here clearly suggest that the role of the forelimbs in demanding suspensory postures (such as arm hanging) results in a preferred limb for these postures due to individual limb strength. This in turn elicits a bias for use of the opposite hand when manipulating the goal during demanding arboreal postures in a symmetrical environment. To further investigate the influence of postures on laterality data for preferred hand for postural support, recorded in relation to available supports relative to the goal in more complex environments (such as a natural canopy environment) is needed. What is clear from this study is that arboreal suspensory postures should be included in studies of laterality and that along with increasing complexity (more dextrous tasks), tasks with increasing physical demand (such as energetically demanding postures) can elicit hand preference.

CHAPTER THREE

BONOBOS (*PAN PANISCUS*) USE FUNCTIONAL PROPERTIES OF ARBOREAL SUPPORTS WHEN SELECTING ROUTES TO A HARD-TO-REACH FOOD GOAL

Abstract

For large bodied primates, such as bonobos, moving around the complex and dynamic canopy environment can be risky due to the possibility of falling. Therefore careful choice of supports based on an understanding of the physical environment is vital for safe and energetically efficient arboreal locomotion. Coping with these demands has been linked to the evolution of complex cognition in primates. Captive bonobos were given a choice of two ropes, which varied in their functional properties, to use to access an arboreal food goal such that one rope provided easy access and one required more demanding postures. The ropes differed in their distance from the goal (the easy rope being nearer) or flexibility (the easy rope being flexible and thus able to be manoeuvred nearer to the goal). Bonobos selected the rope that enabled easy access of the goal significantly more often than the demanding rope, this was particularly important for smaller individuals. Furthermore, lateralised individuals preferentially selected the rope on the opposite side to their preferred hand, such that they could access the goal initially with their preferred hand. Similar results were found for a siamang (*Symphalangus syndactylus*) tested in the same way. This suggests that these apes were selecting routes to the goal based on some knowledge of the functional properties of the ropes. Moreover, hand preference may add a further stage to the planning process in support selection. Seemingly simple, yet equally flexible, cognitive processes such as using knowledge of the physical properties of supports during the selection process of route planning, could form the precursors to more complex cognitive abilities.

Chapter contents

3.1 Introduction

For large-bodied primates, such as great apes, moving around a complex three-dimensional arboreal environment is energetically costly (Alexander 1991) and risky due to the possibility of falling (Carter et al. 2008, Jarrell 2011). Therefore careful choice of supports based on knowledge of their physical properties is vital for safe and energetically efficient arboreal locomotion. Indeed it has been suggested that complex cognition such as that demonstrated by extant great apes could have arisen as a response to the demands of travelling in the forest canopy (Chevalier-Skolnikoff et al. 1982, Povinelli and Cant 1995). This study tested whether bonobos housed in a naturalistic setting chose arboreal supports according to their functional properties, such as flexibility and distance from a goal.

Some knowledge of the functional properties of arboreal supports (branches) is implied in accounts of the locomotor strategies of wild apes. The evidence for this is strongest for orangutans, the largest great ape with a predominantly arboreal life-style. Weight bearing supports are discontinuous in the forest canopy and tree crowns are often separated by large gaps, and it is more energetically costly to descend to the ground and climb back into the canopy than to cross gaps directly (Thorpe et al. 2007). Orangutans overcome this by manipulating the compliance of vertical trunks in oscillatory behaviours (tree sway) in which they oscillate a tree trunk back and forth until they can reach across the gap in the canopy and transfer to the neighbouring tree (Thorpe et al. 2007). Also when moving in the periphery of the canopy orangutans use complex locomotor behaviours to distribute their weight across multiple flexible branches enabling them to use more compliant supports than if they were using a single weight bearing branch (Thorpe and Crompton 2006, Thorpe et al. 2009). Myatt and Thorpe (2011) showed that larger male organutans used stiffer supports than smaller females and juveniles when feeding, suggesting they specifically select supports based on diameter or rigidity.

Similarly, Remis (1995) reported that large male gorillas rarely use the periphery (where supports are particularly thin and flexible) and remain in the tree crown (where supports are larger and more stable).

Crossing large gaps between tree crowns, and foraging in the periphery where branches are weak and compliant poses complicated problems for large bodied apes. Choosing supports based on trial and error would be problematic, if a support fails under an individuals' body weight it could be fatal. The risk of serious injury or fatality is increased for apes of larger body mass (Jurmain 1997, Carter et al. 2008, Jarrell 2011). Nevertheless, apes could potentially 'test' a support by applying a proportion of their body weight while supporting themselves on another (safe) support. Chevalier-Skolnikoff et al. (1982) reported that orangutans were observed on some occasions to "slowly and carefully test each potential support with their weight". However, if the next support to be used in a route is on the far side of a gap in the canopy, testing its properties directly before making a decision would be impossible. Therefore, great apes must be able to resolve the problems of discontinuity by using some knowledge of the mechanical properties of canopy supports to forage safely. Indeed, great apes have been shown to understand such issues when using tools (Tomasello and Call 1997, Povinelli 2000, Herrmann et al. 2008, Manrique et al 2010). For example, it has been has been suggested that great apes understand functional properties such as connectedness and contact with a reward (Herrmann et al. 2008, Povinelli 2000) and physical properties such as rigidity (Manrique et al. 2010) and length (Mulcahy et al. 2005). However, it is the demands of arboreal locomotion that would have selected for the ability to understand functional properties of supports used in locomotion and the ability to select these appropriately based on where they need to get to, such as across a gap between tree crowns.

The ability to plan ahead before carrying out a particular action can increase efficiency of movement, energy use, and productivity. However, the term ‘planning’ is used liberally to explain a number of different cognitive processes. At one end of the spectrum it has been argued that apes are able to plan for future events (Mulcahy and Call 2006, Osvath and Osvath 2008), and like other animals (Clayton et al. 2003), demonstrate episodic future thinking. However, evidence of non-human primates possessing this level of cognitive processing has been disputed (Suddendorf and Corballis 2007). Nevertheless, apes are capable of planning for their current needs, such as by identifying the necessary course of action to achieve an immediate goal (Dufour and Sterck 2008, Tecwyn et al. 2012, 2013). Although Tecwyn et al. (2013) found that apes did not position paddles on a puzzle box to enable retrieval of the reward in advance of taking action on the food item itself, it is possible that this was due to a lack of inhibition when shown the food reward. Nonetheless, planning for current needs has been demonstrated in various domains including arboreal locomotion (Chevalier-Skolnikoff et al. 1982), and the use of sets of multiple tools (Boesch et al. 2009).

For apes to plan arboreal routes it is necessary that they possess an understanding of where they are in space and how their body movements will impact upon their surrounding supports (Povinelli and Cant 1995, Hunt 2004). Primates possess simple motor planning abilities that enable selection of a grasping position prior to a hand action that results in a preferred final position, called the ‘end-state comfort effect’ (Weiss et al. 2007, Chapman et al. 2010). Although non-human great apes have not been directly tested for this effect, it is generally accepted that these simple processing abilities evolved at least 65 million years ago in the primate lineage (Chapman et al. 2010). Furthermore, non-human primates possess a sense of self in space or a ‘body schema’ that is updated continuously during movement. This results in an awareness of where their limbs are in space and also where their limbs can reach (Holmes and Spence 2004). It has also been shown that non-human primates can extend their body schema beyond the physical boundaries of their body to include the size or shape of a tool, for instance, while using a stick to extend their reach (Iriki et al 1996, Maravita and Iriki 2004). Limb preference and handedness may also influence how apes select arboreal supports. It has been shown that in a symmetrical arboreal environment individual apes (that were non-lateralised for manipulatory behaviours such as feeding) express a preference for a particular limb for support during suspensory postures (Chapter Two). In this way, the body schema – incorporating individual body specialisations (such as handedness) and anatomical specifics (such as length of limbs and reach) – combined with a knowledge of the mechanical properties of available supports, influences the ability to select supports in arboreal routes. For example, if an individual has a preference for a particular hand for manipulatory behaviours they may select supports that enable the use of that hand further along the route, such as at a food goal.

Previous studies of route planning in great apes have focused on spatial memory (Menzel 1973, MacDonald 1994, MacDonald and Agnes 1999, Gibeault and MacDonald 2000). Studies on other primates have focused on multi-step planning (Cramer and Gallistel 1997, Janson 2014), spatial memory (MacDonald and Wilkie 1990), travel routes and pathways (Valero and Byrne 2007, Di Fiore and Suarez 2007, Asensio et al. 2011), or the ecological trade-off between energy used and quantity of food reward gained (Milton 1981). These studies have shown primates and specifically great apes have good spatial memory and can choose the shortest routes or those that visit preferred food items (Menzel 1973, MacDonald and Agnes 1999, Gibeault and MacDonald 2000). Although it has been argued that there is no evidence for complex multi-step planning in travel routes or otherwise (Janson 2014, Tecwyn et al. 2013) it is agreed that primates are efficient in using short-range planning (Cramer and Gallistel 1997), for instance, by choosing optimal routes between two goals at different distances. Furthermore, it has been suggested that flanged male orangutans plan their direction of travel well in advance and long-call to inform conspecifics of their intended ranging throughout the day (van Schaik et al. 2013). However, studies of route planning have primarily tested routes used in a terrestrial setting, which does not incorporate the same demands as arboreal foraging which is more typical of the natural foraging behaviour of apes. Planning involving selection of supports on the basis of functional properties such as distance from a goal, or flexibility of a support has not been directly tested in apes.

The aim of this study was to determine whether captive bonobos (*Pan paniscus*) consider the physical properties of supports when selecting routes to a hard-to-reach food goal. Bonobos are particularly suitable for this study because they travel and forage arboreally (Susman et al. 1980, de Waal and Lanting 1997), more frequently than their closest relatives *Pan troglodytes* (Doran 1993). They have also been shown to use tools in captivity (Jordan 1982, Gold 2002) but not habitually in the wild (Ingmanson 1996). This suggests they possess the cognitive abilities necessary for tool use but that in the wild this adaptation serves a different function, such as, for coping with complex relationships or play (Ingmanson 1996, Gruber et al. 2010) or for coping with the demands of arboreal travel (Chevalier-Skolnikoff et al. 1982, Povinelli and Cant 1995).

3.2 Methods

All data were collected by NKIH from subjects housed at a zoo in the UK between July 2013 and June 2014. At the beginning of the study the zoo housed 11 bonobos in two family groups that have adjacent but separate indoor enclosures and a single outdoor enclosure that each group accessed on alternate days. The indoor enclosures were approximately 167m^2 (5 m in height) furnished with vertical, angled, and horizontal poles, connected with various ropes and flattened hose pipes. Each enclosure also had 3 separate off-show bed areas that the bonobos had access to throughout the day, except when they were being cleaned. The four viewing windows (where the food goal and ropes were positioned) were 1.5 m x 2 m.

Data were collected in the group setting, so that all individuals within the group had access to the experimental equipment during the trials. Two adult females, one adolescent female, and two infants (one male and one female) interacted with the experimental equipment consistently throughout the study (Table 3.1). Arm length was obtained by photographing the bonobos when the limb was held against wire mesh of known dimensions (50 mm squares). Arm length was calculated for each individual from a minimum of 3 photographs to reduce any errors caused by positioning. Arm length was used as a proxy for body size (Aiello 1981). Hand preference was based on consistent bias of hand use for different activities including feeding and manipulating the food goals (Chapter Two).

Table 3.1 Details of study subjects.

Individual	Group	Sex	Age at start of study	Arm length	Hand preference
AdfA	1	F	17	51 cm	Not lateralised
AdfC	1	F	15	56 cm	Right
AdfD	1	F	8	50 cm	Left
InfA	2	F	3	30 cm	Not lateralised
InmB	1	M	3	31 cm	Not lateralised

Adf = adult/adolescent females, Inf = infant female, Inm = infant male. Individuals were housed in two separate groups (1 and 2). Hand preference was consistent handedness for different manipulations and activities (Chapter Two).

A food goal was placed 2 m from the ground above a viewing window (Figure 3.1). To either side of the goal were two ropes (polyester webbing 50 mm wide). Two experiments were carried out in which one rope provided ‘easy’ access to the goal, while the other required ‘demanding’ postures to access the goal. In the first experiment, ease of access as varied by manipulating the distance from the ropes to the food goal, while in the second experiment ease of access was varied by manipulating the flexibility of the ropes. In both experiments the easy rope enabled the bonobos to position themselves closer to the food goal, whereas the demanding rope required a greater reach from the rope to the goal to obtain the food. Each trial was balanced so that the easy rope appeared equally to the left and right of the goal and then pseudo-randomised on each day of the trials. A replica of the food goal was placed elsewhere in the enclosure (in a randomly chosen location averaging 1-1.25 m high which they could reach without climbing) during each trial in order to minimise any aggression or monopolisation of the food reward by any one individual.

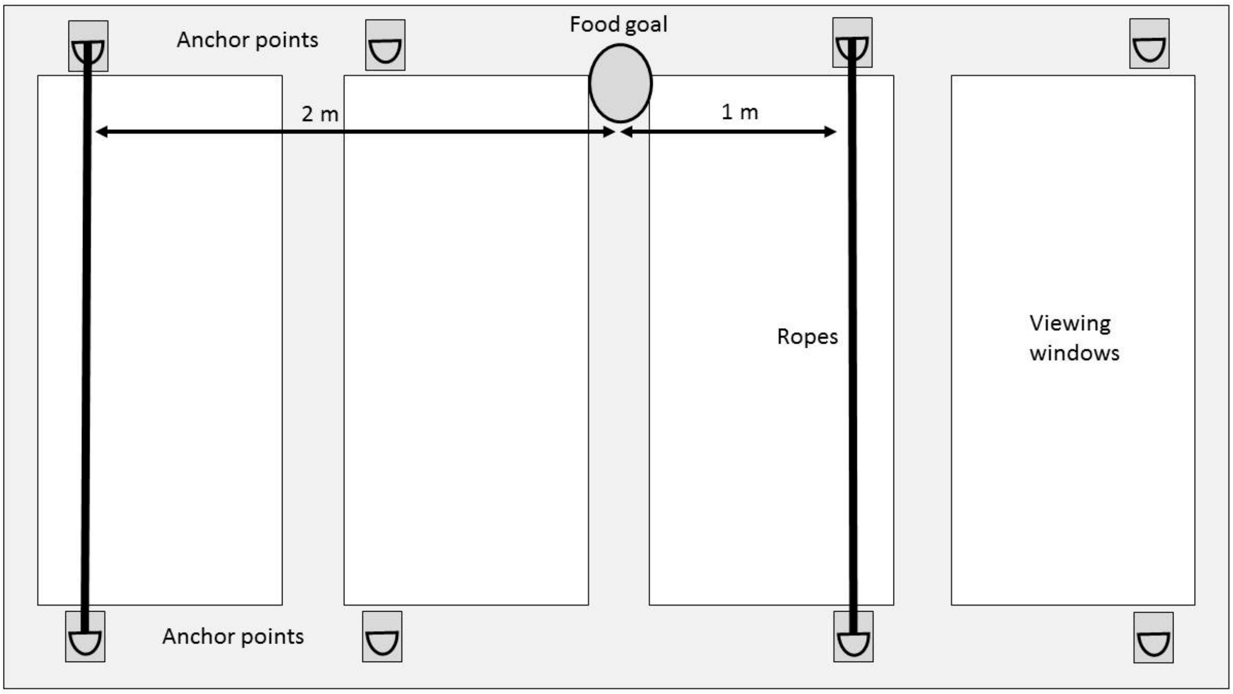

Figure 3.1 Schematic diagram of rope and food goal set up (distance experiment) from the animal's view (not to scale). The easy rope was set at 1 m from the food goal; the demanding rope was set at 2 m from the food goal. Multiple anchor points enabled the experimenter to randomise and balance which side the easiest rope appeared on.

In the distance experiment ropes were 1 m (easy rope) or 2 m (demanding rope) away from the goal. Both ropes were connected to anchor points at the top (2.5 m) and bottom (ground level) of the wall and thus pulled taut (unable to be moved significantly laterally toward the goal). The food goal was a spherical wrought iron cage (0.4 m circumference) with a hollow plastic ball inside. The hollow plastic ball had one small opening through which the subjects could extract food. To enable subjects to swing the flexible rope laterally toward the goal in experiment two the ropes were lengthened and connected to the roof of the enclosure (5 m). Both ropes were attached at ground level (as in the distance experiment) 2 m to either side of the goal. The easy rope (flexible) was 1.5 m longer and so could be manoeuvred toward the goal (mimicking the properties of a liana or vine), whereas the demanding rope was taut and allowed for minimal lateral movement towards the goal. To reduce possible access from the ground, which occurred in the distance experiment (e.g. subjects leapt directly to the food goal from the ground) the goal was reduced in size for the flexibility experiment. The second food goal was a 0.16 m steel mesh cube (mesh size of 50 mm^2) with the same hollow plastic ball inside.

The bonobos had access to the equipment for 2-3 hours in each session. Interactions with the ropes and feeder during each session were videoed from a central position at the viewing window. Videos were watched once at normal speed for each subject that interacted with the food goals so that continuous focal data were collected for each individual for each session (Altmann 1974). Bouts of hand use for interactions with the ropes and goal were recorded in sequences with duration (seconds). A sequence was defined as the series of behaviours from when the individual first approached the equipment, through any interaction with the food goal, to the moment they returned to the ground. Data recorded for each sequence included: initial rope choice (easy or demanding; left or right); goal interactions (touch outer metal cage; power grip inner plastic ball; or precision manipulation e.g. pluck food items from inner plastic ball); posture; and support type. Individual information included: arm length; age (adult; adolescent; infant); and handedness (Chapter Two).

For both experiments the first 30 minutes of interactions with the equipment were videoed (Sanyo Xacti CG10 camera, 30 frames per second). The food reward was usually depleted within the first 15 minutes of each session after which interaction with the goal decreased substantially (with an average of 46 interactions in the first 15 minutes, and an average of 28 in the last 15 minutes). After 30 minutes the interaction level dropped and the observer recorded the same information by hand, however this data is not included in the analysis as interactions after 30 minutes were infrequent and intermittent.

3.2.1 Statistical analysis

Generalised Liner Mixed Models (GLMMs) were used to investigate the influence of multiple variables on initial rope choice (Bolker et al 2009). GLMMs were chosen for statistical analysis because this method deals more appropriately with categorical response variables and unbalanced data (typical of ecological or behavioural response data). By combining properties of both linear mixed models and generalised linear models GLMMs provide a more robust alternative to traditional tests, such as ANOVA (Bolker et al. 2009). Furthermore, GLMM analysis allows for the inclusion of a random effects variable, such as individual, which accounts for variation due to individual choice particularly important in studies with a relatively small sample size. GLMMs were performed in R version 3.2.3 (The R Development Core Team, 2015) using the package lme4 (version 1.1-10), and post hoc analysis was performed using lsmeans (version 2.21-1). Table 3.2 details the variables used in the GLMM analysis. This study investigated individual decision making based on simple functional properties of ropes used to access a hard-to-reach food goal. The functional properties of the ropes in the experiments were controlled and altered (in terms of distance to the goal, flexibility etc.) to test if these individual properties influenced the bonobos' selection. Therefore, initial rope selected by the study subject was chosen as the dependent variable as this was the direct result of a choice made by the individual.

Table 3.2. GLMM factors and factor level description

Factor	Factor levels	Description
Experiment	Distance	Easy rope is 1 m from the food goal
	Flexibility	Easy rope is flexible
Angle of approach	Same side	Subject selected the first rope they came to when approaching food goal
	Other	Subject selected the opposite rope (e.g. they crossed the equipment before selecting a rope to climb)
Initial rope*	Easy	The nearest to the food goal (distance experiment) or the flexible rope(flexibility experiment)
	Demanding	The rope furthest from the food goal (distance), or the taut rope (flexibility)
Left or right rope	Left	Rope to the left of the food goal from the subjects viewpoint
	Right	Rope to the right of the food goal from the subjects viewpoint
Orientation of the easy rope	Left	When the easy rope in the trial occurred to the left of the food goal
	Right	When the easy rope in the trial occurred to the right of the food goal
Arm length	Nearest cm	Length for forelimb in cm
Hand preference	Left handed	Consistent left hand preference
	Right handed	Consistent right hand preference
	Not lateralised	No consistent hand preference

**Initial rope was the first rope climbed by an individual in a sequence that included manipulation of the food goal.*

3.3 Results

A total of 210 sequences were used in the Generalised Linear Mixed Models (GLMMs), 101 from the distance experiment; 109 from the flexibility experiment. Table 3.3 shows the total number of sequences for each experiment recorded for each individual. One sequence was removed for GLMM analysis as it was an outlier (867 seconds, 7.4 standard deviations from mean duration of all sequences) but this did not influence the significance or power of the model, the sequence involved InfA repeatedly swinging on the goal during play with little manipulation of the inner plastic ball.

Table 3.3. Number of sequences recorded for each individual in each experiment and the total number of sequences used in GLMM analysis

Individual	**No. of sequences in distance exp.**	**No. of sequences in flexibility exp.**	**Total no. of sequences (*no. used in GLMMs)***
AdfA	13	17	28 *(28)*
AdfC	13	2	14 *(14)*
AdfD	18	24	30 *(30)*
InfA	55	59	85 *(84)*
InmB	29	55	54 *(54)*

3.3.1 Initial rope choice: easy or demanding

The data were pooled from across the two experiments (distance; flexibility) because there was no significant difference in initial rope choice between the two experiments. The easy rope was selected first in a sequence of behaviours that resulted in manipulation of the food goal in 78.3%

of sequences across all individuals. Figure 3.2 shows that for each individual the easy rope was selected first in a sequence in more than 50% of sequences.

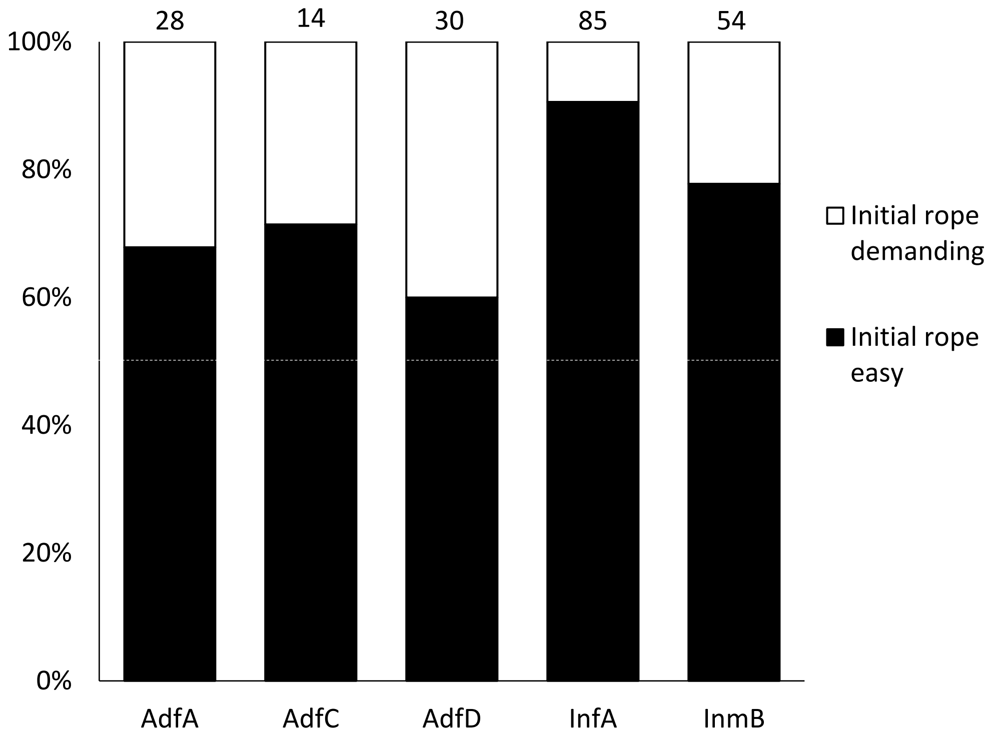

Figure 3.2. Percentage of sequences started with the different ropes for each individual (number of sequences shown above bar). All individuals chose the easy rope initially in more than 50% of sequences (broken white line).

There was no change in choice of initial rope over time (or trials), and no population level preference for selecting the left or the right rope initially in a sequence. Of 210 sequences 112 started with the right rope, 98 started with the left rope.

3.3.2 GLMM: Initial rope choice easy or demanding

All individuals selected the easy rope initially in sequence more often than the demanding rope, however this difference was particularly striking for small individuals. We conducted a binomial generalised linear mixed model (GLMM), in which the dependent binomial variable was which rope (easy or demanding) was selected first in a sequence. Fixed factors were: whether the selected rope was placed to the left or right of the goal; orientation of the easy rope (left or right); angle of approach in relation to rope chosen (same side, or other/unknown); arm length (< 40 cm, ≥ 40 cm); and experiment (distance or flexibility). Individual was included as a random effect (Bolker et al. 2009). Terms whose removal significantly reduced the power (increase in AIC or deviance) of the model were sequentially dropped (Thornton and Samson, 2012). The maximum model (AIC 207.9) showed that arm length influenced the initial rope selected and dropping this term significantly reduced the explanatory power of the model (ANOVA test comparing the two models: $\chi^2 = 5.05$, $p = 0.025$) and so arm length was retained. ANOVA tests comparing sequential models confirmed that removing experiment ($\chi^2 = 0.027$, $p = 0.870$); initial rope chosen on the left or right ($\chi^2 = 0.018$, $p = 0.895$); orientation of the easy rope ($\chi^2 = 0.01$, $p = 0.935$); and angle of approach ($\chi^2 = 0.01$, $p = 0.905$) did not significantly affect the power of the model so these terms were dropped.

Therefore the final reduced model (AIC 200.0, Table 3.4) retained the fixed factor arm length and individual as a random factor. A significantly positive intercept ($Z = 5.05$, $p < 0.001$) meant that all individuals initially selected the easy rope significantly more than the demanding rope. Arm length was a continuous factor and so importance be drawn directly from the model thus further post-hoc pairwise comparisons were unnecessary. Individuals with shorter arm length selected the easy rope initially in a sequence of behaviours significantly more often than individuals with a longer arm length (Z = 3.40, p < 0.001).

Table 3.4. Final GLMMl, Initial rope easy or demanding ~ Arm length + (1 | Individual). Random effects variance = 2.07e-13 (SD 4.55e-07). Individuals with short arms were significantly more likely to select the easy rope first in a sequence.

Variable	**Estimate**	**SE ±**	**Z value**	**p value**
Intercept	3.52	0.70	5.05	< 0.001*
Arm length	-0.06	0.02	-3.40	< 0.001*

* *p ≤ 0.001.*

Individuals fell into two groups based on arm length, the larger individuals were the adults and the adolescent (arm length ≥ 50 cm) and the smaller individuals were the infants (arm length < 31 cm). To investigate how the adults and the adolescent selected ropes the infants (and so the effect of arm length) were removed from the data set. The final model (AIC 87.6) retained just individual as a random factor and retained a significantly positive intercept (Z = 2.61, p = 0.027) meaning the remaining individuals (adults and adolescent) also selected the easy rope initially in a sequence significantly more often than the demanding rope. However, it is important to note that in removing the infants from the data set the overall count of sequences is reduced from 210 to 72 (average of 24 per individual) and the sample size to three individuals.

3.3.3 Initial rope choice: left or right

Two individuals were lateralised, AdfC was right handed and AdfD was left handed (Chapter Two). For these individuals the initial rope chosen was significantly more often the rope on the opposite side to their preferred hand, while non-lateralised individuals showed no significant preference (Figure 3.3). We conducted binomial tests of significance (two tailed, $p = 0.5$) for choice of left or right rope for the lateralised and non-lateralised individuals. The left handed individual selected the rope to the right of the food goal initially significantly more often than the rope to the left of the goal ($p = 0.043$) for 30 sequences. The right handed individual selected the left rope significantly more often than the right rope ($p = 0.002$) for 14 sequences. Non-lateralised individuals showed no significant preference for either the left or the right rope ($p = 0.313$) for 176 sequences.

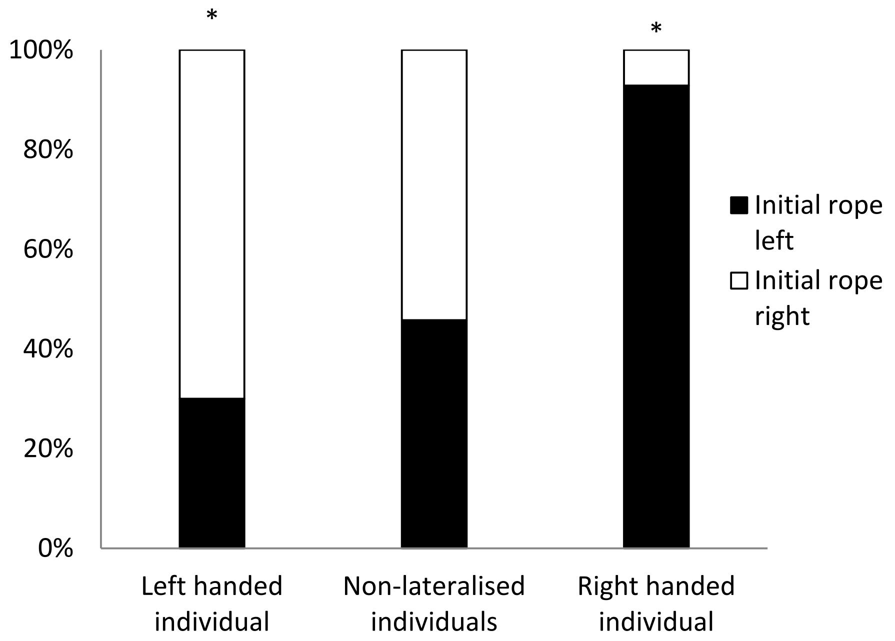

*Figure 3.3. Initial rope chosen (left or right) for lateralised individuals. * $p < 0.05$ for binomial test. The left handed individual chose the right rope initially significantly more often and the right handed individual chose the left rope initially significantly more often. Individuals who were not lateralised ($n = 3$) showed no significant preference for either rope.*

3.4 Discussion

This study tested whether captive bonobos chose ropes to access a hard-to-reach arboreal food goal, according to their functional properties (distance and flexibility). All individuals selected the easy rope (which enabled the individual to maintain the closest proximity to the goal) initially in a sequence of behaviours more often than the demanding rope (which was further from or could not be manoeuvred toward the goal). Small individuals tended to choose the easy rope more often than large individuals, and lateralised individuals chose the rope on the opposite side to their preferred hand whereas individuals that were not lateralised selected ropes on either side of the goal. This study has demonstrated that bonobos, (non-tool users in the wild) employ a knowledge of the functional properties of supports, coupled with a knowledge of the limitations of individual reach, when selecting routes to a hard-to-reach food goal. This is the first time this has been shown for a naturalistic locomotor task as a proxy for arboreal locomotion in the wild.

The easy rope was either nearer to the goal or could be moved closer to the goal and thus provided a less demanding route. Therefore, individuals with shorter arm length could have been predicting from where they would have a better reach and thus selected the easy rope more often. For individuals with a longer arm length, while the easy rope provided a preferable access route allowing them to get closer to the goal, it was not as necessary for them to select this rope in every instance as they could access from the demanding rope. Indeed, the postures used to access the goal were different for individuals with different arm lengths, longer arms allowed individuals to access at arm’s length, whereas individuals with short arms more often required the whole body length (discussed in Chapter Four).

