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Hand use and posture during manipulative behaviours and arboreal locomotion in African apes

by

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A Dissertation Presented in Partial Fulfilment of the
Requirements for the Degree of Doctor of Philosophy

April 2017

Declaration

This is to certify that:

1. The thesis contains only my original work towards the fulfilment of the degree of Doctor of Philosophy at the University of Kent, except where stated otherwise.
2. Acknowledgement has been made in the text to all other material used.

All photographs have been taken by the author, if not stated otherwise.

Johanna Neufuss, April 2017

A handwritten signature in black ink, reading "J. Neufuss". The signature is written in a cursive style with a large, stylized initial "J" and a prominent flourish at the end.



“To many anatomists, opposition is a hallmark of mankind, to many zoologists, it is simply a function of the primate hand.”

(John Napier, 1960)

Abstract

The skill with which primates use their hands to explore and interact with the environment sets them apart from most other mammals. The non-human primate hand serves an important functional role during not only terrestrial and arboreal locomotion, but also enhanced grasping and manipulative behaviours. Understanding how living primates use their hands for these various functions is fundamental for understanding the order Primates and the evolution of humans within this order. While bipedalism and the extraordinary manipulative abilities of our human hand for manufacturing stone tools are considered to be unique, their origins remain controversial. Understanding this evolutionary shift in human hand use from locomotion to manipulation requires comparative studies of hand use in our closest living relatives, the African apes (chimpanzees, bonobos and gorillas). To date, however, little research has been done on African ape daily hand use, including both locomotor and manipulative behaviours, especially in natural environments. This dissertation will address this gap by conducting detailed studies of hand use and posture during two complex manipulative behaviours (i.e., plant-processing, nut-cracking) and arboreal locomotion (i.e., vertical climbing) in the natural environment of African apes.

I conducted the first comprehensive analysis of bonobo palm oil nut-cracking in a natural environment at the Lola ya Bonobo sanctuary, Democratic Republic of the Congo. All eighteen bonobos showed exclusive laterality for using the hammerstone and there was a significant group-level right-hand bias. The study revealed 15 hand grips for holding differently-sized and -weighted hammerstones, 10 of which had not been previously described in the literature. The findings also demonstrated that bonobos select the most effective hammerstones when nut-cracking and that bonobos, despite rarely using tools in the wild, can be efficient nut-crackers with a skill level that is similar to palm oil nut-cracking chimpanzees of Bossou, Guinea.

I further provided the first insights into the manual skills of Bwindi mountain gorillas by examining hand-use strategies, hand grips, and hand-preference (i.e.,

laterality) during the processing of three different plants. Two of these plants are woody-stemmed plants for which the food is more challenging to access in comparison to leaves, lacking physical defenses that are relatively simple to process. Bwindi gorillas used the greatest number of hand actions to process the most complex plant food (i.e., peel-processing) similar to complex thistle feeding by Virunga mountain gorillas. The manipulative actions were ordered in several key stages organised hierarchically. The demands of manipulating natural foods elicited 19 different hand grips and variable thumb postures, of which three grips were new and 16 grips have either been previously reported or show clear similarities to grips used by other wild and captive African apes and humans. A higher degree of lateralisation was elicited for the most complex behaviour of peel-processing but the strength of laterality was only moderate, suggesting that peel-processing is not as complex as thistle leaf-processing by Virunga gorillas.

Finally, I examined for the first time hand use, forelimb posture and gait characteristics during vertical climbing in wild, habituated mountain gorillas (*Gorilla beringei*) of the Bwindi Impenetrable National Park, Uganda, and semi-free-ranging chimpanzees (*Pan troglodytes*) of the Chimfunshi Wildlife Orphanage Trust, Zambia, both within a natural environment. This research revealed that both apes used power grips and a diagonal power grip, involving three different thumb postures. Gorillas showed greater ulnar deviation of the wrist during climbing than chimpanzees, and the thumb played an important supportive role when vertically descending compliant substrates in gorillas. Comparisons of temporal gait parameters showed that large-bodied gorillas exhibited significant longer cycle duration, lower stride frequency and generally a higher duty factor than chimpanzees. This quantitative analysis revealed that mountain gorillas adapt their climbing strategy to accommodate their large body mass in a similar manner found in captive western lowland gorillas, and that chimpanzees showed less variation in their climbing strategy than has been documented in captive bonobos. In summary, this study demonstrates the importance of forceful hand grips and the variable use of the thumb relative to substrate size in both ape species, and particularly in large-bodied mountain gorillas as they face more biomechanical challenges during vertical climbing than smaller-bodied chimpanzees.

