THE EVOLUTION OF HOMINOID ECOMORPHOLOGY

STUDIES OF LOCOMOTOR BEHAVIOUR AND ANATOMY IN HUMAN AND NONHUMAN APES

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ABSTRACT

Locomotor behaviour is the interface between an animal and the surrounding environment, dictating its ability to access food, escape predators and compete for mates. Extant apes have evolved a diverse range of locomotor strategies which allows them to exploit terrestrial and arboreal environments despite their large body size. However, hominins (modern humans and their ancestors) are traditionally defined by their restriction to upright, bipedal posture and locomotion. Reconstructions of locomotor capacity in fossil hominoids allow investigation of the evolution of extant ape locomotor behaviours, including our own bipedal gait. However, these reconstructions rely on a detailed understanding of the relationships between morphology, locomotor behaviour and the environment in extant apes. This thesis explores variation in locomotor behaviour and skeletal morphology among extant apes in order to shed light on these relationships.

The effects of environmental variation on bipedal and knuckle-walking kinematics were investigated in captive chimpanzees (*Pan troglodytes*) and lowland gorillas (*Gorilla gorilla gorilla*). Analysis of video footage of individuals moving through their enclosures shows that locomotor kinematics are sensitive to arboreal support properties in both species, and forelimb kinematics during knuckle-walking contrast with previously suggested differences used to advocate independent evolution of knuckle-walking in *Pan* and *Gorilla*. The results emphasise the influence of environmental context on hominoid locomotion.

The arboreal locomotor behaviour of modern human tree climbers from the UK was explored in the light of claims that adaptations to habitual terrestrial bipedality restrict arboreal capacity. The climbers completed an ecological task of activating four buzzers situated in the peripheral branches of an oak tree. Their behaviour demonstrated that substantial arboreal capabilities are accommodated by modern human morphology, and that humans use similar locomotor strategies to other extant great apes in order to overcome the challenges of the arboreal environment. This provides strong evidence against the presence of a rapid and absolute arboreal-terrestrial transition in hominin evolution.

The variation in five skeletal indicators of habitual bipedality among extant apes was quantified in order to test the reliability of inferring habitual bipedality from skeletal morphology in fossil hominoids. Expression of the anterior inferior iliac spine, obturator externus groove, twisting of the femoral head, angle of the distal tibia articular surface and high lateral lip of the patellar groove of the femur was measured from skeletal specimens of extant apes. There was considerable variation in the expression of these features, particularly within modern humans, suggesting that the absence of any one feature may not reliably indicate a lack of bipedality. Joint ranges of motion (ROM) predicted from skeletal material have also been used to infer locomotor behaviour in fossil hominoids. Flexion/extension ROMs at the hip, knee and ankle were measured from skeletal specimens of extant great apes using digitised photographs. These skeletal measures of ROM varied considerably within extant ape species, and were not strongly related to interspecific differences in passive ROM (maximum ROM in a living animal) and active ROM (the ROM used during positional behaviour). This suggests that interpretations of locomotor capacity in fossil hominoids based on relationships between skeletal measures of ROM and locomotor behaviour in extant apes are unreliable.

These studies highlight the importance of behavioural flexibility in determining locomotor capacity in hominoids, and suggest that fossil hominoids were less restricted in their locomotor repertoires than previous reconstructions suggest. Crown hominoids may share a morphological propensity for considerable behavioural flexibility, rather than phylogenetically constrained sets of locomotor behaviours.

For my Dad,

who taught me to question.

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"Given the evidence, familiar to everyone, that numerous environmental inputs are consistently supplied during normal development, the skepticism of biologists regarding the reliability of environmental factors relative to that of genes has to rank among the oddest blind spots of biological thought"

Mary West-Eberhard, 2005

CHAPTER ONE

GENERAL INTRODUCTION

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POSITIONAL BEHAVIOUR, ECOMORPHOLOGY AND EVOLUTION

Positional behaviour is used to describe an animal’s physical activities, and is made up of two components: posture and locomotion. Locomotion includes any movement that relocates the body’s centre of mass from one place to another, while posture describes any position that does not involve such a shift in centre of mass. Postures are mostly stationary, but also include any non-locomotor movements of body parts. Together, the postural and locomotor behaviours that an animal can exhibit define how effectively it may utilize its surrounding habitat, and as a consequence underlie the success of foraging, predator avoidance and reproductive strategies.

In order to make meaningful comparisons of positional behaviour, both within and between species, it is essential to consider morphological form and function in an ecological context. This approach, known as ecomorphology, was coined by Karr and James (1975) during their exploration of morphological variation among avian populations, before being honed further by Wainwright (1991) when relating jaw morphology to feeding behaviour in labrid fishes. In studies of locomotion, an ecomorphological perspective provides a framework for understanding and quantifying the mechanisms linking morphology, behaviour and ecology. The evolution of positional behaviour is thus linked to the selective pressures presented by an animal’s environment. The selective advantages and developmental mechanisms underpinning the evolution of the exceptional range of positional behaviours exhibited by primates have been a constant focus of anthropological debate; particularly the arboreal strategies of large-bodied hominoids (apes and their ancestors; Figure 1.1), and the supposedly unique form of bipedality seen in hominins (modern humans and extinct species most closely related to humans among extant apes; Figure 1.1). However, as this chapter will illustrate, positional capabilities are facilitated not only through the evolution of specific positional behaviours, but through selection for behavioural flexibility itself, allowing an animal to adapt its behaviour quickly and effectively in response to habitat variation.

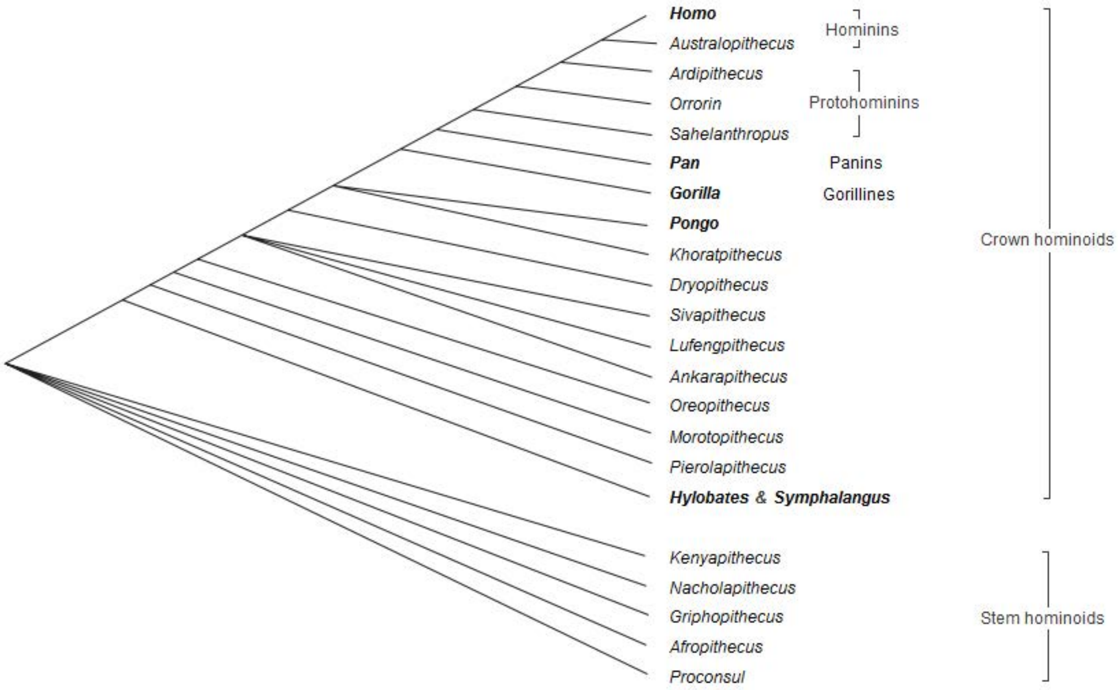

Figure 1.1. Phylogeny of major hominoid genera showing definitions of hominoid groups. Phylogenetic relationships are heuristic and taken from Crompton et al. (2008). Genera containing extant species are in bold text.

Defining and quantifying positional behaviour

The term “positional behaviour” was coined by Prost (1965). He declared the classification of primate locomotion to be “in a state of disorder” following inconsistent reporting of locomotor behaviours by different researchers. He called for a uniform system of locomotor classification that would facilitate the production of detailed, explicit and quantitative datasets. Prost’s call was answered in 1996 when many leading academics in the field created a unified classification system for primate positional behaviour (Hunt et al., 1996). This classification system forms the backbone of the way we describe primate positional behaviour today, and its functional basis and hierarchical nature have allowed subsequent authors to build on the existing framework (e.g. Thorpe and Crompton, 2006). In this classification, postural and locomotor behaviours are categorised into “modes” that are defined in a functional manner. Each mode embraces a family of behaviours that have mechanically similar attributes and subject the animal’s anatomy to similar selective pressures. Submodes are used to describe biomechanical units within each mode (Figure 1.2). The system makes explicit distinctions between key functional parameters such as: whether the limbs that are in contact with supports are bearing more or less than their own mass; whether the torso is held in an upright (orthograde) or horizontal (pronograde) orientation; the number of weight-bearing limbs and weight-bearing supports; and whether the limbs are held in flexed or extended positions (Figure 1.2). Most positional behaviours can be categorized as either posture or locomotion, although in some cases they overlap. Tree sway, for example, which is employed by orangutans and involves increasing oscillation of a compliant tree trunk to reach another support (Cant, 1987; Thorpe and Crompton, 2006), is achieved by maintaining a sequence of postures, but results in locomotion due to movement of the support rather than movement of the animal’s body.

Categorisation allows trained observers to quantify the postures and locomotion of free-living primates in relation to the functional properties of their natural habitats, such as support type and diameter. Such descriptions rely on the observer’s interpretation of the mechanical interaction between the animal and its weight bearing supports. Cues on weight bearing are obtained from factors such as the degree of deformity of supports under the animal; how strongly a support rebounds when the animal unloads it; the position of the torso relative to

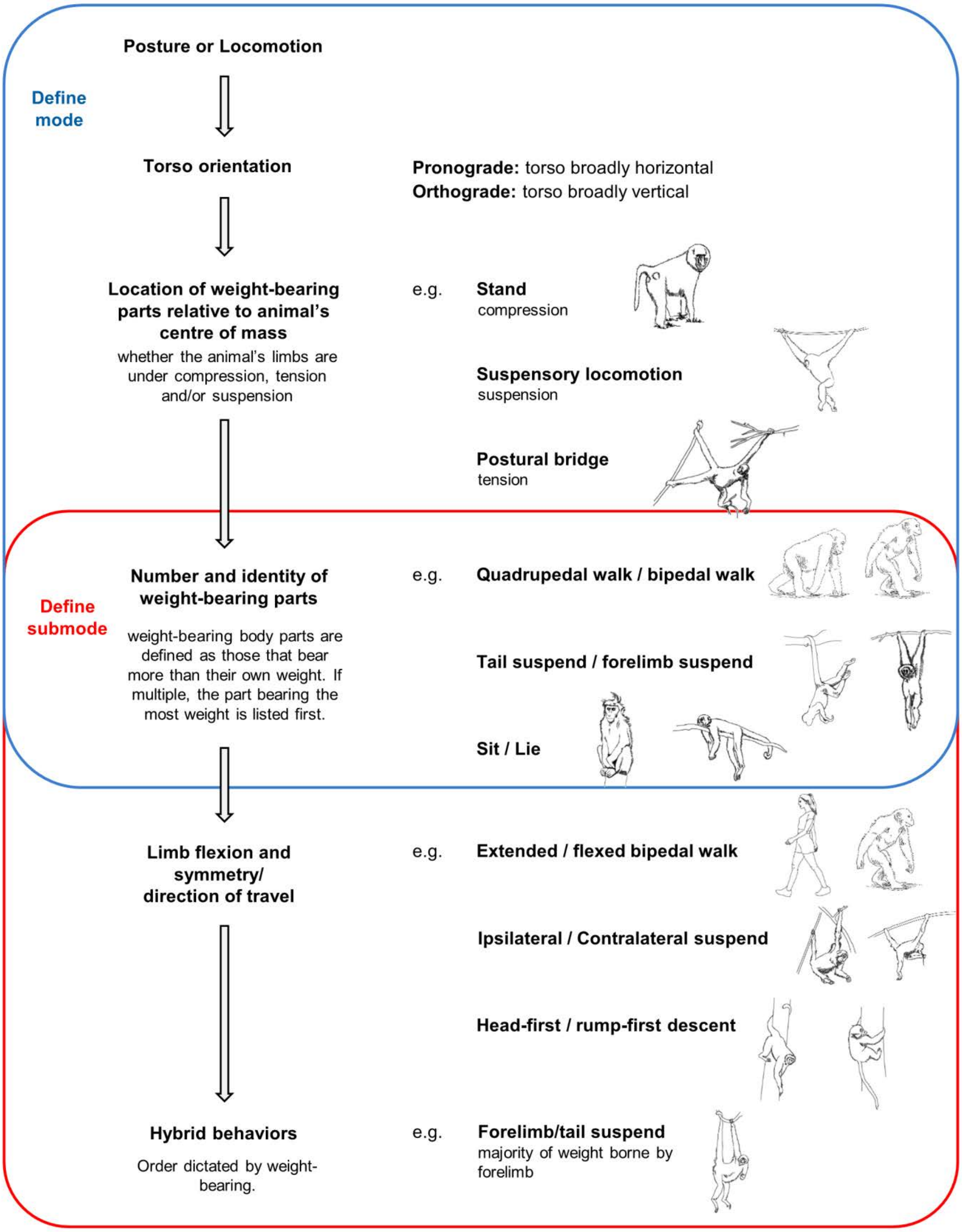

Figure 1.2. Flowchart indicating the hierarchical system in Hunt et al.'s (1996) classification of primate positional behaviour. The blue box includes parameters that define positional modes; the red box includes parameters that define positional submodes. These overlap in the "number and identity of weight-bearing parts" category because these distinctions can be used to define both modes and submodes.

the weight-bearing limbs and support(s); and the appearance of the hands, feet and limbs. However, some differences between gaits cannot be recognized by observation alone. Thus a full interrogation of the relationships between form, function, and behaviour would also include parallel studies into the biomechanics of the observed behaviours. Biomechanical studies of locomotor behaviour involve precise measures of the movements and accelerations (kinematics) and forces (kinetics) that act within or on living organisms. Any one gait cycle taken by an animal can be analysed in terms of its distance and speed, the angles of rotation at particular joints, the forces generated by particular muscles, or the forces and pressures exerted by the animal on the weight-bearing support. This method allows both subtle differences between gaits and dynamic similarities between different locomotor behaviours to be detected. Understanding these is important in explaining how a particular animal transitions from one mode of locomotion to another, and for understanding evolutionary transitions in positional behaviour (Crompton et al., 2010). An example of the latter is the way that biomechanical understanding of locomotion in chimpanzees and modern humans altered hypotheses surrounding the evolution of hominin bipedalism. The dominant theory among anthropologists throughout much of the twentieth century advocated a terrestrial, knuckle-walking origin for bipedalism: that hominins “stood up” from a quadrupedal gait shared with other African apes (Richmond et al., 2001). However, biomechanical disparity between bipedalism and knuckle-walking (Inouye, 1994) provided strong evidence against the development of one behaviour directly from the other, and, alongside a lack of morphologies associated with knuckle-walking in the hominin fossil record (Kivell and Schmitt, 2009), led to the hypothesis being largely refuted (Thorpe et al., 2007b; Crompton et al., 2010).

A biomechanical approach is also useful when quantifying an animal's performance capacity. Performance may simply refer to the maximum speed of a certain locomotor behaviour, or the maximum time an animal can sustain a physically demanding posture (such as hanging from one arm). However, performance can include other aspects of locomotion, such as the ability of a primate to change direction on a branch while maintaining both stability and speed. Biomechanical analyses of performance require instrumented equipment that can accurately measure distances, joint angles, and joint moments of force. As a result, these analyses can only be carried out under the more controlled conditions available in laboratories and zoos (Figure 1.3), and are mostly restricted to the behaviour and mechanics of primates during locomotion at a steady speed in fairly simple environments.

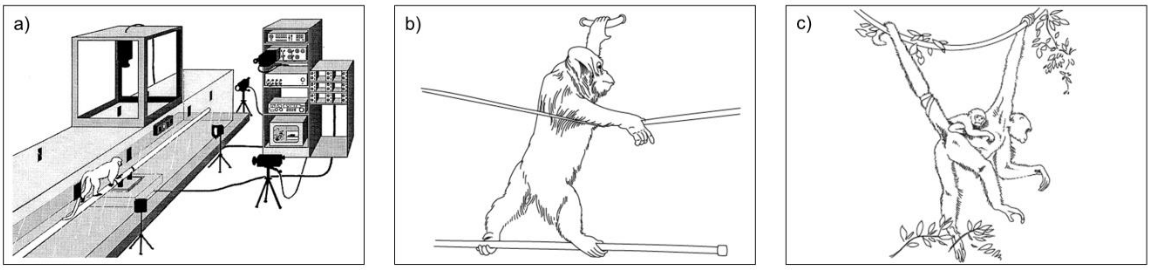

Figure 1.3. Illustration of primate locomotion being studied in laboratory (a; taken from Schmitt, 1999), zoo (b), and natural (c) settings. In the laboratory setting (a), a monkey walks along a horizontal pole which is equipped with a force sensor and filmed from multiple angles. In the zoo setting (b), an orangutan walks along a horizontal pole equipped with a force sensor that has been installed into its enclosure and is filmed from one camera. In a natural setting (c), animals are often obscured by foliage and are generally unrestricted with regards to their direction of travel. Filming locomotion from a specific angle is therefore much more difficult.

At present, it is impossible to obtain equivalent data for complex locomotion in 3D, in natural arboreal habitats. This would require remote sensing of the multiple changes of direction, positional behaviour and supports that typify primate arboreal movement. At some point, this will become possible, and developments in wireless technologies show great promise for the future.

The ecomorphological framework

For a primatologist seeking to understand primates in an evolutionary context, positional behaviour is a vitally important piece of the puzzle. However, simply making a list of all the postural and locomotor behaviours exhibited by a particular primate tells us very little about its life or evolution. In order to understand animals today, and to reconstruct their evolutionary journey, it is essential to look at behaviour in an ecological context (Figure 1.4). Primates must be able to escape from predators, catch mobile prey, compete for mates and access food. Positional behaviour influences the success of all these strategies, and therefore plays a key role in a primate's chances of survival and reproduction, in other words: its evolutionary fitness. But positional behaviour is also linked to, and influenced by, all aspects of a primate's ecology because selective pressures and habitat requirements associated with other core behaviours, such as mating and social interaction, may also influence a primate's positional behaviour in a particular context.

Performance is also essential to understanding this relationship (Figure 1.4). Differences in morphology lead to differences in performance capacity, which in turn result in differences in habitat use. Behaviour mediates the relationships between both morphology and performance and between performance and habitat use (Karr and James, 1975; Garland and Losos, 1994), and is the parameter that is most directly acted on by natural selection. A combination of the observational and biomechanical approaches outlined above therefore allows researchers to explore the relationship between two key concepts: what a primate *can* do when pushed to its performance limits, and how this relates to what it *actually* does in its natural habitat. We can ascertain whether species use their full performance capabilities in the wild, and if so, which ecological contexts are relevant.

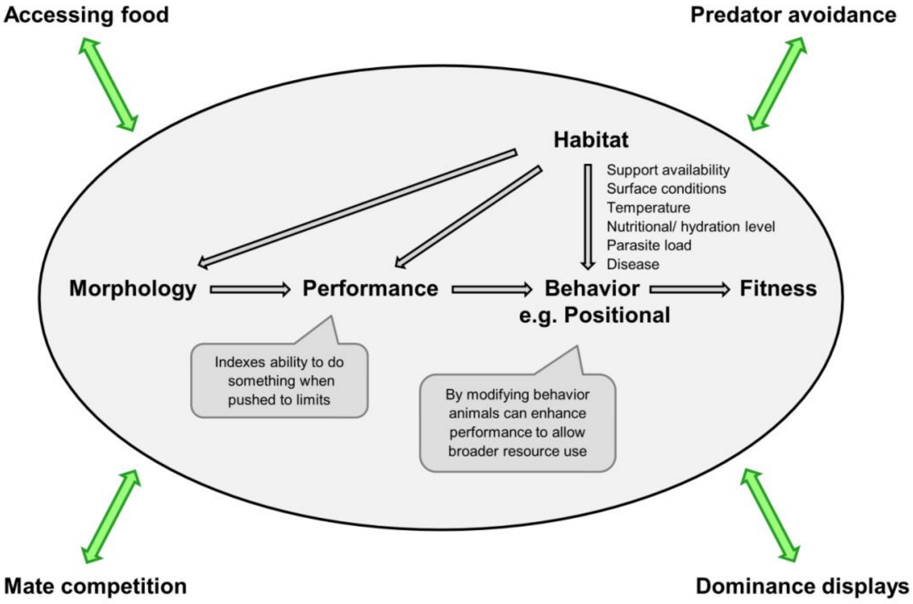

Figure 1.4. The ecomorphological approach. The parameters within the oval depict the ecomorphological framework for interpreting the relationship between morphology, habitat and positional behaviour. The parameters outside of the oval are examples of other behaviours that dictate habitat use and place competing selective pressures on morphology, and will therefore influence the expressed relationship between morphology, habitat and positional behaviour for any given species. Developed from Garland and Losos (1994).

However, an animal’s performance might also be influenced by other factors, such as whether it is raining, rendering the supports wet and slippery; whether the animal is habituated to human observers; or whether an animal is unwell. In order to take account of such factors, field studies need to be of sufficient duration to allow sampling of an animal’s behaviour in a broad range of conditions and across different seasons.

Positional behaviour is also determined by a primate’s own morphology. Morphology is subject to genetic and developmental constraints, yet genes effectively set parameters within which morphology can change throughout ontogeny to accommodate the different behavioural requirements of a primate’s environment (Pilbeam, 2004). However, interpreting the way in which positional behaviour is facilitated and constrained by morphology and ecology is complex. It is practically impossible to know whether any given trait in any given population has reached its selective optimum for a particular selective pressure at the time we study it. In addition, animals do not consistently perform at the limits of their morphological capabilities. Morphology reflects a balance between extreme physical demands, even if infrequent, and the demands of more routine physical activity. A primate may very rarely need to leap five meters in order to escape a predator, but an ability to do so could be essential to survival. Nevertheless, the morphology of bones and muscles is also likely to be refined by adaptations that reduce the energetic cost or risk of routine behaviours (e.g. Pontzer and Wrangham, 2004). Many primates therefore have “compromise morphologies” that reflect a balance between optimization of different positional behaviours or even of different types of behaviours. Finally, it must not be forgotten that morphology is also subject to other demands, such as requirements for bones to protect internal organs or accommodate bone marrow.

ENVIRONMENTAL CHALLENGES TO PRIMATE POSITIONAL BEHAVIOUR

Many primates exploit both terrestrial and arboreal habitats. This presents its own challenges as transitioning between the two can be energetically demanding. Comparatively however, the terrestrial habitat lacks two major challenges of the forest canopy: height above the ground and branch compliance. Extant primates range in size from 30g mouse lemurs to 200kg male mountain gorillas. While avoiding falls is a crucial challenge for any arboreal primate, larger animals are less likely to survive falls from any great height, because the kinetic energy that the body must dissipate on impact increases in proportion to the cube of its linear dimensions and to the square of its terminal velocity (Cartmill and Milton, 1977). The risk of falling also increases with the compliance of a support. The “terminal branch niche” (TBN) at the periphery of tree crowns represents a dynamic network of flexible branches and lianas that vary in orientation, diameter, compliance, and connectedness. However, this niche is where fruit and leaves are most abundant, and where the shortest distances between tree crowns exist. Successful exploitation of the TBN therefore facilitates access to highly desirable food and nest-building resources (van Casteren et al., 2012), as well as providing more opportunities for escaping predators who are unable to move within the TBN or cross gaps between tree crowns at canopy level. The effect of support compliance in the TBN is also magnified for a large animal, whose weight will cause supports to deflect substantially (Grand, 1972), often increasing the size of gaps that must be crossed. Yet even so, many primates of very large size have evolved to be successful within this niche. Indeed ancestral crown hominoids such as *Pierolapithecus catalaunicus* (11.9 million years ago [MA]; Casanovas-Vilar et al., 2008; Hammond et al., 2013) and *Hispanopithecus laietanus* (9.6 MA; Almécija et al., 2007; Alba et al., 2012) were at least as large, and probably larger, than adult female orangutans and were predominantly, if not exclusively, arboreal. It may therefore be a mistake to view large mass exclusively as a problem that must be resolved by positional behaviour, as many studies have assumed. Instead, large size itself may be among the adaptive solutions that evolved in different species, allowing them to exploit the TBN.

SOLUTIONS IN POSITIONAL BEHAVIOUR

For the smallest species, arboreal locomotion may be broadly similar to terrestrial locomotion, as most supports will be stable under their mass, and even small branches will be wide enough, relative to the base of support of the animal, to minimize the risk of falling (Cartmill, 1974). In contrast, the larger-bodied monkeys and apes have evolved several solutions to the challenges of support compliance and of moving between terrestrial and arboreal habitats, examples of which are outlined below.

Gait compliance

Large animals have relatively weaker limb bones than smaller animals, due to scaling laws. Animal mass increases at a cubic rate, whereas mammalian limb bones typically scale close to isometry; this means that if body weight doubles, bone cross-sectional area only increases by a factor of approximately 1.6, and the bone experiences relatively higher stress (Biewener, 2005). Large terrestrial mammals such as horses avoid excessively high bone stresses by adopting extended-leg postures; however, extended-leg postures significantly reduce manoeuvrability and the animal's ability to rapidly accelerate or decelerate (Biewener, 1989). This is an acceptable compromise for large terrestrial mammals, but an unsuitable solution for medium- and large-sized arboreal mammals. These animals must be able to cope with branches that bend under their weight, resulting in relatively large vertical excursions of the animal's centre of mass (Schmitt, 1999). Manoeuvrability is essential for dealing with support compliance and habitat unpredictability more generally.

The TBN creates conflicting demands: the network of multiple branches favours long, gracile limbs for reaching and grasping, yet the small diameter of these branches requires a primate to maintain a low centre of mass to ensure stability. Compliant quadrupedalism is an effective solution to this problem (Schmitt 1999; Figure 1.5). When walking quadrupedally along a branch, above-branch quadrupeds use long strides at a low frequency, allowing them to travel fast, and to continue walking at speeds at which terrestrial mammals may typically need to run. The low stride frequency also increases stability by resulting in longer contact time with the substrate and increasing the duration of multiple-limb support periods.

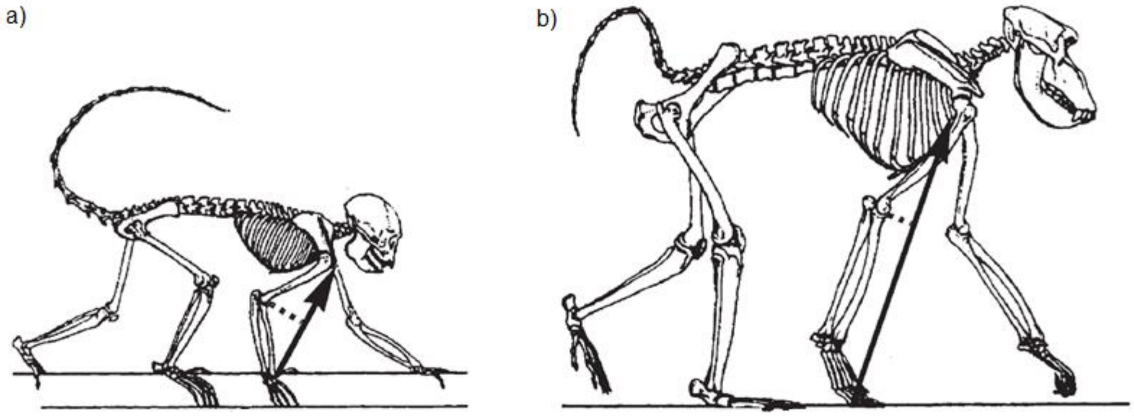

Figure 1.5. Comparison of limb positions in (a) arboreal and (b) terrestrial quadrupedalism. The arboreal primate is using flexed limbs and long, low-frequency strides, resulting in longer contact time with the support. Taken from Schmitt (1999; redrawn from a figure by Stephen Nash in Fleagle, 1988).

Quadrupedal, arboreal primates also flex their limbs to minimize the vertical excursion of their centre of mass (compare terrestrial and compliant quadrupedalism in Figure 1.5). This reduces the tendency to oscillate thin branches at a resonant frequency, which may interfere with the normal frequency of the animal's locomotor pattern. Alexander (1991a) argued that the long, low-frequency strides and flexed limbs of arboreal primates are specific adaptations to the TBN, because it is only on thin, compliant branches that energy losses from branch oscillation are substantial enough to require a compliant gait. Despite being energetically expensive, compliant walking thus allows arboreal primates to successfully negotiate environments that yield high-quality food.

Exploiting branch compliance

The relative compliance of peripheral canopy branches is hypothesized to increase the energetic cost of locomotion, which has been demonstrated by studies investigating the cost of moving along branches and leaping between tree crowns at canopy level in some monkeys and lemurs (Alexander, 1991b). Alexander (1991b) considered that the most important consequence of branch flexibility for the energetics of arboreal locomotion was the loss of potential energy, due to branches flexing under the animals weight. Some authors have reported apparent exploitation of support compliance during locomotion in monkeys, such as in springboard-like pumping of branches before leaping from one tree crown to the next (e.g. Mittermeier and Fleagle, 1976). However, there is no evidence yet that monkeys are able to use support compliance to lower the energetic cost of locomotion, and branch pumping in monkeys may be more associated with testing support strength, or aggressive or mating displays. Orangutans and some other apes, on the other hand, directly exploit support compliance during locomotion. They employ tree sway (Figure 1.6), during which the oscillated tree trunk facilitates bridging the gap to an adjacent tree. This behaviour decreases the energetic cost of gap crossing substantially, compared with jumping between trees or descending to cross at ground level (Thorpe et al., 2007a).

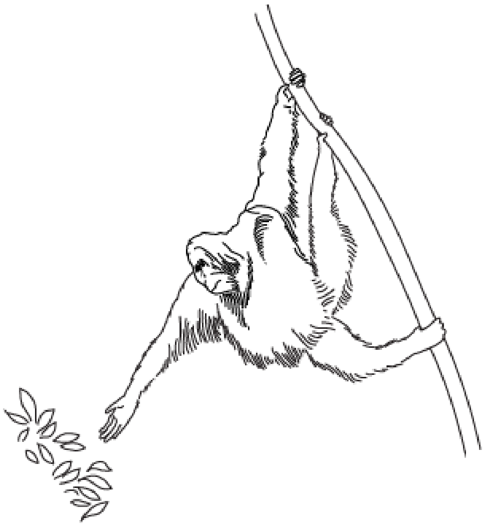

Figure 1.6. An example of tree sway in an orangutan. The orangutan oscillates the branch of an emergent tree in order to transfer to the crown of a lower tree.

Vertical Climbing

For any primate that exploits both terrestrial and arboreal habitats, the most energetically demanding positional behaviour is vertical climbing, as it directly opposes gravity. Hunt et al. (1996) recognized important biomechanical differences between different types of vertical climbing, particularly between those that involved "flexed-elbow" and "extended-elbow" positions (Figure 1.7).

Apes and other primates use flexed-elbow vertical climbing when ascending and descending supports that are thin enough to grip with their hands, such as slender trunks or vertically-hanging lianas (Hunt, 1992). In this behaviour flexed forelimbs are used to keep the body close to the support, while more extended hindlimbs provide propulsion. In contrast, during extended-elbow vertical climbing, propulsion is generated by the humerus retracting in a parasagittal plane against passive tension in the rest of the forelimb, with the hindlimbs often operating in highly flexed positions (Hunt et al., 1996). Extended-elbow vertical climbing is typically employed by apes and large monkeys when climbing up vertical trunks that are too wide to be gripped with the hands and when smaller supports are not available (Hunt, 1992; Kano, 1992; Doran, 1993). The mechanical differences between these two types of vertical climbing demonstrate how primates are able to adapt their positional behaviour to suit both the constraints imposed by body size and the type of supports available, in order to reach the same goal: vertical ascent into the canopy.

Figure 1.7. Comparison of (a) extended-elbow vertical climbing and (b) flexed-elbow vertical climbing.

It was previously thought that quadrupedal knuckle-walking, which is the dominant mode of terrestrial locomotion in chimpanzees and gorillas, was an inherited trait from the last common ancestor (LCA) of the African great apes (Washburn, 1967; Richmond and Strait, 2001). However, increasing fossil evidence suggests that the LCA of great apes had a more orthograde positional repertoire, and that the knuckle-walking of chimpanzees and gorillas in fact reflects a compromise between the energetic demands of vertical climbing and the need for effective terrestrial locomotion (Crompton et al., 2008). Thus the most frequently observed locomotor behaviour in these apes may actually be a “side-effect” of morphology adapted for the most demanding form of locomotion: vertical climbing. This hypothesis is supported by fundamental differences in wrist biomechanics during knuckle-walking between chimpanzees (which adopt extended postures) and gorillas (which adopt neutral postures; Inouye, 1994; Figure 1.8), suggesting that knuckle-walking may have arisen independently, and perhaps in response to different selective pressures (Inouye and Shea, 2004; Kivell and Schmitt, 2009). Indeed, chimpanzees and gorillas engage in similar amounts of knuckle-walking, but chimpanzees do so significantly more in an arboreal context than do gorillas (Inouye, 1994). It is therefore erroneous to assume that knuckle-walking represents the optimal adaptive solution for chimpanzees and gorillas to walking on flat substrates, or that their morphology represents an adaptation to this type of locomotion.

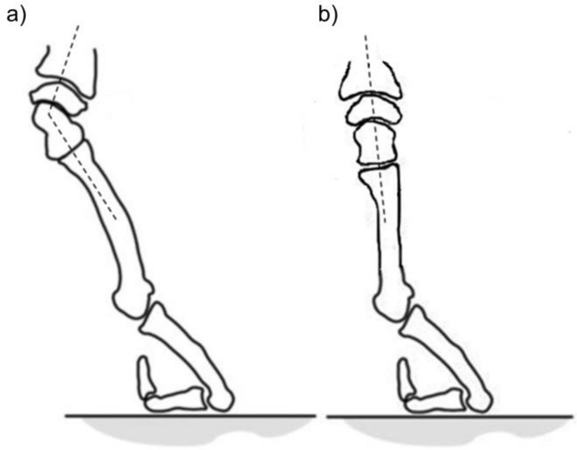

Figure 1.8. Comparison of (a) the extended wrist posture in chimpanzees and (b) the neutral, columnar posture in gorillas during knuckle-walking. Adapted from Richmond and Strait (2001) and Kivell and Schmitt (2009).

Orthograde and pronograde suspension

The suspensory postures and locomotion of primates, and apes in particular, represent a fundamental and ubiquitous positional adaptation to the challenges of the TBN. Suspension underneath a branch avoids the problem of the animal's centre of mass being far above the support during compressive locomotion; they gain stability by, in effect, having already fallen off the support (Cartmill, 1985). Nevertheless, it is a strategy exhibited by different primates in different ways. For the exclusively arboreal Sumatran orangutan (*Pongo abelii*), which can weigh up to 120kg, suspension forms a significant part of its slow and cautious locomotor repertoire. Orangutans move through the canopy by combining both compressive and suspensory behaviours into an irregular and fluidly changing gait, often spreading their weight among multiple supports (Thorpe and Crompton, 2005). While orthograde suspension is most common in orangutans, they are also the only ape to employ pronograde suspension; typically at the periphery of tree crowns when crossing to an adjacent tree (Thorpe and Crompton, 2005; Manduell et al., 2011). The other apes regularly employ orthograde suspension, but have never been observed using pronograde suspension in the wild, despite its biomechanical similarities to knuckle-walking. It is therefore likely that pronograde suspension evolved in the orangutan lineage after its genetic split from the other apes, as a refinement of its exclusively arboreal locomotor repertoire (Thorpe et al., 2009). It has been commonly assumed that the great apes are united by synapomorphic adaptations to orthograde suspension (Keith, 1923). However, one of the most important lines of evidence to emerge relatively recently from new fossil discoveries is that adaptations to orthograde suspension must have evolved not once, but convergently, across several millions of years, in multiple fossil ape species (Crompton et al., 2008).

In the past, many authors have considered orangutans and hylobatids to fall within the same general category of suspensory apes. However, the cautious behaviour of orangutans differs hugely from the fast, forelimb-powered brachiation that dominates the locomotor repertoire of gibbons (Thorpe and Crompton, 2006; Figure 1.9). Brachiation in its strictest sense is a specific form of hand-over-hand suspensory locomotion during which body weight is borne totally by the forelimbs and the trunk rotates almost 180° (Hunt et al., 1996). Among the apes, therefore, only gibbons and siamangs habitually employ true brachiation, but it is also a major form of locomotion in spider monkeys (*Ateles*; Mittermeier and Fleagle, 1976) and muriquis (*Brachyteles*; Mittermeier, 1978). Like gibbons, both have long day ranges and spend the majority of their travelling and feeding time high in the canopy (Milton, 1984), and as some of the largest New World monkeys, have similar body weights (Robinson and Janson, 1986). Their prehensile tails, however, result in fundamental differences from the brachiation style of gibbons, with a more horizontal posture, reduced trunk rotation, and no period of free flight (Turnquist et al., 1999).

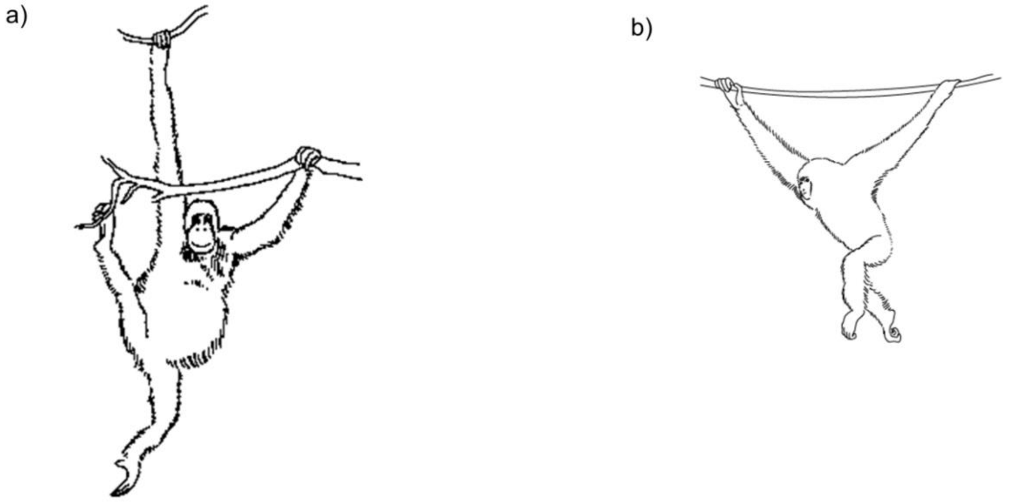

Figure 1.9. A comparison of (a) orthograde suspension in an orangutan while pausing during a bout of locomotion, and (b) brachiation in a gibbon.

Bipedalism

As the predominant form of locomotion in humans, bipedalism has been the focus for much research into primate positional behaviour. Bipedalism is used by all apes and some monkeys, albeit infrequently. Among the nonhuman apes, chimpanzees and gorillas are well known to occasionally employ a flexed, “bent-hip, bent-knee” gait on the ground, but it is orangutans and siamangs that have the largest bipedal component in their locomotor repertoire (Thorpe and Crompton, 2006). Siamangs use bipedalism while travelling along large boughs, using the distinct, running-type gait of hylobatids (Fleagle, 1976). In orangutans, however, bipedalism is associated with the most flexible weight-bearing supports. This suggests that bipedalism could be an important locomotor strategy for large-bodied orthograde apes to access the thinnest branches of the TBN (Thorpe et al., 2007b). Although bipedalism, particularly with extended-knee postures, puts a primate’s centre of mass high above the primary weight-bearing support, it frees the long forelimbs to provide stability by grasping other branches, whilst reaching for food or locomotor supports (Figure 1.10). Research has shown that, like humans and unlike other primates, orangutans respond to increasing support compliance by extending, rather than flexing, their hindlimbs (Thorpe et al., 2007b). In humans, straight-legged terrestrial bipedalism lowers the energetic cost of walking by creating pendulum-like transformations of energy (Alexander, 1991a), but it is unclear whether there is a mechanical as well as an ecological advantage for orangutans using arboreal bipedalism (Thorpe et al., 2007b).

The fact that all apes employ bipedalism, and that it appears to be an important strategy for canopy locomotion, suggests that it evolved long before the human-chimpanzee split, and is likely to have been present in the LCA of all apes (Crompton et al., 2008). There is also biomechanical evidence supporting a natural ability for bipedalism in some monkeys (e.g.

Berillon et al., 2010). All primates, even those that are adapted to pronograde locomotion, are capable of orthograde postures, such as standing, vertical clinging, and suspension, and many also employ some degree of orthograde locomotion, in the form of vertical climbing (Fleagle, 1988; Fleagle and Anapol, 1992; Hunt et al., 1996). As bipedalism is employed by different primates in different ways, it is difficult to identify any precise morphological adaptations to this broad category of bipedal locomotion. However, humans, as the only extant habitual bipeds amongst primates, possess clear adaptations to habitual straight-legged bipedal walking and running such as a low intermembral index, specific features of the pelvis and lumbar spine (Aiello and Dean, 1990), and the ability to store elastic energy in extensor tendons (Alexander, 1991a).

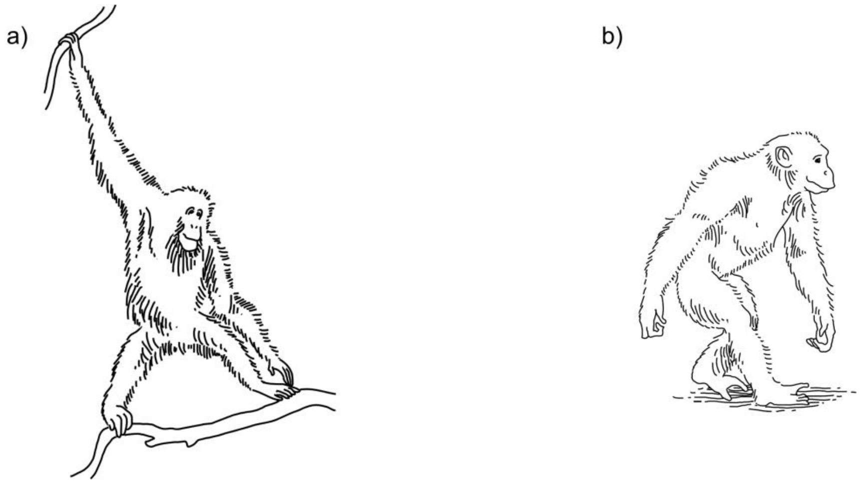

Figure 1.10: Comparison of (a) extended bipedal walking in an orangutan and (b) the flexed, "bent-hip, bent-knee" bipedal gait of a chimpanzee.

The evolution of hominin bipedality

Because positional behaviour in nonhuman primates is generally viewed, first and foremost, as a facilitator of an arboreal lifestyle, the evolution of habitual terrestrial bipedality in the hominin clade is seen as one of the most significant ecological shifts in primate evolution (Lovejoy, 1988; Harcourt-Smith and Aiello, 2004; Crompton et al., 2008). Yet the questions of how, when, and in response to which environmental pressures, bipedalism evolved remain not only unanswered, but subjects of contentious debate between anthropologists. Current evidence suggests that the origins of bipedal adaptations are rooted at the base of the hominoid clade, and are associated with arboreality, rather than terrestriality (Thorpe et al., 2007b; Crompton et al., 2008). However, while this means that adaptations to bipedality were inherited by all hominins, the development of habitual terrestrial bipedalism among different hominin species seems to have been gradual and mosaic in nature (Harcourt-Smith and Aiello, 2004; DeSilva et al., 2013).

Throughout the last century several authors have advocated an arboreal, rather than terrestrial origin for bipedalism, of which some of the earliest were Morton's (1926) "brachiation" model and Keith's (1923) "troglodytian" model. Prost (1980) and Fleagle et al. (1981) suggested that the hindlimb postures used during vertical climbing, often employed by chimpanzees and gorillas, may have preadapted the ape body for bipedalism. However, considerable differences in foot and hand skeletal morphology between chimpanzees and fossil hominin species, and functional and mechanical differences in the hindlimb during vertical climbing and bipedalism (Crompton et al., 2008), render this idea unlikely. Tuttle (1981) proposed a model for the LCA of apes that was morphologically akin to extant hylobatids, advocating a suspensory origin for orthogrady, and hence preadaptation to bipedalism. However, the running-like bipedal gait used by gibbons differs significantly from human bipedalism, casting doubt on the aspects of these models that base the evolution of bipedalism on gibbon locomotor behaviour (Vereecke et al., 2006; Crompton et al., 2008).

Despite these theories' recognition of the importance of the arboreal, as well as terrestrial, environment for the evolution of hominin locomotion, revelation of the close genetic relationship between humans and chimpanzees (e.g. Ruvolo, 1997) stimulated the idea that since chimpanzees move along the ground using knuckle-walking, pre-bipedal hominins must have passed through a terrestrial, knuckle-walking phase (Washburn, 1967; Tuttle, 1974; Wood & Richmond, 2000; Richmond et al., 2001). Although this idea dominated much of the debate surrounding bipedality throughout the latter half of the last century, this "knuckle-walking hypothesis" has been severely undermined by a lack of anatomical features relating to knuckle-walking in the hominin fossil record, the presence of purported "knuckle-walking features" in palmigrade monkeys (Kivell & Schmitt, 2009), and ontogenetic and biomechanical differences between the knuckle-walking of chimpanzees and gorillas (Inouye, 1994; Figure 1.8).

Palaeoenvironmental evidence suggesting that early hominins occupied woodland environments (e.g. WoldeGabriel et al., 2001) reinvigorated the idea that adaptations for bipedalism may have evolved in an arboreal context. Yet rather than returning to vertical climbing or brachiation as the preadaptive model for bipedalism, Crompton et al. (2003, 2008) and Thorpe et al. (2007b) suggested that orthograde clambering and hand-assisted bipedalism were the principal components of the ape LCA locomotor repertoire. This hypothesis took bipedalism from being a relatively recent development in the evolution of ape locomotion to being one of the most ancestral locomotor behaviours in the ape clade, and is supported by an increasing amount of fossil and biomechanical evidence. Early crown hominoids such as *Morotopithecus* (16-20 MA; MacLatchy et al., 2000; Maclatchy, 2004) and *Pierolapithecus* (13 MA; Moyà-Solà et al., 2004) show evidence for orthograde posture and weight-bearing over the hindlimbs, but are not associated with the suspensory or vertical climbing behaviours of living apes. The same, together with strong evidence for both bipedalism and arboreality, is true for protohominins such as *Ardipithecus* (Haile-selassie, 2001; Lovejoy et al., 2009a; b; d) and *Orrorin* (Senut et al., 2001).

It is also important to consider that all extant ape species are capable of bipedal locomotion to a certain extent, and recent research has focused on orangutans, who are one of the most bipedal nonhuman apes (Thorpe and Crompton, 2006; Thorpe et al., 2007b). Crucially, orangutans remain almost exclusively in the ancestral hominoid habitat – the forest canopy – and while bipedalism is by no means their dominant form of locomotion, observations by Thorpe et al. (2007b) suggest that it plays a crucial role in facilitating movement through the peripheral branches of the TBN. These peripheral branches are usually too thin for orangutans to walk along quadrupedally, and bipedalism frees their long forelimbs to provide stability on higher branches while foraging. Orangutans also use heel-strike plantigrady (Crompton et al., 2003), contradicting the claim of Gebo (1992) that this feature was limited to the African apes and associated with knuckle-walking. Thorpe et al. (2007b) hypothesise that bipedalism evolved in an arboreal context as an adaptation to movement along compliant branches, and therefore before the proposed split between the hominin and panin lineages.