All individuals selected the easy rope most frequently, however lateralised individuals favoured the rope that occurred on the *opposite* side to their preferred hand for manipulations (thus allowing initial manipulation of the food goal with their preferred hand). This suggests hand preference, in addition to body size, may also be important in support selection. There is also evidence to suggest that hand preference exhibited during arboreal foraging is due to a preference for a particular hand for maintaining demanding postures (Chapter Two). Therefore lateralisation could be important when selecting supports for locomotion in two ways: for non-lateralised individuals the demand of maintaining arboreal postures can result in a preference for the strongest limb; however, for individuals strongly lateralised for other behaviours such as manipulation, the opposite limb is preferred for support. However, findings for natural canopy environments suggest that the complex and irregular positions of supports can induce ambilaterality regardless of hand preference for terrestrial behaviours (McGrew and Marchant 2007). Therefore, it is important to note that in this study laterality may be relevant for the symmetrical test environment used here. Similarly it has been shown that lateralisation of route choice occurs in other non-primate arboreal species in a symmetrical test environment. Lustig et al. (2013) demonstrated that the majority (six out of eight) of their subjects (*Chamaeleo chameleon*) demonstrated a preference for detouring to a particular side when faced with an obstacle. As with the findings of this study Lustig et al (2013) also demonstrated that the angle of approach had no influence on the chosen detour route. Although they refute the possibility that chameleons demonstrate a bias for a short or long route each time, route choice based on potential energy expenditure has been demonstrated in other non-primate species. Munteanu et al. (2016) demonstrated that a species of frog (*Allobates femoralis*) will avoid obstacles (such as a high wall analogous to a more energy costly route) when returning to a preferred calling site. They conclude that these amphibians can flexibly select their routes based on potential energy expenditure.

To further investigate to what extent apes select arboreal routes based on knowledge of the functional properties of available supports a captive siamangs (*Symphalangus syndactylus*) housed at the same zoo were tested with the same experimental set up. Although only one individual interacted with the equipment the results were consistent with those from the bonobos (appendix Table A3.1). An adolescent male siamang selected the easy rope significantly more often than the demanding rope initially in a sequence of behaviours. This individual was not lateralised and demonstrated no preference for the rope occurring to the left or the right of the goal. Although based on observation of one individual it is possible that the ability to select an appropriate support for arboreal travel, based on knowledge of functional properties of the support, is not restricted to great apes with tool using capabilities. Instead the simple cognitive processes involved in selection of suitable arboreal supports are likely present in lesser apes, and perhaps all arboreal primates.

The complexities faced by large bodied apes traversing the dynamic and discontinuous canopy environment have been key factors contributing to theories for the evolution of complex cognitive abilities such as self-awareness (Povinelli and Cant 1995, Hunt 2004), and generalised problem solving (Chevalier-Skolnikoff et al. 1982). The findings from this study further suggest that the demands of accessing arboreal goals requires knowledge of functional properties of supports along with simple processes (such as body-schema and end state comfort effect). The bonobos selected the most suitable or preferred arboreal routes on the basis of the functional properties of the ropes available. Knowledge of or an ability to predict the behaviour of arboreal supports along with simple internal representations of self are crucial for safe and energetically efficient arboreal locomotion (as can be inferred from observations of wild non-human apes, Chevalier-Skolnikoff et a. 1982, Povinelli and Cant 1995, Remis 1995, Dunbar and Badam 2000, Hunt 2004, Thorpe et al. 2007, Myatt and Thorpe 2011). The evolution of complex cognition in primates was perhaps a manifestation of the reorganisation of computing structures already in place (Vaesen 2012). Therefore, seemingly simple yet equally flexible, cognitive processes (such as motor planning and body schema) and a knowledge of functional properties of supports likely formed the precursors to more complex cognitive abilities such as tool use. And it is the demands of an arboreal lifestyle, particularly for large-bodied apes, that would have selected for this.

CHAPTER FOUR

THE INFLUENCE OF SOCIAL LEARNING AND DOMINANCE RANK ON ROPE CHOICE

Abstract

Captive bonobos, housed in a naturalistic setting, select supports to access a hard-to-reach food goal on the basis of their functional properties (Chapter Three). It has been suggested that the demands faced by large bodied apes traversing a complex and discontinuous canopy environment requires a knowledge of functional properties of supports and simple representations of self (such as body schema and end-state comfort effect). Bonobos were provided with a choice of two ropes to use to access a hard-to-reach food goal, which varied in their functional properties (distance from a goal and flexibility) such that one rope provided easy access and one required more demanding postures. The influence of positional behaviour and limb length on successful access to the food goal was explored. The bonobos were housed in a group setting and the potential influence of social learning and dominance was also investigated. Selection and use of the easy rope resulted in greater success at the goal. Individuals with long limbs used orthograde postures and accessed the goal at arms-length, whereas individuals with short limbs used their whole body length to reach the goal from the rope in pronograde postures. Dominance did not influence rope choice but was important in the order individuals accessed the goal. Individuals selected the easy rope significantly more regardless of which rope the first individual in a trial used to access the food goal, including the demanding rope. Although this could suggest social learning based on observing both errors and successes of conspecifics, this would still require the observing individual to have some knowledge of the functional properties of the ropes. Furthermore, the individuals to access the goal first in a trial selected the easy rope more often than the demanding, without the opportunity of observing another individual, therefore, it is more likely that all individuals were selecting ropes based on their own knowledge of the ropes' functional properties. This further supports the findings of Chapter Three.

Chapter contents

4.1 Introduction

In the previous chapter it was shown that bonobos (and one siamang) selected ropes to access a hard-to-reach food goal according to their functional properties. It was also shown that individual laterality and limb length influenced rope choice. The first aim of this chapter is to further explore the potential benefits of selecting the easy rope (in terms of rate of success) and to discuss the influence of positional behaviour on accessing the hard-to-reach food goal. The findings of the previous chapter suggest the bonobos were using individual knowledge of the functional properties of the ropes to select which one to use to access the food goal. However, the bonobos were tested in a group setting, meaning each individual had the opportunity to observe other individuals selecting and using the ropes and therefore, it could be that they were using social learning to gain relevant information about which rope to select. The second aim of this chapter is to explore the possible influence of social learning and dominance rank on the selection and use of the ropes to access the food goal.

4.1.1 Success rate and positional behaviour

For large bodied apes the demands of foraging arboreally poses two main problems: balancing the energetic demand of traversing the complex environment and successful risk avoidance. Therefore, selecting supports that enable efficient and safe postures is vital to success. Although observations of behaviour can allow inferences to be made about an individuals' support selection based on risk avoidance, direct evidence would require the individual to explain their reasoning and decision making, which is impossible for non-human subjects. Although some studies report muscle activity for various positional behaviours in non-human apes (Tuttle and Basmajian 1974, Tuttle and Basmajian 1978, Stern and Larson 2001), they do not provide complete information regarding energy consumption. Daily energy expenditure can be calculated using the basal metabolic rate (BMR) and the activity pattern of an individual (Key and Ross 1999). However, this is estimated based on species specific BMR and time budget data and therefore not accurate at the individual level for specific bouts of behaviour. Energy expenditure can be determined by the analysis of carbon dioxide (CO_2) production and oxygen (O_2) consumption (Nakatsukasa et al. 2004, Sockol et al. 2007, Rising et al. 2008). However, methods to obtain these data are invasive and impractical outside of the laboratory, where the unnatural social and physical environment confounds the expression of natural behaviours. Nevertheless, observation of positional behavioural repertoires can indicate individual preferences and energetic demand which can be related to individual body specifications such as limb reach, and support availability. For example, some postures are more demanding than others. Bipedalism has been shown to be more energetically costly (as determined by CO_2 production and O_2 consumption) in: *Macaca fuscata* (Nakatsukasa et al. 2004); *Pan troglogytes* (Sockol et al. 2007), and suspensory brachiation to be more energetically costly than above branch quadrupedalism in *Ateles* (Parsons and Taylor 1977). Furthermore, access to food is essential for survival, the food goals used in this study can be considered as a proxy for the kinds of foraging tasks bonobos might face in the wild. Thus, access to the food goal provides a useful measure of rate of success, and thus the potential benefits of selecting supports relevant to limb reach or limb preference.

In the previous study arm length was used as a proxy for body size and it was shown that while all individuals selected the easy rope initially significantly more than the demanding rope during interactions with the goal, this was particularly striking for individuals with short arms. Therefore it is likely that positional behaviours of individuals with different limb lengths will reflect what enables more frequent access or greater success (time spent collecting the food reward) at the food goal, or behaviours which are least demanding (in terms of energy consumption) for that individual. Therefore, it is important to establish the way in which selection of the different ropes (easy or demanding) influences success at the food goal, and whether this is the same across all individuals. The first hypothesis this chapter will address is:

1) Selection and use of the easy rope will result in a higher rate of success, in terms of access to and duration of access of the food goal (success hypothesis).

4.1.2 Social learning and dominance rank

In the previous chapter it was suggested that these bonobos select the easy rope more frequently based on their understanding of the functional properties (distance from the goal and flexibility). However, the group were housed and tested socially so that it was possible for individuals to observe the success of a conspecific accessing the food goal at the start of the trial and learn which rope to select, potentially without any functional understanding of their own. Although in this scenario it would be difficult to explain the rope choice of the first individual to access the food goal in a trial, it could be important for some individuals, such as infants and low ranking individuals, who may socially learn from a parent or more dominant members of the group.

Social learning has been widely studied in apes (for example, Hayes and Galef 1996, Whiten et al. 2004) and there are a number of mechanisms proposed by which apes can acquire new knowledge from conspecifics (see Heyes 1994 and Rendell et al. 2011 for a review). However, this study does not intend to separate the different mechanisms of social learning. What is important here is whether the results (selecting the easy rope more often than the demanding rope, Chapter Three) can be explained by social learning. However, local enhancement, whereby an individual interacting with an object (e.g. the climbing ropes in this study) draws the attention of a conspecific to the object (Heyes 1994) is a possible mechanism by which individuals in this study may have learnt how to access the food goal. Regardless of the way in which an individual may socially learn from another individual, *who* is learning from *whom* is also an important factor when considering the potential influence of social learning on decision making.

Studying goal-oriented behaviours in a social group must consider the influence of dominance. It has been shown in apes that individuals are more likely to copy the behaviour of dominant conspecifics (Horner et al. 2010). Chimpanzees were given the opportunity to observe conspecifics performing various solutions to a foraging task and it was shown that they preferentially reproduced the solution demonstrated by the older, higher ranking individual (Horner et al. 2010). Furthermore, dominance correlates with access to resources (Parish 1994, Furuichi 1997, Wittig and Boesch 2003, Robbins et al. 2007) and therefore may influence how or when an individual gains access to a reward. For instance, an easier access route (as in this study) may be monopolised, or a food reward depleted, by higher ranking individuals before subordinate individuals gain access.

Bonobos are matriarchal (their social hierarchy is female-dominated), and females control access to food (Furuichi 1997, Parish 1994). Parish (1994) found that dominance rank correlated with average time spent fishing at an artificial termite mound in a captive group of bonobos. In the same study the highest ranking female displaced other individuals significantly more often than lower ranking females or a male. Rate of access to the artificial termite mound also corresponded to dominance, with lower ranking individuals gaining more access when the higher ranking females' interest was elsewhere (such as when they had access to the out-door enclosure, or when other novel enrichment devices were provided).

Therefore, it is important to investigate how social learning and dominance may have influenced the findings of the previous chapter. This chapter will test the following hypotheses:

2) Bonobos select the easy rope regardless of which rope the first individual selects at the start of the trial (selection hypothesis). For example, bonobos do not copy the first individual to access the food goal and instead select routes based on some individual knowledge of the functional properties of the available ropes.
3) Higher ranking individuals will access the food goal first during each trial and for longer periods (dominance hypothesis).

4.2 Methods

The methods given here are a summary of the main procedure detailed in Chapter Three. Subject information is given in Table 4.1.

Table 4.1 Details of study subjects

Individual	Group	Sex	Age at start of study	Rank	Arm length	Hand preference
AdfA	1	F	17	1	51 cm	Not lateralised
AdfB	2	F	36	1	51 cm	Not lateralised
AdfC	1	F	15	2	56 cm	Right
AdfD	1	F	8	3	50 cm	Left
InfA	2	F	3	-	30 cm	Not lateralised
InmB	1	M	3	-	31 cm	Not lateralised

Adf = adult/adolescent females, Inf = infant female, Inm = infant male. Individuals were housed in two separate groups (1 and 2). Rank is based on social network analysis of association and grooming data (collected by C. Walters). Hand preference is consistent hand preference for manipulations of the food goal in a terrestrial position and for collecting food from the ground (Chapter Two).

A food goal was placed 2 m from the ground above a viewing window. To either side of the goal were two ropes (polyester webbing 50 mm wide). The distance from the food goal or flexibility of the rope could be manipulated, such that the ropes provided ‘easy’ or ‘demanding’ access to the goal. Bouts of interactions with the ropes and goal were recorded in sequences along with duration (in seconds). A sequence was defined as a series of behaviours from when the individual first approached the equipment, through any interaction with the food goal, to the moment they returned to the ground. Data recorded for each sequence included: initial rope choice (easy or demanding; left or right); goal interactions (touch outer metal cage; power grip inner plastic ball; or precision manipulation e.g. pluck food items from inner plastic ball); and posture. Individual information included: dominance rank (dominant, middle ranking, subordinate, unranked infant). Dominance was calculated from association, grooming, and aggression data collected by C. Walters (2014), a minimum of 20 hours were collected for each individual. Association was defined as an individual being within two arm-lengths of the focal animal, and the interactions: grooming ("using lips and fingers to manipulate the fur of another individual"); dominance and submission (such as displacement, taking or surrendering an object, and rare aggressive behaviours such as lunge at, bite, or slap). Social networks combined these interactions and gave a strength and direction of relationship between each individual. Individuals were ranked according to their position in the social networks drawn for association and grooming data, combined with the number of successful dominance interactions (an interaction was considered successful if the dominant individual replaced the submissive individual or the receiving individual responded with a submissive behaviour such as surrendering a food item) with other individuals. Infants were unranked because only adults performed frequent successful dominance behaviours (total dominance behaviours of both infants was two compared to 40 from the adults). Arm length (described in Chapter Three) was divided into two categories, < 40 cm, ≥ 40 cm and used as a proxy for body size (Aiello 1981); and hand preference (Chapter Two).

GLMMs were used in statistical analysis because they can deal with categorical (binominal) and continuous response variables for non-normal data without the need to transform the data first. GLMMs combine features of linear mixed models (e.g. can include a random effect) and generalised linear models (e.g. for non-normal data) and therefore provide a more robust alternative to ANOVA (Bolker et al. 2009). GLMMs were performed in R version 3.2.3 (The R Development Core Team, 2015) using the package lme4 (version1.1-10), and post hoc analysis was performed using lsmeans (version 2.21-1). Table 4.2 details the variables used in the GLMM analysis. Rate of success and duration of success were chosen as dependent measures to investigate two different measures of success, how often an individual was successful (e.g. whether they accessed the goal and retrieved the food reward on their first attempt in each trail) and how long an individual was successful for (e.g. how long they could access the goal and retrieve the food reward). Both measures were chosen as a means to indicate whether rope choice was relevant to success and in what way.

Table 4.2 GLMM factors and factor level description.

Factor	Factor levels	Description
Initial rope	Easy	The rope nearest to the food goal (distance experiment) or the flexible rope (flexibility experiment)
	Demanding	The rope furthest from the food goal (distance experiment), or the taut rope (flexibility experiment)
Arm length	≥ 40 cm	two adult females and one adolescent female
	< 40 cm	one infant female and one infant male
Experiment	Distance	Easy rope is 1 m from the food goal
	Flexibility	Easy rope is flexible
Left or right rope	Left	Rope to the left of the food goal from the subjects viewpoint
	Right	Rope to the right of the food goal from the subjects viewpoint
Orientation of the easy rope	Left	When the easy rope in the trial occurred to the left of the food goal
	Right	When the easy rope in the trial occurred to the right of the food goal
Hand preference	Left handed	Consistent left hand preference
	Right handed	Consistent right hand preference
	Not lateralised	No consistent hand preference
Angle of approach	Same side	Subject selected the first rope encountered when approaching food goal
	Other	Subject selected the furthest rope encountered (e.g. they crossed the equipment before selecting a rope to climb)

(continued on the next page)

Table 4.2 GLMM factors and factor level description – continued

Factor	Factor levels	Description
Success from initial rope	Yes	Individual reached goal (power grip inner plastic ball; precision manipulation e.g. pluck food items from the inner plastic ball) from the first rope they chose to climb in a sequence
	No	Individual did not reach the goal (the inner plastic ball) from the first rope they chose in a sequence
Orientation of the easy rope	Left	When the easy rope in the trial occurred to the left of the food goal
	Right	When the easy rope in the trial occurred to the right of the food goal
Posture *(1)(orthograde or pronograde)	Orthograde	Orthograde (torso up-right) postures make up the majority of a sequence.
	Pronograde	Pronograde (torso horizontal) postures make up the majority of a sequence.
	Mixed	Sequence is made up of an equal proportion of orthograde and pronograde postures.
Posture (extended or flexed)	Extended	Postures that include the main weight bearing limbs in an extended position make up the majority of a sequence.
	Flexed	Posture that include the main weight bearing limbs in a flexed position make up the majority of a sequence.
	Mixed	Sequence is made up of combination postures, or an equal proportion of extended and flexed postures.

(continued on the next page)

Table 4.2 GLMM factors and factor level description – continued

Factor	Factor levels	Description
Posture (suspensory or mixed) *[(2)]	Suspensory	Postures in which the weight bearing limbs are in a suspensory position make up the majority of a sequence.
	Mixed	Sequence is made up of combination postures, or an equal proportion of compressive and suspensory postures.

*[(1)] *Posture categories are adapted from Hunt et al. 1996.* *[(2)] *Variable was collapsed to two levels (removing compressive postures) as only one individual (AdfB) used compressive postures for whole sequences when accessing the food goal from a barrel on the ground and was not included in GLMM analysis. Majority of a sequence is > 50% of bouts.*

4.3 Results

A total of 210 sequences were collected and used in analysis, 101 from experiment one; 109 from experiment two. A total of 84 sequences began with an alternative initial support (other than the easy or demanding ropes provided) and were removed for analysis. These included sequences in which the subject accessed directly from the ground or from a barrel (AdfB). Of these 35 included the individual returning to a rope for support after initial access of the goal and 49 were instances where an infant had originally chosen one of the ropes but had proceeded to climb briefly out of view above the equipment to then drop down directly onto the food goal.

All adult females accessed the goal directly from the ground at least once, and the adolescent did so 12 times. Also, AdfB accessed the goal a number of times from a barrel she first collected from the back of the enclosure (until the keepers were able to remove this from the enclosure). However, due to the small number of sequences (6) performed by AdfB she was removed from further analysis.

4.3.1 Generalised linear mixed model – rate of success from initial rope

An individual was considered successful if they manipulated the inner plastic ball of the food goal (using either power or precision grip) from the initial rope without returning to the ground or changing to the other available rope. A binomial GLMM was conducted in which the binomial response variable was success from initial rope (yes or no). Fixed factors were: experiment (distance or flexibility); whether the easy rope occurred to the left or right of the goal; arm length [< 40 cm or ≥ 40 cm]; and whether the initial rope was the easy or demanding option. Individual was included as a random factor. Table 4.3 shows the model reduction process: factors were dropped sequentially and those whose removal significantly reduced the power of the model were retained in the final model.

Table 4.3 ANOVA model reduction for maximum GLMM, Success from initial rope ~ Experiment + Initial rope easy or demanding + Initial rope left or right + Orientation of easy rope + Arm length + (1 | Individual). Maximum GLMM (AIC 234.7) revealed no effect of orientation of the easy rope, and initial rope left or right, or arm length.

Variable	**AIC**	**BIC**	**Deviance**	χ^2	**p value**
Maximum model	234.7	257.8	220.7	-	-
- Experiment	236.8	256.6	224.8	4.06	0.044**
- Initial rope easy or demanding	270.5	290.3	258.5	37.79	< 0.001*
- Initial rope left or right	232.8	252.6	220.8	0.04	0.834
- Orientation of easy rope	233.6	253.4	221.6	0.849	0.357
- Arm length	235.9	257.8	223.9	3.176	0.075

** $p < 0.001$*

The final GLMM model (AIC 233.1, Table 4.4) retained whether the initial rope was easy or demanding, and experiment as fixed factors, and individual as the random factor. An individual was more successful from the initial rope when it was the easy rope than when it was the demanding rope (Z = 5.02, p < 0.001).

Table 4.4 Final GLMM, Success from initial rope ~ Initial rope easy or demanding + (1 | Individual). Random effects variance 1.9, sd 1.4.

Variable	Estimate	SE ±	z value	p value
Intercept	1.011	0.708	1.43	0.153
Experiment (flexibility)	0.689	0.344	2.00	0.045**
Initial rope (easy)	2.794	0.574	4.87	< 0.001*

* $p \leq 0.001$, ** $p < 0.05$

4.3.2 Generalised liner mixed model – duration of success

Duration of success was calculated as the total amount of time an individual manipulated the food goal in a sequence, because the longer they manipulated the food goal the more food they were able to retrieve.

A GLMM was conducted with Poisson distribution in which the dependent variable was duration of success in a sequence (in seconds). Duration of success was time spent collecting food reward within a sequence. Fixed factors were: initial rope easy or demanding; success from initial rope (yes or no); experiment (distance or flexibility); postures extended or flexed; postures suspensory or compressive. Two interactions were also included. The first was arm length * postures orthograde or pronograde, after personal observations (NKIH) revealed that small individuals (short arm length) were pronograde more often than large individuals (individuals with long arm length). The second interaction was hand preference * initial rope chosen on the left or right of the goal, because hand preference influenced which rope was selected first in a sequence (Chapters Two and Three). The maximum model (AIC = 11884.6) was reduced using the same method as in the previous model.

The only term that did not significantly reduce the power of the model when removed was postures suspensory or mixed ($\chi^2 = 0.4$, p = 0.516). The final model (AIC 11883) retained all terms except for postures suspensory or mixed. Table 4.5 shows the final GLMM model for factors influencing duration of success.

*Table 4.5 Final GLMM, Duration of success ~ Initial rope easy or demanding + Success from initial rope + Experiment + Postures extended or flexed + Arm length*Postures orthograde or pronograde + Hand preference*Initial rope left or right + (1 | Individual). Random effects variance 0.006, sd 0.07.*

Variable	Estimate	SE ±	z value	p value
Intercept	4.379	0.116	37.65	< 0.001*
Initial rope (easy)	0.503	0.031	16.35	< 0.001*
Success from initial rope	0.366	0.024	15.25	< 0.001*
Experiment (flexibility)	0.154	0.021	7.44	< 0.001*
Sequence postures (extended)	0.347	0.029	12.15	< 0.001*
Arm length (< 40 cm)*Postures (Pron.)	2.035	0.365	5.57	< 0.001*
Initial rope (right)*Preferred hand (right)	-0.939	0.343	-2.74	< 0.006**

* $p \leq 0.001$, ** $p < 0.05$

Most factors had two levels and so importance of levels within the factors could be drawn directly from the model and further pairwise comparisons were unnecessary. Individuals had a significantly longer duration of success when the initial rope chosen in a sequence was the easy rope (Z = 16.35, p < 0.001) and when they were successful from the initial rope they selected

(Z = 15.25, p < 0.001). Individuals also had a longer duration of success in the flexibility experiment (Z = 7.44, p < 0.001).

Extended or flexed postures in a sequence, the interaction arm length*sequence postures orthograde or pronograde, and the interaction hand preference*initial rope left or right required further post-hoc analysis (Table 4.6-4.8). Tukey pairwise comparisons were performed with lsmeans (version 2.21-1). Individuals had a significantly longer duration of success when they used mostly extended postures in a sequence compared to either a mixture of extended and flexed postures (Z = 12.15, p < 0.001) or mostly flexed postures (Z = 24.94, p < 0.001). Sequences with mixed postures resulted in a longer duration of success than in sequences with mostly flexed postures (Z = 20.82, p < 0.001), see Table 4.6.

Table 4.6 Post-hoc analysis for Postures extended or flexed

Factor level	Tukey pairwise	Estimate	SE ±	z value	p value
Sequence postures extended	Mixed postures	0.347	0.029	12.15	< 0.001*
	Flexed postures	1.434	0.058	24.94	< 0.001*
Sequence postures mixed	Extended postures	1.087	0.052	20.82	< 0.001*

** p ≤ 0.001.*

Overall individuals with arm length < 40 cm had longer durations of success when using pronograde postures and individuals with arm length ≥ 40 cm had longer durations of success when using mixed and orthograde postures (Figure 4.1).

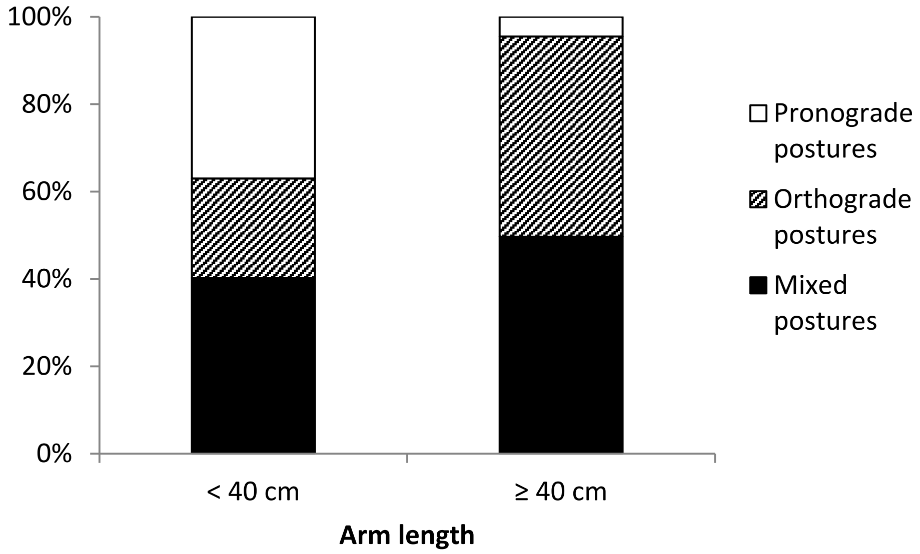

*Figure 4.1 Proportion of duration of success for the interaction Arm length*Postures orthograde or pronograde. Individuals with arm length < 40 cm use more pronograde postures than individuals with arm length ≥ 40 cm, and these individuals use more orthograde and mixed postures.*

Table 4.7 shows the breakdown of the post-hoc analysis for the interaction arm length*postures orthograde or pronograde. Individuals with an arm length < 40 cm had a significantly longer duration of success when they used mostly pronograde postures in a sequence than when they used mostly orthograde postures ($Z = 13.71$, $p < 0.001$). However, they had a significantly shorter duration of success compared to larger individuals (arm length ≥ 40 cm) using mostly orthograde postures in a sequence ($Z = -10.67$, $p < 0.001$) and a mixture of postures in a sequence ($Z = -12.60$, $p < 0.001$). Larger individuals had a significantly longer duration of success when they used a mixture of both orthograde and pronograde postures in a sequence than when they used mostly orthograde postures ($Z = 6.50$, $p = 0.036$) or pronograde postures ($Z = 5.38$, $p < 0.001$).

*Table 4.7 Post-hoc analysis for Arm length*Postures orthograde or pronograde*

Factor level	**Tukey pairwise**	**Estimate**	**SE ±**	**z value**	**p value**
< 40 cm, pronograde postures	< 40 cm, orthograde postures	0.487	0.035	13.71	< 0.001*
	≥ 40 cm, orthograde postures	-1.042	0.098	-13.04	< 0.001*
	≥ 40 cm, mixed postures	-1.503	0.119	-12.60	< 0.001*
≥ 40 cm, mixed postures	≥ 40 cm, orthograde postures	0.461	0.071	6.50	< 0.001*
	≥ 40 cm, pronograde postures	1.951	0.363	5.38	< 0.001*

* $p < 0.001$

The left handed individual had a significantly longer duration of success when selecting the right rope initially in a sequence than the right handed individual (Z = 4.98, p < 0.001) and when they selected the left rope (Z = 3.13, p = 0.022). The right handed individual had a longer duration of success when they selected the left rope initially in a sequence than when they selected the right rope initially in a sequence of interaction with the goal, however this was not significant (Z = 2.28, p = 0.203). Non-lateralised individuals also had a significantly longer duration of success when they selected the left rope initially in a sequence than when they selected the right rope (Z = 9.02, p < 0.001), see Table 4.8.

*Table 4.8 Post-hoc analysis for Hand preference*Initial rope chosen left or right*

Factor level	**Tukey pairwise**	**Estimate**	**SE ±**	**z value**	**p value**
Left handed, right rope	Left handed, left rope	0.169	0.054	3.13	0.022**
	Right handed, right rope	1.754	0.352	4.98	< 0.001*
Not lateralised, left rope	Not lateralised, right rope	0.201	0.022	9.02	< 0.001*
Right handed, left rope	Right handed, right rope	0.771	0.338	2.28	0.203

* $p < 0.001$, ** $p < 0.05$

4.3.3 Duration of success from ‘other’ supports within a sequence

The initial rope chosen in a sequence did not always determine which rope would be used throughout a sequence. For instance, once a subject had reached the food goal, they would often change their posture and their main support, before releasing the food goal and returning to the ground. In this way a sequence may include the following: climb to the goal on the easy rope – access the goal by maintaining a suspensory posture on the easy rope – release the rope and continue manipulating the goal whilst suspended from the goal itself – return to the easy rope and continue to access the goal – release the goal and descend the easy rope. For the majority of sequences success at the food goal was recorded whilst the individual maintained their body weight on the easy rope (167/210, Figure 4.2). However, 118 sequences also included manipulation of the food goal whilst body weight was supported solely by the goal itself. Very few sequences included use of the demanding rope (24), equating to a total of 5.08 minutes of success from the demanding rope across all 210 sequences. The average duration of success from each of the available supports within a sequence was much higher from the food goal itself (34.6 seconds), than from the easy rope (18.8 seconds).

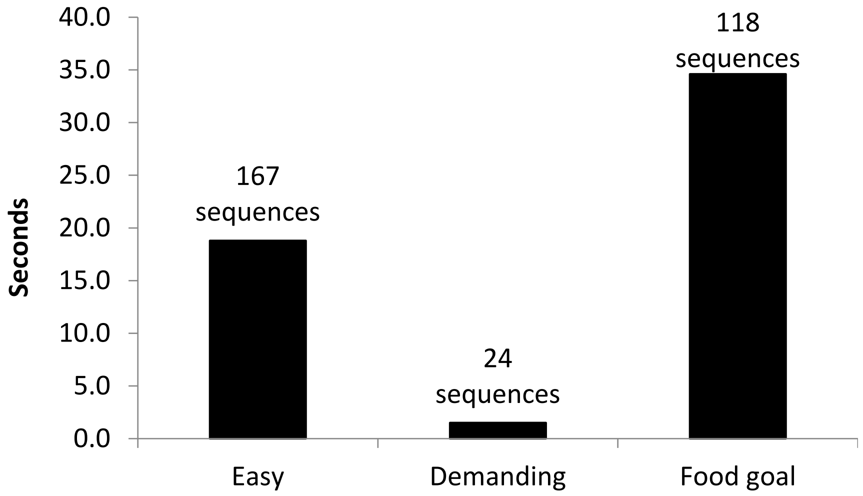

Figure 4.2 Average duration of success in seconds from different supports within sequences, and the number of sequences that bouts of manipulations from each support occurred in

4.3.4 Influence of group presence

All individuals were present or could choose to be present for each sequence within a trial, so could potentially watch and copy the first individual's rope choice. Individuals selected the easy rope initially in a sequence if the first individual in the trial had accessed the food goal from the easy rope (Chi Square test, $\chi^2 = 58.7$, df = 1, $p < 0.001$) or from the demanding rope (Chi Square test, $\chi^2 = 13.52$, df = 1, $p < 0.001$), see Figure 4.3.