Together, this dissertation provides new insights into the functional link between hand morphology and behaviour in African apes in their natural environments that may ultimately generate more informed reconstructions of fossil hominin locomotor and manipulative behaviours. Furthermore, this research shows that the suite of “unique human grips” or “unique human manipulative abilities” that have typically defined humans is getting much smaller the more we learn about African apes, particularly in their complex natural environment where the hand has to adjust to varying foods and arboreal substrates, and where individuals have ample opportunity to learn and develop high manipulative skills.

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Chapter 1

General introduction

The primate hand interacts directly with the environment during numerous daily activities, and thus has evolved to encompass functional adaptations related to both manipulation and locomotion (e.g., Napier, 1967, 1993; Kivell et al., 2016). The non-human primate hand is used for diverse locomotor behaviours in both terrestrial and arboreal environments but is also known for its enhanced grasping ability compared with other mammals (e.g., Cartmill, 1972, 1974; Sylvester, 2006; Garber, 2007; Patel et al., 2015). Bipedal humans, in contrast, have largely removed their hands from the functional requirements of locomotion and are known for their enhanced dexterity relative to other non-human primates (Napier, 1956, 1960; Marzke, 1997). Several studies have investigated the morphological adaptations of the human hand that are thought to promote this dexterity and are generally considered to have evolved in response to tool-related behaviours during human evolutionary history (Napier, 1956, 1993; Marzke, 1983; Susman, 1994; Marzke, 1997; Marzke and Marzke, 2000; Marzke, 2013). However, early bipedal fossil humans (hominins) show a mosaic of ape-like and human-like morphologies that have led to decades of debate over the significance of arboreal locomotion, such as vertical climbing and suspension, in hominin evolution (Stern and Susman, 1983; Latimer, 1990; Hunt, 1996; Stern 2000; Ward, 2002; Schmitt, 2003; Lovejoy, 2009). Vertical climbing, in particular, has long been recognized as playing an important role in the evolution of apes (hominoids) (Cartmill, 1985; Hirasaki et al., 1993; Isler, 2005; Hanna et al., 2008), and has been considered by several authors (Stern, 1976; Probst, 1980; Fleagle et al., 1981; Stern and Susman, 1981, 1983; Tuttle et al., 1991) to be integral to the origins of habitual bipedalism in early hominins. Understanding this evolutionary shift in human hand use from locomotion to manipulation requires a comparative perspective of hand use in our closest living relatives, the African apes (chimpanzees, bonobos and gorillas). African apes offer a valuable functional model as they possess numerous morphological features shared with humans, including several features of the hands, compared with other primates (Lewis 1965, 1969; Tocheri, 2008; but see review in Kivell, 2016). Furthermore, African apes provide us with examples of possible morphological adaptations of their locomotor system to different ecological conditions, their locomotor performance in their natural habitat, manipulative and cognitive abilities, arboreal and terrestrial feeding behaviours and tool-use behaviours. Therefore, African apes can give us a greater insight into the

potential range of behaviours that might be capable with a given bony morphology of their hand.

To date, most studies of African ape manual manipulation have been conducted in captivity, often using very small food objects and unnatural objects (Christel, 1993; Marzke and Wullstein, 1996; Jones-Engel and Bard, 1996; Butterworth and Itakura, 1998; Hopkins et al., 2002; Crast et al., 2009; Hayashi, 2007), or specific tool-use behaviours in the wild (Boesch and Boesch, 1983; Lesnik et al., 2015). Furthermore, although there has been much discussion about African ape terrestrial knuckle-walking hand postures and morphology (Tuttle, 1969, 1967; Richmond, 2001; Begun, 2007; Kivell and Schmitt, 2009; but see Kivell et al., 2013), very little is known about how African apes use their hands, and forelimbs more generally, on arboreal substrates. Thus, we are lacking key information on which anatomical structures of the non-human ape hand are suited for both manipulation and arboreal locomotion such as vertical climbing, both of which are needed to fully interpret the functional significance of morphological variation we see in fossil hominin hands and to reconstruct the evolution of human hand dexterity. The aim of this research is to fill this gap in our knowledge by conducting detailed studies of hand use and posture during complex manipulative behaviours (nut-cracking, plant-processing) and arboreal locomotion (vertical climbing) under natural conditions in African apes.