While adaptations to bipedalism may therefore have been inherited by all crown hominoids, it is becoming increasingly evident that the evolution of terrestrial bipedality among early hominins was of a mosaic nature, with different forms of bipedalism developing in different, and sometimes contemporary, populations (Harcourt-Smith and Aiello, 2004; DeSilva et al., 2013). Variation in foot morphology between protohominins *Sahelanthropus, Orrorin tugenensis* and *Ardipithecus ramidus*, as well as australopiths and early *Homo* species, results in differences between their respective reconstructed bipedal gaits (Day and Napier, 1964; Stern and Susman, 1983; Pickford et al., 2002; Lovejoy et al., 2009a; DeSilva et al., 2013; Parr et al., 2014). These differences have generally been associated with those species' responses to environmental and ecological variation (Napier, 1964; Harcourt-Smith and Aiello, 2004; Wood and Baker, 2011). However, given the potential for morphological plasticity and behavioural flexibility in primates, it is possible that these reconstructions of locomotor behaviour do not capture the extent of intraspecific locomotor variation, and may therefore over-emphasise interspecific differences in positional capacity.

BEHAVIOURAL AND MORPHOLOGICAL FLEXIBILITY

It is not just the specific positional behaviours evolved by primates that allow them to successfully exploit the arboreal environment; it is also the extraordinary diversity of their locomotor repertoires, and their ability to modify their locomotor behaviour according to their environment. A versatile positional repertoire is vital because primates must not only remain stable on a variety of supports for foraging or resting, but must also be able to move fast and efficiently along supports to escape from predators. All of these challenges are intensified by the risk of falling from the canopy. Figure 1.11 illustrates the diversity of locomotor behaviours within the primate Order.

The largest primate species have the most diverse locomotor repertoires, because they must be able to modify their behaviour to meet the challenges associated with moving a large body along a variety of different supports (Grand, 1972; Cartmill, 1974). This is most notable

Figure 1.11. Illustration of the major locomotor modes used by primates.

among the apes, although similarly diverse locomotor repertoires, and ape-like locomotor behaviours, have also been observed in large monkeys (Fleagle, 1988). Yet while we find evidence of striking similarities in locomotor behaviour among different taxonomic groups, there are also examples of significant differences in locomotor behaviour among closely related, even congeneric, species. These often relate to differences in body size or differences in the physical environments inhabited by those species (Doran, 1993; Walker and Ayres, 1996; Byron and Covert, 2004). This mosaic nature of locomotor behaviour may suggest a low level of phylogenetic constraint on positional behaviour in primates. Instead, primates employ a positional repertoire that reflects the demands of their body size, habitat, and other ecological influences, allowing them to retain the key characteristic of primate positional behaviour: flexibility.

For primates, flexible positional behaviour depends on flexible joints. The morphology that permits such behavioural flexibility includes joints with wide ranges of motion, allowing hands and feet to reach out, contact supports, and exert force in a range of orientations, in a complex 3D environment (Payne et al., 2006a; b). Although morphology is subject to genetic and developmental constraints, genes effectively set parameters within which morphology may vary, in response to environmental influences, and in particular, the loads experienced during positional behaviour (Turner and Pavalko, 1998; Pilbeam, 2004; Barak et al., 2011; Shaw and Ryan, 2012). Thus a primate’s musculoskeletal morphology represents both evolutionary (genetic) adaptation and phenotypic accommodation to the challenges of the particular ecological niche it inhabits. The extent to which phenotypic plasticity can affect morphological development was illustrated by Slijper (1942a; b), who described the case of a goat that developed a bipedal hopping gait after being born with a congenital defect of the forelimbs. Dissection of the goat revealed substantial morphological accommodation to this type of locomotion, including changes to both muscle-tendon units and the hindlimb, pelvic and thoracic skeleton. West-Eberhard (2005a) noted that these remarkable alterations took the form of reorganisations of existing structures, rather than the development of new structures, demonstrating the capacity of mammalian morphology for extensive phenotypic accommodation. This capacity is illustrated by the changes to both muscular (Bruton, 2002) and skeletal (Shaw and Stock, 2009) anatomy in response to sport training in modern humans. Many morphological traits that are considered normal for a species may be the result of these adaptive responses to the environment, perhaps including adaptations to bipedal running in the modern human hindlimb (West-Eberhard 2005a; b). Given the forces that it exerts on morphology, positional behaviour is likely to be a particularly strong stimulus for such mechanisms of adaptation.

The extreme versatility of primate locomotor repertoires means that we cannot view an individual locomotor behaviour as an optimal adaptive solution to an individual challenge posed by a particular habitat. Nor can we assume that a morphological feature represents solely an adaptation to one specific aspect of locomotor behaviour. Each morphological element is subject to multiple demands, and represents a compromise solution. This is illustrated nicely by the hypothesis that knuckle-walking in chimpanzees and gorillas may be merely a side-effect of a morphology largely adapted to vertical climbing, meaning that we cannot assume morphological features of the African apes are adaptations to knuckle-walking (Dainton and Macho, 1999; Kivell and Schmitt, 2009). Before we can connect the evolution of positional behaviour, morphology, and habitat in primates, we must be able to differentiate between features that represent derived characteristics of a particular primate group, features that have evolved convergently in separate groups, and features that reflect more ancestral states. This requires both detailed studies of morphology and focused, biomechanical studies of positional behaviour, and is vital for gaining an evolutionary perspective of ecomorphology.

THESIS AIMS

Theories surrounding the evolution of primate positional behaviour, particularly concerning the evolution of hominin bipedality, have usually been based on overly stereotyped views of both locomotor behaviour and morphology in extant species. Humans are presumed to use a much more erect form of bipedalism than nonhuman apes, with the morphology of African apes restricting them to “bent hip, bent knee” bipedalism (Lovejoy, 1988; Crompton et al., 2003; Hogervorst and Vereecke, 2014). Orangutans, however, are capable of hip extension comparable to that in humans (Crompton et al., 2003). In fossil hominoids, the degree of morphological similarity to modern humans is often used as an indicator of the species’ bipedal capabilities, yet this is also sometimes based upon stereotyped interpretations of modern human morphology and without consideration of the morphological variation among humans and nonhuman apes (e.g. Stern and Susman, 1983; Pickford et al., 2002; Lovejoy et al., 2009d). It is also notable that few studies have explored locomotor responses to different habitats in the same species; this is crucial given primates’ ability to move around different environments, and it is inappropriate to characterise a species’ locomotor behaviour based on their response to only one of the habitats they exploit.

This thesis investigates locomotor and morphological variation among extant apes to quantify the behavioural flexibility that they exhibit and the reliability of using certain morphological features to infer locomotor capabilities in fossil hominoids. Kinematic and environmental variation in the bipedal and knuckle-walking gaits of captive chimpanzees and gorillas are considered in Chapter Two. The modern human locomotor repertoire is explored in Chapters

Three and Four by assessing the locomotor responses of tree climbers to the arboreal environment, and their biomechanical requirements compared with terrestrial locomotion. Finally, variation in skeletal morphology among extant apes is studied in Chapters Five and Six to evaluate the reliability of predicting bipedal capabilities and joint range of motion using the skeleton alone. The results of these studies and their implications for reconstructing the evolution of hominoid locomotor behaviour, and bipedalism in particular, are discussed in Chapter Seven, together with recommendations for future research.

CHAPTER TWO

KINEMATIC VARIATION IN THE BIPEDAL AND KNUCKLE-WALKING GAITS OF CHIMPANZEES (*PAN TROGLODYTES*) AND WESTERN LOWLAND GORILLAS (*GORILLA GORILLA GORILLA*):

THE IMPORTANCE OF ENVIRONMENTAL INFLUENCES AND BEHAVIOURAL FLEXIBILITY

Author contributions: chapter written by Emily Saunders and reviewed by Susannah Thorpe and Alice Roberts. Video footage of captive chimpanzees collected by James Ashley (MSci student).

ABSTRACT

Kinematics of bipedalism and knuckle-walking in extant apes have provided important evidence in hypotheses surrounding the evolution of erect bipedality in hominins, and suggest that bipedal adaptations arose in early hominoids as a response to the arboreal environment. However, previous studies have focused on terrestrial locomotion rather than considering variation in gait across both terrestrial and arboreal contexts. This chapter investigates the intra- and interspecific kinematic variation within bipedalism and knuckle-walking in captive chimpanzees (*Pan troglodytes*) and western lowland gorillas (*Gorilla gorilla gorilla*) in order to quantify the effects of arboreal support properties on gait kinematics. Joint angle and spatiotemporal parameters were digitised from video sequences of captive individuals walking in their zoo enclosures. Bipedal kinematics differed between arboreal and terrestrial substrates in both species, and were sensitive to changes in support orientation and diameter in gorillas. Variation in forelimb kinematics during knuckle-walking contrast with previously suggested differences between chimpanzees and gorillas that have been used to advocate independent evolution of knuckle-walking in the *Pan* and *Gorilla* lineages. Results imply that knuckle-walking kinematics are more related to environmental variation than to fundamental interspecific differences. This study highlights the importance of considering the influences of environmental context and behavioural flexibility on hominoid locomotor behaviour.

INTRODUCTION

Habitual upright bipedal locomotion is widely considered to be the single most important defining characteristic of the hominin clade, and is thus a crucial requirement when assigning hominin status to a fossil species (Crompton et al., 2008). Consequently, many evolutionary investigations into fossil hominoids focus on indications of locomotor behaviour, and evidence for bipedalism among the apes (Pickford et al., 2002; Harcourt-Smith and Aiello, 2004; Maclatchy, 2004; Crompton et al., 2008). The question of how, and when, adaptations to bipedal locomotion arose is complex because bipedal capability is displayed by all living apes and some monkeys. Thus while hominins are the only habitual bipeds, it is unlikely that adaptations to bipedal locomotion first arose in the hominin clade (Crompton et al., 2008, 2010).

Reconstructing behaviour from the fossil record

Because locomotion facilitates the interactions between an animal and its environment, the evolution of a locomotor behaviour in a particular clade can only be understood in its environmental and ecological context (see Chapter One). Thus while the locomotor abilities of a fossil species can be partly reconstructed using skeletal morphology, reliable reconstructions must also consider the species' morphology alongside ecological evidence for characteristics such as diet and the ability to use tools, and the terrain and climate of the palaeo-environment associated with the fossil remains.

Skeletal material in the fossil record is the only direct evidence of an extinct animal's morphology. This can be compared with the anatomy of both extant and fossil species to aid phylogenetic placement and reconstruct its probable locomotor capacity. Further information on ecology and behaviour can also be obtained from skeletal morphology; diet can be reconstructed from dental microwear and chemical analysis (Teaford, 1991; Koch et al., 1994), and finer manipulatory capabilities can be estimated from hand morphology (Marzke and Shackley, 1986; Kivell et al., 2011). All of these morphological aspects can only be fully understood in the context of the animal's environment, and palaeo-ecological evidence provides a method with which to test ecomorphological hypotheses. The animal's environment can be reconstructed using stable isotope analysis and indications in the fossil record of the floral profile (Anderson and Arthur, 1983; Bamford, 1999; Pickering et al., 2004), and evidence of other animal species can be used to predict potential predator-prey and competitor interactions (Blumenschine et al., 1994). Any evidence of tools or other material manipulations can also be used to reconstruct cultural aspects (Panger et al., 2002; Marquet and Lorblanchet, 2003; Shea, 2007). Together, these data provide not only an idea of the broad biome that the animal inhabited, but an idea of the resource distribution in the animal's immediate environment and thus the terrain, and perhaps canopy structure, that the animal must have negotiated in order to exploit such resources. Reliable reconstructions of the animal's morphology and environment are thus vital to understanding the evolution of locomotor behaviours. When considering the evolution of bipedalism, skeletal indications of whether a fossil species used bipedal locomotion, or indeed if it could have been accommodated within its morphology, can be tested alongside data that indicates whether bipedalism would have facilitated successful negotiation of its environment and exploitation of resources, and could therefore have been under selection (Lovejoy, 1988).

The importance of living animals in evolutionary reconstructions

These studies aiming to interpret the fossil record rely upon comparative information about the expression of locomotor behaviours and functional morphology across extant ape and other primate clades (Crompton et al., 2008, 2010). Reconstructions of locomotor behaviour from skeletal morphology are only reliable if the relationship between skeletal anatomy and behaviour is understood in extant species; this includes not only the manner that locomotion is reflected in the skeleton, but also the range of behavioural performance capacity that can be accommodated by certain morphological constraints. Relationships between locomotor behaviour and the environment can also be studied in great detail in living primates, such as locomotor responses to different types of terrain or branches of varying functional properties (Cartmill, 1974; Stevens, 2008). These are vital to ecological interpretations of locomotor behaviour in fossil species because they provide data against which to test hypotheses about the locomotor requirements of a species' environment, and thus the manner in which a primate would negotiate a particular habitat. Therefore it is only with detailed information on the morphology, behaviour and ecology of extant primates that we can reliably interpret the primate fossil record, and understand the evolution of locomotor behaviours.

Kinematics describes the movements and rotations of body segments during locomotion, and provides detailed data with which to quantify and compare locomotor behaviours (Sutherland, 2002). Kinematic parameters include speed, footfall patterns and joint angular rotations, and provide more detailed characterisations of locomotor behaviours than can be obtained from observations alone. These data have been used in studies across a variety of taxa to shed light on the relationships between locomotor mechanics and morphology or habitat (Schmitt, 2003; Kivell and Schmitt, 2009; Higham et al., 2015). In studies of fossil species, an understanding of these relationships in extant animals allows more robust interpretations of morphology and locomotor behaviour, and provides insight into possible locomotor mechanics, as well as broad locomotor capacity, in fossil species (Crompton et al., 2003; Schmitt, 2003). Kinematic analysis also allows quantification of the locomotor variation that exists within a species and which can be accommodated by a particular morphology. Some of this kinematic variation may be associated with the different environments that an animal uses, such as the functional properties of the ground compared with those of canopy branches, and can be used to predict the types of habitat that a fossil species would have been able to exploit.

In addition to providing quantitative data on locomotion with which to more reliably interpret the fossil record, kinematics can also be used to identify mechanical similarity between different types of locomotor behaviour, and both within and between individuals and species. Mechanical similarity can indicate an adaptive relationship between two locomotor behaviours, i.e. that one pre-adapted an animal's morphology for the other and thus facilitated its development (Fleagle et al., 1981; Gebo, 1996). It can also indicate the likelihood that a locomotor behaviour employed by two species was inherited from their common ancestor, as opposed to resulting from convergent evolution (Alexander, 1991a; Crompton et al., 2003). This method has been used to reconstruct the evolution of locomotor behaviours, and to identify possible behavioural drivers of speciation (Higham et al., 2015). Perhaps the most significant example in hominoid studies is the kinematic evidence that has been used to refute the "knuckle-walking hypothesis" for the evolution of bipedalism in hominoids (Dainton and Macho, 1999; Kivell and Schmitt, 2009; see Chapter One). Differences between the wrist postures used by chimpanzees and gorillas during knuckle-walking, alongside ontogenetic differences in its expression (Inouye, 1994), have been used to suggest that knuckle-walking, despite being the dominant mode of terrestrial locomotion in nonhuman African apes, may have evolved independently in the *Pan* and *Gorilla* lineages (Kivell and Schmitt, 2009; Figure 2.1). This evidence is crucial, as it suggests that knuckle-walking was not present in the last common ancestor of African apes, and is not related to hominin bipedalism. The knuckle-walking hypothesis is now largely refuted, due in part to the concept that kinematic similarity can aid differentiation between shared locomotor modes that are phylogenetically linked, and those which are the result of convergent evolution (Crompton et al., 2008; Kivell and Schmitt, 2009).

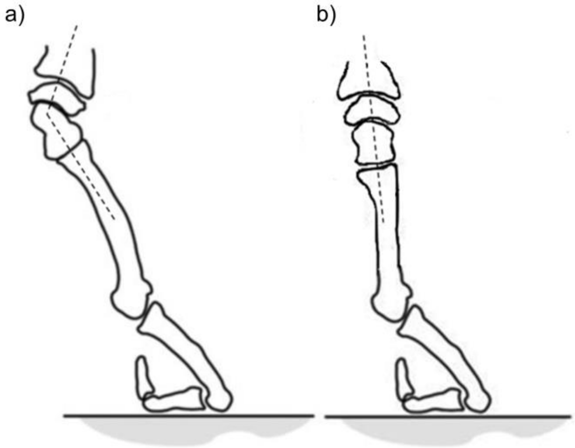

Figure 2.1. A comparison of a) the extended wrist posture in chimpanzees and b) the neutral, columnar posture in gorillas during knuckle-walking. Adapted from Kivell & Schmitt (2009)

The evolution of bipedalism in hominoids

Despite the dominance of the knuckle-walking hypothesis for the evolution of bipedalism throughout much of the last century, several theories, some of which antedate the knuckle-walking model, advocated an arboreal, rather than terrestrial, origin for bipedalism in the hominoid clade (Keith, 1923; Morton, 1926; Prost, 1980; Fleagle et al., 1981; see Chapter One). More recently, Crompton et al. (2008, 2010) suggested that arboreal orthograde behaviours, including hand-assisted bipedalism, were the principal components of the locomotor repertoire of the last common ancestor of crown hominoids. An arboreal origin for bipedal adaptations amongst hominoids is also supported by palaeo-environmental evidence suggesting that many hominin species occupied woodland environments (e.g. Anton, 2003;

Wood and Baker, 2011; Clarke, 2013), as well as evidence from the locomotor behaviour of living apes. The importance of bipedalism as a foraging strategy for chimpanzees (Hunt, 1994; Stanford, 2006), and the use of bipedalism by Sumatran orangutans (*Pongo abelii*) on the thinnest and most compliant branches of the terminal branch niche suggests that bipedal adaptations are ancestral to crown hominoids and evolved before the hominin-panin split (Thorpe et al., 2007b; Crompton et al., 2010; see Chapter One).

In addition to observations on bipedal frequencies, mechanical data suggest similarities between the bipedal gaits of Sumatran orangutans and modern humans, strengthening the support for a phylogenetic link between the two. Orangutans have been reported to exhibit extremes of extension at the hip joint that overlap with the hip extension required for the habitual bipedalism of modern humans, and which differ considerably from those used during the "bent-hip, bent-knee" (BHBK) form of bipedalism typically associated with the African apes (Crompton et al., 2003). Furthermore, orangutans are the only nonhuman ape to have been recorded producing a double-humped vertical ground reaction force curve (plot of vertical force production vs time throughout the stance phase of a stride) during bipedal locomotion that is characteristic of human gait (Crompton et al., 2003, 2010). It must be noted that while strong evidence exists to suggest that general adaptations to bipedal locomotion evolved in early crown hominoids in an arboreal context, and have been retained by all living hominoids, this does not preclude the possibility that the development of habitual, proficient bipedality in the hominin clade involved convergent evolution. While broad adaptations to bipedal locomotion may have been ubiquitous amongst hominins, it is becoming increasingly evident that different forms of terrestrial bipedality evolved in different hominin species as they evolved to meet the specific challenges of their differing environments (Harcourt-Smith and Aiello, 2004; DeSilva et al., 2013).

The importance of considering arboreal locomotion

Despite substantial support for an arboreal origin of bipedalism within the hominoid clade, much of the evidence is based upon terrestrial bipedalism, and the bipedal gaits of extant apes during arboreal locomotion remain little understood. Most research has focused on the terrestrial, BHBK bipedal gait of African apes (Jenkins, 1972; Stern and Susman, 1983; D'Août et al., 2002; Sockol et al., 2007), yet it remains unclear whether BHBK walking typifies arboreal, as well as terrestrial, bipedalism. The arboreal environment differs from the terrestrial environment in both functionality and complexity (see Chapter One), so it cannot be assumed that the mechanical requirements of bipedalism in one context are the same as those required for bipedalism in another. Thus evolutionary hypotheses based on comparisons of extant ape bipedalism have not fully considered the amount of mechanical variation within the bipedal gait of African apes. Furthermore, because increasing evidence suggests that adaptations to bipedality arose in an arboreal context, the use of only terrestrial locomotion to understand such an evolutionary process may be inappropriate.

While the arboreal locomotor repertoire of chimpanzees has been described in several studies (Hunt, 1992; Doran, 1996), the arboreal locomotor strategies of wild gorillas have rarely been investigated (but see Remis, 1995). Gorillas are considered to be the most terrestrial of the apes, yet it has been suggested that the arboreal locomotion of western lowland gorillas (*Gorilla gorilla gorilla*) may be more similar to the orangutan than to the more closely-related chimpanzee (Thorpe and Crompton, 2006). It has also been suggested that when static postures are taken into account alongside locomotor behaviour, gorillas may use bipedalism more than the other nonhuman apes (i.e. during display), and may therefore be better adapted to bipedalism than chimpanzees (although this is not based upon behavioural data; D'Août et al., 2004). Thus an investigation into the terrestrial and arboreal bipedal gaits of nonhuman apes is necessary to establish whether a mechanical link exists between the two.

It is therefore also unknown whether arboreal bipedalism in nonhuman apes resembles the kinematics of modern human gait. The efficiency of bipedal locomotion in modern humans is facilitated by an inverse pendular mechanism that relies on stiff, extended hindlimbs throughout the stance phase of gait (Alexander, 1991a). This results in the body's centre of mass being highest during midstance, i.e. when the hindlimb is extended directly below it, creating a peak in potential energy and a dip in kinetic energy. Throughout a sequence of walking, this results in out-of-phase oscillations of potential and kinetic energy, allowing significant energy conversion from one stride to the next and thus enhancing energetic efficiency. While it has been demonstrated that the mechanics of BHBK walking do not allow pendular transformations of energy (Wang et al., 2003), it is unclear whether the more erect forms of bipedalism used by nonhuman apes do so. Crompton and colleagues (Crompton et al., 2003; Wang et al., 2003) argue that orangutans may be capable of such a mechanism, given the similarities between their bipedal locomotion and that of modern humans. One of the hypotheses concerning an arboreal origin of bipedal locomotion is that a bipedal gait with extended hindlimbs may be a locomotor response to the thin, compliant branches of the terminal branch niche (Thorpe et al., 2007b), yet it is unclear how bipedal kinematics are affected by support diameter, orientation or compliance. It is therefore necessary to characterise the variation in bipedal kinematics that exists within nonhuman ape species, and that is associated with environmental variables.

Differences in wrist kinematics between the knuckle-walking gaits of chimpanzees and gorillas have been attributed to the increased arboreality of chimpanzees and thus greater requirement for a knuckle-walking gait that facilitates movement across a wider range of supports (Kivell and Schmitt, 2009). However, as with bipedalism, it is unknown whether knuckle-walking kinematics change in response to arboreal supports in either species. Furthermore, because the suggestion that knuckle-walking evolved independently in the *Pan* and *Gorilla* lineages is partly based upon fundamental behavioural differences between chimpanzees and gorillas, it is necessary to assess whether these differences remain when both terrestrial and arboreal knuckle-walking is investigated in both species.

Study aims

The aim of this study is to present kinematic analysis of bipedalism and knuckle-walking in common chimpanzees (*Pan troglodytes*) and western lowland gorillas (*Gorilla gorilla gorilla*) in order to investigate the intra- and interspecific variation within each gait. In particular, this includes the impact of arboreal supports on gait kinematics, and whether, once arboreal locomotion is considered, a) the bipedal locomotion of chimpanzees and gorillas is always characterised by a BHBK gait that is mechanically disparate from modern human bipedalism, and b) fundamental interspecific differences in knuckle-walking kinematics are robust. It is hoped that the results will also shed light on the evolution of habitual terrestrial bipedalism, and the viability of the hypothesis that this mode of locomotion evolved from an arboreal locomotor strategy in early crown hominoids.

The following specific questions will be addressed:

- Do chimpanzees and gorillas always exhibit bent-hip, bent-knee postures during bipedal locomotion?
- Do chimpanzees or gorillas ever use a stiff-legged posture during bipedalism that would indicate an inverse pendular mechanism of energy recovery?

- Are there clear kinematic differences between the knuckle-walking of chimpanzees and gorillas when both terrestrial and arboreal locomotion are considered, particularly regarding postures of the forelimb during the knuckle support phase?
- Do the kinematics of knuckle-walking or bipedalism in chimpanzees or gorillas change in response to terrestrial vs arboreal locomotion, or to changes in support angle and diameter?

MATERIALS AND METHODS

Study subjects and experimental setup

Five adult gorillas (all male) and nine adult chimpanzees (two males, seven females) were studied in their captive environments at Paignton Zoo (gorillas) and Twycross Zoo (chimpanzees), UK (Table 2.1). All study subjects had access to both indoor and outdoor enclosures and were filmed from the public viewing area. In compliance with the zoos' ethical guidelines, there was no physical contact with the subjects, and they were untrained and unmarked. Standard video cameras (Panasonic HC-V520, 30 fps) were positioned perpendicular to frequently-used terrestrial and arboreal routes throughout the enclosures. Locomotor sequences were selected from footage of individuals walking at a steady speed in a direction perpendicular to the camera, and in which the subject's stride pattern appeared unconstrained by the enclosure environment (walking along a row of equally spaced supports, for example, would dictate an individual's step length). It is important for the camera to be oriented perpendicular to the study subject so that movements in the sagittal plane, such as joint flexion/extension angles and stride lengths can be accurately measured. Following the method of Watson et al. (2009), sequences in which the subject's locomotion was deemed to be within 10° of perpendicular were selected; Watson et al. (2009) found that within this error margin geometric measurements were not significantly affected. Filming in the same vertical plane as the study subject is also important for accurate angular measurements; all selected sequences were filmed at a camera angle within 10° of horizontal, meaning angular corrections to compensate for vertical camera displacement (Stevens et al., 2006) were not required.

Table 2.1. Gorilla and chimpanzee individuals used in this study.

Species	Individual	Sex	Born	Age (years)	Hindlimb length (m)	N (Bipedal sequences)	N (Knuckle-walking sequences)
G. g. gorilla	G1	M	Captivity	32	0.93	0	1
G. g. gorilla	G2	M	Captivity	12	0.87	6	8
G. g. gorilla	G3	M	Captivity	11	0.72	2	1
G. g. gorilla	G4	M	Captivity	10	0.78	2	1
G. g. gorilla	G5	M	Captivity	10	0.75	0	6
P. troglodytes	C1	M	Captivity	23	0.57	2	2
P. troglodytes	C2	M	Captivity	28	0.45	0	3
P. troglodytes	C3	F	Captivity	8	0.41	1	2
P. troglodytes	C4	F	Captivity	19	0.50	7	1
P. troglodytes	C5	F	Captivity	36	0.50	0	4
P. troglodytes	C6	F	Wild	37	0.57	0	1
P. troglodytes	C7	F	Captivity	26	0.49	0	1
P. troglodytes	C8	F	Captivity	24	0.46	1	0
P. troglodytes	C9	F	Wild	49	0.52	0	1

For the gorillas, 10 bipedal sequences and 17 quadrupedal sequences were selected; for the chimpanzees, 11 bipedal and 15 quadrupedal sequences were selected. Sequences were calibrated using measurements between known points on the weight-bearing supports, and known body measurements for the gorillas. Individual measurements for the gorillas were taken by photographing body segments held flush against a wire mesh of known width.

Sequence digitisation

Sequences were calibrated and then manually digitised frame-by-frame in order to calculate kinematic parameters for each stride sequence. These comprised four spatiotemporal parameters: stride length, stride frequency, speed and duty factor (the proportion of a stride cycle for which the limb is in stance phase, i.e. in contact with the weight-bearing support); and six hindlimb joint angle parameters: maximum and minimum flexion/extension angles at the hip, knee and ankle. An additional six forelimb joint angle parameters were digitised for knuckle-walking sequences: maximum and minimum flexion/extension angles at the shoulder, elbow and wrist.

In all sequences, the limb(s) closest to the camera were digitised. The positions of the inferio-posterior edge of the heel, and for knuckle-walking sequences, positions of the distal end of the third proximal manual phalanx, were digitised using Didge (v.2.3, www.biology.creighton.edu/faculty/Cullum/Didge) in order to calculate spatiotemporal parameters. One complete stride was defined as starting at the initial point of contact of a foot with the weight-bearing support, and ending at the next initial point of contact of the same foot (Alexander, 1977). Stride lengths were calculated using the coordinate positions of the heel and manual phalanx at the points of touch-down, which, together with stride duration, was used to calculate stride frequency and absolute speed. Dimensionless speed was also calculated using the square root of the Froude number:

$$\text{Dimensionless speed} = \sqrt{\frac{v^2}{g \cdot l}}$$

where v is absolute speed, g is acceleration due to gravity, and l is a measurement of body length. Following the method of D'Aoūt et al. (2002) for bonobos, the distance from knee to ankle was used for all individuals as it was the most easily identified measurement in the video frames and hence the most reliable. Duty factor was calculated as the proportion of total stride duration between the point of touch-down of the heel/manual phalanx, and the point when the foot/hand left the weight-bearing support.

Flexion/extension angles at the hip, knee and ankle, as well as the shoulder, elbow and wrist during knuckle-walking sequences (Figure 2.2), were calculated for each frame through digitisation of segment long axes (Isler, 2005) using Kinovea (v0.8.15, www.kinovea.org). For each stride sequence, these joint angles were plotted sequentially against stride duration to show how hindlimb joint angles changed throughout the complete stride. These "joint angle profiles" (Figure 2.3) allowed visual comparison of sequences, and were important for comparing the hindlimb postures of chimpanzees and gorillas during bipedalism with the stiff-legged postures that are typical of human bipedalism. Joint angle profiles were constructed by converting each frame to a percentage of the total stride, thus scaling all sequences to a stride duration of 100. In addition to spatiotemporal parameters, the maximum and minimum angle at each joint from each sequence was used for statistical analysis to allow investigation of the range of kinematic variation that exists in the bipedal and knuckle-walking gaits of chimpanzees and gorillas.

In order to test environmental effects on gait kinematics, the following environmental variables were also recorded for each sequence: whether the individual was arboreal (used for all off-ground supports) or terrestrial; the orientation angle of the weight-bearing support (categorised as 0° [horizontal]; <45°; 45° ≤ 90°; 90°; U-shaped [applicable to compliant supports]); and the diameter of the weight-bearing support (<10cm; 10 ≤ 19cm; 20 ≤ 29cm; ≥30cm). All supports in the apes' enclosures were either rigid or super-compliant suspended ropes or straps, rather than branch-like supports that oscillate at a particular frequency. Thus kinematic responses to the variation in support compliance that apes would encounter in their natural habitat could not be properly tested.

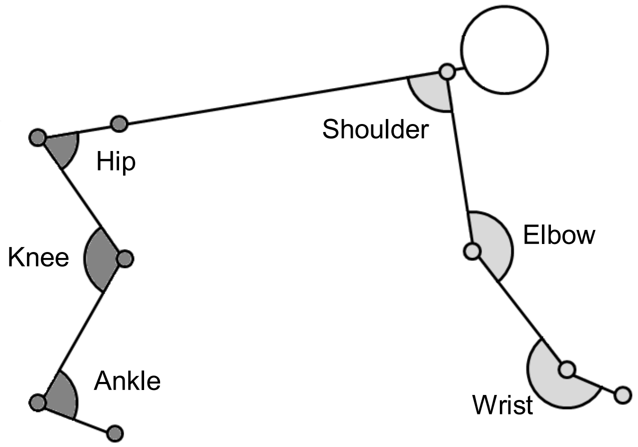

Figure 2.2. Joint angles digitised; those used for both knuckle-walking and bipedalism are shaded dark grey, those digitised for knuckle-walking only are shaded light grey.

Statistical analysis

The effects of arboreality, support angle and diameter on gait kinematics were tested using Multiple Regression models for each kinematic parameter (maximum and minimum joint angles, stride length, stride frequency, dimensionless speed and duty factor). Tests were carried out separately for bipedalism and knuckle-walking in each species. Full Multiple Regression models are reported in Appendix 1.1 – 1.4. Significant differences between the means of kinematic parameters in gorillas and chimpanzees were identified using Independent Sample T Tests. In order to reduce the Type I error rate, a Bonferroni correction was applied to all multivariate analyses. For the chimpanzee data, the effect of sex was tested using Independent Samples T Tests between kinematic parameters for males and females, but no significant differences were present. All statistical tests were completed using R (v2.15.0).

RESULTS

Bipedal kinematics

Intraspecific variation

Both chimpanzees and gorillas exhibited considerable intraspecific variation in hindlimb joint angles during bipedalism (Figure 2.3; Table 2.2). In particular, chimpanzees exhibited huge variation in maximum hip extension, spanning a range of 75°. Maximum hip extension in gorillas was the only joint angle significantly associated with arboreality compared with terrestriality during bipedal locomotion, with terrestrial bipedalism resulting in a higher mean maximum hip angle ($R^2 = 0.997$, F [2,6] = 176.70, $p = 0.053$; t [Support: ground] = 16.17, $p = 0.039$; see Appendix 1.1). Stride frequency was significantly higher during terrestrial bipedalism than during arboreal bipedalism in both chimpanzees ($R^2 = 0.481$, F [1,9] = 8.37, $p = 0.018$, t [Support: ground] = 2.89; see Appendix 1.2) and gorillas ($R^2 = 0.985$, F [2,6] = 107.80, $p = 0.000$; t [Support: ground] = 14.83; $p = 0.000$; Appendix 1.1). In gorillas, duty factor was also significantly higher during arboreal compared with terrestrial bipedalism ($R^2 = 0.912$, F [3,6] = 17.37, $p = 0.004$; t [Support: ground] = -5.89, $p = 0.002$; Appendix 1.1).

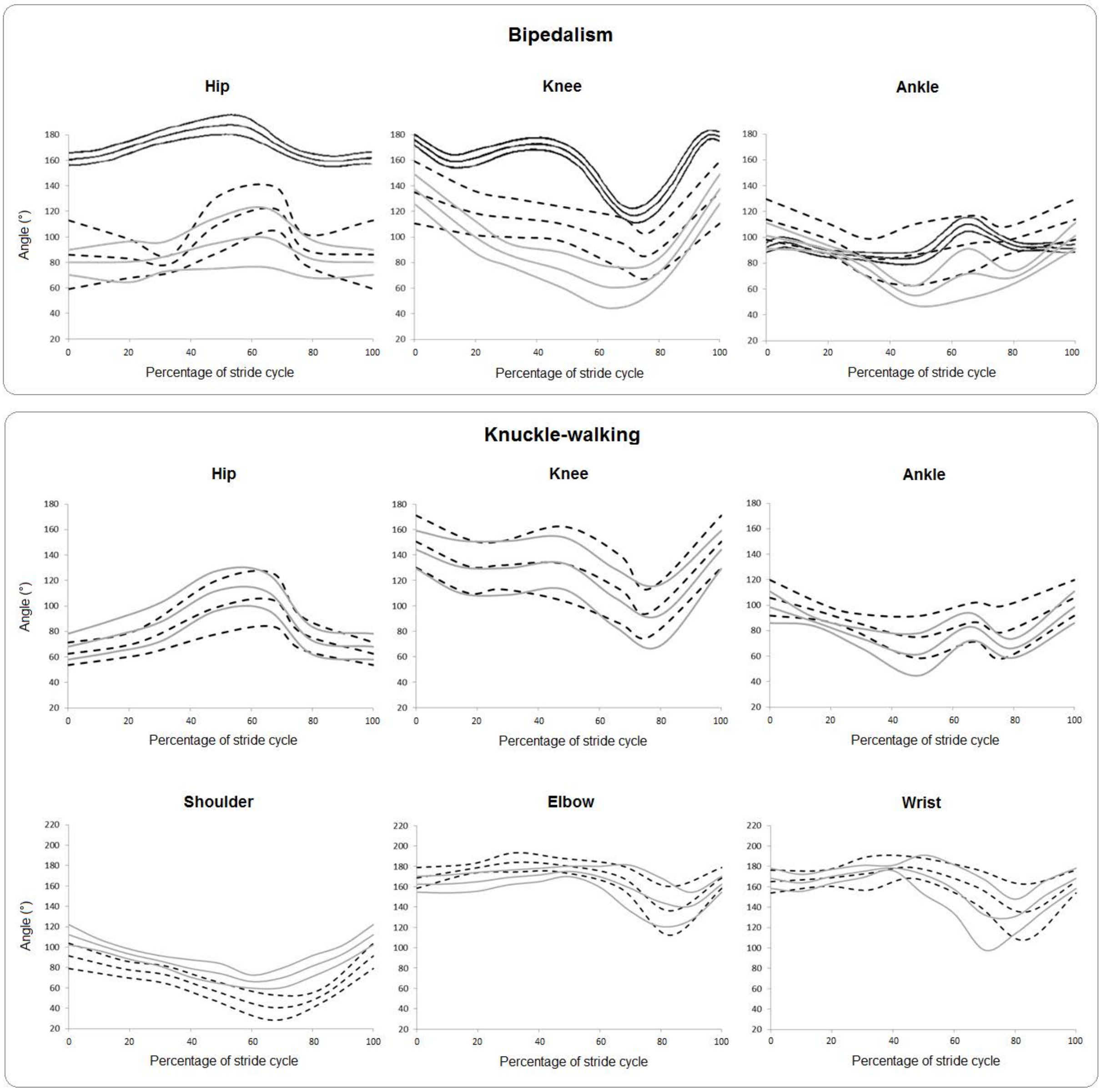

Figure 2.3. Joint angle profiles for bipedal and knuckle-walking in chimpanzees (grey lines) and gorillas (dashed lines). For each joint, the mean (middle line) ± 1 standard deviation (outer lines) are presented. For bipedal sequences, human data are included (solid black lines; taken from D'Août et al., 2002 and Winter, 1991). Note that the angle scale starts at 20°.

Table 2.2. Kinematic parameters calculated for all locomotor sequences. Mean ± standard deviation is presented. Number in parentheses after each entry indicates sample size (some sequences were not used for joint angle analysis if the joint was obscured from view for part of the sequence).

		Bipedalism		**Knuckle-walking**	
		P. troglodytes	*G. g. gorilla*	*P. troglodytes*	*G. g. gorilla*
Spatiotemporal parameters					
Dimensionless speed		1.63 ± 0.86 *(11)*	1.34 ± 1.16 *(10)*	1.44 ± 0.57 *(15)*	0.91 ± 0.37 *(17)*
Stride length (m)		3.57 ± 1.08 *(11)*	4.68 ± 1.50 *(10)*	4.00 ± 0.96 *(15)*	3.97 ± 1.07 *(17)*
Stride frequency (m s^{-1})		0.97 ± 0.41 *(11)*	0.72 ± 0.42 *(10)*	0.74 ± 0.16 *(15)*	0.62 ± 0.11 *(17)*
Duty factor		0.65 ± 0.10 *(11)*	0.70 ± 0.09 *(10)*	0.65 ± 0.06 *(15)*	0.67 ± 0.04 *(17)*
Joint angles					
Hip	Max	109 ± 24.1 *(11)*	119 ± 15.4 *(9)*	127 ± 8.8 *(9)*	111 ± 17.6 *(17)*
	Min	75 ± 15.0 *(11)*	72 ± 13.5 *(9)*	55 ± 8.0 *(9)*	59 ± 8.8 *(17)*
Knee	Max	141 ± 9.5 *(11)*	143 ± 14.8 *(10)*	151 ± 16.4 *(9)*	158 ± 8.8 *(17)*
	Min	51 ± 13.0 *(11)*	81 ± 16.8 *(10)*	79 ± 21.3 *(9)*	87 ± 17.2 *(17)*
Ankle	Max	113 ± 4.9 *(11)*	121 ± 15.9 *(10)*	105 ± 8.8 *(9)*	111 ± 17.1 *(17)*
	Min	53 ± 7.3 *(11)*	77 ± 15.2 *(10)*	51 ± 9.1 *(9)*	68 ± 10.8 *(17)*
Shoulder	Max	-	-	115 ± 7.8 *(9)*	89 ± 6.5 *(17)*
	Min	-	-	62 ± 5.3 *(9)*	39 ± 8.4 *(17)*
Elbow	Max	-	-	178 ± 4.1 *(9)*	185 ± 7.8 *(17)*
	Min	-	-	133 ± 18.3 *(9)*	150 ± 24.5 *(17)*
Wrist	Max	-	-	181 ± 1.4 *(9)*	185 ± 8.7 *(17)*
	Min	-	-	117 ± 23.5 *(9)*	144 ± 22.1 *(17)*

Support angle and diameter were associated with certain kinematic parameters, although only in gorillas (the chimpanzees were rarely recorded walking on angled supports). Interestingly, during all sequences involving angled supports the individuals were walking at an incline, rather than a decline. Walking up an angled support was therefore often used for ascent, but walking down these supports was rarely used for descent; individuals instead chose to drop or vertically descend to the ground. During bipedalism, U-shaped supports elicited higher maximum knee angles ($R^2 = 0.747$, F [3,6] = 5.90, p = 0.031; t [Angle: U-shaped] = 4.20, p = 0.006; Figure 2.4). Stride frequency increased with support diameter ($R^2 = 0.985$, F [2,6] = 107.80, p = 0.000; t [Diameter: 10 ≤ 19cm] = 3.58, p = 0.016), meaning that the gorillas used a faster-moving gait when on the ground and a slower gait when walking along the narrower arboreal supports. Interestingly, although not statistically significant, mean stride frequency in gorillas was highest along horizontal supports, but among all other supports stride frequency increased with support steepness.

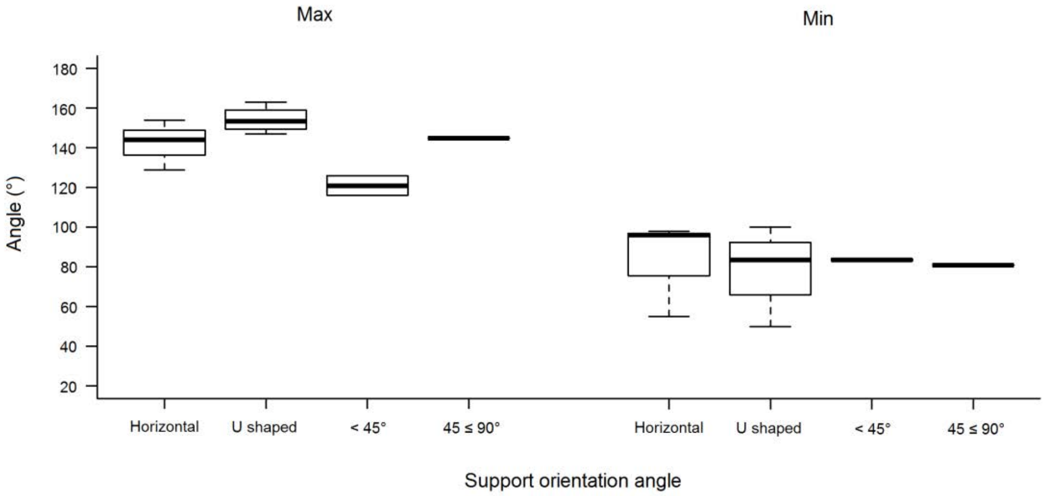

Figure 2.4. Maximum and minimum knee angles during bipedalism in gorillas by support orientation angle category. Boxplots represent the median, interquartile range and total range of the data.

Interspecific comparisons

During bipedalism chimpanzees and gorillas exhibited similar levels of maximum hip and knee extension (Figure 2.3; Table 2.2); however chimpanzees used significantly more flexion at the knee (t [15] = -4.21, p = 0.001) and dorsiflexion at the ankle (t [15] = -4.15, p = 0.001). At the hip, both chimpanzees and gorillas were considerably more flexed than humans throughout the entire stance phase, with their trunk continually bent forward by at least a further 20° (Figure 2.3). However it is the knee that shows the clearest indication that they do not employ straight, stiff hindlimbs during bipedalism, and therefore cannot exploit an inverse pendular mechanism as humans do. At heel strike, the human knee is extended close to 180°. A slight flexion occurs before the opposite foot leaves the ground, but then, critically, the knee extends towards 180° again until after midstance, allowing the torso to pass over a stiff hindlimb. Almost the reverse is true for chimpanzees and gorillas: after near-maximum extension at heel-strike (approx. 140°), the knee then becomes more flexed throughout the stance phase. However, it is important to note the different patterns of knee flexion in chimpanzees and gorillas. Despite both being fundamentally different from the pattern in humans, the knee in chimpanzees reaches a much more flexed position with a mean minimum knee angle of 51°, compared to the mean minimum angle of 81° in gorillas. Chimpanzees also used a higher stride frequency and longer stride length than gorillas during bipedalism, but not significantly so.

Knuckle-walking kinematics

Intraspecific variation

As in bipedalism, there was a large amount of intraspecific variation at some hindlimb joints, particularly in maximum hip extension and ankle plantarflexion in gorillas, and in maximum knee extension and flexion in chimpanzees. The only statistically significant joint angle difference between terrestrial and arboreal knuckle-walking was a higher maximum wrist angle on arboreal supports than on the ground in gorillas ($R^2 = 0.567$, F [2,14] = 5.90, t [Support: ground] = -3.35, p = 0.008; Appendix 1.3). This resulted in interspecific differences in wrist angles being reduced when only the terrestrial knuckle-walking sequences were compared. Stride length and stride frequency were higher during terrestrial compared with arboreal knuckle-walking in both species, but not significantly so.

During knuckle-walking in gorillas, supports <10cm in diameter elicited the highest maximum shoulder angles, yet supports 10 ≥ 19cm elicited the lowest ($R^2 = 0.329$, F [2,14] = 2.70, t [Diameter: 10 ≤ 19cm] = -2.31, p = 0.041; Figure 2.5). Supports <10cm also elicited the highest minimum shoulder angles ($R^2 = 0.397$, F [2,14] = 3.62, t [Diameter: 10 ≤ 19cm] = -2.38, p = 0.036; Appendix 1.3).

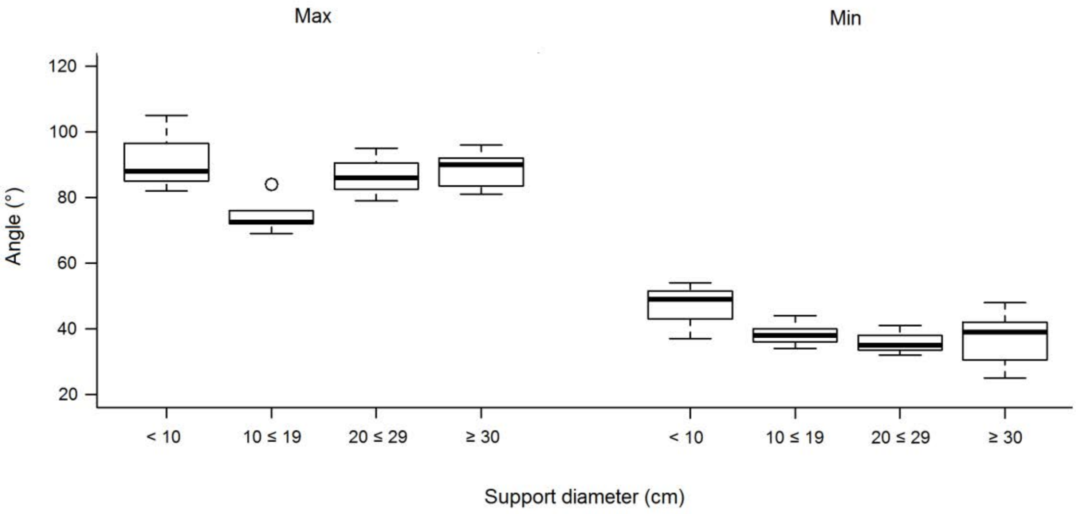

Figure 2.5. Maximum and minimum shoulder angles during knuckle-walking in gorillas by support diameter category. Boxplots represent the median, interquartile range and total range of the data. Circles show data points that fall further than 1.5 x interquartile range.