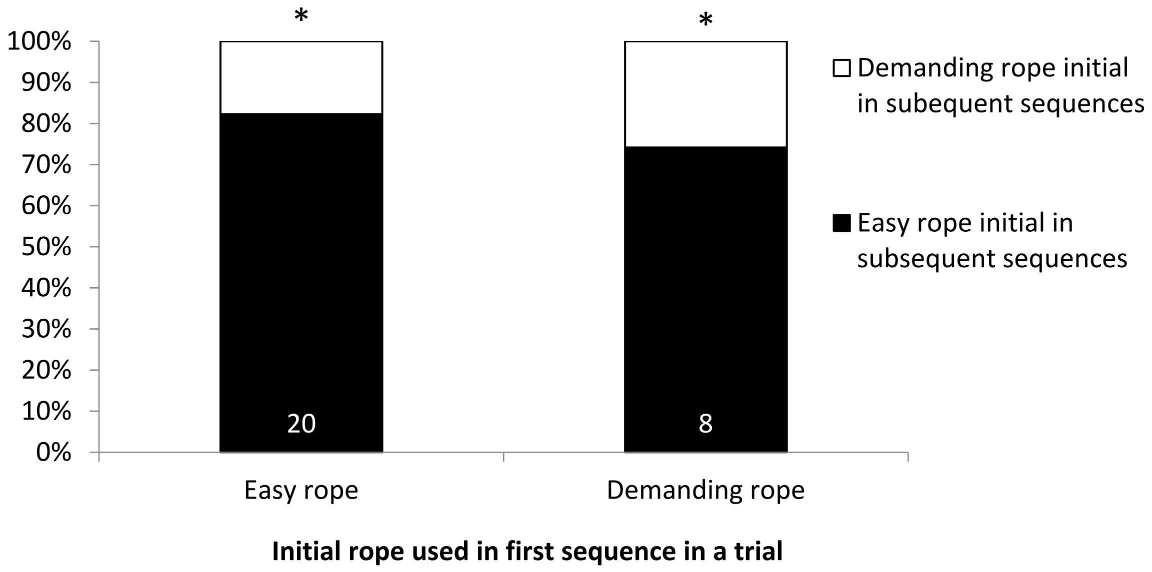

*Figure 4.3 Number of times each rope was chosen first in a trial (in white at the bottom of the bars) and the percentage of initial rope choice for subsequent sequences. If the first individual chose the easy rope in their first sequence, subsequent individuals chose the easy rope. If the first individual chose the demanding rope in their first sequence subsequent individuals chose the easy rope more often. * $p < 0.001$ (χ^2 test, df = 1).*

Table 4.9. Results of chi-square test and descriptive statistics for initial rope choice for the first and subsequent sequences in a trial.

Initial rope choice – first sequence in a trial	**Initial rope choice – subsequent sequences in a trial**		**Total**
	Easy rope	Demanding rope	
Easy rope	116 (82.3%)	25 (17.7%)	141 (100%)
χ^2 = 58.7., *df* = 1, *p* < 0.001			
Demanding rope	43 (74.4%)	15 (25.9%)	58 (100%)
χ^2= 13.5, *df* = 1, *p* < 0.001			

Numbers in parentheses indicate row percentages

Each individual tended to select the same rope throughout a trial period if they had selected the easy rope initially in their first sequence. If an individual selected the demanding rope initially in their first sequence they chose the easy rope in subsequent sequences. However, significance tests could not be performed for all individuals within every trial period because some individuals performed only one sequence during a trial.

4.3.5 Influence of dominance rank

Two adult females and the adolescent female were ranked as dominant, middle ranking, and subordinate respectively, and infants were unranked (see methods). Dominance rank did not influence initial rope choice, and all ranks selected the easy rope initially in a sequence between 60 – 71% of the time. Dominance could not be included in GLMM analysis because it correlated with other variables and created rank deficiency in the model (e.g. all individuals with arm length < 40 cm were un-ranked, only AdfC was beta, and AdfD was subordinate).

However, rank was reflected in the order in which individuals accessed the goal within a trial (Figure 4.4). The lowest ranking individual (AdfD) accessed the food goal first in a trial more often than the middle (AdfC) and highest (AdfA) ranking individuals. The lowest ranking individual also had a shorter average sequence duration (73.4 seconds of which an average of 65.8 seconds was spent successfully gaining food reward). The dominant female had the longest average sequence duration (145.8 seconds, of which an average of 138.5 seconds was spent successfully gaining food reward).

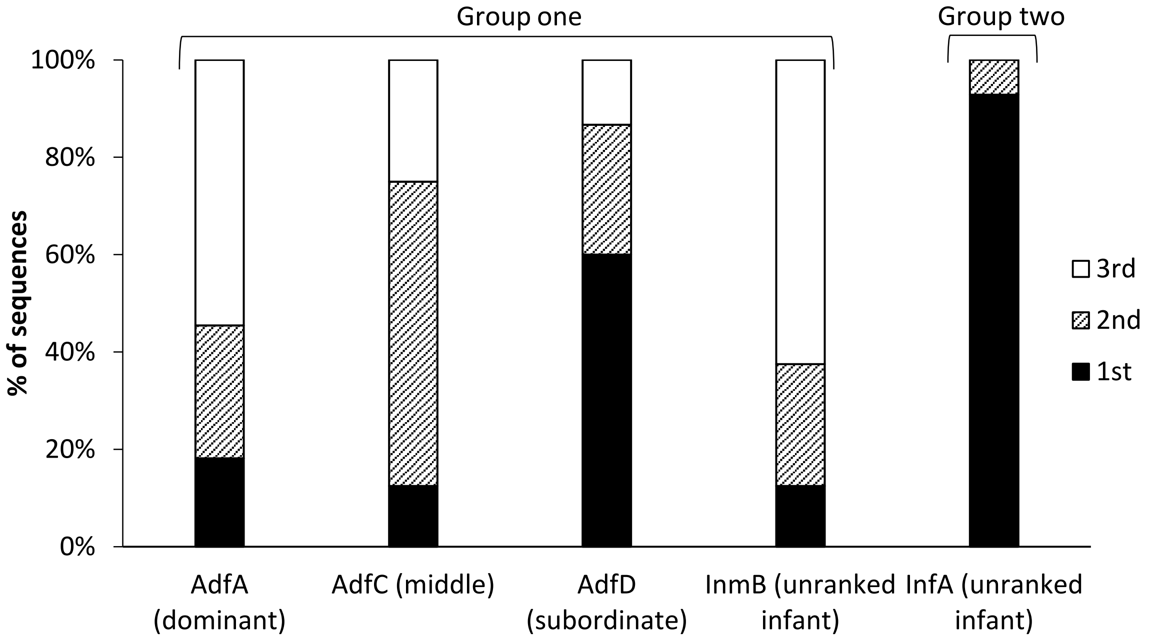

Figure 4.4 Order each individual (and corresponding rank) accessed the goal in all trials. InfA was housed in a separate group with other individuals that did not frequently interact with the test equipment.

InmB follows the same pattern as his mother AdfA. InfA was also housed with her mother (AdfB) in the second group. However, AdfB performed too few sequences (and was consequently dropped from GLMM analysis) and InfA gained initial access to the goal in over 90% of trials, while other individuals in the group rarely interacted with the test equipment.

4.4 Discussion

Sociality and dominance were explored as potential factors influencing rope choice and access of a hard-to-reach food goal. Individuals initially selected the easy rope regardless of which rope the first individual in a trial had used, suggesting they were not socially learning from other individuals in every trial. Selecting and using the easy rope gave the individuals greater success at reaching and increased access to the food goal. Dominance did not influence rope choice, although the subordinate individual accessed the goal first in more trials but overall had shorter sequences (and shorter durations of success) whereas the dominant female had longer durations of success. The findings of this study offer further support to the findings in Chapter Three, in that social learning and dominance cannot explain rope choice, and it is more likely that the bonobos were selecting the ropes on the basis of their functional properties.

4.4.1 Success rate and positional behaviour

The bonobos had a greater rate of success (in terms of reaching the goal and duration of manipulation of the goal) when they selected the easy rope initially in a sequence. This confirms the success hypothesis (1) to be correct: selection of the easy rope benefitted the individual by enabling increased access of the goal. However, limb length influenced the postures used to access the goal. When using the easy rope larger individuals (arm length ≥ 40 cm) were able to access the food goal in orthograde postures, for example climbing thevertical rope and reaching across to the goal whilst maintaining a unimanual forelimb suspensory posture on the rope (see appendix Figure A4.1). In this way the larger individuals were able to access the goal at arms-length. Small individuals (arm length < 40 cm) used more stretched out, pronograde, postures, for example bridging between the rope and the goal in a pronograde suspensory posture, with the feet gripping the rope and a forelimb suspending from the food goal itself (see appendix Figure A4.2). In this way small individuals generally had to use their whole body length to access the goal from a rope. It has been demonstrated for other non-human great apes that flexible locomotor repertoires enable individuals of different body sizes to access hard to reach resources in the canopy environment (Cant 1987, Thorpe et al. 2009, Myatt and Thorpe 2011). This further supports the findings of the previous chapter in that the functional properties of the easy rope provided substantial benefit in terms of greater access of the food goal. Furthermore, individuals with short arm length were infants and selected supports in the same way as adults. This suggests that the ability to select supports based on their functional properties and an awareness of individual reach is developed in bonobos by the age of three years. Bonobos are weaned by the age of five years (Kuroda 1989, De Lathouwers and Elsacker 2006), therefore the infants in this study (three years of age) were still suckling occasionally and being carried by their mothers (de Waal 1995). Although InfA and InmB were carried to the goal on one and two occasions respectively by their mothers, independent locomotion was likely well developed. It has been shown that independent locomotion develops by the age of three in non-human apes (in bonobos less than three years, Doran 1992; in orangutans by the age of three years, Noordwijk and van Schaik 2005). Therefore, it would be vital for survival for even infants of this age to possess some knowledge of the functional properties of supports so as to avoid falling from the canopy.

The average duration of successful manipulations of the food goal for postures maintained on the goal itself was longer than those using either of the ropes. This suggests that using the goal as a support removed potential instability and the restriction associated with individual reach when maintaining a posture on a separate rope. Youlatos (2001) suggested that positional behavioural repertoires are the result of complex interactions between intrinsic factors (such as morphology and body size) and extrinsic factors (such as support availability). The findings of this study further demonstrate that the flexible positional behavioural repertoires of non-human great apes enable successful access of hard-to-reach resources (as has been shown by Hunt 1991, Thorpe et al. 2009, Myatt and Thorpe 2011) by individuals with differing body specifications.

In the previous study it was found that hand preference influenced initial choice of ropes to access the goal: lateralised individuals selected the rope on the opposite side to their preferred hand allowing initial access of the goal with their preferred hand. The findings here suggest that this not only benefited the individual through increased initial access of the goal (success rate) but also through longer duration of successful manipulation of the goal. However, of the two lateralised individuals this was only significant for one individual (AdfD) and although AdfC also selected the rope on the opposite side of her preferred hand this was not significant. However, this could have been due to a small number of sequences recorded for this individual (14).

4.4.2 Social learning and dominance rank

All individuals preferred the easy rope initially in a sequence significantly more than the demanding rope regardless of whether they had potentially observed another individual accessing the goal first using either rope. If only social learning was occurring in this study it would be expected that the first individual to access the goal would do so from either rope and that subsequent individuals to select a rope would do so using the same one regardless of whether it was the easy or the demanding rope. However, this was not the case and the majority of individuals to access the goal first in a trial selected the easy rope initially, and on the rare occasion that they selected the demanding rope (eight out of 28 trials) subsequent individuals still preferred the easy rope.

This suggests that the bonobos were not influenced by the behaviour of the first individual in every trial, however, it is possible that their actions on the ropes and the goal could have stimulated subsequent individuals' use of the ropes through local or stimulus enhancement (Heyes 1994). Individuals can gain information regarding the functional properties of, for example, a tool (in this case the ropes) through observing other individuals interacting with it but may learn how to use the tool themselves through their own manipulations (Tomasello 1996, Tomasello and Call 1997). For instance, if the first individual to access the goal in a trial initially selected the demanding rope other individuals may have used information regarding that individual's postures, limb reach, or distance from the ropes to the goal, when selecting a rope to use themselves. This would imply that they were emulating the results of the behaviour of the first individual (accessing the goal using the ropes), but not imitating their behaviour (selecting the same rope). However, this does not necessarily mean they lacked or were not using some knowledge of the functional properties of supports.

If we consider choosing the demanding rope an 'error' in that it results in a lower rate of success and requires more demanding postures then the bonobos could have been learning from the mistakes of the first individual to access the food goal in a trial (when they selected the demanding rope first). There is evidence for other non-human primates and human children learning from the mistakes of conspecifics or demonstrators (Myowa-Yamakoshi and Matsuzama 2000, Call et al. 2005, Kuroshima et al. 2008). For example, Myowa-Yamakoshi and Matsuzama (2000) demonstrated that chimpanzees were able to learn from the mistakes of a demonstrator (for instance they were able to reproduce a demonstrators strategies for opening a container after seeing a demonstrator fail to do so). Call et al. (2005) similarly demonstrated that chimpanzees were able to emulate the results of a demonstrators actions and that when they observed unsuccessful actions they could employ new methods to achieve the intended goal. Kuroshima et al. (2008) demonstrated that captive capuchin monkeys (*Cebus apella*) were also able to learn from the mistakes of conspecifics. Capuchin monkeys observed another individual fail at opening a container (either from the top or bottom) and were then given the opportunity to attempt to open the container. They successfully switched their behaviour to open the container using the opposite method to the failed conspecifics attempt (for example if the first monkey tried opening from the top and failed, the second observing monkey immediately opened the container from the bottom). Therefore, in this study, if the first individual to access the goal in a trial selected the demanding rope initially the other bonobos could potentially be learning from observing the first individuals 'error'. In this way the bonobos would still be applying knowledge of the functional properties of the supports (gained from observing an individual in more demanding postures using the demanding rope because it is further away).

However, the use of the demanding rope is not a true error in that it could still provide access to the goal, perhaps the outcome of accessing the food reward was more important than considering the potential demand of postures. The majority of subsequent individuals to access the goal in a trial selected the easy rope regardless of the ropes used by the first individual. Also, and perhaps more importantly, the first individuals to access the goal in the majority of trials selected the easy rope without the opportunity to observe another individual (20/28 trials). Furthermore, not all individuals were present and observing the first individual to access the food goal in each trial, all individuals had the freedom to roam throughout their enclosure throughout each trial. Therefore, we cannot explicitly say the bonobos were observing the first individual access the goal at all times, rather that they had the opportunity to do so. This adds further support to the selection hypothesis (2); these bonobos were selecting the ropes based on their functional properties (rather than social learning). This is further suggested by the fact that the first individual to access the food goal in a trial was more often the lowest ranking individual, and therefore, other individuals may have been less likely to copy her (Horner et al. 2010).

Although dominance rank could not be used in the main GLMMs as it correlated exactly with limb length and individual it was found that rank did not influence rope choice (all individuals selected the easy rope initially in the majority of trials). However, dominance influenced the order in which individuals gained access, but the social hypothesis (3) was not supported: the lowest ranking individual gained initial access in a trial more often than the dominant female. However, this does not suggest that the lower ranking individual had better access because the dominant female had longer durations of success at the food goal. In this way the low ranking individual gained access first in a trial but was quickly displaced by the dominant female who then remained at the goal for a longer period, gaining more of the food reward. This pattern of access can be explained by the fact that the dominant female usually accessed another terrestrial food goal initially in a trial. The terrestrial food goal was present during all trials for the purposes of reducing competition and potential aggression (see Chapter Two and Three) and individuals were able to access it in less demanding postures by sitting or standing on the ground.

Therefore, it is likely that the dominant female favoured the other goal initially because this was more easily accessed from the ground and so represented a reward of higher value (such as providing food reward for less energetic exertion). Therefore, while the social hypothesis (3) was not correct for the experimental goal, it was true for the additional terrestrial goal and dominance did influence overall access but not the order of access to the experimental goal. Thus, the findings here support previous findings for captive bonobos (Parish 1994).

Dominance rank has been shown to influence access to resources in wild female: bonobos (Furuichi 1997); chimpanzees (Wittig and Boesch 2003); and gorillas (Robbins et al. 2007). Parish (1994) found that dominant female bonobos attained access of an artificial termite mound more than lower ranking females and a male and for longer periods of time. Parish (1994) also found that a male gained little access to the termite mound; in the current study adult males were present during all trials but gained no access of either the experimental or additional terrestrial food goal.

In conclusion selection of the easy rope benefitted the individual with greater success at the food goal than did selection of the demanding rope (success hypothesis), and body size influenced positional behaviour and success rate. Dominance did not influence rope selection, but did influence access of the food goal (dominance hypothesis) similar to previous studies of other species of wild non-human great apes (Wittig and Boesch 2003, Robbins et al. 2007), and captive and wild bonobos (Parish 1994, Furuichi 1997). Lastly, this study further supports the findings of the previous chapter: that these bonobos were selecting ropes to access the hard-to-reach food goal based on their functional properties (selection hypothesis).

CHAPTER FIVE

SUPPORT CHOICE IN HUMAN ROPE CLIMBERS: COMPARING EXPERIENCED ROCK CLIMBERS, NOVICE ROCK CLIMBERS, AND GYMNASTS

Abstract

Some members of hunter gatherer tribes climb trees for resources such as honey; however, for the majority of humans (*Homo sapiens*) arboreal climbing is rare. However, other climbing is more common, such as rock climbing and using ropes in gymnastics. As we share an arboreal common ancestor with extant non-human apes, human climbing offers an interesting comparison in studies of the decision making involved in arboreal locomotion. Three groups of human climbers (experienced rock climbers, novice rock climbers, and experienced gymnasts) were tasked with collecting a flag situated 2.5 m from the ground by selecting and climbing a vertical rope. Ropes differed in their functional properties in relation to the flag (distance, flexibility, and connectivity) and were presented in pairs within each trial, with one rope offering substantially easier access to the flag (the correct rope). Participants selected the correct rope significantly more often in the distance trial compared to the connectivity trial. It is suggested that this is due to a reduced perception of the relevant functional properties of the ropes, for example, ropes in the distance trial were immediately visibly different (one was near to the goal, the other was further away). These findings suggest that, across different groups of rope climbers, simple processes such as motor planning (for example understanding reach) are used in selection of potential arboreal supports when functional properties are visually obvious. Hand use was also explored in the rock climbers, novice rock climbers preferred to use their dominant hand for postural support rather than using it for the manipulatory task of untying the flag. It is suggested that increased confidence and muscle strength in experienced athletes reduced reliance on the dominant hand for postural support in the symmetrical test environment.

Chapter contents

5.1 Introduction

The demands of travelling in the dynamic and unpredictable environment of the rainforest canopy have been linked to the evolution of cognition in primates (Milton 1981, Povinelli and Cant 1995, Barth et al. 2004). Basic cognitive mechanisms such as knowledge of the physical properties of supports used for locomotion and motor planning could be precursors to complex cognition (Vaesen 2012). It has been shown that non-human apes (bonobos and a siamang) select suitable arboreal supports based on their functional properties such as distance to a food goal (Chapter Three). Determining how cognitive adaptations may have arisen in response to the demands of arboreal locomotion is key to our understanding of the behavioural ecology of non-human primates and potentially to understanding how our own cognitive abilities may have originated. Furthermore, the role of hand preference on selection of arboreal supports in non-human apes is unclear. Bonobos adopting demanding arboreal postures to access a hard-to-reach food goal in a symmetrical test environment showed individual handedness (Chapter Two); whereas in the natural rainforest canopy where available supports are random and irregular in relation to food sources (non-symmetrical), chimpanzees were ambilateral (McGrew and Marchant 2007). However, there is also continuing debate about the existence of population level handedness in non-human primates (see McGrew and Marchant 1997a and Hopkins 1999 for a review), in contrast to the clear population level handedness in humans, where 90% of individuals are right handed (Annet 1985). Therefore, it is also important to consider how handedness may influence support selection and use in predominantly right-handed human participants in a symmetrical test environment.

Some experienced and skilled members of hunter gatherer tribes climb trees unassisted for resources such as honey (Kraft et al. 2014). However, for some tribes tools and technologies are used when foraging in this way. For example, the Batek of Malaysia use vines to bridge gaps between trees (Lye 2004) and the Yanomamö of the Amazon use a pair of wooden "A frames" to overcome defensive spines on the trunks of some species of palms (Chagnon 1992). Further tools for climbing used by hunter-gatherer populations include foot and hand nooses, vines looped around tree trunks, and a series of pegs hammered directly into tree trunks (Kraft et al. 2014). Similarly in western populations the exploration of arboreal environments often involves the use of tools and technologies, such as climbing ropes and winches. The aim of this study was to present human participants with a climbing task in which they were required to select a suitable rope to climb, based on the functional properties of two possible ropes. The findings could then be compared to the performance of non-human apes (bonobos and siamangs) in similar tasks (Chapter Three).

Rock climbing is a popular recreation and a British Mountaineering Council member survey (2010) revealed a total of 80,000 members, of which 74% were rock climbers. Although it is not arboreal travel (i.e. travel in trees) it encompasses similar demands and risks. Rock climbing is energetically demanding because climbers must maintain their own body weight off of the ground (opposing gravity) which requires use of both legs and arms (Mermier et al. 1997, Sheel 2004). Furthermore, it is cognitively demanding because rock climbers must carefully select routes and avoid the obvious danger of falling (Llewellyn et al. 2008, Llewellyn and Sanchez 2008). Therefore, rock climbers represent a useful group of athletes to compare to arboreal apes.

However, rock climbers do not typically use a rope for support (one is attached to a harness primarily for safety purposes) and therefore, testing novice rock climbers (who may rely on ropes as support more frequently) and gymnasts (who climb free hanging ropes) offer an interesting comparison. These groups may use different climbing techniques and differ substantially from non-human apes because humans cannot grip with their feet with the toes closed against the sole as other non-human primates do. However, this study is primarily interested in how human participants decide which supports to select, rather than the biomechanics of different climbing techniques.

Rock climbers were chosen as an interesting comparison to arboreal non-human apes as they have to face many of the same demands, such as the need to avoid falling and the physical demand of maintaining their body weight off of the ground usually using at least one forelimb for postural support. By comparing novice and experienced climbers the influence of training (in terms of knowledge and experience as well as in terms of physical training) and confidence in this environment could be explored. However, rock climbers are required to climb against a rigid climbing wall, which is functionally different from most supports in a natural canopy environment. Therefore, gymnasts climbing a free hanging rope (away from a wall) provide a more biomechanically direct comparison to non-human apes climbing forest vines or vertical ropes in captivity (Chapters Two, Three, and Four).

As an analogue of the decision making of non-human apes when travelling in the canopy three different trials were designed to investigate rope selection based on three functional properties: distance from a goal; flexibility (and so potential distance from a goal); and connectivity. In the distance trial participants were required to judge where they could reach the goal from and select a rope to climb accordingly. The flexibility trial required participants to first judge where they needed to be in terms of proximity to the goal and then decide which rope could be manoeuvred to enable this. The connectivity trial required participants to first judge and decide which rope could be manoeuvred towards the goal in the same way as the flexibility trial but also included an additional manipulatory task (untying the most suitable rope), which added a further stage in the action sequence required to reach the goal. In this way the distance trial provided ropes that were instantly visually different from one another (e.g. near or far from the flag); the flexibility trial required participants to first detect that the ropes would need to be manoeuvred nearer to the rope for an easier reach and then identify which rope could be moved; the connectivity trial required the same process as the flexibility trial but with an additional level of manipulation after identification of which rope could be moved towards the goal, this required participants to perceive that the additional rope restricted the movements of the climbing rope (e.g. connected to) and participants were required to increase their time to action (e.g. they could not climb a rope as soon as they had chosen it). In each trial ropes were presented in pairs with one providing substantially easier access to the goal (nearer or flexible). In this way rope choices were recorded as correct (the easy rope) or incorrect (the more difficult rope).

Hypotheses

1) Increasingly difficult trials will result in fewer correct choices. Across the three different experimental groups (experienced rock climbers, novice rock climbers, and gymnasts) trial one will result in the most correct choices, trial two will have fewer correct choices, and trial three will have the least correct choices.
2) Participants who are right handed will collect the flag with their right hand, and *vice versa* for left handed participants.

5.2 Methods

All data were collected by NKIH between March 2014 and January 2015 at Red Point Climbing Centre, Birmingham, UK, (experienced and novice rock climbers) and King Edward VI High School for Girls, Birmingham, UK, (gymnasts). Participants were recruited from volunteers over the age of 18 (ethical approval was obtained from the University of Birmingham review committee, ERN_14-0072).

In each experiment participants were required to retrieve a coloured flag (the goal) positioned at 2.5m above the ground, between two ropes. Each participant was given three trials in which the functional properties and position of the ropes were different on each trial. The trials thus tested three different properties of the ropes and represented three levels of complexity.

In the distance trial the ropes were 1 m and 1.5 m from the flag respectively, connected at ground level so that they could not be manoeuvred significantly laterally toward the flag. In the flexibility trial both ropes were 1.5 m from the flag, and one was not connected at ground level and thus could be manoeuvred toward the flag. In the connectivity trial both ropes were flexible and 1.5m from the flag, but both ropes were also connected to an additional lateral rope. Participants were required to perform an additional manipulatory task to untie their chosen rope prior to climbing to reach the flag. For each trial the choice of rope was ‘correct’ (nearer to the flag or flexible and thus able to be manoeuvred toward the flag) or ‘incorrect’ (further from the flag or taut and unable to be manoeuvred toward the flag). However, the incorrect route was not impossible, therefore participants were able to successfully access and collect the flag even when selecting the incorrect rope. See Figures A5.1-A5.4 in the appendix for schematic diagrams of rope and flag positioning for the different trials.

The ropes were balanced (so that the position of the correct rope occurred equally to the left and right of the flag across all participants) and then randomised for each participant. The order in which participants received each trial was pseudo-randomised between individuals. Each trial was videoed (Sanyo Xacti CG10 camera, 30 frames per second) from a central position and videos were analysed at a later date. Chosen rope, handedness (which hand was used to touch the goal initially, which hand was used for support at the goal), and how the chosen rope was used as a support for locomotion or posture was recorded.

Arm span (measured from longest finger-tip to longest finger-tip) and unshod height (measured with an upright stadiometer) were taken before each participant started the trials. Participants were given brief verbal instructions (Figure A5.5 appendix) to retrieve the flag using whichever rope they preferred, and were told this may require them to manipulate the rope before climbing but were not informed how or when they may need to do so. All trials in the rock climbers' experiments were overseen by a safety supervisor employed by Red Point Climbing Centre. All trials in gymnasts' experiment were overseen by the captain of the University of Birmingham Gymnastics and Trampolining competition squad.

5.2.1 Rock climbers

Experienced rock climbers (12 participants) had been climbing for more than one year, went climbing more than once a week, and were members of Red Point Climbing Centre. Before each trial participants were given one minute to visually study the apparatus before selecting a rope to climb. Novice rock climbers (10 participants) had never climbed before. Participants were given up to three minutes to visually study the apparatus before selecting a rope to climb.

Ropes were positioned on a ‘slab’ wall which was 4.0 m wide and 6.1 m high and had a slight incline (away from the participant) so that it was not completely vertical. All hand and foot holds were removed from the wall except for six on either side of the flag regularly spaced from 0.5 m to 1.5 m from the ground in the path of the participants. The climbing ropes were 10.2 mm in diameter. To either side of the ropes a safety harness attached to a belay rope was tied out of sight of the equipment (Figure A5.6a in appendix). Participants first selected (verbally or by touching) the rope they wished to use to reach the flag and then were fitted with the respective harness and belay system by the safety supervisor.

5.2.2 Gymnasts

Participants were experienced gymnasts and were members of The University of Birmingham Gymnastic and Trampolining competition squad. Before each trial participants were given one minute to visually study the apparatus before selecting a rope to climb.

Ropes were free hanging standard gymnastic climbing ropes with a diameter of 50 mm. The flag was attached to a rope in the centre which participants were instructed not to climb directly (Figure A5.6b in appendix).

5.2.3 Statistical analysis

Binomial Generalised Linear Mixed Models (GLMM) were used to investigate the influence of multiple variables on rope choice (correct or incorrect) and whether participants used the chosen rope as support when climbing or when collecting the flag (yes or no). GLMMs were chosen in place of traditional statistical tests such as ANOVA because they allow for the inclusion of a random effect (in this case individual) and are the most appropriate method to deal with categorical and unbalanced data. Individual was included as a random factor and fixed factors are detailed in Table 5.1 (Bolker et al. 2009). GLMMs were performed in R version 3.1.0 (2014-04-15 “Spring Dance”) using the package lme4 (version 1.1-6), and post hoc analysis was performed using lsmeans (version 2.13). To investigate how functional properties of the ropes influenced choice, rope choice was chosen as the binomial dependant measure. This enabled correct and incorrect choices to be compared, for example, were participants selecting the correct (in terms of functional property that enabled the least demanding access of the flag) rope or was some other factor (such as handedness) influencing rope choice.

Table 5.1 GLMM terms and descriptions

Factor	Description
Age	Age in years
Gender	Male, female
Arm length	Measured in cm
Height	Measured in cm
Orientation of the correct rope	Left – the correct rope in the trial occurred to the left of the flag Right – the correct rope in the trial occurred to the right of the flag
Chosen rope correct/incorrect	Correct – the easier rope (nearer or flexible) Incorrect – the harder rope (further or taut)
Chosen rope left/right	Left – the first rope the participant climbed occurred to the left of the flag Right – the first rope the participant climbed occurred to the right of the flag
Order of trials	The order the participant received the trials
Experiment	Experienced rock climbers Novice rock climbers Gymnasts
Trial	Distance Flexibility Connectivity

5.3 Results

A total of 28 participants performed each of the three trials (84 trials in total), 12 experienced rock climbers, 10 novice rock climbers, and 6 gymnasts (Table 5.2). Four participants (two experienced rock climbers and two gymnasts) chose the correct rope in every trial although all participants were able to access and collect the flag even when they chose the incorrect rope. All participants successfully retrieved the flag in all trials except for participant 503 on their first trial. There were a total of 47 correct and 37 incorrect choices when the data were pooled across the different experiments and trials.

Table 5.2. Participant information and number of correct choices for each trial – distance, flexibility, and connectivity. Correct choices are 1 and incorrect choices are 0.

				Correct choices (1)			
	Individual	**Gender**	**Age**	**Distance**	**Flexibility**	**Connectivity**	**Total**
Experienced rock climbers	**542**	Female	23	0	1	0	1
	545	Female	21	1	1	0	2
	529	Female	24	1	1	1	3
	501	Male	30	0	1	0	1
	503	Male	27	1	0	0	1
	506	Male	24	1	1	1	3
	510	Male	27	1	1	0	2
	524	Male	24	0	0	0	0
	530	Male	24	1	1	0	2
	535	Male	23	1	1	0	2
	537	Male	26	1	1	0	2
	541	Male	27	0	1	0	1
Novice rock climbers	**846**	Female	22	1	0	1	2
	857	Female	21	1	0	0	1
	867	Female	20	1	0	1	2
	843	Female	21	0	1	0	1
	839	Female	23	1	0	0	1
	847	Female	23	0	0	0	0
	861	Male	22	1	0	1	2
	850	Male	26	1	0	1	2
	874	Male	22	1	0	0	1
	840	Male	26	0	1	1	2
Gymnasts	**767**	Female	19	1	0	1	2
	762	Female	18	1	0	1	2
	765	Female	19	1	1	1	3
	743	Male	22	1	1	0	2
	750	Male	20	1	1	1	3
	764	Male	21	0	0	1	1
			Total	*20*	*15*	*12*	*47*

When the data were pooled across the three experiments the number of correct choices in each trial decreased with increasing difficulty. The majority of participants (20) selected the correct rope in trial one (the distance trial), 15 participants selected the correct rope in trial two (the flexibility trial), and 12 selected the correct rope in trial three (the connectivity trial).