Grasping (or prehension; movements in which an object is seized and held securely partly or wholly within the hand; Napier, 1956) is a hallmark adaptation among primate hands (and feet) (e.g., Napier, 1960, 1961; Cartmill, 1974, 1985; Szalay and Dagosto, 1988; Lewis, 1989). All primates must climb to exploit arboreal food resources in the upper forest canopy. Grasping allows primates to ascend or descend in a highly structured and discontinuous environment. Unlike walking on horizontal or inclined substrates, vertical climbing is not a form of steady locomotion in which primates can rely on limb movements that repeat in regular cycles and a consistent interlimb coordination (or hand/footfall pattern) (e.g., Isler, 2005). The irregularity of climbing upon vertical supports demands a higher amount of neural and visual control of the hands (e.g., Cartmill, 1972, 1974). Vertical climbing requires hand-eye coordination and the conscious estimation of distances and

substrate properties (Schmidt, 2010). It is, therefore, suggested that of all the locomotor modes of primates, vertical climbing is most likely to have promoted the development of cognitive skills during primate evolution (Schmidt, 2010). Prehensile grasping is an important prerequisite for climbing because it provides stability in any position of the three-dimensional environment that primates inhabit (e.g., Grand, 1972; Rose, 1988).

Primates are capable of using different hand grips and postures to accommodate variation in substrate size during vertical climbing, which require compromises in joint mobility and stability, and diverse mechanical demands placed on hand morphology (e.g., Lewis, 1989; Larson, 2007; Drapeau, 2008; but see Schmitt et al., 2016). Many have argued that primate hand morphology is generalised and primitive compared to most other mammals, allowing for greater versatility in hand use (e.g., Napier, 1960, 1961; Tuttle, 1969; Marzke 1971; Jouffroy et al., 1993; Tocheri et al., 2008). Compared to most other primates, the African ape hand exhibits several derived features, of which the potential adaptations to knuckle-walking (e.g., ridges on the metacarpal heads, scaphoid-os centrale fusion, or a distal ridge on the radius) have arguably received the most attention (e.g., Tuttle, 1967; Richmond and Strait, 2000; Inouye and Shea, 2004; Kivell and Begun, 2007). However, the African ape hand also shows several morphologies that are advantageous for arboreal locomotion. Chimpanzees show a reduction while gorillas show a complete loss of ulnocarpal articulation that allows for a greater mobility (i.e., ulnar deviation) of the wrist and hand that is considered adaptive for vertical climbing and suspensory behaviour (Lewis et al, 1970; Cartmill and Milton, 1977; Lewis, 1989; Kivell, 2016; but see Jouffroy and Medina, 2002; Orr and Atkinson, 2016). Furthermore, the fingers are relatively long and the thumb is relatively short, the thumb is highly mobile compared to most non-hominoid primates and the phalanges are curved (Figure 1.1) (e.g., Tuttle, 1969; Lewis, 1989; Kivell, 2016; Patel and Maiolino, 2016; but see Orr, 2016). To securely grasp curved arboreal substrates, curvature of the manual phalanges reduces overall strain experienced by the bone and allows compressive stress from a strong grip to be more evenly distributed along the length of the digits (Figure 1.2) (Sarmiento, 1988; Hunt, 1991; Richmond, 2007). African apes also have several large intrinsic and extrinsic muscles devoted to digital flexion and strong grasping (Tuttle, 1969; Myatt et al., 2012), which better distribute strain along the digits exerted by the locomotor

demands of vertical climbing or suspensory behaviours (Preuschoft and Chivers, 1993; Richmond, 2007). Although the functional importance of the short thumb during arboreal behaviours has traditionally been downplayed (Ashely-Montagu, 1931; Straus, 1942; Tuttle, 1967; Rose, 1988; Sarmiento, 1988), African apes recruit their thumbs in various hand grips when grasping and manipulating objects (e.g., Napier, 1956; Christel, 1993; Marzke and Wullstein, 1996; Engel and Bard, 1996; Pouydebat et al., 2008; Byrne et al. 2001b; Bardo, 2016).