Interspecific comparisons

Kinematic differences between the knuckle-walking of chimpanzees and gorillas were generally characterised by a larger range of motion in the hindlimb joints in chimpanzees, and increased forelimb extension in gorillas (Figure 2.3; Table 2.2). In the hindlimb, chimpanzees had a significantly higher mean maximum hip angle (t [24] = 2.50, p = 0.018), although the larger variation in maximum hip angle in gorillas overlaps the entire range for chimpanzees. While the mean hip extension in chimpanzees was therefore higher, the same level of hip extension was observed in a small proportion of knuckle-walking sequences in gorillas. The mean minimum knee and ankle angles were also significantly lower in chimpanzees (knee: t [24] = -2.04, p = 0.049; ankle: t [24] = -3.55, p = 0.001), although at the ankle (as at the hip), the same level of dorsiflexion was observed in a small proportion of gorilla sequences. In the forelimb, chimpanzees exhibited much higher mean maximum and minimum shoulder angles than gorillas during knuckle-walking (max: t [24] = 8.78, p = 0.000; min: t [24] = 7.30, p = 0.000), which reflects a level of shoulder extension not exhibited by the gorillas in this study. Gorillas also had a higher mean maximum elbow angle (t [24] = -2.58, p = 0.017) and minimum wrist angle (t [24] = -2.63, p = 0.016). Generally, the shoulders were more flexed and the elbow and wrist more extended in gorillas compared with chimpanzees. Both stride length and stride frequency were slightly higher in chimpanzees than in gorillas, but not significantly so (Table 2.2), and there was no difference in duty factor between the species.

DISCUSSION

This study has found kinematic variation in both the bipedal and knuckle-walking locomotion of chimpanzees and western lowland gorillas that sheds new light on our current understanding of these behaviours in the African apes. These findings emphasise the importance of considering differences in the environmental context of locomotion that can elicit intraspecific variation in gait, and which may affect evolutionary hypotheses about locomotor behaviours.

Bipedalism: the bent-hip, bent-knee gait

The African apes have long been associated with a flexed, BHBK terrestrial bipedal gait, and data from this study show the hip and knee to be operating at flexion far below 180°. However, the intraspecific variation in hip and knee extension implies that bipedal locomotion is far from stereotyped, as the BHBK term might suggest. This variation is widened when data from previous kinematic studies are also included, such as that of (Crompton et al., 2003), in which a hip extension of 193° was observed in a bipedal gorilla, overlapping the range of hip extension during human bipedalism. Primates are characterised by extremely plastic locomotor repertoires that allow an individual to adapt its behaviour in response to environmental variation (see Chapter One). The variation in the bipedal gaits of chimpanzees and gorillas, and subsequent overlaps with human gait, demonstrate the importance of considering intraspecific locomotor variation rather than using stereotyped categories. In particular, this study shows the importance of including all relevant environmental contexts when analysing the locomotor behaviour of a species. Many previous kinematic studies of bipedalism in the African apes have reached conclusions based on terrestrial locomotion only, yet here it is apparent that the kinematics of bipedalism change in response to support angle and diameter. The gorillas in this study generally responded to increases in support angle with more hindlimb flexion, and some of this flexion may be due to anterior repositioning of the individual's centre of mass over the hindlimbs to aid balance. Yet some hindlimb flexion may also be a result of the positions of supports that can provide hand assistance to bipedal movement; the gorillas in this study often leant forwards in order to reach supports with their hands. Thus in addition to the impacts of specific properties of the main weight-bearing support on locomotion, the presence of multiple supports in the arboreal environment adds a much greater level of complexity to the mechanisms underpinning locomotion compared with the terrestrial environment. It is likely that the added compliance of supports in the wild would also affect locomotor kinematics, and possibly in a different manner; indeed, orangutans respond to branch compliance by extending, rather than flexing, their hindlimbs (Thorpe and Crompton, 2005, 2006).

Comparison of bipedal gait between African apes and humans

The patterns of flexion at the hip and knee (Figure 2.3) demonstrate the inability of chimpanzees and gorillas to fully extend the hip and the knee at the same time (Fleagle and Anapol, 1992), and hence use the inverse pendular mechanism of energy return that is characteristic of human walking. The hindlimb morphology of chimpanzees and gorillas is generally adapted to generating high power over a large range of motion; proximal muscles have large physiological cross-sectional areas and long moment arms, but the femur and tibia (i.e. the levers) are short (Thorpe et al., 1999; Payne et al., 2006a; b; Myatt et al., 2011). Human hindlimbs, however, are adapted to energetic efficiency through a smaller range of motion, with shorter muscle moment arms and longer bones (Payne et al., 2006a). The long ischial tuberosity in chimpanzees and gorillas creates a long moment arm for the hamstrings, resulting in powerful extensor capabilities in a flexed position; this moment arm is greatly reduced when the hip is extended and the femur is brought towards the origin of the hamstrings, making it difficult to power the hindlimb in an extended position (Fleagle and Anapol, 1992; Hogervorst and Vereecke, 2014).

However, consideration of the plasticity of morphological development counters the assumption that these anatomical differences represent inherited distinctions between humans and African apes that result in inevitable differences in locomotor behaviour. It also prompts the question of whether the morphology of a chimpanzee would allow simultaneous extension of the hip and knee, if from a young age it were exposed to an environment in which extended bipedal locomotion conferred a strong selective advantage. West-Eberhard (2005a) suggests that various morphological adaptations to bipedal running in humans, such as an enlarged gluteus maximus and elongation of the hindlimb bones, may have themselves arisen as adaptive responses to this sort of environment, given the remarkable morphological reorganisations observed in untypically-bipedal mammals such as Slijper's goat (see Chapter One). It is also important to consider that anatomical adaptations in these cases, despite resulting in visibly significant changes to the morphological and behavioural phenotype, are indeed reorganisations of existing structures, rather than generators of new ones. This may also be true for many musculoskeletal differences between humans and African apes that are linked with locomotor differences. Thus if chimpanzees or gorillas were exposed to the wild environment of Sumatran orangutans, who exhibit a more extended form of bipedalism (Thorpe et al., 2007b), they may develop a similar form of locomotion, and, like orangutans, take advantage of more significant energy return (Crompton et al., 2003; Wang et al., 2003). This study found that knee extension during bipedalism in gorillas was highest on U-shaped supports compared with supports of other orientations. These U-shaped supports were, by their nature, super-compliant, while the majority of other supports were rigid. Because none of the supports in the subjects' enclosures replicated the type of oscillatory compliance that characterises branches, kinematic responses to compliance were not tested. However, the knee extension observed in gorillas tentatively suggests that the association between hindlimb extension and support compliance reported for bipedal orangutans (Thorpe et al., 2007b) may also be found in African apes. It is notable that similarities to humans among extant apes are not exclusive to orangutans; gorillas share morphological similarities of the foot with humans, including a long tarsus, resulting in a longer power arm of the foot, and short lateral phalanges (Schultz, 1963). Modelling studies have also shown that the gorilla foot experiences more human-like static loads during bipedal standing (Wang and Crompton, 2004) and joint torque and work during bipedal walking (Wang et al., 2014). These similarities, together with suggestions that the arboreal locomotion of wild western lowland gorillas may be more similar to that of orangutans than to chimpanzees (Thorpe and Crompton, 2006) and that among nonhuman apes gorillas may be highly adapted to bipedal standing (D'Août et al., 2004), support the use of western lowland gorillas as instructive models for understanding the bipedalism of early hominins, and highlight the need for further investigation of their locomotion in different environmental contexts.

Interspecific comparison of knuckle-walking kinematics

This study has found several kinematic differences in knuckle-walking between chimpanzees and gorillas, including a higher average level of extension at the hip and shoulder, and more flexion at the knee, in chimpanzees, as well as more forelimb extension at the elbow and wrist in gorillas. However, the large amount of intraspecific variation in flexion and extension mean that some of these average differences are accompanied by large overlaps in the ranges for each species. Crucially, the wrist postures observed in this study do not fit with the previously reported comparisons between chimpanzees and gorillas that have been used to advocate independent evolution of knuckle-walking in the two genera (Kivell and Schmitt, 2009). The most extended wrist postures recorded during knuckle-walking were employed by gorillas rather than chimpanzees, and gorillas also displayed a much larger range of flexion/extension movement at the wrist (maximum wrist extension ranged from 168° to 196° in gorillas, and from 180° to 184° in chimpanzees). Both of these findings contradict the fundamental interspecific differences reported by Kivell and Schmitt (2009), who associated differences in carpal morphology between chimpanzees and gorillas with the reduced stability of the radiocarpal joint in gorillas. This, they argue, allows a greater range of wrist extension during weight-bearing in chimpanzees, but in gorillas necessitates more columnar loading. While this hypothesis is not supported by wrist kinematics in this study, the authors' assertion that wrist extension may be associated with arboreal locomotion is not precluded. Here, maximum wrist extension in gorillas tended to occur at the point of touch-down during arboreal knuckle-walking; and furthermore, on the most flexible supports (Figure 2.6). These flexible supports were not nearly so prevalent in the chimpanzees' enclosure, and when only terrestrial knuckle-walking sequences were analysed, interspecific differences in wrist kinematics were substantially reduced. It is therefore likely that interspecific kinematic differences observed in the wild are indeed due to the increased arboreality of chimpanzees compared with gorillas, but, crucially, do not reflect the inability of gorillas to exhibit the same locomotor responses as chimpanzees to arboreal supports.

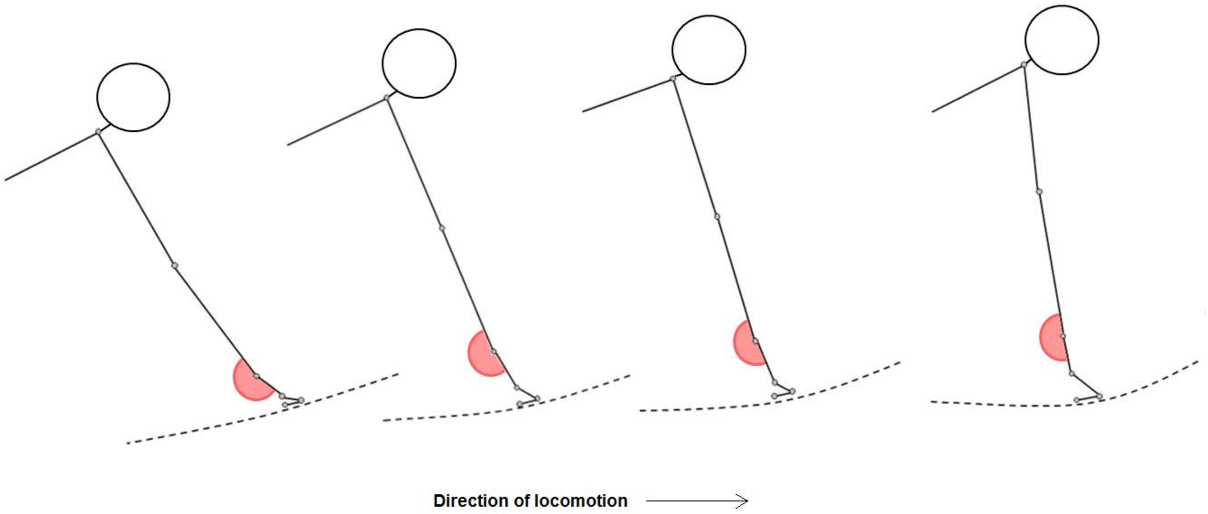

Figure 2.6. Stick figure reproductions of the forelimb during four video frames from an arboreal knuckle-walking sequence in a gorilla, showing the extended wrist posture at the point of touch-down. The orientation of the weight-bearing support is indicated by the dashed line.

The roles of the environment and behavioural plasticity in determining ape locomotion

The variation in bipedal and knuckle-walking kinematics among chimpanzees and gorillas shown here suggests that traditional views of African ape locomotion are far too stereotyped, due in part to a lack of studies that have quantified the variation in locomotor behaviour that exists across the range of habitats exploited by each species. Assessments of both bipedal and knuckle-walking kinematics in nonhuman apes have been based on terrestrial locomotion, despite the importance of the arboreal habitat to hominoid evolution and the evident morphological adaptations to the canopy environment that exist among extant apes. Thus caution must be exercised when basing evolutionary hypotheses on overly narrow proportions of species' full locomotor ranges. This study does not characterise the full locomotor capacity of chimpanzees and gorillas, yet reveals substantial intraspecific variation in locomotor mechanics that confounds the theory that knuckle-walking evolved independently in the *Pan* and *Gorilla* lineages. However, that knuckle-walking must have been inherited from the last common ancestor of *Pan* and *Gorilla* is not an appropriate interpretation of these findings. The revelation that gorillas may be more flexible in their locomotor behaviour than previously thought, shown in their ability to respond to arboreal supports in a manner kinematically similar to chimpanzees, may support the theory that knuckle-walking developed in both lineages as the most effective means of terrestrial locomotion for an animal fundamentally adapted to vertical climbing (Crompton et al., 2010). Chimpanzees and gorillas may not share common inheritance of knuckle-walking, but they may share an inherited capacity for behavioural flexibility that allowed knuckle-walking to develop. This prompts the wider question of how many shared primate locomotor behaviours are not themselves phylogenetically conserved, but are the result of behavioural responses in animals that share phylogenetically constrained morphology and/or an inherited capacity for morphological and behavioural plasticity.

Constraints of captive environments

Intraspecific and intra-individual variation in locomotor kinematics due to environmental differences may be an important cause of disparities between studies, and not only relating to whether a study is analysing locomotion in a terrestrial or an arboreal context. Zoo enclosures generally do not emulate closely the functionality of wild ape habitats in terms of support orientation, compliance, complexity and dynamic nature. Nor do they emulate other ecological factors such as interactions with predators or prey, and the availability and location of food, both of which affect an animal's motivation for locomotion. However, as demonstrated by this study, the constraints of the captive environment can allow isolation of the effects of certain functional properties, such as investigating support angle without compliance. Captive apes can therefore aid understanding of parts of their natural locomotor repertoire, but not its entirety. In a laboratory environment, however, individuals are constrained not only in the weight-bearing supports available to them, but often in the speed of their locomotion, as in studies of locomotion on a treadmill. Pontzer et al. (2014) recorded an average maximum hip angle during bipedalism in chimpanzees of 162°, which was much higher than the previous value of 125° recorded by Jenkins (1972). However, this hip extension was observed during bipedalism on a treadmill moving at an absolute speed of 1.79 ms^{-1}; faster than the absolute speeds recorded by the chimpanzees during bipedalism in this study, which ranged from 0.32 ms^{-1} to 1.72 ms^{-1}. Therefore while data collected on treadmills can provide valuable information about an animal's performance capabilities, it should not be viewed as representative of natural locomotion in the animal's wild environment.

CONCLUSIONS

This research highlights several key characteristics of knuckle-walking and bipedalism in chimpanzees and gorillas that should be considered when attempting to reconstruct the evolution of bipedal locomotion in hominoids. While the bipedal walking gaits of African apes have clear mechanical differences from human bipedalism, they show far more mechanical diversity than the single BHBK category of locomotion might suggest. This particularly comes to light when arboreal bipedalism is considered alongside terrestrial, which is essential not only for ensuring that an ape's full bipedal repertoire is represented, but also because the kinematic responses to different arboreal contexts (e.g. support angle and diameter) are vital for understanding the evolution of bipedalism given the likelihood that it evolved in an arboreal environment. The captive environments used in this study elicited considerable intraspecific variation in bipedal kinematics, demonstrating the flexibility of bipedalism in extant apes, but without clear overlaps with human bipedalism that have been found in some previous studies. However, the lack of functional similarity between the apes' enclosures and their natural habitat highlights the need for kinematic investigations of bipedalism in different environmental contexts in wild African apes, given both their short-term behavioural flexibility in response to environmental differences, and the longer-term influence of environmental factors on behaviour and morphology throughout ontogeny.

This study found differences in wrist posture during knuckle-walking between chimpanzees and gorillas, but which contrast with previously suggested kinematic distinctions that have been used to advocate convergent evolution of knuckle-walking in the two lineages. This study implies that kinematic responses to arboreal supports at the wrist may be universal among African apes, despite interspecific morphological differences. Yet rather than suggesting greater phylogenetic conservancy of knuckle-walking, it is possible that knuckle-walking developed due to shared inheritance of morphological and behavioural flexibility in the *Pan* and *Gorilla* lineages. As with bipedalism, kinematic comparisons of knuckle-walking in chimpanzees and gorillas in different arboreal contexts are now required.

The plasticity of morphological development in primates means that many interspecific differences in the morphological and behavioural phenotype may be caused by responses to different environmental influences throughout individual development. This confounds hypotheses aiming to separate commonly inherited behaviours from those that have evolved independently. While the lack of evidence for knuckle-walking and increasing evidence for orthogrady in the hominoid fossil record still suggest early origins of adaptations to bipedalism in an arboreal context, this study demonstrates how the variation in locomotor behaviour within *Pan* and *Gorilla*, and their associated environmental contexts, must be considered in more detail.

CHAPTER THREE

MODERN HUMAN ARBOREAL CAPACITY CASTS DOUBT ON EARLY HUMAN ARBOREAL-TERRESTRIAL TRANSITION

A manuscript submitted to *Science*

Author contributions: manuscript written by Emily Saunders and edited by Susannah Thorpe and Robin Crompton. Manuscript reviewed by Nardie Hanson, Alice Roberts, Jackie Chappell, Kevin Hunt, Kris D'Août, Russ Savage, Colleen Goh and Ian Redmond. Data collection led by E Saunders and N Hanson. Comparative locomotor datasets contributed by K Hunt, C Goh and I Redmond.

ABSTRACT

The evolution of terrestrial bipedalism in humans is widely thought to have significantly constrained our ancestors' ability to access forest canopy resources, driving a fundamental shift from arboreal to terrestrial life. Nevertheless, increasing palaeontological evidence suggests that hominins exploited woodland and forest habitats for millions of years after they evolved proficient bipedalism. We carried out field experiments on professional tree climbers to test fundamental hypotheses regarding whether bipedal hominins can access and exploit the flexible peripheral branches of tree crowns. Our results show that a bipedal hominin body plan supports considerable, and previously unrecognized, behavioural and mechanical flexibility that allows significant arboreal capabilities. Continued exploitation of key arboreal resources would thus have been possible for all bipedal hominins, despite their increasingly modern postcranial morphologies.

INTRODUCTION

The transition from arboreal to terrestrial life is considered to be one of the most important ecological events in human evolution. Though widely thought to have been rapid and absolute, it has become apparent that early protohominins (e.g. *Orrorin tugenensis* and *Ardipithecus ramidus*); archaic hominins (including *Australopithecus prometheus, Au. afarensis and Au. sediba*); fossils traditionally assigned to *Homo habilis* (e.g. OH-62; Clarke, 2013) and *Homo naledi* (Kivell et al., 2015), all combine adaptations to arboreal and terrestrial habitats (Senut et al., 2001; Clarke, 2002, 2013; Green et al., 2007; Lovejoy et al., 2009c; Wood and Baker, 2011; Churchill et al., 2013), while *Homo erectus*, with an essentially modern postcranial morphology, had re-occupied rainforest in Java by 1.7 million years ago (Anton, 2003). A radical rethink of this ecological transition and its role in driving the origins of our genus is thus required.

For early hominins, exploiting the forest canopy would have required the ability to ascend from the ground into tree crowns, to change height within the canopy and to travel horizontally within, and even between, trees through the peripheral branches of tree crowns. Analogy with modern rainforest hunter-gatherer populations, that climb to heights of up to 50m to access honey and other prized resources (Venkataraman et al., 2013a; Kraft et al., 2014), reveals how hominins may have ascended tall, challenging tree trunks. However, we cannot fully reconstruct ancient hominin ecology until we understand whether they could access and move around the highly flexible and challenging peripheral branches of trees, where fruits and other key arboreal resources are most abundant. Since the vertical climbing abilities of rainforest hunter-gatherers are facilitated by muscular plasticity rather than skeletal adaptations (Venkataraman et al., 2013b), this question cannot be addressed by palaeontological study alone.

Here we quantify the locomotor abilities and hindlimb mechanics that allow professional, European tree climbers to access and exploit woodland canopy, compared to those required for terrestrial bipedalism. These climbers have extensive experience of climbing in tropical and temperate forests throughout the world. Moreover, most contemporary rainforest populations fall into the "pygmy" phenotype, typified by a maximum height of 155cm (Perry and Dominy, 2009), relatively short lower limbs, and long upper limbs and trunk (Pontzer, 2012). While these body proportions are similar to those classically associated with australopith skeletons such as AL 288-1 ("Lucy"), the limb proportions and statures of other australopiths, such as *Au. prometheus* (StW 573), and later hominins fall within the range of modern European humans. Our study thus provides a new model of hominin arboreal capacity that can be applied to the morphologies of a wide spectrum of ancient hominins, to better understand our ancestors' ability to exploit key arboreal resources.

Palaeo-environments in East and South Africa involved a great diversity of localized habitats and environmental cyclicity in the late Miocene/early Pliocene: for example, *Ar. ramidus* is associated with woodland habitats (White et al., 2015) whereas Sterkfontein, at the time of StW 573, was characterised by patches of relict Miocene riverine forest tall enough to bear vines (Bamford, 1999), similar to contemporary tropical afromontane moist broadleaf forest (Appendix 2.1). We selected an English oak tree (*Quercus robur*) with a broad, low canopy as a generic model and suspended a vertical rope to replicate a vine on one side. We studied eight climbers performing an ecological task to ascend the tree to activate four buzzers, deployed as fake-food goals, in the peripheral branches (Figure 3.1), to test the core hypothesis that, by acquiring effective terrestrial bipedality, early hominins would have suffered "severe constraints on arboreal competence" (Latimer et al., 1987; Lovejoy, 1988; Latimer, 1991).

Figure 3.1. Oak tree (*Quercus robur*) used for the study. Locations of the four food buzzers are marked in red circles; size of the circle indicates position of the buzzer, with smaller circles towards the back and larger circles towards the front of the tree crown. The position of the vertical rope is marked in green and the yellow scale bar shows a 2m height from the ground at the base of the trunk. Buzzer heights (from left to right): 7.23m, 4.72m, 4.10m, 4.47m.

First, we investigated how the climbers accessed the tree crown since understanding of arboreal activity in hominins has been strongly predicated on the idea that an absence of adaptations to vertical climbing meant they could not climb into trees (Latimer, 1991). The tree climbers were thus asked to climb the tree three times to activate the buzzers, each time using a new access route, with their preferred route first and least-preferred route last. We then studied the climbers' locomotion within the canopy to quantify their locomotor flexibility. This included whether quadrupedal locomotion was employed and if so, in what circumstances. The contrasting demands of quadrupedal and bipedal locomotion have been central to all debate on the origins of hominin bipedalism, particularly following the recent claim that *Ar. ramidus* was proficient at both arboreal quadrupedalism and terrestrial bipedalism (Lovejoy et al., 2009c; White et al., 2015). We sought to resolve the debate (Lovejoy et al., 2009c; Crompton et al., 2010) as to whether a large-bodied hominin morphology could serve such apparently contrasting behaviours.

RESULTS AND DISCUSSION

We found the trunk was not the only possible route into the tree, nor was it the most preferred. All climbers easily accessed the tree via the peripheral branches (Figure 3.2), facilitated not by vertical climbing, but by a variety of irregular, scrambling movements including pulling and pushing-up with forelimbs and hindlimbs, jumping, suspension and abdominal flexion to raise the legs. Five of the eight climbers chose this as their preferred route, while two chose the trunk and one selected the rope.

Figure 3.2. A climber enters the tree via peripheral branches.

Once in the tree crown, the climbers' arboreal locomotor repertoire was hugely varied, with less behavioural diversity than orangutans, but similar diversity to the other African apes (Figure 3.3). Bipedalism accounted for an average of only 56% of arboreal locomotion (Appendix 2.2), with the rest of the climbers' repertoire including quadrupedal and tripedal locomotion, scrambling, vertical climbing and descent, suspensory locomotion, and leaps and drops between branches.

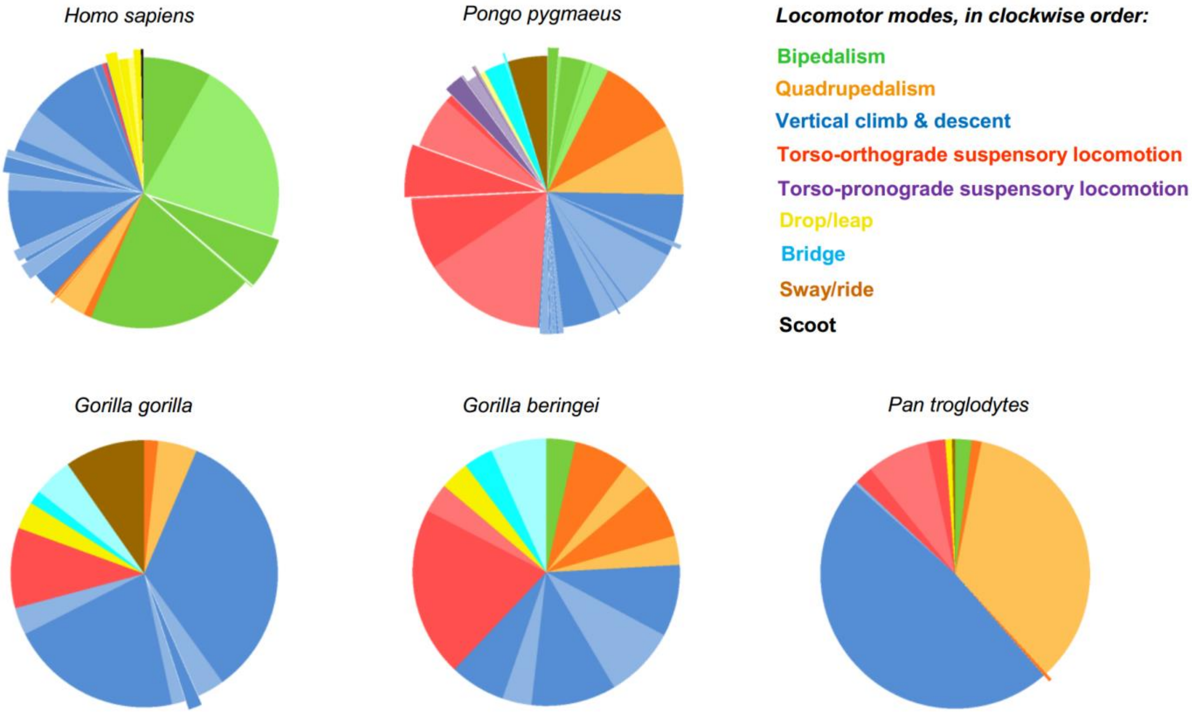

Figure 3.3. Arboreal locomotor diversity in living apes. Percentages of locomotor modes (different colours) and submodes (alternate dark/ light shades) in the arboreal repertoire of humans (this study), orangutans (*Pongo pygmaeus*; Thorpe & Crompton, 2006), western lowland gorillas (*Gorilla gorilla*), mountain gorillas (*Gorilla beringei*) and chimpanzees (*Pan troglodytes*). Submodes not shared with other species are pulled out from each chart. Chimpanzee data were collected with a slightly reduced classification of locomotion than the other datasets, but are broadly comparable. Definitions taken from Thorpe & Crompton (2006) and Hunt et al., (1996). Gorilla data provided by C Goh and I Redmond; chimpanzee data provided by K Hunt.

The climbers used different types of bipedalism, similar to those employed by other great apes (Hunt, 1994, 2016; Thorpe and Crompton, 2006; Crompton et al., 2010). Quadrupedalism made up on average 5% of locomotion; a similar figure to the facultative bipedalism of chimpanzees and thus indicating that humans are facultative arboreal quadrupeds. It was used in both the tree core and periphery, mostly on branches where higher handholds required for hand-assisted bipedalism were absent. Our results therefore suggest that, in addition to muscular plasticity (Venkataraman et al., 2013b), hominins have the capacity for substantial flexibility in their locomotor behaviour. The fact that all participants successfully activated all buzzers in the peripheral branches using different access routes and such a diversity of locomotor behaviours suggests that hominin ability to access and negotiate the forest canopy has been severely underestimated, and unequivocally counters the claim (Latimer, 1991) that arboreal competence is compromised by adaptations to terrestrial bipedality.

We then quantified hindlimb kinematics to compare the mechanical demands of bipedalism and quadrupedalism, and terrestrial and arboreal locomotion. We collected additional data on walking on uneven grassland as the mechanics of bipedalism have been mostly studied on flat ground in the built environment (Wang et al., 2003), but early hominins inhabited mosaic habitats, including rocky areas and irregular terrain (Pickering et al., 2004), and the ability to retain biomechanical efficiency across uneven terrain is a key characteristic of human gait (Matthis and Fajen, 2013). Branches, which vary considerably in compliance, must also place different mechanical constraints on bipedalism than the ground. We found that when the participants walked on grassland they exhibited far more extreme fluctuations of flexion and extension at their hips and knees, but substantially less ankle plantarflexion (sole of the foot bent away from the leg) when the foot left the ground than occurs during bipedalism on flat ground (taken from laboratory data; Winter, 1991; Figure 3.4). Even greater differences were apparent between their arboreal and terrestrial bipedalism, with arboreal movement producing significantly more flexed hip- and knee-joint angles, less ankle plantarflexion around the time of toe-off and more plantarflexion at touch-down, likely reflecting that the climbers often made initial contact on branches with the distal foot (usually the metatarso-phalangeal joints) rather than the heel (Figure 3.4; Appendix 2.3).

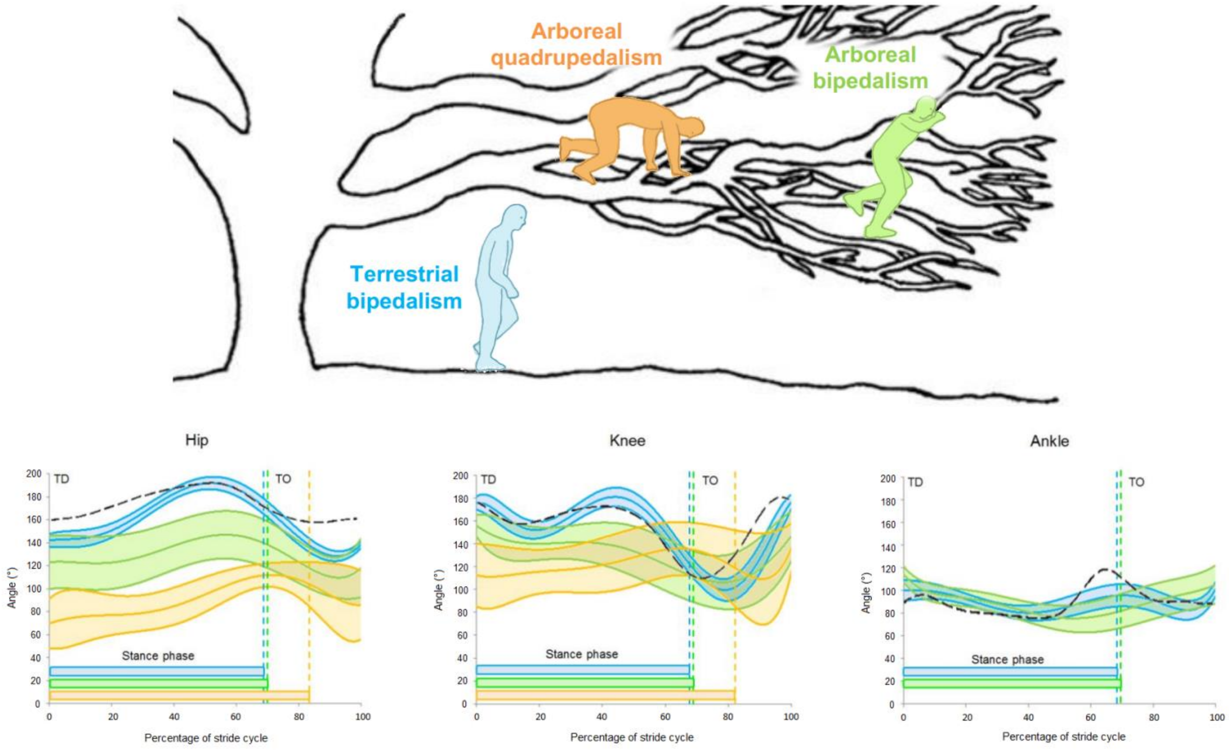

Figure 3.4. Joint angle profiles for the hip, knee and ankle during terrestrial bipedalism (blue; n=7), arboreal bipedalism (green; n=12) and arboreal quadrupedalism (orange; n=8). Lines indicate the mean ± standard deviation for each mode. Black dashed lines indicate mean profiles for terrestrial bipedalism from laboratory data (Winter, 1991). TD = touch-down (start of profile), TO = toe-off (vertical dashed lines).

These results reveal that bipedal kinematics are highly sensitive to environmental variation, and show how analyses of bipedalism on ecologically-valid substrates are essential for understanding the evolution of human morphology and gait. While it has recently become clear that multiple forms of bipedalism existed in ancestral hominins (Harcourt-Smith and Aiello, 2004; DeSilva et al., 2013), our study demonstrates the substantial mechanical variability that can exist within the bipedal gait of a single species.

Comparisons of hindlimb kinematics and muscle activity between bipedalism and quadrupedalism revealed further mechanical diversity. We found that quadrupedalism required much more flexion at the hip and knee (Appendix 2.4) and a particularly distinct pattern of flexion/extension at the hip (Figure 3.4) compared with both terrestrial and arboreal bipedalism. Quadrupedal strides also had longer stance phases, meaning overall contact time between the climbers' feet and the tree was much greater during quadrupedal than bipedal locomotion. These arboreal behaviours also demand much more activity in the thigh and buttock muscles (vastus lateralis and gluteus maximus) than terrestrial bipedalism (see Chapter Four), as well as a huge range of variation in muscle activity which reflects the dynamic nature of the arboreal environment. While proficient arboreal locomotion in bipedal hominins thus requires a combination of mechanically disparate behaviours, it seems these can be comfortably accommodated alongside adaptations to terrestrial bipedality.

CONCLUSIONS

Overall, the surprisingly high arboreal competence and locomotor diversity of modern humans in this study shows that ancestral hominins did not necessarily suffer constraints on their arboreal competence as a result of adaptations to terrestrial bipedality. The ability to move effectively around peripheral branches would have allowed hominins to continue to access highly desirable resources, including fruit which is an important nutritional resource for many contemporary human rainforest populations (Kraft et al., 2014) and other living apes. It would have also provided predator-avoidance options, as large-bodied predators cannot access the peripheral branches, and facilitated sleeping in arboreal nests, which requires flexible branches to weave into strong supportive structures (van Casteren et al., 2012), but offers many benefits in terms of thermoregulation and protection from insect-borne pathogens. We conclude that humans, like the other African apes, exhibit considerable (and previously unrecognised) behavioural and mechanical flexibility. An absolute transition from arboreal to terrestrial life is therefore unlikely to have driven the origins of our genus.

MATERIALS AND METHODS

Experimental Design

The study was carried out on Ringmoor and Turnworth Down (National Trust), Dorset, UK. An English oak tree (*Quercus robur*) was selected for the experiment due to the multiple access routes it provided into the tree crown, and the accessibility of all parts of the tree crown. A 50mm-diameter climbing rope was suspended vertically from the tree to mimic a forest vine, providing an additional access route into the tree. Four manually activated buzzers were placed in the peripheral branches of different areas of the tree (Figure 3.1). Eight male professional tree climbers aged between 25 - 42 years completed the study (Table 3.1). These participants were selected because many had extensive recreational free-climbing (i.e. climbing without the additional support systems) experience since childhood. Written informed consent for all data collection and publication of results, photographs and video footage was obtained from all participants prior to the study.

Table 3.1. Participants used in the study. Number of years' climbing experience is for free-climbing only.

Participant ID	Height (cm)	Armspan (cm)	Weight (kg)	Climbing experience (years)
TrC0315_01	182.2	188.0	89.0	>10
TrC0315_02	186.1	189.3	91.0	2
TrC0315_03	185.5	195.0	80.0	>10
TrC0315_04	183.1	184.5	80.0	4
TrC0315_05	176.4	188.0	77.0	8
TrC0315_06	178.0	190.9	85.0	>10
TrC0315_07	184.5	191.0	95.0	>10
TrC0315_08	179.4	187.0	81.0	8

Each participant was asked to climb the tree, activate the four buzzers, and descend in whichever manner they preferred. They performed this task three times, each time using a new access route such that a participant's first climb used their preferred access route, and their third climb used their least preferred access route (all participants were given the full experimental protocol before commencing their first climb). All participants wore shoes during the experiment. For safety, each participant was attached to a belay system via a secure harness. Three belay ropes were attached to the highest secure branches of different parts of the tree crown, to ensure that participants could travel through all sections of the crown by changing from one belay rope to another when crossing between sections, but without the belay system hampering their progress or movement. Participants were asked to use only the tree and vertical rope for weight-bearing support, rather than the belay ropes. Analysis of video footage confirmed this was predominately the case. The belay system was set up and operated by a qualified Canopy Access Ltd. instructor. In addition to performing the climbing task, each participant performed a three-minute steady walk around a circuit marked on a level, but uneven, section of a pasture field. All climbs were filmed from the ground using three camcorders (all 30 frames per second) mounted on stationary tripods positioned in front of the different areas of the tree, and angled perpendicular to the trajectory from the trunk to the outermost goals. Walking bouts were filmed using a camcorder (at 30 fps) mounted on a tripod and positioned perpendicular to the participants' direction of travel.

Locomotion and Support Use

Participants' positional behaviour and support use was recorded using continuous sampling of video footage. Locomotor or postural mode and submode (see Appendix 2.2 for complete list and explanations of modes), were recorded following Thorpe and Crompton (2006) and Hunt et al. (1996). Orientation and compliance of weight-bearing supports, and the total number of weight-bearing supports used within each locomotor bout, were also recorded. Branch orientation was classified into the following categories: 0 ≥ 20° (horizontal); 20 ≥ 45°; 45 ≥ 70°; 70 ≥ 90° (vertical). Branch compliance was inferred from the extent to which the branches deflected under the climbers' weight with five categories of deflection: none; <2cm; 2 ≥ 5cm; >5cm. For each locomotor bout, and each stride sequence used in kinematic analysis, a compliance score was calculated as the mean compliance category number (i.e. 1 – 4) of the weight-bearing supports used. Support diameter was recorded but not included in any analyses as it was not independent of support compliance and thus resulted in multicollinearity. Frequencies of locomotor behaviours within the climbers' arboreal repertoire were calculated as the mean percentage of time spent by the participants in each locomotor mode/submode. These frequencies were compared to data on the arboreal locomotor repertoires of extant apes published by Thorpe and Crompton (2006).

Kinematic Analysis

Kinematics describes the movements and angular rotations of body segments, and allows quantification and comparison of locomotor behaviours. Sequences of locomotion where the subject's direction of travel was within 10° of perpendicular to the filming angle were selected from the video footage. All selected sequences were filmed at a camera angle within 20° of horizontal, meaning vertical out-of-plane angular corrections were not required (Stevens et al., 2006). Twelve sequences of arboreal bipedalism from seven individuals, and eight sequences of pronograde quadrupedalism from six individuals, were selected for kinematic analysis alongside a sequence from each participant's terrestrial walking bout. Sequences were calibrated using body measurements taken manually from each participant, and manually digitised frame-by-frame. Hindlimb joint angles (flexion at the hip, knee and ankle) were collected by manual digitisation of hindlimb segment long axes in Kinovea (v0.8.15, www.kinovea.org). Ankle joint angles were not digitised from quadrupedal sequences as the participants' feet were often obscured from view. Joint angle profiles (Figure 3.4) were constructed by converting all sequences to 26 time points, such that each sequence was sampled at intervals of 4% of stride duration, and the mean and standard deviation calculated per data point. Coordinates of the back of the heel at the point of touch-down were collected throughout all sequences using Didge (v2.3, www.biology.creighton.edu/faculty/Cullum/Didge) for calculation of three spatiotemporal parameters: stride length, stride frequency and duty factor (the proportion of the stride for which the foot is in stance phase, i.e. in contact with the ground).

Statistical Analysis

Fifteen kinematic parameters were extracted from each stride sequence for statistical analysis. These comprised four angles from the hip, knee and ankle: maximum angle, minimum angle, angle at touch-down and angle at midstance (the point at which the hindlimb is directly underneath the body), and three spatiotemporal parameters: stride length, stride frequency and duty factor. The effects of support type and support compliance on bipedal kinematics were tested using a Multiple Regression model for each kinematic variable. Kinematic analysis did not include support orientation as all sequences were recorded on horizontal supports angled between 0 – 20°. Each model contained two environmental predictor variables: support type (branch or ground) and support compliance score (support orientation excluded as all sequences used roughly horizontal supports). Differences in 11 kinematic variables (excluding ankle angles) between arboreal bipedalism, terrestrial bipedalism and arboreal quadrupedalism were tested using Kruskal-Wallis tests and Dunn tests for post-hoc multiple pairwise comparisons using rank sums.

CHAPTER FOUR

MODERN HUMAN LOCOMOTOR RESPONSES TO THE MECHANICAL DEMANDS OF THE FOREST CANOPY

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ABSTRACT

Nonhuman apes have evolved key locomotor strategies to overcome the challenges of moving a large body around the complex and dynamic structure of the forest canopy. Chapter Three revealed the significant arboreal proficiency of modern humans, facilitated by a diverse locomotor repertoire, despite adaptations to habitual terrestrial bipedality. This chapter explores in detail the locomotor behaviour, kinematics and muscle activity of the climbers during their participation of the task described in Chapter Three in relation to the functional properties of weight-bearing supports. This allows investigation of the mechanical demands posed by the arboreal environment to modern humans, and the specific locomotor strategies that allow a terrestrial biped with modern human morphology to access the different zones of forest canopy. While bipedalism comprised the majority of the climbers' arboreal locomotor repertoire, results show that bipedal kinematics changed in response to support compliance. Modern humans therefore alter both locomotor modes and gait kinematics to achieve effective movement through the canopy. Analysis of muscle activity suggests that the climbers' preferences for their choice of entry route into the tree crown may have been based on reducing the activity required of biceps brachii, rather than the activity required of major hindlimb muscles. These results show that, like other apes, modern humans are able to overcome the challenges of travelling within different forest canopy zones. The results also support the argument that the capacity for behavioural flexibility, rather than specific morphological adaptations, played an important role in facilitating access to arboreal resources throughout hominin evolution.

INTRODUCTION

Despite being habitual terrestrial bipeds, modern humans demonstrate substantial arboreal locomotor capability (Chapter Three). The diversity of their arboreal locomotor repertoire is comparable to other extant African apes (Chapter Three) and is consistent with evidence of arboreal adaptations in early and later hominin species (Senut et al., 2001; Lovejoy et al., 2009c; Wood and Baker, 2011; Clarke, 2013). However, although there is increasing evidence that early hominins were not restricted in their arboreal capacity by adaptations to terrestrial bipedality, they would have needed to meet the particular challenges of moving a large body around the canopy environment. This chapter presents detailed results from the study outlined in Chapter Three on the positional behaviour, ecology and mechanics of arboreal locomotion in modern humans, in order to more fully investigate the locomotor strategies used by hominins in response to the various challenges posed by the canopy environment.

Challenges of the arboreal environment to large-bodied hominoids

The structure of the forest canopy differs significantly from the terrestrial environment. Vertical trunks may be wide and rigid, or thin and flexible, and tree crowns may contain both large boughs at the core as well as peripheral branches which create a complex and dynamic network of supports that differ in orientation, diameter, compliance and connectedness (see Chapter One). For an arboreal animal, these varying support properties not only make achieving stability more difficult in the canopy than on the ground, but make stability a much more crucial aspect of positional behaviour due to the risk of falling from a height. Primate positional behaviour has evolved to meet these challenges (see Chapter One), but body size plays a crucial role in the effectiveness of locomotor strategies. Very small primates may need to cross gaps that are wider relative to their size compared with large primates, yet many branches do not require a substantially different locomotor approach from terrestrial locomotion because they provide a relatively flatter, wider and more rigid weight-bearing surface than they do for larger, heavier animals (Cartmill, 1974). Larger primates generally face greater challenges to their locomotor behaviour than do small primates, because branches provide relatively smaller surfaces for balance and deform to a greater extent under their weight (Grand, 1972). While larger primates are thus at a greater risk of falling than smaller primates, they also have higher chances of fatality from falling, as the kinetic energy that the body must dissipate upon impact increases as a proportion of its linear dimensions (Cartmill and Milton, 1977). Arboreal locomotor strategies of large-bodied primates must therefore reflect a compromise between the need for effective movement through the canopy to access resources, and the constant need for stability on unpredictable weight-bearing supports. Pontzer and Wrangham (2004) suggested that many adaptations to vertical climbing in chimpanzees are maintained by the need to avoid falls, rather than the need for energetically efficient locomotion. In Sumatran orangutans, crossing between two tree crowns at canopy level has been shown to use less energy than descending to the ground and ascending the adjacent trunk (Thorpe et al., 2007a). This behaviour illustrates how both large body size and support compliance may not always be a hindrance to arboreal locomotion; orangutans may utilise both to their advantage when crossing large gaps in the canopy (Thorpe et al., 2007a)

Apes also have particularly diverse locomotor repertoires to meet the increased challenges of canopy locomotion compared with those faced by smaller primates. These include strategies such as suspension underneath branches, hand-assisted bipedalism and unpatterned, scrambling locomotion; all of which are considered to be specific adaptations to moving a large body around the different zones of forest canopy (Grand, 1972; Cant, 1992; Thorpe and Crompton, 2006; see Chapter One). Of these strategies, the suggestion that large-bodied apes extend their hindlimbs to aid arboreal locomotion (Thorpe et al., 2007b) is of particular interest. Extension at the hip and knee is considered a characteristic trait of modern human terrestrial bipedality (Crompton et al., 2003; Lovejoy, 1988), and it has been claimed that primates "cannot travel arboreally with extended limbs" (Schmitt, 1999) due to the restrictions on balance imposed by grasping branches. Schmitt (1999) considered that the compliant gait of quadrupedal primates, characterised by flexed limbs and long, slow strides, is a particularly important adaptation to the thin, flexible branches of the terminal branch niche (TBN) for medium- and large-sized primates. A compliant gait increases balance and stability while maintaining efficient walking speed, and is necessary because, in the absence of claws, primates must grasp branches with their hands and feet during arboreal locomotion (Cartmill, 1985; Schmitt, 1999). Schmitt (1999) proposed that walking on branches with stiff, rather than compliant, hindlimbs would be disadvantageous because it would produce both higher impact forces and amplified oscillation of branches through larger vertical excursions of the individual's centre of mass. However, observations of orangutans suggest that they extend, rather than flex, their hindlimbs during bipedal locomotion in response to the compliance of TBN branches (Thorpe et al., 2007b). The hypothesis that locomotion with stiff hindlimbs could be an adaptation to substrate compliance is in direct conflict with Schmitt's (1999) argument that compliant walking is necessitated by branch oscillations caused by the weight of large-bodied primates. However, the compliant gait model describes quadrupedal locomotion, and its relevance to bipedalism is unclear. Bipedalism not only differs mechanically from quadrupedalism, but allows the forelimbs to reach food or provide balance on higher supports. Thus the supposed disruption to quadrupedal gait of branch oscillation described by Schmitt (1999) may not be as apparent for bipedal locomotion. This locomotor response in orangutans not only has implications for the arboreal origins of erect bipedal locomotion (Thorpe et al., 2007b; see Chapter One), but suggests that variation in body size and substrate functionality result in a more complex relationship between the canopy environment and primate locomotion than just the use of compliant walking in response to thin, flexible branches.