5.3.1 GLMM analysis of rope choice

To investigate rope choice a binomial generalised linear mixed model (GLMM) was used, in which the dependent binomial variable was which rope was chosen (correct or incorrect). Fixed factors were: individual information (age, gender, arm length, and height); orientation of the correct rope (to the left or the right of the flag); chosen rope occurring to the left or the right of the flag; the order the participant received the trials; and trial (distance, flexibility, or connectivity). Individual was included as a random factor (Bolker et al. 2009) nested within experiment because different individuals participated in the three different experiments.

Terms whose removal significantly reduced the power of the model (by increasing the AIC or deviance) were sequentially dropped (Thornton and Samson 2012). The maximum model (AIC 129.5, Table 5.3) showed that trial (distance, flexibility, or connectivity) significantly influenced the choice of the correct rope and dropping this term significantly reduced the power of the model (ANOVA test comparing the two models: $\chi^2 = 6.6$, $p = 0.038$). ANOVA tests comparing sequential models confirmed that removing: age ($\chi^2 = 0.3$, $p = 0.568$); gender ($\chi^2 = 0.04$, $p = 0.845$); arm span ($\chi^2 = 1.1$, $p = 0.298$); height ($\chi^2 = 2.2$, $p = 0.137$); orientation of the correct rope ($\chi^2 = 1.2$, $p = 0.275$); chosen rope occurring to the left or right of the flag ($\chi^2 = 0.3$, $p = 0.404$); the order the participant received the trials ($\chi^2 = 0.3$, $p = 0.849$); and experiment

($\chi^2 = 3.4$, $p = 0.184$) did not significantly affect the power of the model and so these terms were dropped.

Table 5.3. ANOVA model reduction of maximum GLMM, Rope choice ~ Age + Gender + Arm span + Height + Orientation of the correct rope + Chosen rope occurring to the left or the right of the flag + Order of the trials + Trial + (1 | Experiment/Individual). Only the term "Trial" significantly influenced the power of the model and thus was retained in the final reduced model.

Variable	**AIC**	**BIC**	**Deviance**	χ^2	**p value**
Maximum model	129.5	166	99.5	-	-
- Age	127.8	161.9	99.8	0.325	0.568
- Gender	127.5	161.6	99.5	0.038	0.845
- Arm span	128.6	162.6	100.6	1.084	0.298
- Height	129.7	163.7	101.7	2.211	0.137
- Orientation of correct rope	128.7	162.7	100.7	1.192	0.275
- Chosen rope	128.2	162.2	100.2	0.696	0.404
- Order of trials	125.8	157.4	99.8	0.327	0.849
- Trial	132.1	163.7	106.1	6.561	0.038*
- Experiment	128.9	160.5	102.9	3.386	0.184

* $p < 0.05$

Therefore the final reduced model (AIC 118.5, Table 5.4) retained the fixed factor trial (one, two, or three) and individual (nested within experiment) as a random factor. The power of the final reduced model and the maximum model did not significantly differ ($\chi^2 = 9.0$, $p = 0.433$).

Table 5.4 Final GLMM, Rope choice ~ Trial + (1 | Experiment/Individual)

Variable	**Estimate**	**SE ±**	**z value**	**p value**
Intercept	-0.435	0.387	-1.13	0.261
Trial (one)	1.352	0.570	2.372	0.047*

* *p < 0.05*

Tukey pairwise comparisons of each level the factor trial (distance, flexibility, or connectivity) were performed with lsmeans (version 2.13). This revealed that the correct rope was selected significantly more in trial one (the distance trial) than in trial three (the connectivity trial), Z = 2.4, p = 0.047 (Figure 5.1). However, there was no significant difference in the choice of the correct rope between trial one and trial two (the flexibility trial), Z = 0.8, p = 0.676, or trial two and trial three (Z = 1.6, p = 0.250).

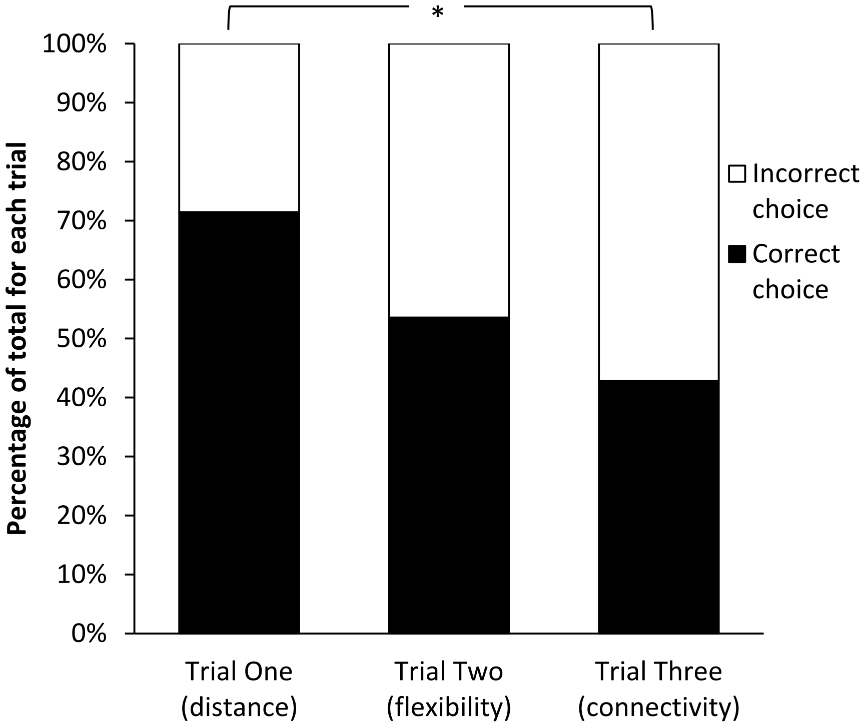

Figure 5.1. Percentage of correct and incorrect choices for each trial. The distance trial accounted for significantly more correct choices than the connectivity trial in glmm analysis ($p < 0.05$).*

All participants were right handed and therefore this could not be included in GLMM analysis, however, scores for which hand (left or right) was used for manipulating the flag and for postural support across the experiments are shown in Table 5.5 with binomial test results.

Table 5.5. Hand use across all participants for each experiment. The majority of experienced rock climbers did not use a rope as a support whilst collecting the flag. The nature of the task required all gymnasts to use one hand as support when collecting the flag.

Experiment	**Rope chosen to climb** count (L/R) binomial test	**First hand to touch the flag** count (L/R) binomial test	**Hand used as support whilst collecting the flag** count (L/R) binomial test
Experienced rock climbers	(26/10) $p = 0.01$*	(11/25) $p = 0.03$*	(5/2) $p = 0.45$
Novice rock climbers	(9/21) $p = 0.04$*	(21/9) $p = 0.04$*	(7/17) $p = 0.06$
Gymnasts	(12/6) $p = 0.24$	(6/12) $p = 0.24$	(12/6) $p = 0.24$

* $p < 0.05$.

5.3.2 *Investigating rope use for support in the rock climbers*

Experienced and novice rock climbers were tested under the same conditions in experiment one and two. To investigate how experience of climbing and the different trials influenced the use of the chosen rope for support (whilst climbing and whilst untying the flag) binomial generalised linear mixed models (GLMMs) were used, in which the dependent binomial variable was whether the rope was used for support (yes or no). Fixed factors were: trial (distance, flexibility, or connectivity); and experiment (experienced or novice climbers). Individual was included as a random factor (Bolker et al. 2009) nested within experiment because different individuals participated in the three different experiments. Data for the gymnasts were omitted.

5.3.2:i Use of the rope for support whilst climbing

ANOVA tests comparing sequential models confirmed that removing experiment ($\chi^2 = 0.02$, p = 0.881) did not significantly affect the power of the model and so this term was dropped (Table 5.6). The final reduced model (AIC 33.7) retained the fixed factor trial.

Table 5.6. ANOVA model reduction of maximum GLMM, Rope used for support during climb ~ Trial + Experiment + (1 | Experiment/Individual).

Variable	**AIC**	**BIC**	**Deviance**	χ^2	**p value**
Maximum model	56.6	87.3	23.6	-	-
- Trial	41.2	49.9	33.2	9.529	0.009*
- Experiment	33.7	44.6	23.7	0.023	0.881

** $p < 0.05$*

Tukey pairwise comparisons of each of the three trials were performed with lsmeans (version 2.13), see Table 5.7. This revealed that participants used the rope as support during climbing to the flag significantly more often in trial three than in trial one (Z = 3.1, p = 0.006) and trial two (Z = 4.8, p < 0.001), and more in trial one than in trial two (Z = 3.4, p = 0.002).

Table 5.7. Final GLMM, Rope used for support during climbing ~ Trial + (1 | Experiment/Individual) and post-hoc comparisons of factor levels

Variable	Estimate	SE ±	z value	p value
Intercept	44.6	7.018	6.360	< 0.001*
Trial				
(one*two)	15.6	4.537	3.439	0.002**
(two*three)	-30.4	6.348	-4.794	<0.001*
(three*one)	14.8	4.858	3.053	0.006**

* $p < 0.001$, ** $p < 0.01$

5.3.2:ii Use of the rope for support whilst untying the flag

ANOVA tests comparing reduced models revealed that experiment ($\chi^2 = 24.0$, $p < 0.001$) and trial ($\chi^2 = 9.7$, $p = 0.008$) significantly influenced the power of the model and so these terms were retained in the final model (Table 5.8). The final model (AIC 35.7) retained the fixed factors experiment and trial.

Table 5.8. ANOVA model reduction of maximum GLMM, Rope used for support whilst collecting the flag ~ Experiment + Trial + (1 | Experiment/Individual).

Variable	AIC	BIC	Deviance	χ^2	p value
Maximum model	35.7	48.8	23.7	-	-
- Trial	41.3	50.1	33.3	9.667	0.008**
- Experiment	57.7	68.7	47.7	24.031	< 0.001*

* $p < 0.001$, ** $p < 0.01$

The chosen rope was used as support whilst untying the flag significantly more often by participants in experiment two (novice rock climbers) than in experiment one (Z = 5.5, p < 0.001). See Table 5.9. Further to this, novice rock climbers used only one hand to remove the flag on every occasion (e.g. by repeatedly tugging the flag until it came loose), whereas the experienced rock climbers used both hands to untie the flag (e.g. by first releasing the rope and leaning against the climbing wall) in 29/36 trials.

Table 5.9. Final GLMM, Rope used for support whilst collecting the flag ~ Experiment + Trial + (1 | Experiment/Individual) and post hoc comparisons of factor levels

Variable	Estimate	SE ±	z value	p value
Intercept	-14.5	5.330	-2.717	< 0.001*
Experiment (two)	60.1	10.893	5.516	< 0.001*
Trial				
(one*two)	-14.9	4.981	-2.985	0.008**
(two*three)	-15.6	4.590	-3.410	0.002**
(three*one)	30.5	6.653	4.587	< 0.001*

* *p < 0.001, ** p < 0.01*

Tukey pairwise comparisons of each level of the trial factor were performed with lsmeans (version 2.13). This revealed that the chosen rope was used for support whilst participants collected the flag in trial three significantly more often in trial one (Z = 4.6, p < 0.001) and trial two (Z = 3.4, p = 0.002), and in trial two significantly more than in trial one (Z = 3.0, p = 0.008).

Figure 5.2 summarises the results of the GLMMs investigating use of the chosen rope for support. Novice rock climbers used the rope for support when collecting the flag in significantly more trials (80% of trials) than experienced rock climbers (25% of trials). However, experienced rock climbers used the rope for support at some stage during their climb up to the flag in more trials (89%) than did novice rock climbers (63%) but this was not significant.

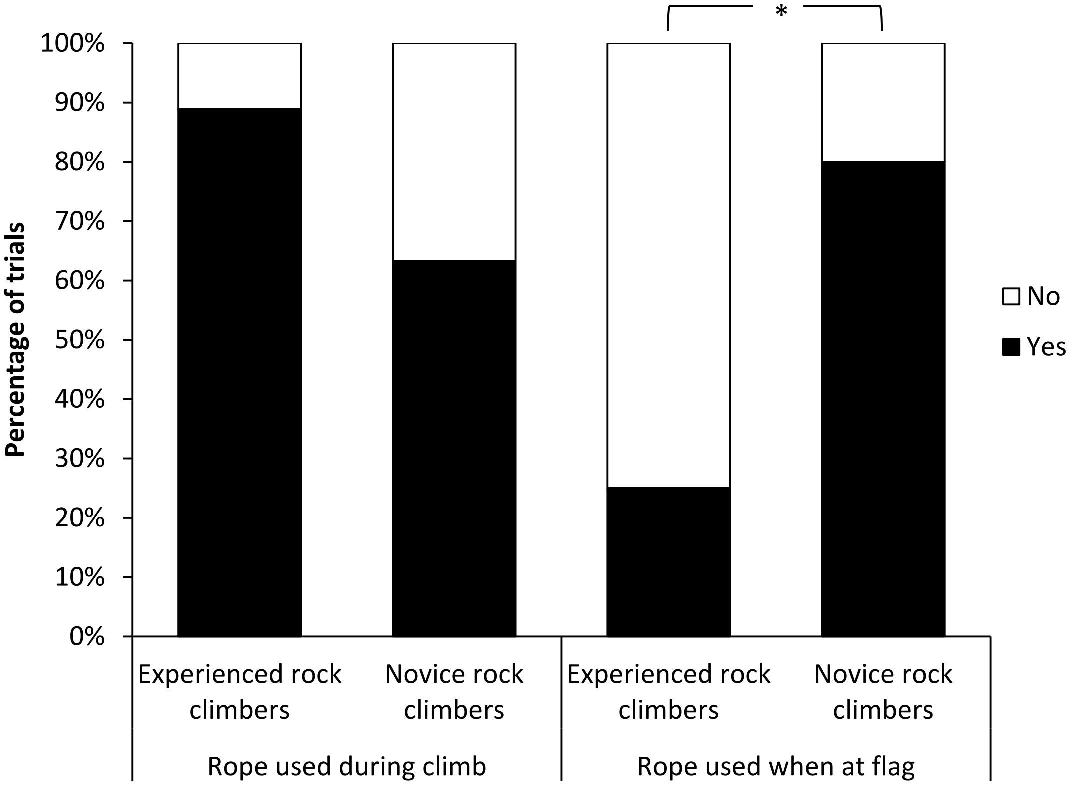

*Figure 5.2. Percentage of trials for which the chosen rope was used for support during climbing to the flag and whilst untying the flag for experienced and novice rock climbers. Novice rock climbers used the chosen rope for support when collecting the flag significantly more than the experienced rock climbers (Binomial GLMM, * $p < 0.001$).*

5.4 Discussion

Three groups of participants (experienced rock climbers, novice rock climbers, and gymnasts) were tested in a climbing task in which they were required to select and climb a rope to collect a centrally placed flag. Each participant completed three trials in which the functional properties of the ropes differed. Overall, the distance trial accounted for significantly more correct rope choices than a multipart trial that required participants to perform an additional task of untying their chosen rope before climbing (connectivity). Trial also influenced whether the chosen rope was used for support during climbing and whilst untying the flag, with the connectivity trial accounting for significantly more rope use amongst the rock climbers. Novice rock climbers relied on their chosen rope as support when collecting the flag significantly more than experienced rock climbers. These findings suggest that for human participants the type of trial and individual experience are important in determining success in arboreal locomotion tasks.

Although success was relevant to trial, due to the nature of the study participants were given limited instruction to avoid leading their actions. In this way participants were unaware of how the ropes would change between trials and therefore may have opted to select a rope before perceiving the additional level of action required for the connectivity trial (releasing the chosen rope from an extra lateral rope before climbing). Indeed 68% of participants did not untie their chosen rope in the connectivity trial and instead climbed and reached across using a biomechanically demanding posture from the rope whilst it was still tied back to the additional lateral rope. Selection of the incorrect rope in this way did not result in failure, and participants were able to reach the flag from the ‘incorrect’ rope in all trials. Therefore, participants may have over-simplified the aim of the task to merely ‘collect the flag’ ignoring relevant information about the ropes. The participants may not have been looking for a problem to solve, indeed one participant stated after the trials that they had had no strategy and had been selecting ropes at random.

Furthermore, as soon as participants viewed the equipment in the distance trial the correct rope was visibly different from the incorrect rope; it was nearer to the flag. Both ropes in the flexibility and connectivity trials were the same distance from the flag and differed in a less obvious way, and both required the participant to select the flexible rope based on its potential manoeuvrability. The flexible rope was unattached at ground level which would have required the participant to study the equipment in more detail before acting. Gaze (where an individual looks) is dependent on the task or goal (Rothkopf et al. 2007) and in situations where a goal is specified (such as the flag in this study) gaze is fixated on this object initially before action (Land and Hayhoe 2001, Land 2007). Therefore, the most likely response when instructed to collect the flag was to locate the flag, thus drawing the participants' eyes upwards and away from other relevant information regarding the suitability of the ropes. There is little doubt as to whether the participants were able to solve all three of these relatively simple trials including the connectivity trial, for example, Silva et al. (2008) demonstrated that human participants understand connectivity and contact in tool-use tasks. Therefore, the low frequency of correct choices in the connectivity trial does not suggest the participants were unable to solve the problem of connectivity but instead did not perceive it.

In this way participants lacked the ability to inhibit their immediate response upon seeing the equipment which could have resulted in more incorrect choices. The ability to inhibit an action has been shown to influence performance in planning tasks such as the Tower of Hanoi (TOH) and Tower of London (TOL) (Welsh et al. 1999, Zook et al. 2004). However, Diamond (2002) suggested that inhibitory abilities develop by early adulthood in humans; therefore, it is assumed that these participants had mature levels of inhibitory control. Perhaps then, due to the limited instruction given prior to the climbing task (to avoid leading decision making) and the fact that the arrangement of the ropes allowed the participants to access the flag regardless of the rope chosen (albeit in a more biomechanically demanding posture) participants were not fully aware of what was required of them. If the ropes differed more obviously or provided a possible and an impossible option selection of the correct rope may have been consistent over all the trials.

5.4.1 Use of the rope for support

Both experienced and novice rock climbers used the chosen rope as support during climbing to the flag, however, this was significantly more for the connectivity trial than for the flexibility and distance trials. Experience influenced the use of the chosen rope for support during climbing to the flag and whilst collecting the flag.

Novice rock climbers relied on the chosen rope for support whilst collecting the flag significantly more often than experienced rock climbers. All participants were dominant in their right hand (right handed). The novice rock climbers also selected the rope to the right of the flag. In this way, they used their right hand for postural support (rather than manipulation), it is likely this is because their right hand was their stronger limb. It has been shown that grip strength for the right hand is 10% stronger in right handed individuals of the general population (Petersen et al. 1989, Incel et al. 2002). The dominant hand is also associated with enhanced motor performance such as strength, speed, and accuracy (Goble and Brown 2008, Janssen et al. 2011, Hughes et al. 2011). Donath et al. (2011) demonstrated that non-elite climbers with less climbing ability and experience exhibited asymmetric loading of the dominant limb during climbing on a symmetrical route. Furthermore, they showed that the asymmetric loading of the dominant hand decreased as climbing ability increased. Therefore, it is clear that handedness plays an important role in support selection and use in human participants in a symmetrical environment, similar to findings for non-human apes (Chapter Two). However, the degree to which the preferred hand is relied upon for support is also influenced by experience in human participants.

Experienced rock climbers chose the left rope significantly more often, and thus were able to use their right hand initially when untying the flag. The experienced group climbed regularly (more than once a week) and it is likely that their confidence and thus their aptitude for taking calculated risks was higher (Llewellyn and Sanchez 2008) than for the novice rock climbers. This may have reduced their need to use their right hand in postural support. Similarly, the gymnast group were also experienced (training more than once a week) and although the effect was not significant they also showed a tendency for using their right hand initially at the flag (necessarily supporting their body weight with their other arm). Furthermore, muscle strength increases with training and it possible that the difference in strength between the dominant hand and the non-dominant hand is less important in trained athletes. Therefore, the experienced rock climbers and the gymnasts were less likely to rely on this hand for postural support, freeing it for the more complex manipulatory task of untying the flag. Indeed, all of the novice rock climbers removed the flag with one hand (for instance by repeatedly tugging it until it came loose), whereas the experienced rock climbers actively untied it with both hands on 29 out of 36 occasions.

Conclusion

A combination of a reduced perception of the relevant functional properties of the ropes (such as one being unattached at ground level and so flexible) and the additional level of required manipulation in the connectivity trial increased the complexity of the trial enough to result in significantly fewer correct choices. These findings suggest that, across different groups of rope climbers, simple processes such as motor planning (for example understanding reach) are used in selection of potential arboreal supports when functional properties are visually obvious.

Experience also influenced how ropes were selected and utilised during the task. For the novice rock climbers the demands of the task elicited a preference for the dominant hand for postural support rather than for the manipulatory task of untying the flag, whereas the experienced climbers could use their preferred hand to collect the flag. This highlights a need for complimentary qualitative data in the form of post-task interviews to determine why participants made the choices they did. Indeed, one novice rock climber commented that they chose the rope occurring to the right of the flag on all trials because they wanted to “hold on” and support themselves with their right-hand (their dominant hand).

CHAPTER SIX

INVESTIGATING THE ECOLOGICAL FACTORS INFLUENCING DECISION MAKING IN HUMAN TREE CLIMBERS

Abstract

The forest canopy is a complex environment in which supports are compliant and discontinuous. For large bodied primates locomotion is energetically costly and risky due to support deformation and potential failure, therefore careful selection of supports is important for safe and efficient locomotion. However, factors influencing decision making in non-human arboreal apes can only be inferred from observation of natural behaviours. From this it has been predicted that energetic efficiency would be traded-off for risk avoidance. Human participants offer the opportunity to investigate the importance of different ecological factors in decision making through verbal communication. Eight human participants were tasked with collecting four goals (each participant climbed three times) placed in the periphery of a tree canopy as an analogue of arboreal foraging in non-human apes. Thematic analysis of post-climb interviews revealed risk avoidance and ease/efficiency were the most important factors influencing their decision making whilst moving around the canopy (participants fell equally into each group). Observations of positional behaviour, support use, and electromyography (of six muscles in the fore- and hind limbs) were compared between the two groups of climbers. The ease/efficiency group performed more bipedalism (and produced more force in a hind limb muscle) than the risk group. The risk group were slower overall, but saved time after their first climb suggesting route memory enabled individuals to reduce time spent travelling. The findings provide direct verbal evidence that risk and efficiency are important factors in decision making in a natural canopy environment. Furthermore, following known travel routes or using familiar supports may enable individuals to increase the speed of arboreal travel. The findings of this study suggest that cognitive processes such as memory are important in balancing the risk avoidance – energetic efficiency trade-off in arboreal locomotion for large bodied non-human apes.

Chapter contents

6.1 Introduction

The demands of balancing energetic expenditure and intake are a fundamental driving force of evolution. The arboreal environment poses particularly complex demands on large bodied primates such as the great apes because there is often a trade-off between avoiding potentially fatal falls and energetic efficiency (Pontzer and Wrangham 2004). Resources (for example, food and the shortest gaps between tree crowns) often lie at the end of branches, termed the terminal branch niche (Grand 1972, Cant 1992). Supports in the terminal branch niche are compliant and increase both the risk of falling and the energetic demands of locomotion for many species (Alexander 1991, Demes et al. 1995) due to supports deforming, and potentially failing, when body weight is applied. Furthermore, gaps in the canopy separate potential supports in a travel route and it has been shown for orangutans that detouring these (by climbing to the ground and back into the canopy again) can incur a substantial energetic cost (Thorpe et al. 2007). Consequently, large bodied non-human apes have evolved behavioural (Thorpe et al. 2009, Myatt and Thorpe 2011), anatomical (Fleagle 1999), cognitive (Chevalier-Skolnikoff et al. 1982, Povinelli and Cant 1995), and to some extent physiological (Pontzer et al. 2010) solutions to the ecological complexities of travelling in the canopy. For example, the only predominantly arboreal great ape, the orangutan (*Pongo spp*.), possesses a number of adaptations that facilitate access to the terminal branch niche, such as flexible locomotor and postural repertoires that reduce risk and conserve energy when using compliant supports (Thorpe et al. 2009, Myatt and Thorpe 2011). The typical ape anatomy includes long forelimbs and short hind limbs and humans as great apes, have retained relatively long arms (Preuschoft 2002). Furthermore, it has been shown that longer arm span and shorter legs are particularly important in reducing energetic expenditure during arboreal locomotion in athletes (Halsey et al. in prep).

It is beneficiary for apes that rely on patchily distributed and seasonally fluctuating resources (such as ripe fruit in the rainforest canopy) to possess the ability to remember travel routes and locations of fruiting trees (Milton 1981) and the ability to plan daily travel in advance of action (van Schaik et al. 2013) because searching randomly could result in an unnecessary waste of energy. Memory is also important in individual confidence in and use of supports on the smaller scale of selecting supports within a route. Halsey et al. (in prep) demonstrated that course repetition and familiarity of routes significantly reduced the time it took human participants to complete an obstacle course. Furthermore, at the support-by-support level it is necessary for large bodied apes negotiating weak and compliant supports in a discontinuous environment to possess an awareness of how their bodies will influence the supports around them and to be able to predict how supports may behave without physically testing them. Simple cognitive abilities such as a knowledge of functional properties of supports combined with an awareness of where your body is in space (body schema) and motor planning abilities may be necessary in the efficient and safe selection of arboreal supports (Chapter Three). These simple processes may have formed the precursors to complex cognition such as an awareness of self and general problem solving (Chevalier-Skolnikoff et al. 1982, Povinelli and Cant 1995). Therefore, the demands of balancing risk avoidance and energetic efficiency during arboreal locomotion is cognitively demanding yet it is unclear in what way these factors may influence an individual's decision making.

The overestimation of energetic demand results in the avoidance of demanding travel routes in humans. For example, participants who overestimated the steepness of stairs tended to avoid these and instead preferred less strenuous alternatives such as escalators (Eves et al. 2014). However, although balancing energetic intake and expenditure is essential for survival, in terms of arboreality, avoiding falls from the canopy is potentially more important. Pontzer and

Wrangham (2004) demonstrated that chimpanzees retain adaptations to safe arboreal locomotion at a significant energetic cost to their daily travel budgets. In terms of energy expenditure it could be possible for short term mistakes to be made and an energy debt repaid later on. For example, although apes optimise foraging routes they do not do so perfectly and sometimes perform unnecessary travel between resource sites in foraging trips (Janson 2014) which could potentially waste energy. Furthermore, chimpanzees increase hunting, an energetically costly activity (Boesch 1994), during times of abundance when potential energy spent failing to capture prey can be regained from other food sources (Gilby and Wrangham 2007). An energy debt would only be problematic and thus decrease fitness if it was not regained before the animal depleted its energy reserves (MacArthur and Painka 1966, Pyke 1984). However, a risk debt cannot exist: if a ‘bad’ decision is made in terms of taking a risk that results in a fall it could be fatal. Falling poses a serious risk of bone trauma and fracture for larger apes (Jurmain 1997, Carter et al. 2008) and the risk of fatality from these injuries is high in apes (Bulstrode 1990, Jurmain 1997) meaning if an ape does not die right away from a fall from the canopy they are likely to die later from the injuries sustained. Therefore avoiding the risk of falling during arboreal locomotion is likely more important in decision making than energetic expenditure.

Similarly to overestimation of potential energetic expenditure, overestimation of distances has been related to risk avoidance, specifically the overestimation of height to avoid falling (Evolved Navigational Theory, Jackson and Cormack 2008). For example human participants judged vertical distances to be greater when viewed from the top of a vertical structure than when viewed from the bottom, because the risk of falling during descent is greater than the risk of falling during ascent (Jackson and Cormack 2007). Jackson and Willey (2011) also found human participants over estimated horizontal distances of routes that involved a risk of falling when compared to horizontal routes that did not. However, avoiding risk when travelling arboreally may result in increased energetic expenditure, such as by requiring a longer route to detour a potentially risky support, or by requiring more time to test novel supports before use, therefore, risk avoidance becomes an energetically expensive trade-off.

The psychology of decision making involved in arboreal locomotion of non-human apes can be inferred from observations of behaviour. For example: large male gorillas avoid the periphery of the canopy where supports are compliant and weak (Remis 1995); large male orangutans use larger branches than females (Cant 1987); whereas Thorpe et al. (2011) found adult females to be more risk averse. Furthermore, orangutans employ multiple points of contact and unique positional behaviour repertoires when in the periphery (Thorpe et al. 2009, Myatt and Thorpe 2011), which could infer risk avoidance. Observing non-human apes in captivity provides the opportunity to systematically test the possible cognitive processes involved in arboreal support selection and use (Chapter Three). However, by studying human participants it is possible to further investigate the psychology underpinning decision making by asking participants to verbally explain which ecological factors of the canopy environment influence their decision making during arboreal locomotion.

Rock climbing offers some similarities to arboreal travel in humans, for instance it is an energetically demanding and potentially risky activity in which fore- and hind limbs are used in propulsion and balance. It is therefore, a cognitively complex task (Green and Helton 2011, Di Paola et al. 2013). Some studies exploring the psychology of rock climbing in humans (Llewellyn et al. 2008, Draper et al. 2010, Pezzulo et al. 2010) have shown that rock climbers are more likely to take calculated risks and attempt harder climbs when they are more confident in their own abilities and efficacy (Llewellyn et al. 2008). Climbers have also reported lead-rope climbs (in which the individual secures the safety line as they go and are not attached to a safety line already in place) are “mentally more demanding” than top-rope climbs in which the individual is attached to a safety rope already in place spanning the whole climb (Draper et al. 2010). Pezzulo et al. (2010) found that expert climbers performed better than novice climbers on a memory recall task in which they were required to detail previously viewed climb routes of different levels. Experts were able to recount easy and difficult routes they had seen whereas novice climbers were only able to recall details of easy routes. Most studies however, have focused on competitive attainment (Boyd and Munroe 2003, Pezzulo et al. 2010), or the influence of psychological processes on physiological responses (Draper et al. 2008, Draper et al. 2010) and have not investigated arboreal locomotor ecology, an understanding of which is essential for research in primate and human evolution. Furthermore, the physical properties of the solid hand and foot holds used by rock climbers differ substantially and functionally to the compliant and discontinuous supports available in a forest canopy.

Kraft et al. (2014) touched on some of the psychological demands (such as stress and the need to overcome fear of falling) required by members of hunter gatherer populations who climb for resources such as honey. They found that tree climbing is a revered and well respected skill of predominantly older men because of the risks involved. However, these factors were used to explain the differences in climbing behaviours between different age and sex groups and did not explore individual decision making. Studies of human locomotion are generally concerned with the origin of bipedalism in humans and are often focused on terrestrial locomotion (Li et al. 1996, Crompton et al. 1998, Schmitt 2003) and also do not include correlates with decision making. All modern humans are intelligent, terrestrial bipeds. However, bipedalism (which allows large bodied orangutans to negotiate multiple compliant supports thus enabling access of the terminal branch niche, Thorpe et al. 2007) and cognition (as an adaptation to arboreal locomotion in a complex and discontinuous environment, Povinelli and Cant 1995, Chevalier-

Skolnikoff et al. 1982) evolved as a response to the demands of arboreal travel in a common ancestor of all the great apes (including humans). It is therefore important, that these adaptations are investigated in modern humans in a natural canopy environment.