Figure 1.1: Hand proportions in gorillas (left) and chimpanzees (right).



Figure 1.2: Gripping arboreal substrates in chimpanzees (left). The dorso-ventral curvature of the manual phalanges maintains a uniform distance (blue arrows) between the bone and substrate, so that pressure is more evenly applied along the length of the digit (right).

Although there has been much discussion about the morphology in the African ape hand in association with vertical climbing and other forms of arboreal locomotion, and forelimb more generally, we know comparatively little about how these apes actually use their hands and forelimbs to grasp, stabilize and propel themselves within a natural arboreal environment (e.g., Sarmiento, 1988, 1994; Hunt, 1991; Marzke, 1992; Preuschoft and Demes, 1994; Preuschoft, 2002). Vertical climbing is an important component of the African ape locomotor repertoire, even in mountain gorillas which are considered the least arboreal of all African apes (e.g., Remis, 1998; Crompton et al., 2010; Hunt, 2016; Crompton, 2016). For small-bodied primates, vertical climbing is as easy (i.e., no increase in both mechanical challenges and relative energetic costs) as horizontal walking, but for larger-bodied primates it is not (Hanna et al., 2008, 2011). Primates larger than 1 kg appear to use their forelimbs mainly in tension and the hindlimbs mainly in compression, both when ascending and descending vertical substrates (Preuschoft, 2002; Hanna et al., 2017). Thus, it is therefore critically important for large-bodied great apes to hold firmly on arboreal substrates when their forelimb is in tension. A few studies have investigated spatio-temporal variables (i.e., stride frequencies, stride - and step lengths, and support phase) and gait characteristics of vertical climbing in great apes, most which have been conducted in captivity (Isler, 2002, 2005; Schoonaert et al., 2016). Only one naturalistic study compared the gait parameters of vertical climbing in rehabilitated and wild Sumatran orangutans to captive individuals (Isler and Thorpe, 2003). A preliminary study on captive chimpanzees described climbing patterns and limb joint kinematics (Nakano et al., 2006), but gait parameters of “forelimbs and hindlimbs” have not been examined. Current knowledge about the spatio-temporal gait characteristics of gorilla vertical climbing stems solely from a captive study of two adult western lowland gorillas using only one type of locomotor support, a vertical rope (Isler, 2002). This comparative study showed that climbing in gorillas was less diverse in gait patterns compared to bonobos and the forelimb/hindlimb support phase (duty factor) was generally higher. In addition, vertical climbing was more challenging for adult male gorillas, likely due to their larger body mass compared to female gorillas and bonobos (Isler, 2002, 2005).

To better understand how species or subspecies differences in morphology may relate to or be adaptive for vertical climbing, we need more research on forelimb

gait parameters and how the digits grasp various natural substrates in mountain gorillas and chimpanzees, particularly in regards to the functional role of their thumb. Moreover, perhaps because vertical climbing is a very physically demanding form of locomotion in larger-bodied great apes (hominids), it is a good link to study forceful hand grips that are important to more secure climbing and needed for object manipulation such as stone tool use, as well as hominin tool manufacture. The frequent use of vertical supports may also influence hand biomechanics toward ulnar deviation in African apes, as observed in gibbons (Van Horn, 1972) and several strepsirrhines (Jouffroy and Lessertisseur, 1979; Lemelin and Schmitt, 1998; Reghem et al., 2012), further enhancing hand mobility and manual grasping for non-locomotor behaviours.

Primates use their hands not only for locomotion, but also for forceful manipulation, during feeding and also for manipulating non-edible objects such as tools during their daily life (Beck, 1980; Bently-Condit and Smith, 2010). Object manipulation is an important survival skill and has been assumed to be a precursor of tool-use (Marzke, 2006; Call, 2013). However, the hand itself possesses a greater potential for manipulation than is typically realised, whether in humans or non-human primates. For instance, humans can further exploit their potential skills after long-term intensive training and become experts in areas that require outstanding manipulative capabilities, such as professional piano players and rock climbers (e.g., Watson, 2006; Heldstab et al., 2016). Captive chimpanzees and bonobos can further improve their manipulative abilities and become more skilled in tool-use in both efficiency and diversity (Hirata et al., 2009; Gruber et al., 2010; Haslam, 2013; Hayashi, 2015). Moreover, “Kanzi” the bonobo, learnt stone tool-making skills and demonstrated that human-like hands are not necessary for removing flakes from stone cores with a hammerstone and use them as cutting tools (Toth et al., 2006; Toth and Schick, 2009; Roffman et al., 2012).