Muscle activity

In addition to limb kinematics, patterns of muscle activity can also be used to assess the varying mechanical demands of arboreal substrates and the differences in locomotor solutions that they elicit. Activities that require minimal muscle activity can also indicate behaviours that are likely to have been most influential on the development of musculoskeletal morphology (Wall-Scheffler et al., 2010). For example, the enlarged gluteus maximus in humans is often associated with bipedality, and has been shown to be most important for activities where hip extension provides propulsion, such as inclined walking (Lay et al., 2006), running and ladder- or stair-climbing (Zimmermann et al., 1994; Bartlett et al., 2014). Bartlett et al. (2014) suggested that a large gluteus maximus is primarily an adaptation to the rapid, powerful movements required during sprinting, rather than constant but submaximal tasks such as endurance running. The hypothesis that vertical climbing was the precursor to bipedal locomotion in hominoids was based on the use of gluteal muscles during vertical climbing in chimpanzees (Prost, 1980; Stern and Susman, 1981), and although this hypothesis has mostly been disregarded (Crompton et al., 2008), it is likely that these rapid bursts of gluteal activity may be important for canopy locomotion as well as sprinting in humans. While a large gluteus maximus is therefore important for terrestrial bipedalism, it may also play a significant role in facilitating the combination of terrestrial bipedal and arboreal capabilities. This study allows comparison of the activity requirements of major hindlimb muscles during arboreal and terrestrial locomotion, and investigation of the importance of forelimb muscle activity during arboreal movement in a terrestrial biped.

Arboreal locomotion in hominins

Despite being habitual terrestrial bipeds, modern humans are able to exploit different routes into the tree crown, rather than being restricted to the climbing of vertical trunks described by Venkataraman et al. (2013a; b), and successfully access different canopy zones (Chapter Three). Climbing ability has been linked to adaptations in soft tissue morphology among the Twa population in Uganda, but without accompanying skeletal changes (Venkataraman et al., 2013a; b). The authors argue that this implies a strong role for phenotypic plasticity, rather than genetic factors, in facilitating arboreal locomotion in modern humans. Although climbing is prevalent among many hunter-gatherer communities, climbers risk substantial fitness consequences in terms of the risk from falling: Risser et al. (1996) reported that the chance of fatality from falling in modern humans rises from 44% to 100% when height in the canopy increases from 12m to 20m. Given the risk associated with climbing, it is likely that climbing confers a fitness advantage, either as a direct consequence of attaining desirable arboreal resources, or through sexual selection (Venkataraman et al., 2013b). Consequently, a role for genetic inheritance in determining climbing ability cannot be ruled out, even if morphological plasticity is indeed the major determining factor. The climbers used in this study, however, are part of a population in which a) tree climbing is not a common activity among adults, and b) improved tree climbing ability is unlikely to confer any selective advantages. It is therefore reasonable to assume that their arboreal performance capacity is not a result of population-specific genetic adaptations.

Study aims

Chapter Three demonstrated how substantial arboreal capacity is facilitated in modern humans by diverse locomotor repertoires that are comparable to those of extant apes. The study also revealed that entering the tree crown via low-hanging peripheral branches, which reduced the distance that an individual must climb completely vertically, was the preferred access route among the climbers, rather than climbing the trunk or a vertical rope. However, while vertical climbing is an energetically expensive form of locomotion for modern humans, the mechanical requirements of different access routes and different locomotor behaviours, and whether these requirements influence arboreal behaviour, are unclear. This chapter presents detailed information on the ecology and mechanics of arboreal locomotion in modern humans to investigate their locomotor responses to the challenges posed by arboreal supports, and thus shed light on the specific mechanisms that allow a habitual terrestrial biped to exploit the forest canopy. This includes the effects of support diameter, orientation and compliance on locomotor behaviour, hindlimb kinematics and activity in six muscles used during climbing. These data will allow characterisation of the mechanical demands of the canopy environment, and the extent to which they vary from the demands of the terrestrial environment. It is hypothesised that, like other extant apes, the climbers would alter their locomotor behaviours in response to variation in these support properties. It is also hypothesised that support compliance would elicit greater hindlimb extension during bipedalism, as has been observed in orangutans. Finally, given the trends in the participants' entry route choices (Chapter Three), it is hypothesised that activity in some muscles measured will be lower during the climbers' most preferred entry routes, and during the most frequently used locomotor behaviours. Since the presence of specific genetic adaptations to climbing is unlikely in the subjects of this study, this data will allow further investigation of the mechanisms behind hominin arboreal capacity.

MATERIALS AND METHODS

See Chapter Three for experimental design, recording of locomotor ecology and methods of kinematics data collection and analysis.

Surface Electromyography

Electromyography (EMG) data were collected throughout each participant’s three climbing tasks and their walking bouts for six muscles: vastus lateralis (thigh), gluteus maximus (buttock), gastrocnemius (lateral head; lower hindlimb), biceps brachii and triceps brachii (upper forelimb) and extensor carpi ulnaris (lower forelimb). These muscles allowed analysis of different parts of the hindlimb and forelimb, and were chosen because their locomotor functions relate strongly to climbing. In humans, vastus lateralis, gluteus maximus and gastrocnemius are used during different types of climbing (Asplund and Hall, 1995; Venkataraman et al., 2013a; Bartlett et al., 2014), and are important during inclined and uneven, as well as level, walking (Zimmermann et al., 1994; Cappellini et al., 2006; Lay et al., 2006; Lichtwark and Wilson, 2006). The morphologies of gastrocnemius and gluteus maximus have also both been related specifically to vertical climbing of tree trunks (Prost, 1980; Fleagle et al., 1981; Venkataraman et al., 2013a; b). Because of their major roles in forelimb flexion and extension, the morphology of biceps and triceps brachii has also been related to vertical climbing in nonhuman primates (Hunt, 1991a; Hirasaki et al., 2000), and comparisons of the vertical climbing gaits of spider monkeys and Japanese macaques have revealed differences in the specific functions of biceps and triceps brachii, relating to variation in the use of active elbow flexion/extension and shoulder extension throughout the stance phase (Hirasaki et al., 2000). These muscles are also important during rock climbing in humans (Koukoubis et al., 1995), and excessive use of pull-up manoeuvres during rock climbing have been associated with injuries to both biceps and triceps brachii (Holtzhausen and Noakes, 1996). Extensor carpi ulnaris is particularly active during rock climbing in humans (Jin et al., 2006), and together with flexor carpi ulnaris, has been related to the possibility of rock climbing in *Homo neanderthalensis* and arboreal climbing in *Australopithecus afarensis* (Ward et al., 1999).

Data were collected using wireless surface electrodes which were applied according to SENIAM guidelines to the muscles on each participant's right side, and recorded using a Trigno Mobile System (Delsys, Inc.) data logger strapped around the participant's waist. EMG data were synchronised to the video footage of locomotor behaviour using two on-camera cues: the start of EMG recording was captured using visual and audio confirmation, and each participant was instructed to jump into the air before each climb, which created a spike in the vertical-axis accelerometry data collected by the wireless electrodes that could be manually synchronised to video footage. Raw EMG signals were processed using a 4^{th} order high-pass Butterworth filter at 20 Hz to remove motion artefacts, and smoothed using a 4^{th} order low-pass Butterworth filter at 6 Hz. The signals collected during the participants' climbs were then normalised as a percentage of a mean walking EMG signal for each participant, calculated from a normal 10 second period of their terrestrial walking bout. The normalised signals were split into time windows based on the positional behaviour recording from video footage, so that mean EMG amplitudes could be obtained for all locomotor sequences. All signal processing was carried out in MATLAB (MATLAB and Signal Processing Toolbox Release R2015b, The Mathworks Inc., Natick, Massachusetts, United States) using custom-written code.

Statistical Analysis: locomotor ecology and EMG

Multinomial Logistic Regression was used to identify associations between locomotor behaviours and support properties (support orientation, compliance and total number of weight-bearing supports). Differences in muscle activity between arboreal locomotor behaviours and support properties, and between access and exit routes, were compared using Multiple Linear Regression models for each muscle. Tests comparing different locomotor behaviours included bipedalism, quadrupedalism and suspensory locomotion, without vertical climbing or descent. This allowed comparison between behaviours that are defined by an individual's posture and weight-bearing limbs, and thus investigation of the reasons behind locomotor choices when direction of locomotion is similar. Vertical climbing and descent were excluded as they are defined instead by vertical direction, which itself dictates factors such as support orientation and muscle activity.

RESULTS

Locomotor ecology

Compared with the arboreal locomotor repertoires of nonhuman apes, the frequency of bipedalism is much higher and the frequency of suspension is considerably lower in humans (Table 4.1). However, the percentage of vertical climbing and descent is within the range of frequencies for other species. The frequency of quadrupedalism in modern humans (5%) is similar to that of bipedalism in nonhuman apes, particularly chimpanzees (3-7%), western lowland gorillas (5%) and orangutans (7%). In this study, quadrupedal locomotion most often took the form of pronograde and orthograde scrambling among multiple supports, rather than being used to walk along one support; and according to Multinomial Logistic Regression, quadrupedalism was associated with a higher number of supports compared with bipedalism and suspension (coefficient = 0.433; p = 0.001; Appendix 2.5). Differences in support compliance and orientation did not appear to elicit particular locomotor behaviours (Appendix 2.5). While the majority of arboreal locomotion was hindlimb dominated, the participants also utilised both orthograde and pronograde suspension (although frequencies were below 0.5%; see Appendix 2.2). During pronograde suspension, rather than grasping supports with the feet, the participants would hook the hindlimb over a branch so that the branch was held underneath the knee or ankle joint. The participants also used leaps to cross gaps between

Table 4.1. Frequencies of arboreal locomotor modes in modern humans (data from this study) and nonhuman apes (adapted from Thorpe & Crompton, 2006). See Appendix 2.2 for submode frequencies and explanations. QW = quadrupedal walk; VC/VD = vertical climb/descent; BW = bipedal walk.

Species				*Orthograde suspension*							
	QW	**VC/VD**	**BW**	**Clamber/ transfer**	**Brachiate/ swing**	**Drop/ leap**	**Pronograde suspension**	**Sway**	**Ride**	**Bridge**	**No. bouts**
Homo sapiens [1]	5	33	56	0	0	4	0	0	0	0	652
Pongo pygmaeus [2]	12	21		49	11	0	1	6			4,360
Pongo pygmaeus [3]	18	25	7	21	14	2	4	6	1	3	1,504
Pongo pygmaeus [4]	18	26	7	22	13	1	3	7	1	2	2,811
Pan troglodytes schweinfurthii [5]	36	49	7	5	5	0					223
Pan troglodytes verus [6]	22	68	3		7	1		0		0	1,417
Pan paniscus [7]	32	53	1		9	4		0		0	1,461
Gorilla gorilla gorilla [8]	19	48	5	17	3		0	8			122
Gorilla gorilla beringei [9]	53	40	2		5	0		0		0	153
Gibbon [10]	1	16	2	0	67	14	0	0	0	0	Small
Hylobates syndactylus [11]	0	32	8	0	59	2	0	0	0	0	Small

[1] Present study
[2] Cant (1987), adult females only
[3] Thorpe and Crompton (2006)
[4] Thorpe and Crompton (2006), adults only
[5] Hunt (1991b)
[6] Doran (1996)
[7] Doran (1996)
[8] Remis (1995), adults only, wet season only
[9] Doran (1996)
[10] Fleagle (1980); Gittins (1983); Srikosamatara (1984); Hunt (2004)
[11] Fleagle (1980); Gittins (1983); Hunt (2004)

supports within the tree crown, which were only used near the tree core where at least the landing branch was larger and more rigid. Leaps were carried out in an upright position, with both propulsion and landing by the hindlimbs, and forelimbs providing stability upon landing. The frequency of leaps and drops in the human arboreal repertoire (4%) is the same for bonobos, and higher than the frequencies observed for all other great apes.

Kinematic responses to support compliance

Multiple Regression analysis of bipedal kinematics revealed that compliant supports elicited greater extension at the hip ($R^2 = 0.662$, F [2,16] = 15.64, p = 0.000; t [Compliance score] = 2.19, p = 0.044) and knee ($R^2 = 0.677$, F [2,16] = 16.77, p = 0.000; t [Compliance score] = 2.31, p = 0.035; Figure 4.1), as well as longer strides ($R^2 = 0.763$, F [2,16] = 24.14, p = 0.000; t [Compliance score] = 2.37, p = 0.032; Appendix 2.3), compared with more rigid supports.

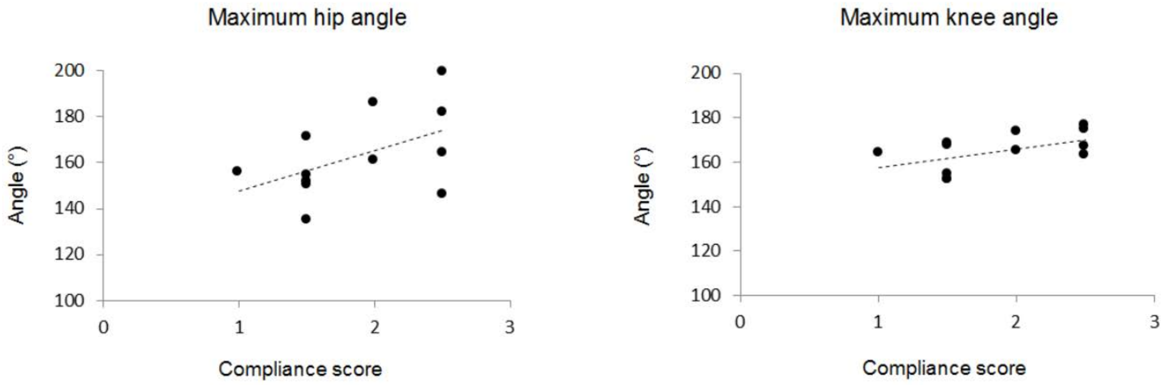


Figure 4.1. Graphs showing the maximum hip and maximum knee angle against compliance score. Compliance score calculated from the amount of branch deflection under the participants' weight. Dashed lines indicate linear regression.

However, constructing hindlimb joint angle profiles from the bipedal sequence on the most compliant branch and from the sequence on the least compliant branch (Figure 4.2; sequences not from the same individual) revealed that neither stride retained an extended hip or knee throughout the stance phase, as in terrestrial walking. On the compliant branch, the hip flexed to a greater extent than on the rigid support after touch-down, but then extended again just before toe-off, reaching a larger angle than was observed on the rigid branch. The knee also flexed throughout the stance phase during the stride on the most compliant branch, and remained more flexed than the knee profile on the rigid branch until just before the last touch-down.

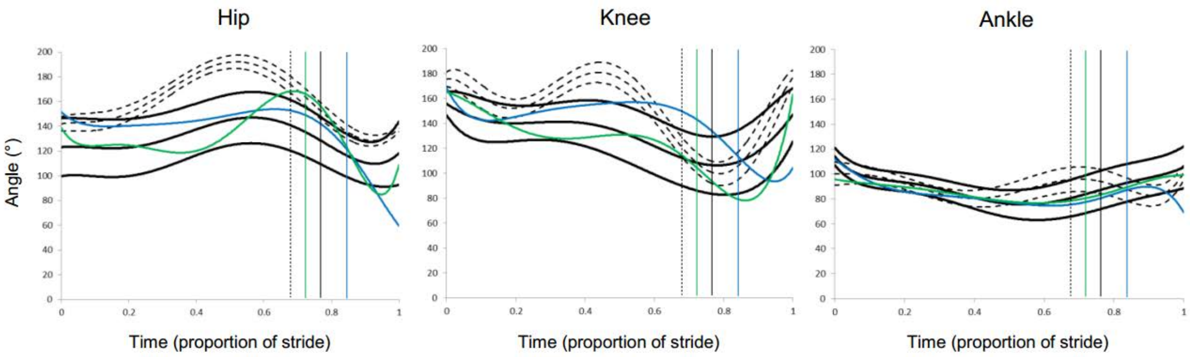


Figure 4.2. Joint angle profiles throughout one stride cycle for terrestrial bipedal walking (dashed black lines) and arboreal bipedal walking (solid black lines). Three lines for each type indicate the mean and standard deviation across all sequences. Blue lines show the angle profiles for the arboreal sequence on the least compliant branch. Green lines show the angle profiles for the sequences on the most compliant branch (not from the same individual). Vertical lines indicate the mean point toe-off.

Entry and exit route choices

The vertical rope was the least preferred access route for the majority of climbers, and generally elicited slower vertical speeds (Table 4.2). After accessing the four goals, most participants chose to descend to the ground via the trunk or a low-hanging branch rather than using the vertical rope (Table 4.2).

Table 4.2. Entry and exit routes used by the participants. Note that participant TrC0315_07 did not wish to ascend the rope, and so chose to enter the tree via a different low-hanging branch on his last climb.

		Entry period			*Exit period*		
Participant ID	**Climb no.**	**Entry route**	**Route height (m)**	**Vertical speed (m/s)**	**Exit route**	**Route height (m)**	**Vertical speed (m/s)**
TrC0315_01	1	branch	2.43	0.16	trunk	1.93	0.92
	2	trunk	1.93	0.27	rope	6.95	0.43
	3	rope	4.23	0.12	branch	2.43	0.69
TrC0315_02	1	branch	2.43	0.22	trunk	1.93	1.61
	2	trunk	1.38	0.22	trunk	1.72	0.43
	3	rope	5.32	0.17	branch	2.43	0.71
TrC0315_03	1	branch	2.43	0.19	trunk	1.93	2.41
	2	trunk	1.93	0.38	branch	2.43	0.46
	3	rope	4.40	0.18	branch	3.06	0.62
TrC0315_04	1	rope	5.93	0.18	branch	2.70	0.71
	2	branch	2.43	0.28	rope	6.95	0.64
	3	trunk	2.11	0.19	trunk	1.93	0.48
TrC0315_05	1	branch	2.43	0.11	trunk	1.93	0.42
	2	trunk	1.93	0.62	trunk	1.80	0.12
	3	rope	5.88	0.29	trunk	1.93	0.51
TrC0315_06	1	trunk	2.70	0.38	branch	2.70	0.66
	2	branch	2.58	0.29	rope	6.95	0.52
	3	rope	5.88	0.18	branch	2.70	0.90
TrC0315_07	1	branch	2.58	0.22	trunk	2.58	0.23
	2	trunk	1.93	0.92	branch	2.70	1.59
	3	branch	1.90	0.11	trunk	1.93	1.21
TrC0315_08	1	trunk	1.93	0.45	branch	2.70	0.59
	2	branch	2.43	0.32	trunk	1.93	0.25
	3	rope	5.88	0.24	branch	2.70	0.51

The goal positioned above the vertical rope (Chapter Three, Figure 3.1) was accessed last in the goal sequence eight times, by seven participants. During five of these eight occasions, participants chose to return to the core of the tree and descend using the trunk, rather than descend on the rope itself. However, vertical speed was not always faster during descents on the rope compared with those participants who descended through the tree core.

Muscle activity

EMG measurements revealed different patterns of muscle activity between the three entry routes used by the participants to access the tree crown. Because patterns of muscle activity differed between individuals, data were plotted separately for each participant to allow investigation of differences in muscle activity between entry routes across all participants (Figure 4.3). Multiple Regression analysis (Appendix 2.6) showed that overall, biceps brachii activity was highest during ascent on the vertical rope and lowest during trunk ascent ($R^2 = 0.760$, $F [4,14] = 11.08$, $p = 0.000$; t [Route: rope] = 2.72, $p = 0.001$; t [Route: trunk] = -3.03, $p = 0.009$), and gluteus maximus activity was significantly higher during ascent through peripheral branches than during trunk ascent ($R^2 = 0.692$, $F [4,19] = 10.66$, $p = 0.000$; t [Route: trunk] = -1.76, $p = 0.035$; Figure 4.3). Although not statistically significant after correction, vastus lateralis reflected a similar pattern to gluteus maximus activity, being highest during branch or trunk ascent in all participants, and lowest during rope ascent in six participants (Figure 4.3). Although EMG measurements were not significantly associated with climb number (Appendix 2.6), it is also notable that muscle activity was lowest during the participants' third climb (and therefore least preferred access route) in all participants for gluteus maximus, and in six participants for vastus lateralis, regardless of the nature of that route. During the climbers' exit from the tree crown, patterns of muscle activity emulated those during the climbers' entry routes: biceps brachii activity was significantly higher during rope descent than branch or trunk descent ($R^2 = 0.691$, F [4,15] = 8.40, $p = 0.001$; t [Route: rope] = 4.60, $p = 0.000$; Appendix 2.7). Although not statistically significant after correction, vastus lateralis activity was higher during trunk descent than branch or rope descent (Figure 4.4; Appendix 2.7).

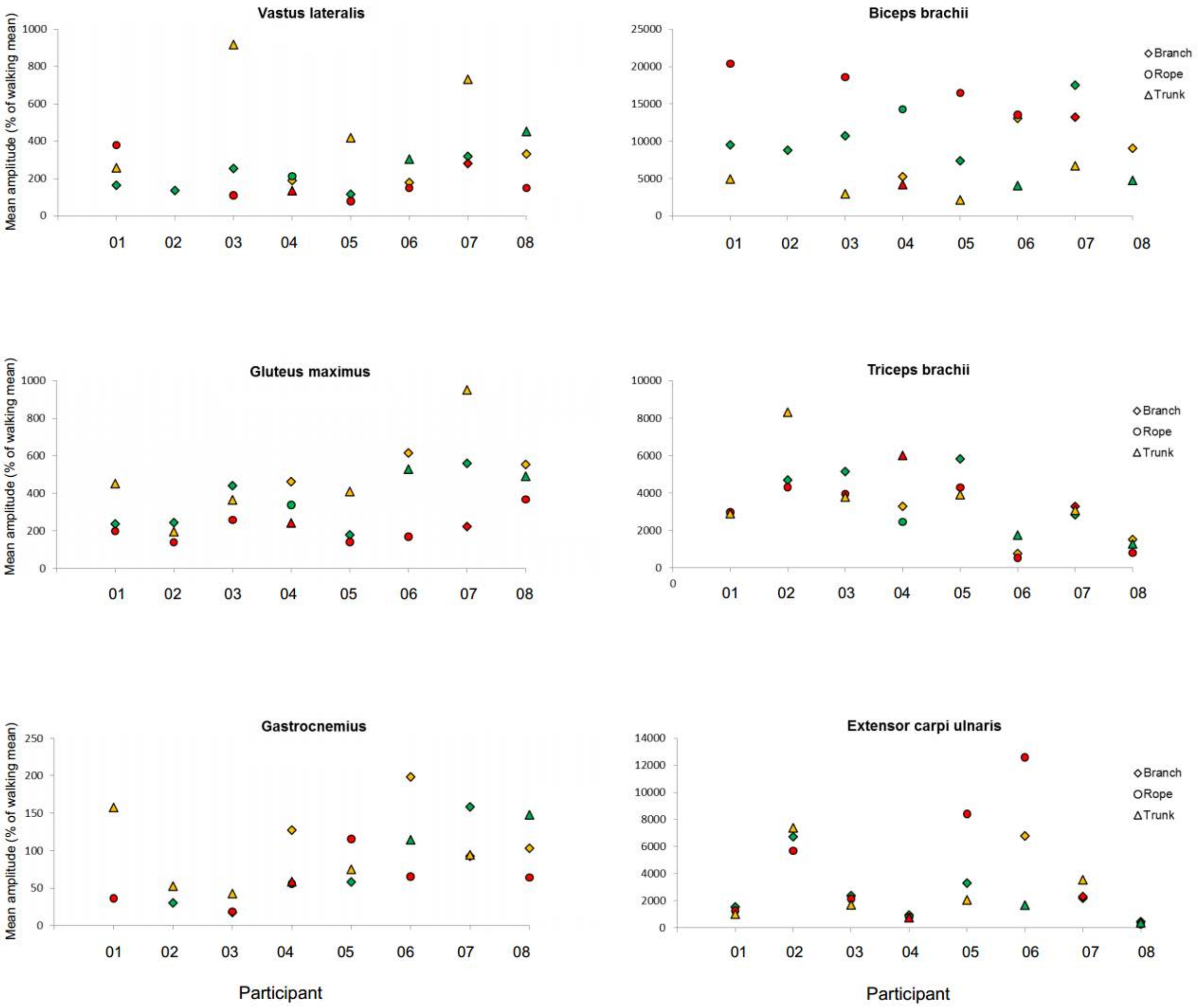


Figure 4.3. Mean EMG activity for each of the eight participants during the entry period of each climb. Route choices are indicated by symbols and are coloured to denote climb number: green = climb one; orange = climb two; red = climb three. Due to loss of electrode signal, data from some muscles for the entry period of some climbs were unavailable (e.g. vastus lateralis activity from participant 02's second and third climbs).

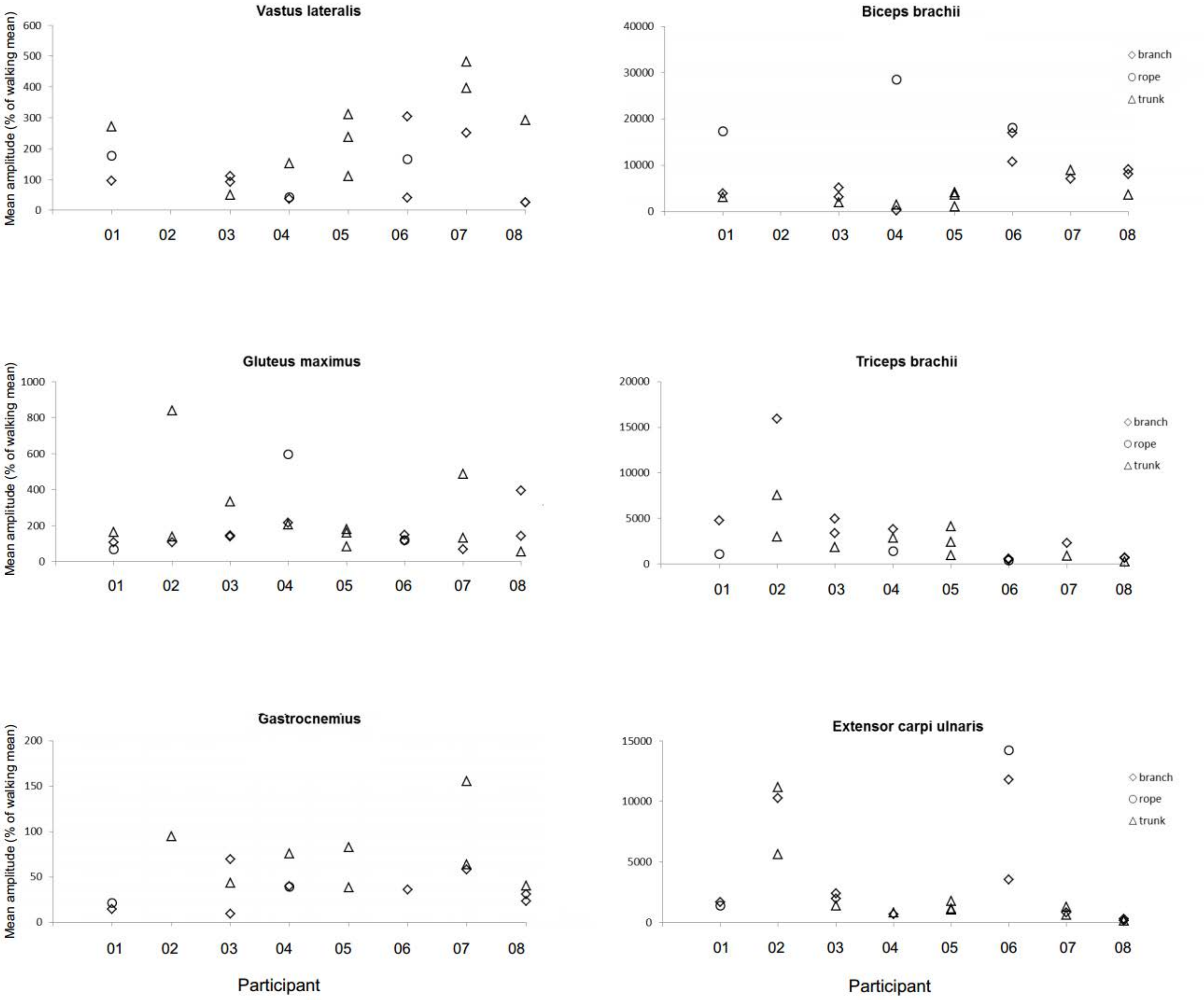


Figure 4.4. Mean EMG activity for each participant during the exit period of each climb. Route choices are indicated by symbols. Climbs are not colour-coded as participants were not instructed in their selection of exit route. Due to loss of electrode signal, data from some muscles for the exit period of some climbs were unavailable.

Activity in biceps brachii was also significantly higher during suspension than bipedalism or quadrupedalism ($R^2 = 0.124$, F [5,147] = 3.45, $p = 0.003$; t [Locomotor mode: suspension] = 4.02, $p = 0.000$; Appendix 2.8a). However, while arboreal bipedalism and quadrupedalism generally used much higher muscle activity than terrestrial bipedalism (Figure 4.5), they were not significantly different from each other (Appendix 2.8a). The gastrocnemius was the only muscle to use more activity during terrestrial bipedalism than the arboreal behaviours (Figure 4.5), and was also higher on steeper supports, both when all arboreal locomotion was considered ($R^2 = 0.052$, F [5,324] = 2.94, $p = 0.008$; t [Support orientation] = 3.19, $p = 0.002$; Appendix 2.8a), and when only bipedalism was analysed ($R^2 = 0.062$, F [3,292] = 4.78, $p = 0.001$; t [Support orientation] = 3.57, $p = 0.001$; Appendix 2.8b). Biceps brachii activity was also higher on compliant supports during arboreal bipedalism, but was not statistically significant after correction (Appendix 2.8b).

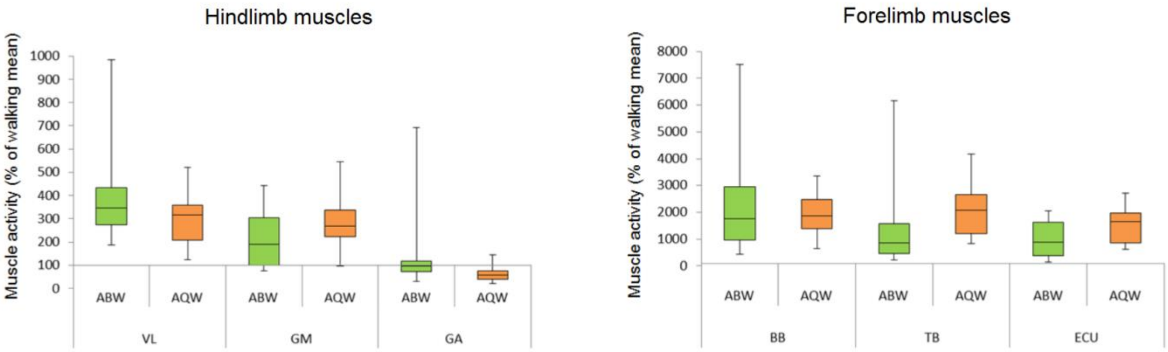


Figure 4.5. Mean muscle activity during arboreal bipedalism (ABW, in green, n=12) and arboreal quadrupedalism (AQW, in orange, n=8) in three hindlimb muscles: vastus lateralis (VL), gluteus maximus (GM), gastrocnemius (GA) and three forelimb muscles: biceps brachii (BB), triceps brachii (TB), extensor carpi ulnaris (ECU). EMG values for each participant are normalised as a percentage of their terrestrial bipedal EMG, which is represented by the x axis at 100%. Boxplots indicate median and interquartile range and error bars show the data range.

DISCUSSION

The arboreal locomotor repertoire of modern humans

Arboreal locomotion in the climbers was dominated by different forms of bipedalism, and they rarely used suspensory locomotion, which is a significant part of most other apes' locomotor repertoire (Table 4.1). However, despite these differences in locomotor frequencies, the arboreal locomotor repertoire of modern humans contains a similar diversity of behaviours to those of other hominoid species (Appendix 2.2). The frequency of vertical climbing and descent in modern humans is higher than in orangutans (Table 4.1), who typically travel between trees at canopy level, but lower than the African apes, who use more terrestrial locomotion than orangutans and are thus required to climb into the canopy more often for arboreal resources (Thorpe and Crompton, 2006). The frequency of vertical climbing and descent is most similar to that in siamangs, although it is likely that a significant amount of the vertical climbing recorded by Fleagle (1980) may in fact be orthograde clamber (Thorpe and Crompton, 2006). The behaviour of the climbers also revealed the importance of spreading weight across multiple supports during arboreal locomotion in humans. Although quadrupedalism comprised a similar percentage of their locomotor repertoire as bipedalism in nonhuman great apes, thus indicating that modern humans are facultative quadrupeds, it usually took the form of scrambling locomotion and was associated with multiple supports, rather than being employed to walk along single supports as is common in chimpanzees (Hunt, 1992). Thorpe & Crompton (2006) suggest that the dominance of orthograde behaviours in the apes' positional repertoire is what distinguishes them from Old World monkeys; this is maintained when human arboreal locomotion is included. However, the key characteristic of human arboreal locomotion that separates it from that of the other apes is the dominance of hindlimb use for weight-bearing, compared to the importance of forelimb weight-bearing in other species.

In interspecific comparisons of locomotor behaviour it is important to note the variation in locomotor frequencies that results from disparities between studies. Because the purpose of arboreal locomotion is to facilitate access to canopy resources, it is to be expected that seasonal or geographical differences in observations will result in different measurements of arboreal locomotor frequencies due to changes in resource distribution, resource abundance or forest structure. For example, the higher frequencies of vertical climbing/descent and bipedalism in western lowland gorillas (Remis, 1995) compared with mountain gorillas (Doran, 1996) may reflect fundamental interspecific differences; but they may also reflect the fact that data for lowland gorillas was only collected during the wet season when fruit abundance, a key incentive for climbing, is highest (Remis, 1995). Similarly, the tree used for the present study did not reflect dense forest structure in that it was not accessible from neighbouring tree crowns. This is an important access route for nonhuman apes (Thorpe et al., 2007a), and participants who had previously climbed in dense forests reported that they would often choose to travel between trees without descending to the ground if it were safe to do so. Both the structure of the tree used in this study and the distance to neighbouring trees may have elicited different locomotor frequencies, such as a low percentage of suspensory behaviour, compared with other trees. Thus the locomotor frequencies recorded here may not accurately reflect the climbers' behaviour when in more dense forest; yet even in this more constrained environment, they still demonstrate considerable locomotor flexibility. Although it is not possible to describe the locomotor repertoires of all hominoid species in exactly the same habitat – not only due to ethical considerations of each species' welfare, but also due to the fact that locomotor behaviour can only be understood in the context of each species' natural habitat – these disparities should be taken into account when comparing locomotor repertoires. For example, Remis (1999) found that the arboreal behaviour of male and female western lowland gorillas was influenced in different ways by tree structure and fruit distribution; and, although extended-elbow vertical climbing is common among African apes when ascending trunks (Hunt, 1992; DeSilva, 2009), it has been shown that chimpanzees and bonobos will instead choose to ascend via flexed-elbow vertical climbing on smaller diameter supports when a variety of supports are available (Hunt, 1992; Kano, 1992; Doran, 1993). In a similar manner, the reliability of interspecific comparisons of locomotor behaviour would increase if all field studies were to quantify support availability alongside support use.

Mechanical variation within modern human arboreal locomotion

For modern humans, effective travel within the forest canopy requires substantial variation in locomotor mechanics that differs from terrestrial locomotion. During arboreal locomotion, the hindlimb kinematics of quadrupedalism were very different from those during bipedalism, yet activity in all hindlimb and forelimb muscles tested did not differ significantly between the two behaviours. Muscle activity was generally higher during both arboreal behaviours compared with terrestrial bipedalism in all muscles except the gastrocnemius, in which activity was generally lower during arboreal locomotion. This suggests that increased muscle activity is required for arboreal locomotion compared to terrestrial walking, regardless of locomotor behaviour. The fact that activity in forelimb muscles was not significantly higher during quadrupedalism emphasises the importance of hand assistance for balance during all arboreal locomotion; indeed, bipedal locomotion was never observed without hand assistance. This suggests a greater reliance on forelimb use during bipedalism than in Sumatran orangutans, in which approximately 60% of bipedal locomotion is hand assisted (Thorpe and Crompton, 2005, 2006). This may relate to the ability of orangutans to grasp branches with their feet (Thorpe and Crompton, 2006), which the participants of this study, who were shod, were unable to do. Quadrupedalism was used by all participants in both the tree core and periphery, and usually when balance was compromised due to unavailability of branches high enough to be grasped while in an upright posture. Despite having an arboreal locomotor repertoire dominated by hindlimb weight-bearing compared with other extant apes, modern humans rely on almost constant use of all four limbs to achieve effective canopy locomotion.

Despite the dominance of hindlimb weight-bearing, the participants occasionally utilised orthograde suspensory locomotion, which involved bearing almost all their body weight from the forelimbs and was associated with significantly higher activity in biceps brachii than bipedalism and quadrupedalism. They also displayed some of the more acrobatic locomotor behaviours used by other extant apes, such as leaps and drops. It is therefore likely that the whole arboreal locomotor repertoire of modern humans encompasses much more mechanical variation than is captured during investigation of bipedalism and quadrupedalism alone.

Locomotor responses to support compliance and orientation

Interestingly, although bipedalism is suggested to be an important locomotor strategy for large-bodied apes in particular relation to the challenges of branch compliance, it was not associated with compliant branches more than other locomotor behaviours in this study. Results suggest that modern humans may prioritise spreading their weight over multiple supports in response to the canopy environment, as opposed to choosing a particular locomotor strategy to suit the functional properties of one weight-bearing support. However, analysis of bipedal kinematics revealed particular responses to support compliance compared with other support properties, characterised by increased hindlimb extension and longer strides. This shows that while bipedalism is not the only locomotor strategy used on compliant supports in modern humans, there is a particular kinematic profile of bipedalism that is used on compliant supports. Hindlimb extension on compliant branches in orangutans has been associated with the extended postures of terrestrial bipedalism in humans (Thorpe et al., 2007b). However, the profiles of hindlimb extension during bipedalism on compliant branches recorded here (Figure 4.2) do not appear to be linked with the stiff hindlimb postures that facilitate the pendular mechanism of energy return during terrestrial walking in humans (Alexander, 1991a). Thus while it appears that a particular type of bipedal locomotion is associated with compliant supports in modern humans, the kinematics are different from terrestrial gait; perhaps more so than those of arboreal bipedalism on rigid branches (Figure 4.2).

Although not statistically significant after Bonferroni correction, activity in biceps brachii was generally higher on compliant compared with rigid supports. This may indicate an increased reliance on the forelimbs for balance (and possibly increased weight-bearing) when walking on compliant supports in order to maintain stability, and increased hindlimb extension may be due in part to the participants reaching to grasp supports with the hands. The mechanical disparities between bipedalism on compliant branches and on the ground mean that caution must be exercised when using the association between branch compliance and hindlimb extension to support an arboreal origin of bipedal adaptations in the hominoid clade. This hypothesis is supported by the possibility of a particular profile of bipedal hindlimb kinematics that aids travel along compliant branches, perhaps by facilitating forelimb assistance; but is not supported by a kinematic link between terrestrial walking in modern humans and bipedalism on compliant supports.

In addition to the effect of support compliance, the only other statistically significant effect of support properties was that gastrocnemius activity, despite being generally highest during terrestrial bipedalism, was higher on steeper supports, both within arboreal bipedalism and across all arboreal locomotion. This increased gastrocnemius activity was present during both inclined and declined walking at an angle of <70°, but not during vertical movement (70 – 90°) in either direction. During terrestrial bipedalism in modern humans the gastrocnemius is an important facilitator of plantarflexion movement just before toe-off (Cappellini et al., 2006), and Lichtwark and Wilson (2006) reported increased gastrocnemius activity in modern humans walking on a treadmill inclined at 10° compared with walking on a horizontal substrate. However, despite the fact that walking on an incline increases dorsiflexion and causes the gastrocnemius to contract at longer fibre lengths, the authors concluded that higher EMG measurements were not caused by a requirement for increased activation to achieve the same required force, due to the parallel elastic component of muscle (which is responsible for resting tension, and thus acts to shorten the muscle independent of contraction; Alter, 2004, p. 62–63). Instead, Lichtwark and Wilson (2006) suggested that increased gastrocnemius activity may be a result of higher velocity contraction during inclined walking. This change in contraction velocity may also be responsible for increased gastrocnemius activity on inclined branches, and the lower overall gastrocnemius activity during arboreal compared with terrestrial locomotion may be related to the lower arboreal stride frequencies. The triceps surae muscles are also important in standing balance in humans, when the body's centre of mass is typically in front of the ankle joints (Morasso et al., 1999; Loram and Lakie, 2002). While the medial head of the gastrocnemius is associated more with balance than the lateral head (studied here) in a standing posture, it is thought that the medial and lateral heads may be adapted to optimal force production in different ankle flexion positions (Heroux et al., 2014). It is therefore also possible that the ankle positions required for locomotion on angled branches result in increased recruitment of the lateral head of gastrocnemius for balance.

Choice of entry and exit routes

The climbers' choices of access route demonstrate that modern humans are not restricted to ascending vertical trunks in order to reach the tree crown, and that entering via low-hanging branches may often be preferred to ascending via the trunk. Whether this is associated with proximity to resources in the tree crown periphery, or specific aspects of the routes relating to stability and ease of locomotion, is unknown and may differ between individuals. However, comparisons of muscle activity between entry and exit routes suggest that force requirements in the forelimb muscles may be a contributing factor in the climbers' preferences. The rope, which was generally the least preferred access route for the climbers, used higher activity in biceps brachii, and lower activity in vastus lateralis and gluteus maximus than other routes during both ascent and descent. Furthermore, vastus lateralis and gluteus maximus activity was generally lowest during the climbers' third choices of entry route, regardless of which route they took; this was even the case for participant 04, who was the only participant to ascend the rope on his first climb, and the trunk on his last. This implies that when choosing entry routes into the canopy, the participants were not aiming to reduce the activity required by these major hindlimb muscles, but may have been reducing the activity required of biceps brachii.

The climbers' behaviour implies that in a tropical forest environment they would not select vertically suspended lianas as their preferred access route to the canopy. However, while the trunks ascended frequently by the Twa population also require long bouts of vertical climbing (Venkataraman et al., 2013a), their diameter and rigidity may elicit a form of climbing that requires less force to be produced by the forelimb muscles. Indeed, the type of climbing referred to as “changwod” by the Jahai climbers of Malaysia (Skeat and Blagden, 1906; Schebesta, 1929; Kraft et al., 2014) and used by many indigenous climbing populations (Oxlade, 2004; Endicott and Endicott, 2008; Kraft et al., 2014), appears to use a similar mechanism to extended-elbow vertical climbing in chimpanzees (Figure 4.6; Hunt, 1992; DeSilva, 2009), during which propulsion is achieved mainly through humeral retraction and hip extension (Hunt et al., 1996). However, in the presence of a variety of vertical supports, nonhuman apes reportedly climb using flexed-elbow vertical climbing, which is typically used on smaller-diameter supports that can be gripped in one hand and during which forelimb flexion is used to pull the body upwards, and usually ascend larger trunks only when smaller supports are unavailable (Cant, 1987; Hunt, 1992; Kano, 1992; Doran, 1993). Although like nonhuman apes, and unlike many hunter-gatherer climbers, extended-elbow vertical climbing was rarely used by the climbers in this study, their flexed-elbow vertical climbing usually followed a different gait pattern from that of nonhuman apes. The forelimb gait of flexed-elbow climbing in nonhuman apes typically follows a hand-over-hand pattern (Hunt et al., 1996), but in this study the participants often gripped the support with their hands one after another, and then pulled the body upwards with both (Figure 4.6). On the vertical rope, participants 01, 02 and 06 combined this with a rope-climbing locking mechanism in the hindlimbs, during which the rope was wrapped around one foot and clamped with the other foot, enabling compressive support on one hindlimb. The hindlimb postures of these three climbers suggested that the hindlimb locked in a compressive position provided more propulsion than the other hindlimb, although the forelimbs facilitated the most upwards motion. This may have contributed to differences in measured vastus lateralis activity between participant 01, who used the right hindlimb in the locked position, and participant 06, who used the left hindlimb. Muscle activity was measured in the right leg in all participants, and thus for the compressive hindlimb in participant 01, and the non-compressive, clamping hindlimb in participant 06. Vastus lateralis activity during rope entry was higher than during trunk or branch entry in participant 01, but was lower than other routes in participant 06. In general, differences between the climbing behaviour of modern humans and nonhuman apes suggest that body proportion differences may result in differences between their choices of vertical support selection. However, while there are patterns in entry route choice among the climbers, the similarity in vertical speed between the different routes demonstrates the proficiency with which the participants were able to exploit these different access routes.

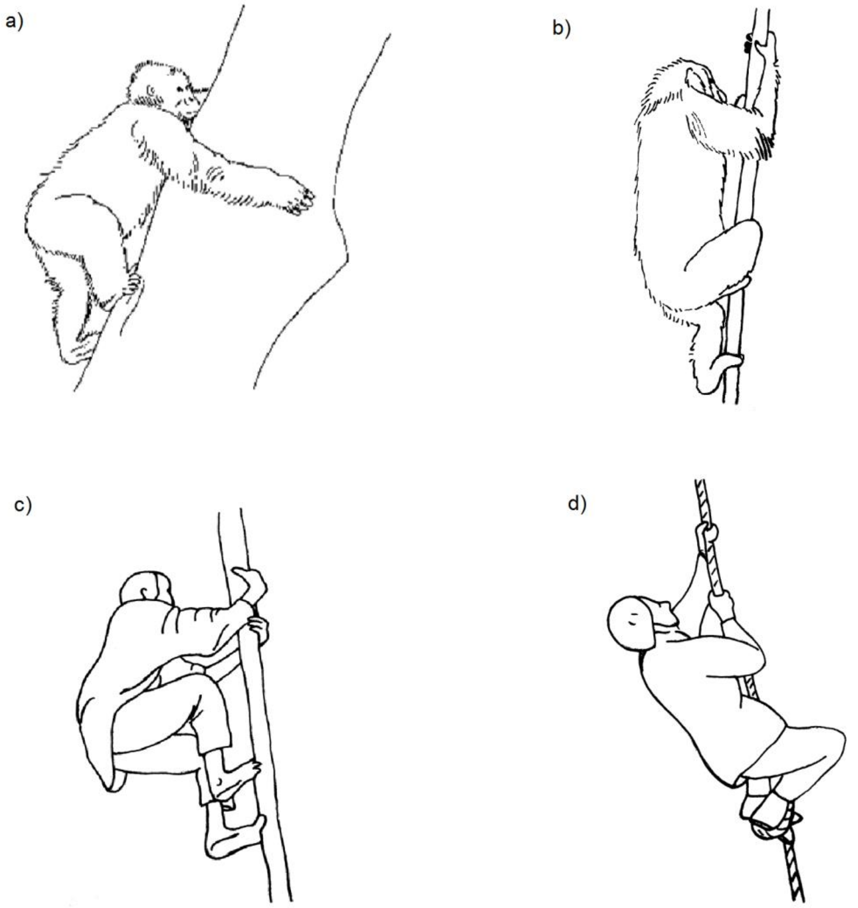


Figure 4.6. Different types of vertical climbing used by modern humans and African apes. a) Extended- elbow vertical climbing in a gorilla. b) Flexed- elbow vertical climbing in a chimpanzee. c) “Changwod” climbing in a Twa man. d) Foot-lock climbing on a rope in a UK climber.

The importance of behavioural flexibility

Increased muscle activity has been used to indicate behaviours for which muscles are not optimally adapted, as natural selection would favour morphologies that reduce the muscle activity required during frequently used behaviours (Wall-Scheffler et al., 2010). The generally higher muscle activity required during arboreal locomotion compared with terrestrial walking in this study thus demonstrates how modern human morphology is best adapted to terrestrial bipedalism. However, this does not rule out any influence of arboreal capacity on modern human morphology, nor the possibility that human morphology reflects the most optimal solution to both effective terrestrial bipedalism and proficient arboreal locomotion. For example, this study shows that gastrocnemius activity is actually lower during arboreal locomotion than during terrestrial walking, but may be important in facilitating both propulsion and balance on angled branches. Furthermore, while ascent into the tree crown via the trunk or peripheral branches generally required higher muscle activity in the gluteus maximus and vastus lateralis than ascent on the rope, the former routes were preferred by the climbers. Therefore, despite appearing to be optimally adapted for terrestrial bipedalism, these muscles may also be important facilitators of those arboreal access routes which are easiest, are associated with the lowest risk, or are most energetically efficient. This supports the argument that morphological adaptations to terrestrial bipedality do not lessen arboreal capacity, and may actually reflect adaptations to a morphology that allows effective terrestrial locomotion alongside proficient arboreality; i.e., that allows substantial behavioural flexibility (see Chapter Two).