Although risk avoidance and energetic efficiency may be the most important factors influencing decision making in arboreal locomotion any decisions made will be based on what supports are available. For example, if a resource is situated in the terminal branch niche then an individual can only use the supports available in that area, which are typically thin and compliant. Furthermore, since the arboreal environment is discontinuous, rather than continuous like most terrestrial substrates, supports determine routes much more strongly. In this way large gaps that cannot be crossed safely and break up the straight line route to a resource may require the individual to take a longer route around the gap. Arboreal locomotion and support use in apes is related to individual factors such as body size (Cant 1987, Thorpe et al. 2009, Myatt and Thorpe 2011) and support availability or habitat structure (Manduell et al. 2012). Thus, decision making determined by the risk avoidance/energetic efficiency trade-off could be dependent on the availability of functional supports in the environment. Therefore, it is important to first establish support availability relative to potential routes of travel before addressing what factors are considered in decision making. Furthermore, certain ecological factors may be more important in decision making for certain individuals. For instance, individuals with a large body mass may be restricted to different routes in the canopy compared to smaller individuals (Cant 1987, Remis 1995), or a confident individual may take more calculated risks than someone with less experience (Llewellyn et al. 2008). Furthermore, younger individuals may take more risks (Wang et al. 2009). This is also true of non-human apes taking more physical risks during arboreal locomotion, for instance: by using more compliant supports although this is likely due in part to body size (Thorpe et al. 2009, Myatt and Thorpe 2011); and by exhibiting more risky behaviours (Doran 1992, 1997). Play incorporating risky locomotor behaviours such as leaping has been attributed to physical flexibility training in juvenile primates (Fontaine 1994). Consequently, the routes selected by an individual will be dependent on what supports are available, individual morphology, and what factors they personally consider important in decision making. It is therefore important to establish in what way observed behaviours, support use, and chosen routes are dependent on individual psychology and morphology.

Aims and hypotheses

Participants performed three climbs for which they were required to select a different access point, collect four goals in the periphery of the canopy, and exit the canopy in any way they preferred. The novelty of this study required exploratory research questions especially in terms of the participant interviews as it was important to allow their responses to come naturally. This was to avoid prompting them to self-classify, or to bias their physical performance by leading them with unnecessary constraints (such as by asking them to perform the task in the most energetically efficient way or as quickly as possible). However, the combination of qualitative data (participant's personal experiences) and quantitative data (physical behaviour such as locomotion; support use; muscle force generation) enabled some testable hypotheses. For example, by cross analysing what the participants said they did with the observational behavioural data of what they actually did.

1) Participants will refer to risk avoidance more than energetic efficiency when asked to explain the factors most important in their decision making while moving around the canopy (Risk hypothesis). Risk should be more important in decision making because a 'risk debt' cannot exist, also participants are not required to complete the task in terms

of efficiency in any way (they are not constrained by time or energetics as these are not specified in their instructions). Therefore, all participants will exhibit similar patterns of muscle force production as a proxy for energetic expenditure when individual differences are accounted for.

2) The routes participants take between the goals will be dependent on the access point and participants' individual preferences (Route hypothesis). In this way the first goal collected will depend on the access point and the order the subsequent goals are collected will depend on participants preferred route sections, and the exit point will depend on the final goal collected. Furthermore, route repetition is likely to reflect a reduction in potential risk due to memory of supports and an increased confidence.
3) All individuals will adopt similar locomotor and postural behaviours on particular supports because these behaviours are dependent on the supports available (Environment hypothesis). In this way route sections will be made up of particular support types and thus will be associated with different positional behaviours (for example, a section that includes large, rigid, and horizontal supports will be associated with bipedalism as these supports are most similar to the ground and thus allow the participants to exhibit their natural locomotion).

6.2 Methods

6.2.1 General procedure

Eight recreational and professional tree climbers (all male and all right handed) participated in the study, carried out on 13th and 14th March 2015 (ethical approval was obtained from the University of Birmingham review committee, UK, ERN_15-0002). Table 6.1 gives participant information, body measurements, and climbing experience. Each participant identification is used throughout analysis and discussion.

Table 6.1 Participant information. All participants climbed as part of their profession (attached to a safety line), however, five participants also climbed recreationally which included free climbing.

Participant identification	Age	Height (m)	Weight (kg)	Arm span (m)	Climbing experience in years (professional or recreational)
One	34	182.2	89	188.0	Since child (both)
Two	42	186.1	91	198.3	> 10 years (both)
Three	25	185.5	80	195.0	6-10 years (both)
Four	37	183.1	80	184.5	3-5 years (professional)
Five	29	176.4	77	188.0	6-10 years (both)
Six	35	178.0	85	190.9	> 10 years (both)
Seven	32	184.5	95	191.0	> 10 years (professional)
Eight	27	179.4	81	187.0	6-10 years (professional)

The climbing task took place in a common oak tree (*Quercus robur*) on Ringmoor and Turnorth Down near Turnworth, Dorset, UK (50.876038, -2.271232). The tree was selected for its low-hanging branches that provided multiple entry routes into and accessibility of all parts of the crown. A climbing instructor from Canopy Access Ltd rigged the tree with a belay system and the task goals prior to the experiment and supervised each climb and operated the belay system. The task goals consisted of four manually-activated coloured buzzers serving as goals (blue, purple, orange, and green) that were placed at different points in the periphery of the tree canopy (selected so that they were relatively equal distances from the main trunk and potentially accessible from multiple directions from in the canopy). Three stationary belay lines were rigged so that each goal could be accessed safely. The belay system was designed to cover as much of the tree crown as possible while minimising the number of points at which the climbers would need to change their belay line. The belay line was attached to both the supervisor on the ground and the participant, and was passed over branch in the crown higher than they climbed, so that if they should fall they would be suspended safely on the belay line. A vertical climbing rope (50mm diameter) was suspended from a branch to mimic a rainforest vine and provided another potential access route into the canopy. Figure 6.1 is a schematic diagram of the locations of the goals in the tree and details the height in the canopy, straight line distances between the goals, and the diameters of the main branches used as foot-holds when accessing each goal. Figure 6.2 shows a photograph of the tree with the goal locations circled in their respective colours.

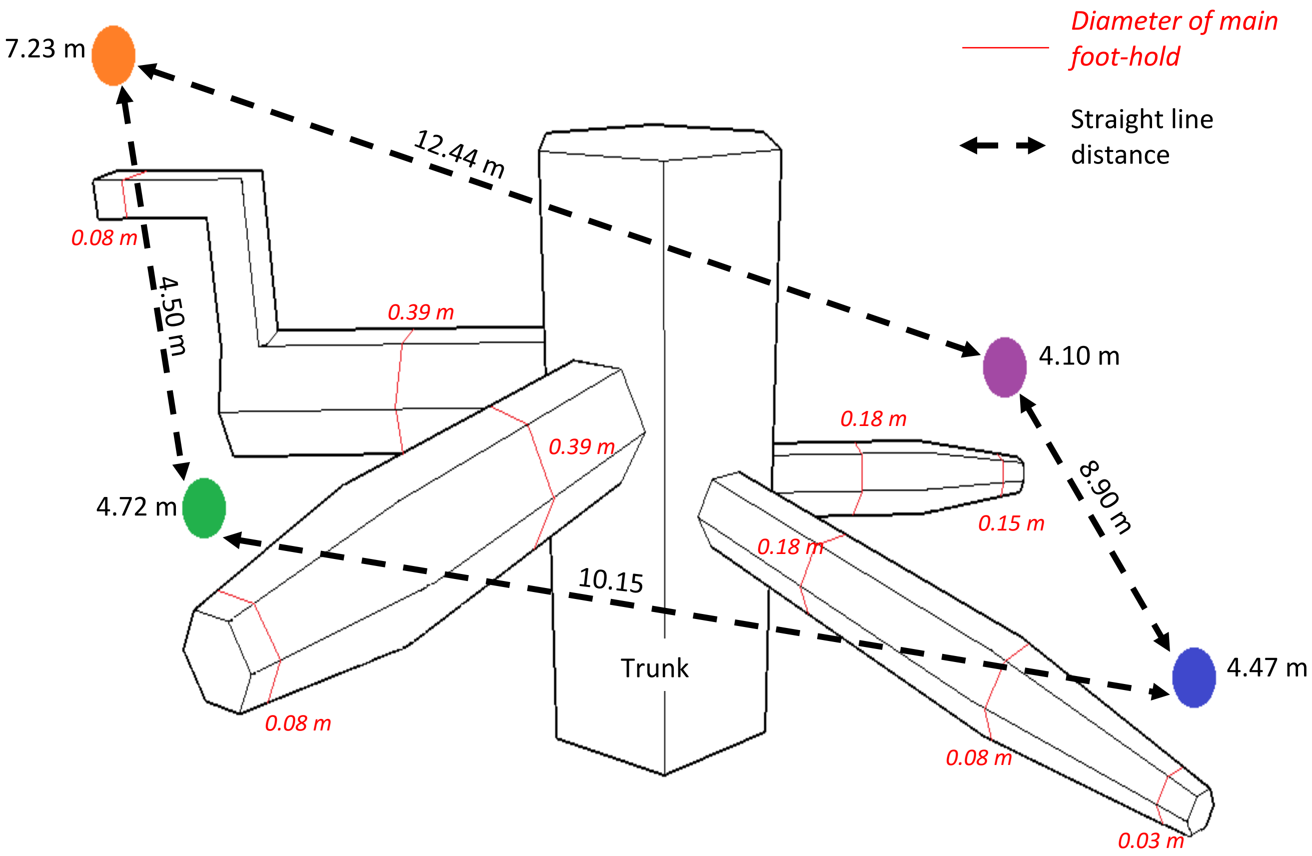

Figure 6.1 Schematic diagram of heights in metres of the goals (shown in coloured circles) above ground level, the beneath the orange goal there was a deep depression in the ground and the height shown is from the bottom of this, the height above the base of the trunk was 6.18 m. Straight line distances in metres (dashed arrows), and diameter in metres of the main foot-holds leading to each goal (red). Not to scale.

Figure 6.2 Photograph of the tree (Quercus robur) used for the climbing task. Goal locations are circled in their respective colours.

Body measurements (arm span measured from longest finger-tip to longest finger-tip; and height measured with an upright stadiometer whilst wearing the shoes they would be climbing in) were taken and participants were given a short questionnaire detailing their climbing experience and hand preference. Participants were also fitted with wireless surface electrodes to measure surface electromyography (EMG) and electrocardiography (ECG) data using the Trigno Mobile System (Delsys, Inc.) EMG data were collected for six muscles used in climbing: *Vastus lateralis,* (lower hind limbs) *Gluteus maximus, and Gastrocnemius* (upper hind limbs); and *Biceps brachii, Triceps brachii*, (upper forelimbs) and *Exensor carpi ulnaris* (lower forelimbs). These data were collected during periods of resting, walking, and running (each session lasting three minutes) in addition to during the climbing tasks, and allowed comparison of energy expenditure during the different climbing routes used by the participants (methods detailed in Saunders 2016).

Participants were asked to climb the tree three times, and on each climb to collect all four goals (by sounding the buzzers), before descending to the ground in any way they preferred. They were asked to select three different entry points into the tree crown and detail the order they intended to collect the goals (although they were informed they could change their minds at any time during the task). Participants were given scripted verbal instructions (Figure A6.1a in appendix) and up to 10 minutes planning time, during which they could visually inspect the canopy and goal locations from the ground. They were then asked to perform the three climbs in the presence of the researchers. Each climb was videoed from a central position from the ground (Sony Handycam HDR-PJ10, 30 frames per second).

After the participants had completed three climbs they were interviewed by NKIH about their decision making, and route and goal preferences (Figure A6.1b in appendix). Questions were scripted and conversations were recorded by dictaphone (Sony ICD-PX240) and transcribed at a later date. Finally, participants were given a paper questionnaire asking about their use of the belay system and their personal aims and preferences when climbing in other situations.

6.2.2 Video data extraction and analysis

Continuous focal data were collected for each participant (Altmann 1974) by NKIH and E. Saunders. A 25% sample of the videos were first coded by both researchers together. The remaining videos were coded equally by NKIH and E. Saunders with a further 25% overlap, an inter-observer reliability score of over 94% was obtained. Positional behaviour (locomotor or postural mode) was recorded together with support information and limb use. Hand use when sounding the buzzers was also recorded (Table 6.2). Each climb was divided into five route sections for analysis: access point – goal one: goal one – goal two; goal two – goal three; goal three – goal four; and goal four to exit. Analysis was conducted in R version 3.2.3 (R Development Core Team 2015) using the following packages: lme4 (1.1-10); lsmeans (2.21-1); foreign (version 0.8-66), ggplot2 (version 2.0.0), nnet (version 7.3-11), and reshape2 (version 1.4.1).

Table 6.2 Positional behaviour (adapted from Hunt et al. 1996), support information, and limb use collected from videos

Variable	Mode	Details
Locomotor mode	Bipedalism	Weight borne by the hind limbs in an up-right position, included hand assisted, flexed, and extended bipedal walk.
	Quadrupedalism	Weight borne by three or more limbs with the trunk in a pronograde position, including quadrupedal and tripedal walk.
	Vertical climb	Ascent > 45°, included propulsion from hind limbs such bipedal push-up, weight borne by fore- and hind limbs such as flexed elbow, and weight borne by forelimbs such as bimanual pull-up.
	Vertical descent	Descent > 45°, included weight borne by fore- and hind limbs such as fire pole slide and rump-first descent, weight borne by hind limbs such as step down.
	Leap or jump	Leaping or jumping, hind limb propulsion
	Drop or suspension	Drop from forelimb suspension, or locomotion in which weight is borne by limbs in suspension.
Posture	Orthograde stand	Weight borne by hind limbs with the trunk in an up-right position, including modes with flexed and extended limbs, monopedal and bipedal stand.
	Other	Other postures included: sit (weight borne by ischium), suspend (weight borne below support by either forelimbs or hind limbs), pronograde stand (weight borne by two or more limbs with the trunk in a horizontal position).
Limb use	Percentage of weight borne by each limb	Estimated weight borne by each limb

(continued on the next page)

Table 6.2 continued.

Variable	Mode	Details
Support type	Branch	Supports in the tree canopy.
	Trunk	Central trunk only.
	Vertical rope	Artificial climbing rope.
Orientation of support	Horizontal	Within 20^o of horizontal.
	$\leq 45^o$	Between 20^o and 45^o.
	$> 45^o$	Between 45^o and 70^o.
	Vertical	Within 20^o of vertical.
Diameter of support	< 5 cm	Supports with a diameter of less than 5 cm
	5 ≤ 10 cm	Supports with a diameter between 5 – 10 cm
	10 ≤ 20 cm	Supports with a diameter between 10 – 20 cm
	> 20 cm	Supports with a diameter of over 20 cm (including ground)
	multiple	Multiple supports of different diameter categories were used by one limb within one bout.
Hand use at goal	Dominant	Hand used to sound the buzzer.
	Posture	Limb used in postural support.

6.2.3 Thematic analysis

Interviews took place immediately after the climbing task to enable the participants to describe their climbing and decision making using the tree as reference. A combination of targeted questions such as, “which was your preferred goal to reach?” with more exploratory questions such as “why was this?” captured as much detail as possible. Questions were generated to encompass each part of the climb, from the access point through collecting the goals to exiting the tree, and targeted questions were chosen to highlight any factors influencing decision making. Thematic analysis is a widely used method for identifying and reporting patterns (themes) within data (Braun and Clark 2006). Unlike grounded theory (see Charmez 1996) this method is not restricted by pre-existing theory and can be used to report recounts of events, experiences and what the experiences meant for participants (Braun and Clark 2006). In this way the themes that emerged represented the participants' answers and language. This method was useful here because thematic evaluation of the participant's interviews (what they said) was described and compared to quantitative data of their observed behaviours (what they did in the canopy).

Text was analysed as a proxy for personal perceptions and feelings of participants (Tesch 2013). Transcripts of interviews were first annotated in a standard interview template detailing the original text and line-by-line exploratory comments for each individual (for example reoccurring words and statements). Transcripts were then re-read and emergent themes from all individuals were detailed (for example language or topics that reoccurred across multiple individuals). Emergent themes common to multiple individuals were used to determine what factors the participants associated with decision making whilst moving around the canopy. Whilst this method would be replicable with different participants, in a different tree, or under different instruction (such as with an added level of competition), thematic analysis reveals themes that are relevant to the individual and so is dependent on the participants own use of words or terminology.

6.3 Results

All eight participants completed three climbing trials (sounding all four buzzers), each starting with a different way of accessing the canopy. Figure 6.3 is a schematic diagram of the tree including the number of times each route section was used across all participants.

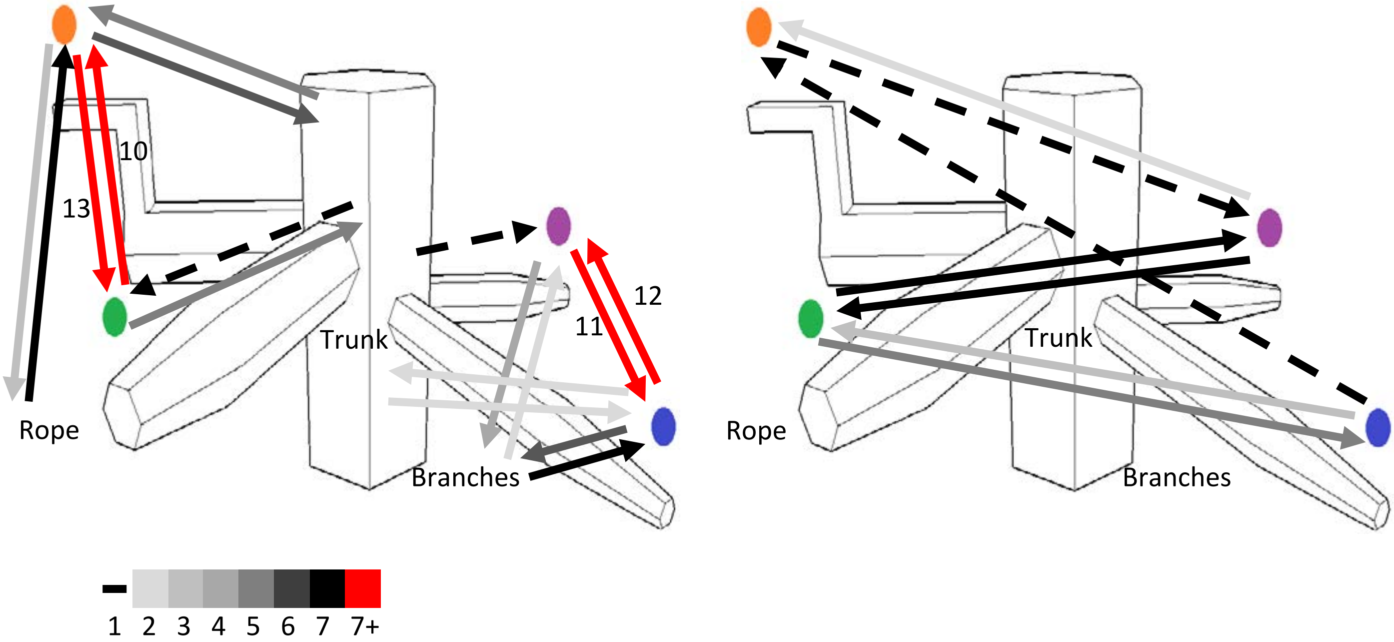

Figure 6.3 Scematic drawing of the tree (not to scale) showing route sections and the number of times each route section was used across all participants. a) route sections within each side of the canopy, b) route sections that crossed the trunk.

To investigate the potential factors influencing route choice an effiency index score was calculated for each section (access point – goal one: goal one – goal two; goal two – goal three; goal three – goal four; and goal four to exit) of each climb as follows. The access point (each participant was instructed to use three different access points), the order the goals were collected in, and the exit point were chosen by the participant on each climb. At each stage of a route the potential subsequent steps (out of the five route sections in each route) were ranked according to the straight line distance (shortest distance = 0, to furthest distance = 3), level of back-tracking required (from current point only = 0, within the same side of the tree = 1, across the trunk = 2), and change in belay required (no = 0, yes = 1). Change in belay was considered potentially important to efficiency of the climb because it required the particiant to pause and adopt a stable posture in which their hands were freed from postural support or balance so they could manipulate the belay system. Scores also reflected the stage in the climb because the number of options decreased with each section completed. For example, each climb had to include five sections (accessing the canopy, collecting all four goals, and exiting the canopy). Therefore, upon accessing the canopy the participant has four options to choose from and their next stage in the climb could be to collect any of the four goals. However, after they have collected their first goal they have a choice of the three remaining goals and so on until the only option remaining, at the end of the climb, is to exit the canopy. From the section scores overall efficiency index scores were calculated for each climb for each participant. One point was deducted from the overall efficiency index score for each route section that a participant repeated. In this way, small scores (0 being the optimum) reflected optimum route choices in terms of the factors used to determine the efficiency score only (straight line distance, required back-tracking, required change in belay line). Table 6.3 gives the chosen access point, the order the goals were collected in, chosen exit point, efficiency index score, and total time (from when the access point in the tree became the main weight bearing support to the time they touched the ground after sounding all four buzzers, minus any time the participants paused to change belay lines or release the belay rope) of each climb for each participant.

Table 6.3. Climb information for each participant. Goal order is the order in which the goals were collected in each climb (b = blue, g = green, o = orange, p = purple). To calculate the efficiency index score each possible subsequent step in a route was ranked according to straight line distance, required back-tracking, required belay changes, and number of repeated route sections. An optimum score is 0.

Participant	Climb number	Access point	Goal order	Exit point	No. of repeated sections	Efficiency index score	Duration of climb (s)
One	1	Branches	bpog	Trunk	0	1	309.6
	2	Trunk	pbgo	Rope	0	0	231.6
	3	Rope	ogpb	Branches	2	0	226.1
Two	1	Branches	bpgo	Trunk	0	2	321.0
	2	Trunk	bpgo	Trunk	4	3	271.9
	3	Rope	ogpb	Branches	0	0	327.1
Three	1	Branches	bpgo	Trunk	0	2	270.9
	2	Trunk	ogpb	Branches	0	4	215.6
	3	Rope	ogpb	Branches	4	0	219.7
Four	1	Rope	ogbp	Branches	0	3	302.1
	2	Branches	bpgo	Rope	1	0	155.3
	3	Trunk	bpgo	Trunk	3	4	194.3
Five	1	Branches	bpog	Trunk	0	1	162.7
	2	Trunk	ogpb	Trunk	1	5	211.1
	3	Rope	ogpb	Trunk	4	2	217.7
Six	1	Trunk	gopb	Branches	0	1	150.7
	2	Branches	bpgo	Rope	1	1	146.3
	3	Rope	ogbp	Branches	1	1	153.6
Seven	1	Branches	pbog	Trunk	0	3	161.7
	2	Trunk	ogpb	Branches	2	4	200.0
	3	Branches	pbgo	Trunk	2	4	187.8
Eight	1	Trunk	ogbp	Branches	0	5	166.4
	2	Branches	bpgo	Trunk	1	2	149.8
	3	Rope	ogbp	Branches	4	1	146.7

All participants had low efficiency index scores overall, the lowest possible score was zero and five was the highest scored by any participants (participants five and eight for their second and first climb respectively). Figure 6.4 shows an optimum route starting from the braches (this route was selected twice) and the most common route starting from the branches (selected three times out of nine). They differ only in the chosen exit point, the preferred route using the trunk rather than the closer vertical rope to exit the canopy.

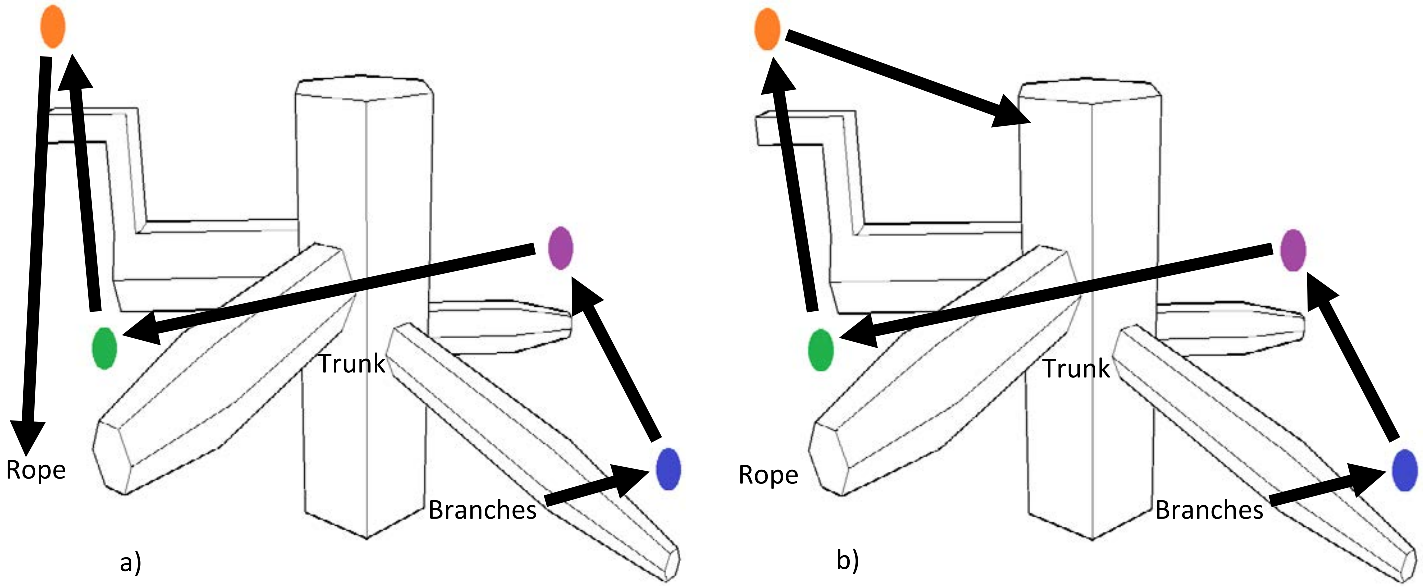

Figure 6.4 a) Optimum route starting from the branches based on an efficiency index score of zero (selected twice by participants). b) Most common route selected starting from the branches (selected three times by different participants).

In this way the order that the goals were collected was dependent on the access point, and likewise the exit generally reflected the last goal collected in a route. When accessing via the low branches the majority of participants (7) collected the blue goal first. When accessing via the trunk half of the participants (4) collected the orange goal first. When accessing the canopy via the vertical rope all participants that used the rope (7) collected the orange goal first. The orange goal was collected last most frequently (9 climbs), of these participants exited via the trunk six times and via the rope three times. Participants exited via the trunk on all occasions when the green goal collected last (three climbs). The blue goal was collected last eight times and participants exited via the low branches six times and the trunk twice. Six participants repeated the order they collected the goals in 2/3 climbs, regardless of the access point differing on each climb. However, the repeated order differed between individuals (Table 6.3).

Five of eight participants chose the low branches as their first way of accessing the canopy, six of the eight said they preferred this as an access point. Six participants also said they preferred the low branches as a point of exiting the canopy. However, this was only selected 42% of the time (on 10 out of 24 climbs), whereas the trunk was selected 54% of the time (13 of 24 climbs). The least preferred way of accessing and exiting the canopy was via the vertical rope. This being chosen as the preferred access point by one participant and never as a preferred way of exiting the canopy. The orange goal was preferred by half of the participants, two participants preferred the blue goal, one preferred the purple goal, and one participant had no preference.

6.3.1 Profile of the tree

Although participants generally had low efficiency index scores, on only five climbs out of 24 did they score 0, and select the optimum route (in terms of the factors used to calculate the efficiency index score). Furthermore, an efficient score did not necessarily result in a shorter duration of climb. To investigate other potential factors that influenced route choice, the tree was profiled according to support types and most frequent positional behaviours used in the different route sections.

Support availability and use differed across different areas of the tree and thus the different route sections (see Figure 6.1). The branches access point consisted of low (~ 2 m from the ground) horizontal, thin branches (ranging from 8 cm – 2 cm diameter). The blue and purple goals (4.47 m and 4.1 m from the ground respectively) were placed in an area consisting of horizontal branches tapering from > 40 cm – 2 cm diameter. The trunk area consisted of the largest branches of > 40 cm diameter. Two large branches (> 40 cm diameter) lead from the trunk to the green and orange goals. The green goal was 4.72 m from the ground on a relatively horizontal branch that tapered from > 40 cm diameter to 8 cm diameter. The branch that lead to the orange goal inclined from < 45° to vertical (> 40 cm – 8 cm diameter) to 7.23 m high. The vertical rope was suspended from the large branch leading to the orange goal.

To further characterise the different route sections a multinominal logistic regression model was conducted because this method enables a categorical dependant variable (with more than two levels). Route section (e.g. branches – blue goal, blue goal – purple goal etc.) was chosen as the dependent categorical variable because each route section differed in terms of the physical environment (e.g. functional supports, height above the ground, distance to the nearest goal etc.) and represented a direct observable result of participant decision making during canopy locomotion (e.g. which route they chose to take to collect all of the goals). Independent variables were proportion of: vertical climb; vertical descent; bipedalism; quadrupedalism; leap and jump; drop and other suspensory locomotion; orthograde stand; and other postural modes within route section. The reference category for the dependent categorical variable (route section) was specified as the blue goal – the purple goal. This was chosen as a baseline to which all other levels would be compared to because it was the most frequently used section with the shortest straight line distance between two goals. Frequency of the different locomotor and positional modes differed significantly from those that occurred between the blue and purple goal in 13/22 route sections used (Figure 6.5).

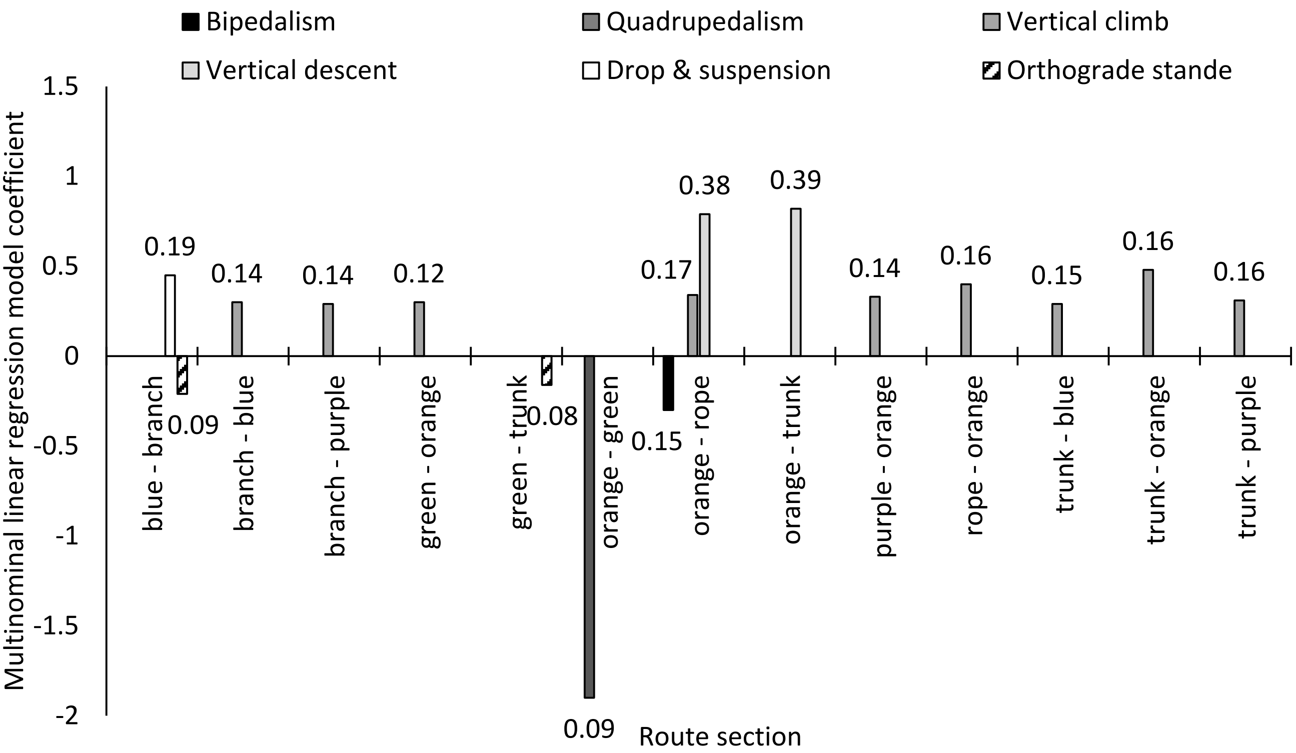

Figure 6.5. Significant ($p < 0.05$) coefficients (for 13/22 route sections) from multinominal linear regression model Route section ~ Bipedalism + Quadrupedalism + Vertical climb + Vertical descend + Leap & jump + Drop & suspension + Orthograde stand + Other postures. Leap & jump and Other postures are not shown here as these were not significantly different for any sections. The baseline for pairwise comparisons was the route section 'blue – purple'. Standard errors are shown above the bars.