Numerous frameworks have been designed for analysing behavioural complexity in object manipulation and tool use of non-human primates, such as the number of acts in the manipulative repertoire of a given species (Torigoe, 1985; Fragaszy and Adams-Curtis, 1991; Takeshita and Walraven, 1996; Byrne et al., 2001a); the number of objects manipulated (Matsuzawa, 1991; Takeshita and

Walraven, 1996); the novelty of the task (Fagot and Vauclair, 1991); the degree of precision in motor patterns such as hand grips and digit role differentiation (e.g., Costello and Frigaszy, 1988; Byrne and Byrne, 1991; Fagot and Vauclair, 1991; Marzke, 1997; Byrne et al., 2001a; Crast et al., 2009; Pouydebat et al., 2009); the extent of bimanual asymmetrical coordination and manual specialisation (e.g., Fagot and Vauclair, 1988; Sugiyama et al., 1993; Hopkins, 1995; Spinozzi et al., 1998; Byrne et al., 2001a; Leca et al., 2010); and the hierarchical complexity in the organizational structure of behavioural units (e.g., Byrne and Byrne, 1991; Matsuzawa, 1996; Hayashi, 2007a; Boesch et al., 2009; Hayashi, 2015; Heldstab et al., 2016). All of these frameworks offer different insights into “complexity” that can be complementary or contradictory, depending on the goals of the research or questions being asked. However, in reports on how primates use their hands to manipulate objects, many researchers agree on the importance of systematically and quantitatively describing the different types of hand-use strategies (Byrne and Byrne, 1991, 1993; Fragaszy and Adams-Curtis, 1991; Leca et al., 2011; Heldstab et al., 2016) and to consider anatomical and/or functional implications such as grips and hand movements (e.g., Marzke and Wullstein, 1996; Marzke, 1997; Pouydebat et al., 2008; Marzke et al., 2015; Bardo, 2016). For example, much work looking at laterality (the preference for using one hand over the other for a particular task or across tasks; Marchant and McGew, 1994, 2013) in great apes has found a positive relationship with task complexity (e.g., Fagot and Vauclair, 1991; but see review in Cashmore et al., 2008). Based on this research, the ‘task-complexity’ model posits that complex manipulative behaviours, such as precise bimanual coordinated asymmetrical actions (i.e., coordinated use of both hands, with each doing something different), should elicit greater laterality at the individual and group level than simple tasks, such as reaching for an object with one hand (e.g., Fagot and Vauclair, 1988; Sugiyama et al., 1993; Hopkins, 1995; Spinozzi et al., 1998; Byrne et al., 2001a; Leca et al., 2010; Lambert, 2012).

In contrast to laterality, the repertoire of hand grips, thumb postures and hand-use strategies during both simple and complex manipulative behaviours are not well characterised among African apes, especially under natural conditions (Boesch and Boesch, 1993; Byrne et al., 2001a; Marzke et al., 2015; Lesnik et al., 2015). Most previous work on ape manual manipulation has been done in zoos, often

involving standardised objects of small size or of uniform shape (e.g., grapes, raisins, cylindrical sticks, wooden cubes) that are suitable for cross-species comparisons, but are unlikely to demonstrate the potential manipulative range of their subjects (Parker, 1974; Torigoe, 1985; Jordan, 1982; Christel, 1993; Engel and Bard, 1996; Marzke and Wullstein, 1996). While many studies focused primarily on a thorough analysis of grasping behaviour, it is clear from these studies that African apes cannot be assumed to lack ability to perform more elaborate prehension movements like precision grips (e.g., Christel, 1993; Engel and Bard, 1996; Christel et al. 1998; Pouydebat et al., 2006a,b, 2009; Reghem et al., 2014). However, little detail is given in these studies to allow an understanding of what the hands can do, when they manipulate an object. They also often use novel tasks that would require more time to further exploit potential skills (Jordan, 1982; Christel, 1993; Bardo et al., 2016). For example, “Kanzi” the bonobo showed that stone tools can be made by non-human primates after long-term training, using different techniques and grip types than observed in humans (Toth et al., 1993; Schick et al., 1999). Ultimately, tightly controlled captive studies may be essential for observing the limits of manipulative ability; however, at this stage the need is instead for discovering the range of potential manual skills that are expressed in the natural behaviour repertoire of the species.