The diverse locomotor repertoire of the climbers provides additional evidence that substantial arboreal capacity can be facilitated by behavioural flexibility alone, rather than through population-specific genetic traits or phenotypic plasticity. Venkataraman et al. (2013a; b) demonstrated how repeated ankle dorsiflexion during climbing of vertical tree trunks was accompanied by significantly longer gastrocnemius fibre lengths in Twa climbers compared with a neighbouring, non-climbing population. However, the climbers in the present study did not exhibit repeated use of such a specific posture during their arboreal activity. Furthermore, while significant locomotor diversity is apparent in the climbers’ arboreal behaviour, their overall locomotor repertoire is still dominated by terrestrial bipedality, which will be the behaviour most reflected in their anatomy. Thus, although morphological comparisons between the climbers observed here and non-climbing individuals have not been made, the large range of mechanically disparate locomotor behaviours within the climbers’ arboreal repertoire is unlikely to be facilitated by population-specific morphological adaptations.

Despite the fact that the majority of modern humans are exclusively terrestrial, the behavioural and mechanical flexibility exhibited by the climbers in this study demonstrate that modern humans are indeed “just another ape”. Humans from geographically and culturally different populations are able to exploit arboreal resources, and like other extant hominoids, are capable of a large range of mechanically disparate locomotor behaviours that are not associated with specific skeletal adaptations. Modern humans share specific locomotor responses to the arboreal environment with nonhuman apes, and orangutans in particular, such as their use of hand-assisted bipedalism, quadrupedal scrambling locomotion and hindlimb extension in response to support compliance (Thorpe and Crompton, 2006; Thorpe et al., 2007b). Furthermore, modern humans may also have a morphology that is characterised by adaptations not only to bipedality, but also to behavioural flexibility, which is perhaps the most significant feature of nonhuman primate locomotion (see Chapter One). Thus the same adaptations that are thought to have enabled large-bodied apes to retain substantial arboreal capacity are also used by modern humans, and are likely to have been important for the evolution of all large-bodied crown hominoids, including hominins.

CONCLUSIONS

The arboreal environment demands a mechanically diverse locomotor repertoire in modern humans in order to achieve effective canopy locomotion and overcome the challenges posed by the variation in support functionality. Important arboreal strategies for a terrestrial biped include the use of all four limbs to provide stability and the ability to move in a range of postures with an unpatterned gait. This study implies that when climbing into the tree crown, a hominin adapted to terrestrial bipedality would not be restricted in their choice of entry route, but may opt to reduce the work required of forelimb muscles, rather than hindlimb muscles, during climbing. It is apparent that substantial behavioural flexibility, rather than specific morphological adaptations, allows modern humans to perform a variety of locomotor behaviours in order to exploit different canopy zones, and to alter gait kinematics in response to substrate. Compliant supports elicited more hindlimb extension during bipedalism, although further investigation of gait kinematics did not suggest a link between this particular locomotor response and the stiff hindlimb extension that facilitates effective terrestrial walking in humans. This capacity for mechanically flexible locomotor behaviour is likely to have played a crucial role in allowing early hominins to access arboreal resources.

CHAPTER FIVE

VARIATION IN SKELETAL INDICATORS OF BIPEDALITY AMONG MODERN HUMANS AND NONHUMAN APES

Author contributions: chapter written by Emily Saunders and reviewed by Alice Roberts and Susannah Thorpe

ABSTRACT

The ability to infer habitual bipedality in a fossil hominoid depends on the presence of reliable skeletal predictors of bipedalism. However, the relationship between habitual bipedality and skeletal morphology in hominoids is not fully understood, due in part to a lack of comprehensive descriptions of the extent of variation in several key predictors of bipedality among modern humans and nonhuman apes. This study aims to investigate the reliability of certain skeletal indicators by describing the variation among modern humans and nonhuman ape species in five such predictor features: prominence of the anterior inferior iliac spine; the obturator externus groove; twisting of the femoral head; the angle of the distal tibial surface relative to the shaft; and the high lateral lip of the patellar groove of the femur. Sensitivity and specificity tests reveal the reduced reliability of these features in predicting habitual bipedality, and considerable variation among modern humans in particular demonstrates that caution must be advised when using the absence of any one feature to infer a lack of habitual bipedalism in a fossil hominoid species. Results suggest that a pronounced anterior inferior iliac spine, anterior twisting of the femoral head and a high lateral lip of the patellar groove of the femur may be the most reliable predictors of habitual bipedality among the features studied here. However, it is noted that full locomotor capacity is not necessarily reflected in skeletal morphology, and that inferring constraints to locomotor behaviours in fossil hominoids may not always be appropriate.

INTRODUCTION

The relationship between form and function

When fossil hominoid remains are discovered, skeletal indicators that the species would have been capable of proficient terrestrial bipedality are among the key features used to confer hominin status (Pickford et al., 2002; White, 2006; Crompton et al., 2008). Yet reliable reconstructions of an individual's behaviour from skeletal indicators rely on sufficient understanding of the relationship between form and function; in this case, the relationship between habitual bipedal locomotion and skeletal morphology. Much of an animal's musculoskeletal morphology develops as a response to the stresses experienced by the body during positional behaviour, within the broader parameters of genetic constraint (Pilbeam, 2004). Although the precise roles of genetic and environmental factors underlying morphological variation, and the relationship between them, is far from being well understood, it is possible to investigate the relationship between form and function by comparing detailed data on anatomy and locomotor repertoires in different species.

Identifying proficient terrestrial bipedalism in a fossil hominoid specifically relies on understanding how bipedal locomotion is reflected in the skeleton among extant hominoids. This is made complex by two overriding factors. The first is that skeletal morphology represents an adaptation to an animal's locomotor repertoire as a whole rather than to one mode of locomotion, and modern humans are capable of a wide range of locomotor behaviours (Chapter Three; Kraft et al., 2014). The second is that modern humans are not the only extant hominoids capable of bipedalism, despite being the only habitually bipedal ape. Modern humans show substantial behavioural flexibility when moving around different environments, and while terrestrial bipedalism is the universally dominant form of human locomotion, variation exists between populations in the extent to which other locomotor modes are practised (Kraft et al., 2014). In many populations, for example, the ability to climb trees facilitates access to desirable resources, and is likely to be under sexual selection in males as it confers higher social status (Endicott and Endicott, 2008; Kraft et al., 2014). Ward (2002) suggested that the retention of skeletal adaptations to climbing may have been crucial for survival in hominins due to the resource access and predator avoidance that they would have facilitated. However, due to its dominance in the human locomotor repertoire, it is likely that terrestrial bipedalism exerts a particularly strong influence on musculoskeletal development and is thus associated with widespread morphological adaptations across the skeleton. Many peculiarities of modern human anatomy, compared with other extant apes, are interpreted as derived adaptations to habitual bipedalism, and the increased prevalence of modern human-type traits in later hominins suggests that increasing efficiency of bipedal locomotion played a significant role in improving evolutionary fitness throughout the hominin lineage (Lovejoy, 1988; Pontzer, 2012).

Bipedalism in nonhuman apes

Bipedalism is used in some form by all extant nonhuman apes and some monkeys. Evidence from the locomotor repertoires of extant apes and indicators of orthograde posture in the hominoid fossil record suggest that hand-assisted bipedal locomotion was used by the earliest crown hominoids, and that adaptations to bipedalism thus evolved long before the hominin-panin split (Thorpe et al., 2007b; Crompton et al., 2008). Therefore it is not the use of bipedalism itself, but its dominance of the locomotor repertoire, that is unique to the hominin clade. Identifying skeletal indicators of bipedality with which to confer hominin status in fossil species therefore relies on the ability to separate morphological adaptations to habitual bipedal locomotion from those enabling the occasional use of bipedalism that is observed in nonhuman apes. In addition to differences in frequency of bipedalism, kinematic evidence reveals a variety of gaits among extant apes. For example, the hindlimb mechanics of African apes during bipedalism are substantially different from those required for terrestrial bipedalism in modern humans (Chapter Two; Crompton et al., 2010), and both modern humans (Chapter Four) and nonhuman apes (Chapter Two; Thorpe et al., 2007b; Crompton et al., 2010) alter bipedal kinematics in response to substrate changes.

The evolution of bipedalism in the hominin clade

It is becoming increasingly evident that the evolution of proficient terrestrial bipedalism was gradual and mosaic in fashion, as contemporaneous hominin populations adapted to different environments (Harcourt-Smith and Aiello, 2004; DeSilva et al., 2013). For example, the foot of *Homo habilis* has been described as primitive in comparison to later hominins (Lisowski, 1967; Wood, 1974; Kidd, 1999) and has thus been used as a model for the early evolution of the modern human foot. However, alternative interpretations which advocate a more modern human-like bipedal gait in *H. habilis* (Day and Napier, 1964), as well as disparate foot morphologies in earlier protohominins *Orrorin* (Pickford et al., 2002) and *Ardipithecus* (Lovejoy et al., 2009a), imply alternative evolutionary scenarios for human foot morphology and locomotion (Harcourt-Smith and Aiello, 2004). There is no clearly “primitive” and “derived” state of overall foot morphology within early hominins: each foot presents a mosaic of apparently primitive and derived characters. The mosaic nature of talar, navicular and hallux morphologies in *H. habilis* (OH 8; Day and Napier, 1964), and the more modern human-like foot of *H. ergaster* (KNM-ER 813; Wood, 1974) as well as the earlier *Australopithecus afarensis* (Sarmiento and Marcus, 2000; Harcourt-Smith, 2002; Parr et al., 2014) and *Au. prometheus* (Stw 573; Clarke and Tobias, 1995; Harcourt-Smith, 2002), suggest that different bipedal gaits were present among different Plio-Pleistocene hominins.

Au. sediba is also suggested to have used a very particular, hyperpronated bipedal gait with extreme medial weight transfer (DeSilva et al., 2013), which differs substantially from the reconstructed gait of other australopiths. The development of efficient terrestrial bipedalism in hominins therefore appears to have evolved via multiple pathways. Several authors (e.g. Stern and Susman, 1983; Harcourt-Smith and Aiello, 2004; DeSilva et al., 2013) have suggested that this bipedal diversity may have occurred due to different levels of arboreality being retained, or reacquired, by different hominin species. Because morphology represents a compromise to the varying demands placed on the body, the degree and mode of arboreal locomotion in any given species is likely to have produced different requirements for, and compromises to, adaptations to terrestrial bipedality.

To investigate the driving mechanisms behind this interspecific morphological variation, it is necessary to take an ecomorphological approach. Napier (1964), for example, construed the more modern human-like pelvic morphology of *Au. africanus* compared with *Paranthropus robustus* as evidence for the *Au. africanus* lineage being associated with an open savannah environment, compared with the woodland habitat of *Par. robustus*. This, he argued, would have allowed the development of more specialised morphological adaptations to terrestrial bipedality in *Au. africanus*. However, although palaeo-ecological evidence from different sites provide conflicting reconstructions of the environment inhabited by *Par. robustus* (e.g. Shipman and Harris [1988] implied a preference for closed and wet, rather than open and dry, habitats using data from four sites in Eastern Africa; while Reed [1997] associated *Par. robustus* from Koobi Fora with open habitats near water), Wood and Constantino (2007) concluded that the majority of palaeo-ecological evidence indicates that *Par. robustus* was one of the first hominins to occupy open environments. Furthermore, a first metatarsal attributed to *Par. robustus* was used by Susman and Brain (1988) to infer more committed, modern human-like, form of terrestrial bipedality than existed in *Au. africanus*. However, morphological and chemical evidence for the diet of the two species implies that both occupied broad dietary niches compared with other hominins (Cerling et al., 2013), and were subsisting on terrestrial resources such as grasses, storage organs and even meat (Sillen et al., 1995; Sponheimer and Lee-Thorp, 1999), as well as the arboreal fleshy fruits and leaves with which *Au. africanus* has long been associated (Grine, 1986; Scott et al., 2005). Palaeo-ecology thus provides evidence against which to test ecological interpretations of hominin morphology. However, caution must be exercised to avoid extreme environmental determinism, such as the idea that a hominin occupying woodland environments would be adapted to climbing. The part of an animal's habitat that influences musculoskeletal morphology consists of the structures in its immediate vicinity with which it interacts in order to exploit resources; not its broader ecological biome. Furthermore, the underlying assumption that arboreal competence is compromised by skeletal adaptations to terrestrial bipedalism (Latimer et al., 1987; Latimer, 1991), or that the retention of arboreal behaviour would negate the development of efficient bipedality (Stern and Susman, 1983), may be questionable. It is becoming clear that substantial behavioural flexibility is accommodated by a hominin body plan (Chapter Three) and that arboreal competence may not necessarily be accompanied by skeletal adaptations (Venkataraman et al., 2013b). Thus if a species already has morphology which supports a natural capacity for behavioural flexibility, the previously conceived tight link between morphology and environment is loosened, and we must consider that an ecological shift would not always be accompanied by a shift in skeletal morphology.

Interpreting the fossil evidence

Understanding how bipedalism has evolved within the hominin clade depends on our reconstructions of the locomotor repertoires of extinct hominins being as accurate and reliable as possible. Interpretation of fossil material itself using data from extant hominoids is challenging; the hominoid fossil record is sparse, and fossil remains are, by their nature, fragmentary. Skeletons such as the one-third complete AL 288-1 ("Lucy") that give a reliable impression of morphology across many parts of one individual's postcranium are rare. It therefore becomes difficult to predict an individual's full range of locomotor capabilities, and even harder to assess the extent of skeletal variation that may exist across a species, as well as the amount of variation that can accommodate a certain behaviour. Reliable reconstructions thus rely on comparison with specific skeletal adaptations to bipedalism in the modern human skeleton, which are then used as crucial indicators of terrestrial bipedality and hominin status. Such indicators of habitual bipedality include a central, rather than posterior, position of the foramen magnum (Dart, 1925; Schultz, 1955); features of the pelvis and femur relating to hip joint orientation, such as a high bicondylar angle (Aiello and Dean, 1990; Lovejoy, 2007) and anteriorly twisted femoral head (Asfaw, 1985); and features relating to talocrural and pedal orientation, such as a flat distal articular surface of the tibia (Latimer et al., 1987; DeSilva, 2009). Because these features inform so much of our understanding of human evolution, it is vitally important that they are reliable. However, several such indicators appear to be based on assumptions about how habitual bipedalism is reflected in skeletal anatomy that lack supporting evidence from a sufficiently large sample size of extant apes (see descriptions of features included in this study below). Without data on the inter- and intraspecific variation in these morphological features, we cannot gauge their reliability in predicting proficient terrestrial bipedality.

As anatomical variation is ubiquitous in mammal species, it is likely that all morphological features taken to be indicators of bipedalism will exhibit variation. Quantifying this variation across both humans and nonhuman apes would allow us to ascertain whether a feature is always present in the skeletons of habitual bipeds, in which case its absence in a fossil hominoid may indicate a lack of bipedality; or indeed whether a feature is ever seen in extant nonhuman apes, in which case we cannot reliably associate it with habitual bipedality. Using the analogy of diagnostic tests in medicine, we can use variation among extant apes to characterise the reliability of a particular skeletal indicator in terms of its sensitivity and specificity (Altman and Bland, 1994; Akobeng, 2007). A test may produce a certain rate of false negatives (in this case, skeletons of habitual bipeds that lack the indicator feature) and false positives (skeletons of non-bipeds that exhibit the feature). The sensitivity of a test describes its power to detect true positives, and can be expressed as the ratio: true positives/ (true positives + false negatives). In the case of predicting habitual bipedality among extant apes, this sensitivity ratio would only involve modern humans. The specificity of a test relates to how often it generates false positives, and can be similarly expressed as the ratio: true negatives/ (true negatives + false positives). This ratio would thus involve only nonhuman apes. One can also characterise indicator features in terms of positive or negative predictive value. Positive predictive value (PPV) describes the proportion of positive identifications that are true: true positives/ (true positives + false positives). Negative predictive value (NPV) describes the proportion of negatives that are true: true negatives/ (true negatives + false negatives). Having these measures for each skeletal predictor of bipedality would provide a researcher with a means of gauging the reliability of that indicator, and how much trust to place in its predictions. An important aim of this study, in order to maximise the usefulness of the data collected, was to produce these statistical measures for each morphological feature. In order to be considered as a relatively reliable indicator of a more proficient, habitual form of terrestrial bipedality than exists in nonhuman apes, a morphological feature would be expected to occur in most modern humans (i.e. be highly specific), and to be absent in most nonhuman apes (i.e. be highly sensitive). An ideal indicator would be 100% specific and 100% sensitive.

Study aims

This study quantifies the variation in five skeletal features in samples of modern humans and extant nonhuman ape species in order to test their reliability in inferring habitual terrestrial bipedality. The skeletal features included in the study have been used to infer terrestrial bipedality in both protohominins (*Ardipithecus* and *Orrorin*) and archaic hominins (*Australopithecus, Paranthropus* and *Homo*). Presence of these features has been used to indicate substantially increased reliance on bipedal locomotion compared with extant apes. Some features used to infer bipedality in fossil hominoids, but that have been dealt with extensively elsewhere, such as long bone proportions (Schultz, 1937) and femoral condyle morphology (Sylvester and Pfisterer, 2012), have been omitted from this study. Features that involved techniques too time-consuming for a study which was predicated on large sample sizes (e.g. caudal patterns of spinal morphology) were also omitted. Some of the skeletal features included in the study have been investigated in extant apes (see feature descriptions below); however, it is notable that most studies have compared modern humans to chimpanzees and gorillas due to their close genetic affinity, but not to Asian apes – particularly orangutans which have been shown to be the most bipedal of nonhuman apes (Thorpe and Crompton, 2006). The present study aims to address this omission, as well as to increase the sample sizes within modern human and African ape species. Many studies have focused almost exclusively on samples of modern humans from European or contemporary North American populations; while it is beyond the scope of this study to characterise the variation present across a diverse, global species, the study aims to capture at least some of that diversity by including both European and Southeast Asian (Thai) samples of human skeletal material.

SKELETAL FEATURES INVESTIGATED IN THE STUDY

Anterior inferior iliac spine (AIIS)

The AIIS is the attachment site for rectus femoris, which flexes the hip and contributes to knee extension, and the iliofemoral ligament, an important resistor of hyperextension at the hip during erect posture (Aiello and Dean, 1990). Its relationship to these two structures, and supposed uniqueness to hominin pelves, links the AIIS functionally with terrestrial bipedality. Development of the AIIS is thought to have been a consequence of widening at the iliac isthmus and triradial epiphysis in hominins, and has been used to infer bipedalism in *Oreopithecus bambolii* (Rook et al., 1999), *Ardipithecus ramidus* (Lovejoy et al., 2009d), *Au. afarensis* (Stern and Susman, 1983; Haile-Selassie et al., 2010; Lovejoy and McCollum, 2010), *Au. africanus* (Toussaint et al., 2003), *Au. prometheus* (Dart, 1957), *Au. sediba* (Berger et al., 2010), *Par. robustus* (Gommery and Thackeray, 2008) and *H. erectus* (Simpson et al., 2008) . However, despite widespread use of this predictor feature, Lovejoy and McCollum (2010) suggest that a protruding AIIS can be found in gorilla pelves and is therefore not unique to modern humans among extant apes, implying that its presence should not be used to infer habitual bipedality or hominin status. Walker (1974) also associated observations of an AIIS in prosimians, as well as koalas, to vertical clinging and leaping ability.

Obturator externus groove (OEG)

The obturator externus muscle arises from the inferior pubic ramus and ischium, and ends in a tendon that passes along the back of the femoral neck and inserts into the trochanteric fossa. It acts as a lateral rotator of the thigh and contributes to thigh adduction, but is also considered to be an important stabiliser of the hip joint during extension (Stern and Larson, 1993). When the hip is extended the obturator externus tendon presses against the femoral neck and can, over time, leave a groove (Aiello and Dean, 1990; Figure 5.1). The OEG is a feature that is used to infer frequent use of erect postures and thus bipedality. Presence of an OEG has been used to infer bipedalism in *Au. afarensis* (Lovejoy et al., 1982, 2002; although has been questioned by Stern and Susman, 1983), and *Or. tugenensis* (Day, 1969; Pickford et al., 2002; Galik et al., 2004), and is seen as a crucial bipedal adaptation (Day, 1969; White, 2006). Stern and Larson (1993) argued that bipedalism would have more influence on the formation of an OEG than climbing behaviours due to the more extended hip postures; however, Crompton et al. (2008) note the extremely extended hip postures used during quadrumanous climbing and bridging behaviours in many primates, including orangutans and atelines, which could also contribute to groove formation.

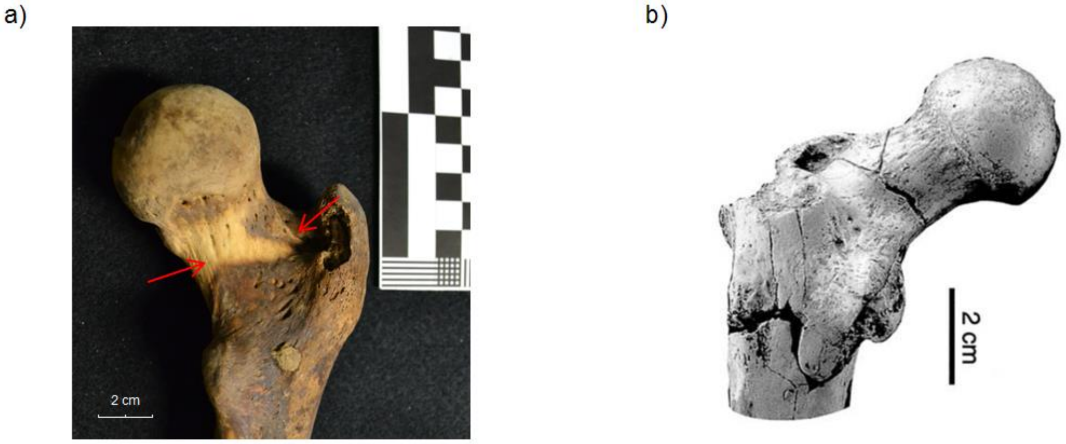


Figure 5.1. Location of the obturator externus groove a) in a modern human femur (between red arrows) and b) on the femur of *Orrorin tugenensis* (taken from Pickford et al., 2002).

Lovejoy et al. (2002) reported a total absence of an OEG in nonhuman African apes (60 chimpanzees, 95 western lowland gorillas), but found a groove in 30 out of 50 modern human Amerindian femora. OEGs have also been reported present in some species of cercopithecoid and platyrrhine monkeys, together with interspecific variation in the direction of the groove, although sample sizes were not indicated (Stern and Susman, 1983; Bacon, 1997). Presence of a "true" OEG is thus disputed within both extant and fossil hominoids. Lovejoy et al. (2002) argue that these discrepancies arise largely due to authors such as Stern and Susman (1983) and Stern and Larson (1993) erroneously interpreting smooth depressions of bone surface as grooves caused by tendon contact. It is also notable that some confusion may have arisen as a result of the OEG being referred to by several authors (e.g. Richmond et al., 2001; Senut et al., 2001; Crompton et al., 2008) as the "intertrochanteric line/groove", which is instead the boundary between the shaft and neck of the femur on its anterior side, and the attachment site of the iliofemoral ligament.

Anterior twist of femoral head

In modern humans, the femoral head is thought to be positioned anteriorly on the femoral neck compared with other primates, such that when looking at the femur from a superior view the articular boundary passes from anterolateral to posteromedial (Figure 5.2, type A). In nonhuman apes, the femoral head tends to be positioned posteriorly on the femoral neck, resulting in the reverse effect from the modern human condition when viewed superiorly (Figure 5.2, type C; Stern and Susman, 1983; Asfaw, 1985). The specific function of this trait has not been explored in detail, but has been related to increased hip abduction ability in nonhuman apes compared with modern humans (Stern and Susman, 1983). Specific association between anterior femoral head orientation and habitual bipedality appears to stem only from its supposed uniqueness to modern humans among extant apes, and it has been suggested that its function links to other femoral indicators of bipedalism, such as the OEG (Pickford et al., 2002). It has been used to infer bipedalism in *Or. tugenensis* (Pickford et al., 2002) and its absence used to advocate a different, perhaps less erect, form of bipedalism in *Au. afarensis* (Stern and Susman, 1983), although the authors note the considerable difference in femoral head morphology between AL 288-1, which appears distinctly nonhuman, and AL 333-3, which appears more modern human-like. The femoral head morphology of AL 288-1 has been attributed to increased arboreality and need for substantial hip abduction (Stern and Susman, 1983).

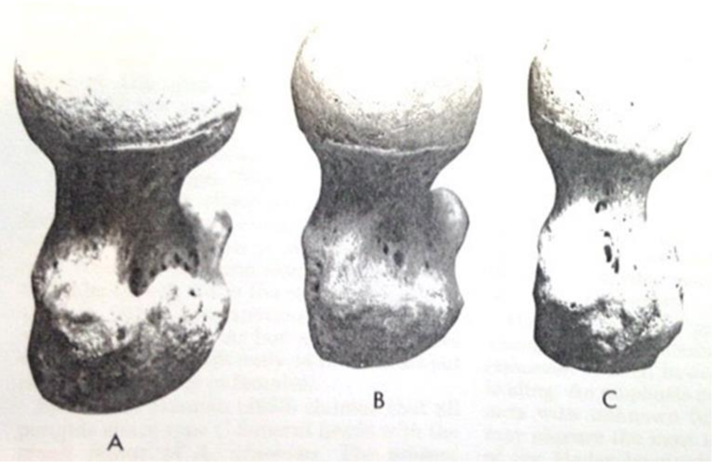


Figure 5.2. Photographs showing different orientations of the left femoral head, taken from Asfaw (1985). In type A, the “human condition”, the articular margin passes from anterolateral to posteromedial. The intermediate type B shows equal anterior-posterior distribution of the articular surface. In type C, the “ape condition”, the margin passes from anteromedial to posterolateral.

Asfaw (1985) described a marked variation in anterior twisting in a sample of 532 prehistoric modern humans and a small sample of nonhuman apes and monkeys (2 chimpanzees, 2 gorillas, 3 orangutans, 7 baboons). He found that frequencies of each type of femoral head coverage also varied between the different prehistoric sites sampled, although all were within

California, and did not find the human condition in the nonhuman sample, but considered whether, with a larger sample size, it may be found in some African apes. Stern and Susman (1983) also reported that the reverse of the "human condition" was universal among chimpanzees and "all other anthropoids" (species and sample sizes unknown), but found less variation than Asfaw (1985) among modern human skeletal material from Africa (n = 31), the Indian subcontinent (sample size unknown) and Australia (n = 3).

High lateral lip of patellar groove of femur

In modern humans, the patellar surface of the distal femur is characterised by a more anteriorly prominent lateral margin, referred to as a 'high lateral lip' when the femur is observed from an inferior view (Figure 5.3). This serves to reduce the tendency towards lateral patellar dislocation during knee flexion, caused by the high bicondylar angle and subsequent lateral forces produced by the quadriceps (Lovejoy, 2007). Tardieu (1999) described a pronounced lateral lip of the patellar groove in neonatal femora, indicating that its development may be due to the genetic programme of development, acting in the absence of any stresses which are later placed on the femur during bipedal locomotion. It also appears in the absence of a bicondylar angle, which develops over the first seven years in response to increased standing and walking (Tardieu et al., 2006), and does not develop in children who do not walk (Tardieu and Trinkaus, 1994). The lateral lip of the patellar groove has been used to advocate terrestrial bipedality in *Au. africanus* (Le Gros Clark, 1946; Heiple and Lovejoy, 1971), *Au. sediba* (DeSilva et al., 2013) and *Au. afarensis* (Lovejoy, 2007), although its prominence has been disputed in the latter (Stern, 2000).

The prominence of the lateral lip has been characterised in a variety of ways. Comments on the height of the lateral lip based upon observations is common throughout hominin fossil literature (Le Gros Clark, 1946; Heiple and Lovejoy, 1971; Stern and Susman, 1983; Stern, 2000; Ward, 2002). More specific measurements include ratios of the total heights of the two condyles when viewed from an inferior aspect (Halaczek, 1972; Wanner, 1977) and angles that describe the steepness of the two sides of the trochlear groove, which are influenced by groove depth as well as prominence of the lateral lip (Tardieu et al., 2006). DeSilva et al. (2013) report one of these, the lateral trochlear groove angle, for 32 modern humans to compare with several australopith and early *Homo* fossils.

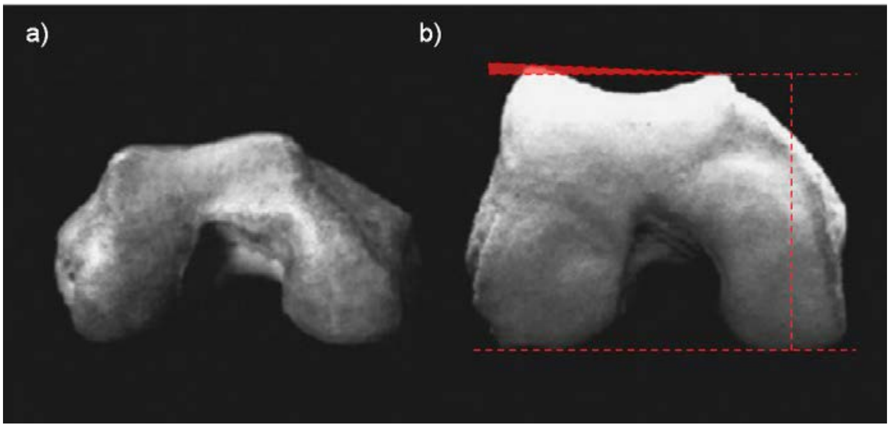


Figure 5.3. Inferior view of distal femora (lateral to the left) of a) a chimpanzee and b) a modern human, showing the patellar groove at the top. The lateral lip of the patellar groove is higher in the human femur. Taken from Lovejoy (2007). Red lines indicate the condylar tangent angle (Halaczec, 1972) measured from the medial to lateral lip (see Materials and Methods).

The lack of a pronounced lateral lip in extant nonhuman apes has been frequently noted to support its validity in designating hominin status (Heiple and Lovejoy, 1971; Stern and Susman, 1983; Ward, 2002; Lovejoy, 2007; DeSilva et al., 2013). However, Wanner (1977) described marked variation among 32 modern humans in patellar groove morphology, and

Kern and Straus (1949) found that while the lateral lip was generally higher in modern humans compared with other apes, it was also high in some cercopithecoid monkeys (n = 42 modern humans, 32 gorillas, 34 chimpanzees, 28 orangutans, 1-17 per monkey species). The reliability of a high lateral lip of the patellar groove as a hominin character, as well as the correct measurement method, is disputed.

Distal surface of tibia perpendicular to tibial shaft

The combination of a high bicondylar angle and a tibia with a shaft oriented perpendicular to the ankle joint in the coronal plane (Figure 5.4) is considered one of the most important morphological adaptations to bipedalism, as it positions both the knee and ankle joints directly underneath the body's centre of gravity (Heiple and Lovejoy, 1971; Latimer et al., 1987; DeSilva, 2009).

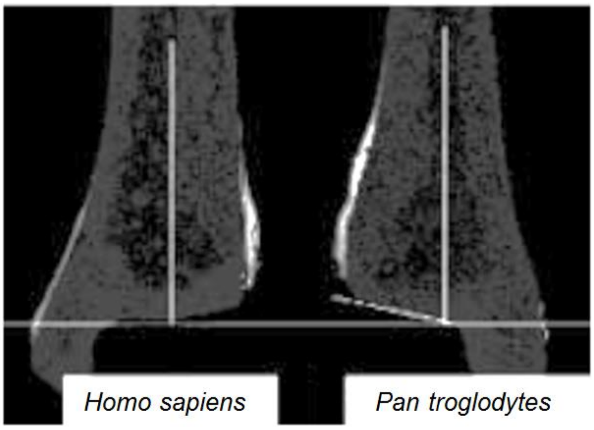


Figure 5.4. Perpendicular angle of the talar surface relative to the tibial shaft in a modern human compared to an oblique angle in a chimpanzee. Adapted from DeSilva (2009).

This morphology of the tibia has been used to support bipedal capabilities of almost all known archaic hominins (e.g. fossils attributed to *Australopithecus* and *Homo*; Heiple and Lovejoy, 1971; Latimer et al., 1987; Ward et al., 1999; DeSilva, 2009; Zipfel et al., 2011). Talar orientation in *Ar. ramidus* and *Or. tugenensis* is unknown, but Lovejoy et al. (2009a) stated that despite indicators of bipedality, other aspects of foot morphology in *Ar. ramidus* suggest a much more mobile ankle than is seen in later hominins. DeSilva (2009) reported an average angle of 91° (± 2.4) in a sample of 28 (mostly Amerindian) human tibiae, 102.6° (± 4.4) in 31 chimpanzees and 105.7° (± 2.5) in 29 western lowland gorillas, but did not investigate other extant ape species.

MATERIALS AND METHODS

Skeletal material

Skeletal specimens of non-pathological, adult hominoids (Table 5.1) were studied using collections at the Museum of London (*Homo sapiens*; post-medieval), Chiang Mai University, Thailand (*H. sapiens*; 20th century), the Powell-Cotton Museum, Kent (*Pan troglodytes, Gorilla gorilla gorilla*), the National Museum of Scotland (*Pa. troglodytes, G. g. gorilla, Pongo Pygmaeus, Po. abelii*), the Natural History Museum, London (*G. g. gorilla, Po. pygmaeus, Hylobates*), the Royal Museum for Central Africa, Brussels (*Pa. paniscus, G. g. gorilla, G. beringei beringei, G. b. grauri*), the Museum für Naturkunde, Berlin (*Po. pygmaeus, Hylobates, Symphalangus syndactylus*), and the Anthropological Institute and Museum, Zurich (*Po. pygmaeus, Po. abelii, Hylobates, Sy. syndactylus*). All nonhuman specimens were wild-shot individuals, apart from those at the National Museum of Scotland; these captive individuals fell inside the range of variation for each wild-shot species in each morphological feature and did not affect the results (means compared using Independent

Samples T Tests). For specimens without information on age at death, adult status was confirmed using full epiphyseal fusion. The sex of a small number of individuals was undeterminable, notably within hylobatids; in these cases individuals were included in broader interspecific analyses but excluded from intraspecific analyses.

Ten percent of all measurements (both manual and digital) were repeated on a different day to ensure reliability of data collection and to reduce specimen measurement interdependence (i.e. the likelihood that categorisation of a specimen would be influenced by the specimen(s) previously observed by the researcher). All angle measurements were within 2° of original measurements, and most categorisations did not differ (but see AIIS section below).

Table 5.1. Sample sizes of ape skeletons used for each morphological feature.

Species	***n* (male, female)**				
	Anterior inferior iliac spine	Obturator externus groove	Anterior twist of femoral head	High lateral lip of patellar groove	Angle of talar surface of tibia
Homo sapiens (UK)	12 (8,4)	31 (21,10)	24 (17,7)	26 (19,7)	28 (21,7)
Homo sapiens (Thai)	37 (17,20)	38 (17,21)	38 (17,21)	37 (17,20)	36 (17,19)
Pan troglodytes	66 (22,44)	66 (22,44)	65 (22,43)	65 (21,44)	61 (20,41)
Pan paniscus	16 (7,9)	16 (7,9)	14 (6,8)	16 (7,9)	16 (7,9)
Gorilla gorilla gorilla	47 (23,24)	52 (28,24)	51 (28,23)	51 (28,23)	50 (26,24)
Gorilla beringei beringei	5 (2,3)	5 (2,3)	5 (2,3)	4 (1,3)	5 (2,3)
Gorilla beringei grauri	14 (7,7)	15 (8,7)	14 (8,6)	15 (8,7)	15 (8,7)
Pongo pygmaeus	32 (15,12)	25 (13,12)	25 (13,12)	24 (12,12)	23 (12,11)
Pongo abelii	3 (1,2)	4 (2,2)	4 (2,2)	4 (2,2)	4 (2,2)
Hylobates lar	22 (12,10)	25 (13,12)	25 (13,12)	25 (13,12)	24 (13,11)
Hylobates moloch	5 (2,2)	6 (3,2)	6 (3,2)	6 (3,2)	6 (3,2)
Hylobates muelleri	2 (2,0)	1 (1,0)	1 (1,0)	1 (1,0)	3 (2,0)
Hylobates pileatus	2 (2,0)	2 (2,0)	2 (2,0)	2 (2,0)	2 (2,0)
Hylobates sp.	4 (2,1)	5 (2,1)	5 (2,1)	5 (2,1)	5 (2,1)
Symphalangus syndactylus	4 (3,1)	6 (3,3)	6 (3,3)	6 (3,3)	6 (3,3)

Assessment and recording of skeletal features

Anterior inferior iliac spine

Despite such widespread use of the AIIS in predicting bipedality in fossil hominins, no common method of characterising AIIS protrusion for comparative study appears to exist. For this study, protrusion of the AIIS site was observed and recorded using the following categories: none; very slight (shallow protrusion of bone visible at AIIS site); slight (small protrusion of bone visible); moderate (marked protrusion of bone); pronounced (very large and protruding area of bone; see Figure 5.5 for examples). Care was taken not to record protrusion as a result of 'drop off' from the iliac shelf in error. To ensure reliability of recording specimens were also photographed and categorised in a random order at a later date. Two percent of observations differed from their original categorisation and were altered as a result.

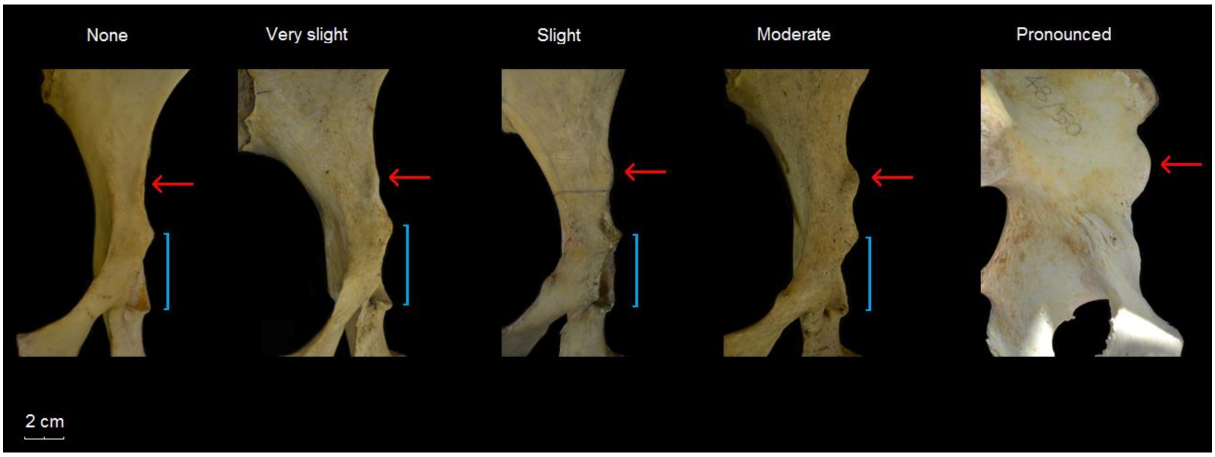


Figure 5.5. Examples of the categories used for recording of AIIS expression in chimpanzee (none – moderate) and human (pronounced) pelves. AIIS is shown by the red arrow. The position of the acetabulum is indicated by the blue bars.

Obturator externus groove

As noted by Lovejoy et al. (2002), presence of an OEG is not always clearly visible, but can be palpated. Thus the presence of a palpable groove was recorded. Grooves were further categorised into the following groups in order to compare rugosity: very slight (a slight depression palpable and perhaps visible when rotating the femur under light); slight (a clearly palpable groove with visible, shallow depression); moderate (a clearly palpable and visible groove); pronounced (a deep, gully-type groove). To be recorded as an OEG, depressions must cover a significant distance across the femoral neck (i.e. extend over halfway across the visible posterior aspect of the neck), and appear as a distinct furrow (even if shallow) rather than a smooth continuation of bone – which has been used in the past to indicate presence of a groove (Stern and Susman, 1983; Stern and Larson, 1993), but in error, according to Lovejoy et al. (2002).

Anterior twist of femoral head

Following the method of Asfaw (1985), the femoral head was photographed from a superior aspect and classified into one of the following three categories (Figure 5.2):

A. articular margin of femoral head passes from anterolateral to posteromedial

B. articular margin passes perpendicular to the long axis of the femur

C. articular margin passes from anteromedial to posterolateral.

Angle of distal tibial articular surface

The distal tibia was marked at the medial and lateral edges of the talar articular surface and photographed from an anterior view (Figure 5.6). These locations on the bone were identified by articulating the talus and tibia to ensure that only the talar surface of the tibia was included for analysis. The angle between the two edges relative to the long axis of the tibial shaft was digitised manually and calculated using Kinovea (v0.8.15, www.kinovea.org).

Figure 5.6. Photograph of the left tibia of a chimpanzee (lateral towards the top). The angle of the distal articular surface relative to the shaft is shown in red. Green crosses indicate the position of marks on the bone showing the location of the medial and lateral edges of the talar articular surface.

High lateral lip of patellar groove of femur

The femur was photographed from an inferior view and the condylar tangent angle (angle of elevation from the medial to lateral lips of the patellar groove; Halaczek, 1972) digitised manually and calculated using Kinovea (Figure 5.3). This measurement characterises the difference in height between the medial and lateral lips without influence of trochlear groove depth, thus reflecting the feature that has been most widely considered during studies of fossil hominins.

Statistical Analysis

Significant differences in the expression of morphological features between humans and nonhuman apes were investigated using the Chi Squared Test for presence/absence data

(AIIS, OEG and anterior twist of femoral head) and a two-tailed T Test for continuous data (angle of distal tibia and angle of lateral lip of patellar groove of femur). To investigate overlaps between the morphology of humans and nonhuman apes, and to assess further the reliability of each feature for predicting bipedality, sensitivity (true positives/ [true positives + false negatives]), specificity (true negatives/ [true negatives + false positives]), PPV (true positives/ [true positives + false positives]) and NPV (true negatives/ [true negatives + false negatives]) were calculated for each morphological feature, and at various threshold values for continuous variables (see Table 5.2). The value of skeletal indicators of bipedality lies in the power of each feature to predict a higher level of bipedality (which may relate to increased proficiency and/or increased dependence on this locomotor mode) than is shown in nonhuman apes. Therefore, human specimens exhibiting the feature were categorised as true positives, and nonhuman apes lacking the feature as true negatives.

Combinations of predictor features

In addition to investigating the value of each individual feature, the combinations of features that were most likely to reliably predict bipedality were identified using minimum Redundancy Maximum Relevance Feature Selection (mRMR; Peng et al., 2005). This method was developed for identifying genes whose expression most closely associates with phenotype variation (Ding and Peng, 2005), and is necessary because predictor features that are most reliable when considered individually are not necessarily the most reliable when considered in a combination (Cover, 1974). During mRMR, features are scored based not only on the probability that they reliably predict the target response (maximum relevance), but also on their distance from other predictor features in the dataset (minimum redundancy), thus describing a larger portion of the dataset. By this method, the highest scoring combinations therefore include features that are less dependent on each other, while maintaining maximum relevance to the target response. These combinations have been shown to be more robust in predicting a target response variable than selecting features that are individually most relevant, but that may be closely interdependent (Ding and Peng, 2005; Peng et al., 2005). Specimens were given a binary score for each feature based on presence or absence, due to the combination of different predictor variable types in the dataset, and because mRMR is generally more robust when used for categorical data than continuous as it allows more precise calculation of mutual information between variables (Peng et al., 2005). For the AIIS and OEG, specimens scored 0 if none were present and 1 for any recorded expression (i.e. even very slight presence). An additional dataset was produced in which specimens only scored 1 for these two features if moderate or pronounced expression was recorded. For twisting of the femoral head, specimens were scored 0 for types B and C (posterior twist), and 1 for type A (anterior twist). For angle of the distal tibia, specimens scored 0 for an angle >100°, and 1 for an angle <100° (based on diagnostic values; see Table 5.2). For angle of the lateral lip of the patellar groove, specimens scored 0 for an angle ≤0°, and 1 for an angle >0°. The target response variable described habitual bipedality; nonhuman apes scored 0 and modern humans scored 1. mRMR analysis was conducted using the mRMRe package for R (De Jay et al., 2012). Finally, each specimen was also scored based on how many bipedal indicator features it exhibited, in order to investigate whether the number of bipedal indicators present differed between humans and nonhuman apes. The total score for each specimen was calculated as the sum of individual feature scores used for mRMR analysis. All statistical analyses were performed using R (v3.3.1).

RESULTS

Most features had high predictive scores (Table 5.2), but overlaps between humans and other ape species demonstrate certain problems with their reliability, reflected in measures of sensitivity and specificity. These are discussed individually below. All morphological features were significantly different between the human and nonhuman ape samples (Tables 5.3 and 5.4), with humans exhibiting bipedal indicators to a much higher degree.

Table 5.2. Sensitivity, specificity, positive predictive value (PPV) and negative predictive value (NPV) of each feature for predicting substantial capacity for terrestrial bipedality.

Predictor feature	Sensitivity	Specificity	PPV	NPV
AIIS (any visible)	1.00	0.39	0.26	1.00
AIIS (moderate/ pronounced)	0.98	0.96	0.86	1.00
OEG (any visible)	0.77	0.87	0.67	0.92
OEG (moderate/ pronounced)	0.18	1.00	0.93	0.78
Anterior twist of femoral head	0.64	1.00	1.00	0.90
Angle from medial to lateral lip of distal femur (> 0°)	0.96	0.91	0.77	0.99
Angle from medial to lateral lip of distal femur (> 5°)	0.48	1.00	0.97	0.86
Angle of distal tibia surface (≤ 90°)	0.25	1.00	0.95	0.80
Angle of distal tibia surface (≤ 95°)	0.69	0.97	0.88	0.91
Angle of distal tibia surface (≤ 100°)	0.94	0.89	0.74	0.98

Table 5.3. Chi Squared Test for significant differences in presence/absence of categorical bipedal indicator features between humans and nonhuman apes.

Morphological feature	χ^2	df	p
Anterior inferior iliac spine	26.047	1	0.00 ***
OEG	111.42	1	0.00 ***
Anterior twist of femoral head	162.99	1	0.00 ***

Table 5.4. Two-tailed T Test for significant differences in angles of distal tibia and lateral lip of patellar groove of femur between humans and nonhuman apes.

Morphological feature	**t**	**df**	**p**
Angle of distal tibia	-25.483	232	0.00 ***
Angle of lateral lip of patellar groove	23.391	231	0.00 ***

Anterior inferior iliac spine

The AIIS was generally more pronounced in humans, but was present at least in "very slight" form within all nonhuman ape species except Sumatran orangutans (Figure 5.7). Moderate AIIS expression, which was the most common form in humans, was also found in 11% of chimpanzees and 6% of western lowland gorillas. There was considerable intraspecific variation; it is notable that only a minority of chimpanzees (27%), bonobos (6%) and western lowland gorillas (28%) had no visible AIIS expression. In humans and bonobos AIIS expression appeared more pronounced in males than females, although the opposite effect was observed in chimpanzees and western lowland gorillas.