6.3.2 Thematic analysis of post-climbing task interviews

Interview questions were geared toward understanding participants' decision making, what factors they considered, how they felt about the climbing task, and their preferences and reasoning. There were three main ways the participants discussed their decision making. They described the physical environment; discussed their mental processing (such as memory or learning); and described their reasoning. The way they described their physical environment and the processes behind their decision making were mainly used in support of their reasoning, for example, by giving a physical description of a branch they chose or by explaining a route preference based on memory. Although these areas do not form the main focus of this study they are outlined below as they give more context to the main focus of this study, their reasoning, which is where the main themes for discussion emerged.

Describing their physical environment and positional behaviour

Participants described their physical environment (40 responses) when referring to their decision making and often gave detailed descriptions of the physical properties of the canopy and supports available and also their positional behaviour. This occurred most often when the participants were emphasising their reasoning or describing what they did during the climb. Participants described the physical properties of supports such as “bendy”, or “snappy”. In this way they would also describe how they would use certain supports: “stand in the bottom of a U shape”; “I was using dead ones as support but my foot was right in against the junction”. Finally, they also explained how they read or understood certain cues such as by visual inspection or by sound: “I might hit it, sound it, and you know listen to the acoustics”. Participants also described the movements they made (23 responses). The most common reference was to bipedalism (“it’s a question of walking along”) and the use of their hands for balance and stability: “the higher branches I was using just mainly for my hand support to keep my upper body, kind of stopping me wobble”.

Discussing mental processes involved in decision making

Although participants discussed mental processes involved in their decision making (32 responses), these responses do not allow us to infer the cognitive processes involved in the decision making being discussed. However, their answers do reflect how they perceived the problem they faced and this is likely to have influenced how they approached it and so represents direct evidence for the factors influencing individual decision making. Participants discussed: planning, emotions (such as confidence and committal), memory or learning, behavioural flexibility, and interpretation of the physical environment. Participants implied planning by discussing their preparedness through having alternative methods in mind if the supports changed and they had to alter their course of action: “if it does break I’ve still got at least two or three other points of contact”. Planning was also implied in relation to the belay system the participants were using, “you’ve got to think about where the lines’ got to go”. Participants also referred to aspects of learning and memory: “there is an element of route memory”; or inferred that they possessed route memory: “I had already done that route once so I knew where I was going”. Participants also discussed their own behavioural flexibility and problem solving: “I was tangled up in it…I had to detangle myself and then find the three targets”. This refers to both the physical problem of untangling the belay rope and then the problem of relocating the goals.

Reasoning

The main themes for discussion emerged when participants were giving answers to questions about the factors they considered when accessing the canopy, when moving between the goals, and when exiting the tree. Three main themes emerged and these were: ease and efficiency; risk; and emotion. These themes refer directly to the participants own reasons given in their own words for making decisions. These encompass all reasons given by all participants, however not all participants referred to all themes. Figure 6.6 details the frequency with which each participant discussed each theme as a proportion of all the themes they used in the discussion topics (accessing the canopy, preferred goal, movement in the canopy, and exiting the canopy).

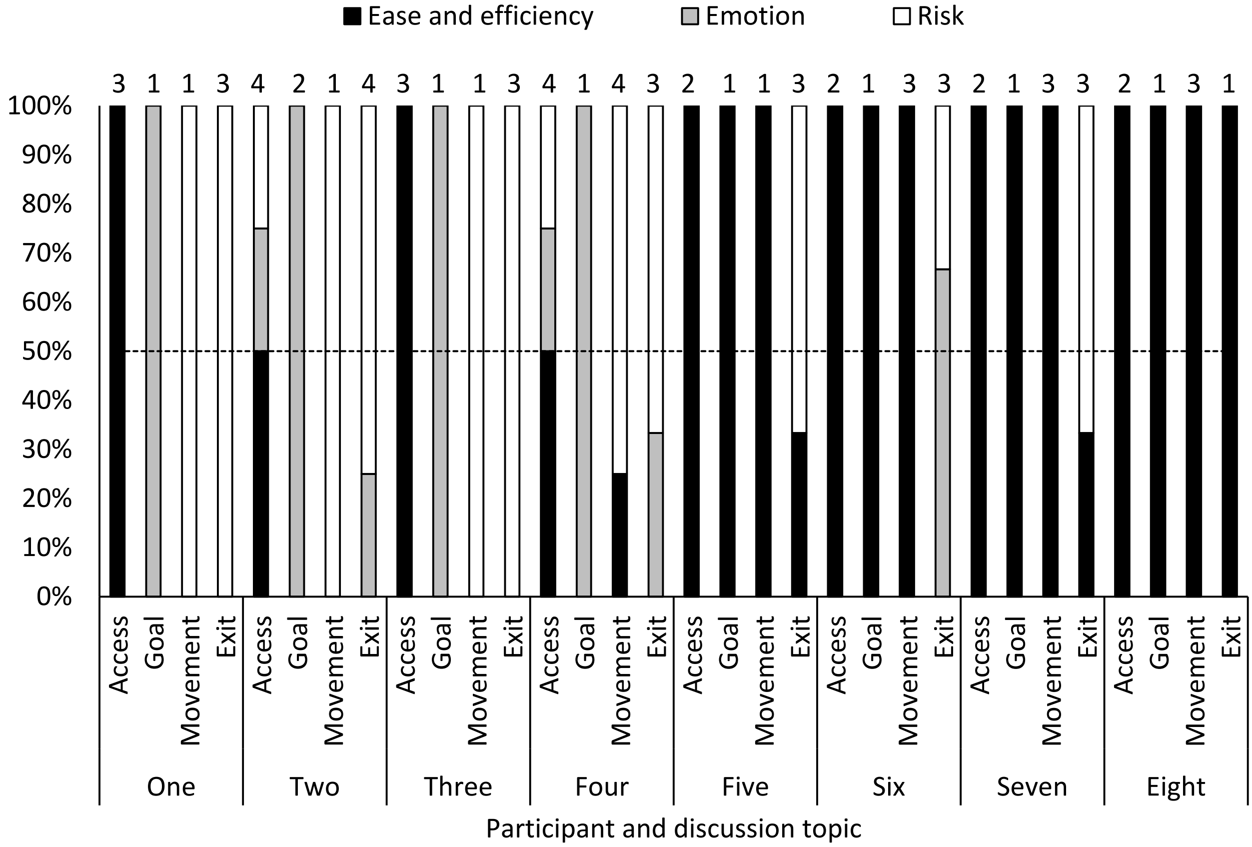

Figure 6.6. Themes each participant used as a proportion of all the themes they used during the four discussion topics. Discussion topics were accessing the canopy, preferred goal, movement in the canopy, and exiting the canopy. Number of responses in each discussion topic is shown above the bar.

Theme one – Ease and efficiency

Ease and efficiency were the most common reasons given across all participants (78 responses), the use of the word ease or easy was present in most interviews: e.g. “I went for the first easy three targets”; “the ease of access”. This theme encompasses the use of different synonyms such as reducing difficulty and effort for example, “probably the less strenuous way” and when explaining why something (a goal or a route) was less desirable, “the most difficult one”. Furthermore, they implied efficiency by avoiding back-tracking or retracing their steps: “I didn’t have to back-track, which was my main reason”. They also used more precise terms such as energy consumption: “a lot more energy spent”; “in terms of energy efficiency”. Participants also spoke of efficiency: “because it was most efficient”; “the most efficient way was route one”. This theme was often used in conjunction with a description: “it just felt most efficient because all the holds, I didn’t have to jump into the tree”.

Theme two – Risk

Discussion of issues related to risk avoidance was common to all participants (25 responses) except one (participant 8), however the word or variations of ‘risk’ were not used directly. Instead most participants implied risk avoidance by describing physical properties of branches they may avoid: “without being on the snappy branches so I didn’t break any off”; “where it is least likely to fail and snap off”. Risk avoidance was also implied through avoiding slips and falls: “I didn’t want to jump and then fall from too high”; “and hope you don’t fall”.

Theme three – Emotion

The final theme emotion (21 responses) occurred most often when participants were talking about positive emotions such as fun: “that was more fun”; “I think purely just for fun”, thrills: “slightly more thrilling”, or enjoyment: “you’re kind of asking someone who just enjoys climbing”. Interest was also important in this theme and again given by participants to explain why they preferred a particular aspect of the route: “It was the most interesting one to get to”. Similarly, emotion also encompasses participants using challenge as a reason for a particular preference: “I quite liked the orange one, because it was more of a challenge”.

Due to the timing of the interview (after the participant had completed all three climbs) these themes applied to all climbs, and it was not possible to extract themes for individual climbs. Although the first question in each interview asked the participant to recall each climb in order and recount in their own words what they did, this did not tend to lead to discussion regarding their decision making (as it was led by the participant before they were asked to discuss the factors that they took into account when making decisions). Furthermore, each participant did not fall into one theme through-out all of their discussion, hence why the themes taken forward in the cross analysis of the reasoning themes and observational data (this chapter, Section 6.3.3) were those that were extracted from their discussions specifically about their movements within the canopy. This was selected as the most important discussion topic to concentrate on for this analysis as it included all routes taken between the goals which is the focus of this study.

6.3.3 Cross analysis of reasoning themes and observational data

Participants were grouped according to the most frequent theme they used when discussing their movements in the canopy between the goals, hence forth, the ‘movement theme’. Four participants considered risk (totalling 7 responses), and four considered ease and efficiency (totalling 10 responses) the main factor influencing their decisions when moving within the canopy. Emotion did not feature in any participants’ discussions about their movement within the canopy.

To investigate how the themes may have influenced bouts of behaviour in the canopy a multinominal logistic regression model was performed, in which the dependant variable was the movement theme category (risk or ease and efficiency). Independent factors were: duration of bout (seconds); diameter of support used by the forelimbs; diameter of support used by the hind limbs; proportion of weight borne by the forelimbs; number of weight bearing limbs; orientation of supports; and efficiency index score for the route section. Table 6.4 shows a breakdown of the model. Participants who considered risk the main factor influencing their decision making had significantly longer durations of bouts (Z = 3.91, p < 0.001) and a significantly lower efficiency index score (Z = -2.3, p = 0.021).

Table 6.4 Multinominal logistic regression model, Movement theme ~ Duration of bout + Diameter of support for forelimbs + Diameter of support for hind limbs + Orientation of supports + Number of weight bearing limbs + Proportion of weight borne by forelimbs + Efficiency index score.

Variable	**Estimate**	**SE ±**	**z value**	**p value**
Intercept	-2.31	0.87	-2.64	0.008**
Duration of bout	0.14	0.04	3.91	< 0.001*
Diameter support fl.	0.10	0.08	1.20	0.229
Diameter support hl.	-0.12	0.10	-1.30	0.193
Orientation of supports	0.02	0.06	0.34	0.735
No. weight bearing limbs	0.36	0.20	1.79	0.073
Prop. weight borne fl.	-0.25	0.64	-0.40	0.691
Efficiency index score for section	-0.25	0.11	-2.30	0.021**

* $p \leq 0.001$, ** $p \leq 0.05$

The movement themes also influenced total duration of climbs. Participants who gave risk as the main factor influencing their decisions when moving in the canopy had significantly longer climbs than those who said ease and efficiency were more important (Kruskal-Wallis test, χ^2 = 12.403, df = 1, p < 0.001). Furthermore, for the risk group the time saved between climb one and two was significantly greater than for the ease and efficiency group ($\chi^2 = 5.333$, df = 1, p = 0.021), indicating this group was particularly cautious in their first exposure to the tree. However, there was no significant difference in duration between climb two and three ($\chi^2 = 0.75$, df = 1, p = 3.865), and total time difference across all climbs ($\chi^2 = 3$, df = 1, p = 0.083). Figure 6.7 shows the duration of each climb for each participant grouped according to the movement themes.

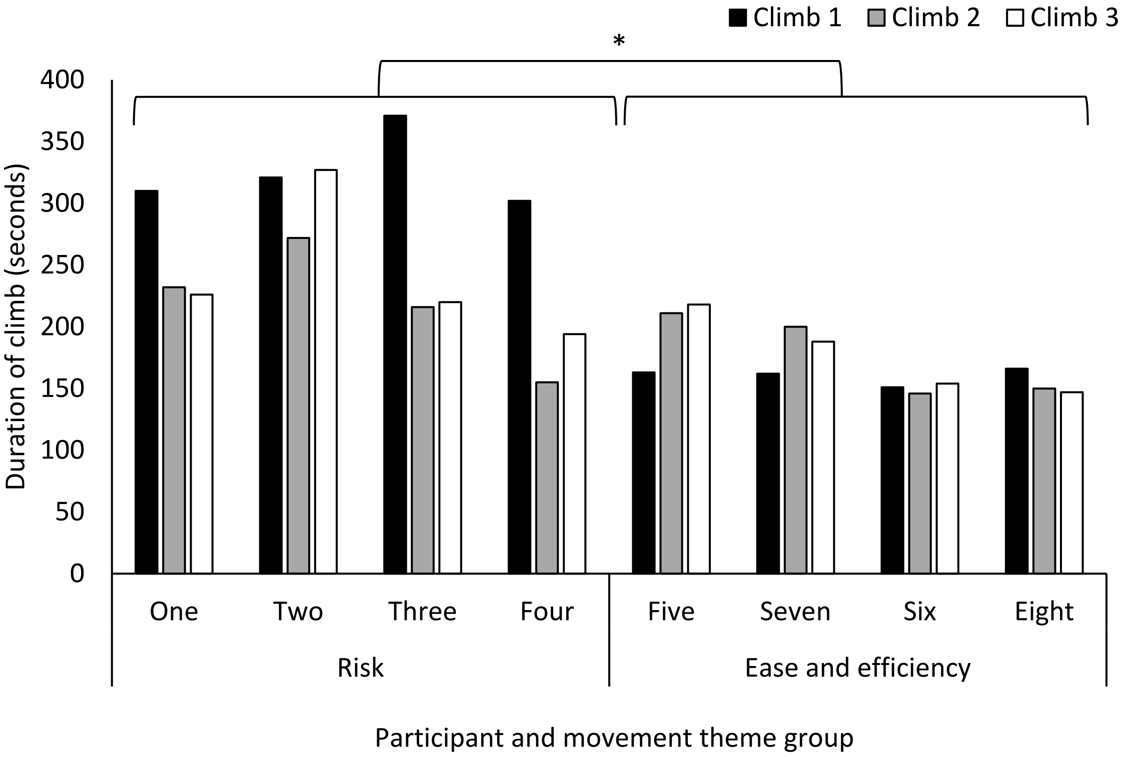

*Figure 6.7 Duration of each climb for each participant grouped according to movement themes. The risk group had significantly longer climbs than the ease and efficiency group (*Kruskal-Wallis test, $\chi^2 = 12.403$, df = 1, p < 0.001).*

Locomotor and postural modes could not be included in the multinominal logistic regression model because this analysis method cannot include cells with zero frequency (UCL Statistical

Consulting Group, 2015) and some locomotor modes did not occur with certain support types and for every individual in the movement theme groups. However, when frequency of locomotor and postural modes were compared across the movement themes there was no significant difference for any modes except bipedalism; the ease and efficiency group used bipedalism significantly more often than the risk group (χ^2 = 7.28, df = 1, p = 0.006). Figure 6.8 compares frequency of each locomotor and postural modes for the movement themes.

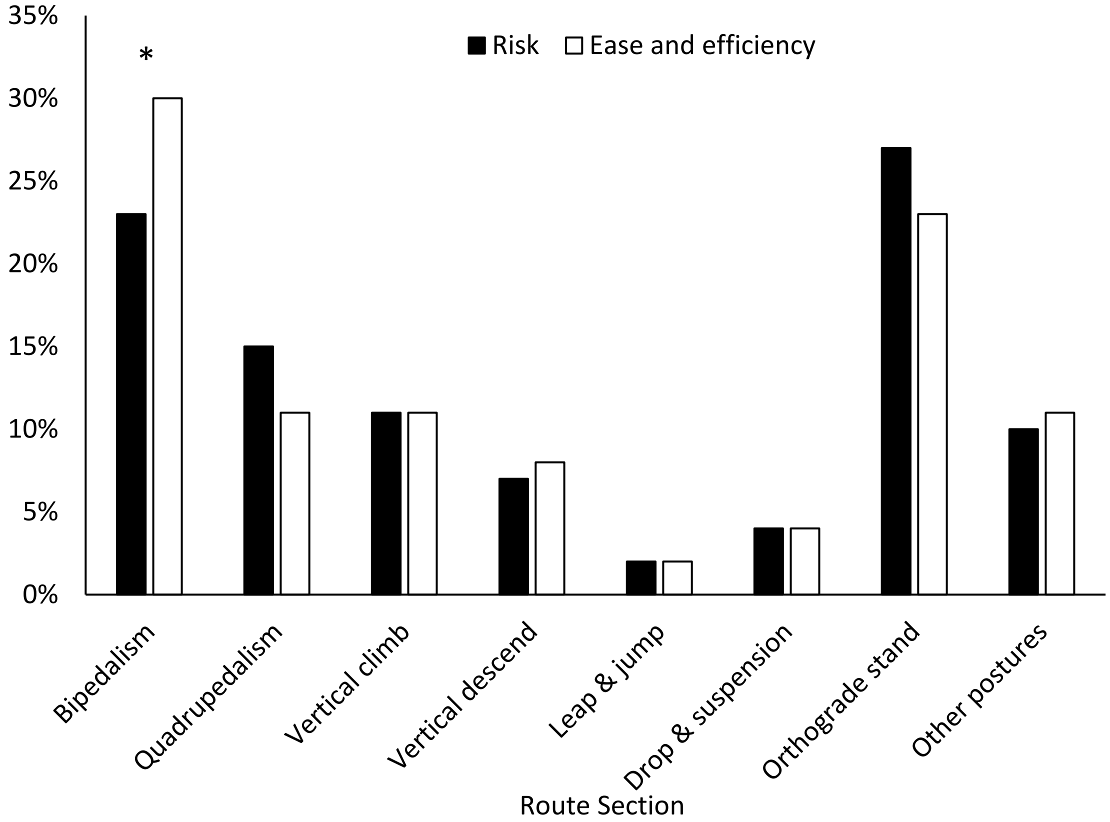

Figure 6.8. Positional behaviour as a percentage of all modes used by each movement theme. The ease and efficiency group performed significantly more bipedalism than the risk group (χ^2 = 7.28, df = 1, p = 0.006), however, there were no other significant differences between the movement groups.*

6.3.4 Muscle use and force production

Electromyography were collected for six muscles used in climbing, in the hind limbs: vastus lateralis; gluteus maximus; gastrocnemius, and in the forelimbs: biceps brachii; triceps brachii; and extensor carpi ulnaris. For each muscle, the mean EMG for each bout of behaviour was normalised against the mean EMG for terrestrial walking (for a bout of three minutes) for each individual. A GLMM was then conducted for each muscle in which the dependent factor was the mean EMG for each bout across all trials, movement theme was the only fixed factor and individual was included as a random factor (Bolker 2009). A GLMM was selected because they are the most suitable model for unbalanced and non-normal data and can incorporate a random effect, thus provides a more robust alternative to classical statistical analysis such as ANOVA which may require data to be transformed or pseudo-balanced. The mean EMG for each bout was selected as the dependant variable to investigate whether participants that fell into the movement themes differed in muscle activation (for example, were those participants that considered ease and efficiency most important when moving around the canopy also expressing less muscle activation, as a proxy for energetic exertion). Table 6.5 gives a break-down of the GLMM models for each muscle. Individuals in the ease and efficiency group produced higher forces in the vastus lateralis (in the hind limb) than individuals in the risk group ($Z = 3.24$, $p < 0.01$). No other muscles were significantly different for the movement theme groups. Due to the use of multiple separate models, a post-hoc Bonferroni correction ($N = 6$) was made but this did not influence the significance for any of the muscle.

T*able 6.5. GLMMs for Muscle ~ Movement theme + (1|Individual) for each muscle. Results shown are for the risk movement theme (no further pairwise comparisons were necessary as the movement theme had only two levels). There was no significant difference in muscle force production across the two movement themes, except for the vastus lateralis. The ease and efficiency group produced greater forces in the vastus lateralis compared to their mean EMG for walking on the ground than the risk group.*

Muscle	Random effects variance *(SD)*	Estimate	SE ±	Z value	p value	Adjusted p value $^{(1)}$
Intercept	0.033	5.71	0.09	63.32	< 0.001*	
Vastus lateralis	*(± 0.180)*	-0.41	0.13	-3.24	0.001*	0.007**
Intercept	0.109	5.54	0.16	33.64	< 0.001*	
Gluteus maximus	*(± 0.330)*	-0.24	0.23	-1.02	0.306	0.364
Intercept	0.112	4.53	0.17	27.07	< 0.001*	
Gastrocnemius	*(± 0.334)*	-0.44	0.24	1.88	0.061	1.0
Intercept	0.079	8.45	0.14	60.67	< 0.001*	
Biceps brachii	*(± 0.282)*	0.09	0.20	0.46	0.649	1.0
Intercept	0.315	7.07	0.28	25.41	< 0.001*	
Triceps brachii	*(± 0.561)*	0.68	0.39	1.72	0.085	0.508
Intercept	0.699	7.13	0.41	17.41	< 0.001*	
Extensor carpi ulnaris	*(± 0.836)*	0.11	0.58	0.20	0.846	1.0

* $p \leq 0.001$, ** $p < 0.01$. $^{(1)}$ *Bonferroni correction (N = 6) for comparing multiple models.*

Although the ease and efficiency group used bipedalism more frequently than the risk group there was no difference in muscle use during bipedalism between the movement theme groups. Table A6.1 (appendix) shows the breakdown of the GLMMs for each muscle for bipedalism only. As with the overall data, the ease and efficiency group produce significantly higher forces in the vastus lateralis than the risk group (Z = 3.91, p < 0.001*). There were 12 outliers across the six muscles ranging from 5.4 to 20.1 standard deviations from the mean of the sample, removing these outliers did not affect the power of the model or the significance of the factors. Table A6.2 (appendix) details the outliers removed. Figure 6.9 shows the mean EMG for the vastus lateralis for the movement themes (with outliers removed), plots for the other muscles are in Figure A6.2a-d (appendix).

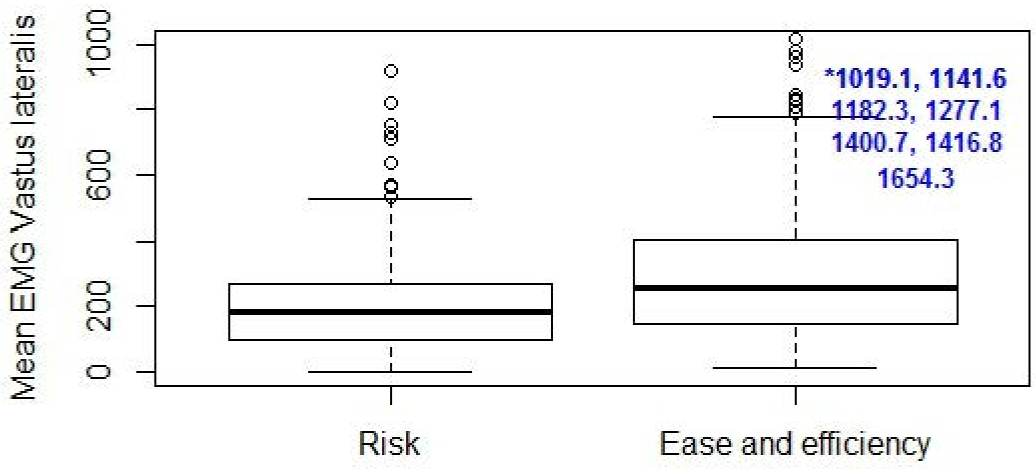

Figure 6.9. Mean EMG for Vastus lateralis for the movement themes. Individuals in the ease and efficiency theme produced significantly higher forces in the Vastus lateralis than individuals in the risk theme (GLMM, Z = 3.24, p < 0.01). Data points missing from the plot due to the scale are shown in blue.

6.4 Discussion

The factors influencing decision making in Western, recreational and professional, human tree climbers were investigated using a combination of behavioural observations, electromyography of six muscles used in climbing, and thematic analysis of individuals' own verbal accounts of their decision making. It was proposed: that participants would refer to risk avoidance as the factor influencing decision making as more important than energy efficiency (Risk hypothesis), and that routes chosen would depend on the access point and the order the goals were collected (Route hypothesis). Finally it was proposed that, since availability of different supports would restrict positional behaviour, participants would demonstrate similar locomotion in the same route sections (Environment hypothesis).

The Environment hypothesis was partially supported by the results of this study as routes and positional behaviour within route sections were to some extent restricted by the available supports. However, this was primarily only important for vertical locomotion (climb and descend), for instance, these locomotor modes occurred most often in route sections to the highest goal (orange) or ones that included the vertical rope. Whilst this may seem an obvious finding it does demonstrate that the availability of different supports influences human locomotion in a canopy environment as has been found with other apes (Manduell et al. 2012). Furthermore, bipedalism occurred in all route sections (even for the section between the vertical climbing rope and the highest goal, although at a reduced frequency). This suggests that despite being habitual terrestrial bipeds, human bipedalism is flexible enough to cope with the complex diversity of support types available in a natural canopy, at least for the short period of time the participants were recorded climbing in this study. Furthermore, the participants used bipedalism on thin and compliant supports in the periphery of the canopy, as has been shown in wild orangutan locomotor repertoires (Thorpe et al. 2009).

The order the goals were collected in was generally dependent on the access point, as the exit point was generally dependent on the last goal collected (the Route hypothesis). All participants selected routes with relatively low efficiency index scores. Low efficiency index scores indicated that chosen routes were made up of: short straight-line distances; a low level of back-tracking within a route; minimal number of changes in belay line; and potentially frequent repeated sections within a route. However, individual differences did occur in the order that the goals were collected, some route sections and routes were used more frequently across all participants, and all participants repeated some sections across their climbs. There is evidence for similar behaviour in non-human primates. Sympatric species (*Ateles belzebuth* and *Lagothrix poeppigii*) non-human primates also use and share repeated arboreal travel routes in the wild (Di Fore and Suarez, 2007); non-human great apes use specific support types within a canopy (Thorpe et al. 2009, Remis 1995); and locomotion is dependent on available supports (Manduell et al. 2012). Therefore, the assumption could be made that the overlap of repeated routes and route sections between individuals seen here is representative of the available supports, and task constraints, such as the requirement to collect all four goals. For instance, if an individual is required to collect all four goals, in three different climbs and these are situated in the same location on each climb then it is likely that there will be some route section repetition. However, little is known about the support-to-support routes used within a canopy that make up whole travel routes to different resources for wild non-human great apes. Therefore it is difficult to explain the factors resulting in individuals sharing similar routes and repeating routes themselves without some insight into the individuals' decision making.

Interview and questionnaire data is often plagued with issues of subjectivity during analysis, therefore, thematic analysis was used to reveal themes which were common to participants (although not all participants discussed all themes). Although some rational interpretation is required (e.g. not all participants use the same terminology or vocabulary) this method is not restricted by pre-existing theories (Braun and Clarke 2006) and so subjectivity is minimised. Also, the interview questions consisted of some targeted questions (such as "which was your favourite climb?") which required straight-forward answers that would be difficult to misinterpret thus further reducing the potential influence of subjectivity. Four participants reported that risk avoidance was the most important factor influencing decision making (the Risk hypothesis); however, the remaining four participants identified ease and efficiency as the most important factor influencing their decision making. The participants reported the factors influencing decision making post-hoc to the climbing task and this could have resulted in them unknowingly separating their rational decision making from their intuitive decision making. Intuition draws on long-term memory and sensory inputs from the environment (Betsch 2008). Decisions based on intuition can be considered an automatic and fast response to a situation or the environment, whereas rational decision making results in slow, controlled, and flexible responses (Kahneman 2002). Although decision making generally involves aspects of both cognitive systems (Meyers 2010, Sadler-Smith and Shefy 2004), accessibility of the thought processes influencing decision making (by the individual doing the recalling) may be influenced by their current (at the time of the interview) rational thought process (Betsch 2008). Despite this, gaining direct verbal evidence of these factors influencing decision making in canopy locomotion in the participants' own words is of considerable importance in light of the presumed risk avoidance/energy efficiency trade-off in non-human great ape arboreal locomotion. Of any number of potential influencing factors these participants selected the two factors that are important in the decision making of other apes during arboreal locomotion (as can be inferred from observations of wild non-human apes in forest environments: Chevalier-

Skolnikoff et al. 1982, Povinelli and Cant 1995, Remis 1995, Hunt 2004, Thorpe et al. 2007, Myatt and Thorpe 2011).

There were few differences between the two groups of participants in terms of support use, locomotor repertoires, or muscle use. However, the ease and efficiency group used significantly more bipedalism (and the mean activation of their vastus lateralis in the hind limb was higher) than the risk group. Humans are bipedal and therefore the most efficient form of travel is bipedal walking (Cavagna et al. 1976, Sockol et al. 2007), by selecting their habitual locomotor mode the ease and efficiency group could have believed they were being more efficient regardless of the environment. Bipedalism could therefore be perceived as a way of increasing efficiency during arboreal travel. However, bipedalism could also be selected to reduce the risk of falling. For instance, it has been shown that other apes use upright and bipedal postures when in the canopy despite not being habitual bipeds (chimpanzees [Hunt 1992], bonobos [Susman et al. 1980, Doran 1993], chimpanzee postures [Stanford 2006], orangutans [Thorpe and Crompton 2006]). Furthermore it has been shown that this enables the most efficient and safest use of the terminal branch niche (Thorpe et al. 2007). For example, hand-assisted bipedalism enables orangutans to forage with a free forelimb whilst still supporting themselves from above and below on flexible branches (Thorpe et al. 2007).

Alternatively, bipedalism may have been selected less by the risk group because it could have been considered less safe. It has been shown that height and slope of a substrate (Simeonov et al. 2003) and disturbances in the visual field increase postural sway (Musolino et al. 2006, Palmisano et al. 2009). Humans also have long legs and therefore during bipedalism the centre of mass is held in a high position above the main weight bearing support in a relatively unstable posture (Hunt et al. 1996). Therefore, in a dynamic canopy environment, high from the ground, an individual may suffer from decreased balance, thus reducing their use of bipedal postures.

However, it has been shown that even light hand-touches of a compliant and non-weight bearing support improves postural sway (Johannsen et al. in prep). The use of compliant supports in this way could increase the feeling of stability, indeed one participant in this study reported that "it was really just a balance thing, probably a psychological thing more than anything, that branch was never going to hold my weight" when asked why they had bent a thin branch towards themselves whilst bridging a gap between two larger branches in a bipedal posture. Therefore, it could be assumed that the risk group would use more hand-assisted modes of bipedalism, however, the frequency of bipedalism used in analysis in this study combined all modes, including hand assisted.

Despite the few differences in behaviour (and support and muscle use) between the two groups, the ease and efficiency group were more efficient in terms of reduced time spent climbing or increased speed with which they completed the task. The risk group took longer to complete the task overall, but reduced their climbing time after their first climb. This could be due to knowledge or confidence in the supports and routes available. Indeed, during the post climb interviews the risk group made more frequent references indicating confidence due to route memory (eight times) than the ease and efficiency group (once). Similarly Halsey et al. (in prep.) found an increase in the speed with which parkour athletes completed an obstacle course when they repeated the course a number of times. This suggests consideration of risk may decrease in importance over time using familiar routes or in a familiar canopy.