A wide repertoire of hand grips has been defined so far in humans and non-human primates in both wild and captive studies during object manipulation (e.g., Napier, 1956; (Boesch and Boesch, 1993; Marzke and Wullstein, 1996; Gumert et al., 2009; MacFarlane, 2009; Pouydebat et al., 2011; Bullock et al., 2013; Marzke et al., 2015, Bardo, 2016). These hand grips are divided into four categories, for which there are variations of the grips within each category based on the contact areas and particular digits used.

(1) Precision grips: Object is held in contact between the thumb and fingers without involvement of the palm (Figure 1.5a) (Napier, 1956; Schneck, 1987, Marzke and Wullstein, 1996; Jones-Engels and Bard, 1996; Byrne et al., 2001; Gumert et al., 2009; Pouydebat et al., 2011; Marzke et al., 2015; Lesnik et al., 2015; Bardo, 2016).

- (2) **Power (palm) grips:** Object is held by an active involvement of the palm, the thumb and one or several fingers (Figure 1.5b) (Napier, 1956; Marzke and Wullstein, 1996; Jones-Engels and Bard, 1996; Pouydebat et al., 2011).
- (3) **Hook grips:** Object is held mainly by the flexed fingers, whereby the thumb and the distal part of the palm can be also involved (Figure 1.5c) (Napier, 1956; Marzke, 1992; Marzke and Wullstein, 1996; Marzke et al., 2015; Bardo, 2016).
- (4) **Compound grips:** More than one object is held in one hand by using two distinct hand grips simultaneously (Figure 1.5d) (Napier, 1956; Macfarlane, 2009; Jones and Fragaszy, 2015). For example, two small fruits are held in the same hand, one gripped by the tips of the thumb and index finger, while the other is gripped by the palm and fourth and fifth digits. These grips require that the digits operate independently to some degree to accommodate multiple objects or multiple grips. The combined grip can also be termed as ‘asynchron use of digits’, according to the terminology of Heldstab et al. (2016).