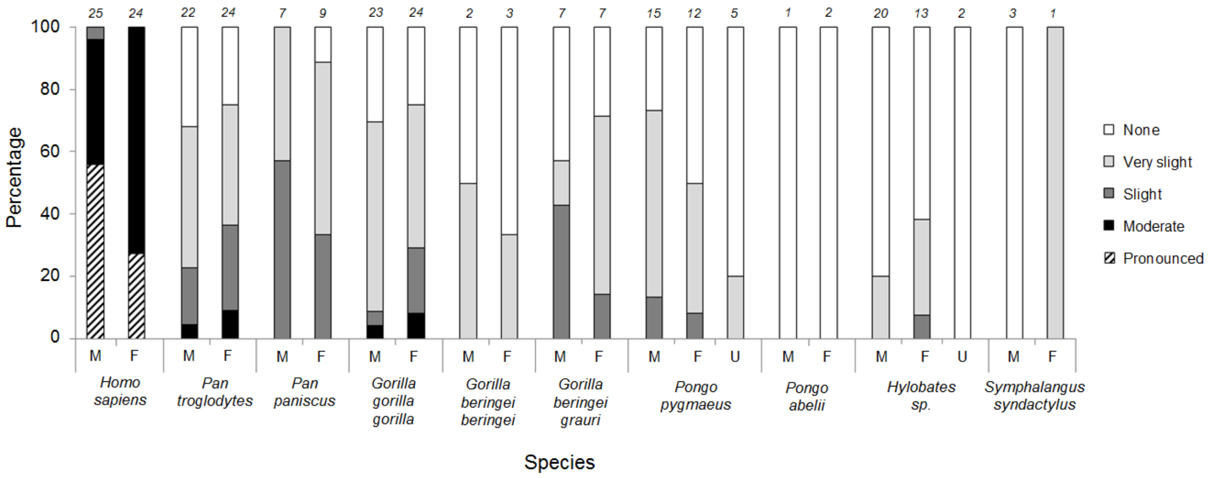


Figure 5.7. Frequency of AIIS expression in extant apes. M = male; F = female; U = unknown sex. Numbers above bars indicate sample size.

Sensitivity of the AIIS in predicting bipedality was very high due to consistent expression among humans, but its prevalence across nonhuman apes meant that specificity and PPV were low when using any visible AIIS as a predictor (Table 5.2). Specificity and PPV increased hugely when the threshold was increased to at least moderate AIIS expression, which was rare among the nonhuman sample. Therefore, lack of an AIIS in a fossil species is a reliable indicator that the species was not a committed biped; however, presence of an AIIS is not always a reliable indicator of bipedal capacity beyond that of nonhuman apes, and a threshold of at least moderate AIIS expression should be used to predict terrestrial bipedality. *Au. afarensis* (Stern and Susman, 1983; Haile-Selassie et al., 2010) and *Ar. ramidus* (Lovejoy et al., 2009d) appear to exhibit at least moderate expression of the AIIS, supporting the authors' claims of bipedality. However, the results presented here have implications for reconstructions of *Or. bambolii*, as photographs of the pelvic morphology of IGF 11778 (Rook et al., 1999) show an AIIS that appears closest to the "slight" category of expression. While the overall pelvic morphology of *Or. bambolii* is more similar to humans than to other extant apes and therefore indicates vertical weight-bearing, it is possible that the AIIS is not functionally linked with human-like bipedal locomotion.

Obturator externus groove

Presence of a visible OEG was rare among nonhuman apes and variable among humans (Figure 5.8). The most common state found in humans (observed in 41%) was the presence of only a very slight groove, which was also found in 45% of chimpanzees. A pronounced groove was never observed in any species, and a moderate groove was found in only 18% of humans, and also on the left femur of a female bonobo (Appendix 3; the right femur was not available so symmetry of the OEG in this individual is unknown). In humans, expression was more common in females than males: of the 16 individuals without an OEG, 13 were male, whereas the relative proportion of males and females within the other categories of expression were similar. A similar effect was observed in chimpanzees, where a groove was observed in 36% of females but only 18% of males. However, among hylobatids, OEG expression was more common in males.

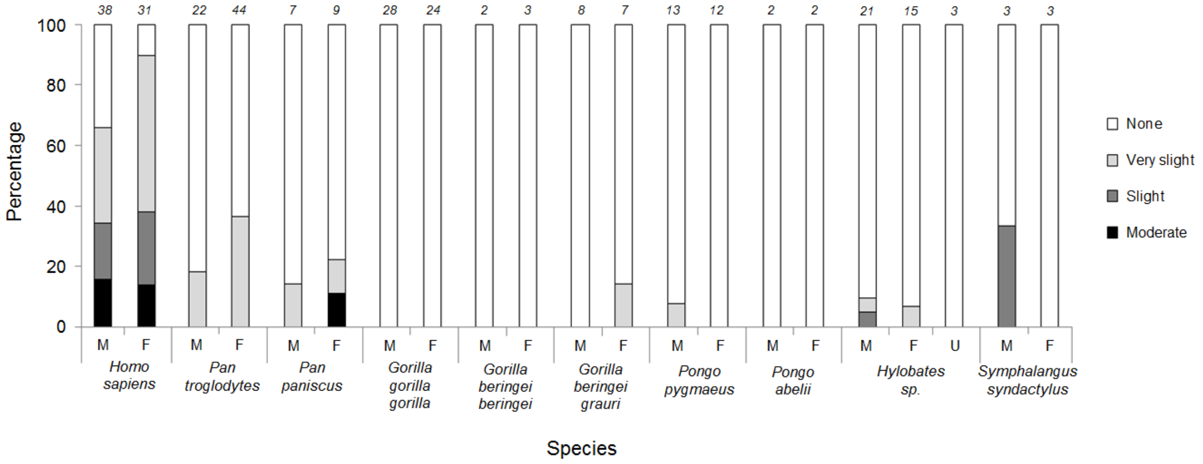
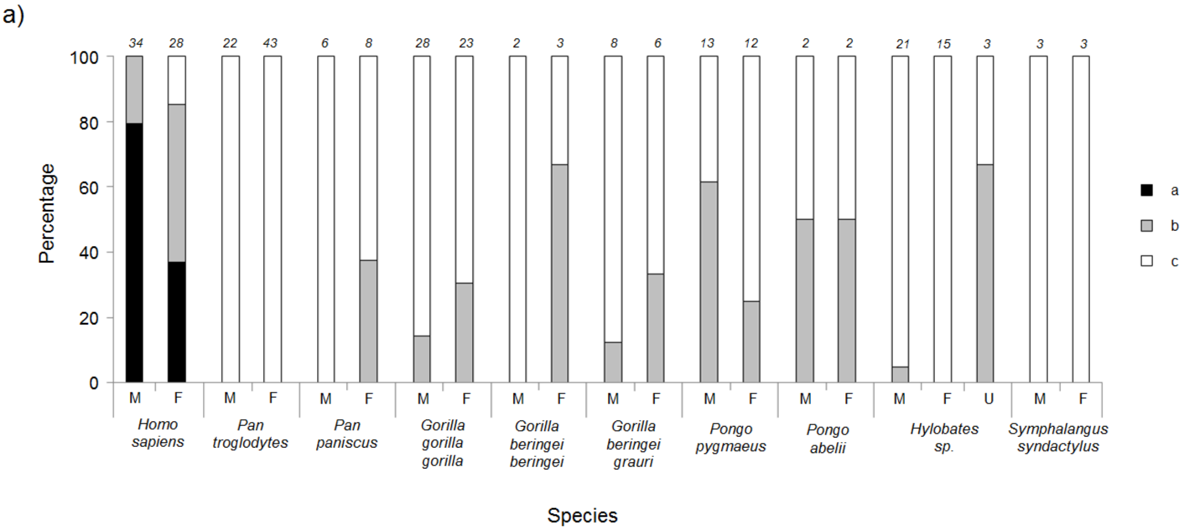


Figure 5.8. Frequency of obturator externus groove expression in extant apes. M = male; F = female; U = unknown sex. Numbers above bars indicate sample size.

Specificity of predicting bipedality using any visible OEG was fairly high, due to most nonhuman apes lacking a visible groove. Sensitivity was lower, due to the variability among humans, and particularly the lack of a groove in 23% of humans. However this percentage was much lower than that of nonhuman apes without a groove, resulting in high NPV. PPV was lower due to the presence of a groove in some nonhuman apes, particularly in chimpanzees. When the predictor threshold was increased to clear presence of a groove (i.e. at least moderate expression), specificity and PPV increased, but sensitivity and NPV dropped, due to the small proportion of humans exhibiting a moderate groove. In a hominoid fossil, a clear OEG is therefore a likely indication of bipedality; however, the variability among modern humans, and lack of a groove in nearly a quarter of humans, shows that a substantial proportion of committed terrestrial bipeds may be expected to lack this feature. This calls into question the reconstructions of non-hominin femora, such as P.67.50, which was reassigned from *Homo sapiens* to *Pan* based on, among other features, absence of an obturator externus groove (DeSilva et al., 2006). A groove has been described for many fossil hominin species (although partly due to its significance in assigning hominin status), although some (most notably both species of *Ardipithecus*) are not yet associated with a preserved femoral head and neck. Sex differences among modern humans and chimpanzees also indicate that, based on this feature alone, females may be more likely to be classified as proficient bipeds than males.

Anterior twist of the femoral head

An anterior twist of the femoral head was unique to humans among the study sample, although was more common among males (Figure 5.9a). Seventeen of the 24 individuals who lacked anterior twisting were female, four of which expressed the condition typical of nonhuman apes of a posteriorly twisted femoral head. These four females were from the modern Thai population, which generally exhibited more variation in femoral head position than the post-medieval UK population, and which was responsible for the difference between males and females (Figure 5.9b). In the UK population, the majorities of both males and females exhibited type A, but in the Thai sample the majority of females exhibited type B, and similar numbers of females exhibited type A and C. The intermediate form (no twist in either direction) was observed in all species except chimpanzees and siamangs. The fact that anterior twisting was not observed in the femora of nonhuman apes resulted in very high specificity and PPV. The variability among humans, however, resulted in lower sensitivity, although the NPV remained high.



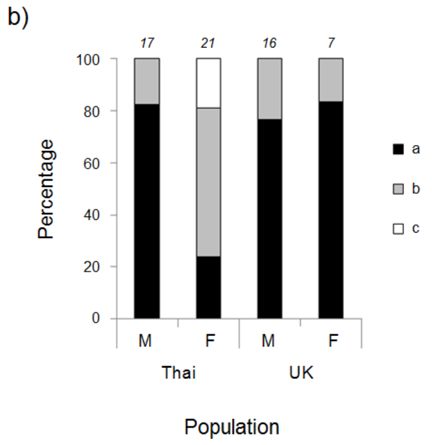


Figure 5.9. Frequency of expression of anterior twisting of the femoral head among a) all extant apes and b) different populations of modern humans. M = male; F = female; U = unknown sex. Numbers above bars indicate sample size.

High lateral lip of patellar groove of femur

While humans generally had a higher lateral than medial lip of the distal femur than nonhuman apes, the modern human range was not completely distinct and was overlapped, particularly by the data ranges of hylobatids, female chimpanzees, male western lowland gorillas and Bornean orangutans (Figure 5.10). Predicting bipedality using an elevation angle threshold of >0° had high sensitivity, specificity and NPV, and reasonably high PPV. When the threshold was increased to >5° the specificity and PPV increased, but sensitivity dropped due to the high proportion of human specimens under the threshold. It is likely that increasing the number of siamang specimens would decrease the specificity and PPV of the high lateral lip as an indicator of terrestrial bipedality, as the siamang sample is small (n=6), yet half of the individuals have an elevation angle of >0°. When analysing fossil specimens it would be unwise to increase the threshold beyond >0° for inferring bipedality, but also essential to consider that a positive identification is not always associated with terrestrial bipedality.

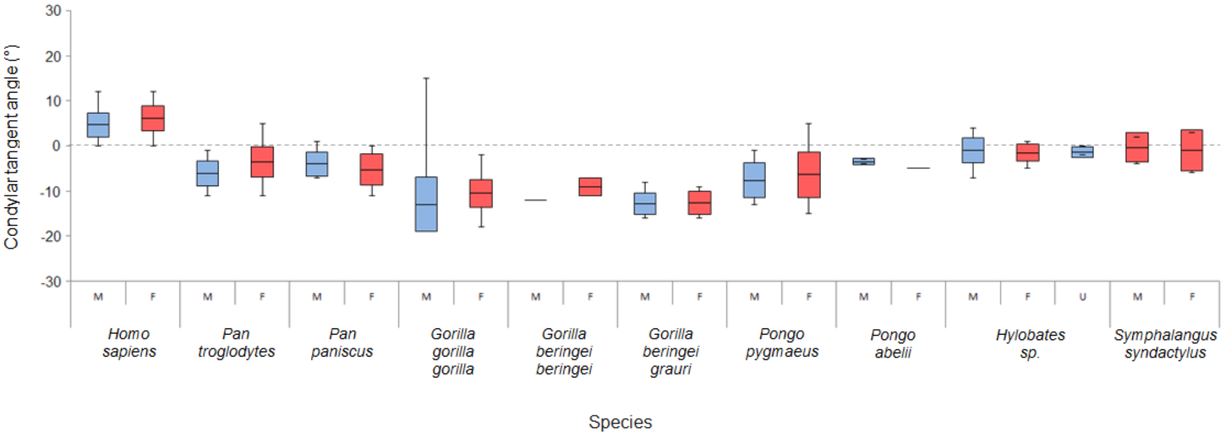


Figure 5.10. Condylar tangent angle from the medial to lateral lip of the patellar groove of the femur when viewed from an inferior aspect in extant apes. Boxes indicate the mean and standard deviation, error bars indicate data range. M = male; F = female; U = unknown sex.

Angle of distal tibial surface relative to shaft

The angle of the distal surface of the tibia relative to the shaft was generally lower in humans, but again the range of data overlapped those for other species, most notably mountain gorillas and gibbons (Figure 5.11). The mean angle for modern humans was 94°, and ranged from 87° to 103°; overlapping the gibbon sample mean at 101°. When ≤90° was used as a threshold for bipedality, sensitivity was very low because the majority of human specimens were above 90°. Sensitivity increased as the threshold was raised, and was high at 100°, although PPV decreased due to angles below 100° also being found in mountain gorillas, Sumatran orangutans, gibbons and siamangs. These results demonstrate the extent of overlap between humans and nonhuman apes once species other than chimpanzees and western lowland gorillas are considered.

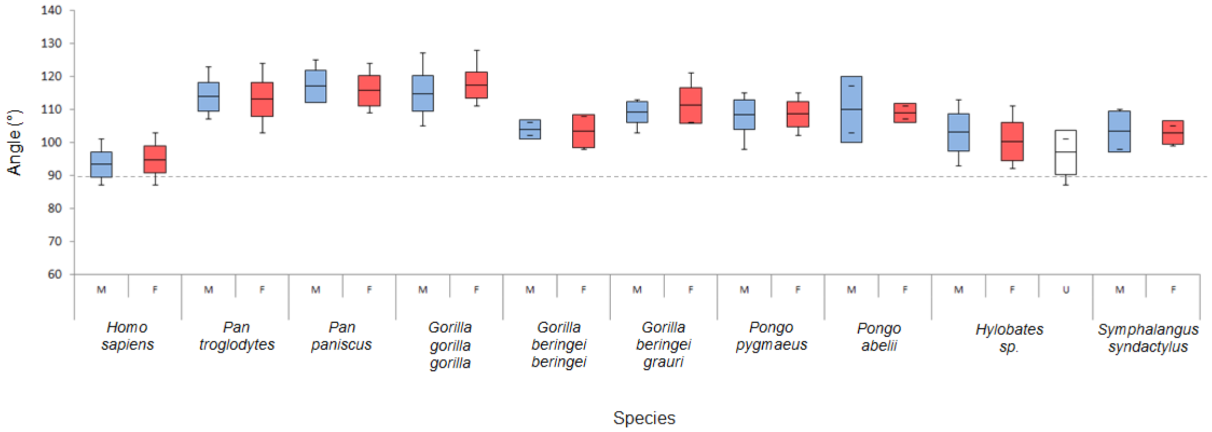


Figure 5.11. Angle of the talar surface of the tibia relative to the long axis of the shaft when viewed from an anterior aspect in extant apes. Boxes indicate the mean and standard deviation of data, error bars indicate data range. M = male; F = female; U = unknown sex.

The presence of multiple bipedal indicators

The combined scores from all indicator features reveal the clearest difference between modern humans and nonhuman apes (Figure 5.12); three was both the highest score in nonhuman apes and the lowest score in humans. There were no considerable sex-related differences, although the variation in OEG and femoral head position among modern human females was reflected in their lower scores compared with males.

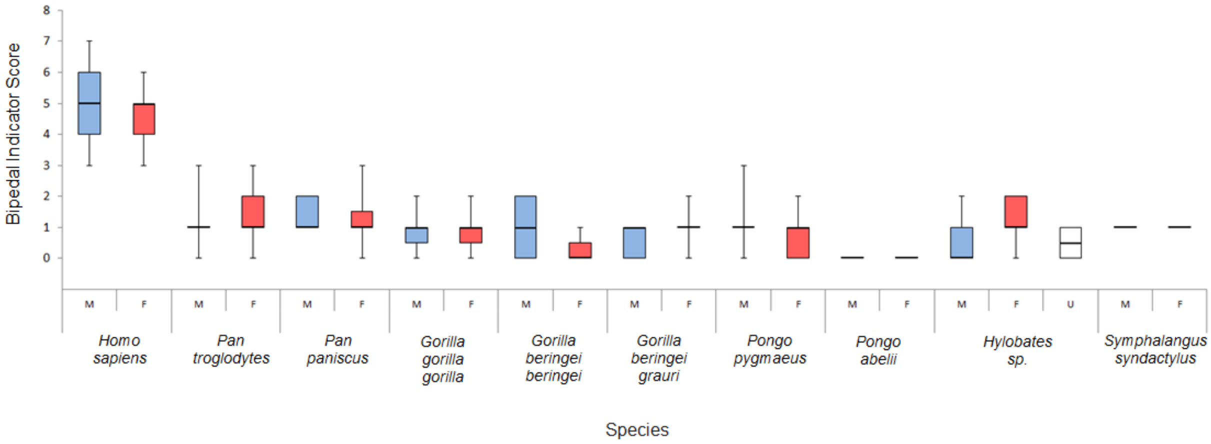


Figure 5.12. Total bipedal predictor scores in extant apes (see Methods for calculation). Boxes indicate median and interquartile range of data, error bars indicate data range. M = male; F = female; U = unknown sex.

Tables 5.5 and 5.6 show the most powerful combinations of predictor features identified by mRMR feature selection. Anterior twist of the femoral head and the angle of the lateral lip of the patellar groove were consistently selected in the top three features, and the angle of the distal tibial surface was consistently low-ranking. The AIIS ranked lowest when any recorded expression (i.e. including very slight expression) was scored as present (Table 5.5), but ranked highest when only moderate or pronounced expression was scored as present (Table 5.6). The OEG, however, ranked third when any expression was scored as present, but ranked lowest when only moderate or pronounced expression was scored. This is consistent with the individual predictive values described above, where the AIIS was prevalent among humans but also present in very slight or slight form in many nonhuman apes, whereas the OEG was absent in many modern humans. The mRMR method suggests that when predicting proficient, habitual bipedality, the most powerful combination of predictor features is the AIIS (providing only at least moderate expression is scored), anterior twisting of the femoral head and the angle of the lateral lip of the patellar groove.

Table 5.5. mRMR scores for morphological predictor features. Features are listed in order of combination value, such that the most powerful combination of two features would be 1 and 2; the most powerful combination of three features would be 1, 2 and 3, etc.

Predictor feature		mRMR score
1	Anterior twist of femoral head	0.433
2	Angle of lateral lip of patellar groove	0.082
3	OEG (any visible/palpable expression)	0.078
4	Angle of distal tibial surface	0.041
5	AIIS (any visible expression)	0.031

Table 5.6. mRMR scores for morphological predictor features (see Table 5.5 for explanation).

Predictor feature		mRMR score
1	AIIS (at least moderate expression only)	0.816
2	Angle of lateral lip of patellar groove	0.085
3	Anterior twist of femoral head	0.116
4	Angle of distal tibial surface	0.046
5	OEG (at least moderate expression only)	0.015

DISCUSSION

Reduced reliability of predictor features due to variation

Results suggest that the most reliable predictor of habitual/proficient bipedalism is the presence of multiple morphological indicators, rather than the presence of any one. Naturally this is employed when analysing more complete fossil specimens, particularly as many fossil species exhibit somewhat conflicting morphologies, but it suggests caution must be taken when assigning vital significance to one feature. The OEG, for example, has been cited as "critically important" to bipedal function (White, 2006), but was found in this study in 33% of nonhuman apes, and was completely absent in 8% of modern humans. Furthermore, features which included marked OEGs in *Or. tugenensis* were used to deduce that the species "must be a hominid in the narrow sense of the term" and "must have been a habitual biped" (Pickford et al., 2002). While the modern humans that exhibit a groove in this sample have more pronounced grooves than nonhuman apes overall, it must be noted that they rarely showed such clear grooves as are implied for *Or. tugenensis* (Pickford et al., 2002; Galik et al., 2004; see Figure 5.1) or *Au. afarensis* (Lovejoy et al., 2002). Thus despite being considered such a fundamental part of bipedal adaptations, the relationship between the OEG and positional behaviour is not yet fully understood. The strong grooves exhibited by some early hominins cannot be said to be unequivocally linked to bipedality because the variation among modern humans demonstrates that habitual bipedalism does not always result in groove formation. Yet the lack of OEGs among nonhuman apes counters the argument that other locomotor behaviours used by extant apes were the cause of the pronounced grooves in *Or. tugenensis* and *Au. afarensis*. The reliability of the OEG in predicting habitual bipedality is therefore particularly compromised when using its absence to predict a lack of bipedal capabilities. DeSilva et al. (2006), for example, attributed a proximal femur from Kikorongo, Uganda (with unknown age but likely prior to 8 KA and originally attributed to *Homo sapiens*), that lacked an OEG and intertrochanteric line, to *Pan*, but only tentatively, given the range of morphological variation among modern humans.

The variation among humans in this study, both within and between sexes, raises important questions about relying on the *absence* of a certain morphological feature as evidence for a lack of proficient/habitual bipedalism, or indeed for a form of bipedal locomotion which would have differed substantially from that used by modern humans. The lack of anterior twisting of the femoral head in *Au. afarensis*, for example, was used by Stern and Susman (1983) to infer a "distinct" bipedal gait from that seen in modern humans. Yet, in this study, anterior twisting is found lacking in 36% of modern humans, and the "ape-like" condition of a slightly posteriorly positioned femoral head, as is found in AL 288-1, is present in 6% of humans. This is mainly due to variation among the Thai human sample, with anterior twisting being more common in males. Those who lack anterior twisting are from different regions of northern Thailand and have no pathological indications of reduced locomotor ability; it is therefore unlikely that variation in expression of this feature in modern humans relates to bipedality. This does not, however, exclude the influence that other frequently-used postures, such as squatting (which is more common among Asian populations), may have on femoral head development, without a change in bipedal frequency (Bridger, 1991; Blair, 1994). Nor does it preclude the possibility that expression in these individuals is linked to frequent use of locomotor behaviours requiring substantial abduction at the hip, such as climbing. When one considers the extent of bipedal flexibility in modern humans, and that the condition in a probable female *Au. afarensis* was similar to that in a minority of female modern humans, it becomes unfeasible to adopt anterior twisting of the femoral head, on its own, as an indicator that *Au. afarensis* possessed a peculiar type of bipedal locomotion, mechanically disparate from that of modern humans. While the femoral morphology of *Au. afarensis* is more difficult to interpret, the lack of anterior twisting in extant nonhuman apes confirms Pickford et al.'s (2002) assertion that femoral head positioning in *Or. tugenensis* is "clearly outside the range of variation that occurs in [chimpanzees]", and counters Asfaw's (1985) prediction that larger sample sizes of African apes would yield more variation.

The discrepancy between the two modern human populations in orientation of the femoral head demonstrates the importance of including samples from more than one human population. Geographically disparate populations are likely to show variation in positional behaviour, either through differences in habitat and resource use, or differences in the cultural importance of certain activities. There may also be inter-population variation in genetic constraints on musculoskeletal development. These sources of variation will influence morphology, and should be considered in comparative studies of humans and nonhuman apes in order to make reliable conclusions about interspecific differences.

Inclusion of Asian apes

Some features, which have previously been pronounced absent in chimpanzees and western lowland gorillas, have been found here in other nonhuman apes, most notably OEG expression in gibbons, siamangs and bonobos, and a low distal tibial angle in gibbons and mountain gorillas. A low distal tibial angle was described by Latimer et al. (1987) as a hugely important adaptation to, and thus clear indicator of, terrestrial bipedality that would preclude significant arboreal activity, and which is "unequivocally present" in Hadar specimens (including AL 288-1). However, in this study, the angle reconstructed in AL 288-1 also falls within the range for gibbons, which are substantially arboreal. Furthermore, in both the distal tibial angle and twist of the femoral head, the condition in chimpanzees, among all nonhuman apes, tends to be the most different from that seen in humans. Although chimpanzees have the lowest percentage of bipedalism in their locomotor repertoire among nonhuman apes, the morphological variation in these indicator features between nonhuman ape species is unlikely to be simply related to bipedal frequency, as Sumatran orangutans, bonobos and siamangs (who have the highest percentages of bipedalism in their locomotor repertoires of approximately 7%, 6% and 6% respectively), do not appear substantially more human-like than the other nonhuman apes.

However, there is a small amount of evidence that the OEG and distal tibial angle, which are both observed in gibbons, may relate to bipedality but are influenced by relative substrate size during locomotion. Hylobatids have been reported to use bipedal locomotion along branches and do not engage in quadrupedal walking to the same extent as larger nonhuman apes (Fleagle, 1980; Gittins, 1983), but their smaller body size may mean that the mechanical requirements of bipedalism on wider branches are similar to those on the ground. It is therefore possible that these particular similarities between modern humans and hylobatids, which do not exist between humans and the much larger orangutans, are partly due to similarities in the functional requirements of bipedalism. This response to relative substrate size may also explain the low distal tibial angle observed in mountain gorillas, which are not particularly bipedal, but are considered highly terrestrial in comparison to other nonhuman apes. Thus apes that are largely terrestrial and those that are arboreal, but small in size, may exhibit converging adaptations based on similar mechanical requirements of their locomotor substrate. Orangutans, despite being the most bipedal of nonhuman apes, may therefore face some of the most mechanically disparate challenges to their locomotion from those faced by humans, due to their large body size and almost exclusively arboreal lifestyle (Thorpe and Crompton, 2005). The lack of an OEG in orangutans runs counter to Crompton et al.'s (2008) suggestion that scrambling and bridging behaviours, which are used by orangutans and can require extreme hip extension, are likely to lead to OEG formation. Once again, this demonstrates the need to test mechanically viable hypotheses against observations.

Predicting habitual bipedality in fossil hominoids

While the predictive values of these morphological indicator features are reasonably high, these results demonstrate the problems with reliability that relate to the amount of variation in these features among extant apes. When interpreting the morphology of fossil hominoids, compromises to reliability are most significant when only one characteristic is used to infer bipedalism. Given the fragmentary nature of fossil remains, it is hoped that the estimates of sensitivity and specificity produced here may prove useful to researchers by providing an indication of the relative reliability of these features as indicators of habitual bipedality. In cases where fossil skeletons are more complete, results suggest that the presence of at least three of the bipedal predictors studied here is a more reliable method for indicating habitual bipedality than the presence of one. The most powerful combination of three features from these five is a prominent AIIS, a high lateral lip of the patellar groove of the femur, and an angle of <100° of the distal tibial articular surface.

The morphological variation among modern humans in features that are seen as functionally important for bipedalism questions the significance of using the absence of certain features as evidence for either a lack of bipedal capabilities, or a different form of bipedal locomotion from modern humans. Recent observations on the flexibility of modern humans in regard to their locomotor repertoires in general, and bipedal mechanics in particular, warn against assuming stereotyped forms of locomotion in hominins. Furthermore, Venkataraman et al. (2013b) demonstrated how muscular adaptations to locomotion do not necessarily require skeletal adaptation. It is therefore likely that we underestimate the locomotor abilities of early hominins who lack modern human-like morphology. The skeletal morphology of *Au. afarensis*, for example, falls partially into the range for nonhuman apes but also into the range for modern humans, suggesting it may have been capable of a more flexible bipedal gait than traditionally assumed, and not necessarily fundamentally different from modern humans.

CONCLUSIONS

Reliability of the skeletal indicators considered here is compromised due to considerable intra- and inter-specific variation, and researchers should be aware of the predictive value of each feature as inferred from sensitivity and specificity tests. Most features show variation among modern humans and can be found to some degree in extant nonhuman apes, and we should not underestimate either the morphological variation or behavioural flexibility that may have occurred in a fossil hominoid species. In particular, researchers seeking to infer locomotor behaviour and assess hominin status should consider that absence of a particular feature is a fairly common occurrence in modern humans, and thus should not be taken to imply absence of bipedalism as a significant component of an individual's locomotor repertoire. A combination of at least three predictor features provides a more reliable indication of habitual bipedalism.

CHAPTER SIX

RELIABILITY OF PREDICTING RANGE OF MOTION AT HINDLIMB JOINTS FROM SKELETAL MORPHOLOGY IN EXTANT GREAT APES

Author contributions: chapter written by Emily Saunders and reviewed by Alice Roberts and Susannah Thorpe

ABSTRACT

Some reconstructions of locomotor behaviour in fossil hominoids, particularly in *Australopithecus afarensis*, have been based on predictions of joint range of motion (ROM) measured from skeletal material. However, it is unclear whether skeletal measures of ROM are associated with measures of passive ROM (maximum ROM capability in a living animal) or active ROM (the ROM used during positional behaviour) in extant apes. Thus reconstructions of locomotor behaviour based on skeletal ROM may be unreliable. In this study flexion/extension ROM at the hip, knee and ankle was measured from skeletal material in extant great apes, and compared with published data on passive and active ROMs where possible. Results revealed considerable intraspecific variation and few clear interspecific differences in skeletal ROMs. Comparisons of skeletal, passive and active ROMs at the hip suggest that inferences of locomotor capacity in fossil hominoids based on differences between extant apes may be unreliable. Furthermore, interspecific variation in active ROM demonstrates how different species are able to achieve the same locomotor behaviours with different joint kinematics. This study highlights the importance of morphological and behavioural flexibility in ape locomotion, and supports the argument that locomotor capacity in extinct hominoid species may have been less restricted than reconstructions from skeletal morphology suggest.

INTRODUCTION

Determinants of ROM

Musculoskeletal morphology at each joint reflects a trade-off between mobility, which allows larger displacements of body segments, and stability, which reduces the likelihood of dislocation (Aiello and Dean, 1990). Fibrous joints (e.g. cranial sutures) and cartilaginous joints (e.g. symphyses), which fuse throughout ontogeny, allow very little movement and are thus the most stable (Adams, 2015). Synovial joints, which are lubricated by synovial fluid, allow much greater movement, and the joint that is most mobile in humans – the shoulder – is consequently the least stable and thus the most commonly dislocated (McFarland et al., 1996; Adams, 2015). The stability of synovial joints, and therefore the limit of their range of motion (ROM), is determined by all aspects of musculoskeletal anatomy around the joint: morphology of bone and fibrous tissue/cartilage around the articulating surfaces, stabilising ligaments and muscle-tendon units. The hip joint, for example, is rotated in a variety of planes by 15 muscles, but is primarily a weight-bearing joint and thus requires substantial stability. The chance of femoral head dislocation is reduced by concavity of the acetabulum and the presence of acetabular labrum cartilage, which together increase the depth of the joint (Rális and McKibbin, 1973). ROM (particularly maximum extension and abduction) is heavily restricted by the iliofemoral, pubofemoral and ischiofemoral ligaments, and by the surrounding muscles, particularly strong posterior muscles such as the gluteals, which are compensated for by the stronger presence of stabilising ligaments anteriorly (Aiello and Dean, 1990). All of these determinants of joint ROM change throughout ontogeny in response to both internal and external environmental factors (Calguneri et al., 1982; Bini et al., 2000; Pilbeam, 2004).

In addition to these functional constraints on joint ROM by the musculoskeletal system, ROM is also restricted by factors such as an individual's size and thus the amount of flesh surrounding a joint, and in humans, joint ROM generally decreases with BMI (Bini et al., 2000; Soucie et al., 2004). Pathology can also be associated with ROM; in humans, osteoarthritis of the hip joint, for example, results in reduced flexion/extension ROM which causes pain when walking (Hurwitz et al., 1997), and in the elderly, small joint ROM is thought to be a major contributing factor to gait instability (Kang and Dingwell, 2008).

Joint stability at major limb joints is crucial not only because these joints might be subject to substantial weight-bearing, but also because severe dislocation can disrupt blood supply and innervation to the distal body segment (Ganz et al., 2001). Yet despite these risks, extant apes generally have very mobile limb joints (Payne et al., 2006a; b; Thorpe and Crompton, 2006; Hammond, 2014). It is therefore likely that the advantages of increased ROM – perhaps to facilitate effective movement through the forest canopy – outweighed the disadvantages associated with joint dislocation throughout the evolution of locomotor anatomy in hominoids.

The importance of ROM

The extent to which an animal can displace weight-bearing body segments via joint rotation is a key determinant of locomotor capacity (Walker, 1974; Jenkins and Camazine, 1977; Grand, 1984; Crompton et al., 2008; Schmidt and Krause, 2011). In modern humans, while the ROM required at each major hindlimb joint during normal locomotor behaviour is generally smaller than the ROM required during other activities, such as transferring between standing and sitting or squatting (Mulholland and Wyss, 2001), the kinematics of effective terrestrial bipedalism rely particularly on sufficient dorsiflexion ROM at the ankle and metatarsophalangeal (MTP) joints (Hetherington et al., 1990; Dobkin, 2003, p 252–254). Nevertheless, a terrestrial lifestyle has been linked with substantial underutilisation of joint ROM in modern humans (Alexander, 1994), and the arboreal environment is thought to demand a much greater ROM in both hindlimb and forelimb joints to allow efficient locomotion through complex networks of branches. Hammond (2014) and Chan (2008) suggested that non-suspensory hominoids underutilised forelimb ROM compared with suspensory hominoids, and Hunt (2016) noted how nonhuman apes, being large-bodied, rely upon joint ROMs that allow effective movement and stability, as well the ability to reach food, within the terminal branch niche environment. In chimpanzees, this is facilitated by muscular adaptations that allow substantial power to be produced through a large ROM (Payne et al., 2006a; b).

Predicting ROM from the skeleton

Several authors have used skeletal predictions of ROM at certain joints in fossil hominoids to aid interpretation of positional behaviour in extinct species (Latimer et al., 1987; Latimer and Lovejoy, 1990; Richmond and Jungers, 2008). However, because joint ROM is affected by a wide range of factors relating to soft tissue anatomy as described, the extent to which meaningful information on ROM can be extracted from skeletal material alone is unclear. Inferring locomotor behaviour from such information also relies on two assumptions: that skeletal morphology can reliably predict an animal’s full ROM capacity at a given joint, and that full ROM capacity is related to the actual ROM used by the animal during locomotor behaviour. These three components are referred to as: skeletal ROM (a measure of full ROM for a given joint from skeletal morphology alone); passive ROM (the total ROM at a given joint of which an animal is capable, measured from the living individual); and active ROM (the ROM that an animal uses during positional behaviour).

Latimer et al. (1987) argue that the ROM to which a joint is adapted can be reliably inferred from skeletal material by assuming that any position in which maximum congruence is maintained between the two articulating surfaces would have been possible for the animal in question. Articular congruence refers to the level of overlap between two articulating surfaces perpendicular to the plane of rotation; in a hinge or ball-and-socket joint, for example, articular congruence would decrease if rotation occurred to the extent that a smaller proportion of the convex surface was in contact with the concave surface. When a joint rotates to the extent that articular congruence decreases, particularly during weight-bearing, the animal risks injury due to increased tensile stress in the stabilising ligaments and transarticular pressure caused by reduced cartilage contact and increased muscle activity (Latimer et al., 1987; Latimer and Lovejoy, 1990). In addition to assuming that passive/active ROM can be reliably predicted from skeletal material, this method also assumes that the presence of cartilage does not significantly alter the relative geometry of the two articular surfaces, and thus the level of congruence that can be maintained between them during rotation.

The method of inferring joint ROM by rotating bones (either manually or virtually using scanned images), while maintaining full congruence of the articular surfaces, has been employed in the analysis of the most complete *Australopithecus afarensis* skeletons to reconstruct the species' locomotor behaviour. Latimer et al. (1987) calculated a large skeletal ROM at the talocrural joint (from the talus and tibia only) in AL 288-1 ("Lucy") that exceeded the skeletal ROM not only in modern humans, but also in African apes. However, the authors cited intraspecific and possible allometric variation in skeletal talocrural ROM among extant hominoids, as well as other, more modern human-like features of the AL 288-1 pedal skeleton, as evidence against altering their reconstruction of *Au. afarensis* as a habitual biped restricted to terrestrial locomotion. Latimer and Lovejoy (1990) likened the greater percentage of dorsiflexion and smaller percentage of plantarflexion in the ROM at the MTP joint in AL 333-115 to that in modern humans, in order to argue against pedal prehensile capability – and thus arboreal locomotor capacity – in *Au. afarensis*. However, the total skeletal ROM at the MTP joint for AL 333-115 is estimated at 120°; in modern humans, passive ROM does not exceed 100° (Nawoczenski et al., 1999). Therefore, if one assumes that skeletal ROM relates to passive ROM, a similar percentage of ROM may be allocated to dorsiflexion in both species, but the absolute passive ROM in AL 333-115 would have been greater, meaning that *Au. afarensis* would have had greater plantarflexion capabilities than modern humans. This renders the argument that *Au. afarensis* was restricted to a more modern human-like form of locomotion less plausible. Thus although *Au. afarensis* morphology clearly displays evidence of modern human-like bipedalism, it is surprising that Latimer et al. (1987) did not interpret the large skeletal ROMs at the talocrural and MTP joints as reasons to take more caution in their rejection of arboreal capacity in the species.

Sources of error in skeletal ROM

The studies of Latimer et al. (1987) and Latimer and Lovejoy (1990) have compared skeletal ROM between hominoid species, yet it is unclear how these skeletal ROMs relate to passive and active ROMs, and thus to locomotor behaviour in living animals. Evidence suggests that tight links cannot always be drawn between skeletal morphology and locomotor function in hominoids. Despite being habitual bipeds, the skeletal morphology of modern humans can accommodate substantial behavioural flexibility (Venkataraman et al., 2013b; Chapter Three), and humans may significantly underutilise their passive joint ROM during routine activity (Alexander, 1994). Furthermore, morphological features in modern humans that have been associated with habitual bipedalism show considerable intraspecific variation (Chapter Five). There is also conflicting evidence about whether locomotor behaviour is indeed affected by passive ROM; Cornwall and McPoil (1999) found that passive flexion/extension ROM at the ankle was significantly associated with gait kinematics in modern humans, but this was contradicted by the findings of Turner et al. (2007). It is therefore likely that the link between locomotor anatomy and behaviour in modern humans is not as tight as has sometimes been assumed during studies of fossil hominoid morphology. Hominoid morphology reflects a compromise between the demands of different locomotor behaviours, and extant great apes rely on particularly broad positional repertoires (see Chapter One). It is unlikely that measurements of passive ROM are closely related to all behaviours in the ape locomotor repertoire; yet it is unclear whether passive ROM relates to frequently used behaviours, or to important behaviours that may be required less frequently but which rely on the extremes of joint ROM. Therefore, even if skeletal ROMs were closely linked to passive ROMs, this may not translate into reliable predictions of either full locomotor capacity or the most commonly used locomotor behaviours. Thus comparisons of skeletal, passive and active ROMs can be used to highlight differences between what an animal appears to be adapted to (from skeletal ROM), what its performance capabilities are (passive ROM), and what it does during positional behaviour (active ROM).

It is therefore necessary to investigate intra- and interspecific variation among extant hominoids in measurements of a) skeletal joint ROM, b) passive ROM and c) active ROM used during locomotor behaviour. This will allow assessment of whether passive and active ROM can be reliably inferred from skeletal material. While the most robust means of comparing skeletal, passive and active ROM would be to measure all three in the same individual, this would be unfeasible for nonhuman apes as it would require either scans or studies lasting the duration of the subjects' adult life in order to obtain skeletal information, both of which would only permit small sample sizes. However, measurements of skeletal, passive and active ROM in separate individuals can still reveal whether interspecific differences in one measurement of ROM are reflected in another measurement. Thus while it is unlikely that skeletal ROM accurately reflects an individual's passive ROM due to soft tissue constraints, similar relative interspecific differences in the two measurements would imply a relationship between skeletal and passive ROM. Such data will provide useful information about the reliability of interpretations of fossil hominoid locomotion based upon skeletal ROM and comparison with locomotor behaviour in extant species.

Study aims

This study investigates variation in skeletal flexion/extension ROM at the hip, knee and ankle from skeletal specimens of humans and nonhuman great apes. These data are compared with published measurements of passive and active ROM from samples of living apes where possible. Active ROMs are taken from available data during bipedalism, quadrupedalism and vertical climbing in order to investigate interspecific differences that relate to these relatively frequently used locomotor behaviours. Although an animal's true active ROM would include its full positional repertoire, skeletal ROMs are often considered in the light of these three behaviours, meaning that the comparisons made here are highly relevant to reconstructions of fossil hominoids (Latimer et al., 1987; Latimer and Lovejoy, 1990; DeSilva, 2009; DeSilva et al., 2013). Also, increasing evidence showing the extent of locomotor flexibility in living hominoids (Thorpe and Crompton, 2006; Hunt, 2016; see Chapter One) may well render collection of true active ROM data unfeasible. It is hypothesised that active ROM in each species represents only a portion of passive ROM, and in turn, that passive ROM comprises only a portion of skeletal ROM (Figure 6.1). Investigating the nature of these relationships, and considering them alongside extant ape locomotor ecology, will aid identification of the elements of behaviour that can be reliably predicted from skeletal morphology alone. Findings on the reliability of inferring locomotor behaviour from skeletal ROMs are then used to reassess reconstructions of locomotor capacity based on skeletal ROM in *Au. afarensis*.

Figure 6.1. Illustration of articulated talus and tibia to demonstrate the hypothesis that skeletal ROM is larger than passive ROM, which in turn is larger than active ROM used during locomotion. Anterior is towards the left, superior is towards the top.

MATERIALS AND METHODS

Skeletal material

Skeletal specimens of non-pathological, adult great apes (Table 6.1) were studied using the collections and inclusion criteria described in Chapter Five. In order to make measurements of joint ROM reliable, individuals with any damage to bone that affected the relevant articular surfaces were also excluded.

Table 6.1. Great ape specimens used to measure skeletal ROM at the hip, knee and ankle

Species	***n* (male, female)**		
	Hip	**Knee**	**Ankle**
Homo sapiens	38 (22,16)	59 (36,23)	51 (31,20)
Pan troglodytes	56 (17,39)	57 (17,40)	55 (16,39)
Pan paniscus	13 (6,7)	16 (7,9)	14 (6,8)
Gorilla gorilla gorilla	38 (16,22)	45 (21,24)	44 (20,24)
Gorilla beringei beringei	2 (0,2)	5 (2,3)	4 (1,3)
Gorilla beringei grauri	9 (6,3)	15 (8,7)	13 (6,7)
Pongo pygmaeus	14 (8,6)	15 (9,6)	10 (6,4)

Measurements of skeletal ROM at the hip, knee and ankle

Skeletal ROMs were obtained following the maximum congruence method used by Latimer et al. (1987), but using digitised photographs rather than manual rotation of bones. The method of determining flexion/extension ROM at the hip and ankle involved digitising the full lengths of the two relevant articular surfaces from photographs taken perpendicular to the plane of rotation, before subtracting the length of the concave surface from that of the convex surface in order to obtain the maximum possible angle of rotation (Figure 6.2). Because maximum congruence dictates that bones will maintain full articular surface contact during rotation in a given plane, the limits of the articular surfaces represent the limits of joint ROM. Consider a ball-and-socket joint, as illustrated in Figure 6.2: the maximum amount of rotation allowed by the rotating bone alone (i.e. the ball) can be obtained using the bone’s convex surface limits and centre of rotation. However, to maintain maximum congruence the whole length of the concave articular surface (i.e. the socket) must remain in contact with a portion of the convex surface. This portion of the convex surface can be removed by subtracting the length of the concave surface (shown by the red arrow in Figure 6.2), leaving only the part of the convex surface that can rotate fully out of the joint socket (shown by the green arrow in Figure 6.2). This remaining part of the convex surface represents the total rotation potential of the joint in that plane, and skeletal ROM can be measured as the angle from the centre of rotation to its two outer limits.

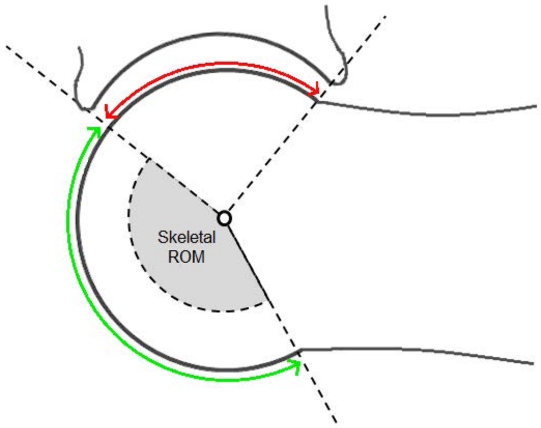


Figure 6.2. Method of skeletal ROM calculation based on the maximum congruence method of Latimer et al. (1987). The portion of the convex articular surface in contact with the concave articular surface is removed by subtracting the concave surface length (red arrow) from the convex surface length. The remaining arc (green arrow) represents the full rotation potential of the joint in that plane. The resultant angle formed from the centre of rotation thus represents the angle of skeletal ROM.

To obtain the articular arcs for the hip joint, the innominate and sacrum were oriented with the pubic symphysis and central sacrum in the same vertical plane and the innominate clamped in position, thus orienting the plane of flexion/extension rotation to the vertical. The femur was then manually rotated inside the acetabulum while keeping the posterior aspects of the femoral condyles perpendicular to the vertical plane, thus resulting solely in flexion/extension movement without abduction/adduction or internal/external rotation. This position was maintained by sight using a custom-built platform device (Figure 6.3).

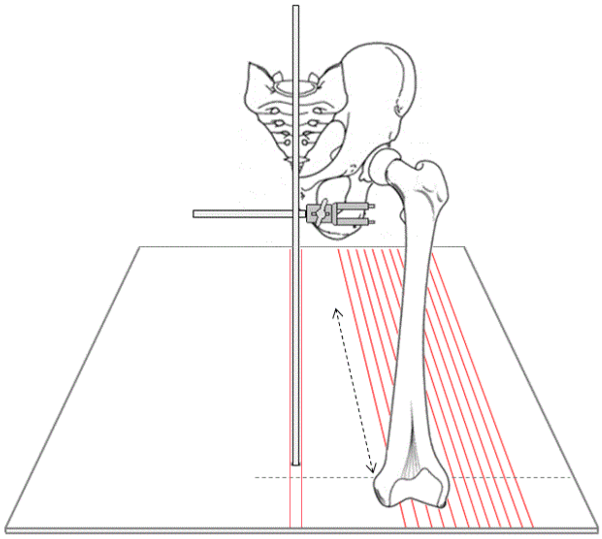


Figure 6.3. Illustration of the device used to determine limits of flexion and extension at the hip for calculation of skeletal ROM (not to scale). The device was a board 1.5m long with lines drawn along its length at 1cm intervals, which was placed over the base of a clamp stand. The innominate was positioned with the centre of the sacrum and pubic symphysis aligned in the vertical plane, parallel to the length of the board (achieved by sight using central red lines). The innominate was then clamped in position using a padded grip. The femoral head was placed inside the acetabulum, and the femur oriented with the inferior surfaces of the condyles flat and the posterior surfaces perpendicular to the length of the board. The femur was then manually rotated along the red lines by sight, thus reflecting flexion/extension without abduction/adduction (shown by the direction of the arrow).