In terms of non-human great ape ecology, an arboreal ape using known pathways or routes could similarly save time spent travelling with increased experience of a route or after learning what functional supports are available within a route. Non-human primates use goal oriented routes in the wild (Di Fore and Suarez 2007, Valero and Byrne 2007, Asensio et al. 2011). Furthermore, non-human great apes have good spatial memory (Menzel 1973, MacDonald and

Agnes 1999, Gibeault and MacDonald 2000) and can select efficient terrestrial travel routes (in terms of distance, time, and preferred resources). In this way, cognitive processes such as memory of routes may increase the efficiency of arboreal locomotion (as demonstrated by Milton 1981) by enabling an individual to reduce the time or speed compensations made when concentrating on avoiding the risk of falling.

Furthermore, for social species speed and time spent travelling may be important in scramble and contest competition within a group. Scramble competition occurs when all individuals within a group have access to a resource and contest is when individuals dominate a resource (van Schaik and van Noordwijk 1988). It has been shown that during foraging in non-human primates goal oriented travel is faster than random searching (Beisner and Isbell 2009, Pochron 2001, Noser and Byrne 2010), and Di Bitetti and Janson (2001) demonstrated that reaching the location of a food resource before other group members resulted in an increase in the finders share of the food (in capuchin monkeys). Furthermore, in Chapter Four it was shown that a low ranking female bonobo was able to access a food goal by reaching it quickly before being displaced by the dominant female. Therefore, speed of travel could be important in the increase of an individuals’ acquisition of resources in light of intra-group competition. Moreover, non-human great apes have been shown to share food in exchange for other benefits such as grooming and agonistic support (de Waal 1989, Mitani and Watts 2001) and to appease beggars and scroungers, thus reducing the cost of defending a resource (Gilby 2006). Therefore, while speed of travel may increase an individuals’ access to resources (thus directly increasing fitness) in the more complex social systems of non-human great apes access to resources might also mediate other important social benefits (thus increasing fitness indirectly). Although some fast locomotion is associated with greater energetic costs (Cavagna et al. 1976) less time spent travelling could increase net daily energetic efficiency (Leonard and Robertson 1997, Key and

Ross 1999, Pontzer and Wrangham 2004), therefore regardless of foraging strategy (selfish or social) speed could be important in increasing an individuals' fitness.

Finally, it was not specified in the task to collect the goals as quickly as possible, or as efficiently as possible, instead participants were asked to collect the goals in whatever way they preferred. The differences between the groups could therefore be a manifestation of differences in personal competitiveness between individuals and therefore demonstrates the need for more in-depth personality profiling. For example, often in sports competitive orientation, self-confidence, and self-efficacy are important in performance (Martin and Gill 1991, Feltz 1988). Competitiveness is a measurable personality trait also influencing performance (Smither and Houston, 1992). Similarly, personality may influence a participants' aptitude for taking risks or adventure seeking and therefore how they perceive physical risks (Levenson 1990). Therefore it would be useful to measure these traits alongside thematic analysis of the factors influencing decision making in individuals.

It could be argued that the different participants may have fallen into these two groups based on the routes that they followed. For instance, it might be expected that individuals travelling at greater heights or on more compliant or insecure branches could refer to risk avoidance more often due to the greater risk of injury associated with a perceived greater risk of falling (Jackson and Cormack 2008). However, as discussed there were few differences in the routes taken by participants in the different groups, other than the risk group having a lower efficiency index score (meaning they selected the most efficient routes in terms of required belay changes, repeated sections, and distance). All participants shared some route sections (in terms of the order the goals were collected) and similar support use within climbs, and as discussed this is likely due to the restriction of the physical environment and the nature of the task, for example, all goals had to be collected on each climb so there is likely to be some cross-over between participants in terms of the routes taken. Therefore, it is unlikely that the division of the participants into the groups is based on their use of the physical environment. Finally, experience could influence the factors on which participants based their decision making, in that those with more experience may be less likely to consider risk avoidance the most important factor because of greater self-confidence (Llewellyn et al. 2008). However, neither the risk nor the ease and efficiency group was made up of more or less experienced participants, and both groups included participants with a range of experience from at least 3-5 years or since childhood. Furthermore, participants in both groups usually climbed professionally or both professionally and recreationally so there was no division in terms of current experience.

In conclusion, overall route choice and locomotor behaviours tended to reflect the available supports in the environment. Furthermore, avoiding the risk of falling and ease and efficiency were the most important factors influencing decision making in these climbers. Whilst there were few differences between these groups, the risk group traded-off time spent travelling or speed for safety. However, these individuals were able to reduce their time spent travelling after their initial climb suggesting that cognitive processes such as memory may increase confidence in known routes or supports, and thus be important in increasing efficiency of arboreal locomotion.

CHAPTER SEVEN

GENERAL DISCUSSION

Chapter contents

7.1 Summary of the main research questions

Chapter One detailed two research questions that referred to within-route support selection and the ecological factors influencing decision making during arboreal locomotion. These were:

Do non-human great apes select supports within a route based on a knowledge of the functional properties of the supports and to what extent is decision making influenced by an individuals' anatomy such as limb reach, or preference?

And:

Which ecological factors are important in decision making in the canopy environment?

By bringing together the information gathered in answer to these main questions this thesis hopes to further our understanding of the role of the arboreal environment in the evolution of cognitive processes such as a knowledge of functional properties of supports and memory of known routes, and the ecological factors that may have selected for these. The main findings of the studies presented here were: 1) that non-human apes have some knowledge of the functional properties of individual supports within a route to a hard-to-reach food goal and they select the least demanding support most frequently; 2) individual anatomy (such as limb reach and body size), specialisations (such as handedness), and experience can influence support selection and use; 3) risk avoidance and energetic efficiency are the most important ecological factors influencing decision making during arboreal travel, as reported by human tree climbers; and 4) there is a trade-off in efficiency (in terms of time spent travelling) when risk avoidance is considered, however, this can be reduced when individuals follow the same routes due to memory and an increased confidence in the available supports. These findings show the importance of both environmental influences and individual preferences on arboreal locomotion, and the link between them: that decision making during arboreal locomotion is dependent on the interaction between the individual and the environment.

7.2 Selection of supports within a route

It has been suggested that the demands of the arboreal environment may have selected for complex cognitive abilities, such as a concept of self (Povinelli and Cant 1995) and higher intelligence and general problem solving (Chevalier-Skolnikoff et al. 1982). It was predicted that careful selection of supports would be necessary for safe and efficient arboreal locomotion but that testing every support before use would not be practical or possible in all situations (for instance, during rapid locomotion, such as when fleeing aggression from conspecifics, or if the next support in a route was located on the other side of a large gap in the canopy). Therefore, apes must possess some knowledge of the functional properties of supports and select suitable routes accordingly. It is well known that non-human apes possess some knowledge of causality and the functional properties of objects in their physical environment as demonstrated by their ability to select the appropriate tools for a task based on properties such as length (Mulcahy et al. 2005), rigidity or flexibility (Manrique et al. 2010), or connectivity (Herrmann et al. 2008). However, the selection of supports for locomotion based on knowledge of functional properties had not been investigated. Chapters Three and Four demonstrated that bonobos (non-tool users in the wild) and a siamang selected supports based on functional properties such as distance from a food goal and flexibility.

7.2.1 The role of the individual

Merely possessing knowledge of the functional properties of a support would not be enough to ensure safe and efficient travel; an individual must also possess some understanding of the impact that their body will have on a support. It has been shown that non-human primates possess simple processes such as motor planning (Weiss et al. 2007, Chapman et al. 2010) and body schema (Holmes and Spence 2004). Chapters Three and Four also demonstrated that individual limb reach was important in support selection and the postures adopted when accessing a hard-to-reach food goal. Furthermore, along with anatomy, individual preferences (in bonobos) and experience (in humans) are also important in support selection. It was shown that lateralised bonobos were able to select (and gain greater success from) supports that enabled the use of their dominant hand at the food goal. It has been shown that use of a dominant hand results in enhanced performance in both humans (Goble and Brown 2008, Janssen et al. 2011, Hughes et al. 2011) and in non-human primates (Fragaszy and Mitchell 1990, Byrne and Byrne 1991, King 1995, Rigamonti et al. 1998, Hopkins et al. 2002). Therefore, selecting a support that enables the use of an individuals’ dominant hand could increase fitness, for example by enabling them to gain more efficient access of a food resource.

The ability to select supports based on functional properties of the support, individual anatomy, and individual handedness seen here suggests some level of planning. Although the term planning has been used liberally to explain a broad spectrum of different cognitive processes (from planning for future events [Mulcahy and Call 2006] to planning for an immediate goal [Dufour and Sterck 2008, Tecwyn et al. 2012]), in this case it describes planning for the current needs of an individual, for example, for reaching a food goal. This suggests that the ability to plan efficient arboreal routes requires selection of suitable supports based on knowledge of, or the ability to predict, the behaviour of supports, along with some internal representation of self.

Therefore, it is likely that these seemingly simple, yet flexible, processes could have formed the precursors to more complex cognition (Vaesen et al. 2012), such as that which is required for tool use and future planning.

The studies in Chapters Two – Four were performed with naturalistically housed captive bonobos and siamangs. In reality, non-human apes travelling in a natural canopy would be subject to a number of complex challenges, such as the energetic cost of travel, height from the ground and the danger of falling, and supports that differ in a number of functional properties at any one time, such as compliance, discontinuity, and response to loading. Therefore, in the wild it would be difficult to separate how non-human apes respond to or have knowledge of individual functional properties of supports. Using a naturalistic experimental test environment enabled support selection in relation to individual functional properties such as distance from a food goal and flexibility to be tested. The symmetry of the test environment also enabled other factors influencing support selection and use, such as fatigue in weight bearing limbs and positional behaviour, to be investigated.

7.2.2 Environmental symmetry

Maintaining demanding arboreal postures is energetically costly and can result in fatigue in the limb(s) used to support the body's weight. It has been suggested that for this reason chimpanzees exhibit ambilaterality using both hands equally and indiscriminately in an ant fishing task (Marchant and McGrew 2007). However, this was not the case when handedness was observed in a symmetrical test environment, and in Chapter Two it was shown that non-lateralised bonobos exhibited a preference for the limb used for postural support. This is understandable considering it has been shown that the strength of the dominant limb is enhanced compared to the non-dominant limb in humans (Goble and Brown 2008) and that limb preference may depend on the energetic demand of a required posture in non-human apes (Vleeschouwer et al. 1995, Morcillo et al. 2006, Peters and Rogers 2008). The use of a preferred limb to maintain suspensory postures in the symmetrical test environment of the current study suggests that it is the complexity of the natural arboreal environment that requires ambilaterality rather than fatigue in the limbs used for postural support.

Furthermore, inexperienced human participants in the rope climbing study in Chapter Five also preferred to use their dominant hand in support when collecting a placed flag two meters from the ground. This suggests that with training (and experience) limb dominance becomes less important in postural support. Donath et al. (2011) also found asymmetric loading of the dominant limb in non-elite rock climbers (those with less experience) and demonstrated that this decreased as climbing ability increased. This suggests that limb preference is flexible at the individual level and depends on the demands of a task. Therefore, handedness can be a useful indicator of the demands of an arboreal task both in terms of support selection and in limb use for postural support.

7.3 Whole routes in a natural canopy

The canopy environment is complex and dynamic, with supports that are compliant and discontinuous, and that occur randomly in relation to one another and to resources. It can be inferred from the observation of wild behaviour of non-human apes that energy efficiency and risk avoidance must be important factors influencing decision making during arboreal locomotion (Chevalier-Skolnikoff et a. 1982, Povinelli and Cant 1995, Remis 1995, Dunbar and Badam 2000, Hunt 2004, Thorpe et al. 2007, Myatt and Thorpe 2011). For example, orangutans distribute their weight across multiple thin supports when in the periphery of a tree crown which could reduce the risk of falling if one branch were to break (Myatt and Thorpe 2011), and avoid the energetic cost of detouring large gaps in the canopy (by climbing down to the ground and back up into a neighbouring tree) by utilising the compliance of vertical trunks in tree-sway behaviours (Thorpe et al. 2007). However, direct evidence of any factor influencing decision making is difficult to obtain without verbal explanation from the individual making the decision. In this way human participants offer the unique opportunity to obtain information regarding the ecological factors influencing decision making through verbal communications of their thought process during arboreal locomotion. Therefore, Chapter Six focused on combining quantitative observations of behaviour of human participants climbing in a natural canopy along with qualitative data in the form of interviews after the climbing task.

7.3.1 Factors influencing decision making

The study in Chapter Six demonstrated that efficiency and risk avoidance were the most important factors influencing decision making during arboreal locomotion. However, all participants did not consider these factors equally and the participants fell into two groups, those who considered risk avoidance and those who considered efficiency the most important factor. It was shown that efficiency (in terms of time spent climbing) was traded-off when risk avoidance was considered the most important factor influencing decision making.

7.3.2 Memory of arboreal routes

Although a trade-off in efficiency (time spent climbing) exists when risk avoidance is considered, this compensation was reduced in individuals who prioritised risk avoidance after repeated use of the same canopy. This suggests that, with repeated use of travel routes, knowledge about or confidence in the available supports reduces the time spent considering risk avoidance and thus increases efficiency of locomotion. It has been shown that non-human primates (*Hylobates spp*., *Ateles spp*., and *Lagothrix spp*.) use repeated travel routes (Di Fore and Suarez 2007, Valero and Byrne 2007, Asensio et al. 2011) and follow known pathways along topographical features between known resource sites (Di Fiore and Suarez 2007). While it is therefore likely that large bodied non-human apes also use known routes, however, this is yet to be confirmed with wild observations.

7.4 Conclusion

In this thesis I have presented evidence from a novel experiment investigating arboreal support selection based on the functional properties of supports in non-human apes (bonobos and siamangs) and a comparative study with human rope climbers, and a novel experiment investigating the ecological influences on decision making in human tree climbers in a natural canopy environment. These studies demonstrate that apes (bonobos, a siamang, and humans) use knowledge of the functional properties of supports in selection and use of supports in arboreal routes. Furthermore, this thesis provides direct evidence that risk avoidance and efficiency are important factors influencing decision making during arboreal travel, but that compensations in efficiency (in terms of time spent travelling) made in favour of risk avoidance can be reduced with repeated use of the same environment or known routes. Therefore, it is likely that non-human apes are able to increase the efficiency and safety of arboreal travel both through the use of known travel routes or pathways, and through careful selection of supports, based on the ability to predict how they may be influenced by an individual's body weight, combined with knowledge of their own limb reach or body size. The studies presented here provide evidence that the arboreal environment played a key role in the evolution of fundamental cognitive abilities, such as memory, a sense of self, and knowledge of the physical and functional environment, in non-human apes.

7.4.1 Strengths, weaknesses, and personal development

At the start of this study my aim was to test multiple species of non-human primates (including apes and monkeys) for individual support selection based on the functional properties of supports as in Chapters Three-Four. However, as the study progressed it was clear that this would have limited the scope of the research questions and would have provided only part of the story of how the canopy environment influences decision making during arboreal locomotion. One of the weaknesses of this study is that the sample sizes of the species included are small and exploratory only, indeed only one siamang interacted with the equipment. Whilst testing multiple populations with the same experimental set up would provide the basis for species wide claims and perhaps a stronger phylogenetic basis for evolutionary claims (e.g. by looking at increasingly distantly related species), the fact that the bonobos and the siamang used supports in the same way indicates that this is a potentially cross-species phenomenon and lays the foundations for future studies covering more species and multiple populations of the same species'. A further weakness of this study is that in the experiments in Chapters Three-Five the choice of ropes to access the food goal (bonobos and siamang) or the flag (human rope climbers) was not one of an impossible versus a possible route. This would have provided clearer results of correct or incorrect choices and mistakes, as it was choosing the “incorrect” rope (the demanding rope) did not result in a direct failure to access the food goal or flag and I had to make assumptions of comfort or energy efficiency based on the use of more demanding (stretched out) postures. Although this is a sound rationale, without direct measurement of energetics or muscle activation (which is impractical to collect from a zoo housed animal) it is a limited conclusion. Similarly in the human rope climbing study (Chapter Five) the choice of either of the ropes did not result in failure to reach the flag, therefore, participants were not aware that their choices could have been incorrect. Finally, in the human rope climbing study in Chapter Five I concluded post-hoc that participant interviews after the task would have revealed greater detail about their decision making. I concluded that the participants were perhaps not perceiving the aim of the task (to select the most suitable rope for climbing based on distance, flexibility, or connectivity) from the equipment set up and limited instructions before acting (e.g. before they chose the rope they were to climb). Collecting their views on the task itself could have confirmed this or otherwise.

Despite the limitations which were revealed post-hoc to the data collection for each of the studies in this thesis the strengths of the final product out-weigh these. Overall, this thesis pulls together evidence for the influence of the canopy environment in decision making during arboreal locomotion across the scale of individual support selection to whole route choice. From the physical and individual factors influencing single support selection (Chapters Two-Five) to the broader ecological factors influencing whole route selection in a natural canopy (Chapter Six) this thesis provides a multifaceted insight into decision making during arboreal locomotion. By breaking down support selection based on individual functional properties and the influence of individual body specifications such as handedness and reach, the simple cognitive processes that may be involved in individual support selection within a route are demonstrated. Then by investigating whole route selection in a natural canopy environment the over-arching ecological factors that influence decision making throughout arboreal travel are shown.

Finally, this thesis has demonstrated the importance of and usefulness of humans in studies of non-human primate behaviour and vice-versa. Covering a spectrum of apes, including humans is important because this can provide a phylogenetic base to questions of how behaviours or cognitive processes may have evolved. For example, if an ability to select arboreal supports based on their functional properties such as distance or flexibility is present in more distantly related species it could be argued that this may have evolved earlier in the primate lineage. But I have also shown that humans provide a useful tool in understanding non-human primate behaviour and ecology. For example, from observations of wild behaviour it can be assumed that decision making during arboreal route planning is likely based on risk avoidance and energetic efficiency (Chevalier-Skolnikoff et a. 1982, Povinelli and Cant 1995, Remis 1995, Dunbar and Badam 2000, Hunt 2004, Thorpe et al. 2007, Myatt and Thorpe 2011) and that the complex nature of the canopy environment means that there is likely a trade-off between selecting routes that are least costly in terms of energetic requirement and routes that are safe. However, by using human participants in a natural arboreal environment we can ask them to explain verbally what ecological factors they consider most important when moving in the canopy. Answers to these questions can give insight into what factors are likely to influence other apes in the same environment, and indeed it was found that risk avoidance and efficiency were the most important factors influencing decision making, and that there was some trade-off (in terms of time spent climbing) when considering risk avoidance over efficiency (Chapter Six).Personally these studies have been a journey of my own development as well as development of the overarching research questions. When I started out I was not familiar with the study of physical cognition, in humans or other species, and I was more comfortable in the realms of primate behavioural ecology. However, early on in my studies I immersed myself in the literature and built a sound basis of knowledge of cognitive research in apes and other primates. A real light-bulb moment was when I learnt that cognition is a biological adaptation that enables an individual to decide how they interact with their environment, be it the physical world or with their social conspecifics (Tomasello and Call 1997). Cognition, for me, was no-longer "untestable" and I developed ideas of how I might test for cognitive abilities in apes and how these may be relevant in terms of evolution in an arboreal environment. It is easy to envisage the advantage a species would have if it were able to respond *ad hoc* to challenges in its environment, e.g. to innovate a new foraging technique to access a different food source, or to be able to predict how conspecifics may behave in potentially dangerous social interactions based on previous experience or memory of similar situations. In terms of what I now understand, and how the findings in this thesis sit in the field of primate cognition, I believe cognition is not one single adaptation that can be traced back in the primate lineage to one single ecological selection pressure during evolution. Indeed, cognition has evolved numerous times in different lineages such as cetaceans and birds (see Rogers and Kaplan 2012 for a review) under very different conditions and in response to very different environmental pressures. What my findings seem to suggest is that the complexities of the canopy environment poses quite specific demands on a large bodied ape during arboreal locomotion. In the wider picture of whole route selection factors such as avoiding the risk of falling and maintaining energetic efficiency are key influences on decision making (Chapter Six), however, to be able to carefully select a safe and efficient route an individual must possess some knowledge of the physical environment and their own body and the potential outcomes of interacting with the environment, such as how far one can reach to a food goal, or how one’s own body weight could deform a potential weight bearing support (Chapters Two-Five). Therefore, in terms of cognition, this research lends support to the theory of embodied cognition in that cognition is not an ability or process separate to the body, but the body influences cognitive processes (Wilson 2002, Anderson 2003), such as through body schema and individual lateralisation. Although I argue that the environment influences the decision making process during arboreal locomotion I believe cognition is not held in the environment as well as the brain and the body but is instead processes that determine the interaction with the environment. If an individual’s environment changes their cognitive ability remains and processes that could be applied to one environmental factor (such as knowledge of the functional properties of a potential support in an arboreal route) can be applied in other situations for different gains (such as knowledge of the functional properties of potential tools to access an embedded food resource). In this way, I believe the complexities of the arboreal environment require cognitive processes (such as a knowledge of functional properties of supports; body schema; end-state comfort effect) which could have formed the basis or the mental scaffolding necessary for the development of more complex and abstract cognitive abilities such as those required for developing tools and future planning.

7.4.2 Recommendations for future research

Future research could increase the sample size and species covered in the within-route support selection studies (Chapters Three and Four). While these studies represent the first, to my knowledge, to investigate knowledge of functional properties in support selection during arboreal locomotion it would be important to expand the sample size to enable broader conclusions to be made at the species level rather than for individual populations. Also, because a siamang performed the same as the bonobos, it would be interesting to apply a similar test to further species, including smaller primates and more phylogenetically distant species (such as Old World monkeys). Theories regarding evolution of cognition in response to the demands of the arboreal environment are based on the specific demands faced by large bodied apes (such as Povinelli and Cant 1995). Therefore, it would interesting to see if smaller species also possess a basic knowledge of the functional properties of supports as in indicator of when this phenomenon may developed in the primate lineage or beyond with the testing of non-primate species. For instance it has been shown that different species of primate prefer different canopy strata (such as Cannon and Leighton 1994) and supports of different orientations (such as Garber 1980, Crompton and Andau 1986, Warren 1997), or prefer environments with high connectivity between supports (Madden et al. 2010). However, it is unclear if individual support selection extends to other functional properties such as distance or flexibility. Therefore, standardised and controlled tests (as in Chapters Two-Four) would be necessary.

Furthermore, evidence of limb preference and handedness in non-human primates remains in an inconclusive debate (McGrew and Marchant 1997, Hopkins 1999, Palmer 2002), in which it is generally believed that the complexity of a task influences the strength of laterality (Fagot and Vauclair 1991). This study demonstrated that environmental symmetry and the demands of positional behaviour are also influential in limb preference (Chapter Two). Therefore future studies of handedness and limb preference in non-human primates should take positional behaviour and the demand of maintaining postural support with a forelimb into account when recording and reporting handedness and limb preference in non-human primates. Furthermore, in studies of wild primates limb preference in the natural canopy should be recorded along with support availability relative to positional behaviour as it is likely the random location of available supports that elicits ambilaterality in the canopy rather than fatigue in the limbs used in postural support.

Modern human tree climbers represent a novel and vital experimental resource in the advancement of our understanding of the complexities of the arboreal environment and its role in our own evolution because they offer a controlled sample and can provide information regarding their decision making process in their own words. This study has demonstrated that qualitative data in the form of the participants own words is key to answering important questions regarding decision making during arboreal travel because they can provide direct evidence of the ecological factors influencing decision making, which can only been assumed in non-human apes. Using qualitative analysis of participants own words also bought to light the potential influence of personality type on decision making. Therefore, future research with modern human tree climbers could incorporate robust personality profiles. These methods could also be used in studies with modern hunter-gatherer populations who rely on arboreal resources such as honey. Furthermore, a comparison of pre-, during-, and post-climb interviews could draw out any differences between intuitive and reflective reasoning during decision making (such as Betsch 2008). It would also be interesting to measure oxygen consumption, and thus energetic expenditure, in human climbers to confirm whether or not the use of repeated routes and known supports directly increases energetic efficiency. Indeed, Halsey et al. (in prep.) found that parkour athletes repeating the same experimental obstacle course reduced their energetic expenditure in this way. Furthermore, due to the novelty and explorative nature of this study (Chapter Six) participants were required to climb in whatever way they preferred, giving them control over how they climbed. It would therefore be interesting to investigate how the inclusion of an additional challenge to this study, such as asking participants to complete the climb as quickly as possible or as efficiently as possible, would influence their decision making and energetic efficiency or risk avoidance. This is important as a fundamental characteristic of these climbers is that tree-climbing is, at least in part, a leisure activity. This could mean that increased time spent in the tree is preferred. This is a vast contrast to hunter-gatherers and particularly non-human apes, who rely on arboreal resources, and may be at more risk from falling or predators, meaning their locomotor decisions are more critical to survival.

Finally, it could be predicted that non-human apes would increase their energetic efficiency and safety during arboreal travel if they followed known travel paths. However, evidence for the use of repeated routes or known pathways is lacking for the apes, therefore, future research could include observations and controlled tests of wild and captive non-human ape travel routes. It is important that comprehensive information about both broad tree-to-tree pathways, as well as more fine-grained branch-to-branch support selection is obtained so that a broader understanding of route selection and the factors influencing decision making can be generated, as has been shown in this thesis. This would further build upon the findings of this thesis and enhance our understanding of how the arboreal environment influences decision making and how large bodied non-human apes cope with the energetic demands of this complex environment whilst avoiding the risk of falling.

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Appendices

Chapter Two

Arboreal postures elicit hand preference when accessing a hard-to-reach food goal in captive bonobos (*Pan paniscus*)

Figure A2.1 Video stills of food goal access in the different experiments. a) shows AdfA and AdfB accessing the food goals in the terrestrial position. b) shows AdfD accessing the food goal in the arboreal position.

Chapter Three

Bonobos (*Pan paniscus*) use functional properties of arboreal supports when selecting routes to a hard-to-reach food goal

Table A3.1 Summary of siamang data. Data were collected by NKIH for one adolescent male housed at the same zoo in the UK. Rope selection was pooled from two experiments (distance and flexibility) and is the number of times the easy or the demanding ropes (or the left or the right ropes) were selected initially in a sequence of behaviours. Hand use is the number of times the left or the right hands were used to manipulate the arboreal food goal or in general foraging (scatter feeds or terrestrial grazing). Binomial tests (two tailed, $p = 0.5$) were run in R version 3.1.0 (2014-04-10), and alpha was set at 0.05.

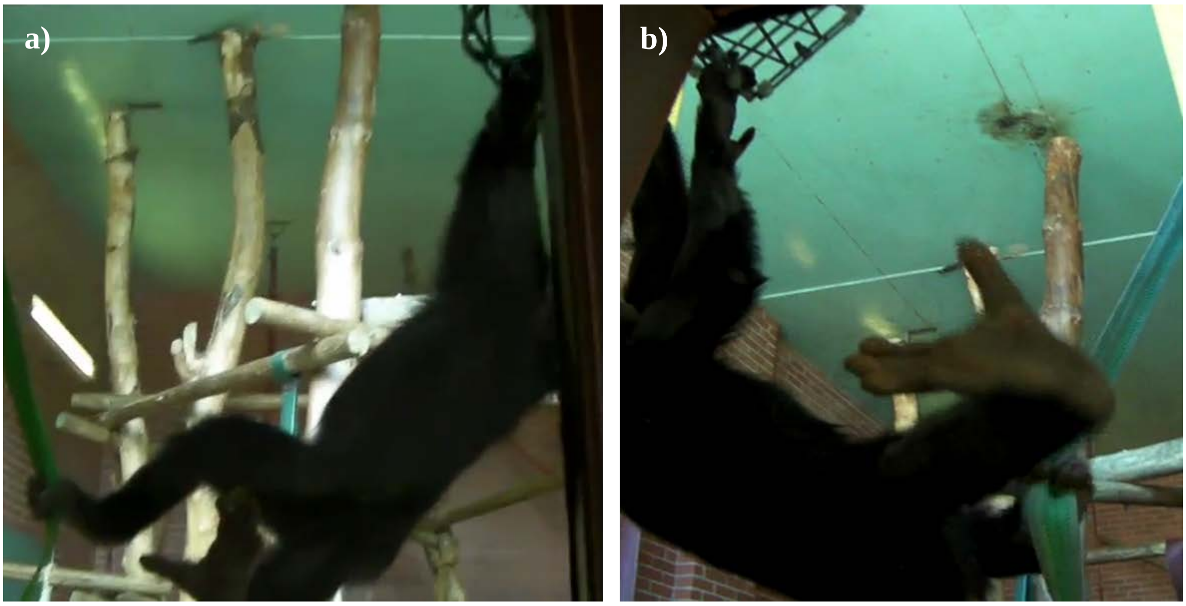
Individual information (age at study)	**Initial rope selection** (easy/demanding) B test	**Initial rope selection** (left/right) B test	**Hand use – arboreal food goal** (L/R) B test	**Hand use – general foraging** (L/R) B test
Male siamang (4 years)	(79/27) **$p < 0.001$**	(48/58) $p = 0.382$	(437/297) **$p < 0.001$**	(112/108) $p = 0.839$

Chapter Four

The influence of social learning and dominance rank on rope choice

Figure A4.1 Video frames of large individuals accessing the food goal from a rope at arms-length (flexed) from the easy rope. a) AdfC on the easy rope and AdfD bottom left dropping from goal, b) AdfA on the easy rope.

Figure A4.2 Video frames of small individuals accessing the food goal from the easy rope in near-pronograde and pronograde postures using the whole body length. a) InmB accessing the goal from the easy rope, b) InfA accessing the goal from the easy rope.



Chapter Five

Support choice in human rope climbers: comparing experienced rock climbers, novice rock climbers, and gymnasts

Figure A5.1. Schematic diagram of equipment set up for the distance trial in the rock climbers experiments. The flag was 2.5 m from the ground. Both ropes were connected at ground level, the correct rope was 1 m from the flag.