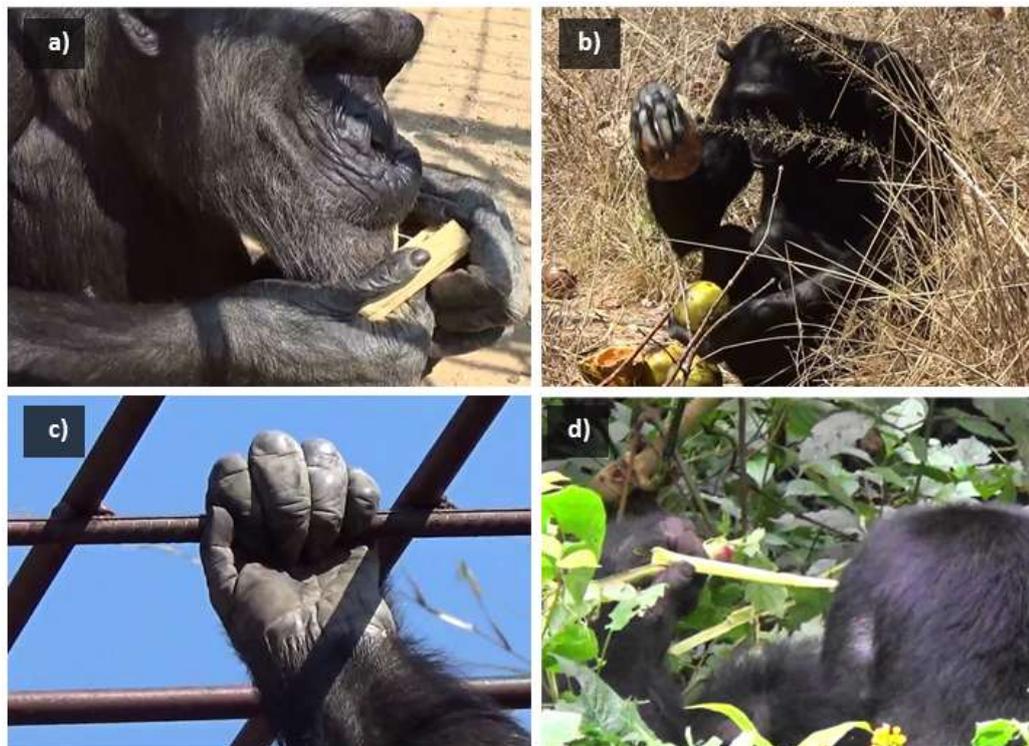


Figure 1.3: Classification of grips: (a) Pad-to-side precision grip in both hands, (b) Power (palm) grip in upper, right hand, (c) Suspensory transverse hook grip, and (d) Compound grip.

To investigate the evolution of a trait, researchers need to study non-human primates in their natural environments; the more natural the behaviour and more diverse the setting, the more informative the results are likely to be (McGrew and Marchant, 1997a). Pouydebat and colleagues (2006a, b, 2009) recorded grasping behaviour in a large sample of semi-free-ranging primates (including great apes, cercopithecines, capuchins). They focused on interspecific differences in grasping techniques to pick up objects of different sizes, showing that precision grasping is used preferentially to pick up small objects by all primates. Macfarlane and Graziano (2009) made a detailed analysis of basic grip behaviour during food manipulation in semi-free-ranging macaques. They could distinguish 15 different grip types according to the contact areas of the hand that were used to grip the object. However, only a few studies focused on a level of analysis above that of reach-and-grasp and involved complex, familiar tasks in wild individuals, such as tool-use and food-processing. They elicited a great range of manipulations and new grip types (chimpanzees: Boesch and Boesch, 1993; Corp and Byrne, 2002; Marzke et al., 2015; Lesnik et al., 2015; mountain gorillas: Byrne et al., 2001a). Hence, we now require more detailed functional analyses of manipulation for complex, familiar tasks to chart the range of manual skills that might be used for varying objects in a natural environment.

While early studies focused primarily on classification of grip types in the human hand only (e.g., Napier, 1956), subsequent studies have attempted to use the behavioural observation of grasping types under controlled conditions to better understand hand functions in non-human primates (e.g., Napier, 1960, 1961; Tuttle, 1969; Christel, 1993; Jones-Engel and Bard, 1996; Marzke and Wullstein, 1996). Since then, many researchers have video recorded their subjects while performing manual tasks in experimental settings and used digitized images to make detailed descriptions of prehension movements, hand postures, grip types and the contact areas between the fingers of the grip and the object (e.g., Butterworth and Itakura, 1998; Christel et al., 1998; Christel and Fragaszy, 2000; Spinozzi et al., 2004; Crast et al., 2009, Borel et al., 2017). Other studies used high-speed cameras during *ad libitum* sampling (Altmann, 1974) in semi-free-ranging individuals (Pouydebat et al., 2006a,b, 2009; Macfarlane and Graziano, 2009) or motion capture techniques to allow a quantification of forelimb motion (Sartori et al., 2013a,b). In the latter

method, a video camera is positioned perpendicular to the direction of motion, allowing an analysis of speed of movement, patterns of contact, and 2D joint and segment angles in each frame. When multiple video cameras are used and synchronized, a 3D approach is possible (e.g., Christel and Billard, 2002; Isler, 2005; Hedrick, 2008; Patel, 2009; Patel and Polk, 2010; Reghem et al., 2014). Outside the laboratory, motion capture of the hand and forelimb is often hampered because of difficulties in calibration of the space and the limited availability of possible camera positions. However, much work is currently under way to develop methodologies that correct 2D out-of-plane angular estimates (Stevens et al., 2006) and completely markerless systems with multiple cameras based on photogrammetric 3D reconstruction (Sellers and Hirasaki, 2014), which can be carried out on semi-free-ranging primates in sanctuaries.