Following the full articular surface congruence method of Latimer et al. (1987), the positions of maximum flexion and extension were taken as the positions at which the acetabulum came into contact with femoral neck rather than articular surface. At each of these two positions, the point at which articular surface contact reduced was marked in pencil on both bones. To obtain the shape of the acetabular articular surface, a carpenter’s profile gauge was inserted between the two marked points and along the middle of the lunar articular surface, and a photograph taken of the resultant impression on the profile gauge. For the equivalent arc on the femoral head, a photograph was taken of the femoral head perpendicular to the plane of flexion/extension (oriented using the posterior femoral condyles), and the articular surface length taken as the visible arc between the two pencil points (Figure 6.4).

To obtain arcs of rotation for the ankle joint, a photograph was taken of the talus from a lateral aspect showing the full anteroposterior contact surface for the tibia, together with another photograph of the impression from inserting the profile gauge along the corresponding anteroposterior surface of the distal tibia at its lateral edge.

The curve of each articular surface was manually digitised from these photographs using TPSDig (v2.18, Rohlf 2015, SUNY, Stony Brook) and recorded as landmark coordinates plotted at every 0.5mm. The length of each concave surface (the acetabulum/distal tibia) was subtracted from the curve of the corresponding convex surface (the femoral head/talus). A circle was then fitted to the remaining curve via generalised least squares (GLS; i.e. by minimising the sum of the distances between each point on the curve and the superimposed circle) in order to locate the logical centre of rotation, and the maximum angle of rotation calculated as the angle from the centre to the two points at each end of the curve (Figure 6.4d).

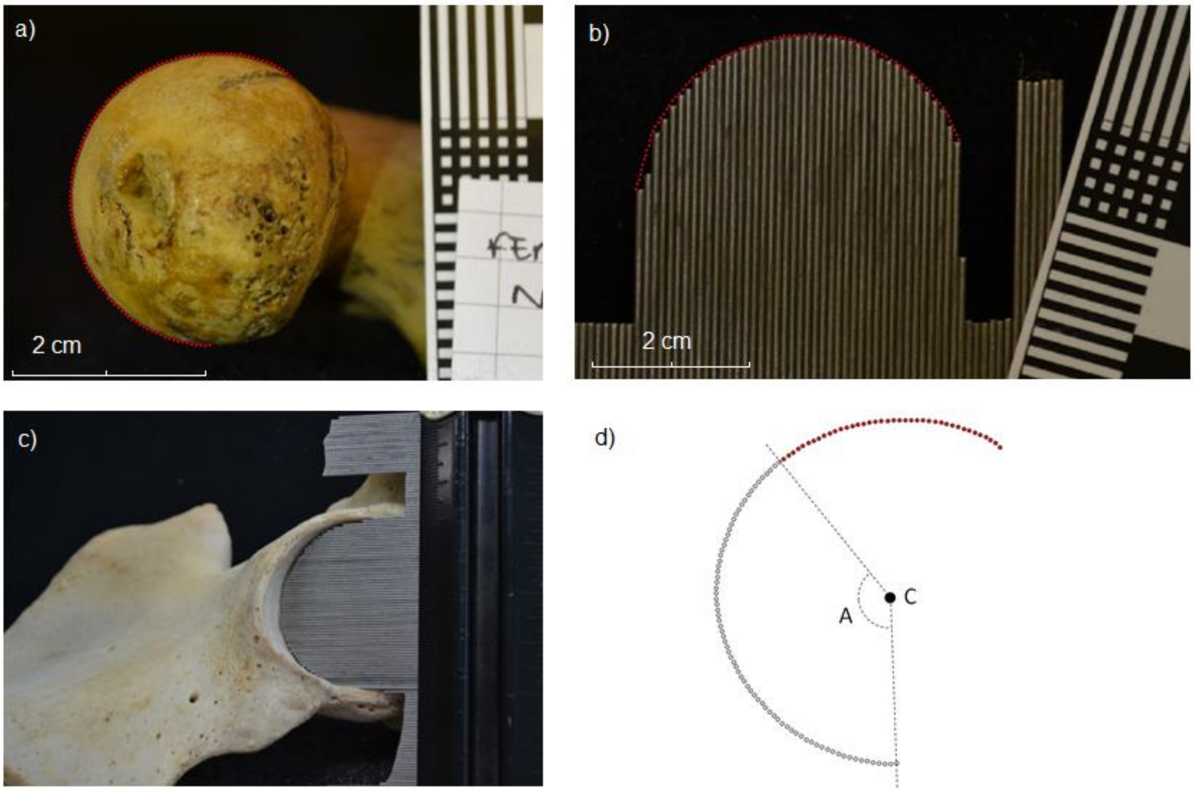


Figure 6.4. a) Photograph of femoral head with outline curve plotted in red. b) Outline curve of acetabulum plotted onto profile gauge impression. c) Insertion of profile gauge into acetabulum. d) Landmarks exported from the outline curve of the femoral head. The length of the acetabular articular surface is subtracted (indicated by red landmarks). The maximum angle of rotation (A) is calculated from the centre of the circle of closest fit (C) to the landmarks at each end of the curve.

This method was not appropriate for obtaining the flexion/extension ROM at the knee joint due to the role of gliding, as well as rotation, of the tibia around the femur, and the different roles of the medial and lateral femoral condyles (Aiello and Dean, 1990), both of which make accurate reconstruction of articular movement from skeletal material alone difficult. However, because the posterior aspects of the femoral condyles rotate fully out of the tibial condyles during extreme extension, the arc of rotation can be characterised merely by the surface of the femoral condyles, from the superior edge to the point adjacent to the position of the posterior-most point of the tibial articular surface when the tibia stops rotating around the posterior femoral condyles and starts to glide across their flatter, inferior aspects (Figure 6.5). Thus a photograph was taken of the medial femoral condyle from a medial aspect and the visible articular surface of the condyle was digitised, starting at the superior edge and continuing along the majority of the flat inferior edge, and recorded using landmarks as described above.

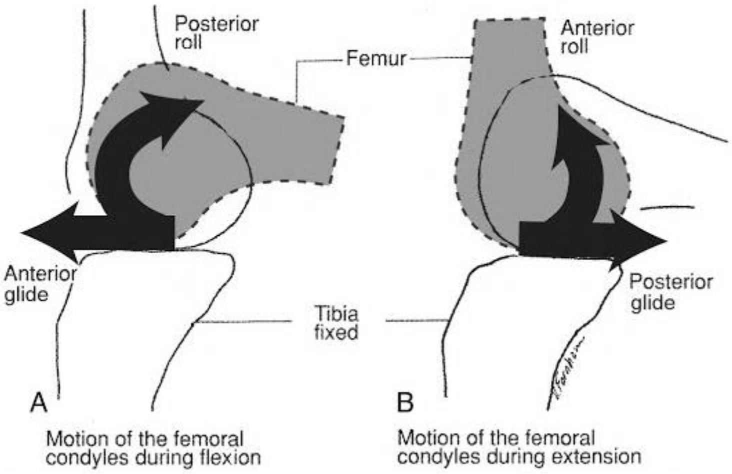


Figure 6.5. Illustration of the roll (rotation) and glide movements of the femur during knee flexion and extension. Taken from Hartigan et al. (2011).

The point on the arc of the femoral condyle that would be adjacent to the posterior edge of the tibial surface at the point when the extending tibia ceases circular rotation and begins to glide across the inferior surface of the femoral condyle was determined using GLS circle fit and cumulative sum (CUSUM) change detection (Taylor, 2000). CUSUM change detection is a statistical technique typically applied to time series analysis to identify data points that deviate above or below a certain threshold in order to detect the point at which a significant alteration from a previous pattern takes place (Taylor, 2000). Firstly, a circle was fitted to the first half of the landmarks on the femoral condyle curve (i.e. the posterior half) using GLS in order to determine the circular rotation of the femur within the tibia. The CUSUM technique was then applied to the "error" of each landmark on the femoral condyle curve; i.e. the distance (measured in mm) between each landmark and the circumference of the superimposed circle, in order to detect the point along the curve at which the landmarks begin to deviate away from the circle. The protocol for the CUSUM method, and subsequent calculation of the circular rotation angle of knee flexion/extension, is as follows (Figure 6.6):

- Data points are plotted in sequence. Here, each data point was the "error" of each landmark; thus, for example, the data point for a landmark positioned exactly on the superimposed circle would be 0.
- A benchmark value is determined, representing the target value for each data point during normal progression (i.e. with no change in pattern). The difference between each data point and the benchmark value are then cumulatively summed in sequence. This method assumes that deviations above and below the benchmark will cancel each other out, averaging 0. Because all data points here represented error values and were therefore positive, the benchmark value could not be set at 0, as the absence of values lower than the benchmark would result in the CUSUM gradually increasing, rather than averaging 0. Here, the benchmark value was set as the average of the first quarter of data points. These were consistently low for each curve analysed, being very close to the superimposed circle.
- In order to determine the point at which normal progression is violated, and data points begin to deviate away from the benchmark, the analysis detects those data points whose CUSUM is above a certain threshold. Here, the threshold above which the CUSUM was deemed to have changed was set at 0.1 standard errors, being highly sensitive, but not

resulting in “false alarms” in any cases, i.e. where the error rises before returning to the benchmark.

- All the data points whose CUSUM deviated significantly from the benchmark value were identified. These represented the landmarks on the femoral condyle curve which deviated significantly from the superimposed circle.
- These landmarks were removed from the curve, the remaining curve thus representing the arc of circular rotation.
- The angle of rotation for knee flexion/extension was calculated as the angle from the centre of the superimposed circle to the first and last landmarks on the curve.

CUSUM analysis was carried out using the qcc package for R (v2.6; Scrucca, 2004).

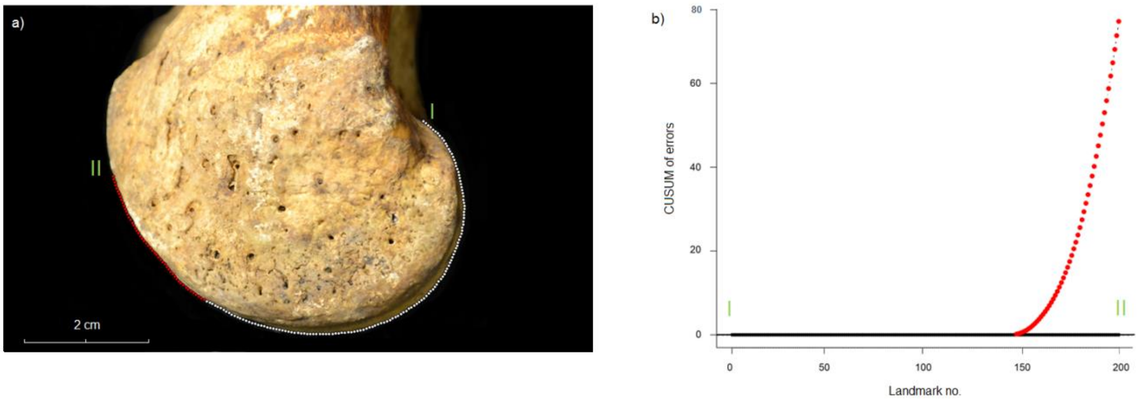


Figure 6.6. Illustration of the CUSUM technique used to determine flexion/extension ROM at the knee. a) The photograph of the medial femoral condyle with the outline curve represented by landmarks positioned every 0.5mm. The curve is plotted from I to II. b) CUSUM plot of the error of each landmark. Each landmark is plotted along the x axis, and the error (the distance between each landmark and the circle fitted to the first half of the landmarks) along the y axis. The CUSUM threshold is set at 0.1 standard errors of the mean of the first quarter of data points. Red data points represent landmarks for which the error is higher than the CUSUM threshold. These landmarks also appear in red on the photograph, and were removed in order to obtain the arc of rotation.

Measurement errors

All stages of measuring skeletal ROM were repeated for 10% of specimens from each species on a different day from their initial measurements. All repeated measures of skeletal ROM were within 10% of the original measurement, and none exceeded a difference of 6°.

Statistical analysis of skeletal ROMs

Significant differences in skeletal ROM at each joint between species and sexes were determined using Factorial Analysis of Variance (ANOVA) with Bonferroni correction and Tukey's HSD post-hoc on the maximum angles of rotation obtained using the methods described above. Because the effect of sex did not appear to be uniform between species, Independent Samples T Tests were also used to investigate sex differences within each species of nonhuman ape. In humans, Factorial ANOVA was used to investigate the effects of sex and population (UK vs Thai individuals). Allometric variation in ROM at each joint was investigated using linear regression models. Lower limb length (femur length + tibia length) was used as a proxy for body size, being the most relevant measurement to the joints studied, and because the allometric relationship between specific long bone lengths and stature varies slightly both within and between species (Ruff, 1987; Duyar and Pelin, 2003). All statistical tests were carried out in R (v3.3.1; R Core Team, 2016).

Passive and active ROM measurements

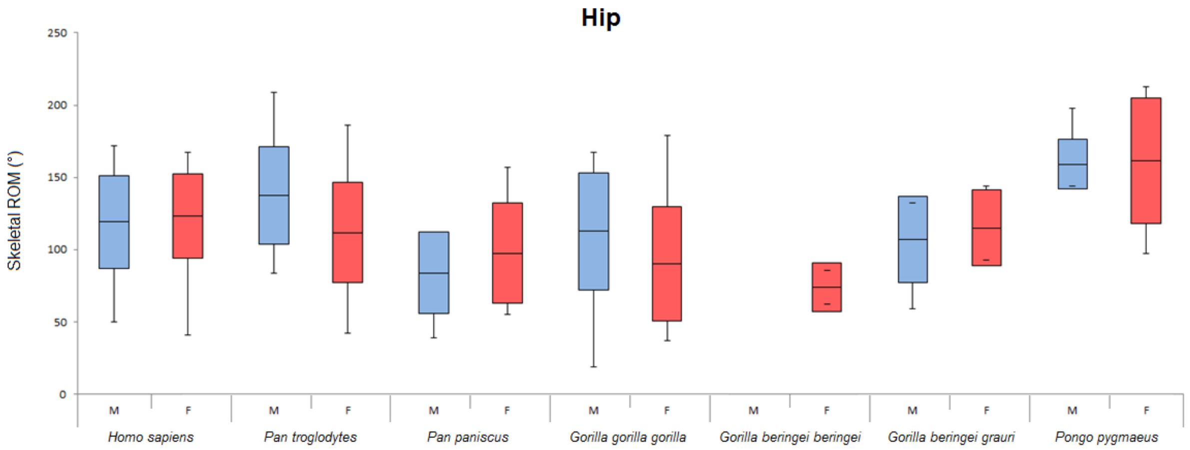
Data on passive flexion/extension ROM at the hip (data for the knee and ankle unavailable for nonhuman apes) were taken from Soucie et al. (2011) for modern humans (20 – 49 age group) and from Hammond (2014) for adult chimpanzees, western lowland gorillas and Bornean orangutans (nonhuman ape subjects were anaesthetised). Data on active ROM during locomotion was available for quadrupedalism, bipedalism and vertical climbing. ROM at the hip, knee and ankle during bipedalism and quadrupedalism was taken from Chapters Two, Three and Four for modern humans, chimpanzees and western lowland gorillas, and from D'Août et al. (2002) for bonobos. ROM at the hip and knee during vertical climbing was available from Isler (2005) for western lowland gorillas, bonobos and Sumatran orangutans. Because these studies differed in data collection method, data resolution, sample sizes and representation of sexes, statistical comparison across studies was not appropriate. These data were plotted in order to provide a preliminary investigation of whether patterns of skeletal ROM are likely to be reflected in patterns of passive or active ROM.

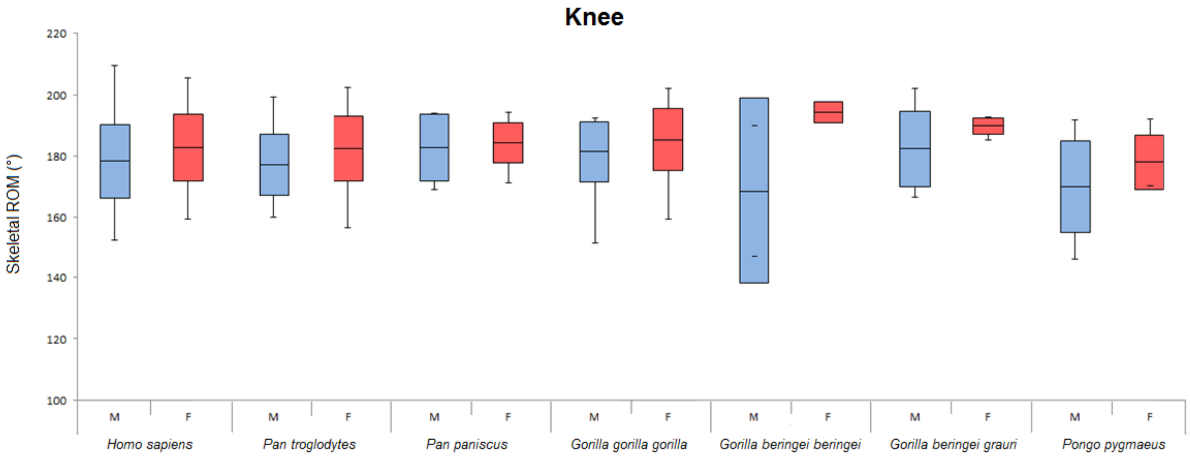
RESULTS

Skeletal ROM at the hip, knee and ankle

Skeletal flexion/extension ROM at the hip, knee and ankle in extant apes was characterised by extensive intraspecific variation and few significant differences between species (Figure 6.7). Factorial ANOVA revealed effects of species on skeletal hip and ankle ROM, and of sex on knee and ankle ROM. At the hip, Bornean orangutans had a significantly larger ROM at the hip than all other species (F [6,157] = 7.16, p = 0.00; Tukey HSD $p < 0.05$ [for all species]), and at the ankle, modern humans had a significantly lower ROM than all other species (F [6,177] = 26.89, p = 0.00; Tukey HSD $p < 0.05$ [for all species]).

Across the whole dataset, females had a larger ROM both at the knee (F [1,198] = 11.89, p = 0.002) and at the ankle (F [1,177] = 6.89, p = 0.028). However, the only significant within-species sex effects observed were in chimpanzees, where hip ROM was larger in males (t [54] = 2.54, p = 0.014) and ankle ROM was larger in females (t [53] = 2.59, p = 0.012). It is notable that the mean knee ROM was largest in females for all species except bonobos,





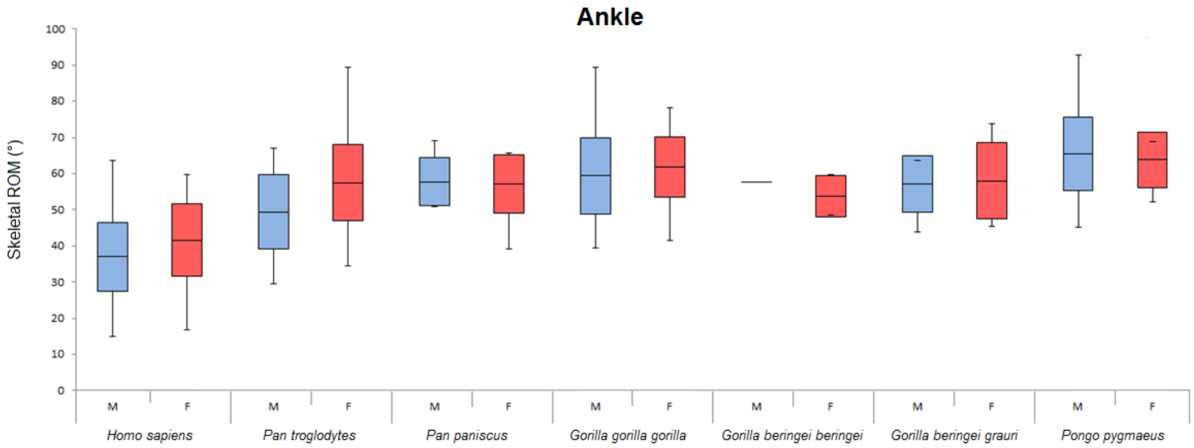


Figure 6.7. Skeletal flexion/extension ROM at the hip, knee and ankle in extant great apes. Boxplots show mean and standard deviation, error bars show the total data range. M = males; F = females.

although not statistically significant, and that the range for male mountain gorillas, while hugely varied, did not overlap with female mountain gorillas (sample sizes for mountain gorillas were too small to be tested individually).

Factorial ANOVA revealed an effect of population, rather than sex, within the skeletal ROM data for modern humans. Thai individuals had significantly larger ROM than the UK population at the hip (F [1,34] = 14.40, p = 0.002) and at the ankle (F [1,47] = 9.17, p = 0.012). Mean skeletal hip ROM in the Thai population was higher than African apes and much closer to that of orangutans, while the mean hip ROM for UK humans was below that of African apes (Figure 6.8). The range of ankle ROM for the Thai population also overlapped much more with other species compared with the UK population, despite the mean ankle ROM of both populations being lower than that for nonhuman apes (Figure 6.8).

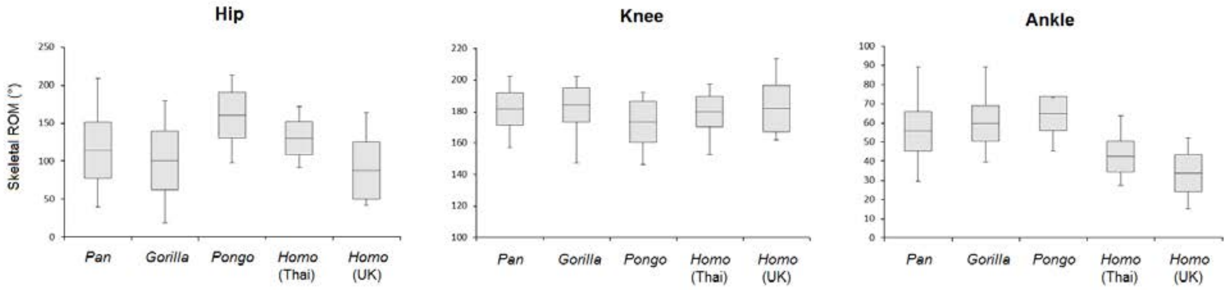


Figure 6.8. Skeletal flexion/extension ROM at the hip, knee and ankle in UK and Thai populations of modern human compared with other ape genera. Boxplots show mean and standard deviation, error bars show the total data range.

The high level of intraspecific variation in skeletal ROM at all three joints was not always associated with sex or population, and resulted in significant overlap between the ranges for different species. Only female mountain and eastern lowland gorillas appeared relatively stereotyped in skeletal ROM at the knee (Figure 6.7), although sample sizes were small. Even at the ankle, where modern humans had statistically lower ROM, the range for female humans overlapped those for all nonhuman apes except male orangutans, and the range for chimpanzees extended well below the mean for female humans (Figure 6.7). Linear regression models found no substantial allometric variation in inferred ROM among nonhuman apes. Ankle ROM appeared to be inversely associated with lower limb length in humans (Figure 6.9), but was not statistically significant (F [1,50] = 3.78, $p = 0.057$, $R^2 = 0.05$).

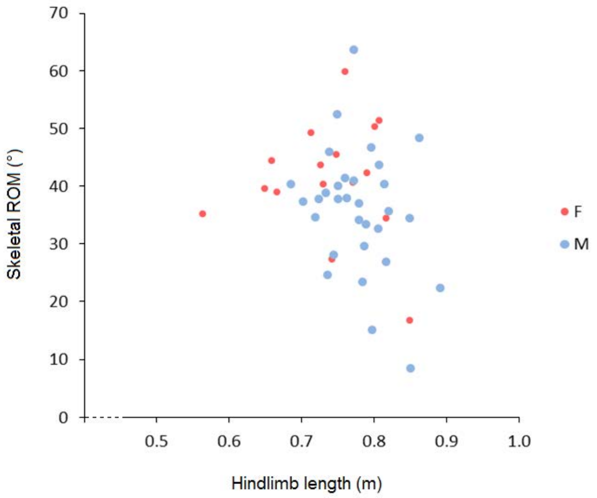


Figure 6.9. Variation in skeletal ankle flexion/extension ROM with hindlimb length (femur + tibia length) in modern humans. M = males; F = females. Linear regression: F [1,50] = 3.78, $p = 0.057$, $R^2 = 0.05$.

Comparison with passive and active ROM at the hip

In male chimpanzees and male western lowland gorillas, skeletal ROM was largest and active ROM smallest, as hypothesised (Figure 6.10; Table 6.2). However, in modern humans, female chimpanzees and female lowland gorillas, passive ROM was larger than skeletal ROM; and in male humans, active ROM was the largest measurement (active ROM was not available for females). In chimpanzees and gorillas, this generally reflects slightly higher skeletal ROM in males, and higher passive ROM in females. In bonobos, for which passive ROM was unavailable, active ROM was larger than skeletal ROM (males and females not separated).

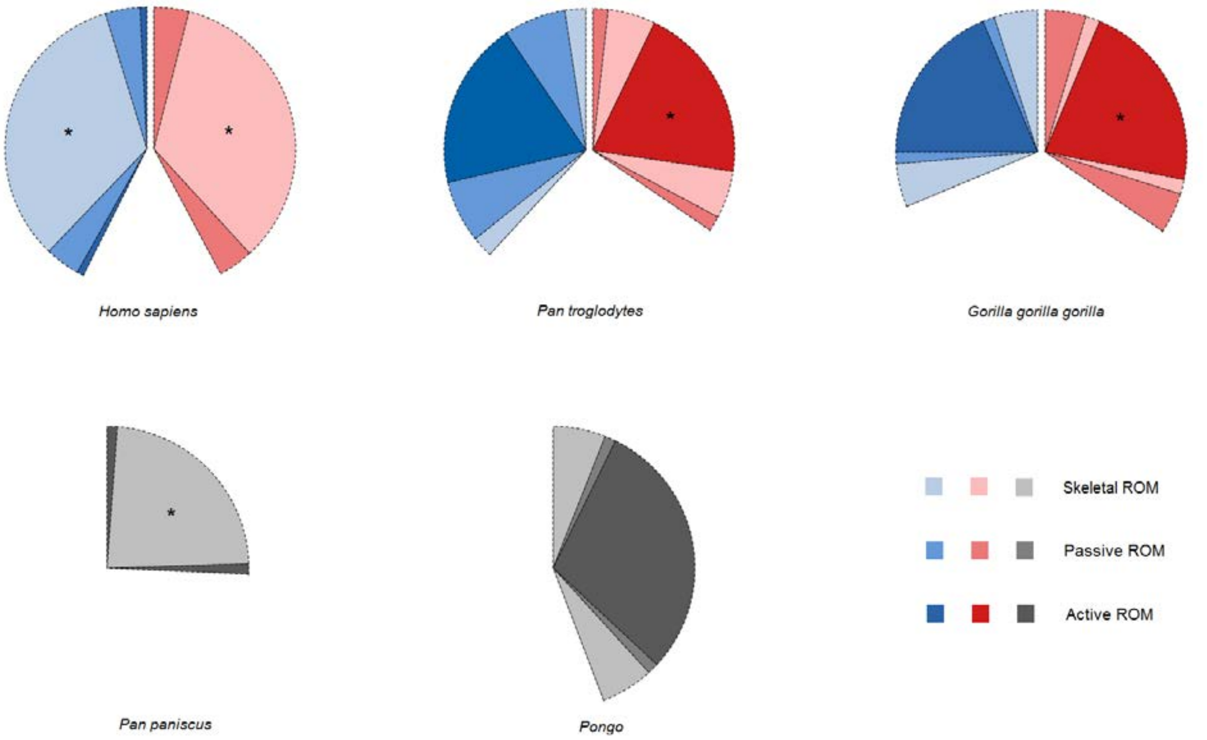


Figure 6.10. Mean skeletal, passive and active ROM at the hip in extant great apes. Males are shown in blue, females in red. For *Pan paniscus* and *Pongo* male and female data are combined. * indicates groups which do not follow the hypothesis: skeletal ROM > passive ROM > active ROM. *Pongo* is included for reference, but it must be noted that skeletal and passive ROM were measured in *P. pygmaeus*, and active ROM is for *P. abelii*.

Table 6.2. Mean skeletal, passive and active flexion/extension ROM at the hip in extant great apes. Passive ROMs taken from Soucie et al. (2011, *H. sapiens*) and Hammond (2014, nonhuman apes). Active ROM measurements include bipedalism, quadrupedalism (Chapters Two, Three and Four; D'Août et al., 2002) and vertical climbing (Isler, 2005). These behaviours are indicated: B = bipedalism; Q = quadrupedalism; VC = vertical climbing. *Pongo* are included for reference, but it must be noted that skeletal and passive ROM were measured in *P. pygmaeus*, and active ROM is for *P. abelii*.

Species	Sex	Skeletal ROM	Passive ROM	Active ROM	Behaviours
Homo sapiens	M	119.2	147.8	153.4	B, Q
	F	123.2	151.9	-	-
Pan troglodytes	M	137.3	120.1	69.0	B, Q
	F	111.9	124.3	72.8	B, Q
Gorilla gorilla	M	112.7	77.0	67.3	B, Q, VC
	F	90.5	124.0	78.7	B, Q, VC
Pan paniscus	M+F	84.1	-	92.5	B, Q, VC
Pongo	M+F	159.1	116.0	106.9	VC

Measurements of passive ROM at the hip imply a greater flexion/extension ROM in humans compared with nonhuman apes (Figure 6.11). Yet this is not reflected in skeletal measurements, which imply that the greatest hip ROM occurs in orangutans (Figure 6.7). The sex effect in passive ROM in western lowland gorillas appeared to be the opposite from skeletal ROM: females had higher passive ROM at the hip than males, but lower skeletal ROM. Sex differences in skeletal ROM in humans, chimpanzees and gorillas were also not reflected in passive ROM, which was comparable between males and females in all three species.

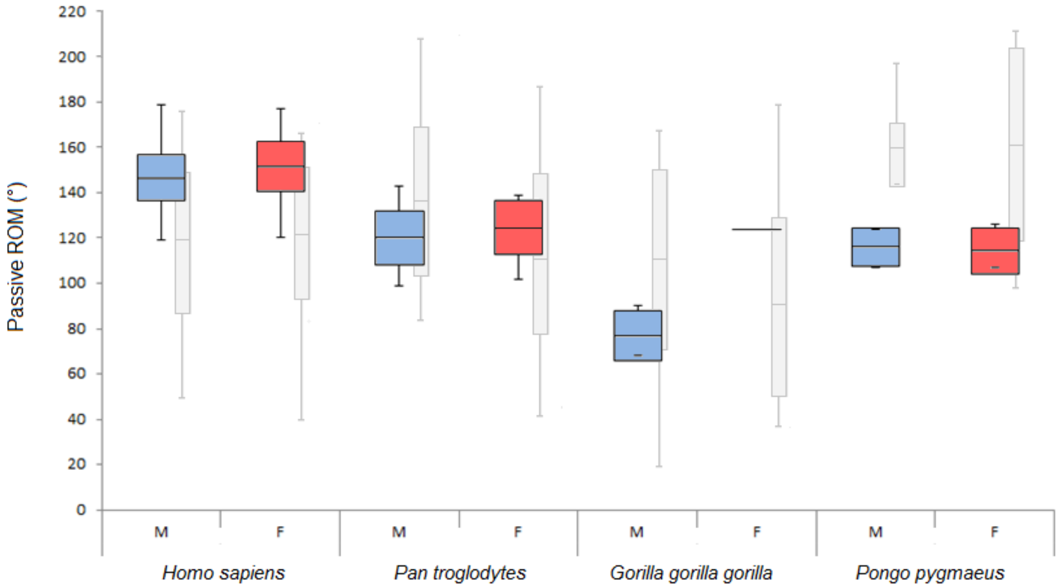
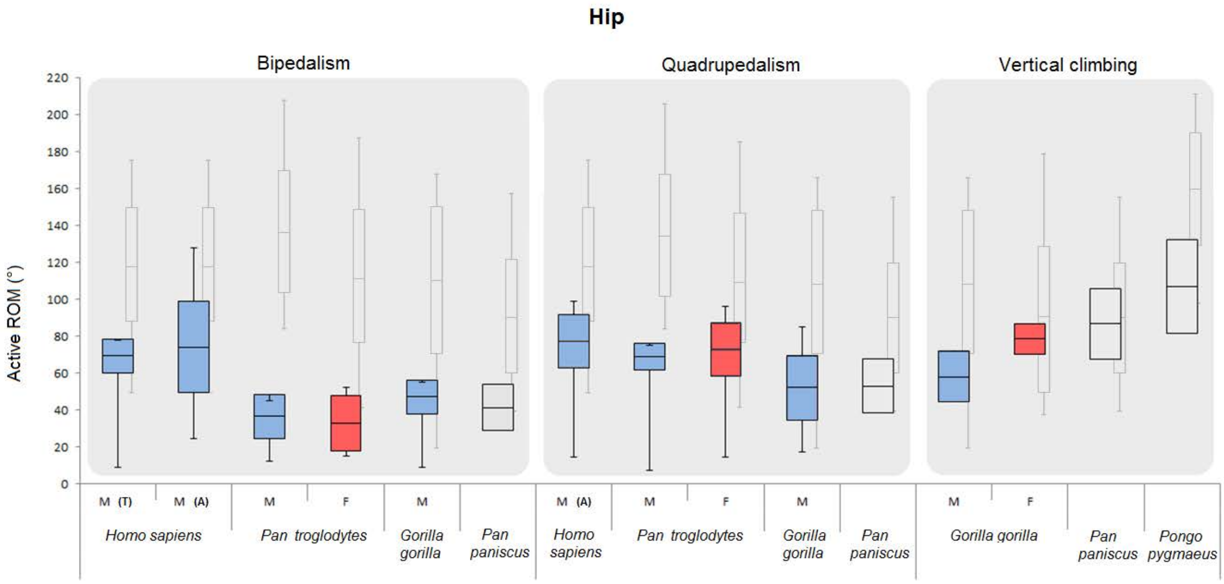
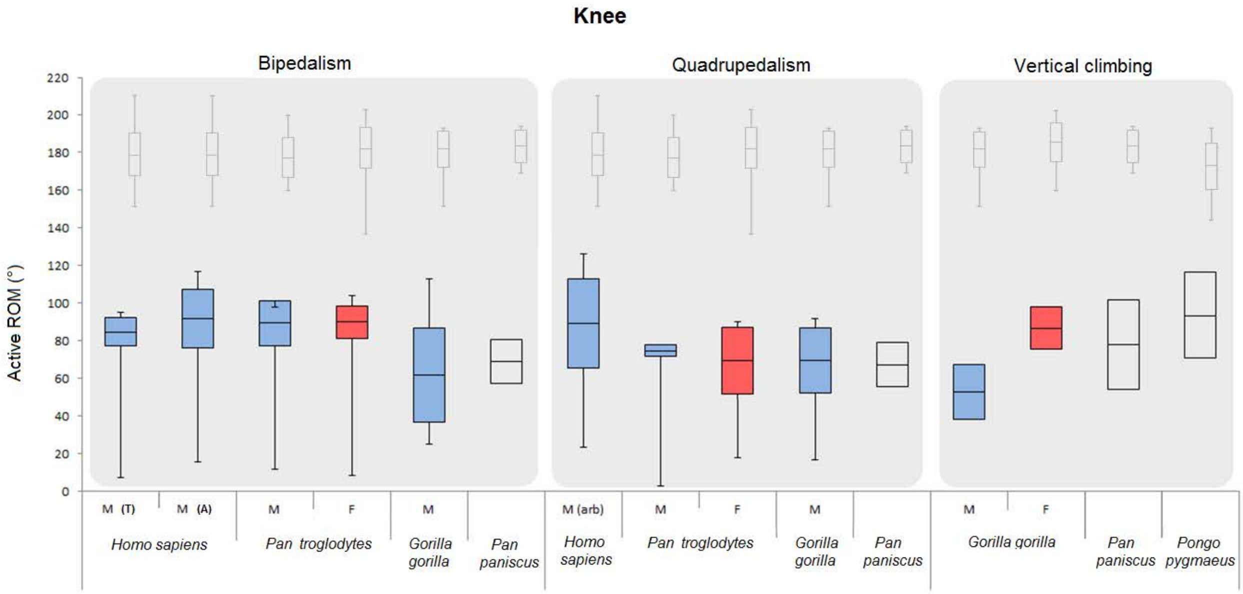


Figure 6.11. Measurements of passive flexion/extension ROM at the hip in modern humans (Soucie et al., 2011) and nonhuman apes (Hammond, 2014). Nonhuman ape specimens were anaesthetised. Boxplots show mean and standard deviation, error bars show the total data range. M = males; F = females. Grey bars behind each boxplot show measurements of skeletal ROM for reference.

Orangutans appeared to use a greater active flexion/extension ROM at the hip during vertical climbing than African apes (Figure 6.12; data for bipedalism and quadrupedalism unavailable), which corroborates with skeletal ROM, but is not reflected in passive ROM. Modern humans appear to use the largest ROM at the hip during bipedalism and quadrupedalism, and also had the largest passive ROM, yet skeletal morphology predicts a lower ROM than chimpanzees and orangutans. Although measurements of passive ROM at the knee and ankle in nonhuman apes are not available, active ROMs show extensive intraspecific variation at all three lower limb joints during locomotion (Figure 6.12).


Hip
Bipedalism
Quadrupedalism
Vertical climbing
Active ROM (°)
0
20
40
60
80
100
120
140
160
180
200
220
M (T)
M (A)
Homo sapiens
M
F
Pan troglodytes
M
Gorilla gorilla
Pan paniscus
M (A)
Homo sapiens
M
F
Pan troglodytes
M
Gorilla gorilla
Pan paniscus
M
F
Gorilla gorilla
Pan paniscus
Pongo pygmaeus


Knee
Bipedalism
Quadrupedalism
Vertical climbing
Active ROM (°)
0
20
40
60
80
100
120
140
160
180
200
220
M (T)
M (A)
Homo sapiens
M
F
Pan troglodytes
M
Gorilla gorilla
Pan paniscus
M (arb)
Homo sapiens
M
F
Pan troglodytes
M
Gorilla gorilla
Pan paniscus
M
F
Gorilla gorilla
Pan paniscus
Pongo pygmaeus

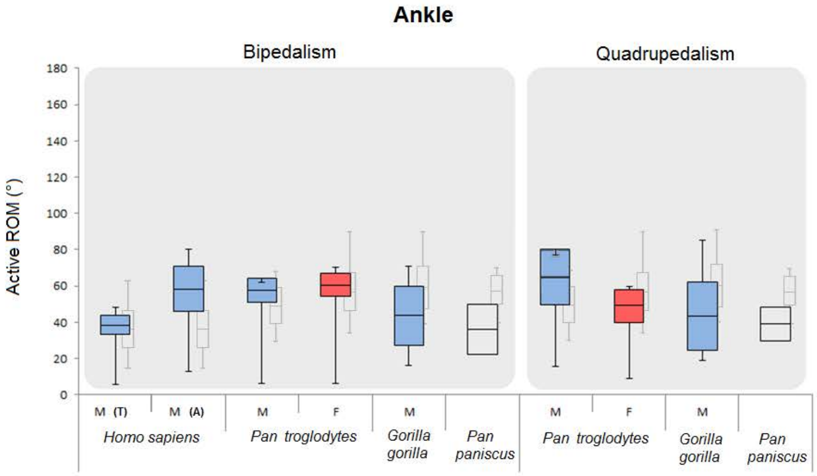

Ankle
Bipedalism
Quadrupedalism
Active ROM (°)
0
20
40
60
80
100
120
140
160
180
M (T)
M (A)
Homo sapiens
M
F
Pan troglodytes
M
Gorilla gorilla
Pan paniscus
M
F
Pan troglodytes
M
Gorilla gorilla
Pan paniscus

Figure 6.12. Active flexion/extension ROMs at the hip, knee and ankle during bipedalism, quadrupedalism and vertical climbing in extant great apes. Data on bipedalism and quadrupedalism taken from Chapters One, Two and Three, and D'Aout et al. (2002). Data on vertical climbing taken from Isler (2005). Boxplots show mean and standard deviation, error bars show the total data range. M = males; F females. T = terrestrial locomotion; A = arboreal locomotion. Grey bars behind each boxplot show measurements of skeletal ROM for reference.

DISCUSSION

Despite a small number of clear interspecific differences, such the large skeletal hip ROM in orangutans and small skeletal ankle ROM in modern humans, considerable intraspecific variation and interspecific overlap exists in skeletal flexion/extension ROM at all three lower limb joints among extant apes. This variation, as well as stark differences between skeletal, passive and active ROM at the hip, casts doubt upon the reliability of using skeletal measures of ROM to predict positional behaviour based upon skeletal differences between extant apes.

Variation in skeletal ROM

Clear interspecific differences in skeletal joint ROM were weakened due to the wide ranges exhibited by each species, and by sex and population effects. At the hip, skeletal ROM in both male and female modern humans, chimpanzees and western lowland gorillas spanned a range of over 100°, which represents 52% of the total range of skeletal hip ROM observed across all species. At the knee and ankle, many species spanned a range of over 40°, which was 63% of the total range of skeletal ROMs observed at the knee, and 54% of the total range at the ankle. Several authors have alluded to a greater ROM in the lower limb joints of females compared with males in hominoid species (Latimer and Lovejoy, 1990; Daniels et al., 1997; Crompton et al., 2003), which was reflected in this study in skeletal ROMs at the knee and ankle. In modern humans, any potential effects of sex were obscured by population effects, with significantly larger skeletal ROMs at the hip and ankle in Thai individuals compared with the UK population. Even before comparisons with passive and active ROMs in extant apes, this high level of intraspecific variation suggests that using interspecific differences in skeletal ROM to infer ROM and behaviour in fossil hominoids is not reliable.

Estimations of passive ROM from skeletal ROM

Measurements of passive ROM reflect an animal's total ROM capacity in life. In this study, both interspecific and sex differences in skeletal ROM at the hip were not reflected in patterns of passive ROM, which suggests that ROM measured from skeletal material is an unreliable predictor of an animal's ROM capacity at this joint. For example, passive ROM measurements imply that little difference exists between chimpanzees and Bornean orangutans regarding hip flexion/extension capacity. Even though orangutans are considered to require a larger range of joint positions than other apes to achieve scrambling locomotion among branches that differ in orientation and diameter (Thorpe and Crompton, 2006; Zihlman et al., 2011), this similarity in passive ROM could be used to demonstrate that chimpanzees and orangutans share a similar maximum capacity for hip ROM, which is utilised more frequently by orangutans. However, this similarity in passive ROM was not reflected in skeletal ROMs, which were much larger in Bornean orangutans than chimpanzees. If orangutans and chimpanzees do have similar passive ROMs at the hip, this is not reliably predicted by skeletal measures of ROM.

Skeletal ROMs that imply different ROM capacities between individuals must assume that soft tissue constraints will either have no effect on skeletal ROM, or have a uniform effect across all individuals and thus reduce passive ROM to the same proportion of skeletal ROM. However, it is possible that the disparities between skeletal and passive ROMs shown here highlight the importance of soft tissue morphology in determining passive joint ROM, which may vary between individuals to a greater extent than skeletal morphology. Indeed, Venkataraman et al. (2013b) demonstrated how an unusually large dorsiflexion ROM at the ankle could be accommodated in modern humans without skeletal adaptations, despite being associated with differences in gastrocnemius morphology. Another possibility is that these results also demonstrate the difficulties involved in predicting ROM in a single plane from a joint such as the hip whose function is to facilitate rotation in multiple planes, and to withstand substantial and multidirectional muscular force exerted during weight-bearing. The articular surface morphology of the femoral head reflects a compromise between the morphological optima for effective flexion/extension, abduction/adduction, and internal and external rotation. The joint must not only facilitate effective movement in these planes, but allow stability of the joint complex during weight-bearing while in positions that place body segments at the extremes of ROM in any one plane. Differences between patterns of skeletal and passive ROMs may therefore be a result of both variation in soft tissue morphology and the conflicting demands of skeletal morphology that are required at any one joint.

Estimations of active ROM from skeletal ROM

The lack of similarity between interspecific patterns of skeletal and passive ROM implies that locomotor capacity cannot be reliably predicted from skeletal estimations of ROM. However, consideration of skeletal and passive ROMs alongside active ROMs used by extant apes during bipedalism, quadrupedalism and vertical climbing revealed further complications in the relationships between the different measurements of ROM. Overall, active ROMs during these behaviours show little association with either skeletal or passive ROMs, yet there is some tentative evidence that frequently-used behaviours may be reflected in patterns of skeletal ROM.

Mean hip ROM observed in male humans during bipedalism and quadrupedalism was larger than both mean passive and skeletal measures of ROM. Mean active hip ROM was also larger than mean skeletal ROM in bonobos. While these comparisons are based on mean values taken from considerably variable samples, and therefore reflect species-level, rather than individual-level, differences, they contradict the hypothesis that skeletal ROM is larger than passive ROM, which in turn is larger than active ROM, at least for the hip joint. One possible explanation is that, while it is logical to assume that maximum joint ROM capacity in an individual can be determined passively, of which a subset will be utilised during physical activity, this ignores the potential short-term effect of repeated activity on joint ROM. McNair and Stanley (1996) demonstrated that in a sample of 21 adult humans, maximum ankle dorsiflexion capacity increased by 1% after 10 minutes of jogging, by 8% after 2.5 minutes of stretching the calf muscles, and by 13% after both jogging and stretching. Thus passive ROM, and possibly therefore active ROM, increases during a bout of physical activity as a result of increased joint laxity. An additional factor to consider is the increased flexion or extension that may be facilitated by weight-bearing during locomotion. In humans, metatarsophalangeal dorsiflexion is generally greater during locomotion than passive measurements due to the weight borne by the joint towards the end of the stance phase of walking (Nawoczenski et al., 1999). We therefore cannot always assume that passive ROM measured in a sedentary or anaesthetised individual represents the full ROM available to them during locomotion.

It is also important to consider that these findings may also imply a lack of consistency between studies. Comparisons of passive ROM measurements between conscious humans and anaesthetised nonhuman apes are necessary due to experimental constraints, but may result in differences between studies. Passive measurements on anaesthetised nonhuman subjects are also particularly constrained in sample size. Studies of active ROM have used slightly different methods of quantifying joint kinematics (D'Août et al., 2002; Isler, 2005), which are also affected by substrate. Nevertheless, while these inconsistencies may contribute to findings of smaller skeletal ROMs reported in one study compared to passive or active ROMs reported in another, one would still expect replication across studies of similar interspecific patterns in joint ROM. These patterns were not repeated across studies of skeletal, passive and active ROMs, which questions the overall reliability of inferring one measure of joint ROM from another based upon observed differences between extant species.

Skeletal ROM and frequently used behaviours

Some interpretations of skeletal morphology assume that this can indicate an animal's full performance capacity (e.g. Latimer et al., 1987), while others assume that morphology reflects an animal's frequently used behaviours, giving little indication of the extremes of behavioural capacity (e.g. Pickford et al., 2002). In this study, while there was little association between skeletal and passive ROMs, there is a small amount of evidence that skeletal ROMs may reflect active more than passive ROMs. At the hip, the relatively high skeletal flexion/extension ROM in orangutans may reflect their increased reliance on arboreal locomotion; this was reflected in measurements of active ROM during vertical climbing (Figure 6.12), but may also be associated with their use of behaviours such as scrambling and bridging, which require extreme hip extension (Crompton et al., 2008). In turn, while mountain gorillas are capable of arboreal locomotion, the relatively small skeletal hip ROM that they exhibit may reflect their more terrestrial lifestyle compared with other ape species (Doran, 1996; Thorpe and Crompton, 2006). Similarly, the low skeletal ROM at the ankle in modern humans may reflect the dominance of terrestrial bipedalism in our locomotor repertoire. Some humans show substantial behavioural flexibility in response to the arboreal environment, which is not necessarily accompanied by skeletal adaptations (Chapter Three; Venkataraman et al., 2013b; Kraft et al., 2014); thus it is likely that some skeletal traits are adaptations to frequently used positional behaviours rather than locomotor extremes. Locomotor behaviours that use unpatterned gaits in nonhuman apes may also be related to skeletal morphology, although ROMs during these behaviours are unknown.