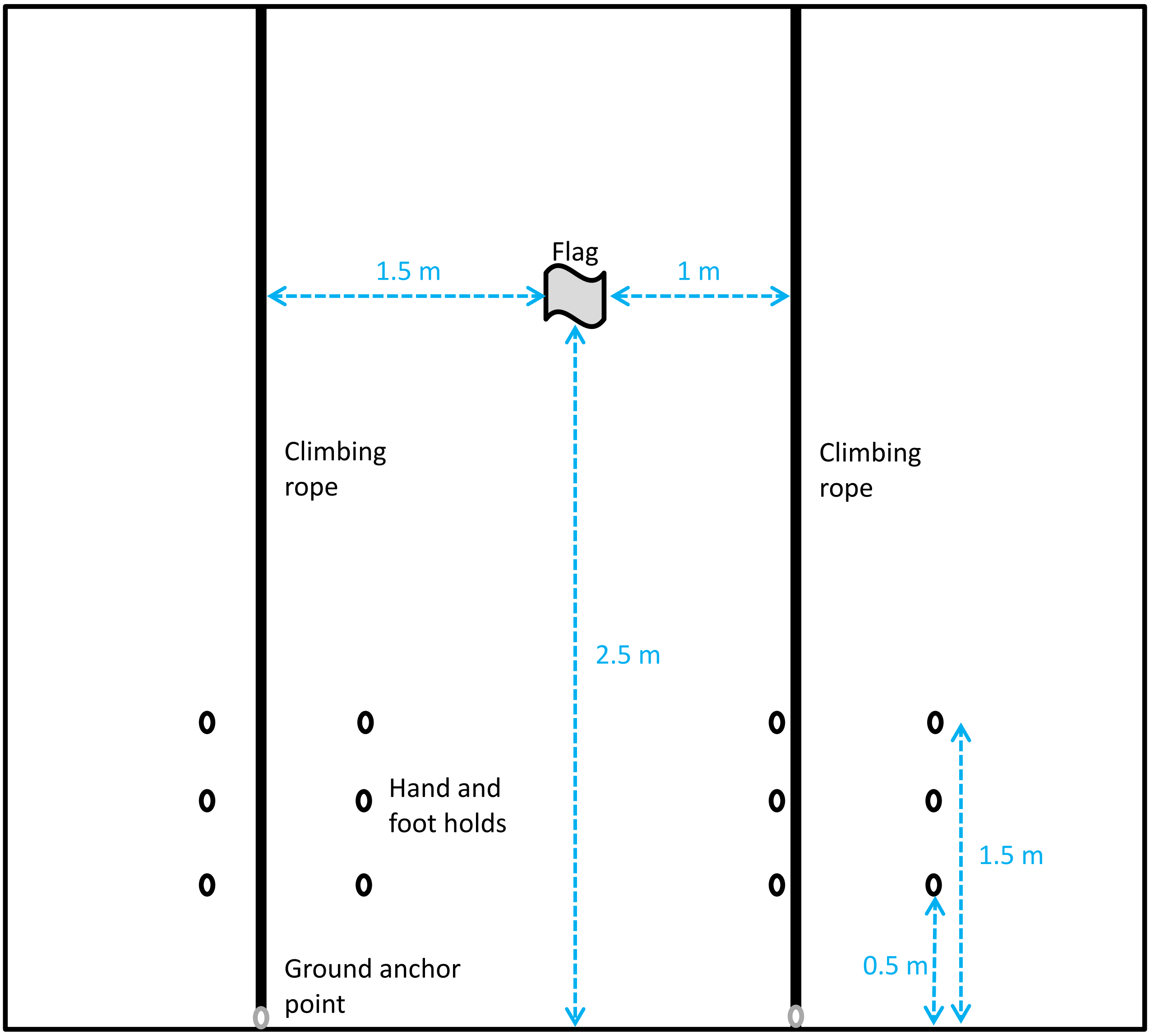


Figure A5.2. Schematic diagram of equipment set up for the flexibility trial in the rock climbers experiments. Both ropes were 1.5 m from the flag, the correct rope was not connected at ground level and so could be moved toward the flag.

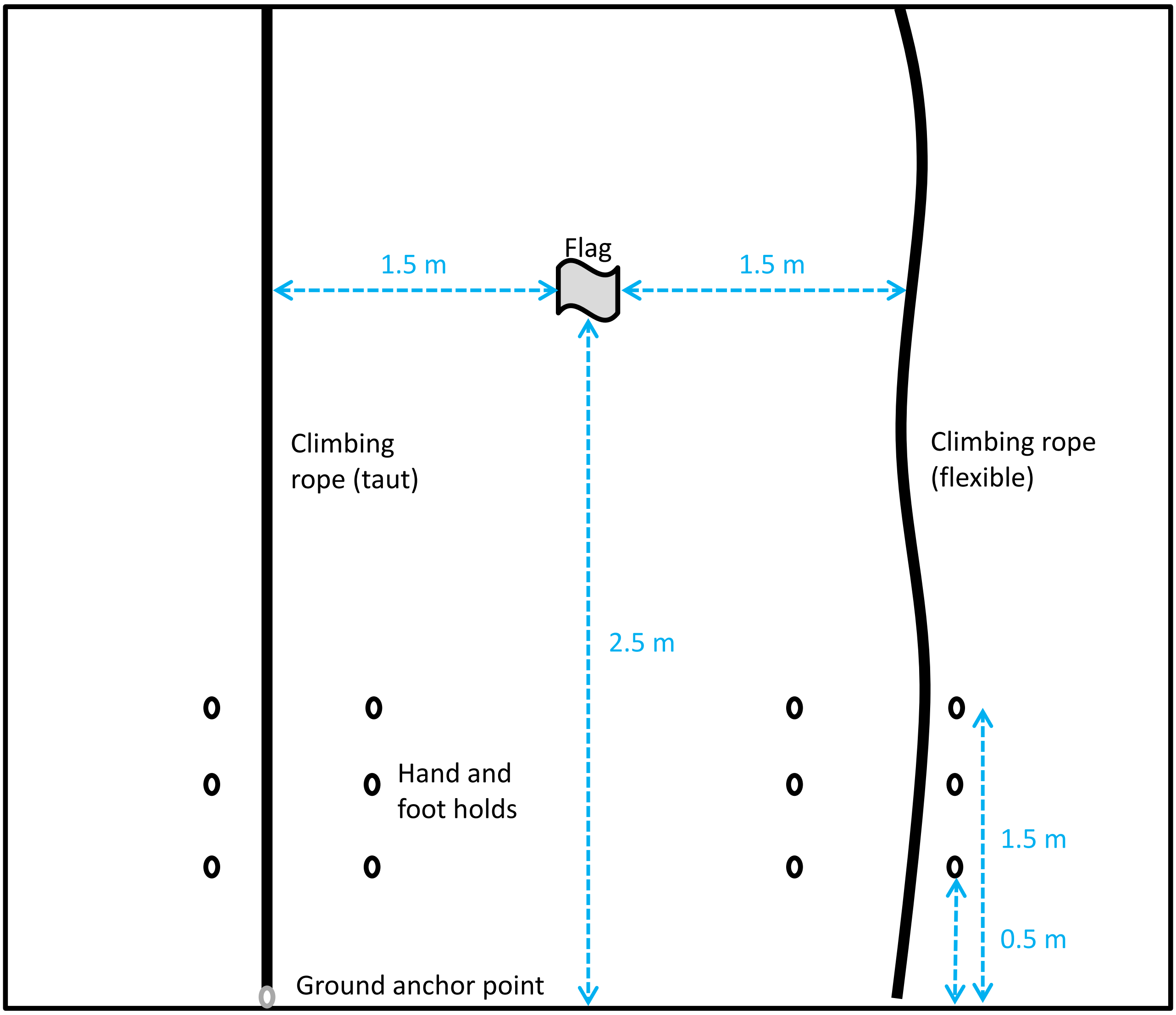


Figure A5.3. Schematic diagram of equipment set up for the connectivity trial in the rock climbers experiments. Both ropes were 1.5 m from the flag, and both were tied to an additional lateral rope. The correct rope was not connected at ground level and so could be moved toward the flag.

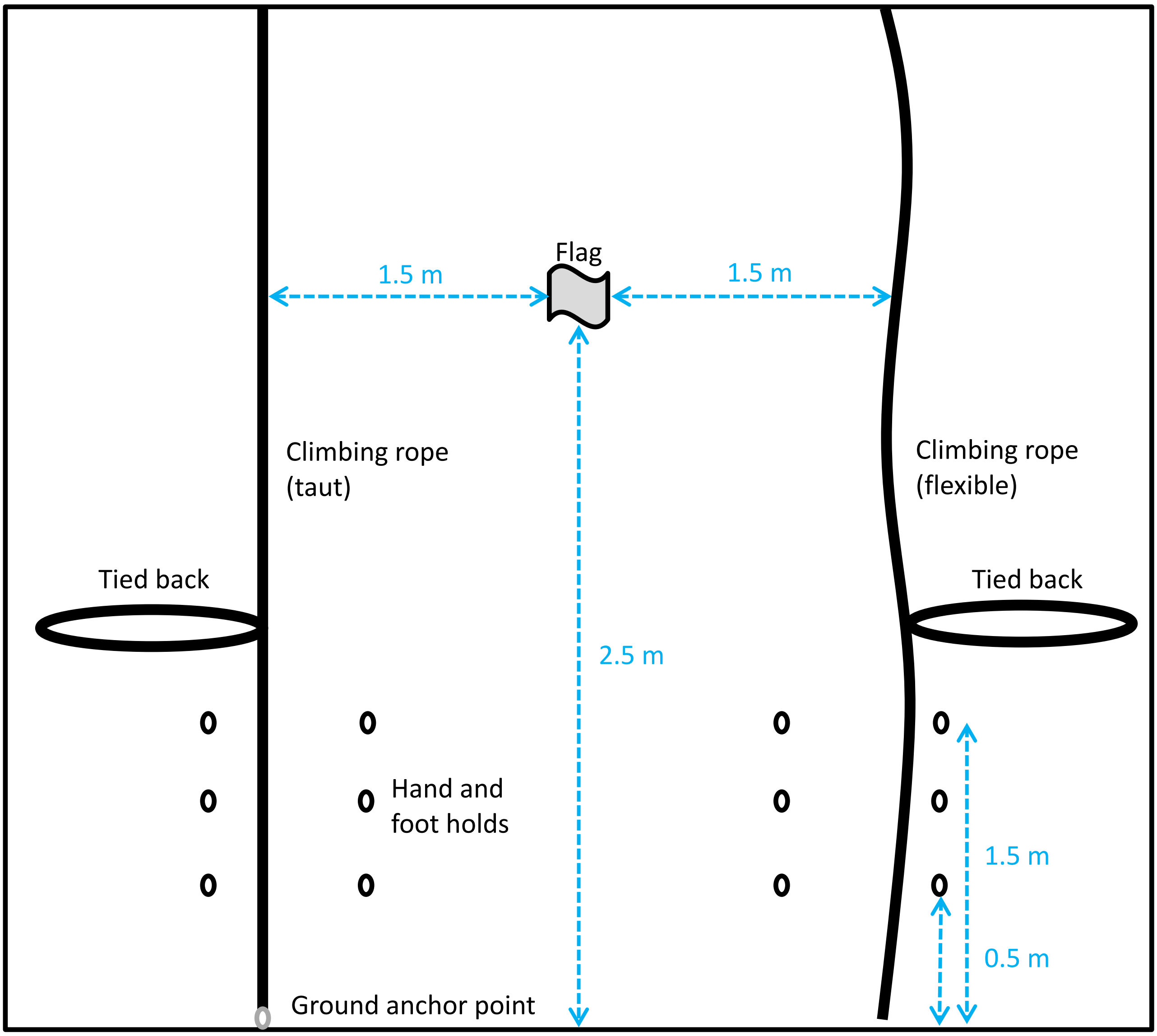


Figure A5.4. Schematic diagram of equipment set up for the distance trail for the gymnasts experiment. The flag was attached to a central rope that participants were instructed not to climb directly. Both ropes were connected at ground level, the correct rope was 1 m from the flag.

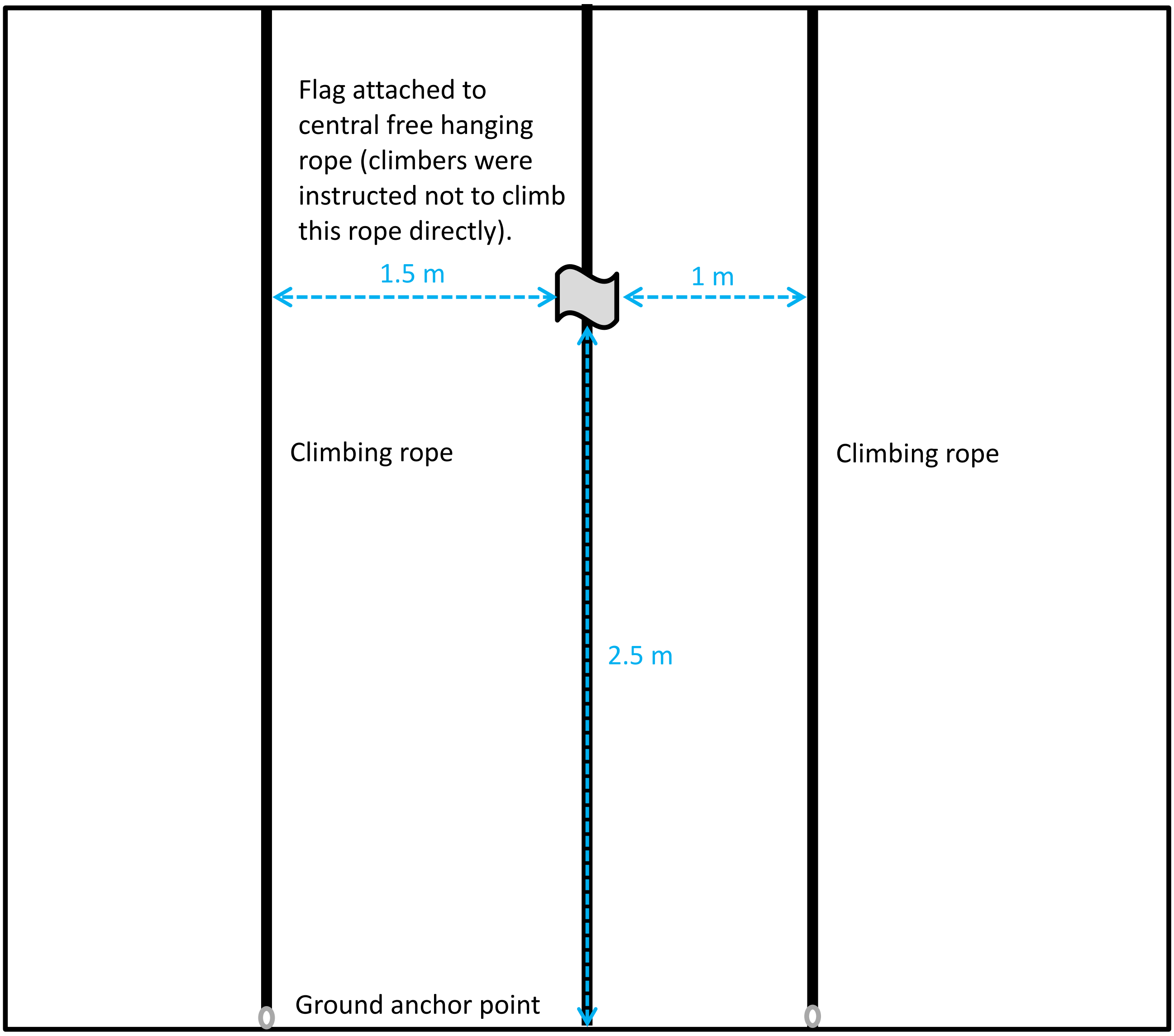


Figure A5.5a Scripted instructions given to participants prior to the climbing task for both the experienced rock climbers and novice rock climbers.

I am now going to give you a set of instructions regarding the climbing task.

I will use scripted instructions to ensure that all participants get the same information prior to and during the climbing task, so that the experimental conditions are the same for everyone.

Do you have any questions before I proceed?

In a moment we will go upstairs to the wall where you will perform the climbing task. At this stage I ask that you avoid studying the wall in any detail until we are in position and ready to start the experiment. This is because I want everyone to have the same exposure to the equipment.

Most or all of the hand and foot holds will be removed from the wall.

In the middle of the wall there will be a flag tied to a carabiner. Your task is to retrieve or attempt to retrieve this using one of the ropes provided.

You may do so in whatever way is most comfortable for you. You may also manipulate or adjust the rope in any way you wish but please do not untie knots at the bottom of the wall, these will be marked with red tape.

When we are in front of the equipment you will have up to one-three minutes *(one for experienced rock climbers and three for novice rock climbers)* to study the wall before starting the task.

Once I have set up the camera and timer, I will say “Go” and you will have two minutes to retrieve or attempt to retrieve the flag.

Once you have retrieved or attempted to retrieve the flag I will ask that you turn your back to the wall while I re-set the wall. You will then be asked to repeat the task a total of three times.

Remember that you are free to opt out at any stage by asking to stop. Do you have any questions before we proceed?

Figure A5.5b Scripted instructions given to participants prior to the climbing task for the gymnasts.

I am now going to give you a set of instructions regarding the climbing task.

I will use scripted instructions to ensure that all participants get the same information prior to and during the climbing task, so that the experimental conditions are the same for everyone.

Do you have any questions before I proceed?

In a moment we will go through to the hall where you will perform the climbing task. At this stage I ask that you avoid studying the ropes in any detail until we are in position and ready to start the experiment. This is because I want everyone to have the same exposure to the equipment.

There will be three ropes, the middle rope has a coloured flag tied to it, and your task is to retrieve or attempt to retrieve this using one of the other ropes provided. Please do not climb the central rope that the flag is tied to.

You may do so in whatever way is most comfortable for you. You may also manipulate or adjust the rope you choose to climb in any way you wish but please do not untie knots at the bottom of the ropes (these will be marked with red tape).

Once we are in front of the equipment you have up to one minute to study it before starting the task. Once I have set up the camera and timer, I will say “Go” and you will have two minutes to retrieve or attempt to retrieve the flag.

Once you have retrieved or attempted to retrieve the flag I will ask that you turn your back to the equipment while I re-set the wall. You will then be asked to repeat the task a total of three times.

Remember that you are free to opt out at any stage by asking to stop. Do you have any questions before we proceed?

Figure A5.6 Video stills of participants collecting the flag. a) Novice rock climber using the near rope and collecting the flag using their left hand whilst supporting their weight on the rope with their right hand. b) Gymnast using the near rope to collect the flag with their right hand.

Chapter Six

Human tree climbers

Figure A6.1a Scripted instructions given to participants prior to starting the tree climbing task.

In a moment we will go up to the tree where the climbing task will take place. In the tree you will see 4 coloured buzzers, these are your goals. Your task is to press all the buzzers or as many as you are able to. You can do this in whatever way you prefer and in any order. Please exit the tree when you have finished.

You will repeat this 3 times with a short break between each climb. Before each climb we will ask you to choose a new way of accessing the canopy, and to briefly outline why you made your choice.

As far as possible please free climb the tree throughout the task without bearing your weight on the safety ropes. The large vertical rope (secured by Canopy Access Ltd) represents rainforest vines and can be used.

After completing all three climbs we will discuss the decisions you made and your chosen access points, followed by a short questionnaire.

Do you have any questions before we proceed?

(Walk to tree)

You can now have up to 10 minutes to study the location of the goals from the ground. Please feel free to walk around the tree as necessary. You do not have to use the whole 10 minutes, just come back to us when you are ready to start.

Please take this time to think of the 3 different ways you will access the tree in your 3 trials. We ask you to start with your most preferred choice, your second climb will then be your second preferred choice, your final climb will be your third preferred choice.

Before we start each climb we will ask you to briefly detail the decisions you have made and the order in which you will attempt to access the goals for that climb. This is so that we can get the cameras into suitable positions. However, you are not restricted to the order you’ve described. You are free to change your mind about how you access the tree and the order you attempt to access the goals at any stage before or during the climb. We just ask that you tell us so that we can manoeuvre the cameras suitably.

Do you have any questions before we proceed? Please remember you are free to opt out or stop the task at any moment.

Figure A6.1b Scripted questions used during the post-climb interview. Each interview was started with a general open question "can you talk me through your climbs in as much detail as possible?", then to ensure the same detail was collected from each participant the scripted questions were used. After the questions NKIH asked individual questions based on notes made during the climb, including any change in duration of climbs or specific positional behaviour used by individuals (such as jumping or bridging).

Now you have used three different ways of accessing the tree which was your preferred way?

Why was this your preferred way of accessing the tree?

Does the order of the different ways of accessing the tree you used reflect your preference?

How did this change?

What factors did you consider when choosing a way to access the tree?

Do the different ways you accessed the tree represent ways you would usually use?

If not, what is different?

Did you collect the goals in the order you thought you would each time?

What changed?

Why?

Which was your preferred goal to reach?

Why?

How did you move from goal to goal? *(specify between goal one and two etc.)*

What factors did you consider when choosing how you travel between and access each goal?

Did any of these things change between each climb, why?

Did the way you feel about the task change over the climbs?

Can you elaborate? Describe in more detail? What specifically are you referring to?

Which was your preferred way of exiting the tree?

Why?

What factors did you think about when choosing a way of exiting the tree?

T*able A6.1. GLMMs for Muscle ~ Movement theme + (1|Individual) for each muscle for bipedalism only. Results shown are for the risk movement theme (no further pairwise comparisons were necessary as the movement theme had only two levels). There was no significant difference in muscle force production across the two movement themes, except for vastus lateralis. The risk group produced greater forces in the vastus lateralis compared to their mean EMG for walking on the ground than the ease and efficiency group.*

Muscle	**Random effects variance *(SD)***	**Estimate**	**SE ±**	**Z value**	**p value**	**Adjusted p value [(1)]**
Intercept	0.03	5.75	0.08	69.41	< 0.001*	
Vastus lateralis	*(± 0.17)*	-0.46	0.12	-3.91	< 0.001*	0.0006*
Intercept	0.16	5.44	0.20	27.65	< 0.001*	
Gluteus maximus	*(± 0.39)*	-0.25	0.28	-0.89	0.371	1.0
Intercept	0.14	4.44	0.19	23.50	< 0.001*	
Gastrocnemius	*(± 0.38)*	-0.35	0.27	-1.32	0.188	1.0
Intercept	0.20	7.98	0.22	35.77	< 0.001*	
Biceps brachii	*(± 0.45)*	0.05	0.32	0.15	0.879	1.0
Intercept	0.41	6.74	0.32	20.95	< 0.001*	
Triceps brachii	*(± 0.64)*	0.75	0.46	1.65	0.099	0.593
Intercept	0.53	6.81	0.37	18.64	< 0.001*	
Extensor carpi ulnaris	*(± 0.73)*	0.22	0.52	0.43	0.665	1.0

** $p \leq 0.001$. [(1)] Bonferroni correction.*

Table A6.2 Details of 12 outliers removed from the data set, removal did not influence the power of the GLMMs (Muscle ~ Theme + (1|Individual)) or the significance of p values. EMG values are mean EMG as a percentage of the mean EMG for walking on the ground for each individual. Mean for the sample was calculated for each muscle for each movement theme group. Positional behaviour is provided for context.

Muscle	Individual (theme)	Positional behaviour	Mean for sample	Outlier value	No. of SD from the mean
Vastus lateralis	Seven (ea. & ef.)	Bipedal jump	307.4	2328	8.2
Gluteus maximus	Seven (ea. & ef.)	Vertical climb	262.9	1499.9	5.4
	Four (risk)	Vertical climb	219.6	1548.8	9.0
	Four (risk)	Vertical climb	219.6	1487.1	8.6
Gastrocnemius	Six (ea. & ef.)	Suspensory drop	92.3	3489.3	20.1
Biceps brachii	Three (risk)	Vertical descend pole slide	5846.1	52555.0	5.9
	Four (risk)	Orthograde scramble	5846.1	55169.3	6.2
Triceps brachii	Two (risk)	Vertical climb	2586.2	21706.3	6.7
	Two (risk)	Vertical descend	2586.2	19002.6	5.8
Extensor carpi ulnaris	Six (ea. & ef.)	Orthograde suspend	1763.9	21015.9	7.8
	Six (ea. & ef.)	Orthograde suspend	1763.9	21542.5	8.0

(ea. & ef.) is ease and efficiency movement theme. SD is standard deviation.

Figure A6.2a. Mean EMG for gluteus maximus for the movement themes. There was no significant difference between the themes (GLMM, Z = -1.02, p = 0.364). Data points missing from the plot due to the scale are shown in blue.

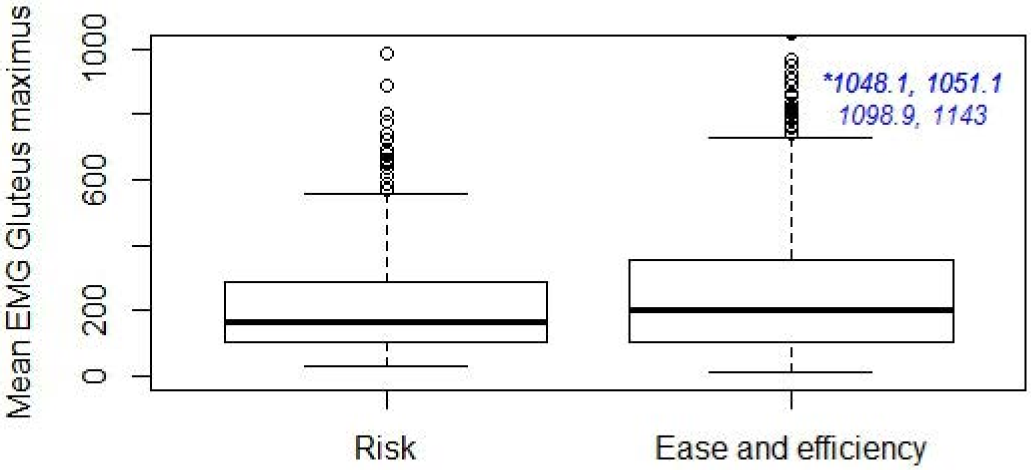


Figure A6.2b. Mean EMG for gastrocnemius for the movement themes. There was no significant difference between the themes (GLMM, Z = 1.88, p = 1.0). Data points missing from the plot due to the scale are shown in blue.

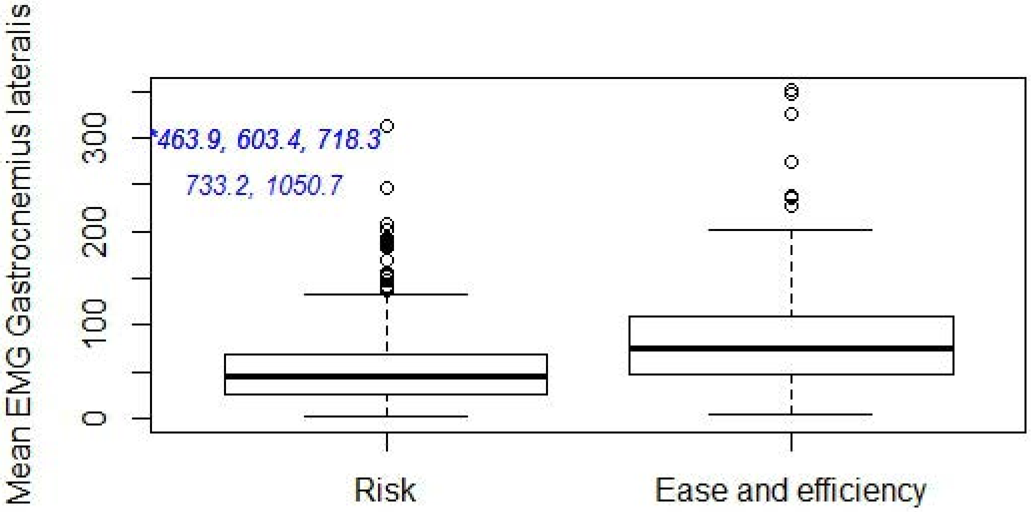


Figure A6.2c. Mean EMG for biceps brachii for the movement themes. There was no significant difference between the themes (GLMM, Z = 0.46, p = 1.0). Data points missing from the plot due to the scale are shown in blue.

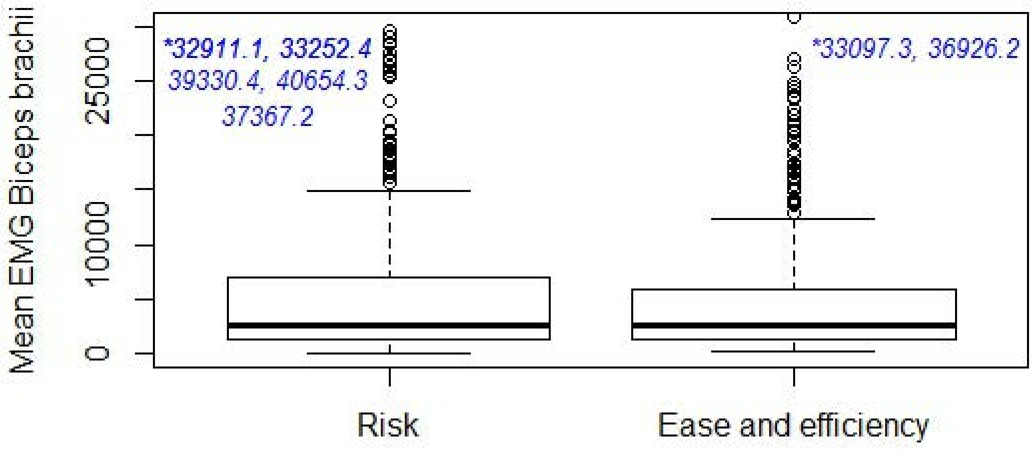


Figure A6.2d. Mean EMG for triceps brachii for the movement themes. There was no significant difference between the themes (GLMM, Z = 1.72, p = 0.508). Data points missing from the plot due to the scale are shown in blue.

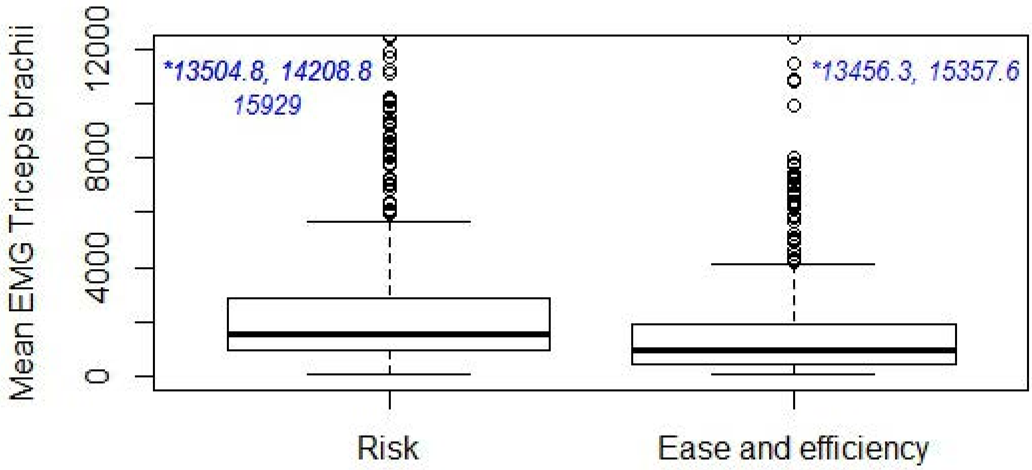
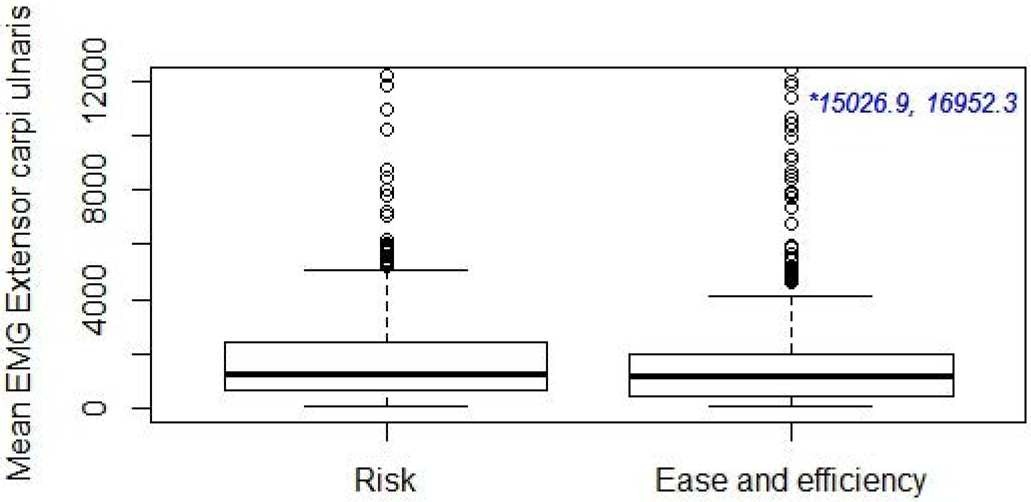


Figure 6.2d. Mean EMG for extensor carpi ulnaris for the movement themes. There was no significant difference between the themes (GLMM, Z = 0.20, p = 1.0). Data points missing from the plot due to the scale are shown in blue.



In loving memory of Kakowet

1980-2016