It is also possible that the large skeletal ROM of Thai modern humans, particularly at the ankle, likely reflects the increased use of squatting-type behaviours (Blair, 1994) or ground-sitting (Alexander, 1972) by Asian populations compared with Europeans. A full squat is the posture that requires the most flexion of the hindlimb while joints are subject to full weight-bearing, and is therefore likely to impact the development of hindlimb joint morphology. Blair (1994) concluded that this impact on joint ROM was more likely to result from a high frequency of squatting, rather than the duration of each squatting bout. Sitting positions may be another contributing factor behind geographical differences in ROM between modern human populations. During a study of varicose vein prevalence, Alexander (1972) noted that while chair-sitting is the dominant activity for many modern Westerners, it was rare or non-existent among many Eastern populations, who spent less time in a resting position and when sitting, used the ground. Transferring from standing to ground-sitting is likely to use a larger ROM at all major hindlimb joints than transferring between standing and chair-sitting (Mulholland and Wyss, 2001). These differences highlight the importance of considering the roles of soft tissue plasticity and behavioural flexibility in determining full performance capacity, neither of which should be ruled out in the case of joint ROMs.

Implications for Australopithecus afarensis and other fossil hominoids

The current study highlights two reasons why inferring locomotor capacity from skeletal ROMs may not be reliable for hominoids. Firstly, differences in passive hip ROM between great ape species were not reflected in skeletal ROMs, meaning there is no robust relationship between the two (at least for the hip) that can be used to infer the potential locomotor capacity of an extinct species. Furthermore, because skeletal ROMs at the hip were not always larger than passive, or indeed active, ROMs, it is not possible to exclude the likelihood of locomotor behaviours that required substantially larger active ROMs than were estimated by skeletal ROMs.

Secondly, interspecific variation in the active ROMs used during certain locomotor behaviours reveals how different species achieve the same type of locomotion using different joint kinematics through behavioural plasticity. Thus an individual's ROM capacity is not necessarily a reliable indicator of its ability to perform a certain locomotor behaviour. For example, orangutans use a much higher flexion/extension ROM at the hip during vertical climbing on a thin support than western lowland gorillas (Figure 6.12; Isler, 2005), yet this does not appear to affect the climbing ability of the two species. Therefore, even if the skeletal ROM at the hip in a fossil hominoid were lower than the ROM used by gorillas during vertical climbing, it is possible that the fossil species achieved effective vertical climbing using different joint kinematics.

These results suggest that previous estimations of joint ROM in *Au. afarensis* may not be reliable, and may underestimate the species' locomotor abilities. Reconstructions of locomotor behaviour in *Au. afarensis* have often been understandably "bipedal-centric", perhaps because discovery of skeletal material showing substantial similarity to modern human morphology led researchers to focus more towards reconstructing the species' bipedal gait than considering its full locomotor capacity (Dart, 1949; Jenkins, 1972; Latimer and Lovejoy, 1990; but see Senut, 1981; Feldesman, 1982a; b; Stern and Susman, 1983). If skeletal morphology is reflective of routinely used behaviours, the ROM at pedal joints described by Latimer et al. (1987) and Lovejoy and Latimer (1990) are consistent with terrestrial bipedality, yet also indicate a higher frequency of arboreal behaviour than in modern humans. Furthermore, evidence from the forelimb (Senut, 1981; Feldesman, 1982a; b) implies substantial arboreal capacity in *Au. afarensis*. The large skeletal ROM at pedal joints in AL 288-1 and AL 333-115 compared with modern humans does not imply severe restriction to terrestrial bipedality, but has been somewhat overshadowed by other morphological features indicative of bipedalism in their locomotor repertoire (Dart, 1949; Jenkins, 1972; Latimer et al., 1987). However, other morphological indicators of bipedalism show substantial variation across extant apes (Chapter Five). It is therefore likely that, when soft tissue plasticity and behavioural flexibility are considered, the locomotor capacity of *Au. afarensis* was even less restricted than that of modern humans, who themselves show substantially diverse locomotor responses to environmental changes.

CONCLUSIONS

There is considerable intraspecific variation and interspecific overlap in skeletal ROMs, and little indication that skeletal hip ROM is related to measurements of passive ROM in living apes. Furthermore, mean ROM values contradict the hypothesis that skeletal ROM is always larger than passive ROM, which is in turn larger than active ROM used during positional behaviour. However, this can only be deduced at the species level, and should be further investigated within individuals. Thus locomotor capacity in fossil hominoids cannot be reliably inferred from skeletal ROM measurements at the major hindlimb joints, despite the possibility that some interspecific differences in skeletal ROM reflect the joint positions used during frequently used behaviours. This is because ROM measurements from skeletal morphology cannot reliably predict the total ROM available to a living hominoid, and because different species can achieve the same locomotor behaviours with different kinematics through behavioural flexibility.

CHAPTER SEVEN

GENERAL DISCUSSION

Author contributions: chapter written by Emily Saunders and reviewed by Alice Roberts and Susannah Thorpe.

SUMMARY OF THESIS AIMS AND MAIN FINDINGS

The investigations described in this thesis aimed to explore the variation in locomotor behaviour and anatomy that exists across extant apes in order to shed light on the evolution of hominoid locomotor behaviour. This included quantifying the variation in gait mechanics that exists during locomotion in both terrestrial and arboreal contexts, as many hominoid adaptations have been associated with the demands of the arboreal environment, yet most studies of humans and nonhuman apes have focused almost exclusively on terrestrial locomotion (Jenkins, 1972; Stern and Susman, 1983; D'Août et al., 2002; Crompton et al., 2003; Sockol et al., 2007; Matthis and Fajen, 2013). The studies described here also included investigating the variation among extant apes in skeletal features that have been used to infer locomotor behaviour, in particular habitual bipedality, in fossil hominoids. This would allow an assessment of the reliability of predicting locomotor capacity from particular aspects of skeletal morphology, and would therefore provide an indication of the reliability of current reconstructions of locomotor capacity in fossil hominoids, as well as useful information for researchers undertaking such reconstructions in the future.

The study described in Chapter Two showed that both bipedal and knuckle-walking kinematics in captive chimpanzees and lowland gorillas are sensitive to environmental variation, differing between arboreal and terrestrial substrates and with functional properties of arboreal supports. These results contradict reports of fundamental differences in knuckle-walking kinematics between the two species, which have been used in the past to advocate independent evolution of knuckle-walking in the *Pan* and *Gorilla* lineages (Kivell and Schmitt, 2009). Instead, the findings suggest that chimpanzees and gorillas respond in a similar manner to substrate differences, and that interspecific differences in wild populations may be due to environmental variation; specifically the increased arboreality of chimpanzees compared with gorillas.

The investigation described in Chapters Three and Four revealed the surprising arboreal proficiency of modern humans, contradicting the commonly-held view that hominin evolution was defined by a clear arboreal-terrestrial transition, and that adaptations to bipedality place severe constraints on arboreal capacity. Like nonhuman apes, modern humans achieve effective arboreal locomotion through a range of mechanically diverse locomotor behaviours.

Chapter Five found considerable intraspecific variation among extant apes in the expression of five skeletal predictors of habitual bipedalism. Sensitivity and specificity tests suggest that caution must be exercised when using these features for predicting habitual bipedality in a fossil hominoid. In particular, phenotypic variation among modern humans indicates that absence of a certain feature is not necessarily associated with a lack of bipedality.

The study described in Chapter Six investigated whether passive and active range of motion (ROM) at hindlimb joints can be reliably predicted from skeletal measures of ROM in extant great apes. Considerable intraspecific variation and a lack of clear interspecific differences in skeletal ROM, alongside inconsistencies when compared with measures of passive and active ROM in living animals, suggest that inferring locomotor behaviour in fossil hominoids from predictions of joint ROM may be unreliable.

BEHAVIOURAL FLEXIBILITY

The idea that morphology, and thus positional capability, is not fully constrained by genetics is well-established, and various studies have documented the role of morphological plasticity in accommodating changes to positional behaviour within an animal's lifetime (Turner and Pavalko, 1998; West-Eberhard, 2005a; Hellier and Jeffery, 2006; Venkataraman et al., 2013). However, this thesis illustrates the role of behavioural flexibility as well as morphological plasticity in determining locomotor capacity. This has several implications for understanding the evolution of positional behaviour, related to the ways that we interpret locomotion in living apes and the morphology of extant and fossil hominoids.

Positional behaviour is ultimately a response to an animal's environment, and specifically to the distribution and functional properties of weight-bearing supports. This means that fundamental interspecific differences in behaviour can only be identified when the species being compared are exposed to a similar locomotor substrate. Therefore, interspecific variation in locomotor behaviour should not be assumed to represent phylogenetically constrained differences if those species have been studied in different environments (e.g. Kivell & Schmitt, 2009). Furthermore, the mechanical profile of a locomotor behaviour in a particular species should be characterised based on the range of gait mechanics exhibited by the species on the different types of substrate in its habitat, rather than the specific gait used in only one environmental context. Chapters Two, Three and Four showed that investigations of bipedalism and knuckle-walking on both terrestrial and arboreal supports result in considerable intraspecific variation in gait mechanics and relatively few clear interspecific differences. In particular, the behaviour of modern human tree climbers revealed both a more varied mechanical profile of human bipedalism and a much broader overall locomotor repertoire in humans than has previously been recorded (e.g. Latimer et al., 1987). This new data strongly suggest that many previous interpretations of extant ape locomotion have over-emphasised interspecific differences, drawing on particularly narrow and stereotyped views of locomotor behaviour in each species (e.g. Lovejoy, 1988; Latimer, 1991; Crompton et al., 2003; Hogervorst and Vereecke, 2014).

The hypothesis that substantial changes to locomotor behaviour can be accommodated through behavioural flexibility alone, without accompanying morphological changes, also loosens the generally perceived tight link between form and function (e.g. Latimer et al., 1987; Cornwall and McPoil, 1999). This has particular consequences for studies aiming to reconstruct the locomotor behaviour of fossil hominoids, because an animal's skeleton may not necessarily reflect its positional capacity. Currently we do not know the extent of musculotendinous variation that can be accommodated by a particular skeletal morphology (e.g. Venkataraman et al., 2013b); nor do we understand the behavioural performance capacity that can be achieved within particular morphological constraints (see Chapters Three and Four). From the data presented here, considerable morphological variation across extant apes (and particularly within modern humans) in the expression of several skeletal features considered to be essential adaptations to habitual bipedality demonstrates the lack of cohesion between morphology and even frequently used behaviours. Furthermore, comparisons of active joint ranges of motion used during certain locomotor behaviours demonstrate how different species are able to achieve similar locomotor strategies via different joint kinematics. In addition, the complexity of the primate musculoskeletal system itself facilitates solutions to positional behaviour challenges: for example, reduced ROM at one joint may be compensated by larger ROM at another.

The potential unreliability of predicting locomotor behaviour with individual aspects of skeletal morphology, alongside the behavioural and mechanical diversity observed in the locomotor repertoires of all extant apes, means that interpretations of skeletal morphology in fossil hominoids are likely to result in overly constrained reconstructions of locomotor capacity. For example, the argument that modern human-like morphology in an early hominin would have severely restricted their arboreal capabilities in favour of more efficient terrestrial bipedality (Latimer, 1991) is unsubstantiated given the significant arboreal capacity of modern humans themselves demonstrated here. It is possible that the hominin clade is defined by adaptations that facilitate the retention of arboreal capacity alongside proficient terrestrial locomotion, rather than adaptations that restrict them to terrestriality. Thus all crown hominoids may share a morphological propensity for behavioural flexibility, rather than particular combinations of positional behaviours that are tightly genetically constrained.

UNDERSTANDING THE EVOLUTION OF LOCOMOTOR BEHAVIOUR

The variation in locomotor behaviour and anatomy across extant apes described in this thesis strongly suggests that any hypotheses about the evolution of hominoid locomotor behaviour must accommodate concepts of both morphological and behavioural plasticity. In general, the concept that locomotor performance is partly facilitated through the capacity for behavioural, as well as morphological, plasticity means that the evolutionary development of specific locomotor behaviours may not follow distinct phylogenetic patterns that can be easily traced through certain lineages. Instead, they may be related to the evolution of morphology that is both plastic and somewhat generalised, and thus able to accommodate substantial behavioural flexibility.

The results of this thesis do not contradict the hypothesis that adaptations to bipedal locomotion developed early in hominoid evolution (Thorpe et al., 2007b). Indeed, given the locomotor flexibility of modern humans and the variation in bipedal gaits across extant great apes described here, there is no reason to discard the possibility of bipedal capacity in the last common ancestor of crown hominoids (Crompton et al., 2008). An arboreal origin for bipedal locomotion is also supported by these results, as modern humans and extant nonhuman apes share bipedalism as an important arboreal locomotor strategy (Chapters Three and Four; Hunt, 1992; Thorpe and Crompton, 2006). However, two specific lines of evidence that have been used to support an early, arboreal origin for bipedalism are called into question. Firstly, the kinematic differences in wrist posture during knuckle-walking between chimpanzees and lowland gorillas, that have been used to advocate independent evolution of knuckle-walking in the two lineages and therefore absence from the hominin lineage (Inouye, 1994; Dainton and Macho, 1999; Kivell and Schmitt, 2009), are not found in knuckle-walking kinematics here. Chimpanzees have been proposed to use more extended wrist postures during knuckle-walking due to their increased arboreality, while gorillas were suggested to be morphologically limited to more columnar loading through the wrist (Inouye, 1994; Kivell and Schmitt, 2009). However, the study described in Chapter Two revealed increased wrist extension in gorillas in response to arboreal supports. Differences observed in the wild are therefore likely to reflect environmental variation, rather than the proposed inability of gorillas to respond to arboreal substrates in a similar manner to chimpanzees. However, this does not suggest that knuckle-walking behaviour in the two species is necessarily phylogenetically linked. Given the locomotor flexibility of extant apes, this finding supports the hypothesis that knuckle-walking developed in chimpanzees and gorillas as the most parsimonious form of terrestrial locomotion in an animal also adapted to vertical climbing (Crompton et al., 2010).

Secondly, the argument that hindlimb extension during bipedal locomotion on compliant branches in orangutans is related to the hindlimb extension characteristic of terrestrial walking in humans (Thorpe et al., 2007b; Crompton et al., 2010) is not supported by kinematics of modern humans on arboreal supports. While modern human tree climbers exhibit more hindlimb extension during bipedalism on compliant branches compared with rigid supports, this does not involve stiff hindlimbs throughout the stance phase of bipedal gait. Hindlimb extension throughout the stance phase is crucial for achieving the inverse pendular mechanism of energy return that allows highly efficient walking (Alexander, 1991a). Thus while arboreal bipedalism on compliant branches may require increased extension at the hip and knee, perhaps to allow the forelimbs to reach handholds for balance, a kinematic link between bipedalism on compliant branches and the mechanism that facilitates energetically efficient terrestrial walking is not apparent in modern humans.

CONCLUSIONS

This thesis demonstrates the substantial behavioural and kinematic flexibility that can be accommodated by the morphology of modern humans and African apes. Studies of extant ape skeletal morphology also revealed considerable intraspecific variation, loosening the perceived tight link between form and function with regards to locomotor anatomy. These studies highlight the importance of behavioural flexibility, in addition to morphological plasticity, in determining locomotor capacity in hominoids, and thus the caution that must be exercised when reconstructing locomotor behaviour in fossil species. In particular, reconstructions which imply that early hominins may have been restricted to terrestrial bipedality are problematic given the considerable locomotor flexibility and variation in skeletal predictors of bipedalism among modern humans. It is hypothesised that some locomotor adaptations retained by modern humans may facilitate arboreal capacity as well as proficient terrestrial bipedality, and that all extant apes may share a morphological propensity for considerable behavioural flexibility.

AREAS OF FURTHER RESEARCH

It is apparent that the relationships between morphology and locomotor capacity in hominoids are not yet understood, which inhibits investigations of hominoid evolution. One avenue of further investigation would be an extensive capture of the range of anatomical and behavioural variation among modern humans, in order to understand the association between gait biomechanics and skeletal anatomy, and to obtain an estimation of the morphological and behavioural variation that exists in one hominin species. This would provide a more comprehensive idea of the performance capacity that can be accommodated by certain morphological constraints. Another, broader, approach would be to obtain a more comprehensive view of the true locomotor capacity of living nonhuman apes. While this would be difficult to obtain under natural conditions, combining studies of kinematic responses to environmental variation in the apes' natural habitats, with more focused zoo-based studies of locomotor mechanics on supports whose functional properties are known, would provide a useful dataset on their behavioural capacity. In particular, this would allow more robust comparisons between phylogeny and patterns of behaviour. Given the current conservation status of many extant apes, particularly mountain and eastern lowland gorillas, and Sumatran orangutans, obtaining this data for wild populations in their natural environment is perhaps the most time-critical area of investigation.

The ontogenetic development of many supposed locomotor adaptations also remains unclear. An understanding of the link between development of skeletal features and locomotor behaviour within modern human individuals would allow identification of the mechanisms behind their development. This has been partly addressed by Tardieu and Trinkaus (1994) and Tardieu et al. (2006), through investigation of features that are present in neonates. However, this still relies on average timings for the onset of walking in humans. A long-term study of both behaviour and morphological development in modern humans throughout ontogeny would perhaps reveal more specific relationships between the two. Another next step would be to tackle the "missing link" of soft tissue morphology that constrains all studies looking to interpret fossil morphology: whether variation in skeletal morphology reflects variation in muscular and tendinous anatomy. It is becoming increasingly evident that muscular adaptations to locomotor behaviour can be accommodated without accompanying skeletal adaptations (e.g. Venkataraman et al., 2013b), and that a propensity for behavioural flexibility may facilitate extensive alterations to locomotor behaviour without any significant morphological alterations (Chapter Three). Understanding the extent to which variation in one reflects the other in modern humans would enable the generation of much clearer hypotheses about the locomotor capabilities of early hominins, rather than assuming that apparent adaptations to one behaviour necessarily involve compromises for another. Ultimately it may be hoped that genetics will provide a key part in the puzzle, enabling better understanding of the contributions of genetic changes and phenotypic accommodation to the evolution of morphology and patterns of locomotor behaviour.

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APPENDIX ONE

KINEMATICS OF AFRICAN APE LOCOMOTION

Appendix 1.1. Multiple Regression models for bipedal kinematic parameters in gorillas. p values in bold text remained significant after Bonferroni correction. * = p value <0.05; ** = p value <0.01; *** = p value <0.001. n=9 sequences for hip models and 10 sequences for all other models.

Model		**R²**	**F**	**df**	**p**	**Predictor variable**	**Estimate**	**SE**	**t**	**p**	
Hip	Maximum	0.997	176.70	2,6	0.053	Support (ground)	28.00	1.73	16.17	**0.039**	*
						Diameter (10 ≤ 19cm)	3.00	2.00	1.50	0.374	
	Minimum	0.926	6.25	2,6	0.272	Support (ground)	27.50	7.79	3.53	0.176	
						Diameter (10 ≤ 19cm)	20.00	9.00	2.22	0.269	
Knee	Maximum	0.747	5.90	3,6	0.031	Support (ground)	21.33	8.34	2.56	0.043	*
						Diameter (10 ≤ 19cm)	24.00	11.19	2.14	0.076	
						Angle (U-shaped)	33.25	7.92	4.20	**0.006**	**
	Minimum	0.014	0.03	3,6	0.993	Support (ground)	-0.50	18.65	-0.03	0.979	
						Diameter (10 ≤ 19cm)	-2.50	25.03	-0.10	0.923	
						Angle (U-shaped)	-4.25	17.70	-0.24	0.818	
Ankle	Maximum	0.736	4.64	3,6	0.066	Support (ground)	19.50	10.31	1.89	0.117	
						Diameter (10 ≤ 19cm)	45.50	12.62	3.60	0.015	*
						Angle (U-shaped)	22.75	8.93	2.55	0.051	
	Minimum	0.212	0.45	3,6	0.729	Support (ground)	14.50	17.10	0.85	0.435	
						Diameter (10 ≤ 19cm)	15.00	20.95	0.72	0.506	
						Angle (U-shaped)	1.00	14.81	0.07	0.949	
Stride length		0.581	2.31	3,6	0.194	Support (ground)	1.39	1.23	1.13	0.31	
						Diameter (10 ≤ 19cm)	-2.55	1.50	-1.69	0.151	
						Angle (U-shaped)	0.28	1.06	0.26	0.806	
Stride frequency		0.985	107.80	3,6	0.000	Support (ground)	0.96	0.06	14.83	**0.000**	***
						Diameter (10 ≤ 19cm)	0.28	0.08	3.58	**0.016**	*
						Angle (U-shaped)	0.02	0.05	0.27	0.798	
Speed		0.959	39.21	3,6	0.001	Support (ground)	2.66	0.29	8.95	**0.001**	**
						Diameter (10 ≤ 19cm)	-0.09	0.36	-0.26	0.808	
						Angle (U-shaped)	0.17	0.26	0.66	0.539	
Duty factor		0.912	17.37	3,6	0.004	Support (ground)	-0.20	0.03	-5.89	**0.002**	**
						Diameter (10 ≤ 19cm)	-0.02	0.04	-0.36	0.733	
						Angle (U-shaped)	-0.00	0.03	-0.08	0.936	

Appendix 1.2. Linear Regression models for bipedal kinematic parameters in chimpanzees. Support diameter removed from models due to intercorrelation with support type (ground vs arboreal). p values in bold text remained significant after Bonferroni correction. * = p value <0.05; ** = p value <0.01; *** = p value <0.001. n=11 sequences.

Model		R^2	F	df	p	Predictor variable	Estimate	SE	t	p	
Hip	Maximum	0.010	0.09	1,9	0.772	Support (ground)	-4.83	16.18	-0.30	0.772	
	Minimum	0.002	0.02	1,9	0.893	Support (ground)	-1.46	10.55	-0.14	0.893	
Knee	Maximum	0.032	0.30	1,9	0.597	Support (ground)	3.88	7.06	0.55	0.597	
	Minimum	0.035	0.33	1,9	0.582	Support (ground)	5.00	8.75	0.57	0.582	
Ankle	Maximum	0.021	0.19	1,9	0.67	Support (ground)	1.50	3.41	0.44	0.670	
	Minimum	0.005	0.04	1,9	0.838	Support (ground)	1.08	5.15	0.21	0.838	
Stride length		0.064	0.61	1,9	0.454	Support (ground)	-0.58	0.74	-0.78	0.454	
Stride frequency		0.481	8.37	1,9	0.018	Support (ground)	0.61	0.21	2.89	**0.018**	*
Speed		0.282	3.53	1,9	0.093	Support (ground)	0.98	0.52	1.88	0.093	
Duty factor		0.031	0.28	1,9	0.607	Support (ground)	0.04	0.07	0.53	0.607	

Appendix 1.3. Multiple Regression models for knuckle-walking kinematic parameters in gorillas. p values in bold text remained significant after Bonferroni correction. * = p value <0.05; ** = p value <0.01; *** = p value <0.001. n=17 sequences.

Model		**R^2**	**F**	**df**	**p**	**Predictor variable**	**Estimate**	**SE**	**t**	**p**	
Hip	Maximum	0.049	0.31	2,14	0.739	Support (ground)	6.55	14.26	0.46	0.654	
						Diameter (10 ≤ 19cm)	-3.50	18.55	-0.19	0.854	
	Minimum	0.002	0.01	2,14	0.989	Support (ground)	-1.00	7.11	-0.14	0.890	
						Diameter (10 ≤ 19cm)	-0.50	9.25	-0.05	0.958	
Knee	Maximum	0.212	1.89	2,14	0.188	Support (ground)	3.34	4.27	0.78	0.447	
						Diameter (10 ≤ 19cm)	12.25	6.34	1.93	0.074	
	Minimum	0.216	1.93	2,14	0.182	Support (ground)	6.32	9.03	0.70	0.496	
						Diameter (10 ≤ 19cm)	26.00	13.40	1.94	0.073	
Ankle	Maximum	0.027	0.19	2,14	0.828	Support (ground)	-0.96	11.02	-0.09	0.932	
						Diameter (10 ≤ 19cm)	8.00	16.34	0.49	0.632	
	Minimum	0.24	2.21	2,14	0.147	Support (ground)	4.34	5.93	0.73	0.476	
						Diameter (10 ≤ 19cm)	18.25	8.79	2.07	0.057	
Shoulder	Maximum	0.329	2.70	2,14	0.111	Support (ground)	-7.70	4.68	-1.64	0.129	
						Diameter (10 ≤ 19cm)	-14.00	6.05	-2.31	**0.041**	*
	Minimum	0.397	3.62	2,14	0.062	Support (ground)	-14.60	5.85	-2.49	0.300	
						Diameter (10 ≤ 19cm)	-18.00	7.55	-2.38	**0.036**	*
Elbow	Maximum	0.014	0.08	2,14	0.924	Support (ground)	-1.30	6.97	-0.19	0.855	
						Diameter (10 ≤ 19cm)	-3.50	8.99	-0.39	0.705	
	Minimum	0.179	1.20	2,14	0.338	Support (ground)	-25.00	18.19	-1.37	0.197	
						Diameter (10 ≤ 19cm)	-8.00	23.48	-0.34	0.740	
Wrist	Maximum	0.567	5.90	2,14	0.023	Support (ground)	-16.25	4.84	-3.35	**0.008**	**
						Diameter (10 ≤ 19cm)	-9.50	6.13	-1.55	0.155	
	Minimum	0.448	3.64	2,14	0.069	Support (ground)	-36.37	14.03	-2.59	0.029	*
						Diameter (10 ≤ 19cm)	-39.50	17.75	-2.22	0.053	
Stride length		0.034	0.23	2,14	0.801	Support (ground)	-0.18	0.63	-0.28	0.782	
						Diameter (10 ≤ 19cm)	0.37	0.93	0.39	0.700	
Stride frequency		0.153	1.17	2,14	0.34	Support (ground)	0.10	0.06	1.53	0.150	
						Diameter (10 ≤ 19cm)	0.07	0.09	0.72	0.486	
Speed		0.154	1.18	2,14	0.338	Support (ground)	0.20	0.22	0.91	0.377	
						Diameter (10 ≤ 19cm)	-0.20	0.32	-0.63	0.538	
Duty factor		0.14	0.98	2,14	0.404	Support (ground)	0.03	0.02	1.04	0.317	
						Diameter (10 ≤ 19cm)	0.05	0.03	1.35	0.201	

Appendix 1.4. Linear Regression models for knuckle-walking kinematic parameters in chimpanzees. Support diameter removed from models due to intercorrelation with support type (ground vs arboreal). p values in bold text remained significant after Bonferroni correction. * = p value <0.05; ** = p value <0.01; *** = p value <0.001. n=9 sequences for joint angle models and 15 sequences for spatiotemporal models.

Model		**R^2**	**F**	**df**	**p**	**Predictor variable**	**Estimate**	**Std Error**	**t**	**p**
Hip	Maximum	0.087	0.67	1,7	0.442	Support (ground)	7.75	9.50	0.82	0.442
	Minimum	0.131	1.05	1,7	0.339	Support (ground)	-8.63	8.41	-1.03	0.339
Knee	Maximum	0.046	0.33	1,7	0.581	Support (ground)	-10.50	18.16	-0.58	0.581
	Minimum	0.347	3.72	1,7	0.095	Support (ground)	-37.75	19.57	-1.93	0.095
Ankle	Maximum	0.010	0.07	1,7	0.799	Support (ground)	2.63	9.93	0.26	0.799
	Minimum	0.239	2.20	1,7	0.182	Support (ground)	-13.38	9.02	-1.48	0.182
Shoulder	Maximum	0.008	0.06	1,7	0.817	Support (ground)	2.13	8.85	0.24	0.817
	Minimum	0.371	4.12	1,7	0.082	Support (ground)	9.63	4.74	2.03	0.082
Elbow	Maximum	0.080	0.61	1,7	0.462	Support (ground)	3.50	4.50	0.78	0.462
	Minimum	0.003	0.02	1,7	0.894	Support (ground)	-2.88	20.77	-0.14	0.894
Wrist	Maximum	0.015	0.17	1,7	0.689	Support (ground)	0.06	0.88	0.41	0.689
	Minimum	0.009	0.07	1,7	0.805	Support (ground)	6.38	24.90	0.26	0.805
Stride length		0.169	2.65	1,13	0.128	Support (ground)	0.95	0.59	1.63	0.128
Stride frequency		0.157	2.42	1,13	0.144	Support (ground)	0.15	0.10	1.55	0.144
Speed		0.209	3.44	1,13	0.087	Support (ground)	0.63	0.34	1.85	0.087
Duty factor		0.038	0.32	1,13	0.590	Support (ground)	0.03	0.05	0.56	0.590

APPENDIX TWO

MODERN HUMAN TREE CLIMBERS

Appendix 2.1. Tropical Afromontane moist broadleaf forest at Knysna, Southern Cape, South Africa (left) and at the Groot river, Eastern Cape, South Africa (right).

Appendix 2.2. Descriptions of locomotor modes and submodes, together with the mean locomotor frequencies used by the climbers. Definitions are adapted from Thorpe and Crompton (2006) and Hunt et al. (1996). New submodes, or those whose definitions differ from those of previous authors, are marked with *.

Locomotor mode, *submode*, description	**Frequency**
Bipedal walk	**56.37**
Extended bipedal walk: hip and knee are extended	8.13
Flexed bipedal walk: hip and knee are relatively flexed	22.02
*Lateral/backwards bipedal walk**	6.15
*Bipedal shuffle**: slow bipedal locomotion with very flexed hindlimbs	0.15
Bipedal scramble: unpatterned bipedal locomotion without continuous gait cycle, often with considerable hand assistance	19.92
Quadrupedal walk	**4.65**
Orthograde scramble: unpatterned, quadrumanous gait, usually using multiple, irregularly-placed supports	0.82
Pronograde scramble: as above, but in pronograde position	3.52
Crutch walk: both forelimbs placed in compression and torso/hindlimbs are swung through the forelimbs	0.12
*Inverted compressive scramble**: as for pronograde scramble, but with the torso facing upwards	0.20
Tripedal walk	**0.51**
Symmetrical tripedal walk: both hindlimbs and one forelimb used in continuous gait cycle	0.32
Orthograde tripedal scramble: as for orthograde scramble, but using only one forelimb	0.08
Pronograde tripedal scramble: as above	0.11
Vertical climb	**18.45**
*Flexed-elbow vertical climb**: propulsion provided by hindlimbs as well as forelimb flexion to pull body upwards	3.08
*Flexed-elbow/foot-lock climb**. Used while climbing a vertical rope. As with flexed-elbow vertical climb, but combined with the rope-climber's locking technique whereby the rope is wrapped round one foot and secured with the other, thereby providing a surface for hindlimb compression	1.91
Extended-elbow vertical climb: propulsion provided by hindlimbs (mainly through hip extension) with relatively extended forelimbs gripping the support and providing some propulsion through humeral retraction	0.46
*Vertical step walk**: Vertical locomotion using bipedal steps with little forelimb assistance	1.36
*Unpatterned vertical climb**: Vertical, irregular, quadrumanous locomotion, typically using multiple, irregularly-placed supports	6.94
Bimanual pull up: Body is lifted by the forelimbs using elbow flexion and humeral retraction	2.02
Bimanual push up: Body is lifted by extended forelimbs under compression	1.86
Bipedal push up: Body is lifted from a crouched position by extending hindlimbs	0.82
Vertical descent	**15.03**
Rump-first vertical descent: rump-first symmetrical descent, similar to flexed-elbow vertical climb	1.49
*Vertical step walk descent**: as for vertical step walk	4.10
*Unpattered vertical descent**: as for unpatterned vertical climb	8.30
*Forelimb suspensory descent**: Body is lowered while in forelimb suspension, typically using forelimb extension	0.29
Firepole slide: vertical support gripped loosely with hands and hindlimbs while the body slides down the support	0.85

Torso-orthograde suspensory locomotion	**0.45**
Orthograde clamber: irregular locomotion similar to orthograde scramble, but with most weight borne by suspended forelimbs	0.05
Forelimb swing: hand-over-hand suspensory locomotion with little torso rotation	0.40
Torso-pronograde suspensory locomotion	**0.22**
Inverted pronograde scramble: irregular, quadrumanous suspensory locomotion	0.22
Drop	**2.45**
Crutch drop: body lifted with both forelimbs extended under compression before dropping down off support	1.36
Bipedal drop: bipedal stand or crouch before drop	0.02
Suspensory drop: body lowered under support by suspended forelimbs before drop	1.07
Leap/jump	**1.58**
Orthograde leap: gap crossing using hindlimb propulsion, with no assistance from forelimbs until landing	0.71
*Bipedal jump**: small leap not used for gap crossing, using hindlimb propulsion but with forelimb assistance	0.87
Scoot: Ischia bear most body weight in a sitting position and slide along the support, body propelled by either hindlimbs or forelimbs	**0.29**

Appendix 2.3. Multiple Regression models for bipedal kinematic parameters. * = p value <0.05; ** = p value <0.01; *** = p value <0.001. n=12 (arboreal sequences), n=7 (terrestrial sequences).

Model		R^2	F	df	p	Predictor variable	Estimate	SE	t	p	
Hip	Maximum	0.662	15.64	2,16	0.000	Support (ground)	49.00	9.55	5.13	0.000	***
						Compliance score	17.31	7.90	2.19	0.044	*
	Minimum	0.722	20.79	2,16	0.000	Support (ground)	36.76	8.68	4.24	0.000	***
						Compliance score	-2.00	7.17	-0.28	0.784	
	Heel strike	0.256	2.80	2,16	0.093	Support (ground)	16.24	13.08	1.24	0.035	*
						Compliance score	-5.14	10.83	-0.48	0.641	
	Midstance	0.564	10.34	2,16	0.001	Support (ground)	38.33	11.27	3.40	0.004	**
						Compliance score	3.55	9.34	0.38	0.709	
Knee	Maximum	0.677	16.77	2,16	0.000	Support (ground)	23.71	4.45	5.33	0.000	***
						Compliance score	8.49	3.68	2.31	0.035	*
	Minimum	0.634	13.84	2,16	0.000	Support (ground)	13.86	6.94	2.00	0.006	**
						Compliance score	-10.98	5.75	-1.91	0.074	
	Heel strike	0.436	6.18	2,16	0.010	Support (ground)	33.05	10.34	3.20	0.005	**
						Compliance score	11.22	8.56	1.31	0.208	
	Midstance	0.541	9.43	2,16	0.002	Support (ground)	32.91	9.26	3.55	0.002	***
						Compliance score	6.53	7.67	0.85	0.407	
Ankle	Maximum	0.198	1.85	2,16	0.191	Support (ground)	-9.25	7.37	-1.26	0.228	
						Compliance score	0.75	6.10	0.12	0.904	
	Minimum	0.444	5.99	2,16	0.012	Support (ground)	13.31	4.33	3.07	0.007	**
						Compliance score	3.90	3.58	1.09	0.295	
	Heel strike	0.405	5.12	2,16	0.020	Support (ground)	-15.07	5.45	-2.76	0.008	**
						Compliance score	-3.82	4.52	-0.85	0.411	
	Midstance	0.249	2.49	2,16	0.117	Support (ground)	8.07	3.62	2.29	0.159	
						Compliance score	5.00	3.00	1.67	0.116	
Stride length		0.763	24.14	2,16	0.000	Support (ground)	0.10	0.01	6.26	0.000	***
						Compliance score	0.03	0.01	2.37	0.032	*
Stride frequency		0.858	48.46	2,16	0.000	Support (ground)	0.45	0.07	6.32	0.000	***
						Compliance score	-0.04	0.06	-0.63	0.538	
Duty factor		0.084	0.74	2,16	0.494	Support (ground)	-0.05	0.04	-1.13	0.277	
						Compliance score	-0.04	0.04	-1.13	0.275	

Appendix 2.4. Kruskal-Wallis models for kinematic parameters to test differences between the three locomotor modes (ABW = arboreal bipedalism [n=12], TBW = terrestrial bipedalism [n=7], AQW = arboreal quadrupedalism [n=8]). Dunn's test of multiple comparisons used as post-hoc test to identify pairwise group differences (p values adjusted using Bonferroni correction). * = p value <0.05; ** = p value <0.01; *** = p value <0.001.

Kruskal-Wallis					*Dunn's Test of Multiple Comparisons*			
	Model	**χ2**	**Df**	**p**	**Group pairing**	**z**	**Df**	**p (adjusted)**
Hip	Maximum	21.438	2	0.000 ***	ABW - TBW	-2.360	2	0.027 *
					ABW - AQW	2.773	2	0.008 **
					TBW - AQW	-4.614	2	0.000 ***
	Minimum	22.64	2	0.000 ***	ABW - TBW	-2.518	2	0.018 *
					ABW - AQW	2.762	2	0.009 **
					TBW - AQW	-4.749	2	0.000 ***
	Heel strike	16.886	2	0.000 ***	ABW - TBW	-1.568	2	0.175
					ABW - AQW	2.905	2	0.006 **
					TBW - AQW	-4.003	2	0.000 ***
	Midstance	22.674	2	0.000 ***	ABW - TBW	-2.520	2	0.018 *
					ABW - AQW	2.764	2	0.009 **
					TBW - AQW	-4.753	2	0.000 ***
Knee	Maximum	13.843	2	0.001 ***	ABW - TBW	-3.034	2	0.004 **
					ABW - AQW	0.823	2	0.616
					TBW - AQW	-3.514	2	0.001 ***
	Minimum	11.406	2	0.003 **	ABW - TBW	-3.105	2	0.003 **
					ABW - AQW	0.035	2	1.000
					TBW - AQW	-2.884	2	0.006 **
	Heel strike	16.399	2	0.000 ***	ABW - TBW	-2.390	2	0.025 *
					ABW - AQW	2.101	2	0.053
					TBW - AQW	-4.049	2	0.000 ***
	Midstance	16.441	2	0.000 ***	ABW - TBW	-2.697	2	0.011 *
					ABW - AQW	1.760	2	0.118
					TBW - AQW	-4.031	2	0.000 ***
Stride frequency		18.414	2	0.000 ***	ABW - TBW	-2.872	2	0.006 **
					ABW - AQW	1.842	2	0.098
					TBW - AQW	-4.263	2	0.000 ***
Stride length		20.834	2	0.000 ***	ABW - TBW	-2.500	2	0.019 *
					ABW - AQW	-4.491	2	0.000 ***
					TBW - AQW	1.800	2	0.108
Duty factor		14.687	2	0.001 ***	ABW - TBW	0.913	2	0.542
					ABW - AQW	-3.087	2	0.003 **
					TBW - AQW	3.561	2	0.001 ***

Appendix 2.5. Multinomial Logistic Regression model showing the association between locomotor mode and individual support properties. Quadrupedalism and suspensory locomotion are compared to bipedalism. * = p value <0.05; ** = p value <0.01; *** = p value <0.001.

	Locomotor mode				
	Quadrupedalism			*Suspension*	
	Coefficient	p		Coefficient	p
Compliance score	-0.034	0.922		-0.619	0.609
Support orientation	0.105	0.469		0.44	0.417
Total N Supports	0.433	0.001	***	-0.328	0.527

Appendix 2.6. Multiple Linear Regression models showing the associations between mean muscle activity and access routes. * = p value <0.05; ** = p value <0.01; *** = p value <0.001.

Model	R^2	F	df	p	Predictor variable	Estimate	SE	t	p	
Vastus lateralis	0.478	3.90	4,17	0.020	Route (rope)	-32.50	103.58	-0.31	1.000	
					Route (trunk)	118.61	105.66	1.12	0.560	
					Climb number	-1.12	51.05	-0.02	1.000	
					Vertical speed	493.95	256.69	1.95	0.101	
Gluteus maximus	0.692	10.66	4,19	0.000	Route (rope)	-115.68	72.78	-1.59	0.128	
					Route (trunk)	-122.93	69.78	-1.76	0.035	*
					Climb number	-27.48	36.39	-0.75	1.000	
					Vertical speed	897.51	171.76	5.23	0.000	
Gastrocnemius	0.151	0.76	4,17	0.567	Route (rope)	-40.95	32.17	-1.27	1.000	
					Route (trunk)	-19.69	30.38	-0.65	1.000	
					Climb number	2.92	16.07	0.18	1.000	
					Vertical speed	64.40	74.55	0.86	1.000	
Biceps brachii	0.760	11.08	4,14	0.000	Route (rope)	6297.60	2311.30	2.73	0.001	**
					Route (trunk)	-6374.90	2104.90	-3.03	0.009	**
					Climb number	125.40	1145.20	0.11	1.000	
					Vertical speed	1415.80	5029.00	0.28	1.000	
Triceps brachii	0.191	1.12	4,19	0.377	Route (rope)	-1251.50	1388.70	-0.90	1.000	
					Route (trunk)	1004.10	1331.60	0.75	0.956	
					Climb number	-175.20	694.30	-0.25	1.000	
					Vertical speed	-5533.60	3277.40	-1.69	0.754	
Extensor carpi ulnaris	0.098	0.52	4,19	0.724	Route (rope)	800.10	2024.60	0.40	1.000	
					Route (trunk)	-1100.60	1941.40	-0.57	1.000	
					Climb number	614.60	1012.20	0.61	1.000	
					Vertical speed	1192.20	4778.20	0.25	1.000	

Appendix 2.7. Multiple Linear Regression models showing the associations between mean muscle activity and exit routes. * = p value <0.05; ** = p value <0.01; *** = p value <0.001.

Model	R^2	F	df	p	Predictor variable	Estimate	SE	t	p	
Vastus lateralis	0.345	2.11	4,16	0.127	Route (rope)	7.63	80.61	0.10	1.000	
					Route (trunk)	141.09	56.78	2.48	0.081	
					Climb number	-24.57	32.42	-0.76	1.000	
					Vertical speed	-41.80	53.28	-0.78	1.000	
Gluteus maximus	0.284	1.89	4,19	0.157	Route (rope)	106.26	117.42	0.91	1.000	
					Route (trunk)	60.33	78.72	0.77	1.000	
					Climb number	-80.52	45.91	-1.75	0.389	
					Vertical speed	93.97	73.55	1.28	1.000	
Gastrocnemius	0.120	0.51	4,15	0.730	Route (rope)	-287.80	565.10	-0.51	1.000	
					Route (trunk)	-132.20	344.70	-0.38	1.000	
					Climb number	247.00	205.90	1.20	1.000	
					Vertical speed	101.60	300.60	0.34	1.000	
Biceps brachii	0.691	8.40	4,15	0.001	Route (rope)	14168.47	3082.29	4.60	0.000	***
					Route (trunk)	-3574.99	2279.97	-1.57	0.750	
					Climb number	220.33	1324.93	0.17	1.000	
					Vertical speed	58.66	2119.08	0.03	1.000	
Triceps brachii	0.154	0.77	4,17	0.557	Route (rope)	-2303.40	2366.40	-0.97	1.000	
					Route (trunk)	-582.00	1682.40	-0.35	1.000	
					Climb number	1133.80	1009.30	1.12	1.000	
					Vertical speed	1254.70	1533.50	0.82	1.000	
Extensor carpi ulnaris	0.171	0.88	4,17	0.499	Route (rope)	5032.10	3431.90	1.47	0.789	
					Route (trunk)	-711.00	1982.70	-0.36	1.000	
					Climb number	587.00	1166.80	0.50	1.000	
					Vertical speed	1792.20	1829.60	0.98	1.000	

Appendix 2.8a. Multiple Linear Regression models showing the associations between mean muscle activity and locomotor modes/ support properties. QW = quadrupedalism; SP = suspension. * = p value <0.05; ** = p value <0.01; *** = p value <0.001.

Model	R^2	F	df	p	Predictor variable	Estimate	SE	t	p	
Vastus lateralis	0.009	0.63	5,337	0.678	Locomotor mode (QW)	-0.37	35.43	-0.01	1.000	
					Locomotor mode (SP)	-10.63	115.64	-0.09	1.000	
					Compliance score	-32.73	19.46	-1.68	0.827	
					Support orientation	-4.82	10.06	-0.48	1.000	
					Total no. supports	8.77	9.10	0.96	1.000	
Gluteus maximus	0.029	1.91	5,386	0.063	Locomotor mode (QW)	42.49	30.26	1.40	0.848	
					Locomotor mode (SP)	12.03	102.71	0.12	1.000	
					Compliance score	-18.38	17.58	-1.04	1.000	
					Support orientation	10.63	8.07	1.32	0.256	
					Total no. supports	14.15	7.66	1.85	0.328	
Gastrocnemius	0.052	2.94	5,324	0.008	Locomotor mode (QW)	-8.49	7.46	-1.14	1.000	
					Locomotor mode (SP)	-27.09	27.74	-0.98	1.000	
					Compliance score	-5.06	4.19	-1.21	0.859	
					Support orientation	6.12	1.92	3.19	0.002	**
					Total no. supports	-1.22	1.84	-0.66	1.000	
Biceps brachii	0.124	3.45	5,147	0.003	Locomotor mode (QW)	950.75	1365.66	0.70	0.896	
					Locomotor mode (SP)	11822.02	2942.87	4.02	0.000	***
					Compliance score	-205.68	1132.18	-0.18	1.000	
					Support orientation	-647.58	484.58	-1.34	1.000	
					Total no. supports	344.74	546.80	0.63	1.000	
Triceps brachii	0.026	0.65	5,149	0.688	Locomotor mode (QW)	390.72	457.76	0.85	1.000	
					Locomotor mode (SP)	242.91	991.27	0.24	1.000	
					Compliance score	-56.75	368.78	-0.15	1.000	
					Support orientation	-90.26	161.14	-0.56	1.000	
					Total no. supports	-197.48	186.59	-1.06	1.000	
Extensor carpi ulnaris	0.043	1.17	5,157	0.327	Locomotor mode (QW)	120.23	273.05	0.44	0.628	
					Locomotor mode (SP)	1064.38	576.03	1.85	0.146	
					Compliance score	307.24	222.93	1.38	1.000	
					Support orientation	60.60	96.23	0.63	1.000	
					Total no. supports	-52.44	111.93	-0.47	1.000	

Appendix 2.8b. Multiple Linear Regression models showing the associations between mean muscle activity and support properties during arboreal bipedalism. * = p value <0.05; ** = p value <0.01; *** = p value <0.001.

Model	R²	F	df	p	Predictor variable	Estimate	SE	t	p	
Vastus lateralis	0.018	1.36	3,299	0.148	Compliance score	-45.26	22.45	-2.02	0.692	
					Support orientation	-3.91	10.94	-0.36	1.000	
					Total no. supports	15.83	9.79	1.62	0.427	
Gluteus maximus	0.024	2.15	3,345	0.074	Compliance score	-13.58	18.39	-0.74	1.000	
					Support orientation	13.39	8.47	1.58	0.098	
					Total no. supports	14.13	7.80	1.81	0.284	
Gastrocnemius	0.062	4.78	3,292	0.001	Compliance score	-5.08	4.36	-1.16	0.546	
					Support orientation	7.15	2.00	3.57	0.001	**
					Total no. supports	-1.63	1.86	-0.87	1.000	
Biceps brachii	0.017	1.36	3,309	0.248	Compliance score	626.64	506.87	1.24	0.304	
					Support orientation	-196.67	240.12	-0.82	1.000	
					Total no. supports	301.48	221.99	1.36	0.702	
Triceps brachii	0.013	1.10	3,329	0.356	Compliance score	174.01	239.06	0.73	0.578	
					Support orientation	-129.35	109.36	-1.18	1.000	
					Total no. supports	131.87	104.58	1.26	0.833	
Extensor carpi ulnaris	0.018	1.56	3,342	0.185	Compliance score	84.71	131.03	0.65	1.000	
					Support orientation	0.36	60.22	0.01	1.000	
					Total no. supports	112.13	55.44	2.02	0.176	

APPENDIX THREE

SKELETAL PREDICTORS OF BIPEDALITY

Appendix 3. Photograph showing a moderate obturator externus groove in the left femur of a female bonobo. The depression in bone surface can be observed between the red arrows running across the femoral neck, and a clear groove could be palpated upon recording.