In the wild, detailed analyses of hand use are more challenging and thus, few studies have been conducted to date (Boesch and Boesch, 1993; Byrne et al., 2001a; Corp and Byrne, 2002; Gumert et al., 2009; Lesnik et al., 2015; Marzke et al., 2015). For example, the study group may not be habituated enough to the presence of humans for allowing close range observations, conditions of observations may be very difficult (e.g., bad visibility due to foliage or height), or the frequency of observations may be too low (e.g., infrequent contact with particular individuals). Some researchers determined hand grips by observation (Boesch and Boesch, 1993) or by manual digitization of their recorded images (Gumert et al., 2009), while others used stop-frame and slow-motion video analyses to be certain of the fine details of fast prehensile movements (Byrne et al., 2001; Marzke et al., 2015). While all these methods are rather time-consuming, the latter is most efficient as information on different hand use behaviours (e.g., grips, hand-posture, contact areas across digits, laterality) and object characteristics (e.g., size, length, weight) can be extracted at once using a behaviour video coding software (e.g., The Observer XT12, INTERACT). Coding software allows one also to determine how often an event or behaviour occurs across species. For this, an ethogram coding of all the potential hand use behaviours needs to be developed in prior to the analysis (see *Appendix D*).

When analysing hand use behaviours, it is important to consider not only variation in the size and shape of objects (e.g., Cutkosky, 1989; Elliott and Connolly, 1984; Santello et al., 2002), but also variation in individual or species hand size

(Pouydebat et al., 2008, 2009). For this, Pouydebat and colleagues (2008, 2009) determined the diameter of the object according to the length of the hand (i.e., from the proximal part of the third metacarpus until the distal part of the third digit) of the species and categorised objects as either small when shorter than the length of the hand or as large when as long as the length of the hand. However, it is almost always impossible to measure directly the actual size of an object or individual's hand under field conditions. Thus, a standardized categorisation scheme is now needed to consistently assess the size of an object relative to the individual without having to carry out measurements and facilitate reliable intraspecific (e.g., larger males vs. smaller females) and interspecific (e.g., smaller bonobos vs. larger gorillas) comparisons in natural environments.

Unlike in non-human primates, the human hand is completely decoupled from habitual locomotion and used only for manipulations (Napier and Tuttle, 1993; but see Bullock et al., 2013 for common human hand use behaviours). Traditionally humans are considered to be unique compared with other primates in their ability to apply high forces with one hand when using precision and power squeeze grips, and to precisely maneuver objects within one hand using the thumb and finger tips (precision handling; Marzke and Shackley, 1986; Marzke, 1997). Several morphological features of the human hand are considered to be distinctive of humans and to facilitate use of these grips, such as a long thumb relative to shorter fingers (e.g., Schultz, 1930; Napier, 1993; Almécija et al., 2015), well-developed intrinsic thumb muscles (e.g., Tuttle, 1969; Marzke et al., 1999) and a high mobile first carpometacarpal joint (Taylor and Schwarz, 1955; Napier, 1962; Marzke, 1992, 1997; Tocheri et al., 2008).

Humans are also considered unique among primates in having a wide-spread occurrence of right-handedness (i.e., 80-90 % of all human populations; McManus, 1991; Llaurens et al., 2009). In contrast, investigations of captive and wild non-human primates revealed no clear evidence of species-level manual lateralization (e.g., Colell et al., 1995; Papademetriou et al., 2005), perpetuating the idea that population-level right-handedness is a characteristic unique to humans. However, experimental parameters (e.g., terminology, behavioural tasks, analysis procedures) have varied across studies, potentially contributing to inconsistent cross-species

findings (e.g., McGrew and Marchant, 1997; Cashmore et al., 2008; Marchant and McGrew, 2013; Hopkins et al., 2013). Although studies on human handedness often treat manual behaviour with dichotomous distinctions (left, right), hand laterality is multidimensional and exist on a gradient. To demonstrate the multidimensionality of lateralized manual behaviour, Marchant and McGrew (2013) suggested a basic category framework that defines manual laterality at both the individual and group levels. This framework generates four different types of manual laterality and allows comparisons within and between individuals, populations, and species: (1) handedness, where multiple tasks are performed by multiple individuals with the same hand; (2) hand-preference, which refers to a single task performed by a single subject; (3) manual specialisation considers multiple tasks performed by a single individual; (4) task specialisation refers to a single task performed by multiple individuals.

Non-human apes have now been extensively investigated for lateralized manual behaviour, and researchers have identified numerous factors that can influence laterality: task type, task complexity, speed of the task, body posture, hand-use strategy, rearing history and setting (e.g., Forrester et al., 2012, 2013; Hopkins, 2013; Marchant and McGrew, 2013; Pouydebat et al., 2014). However, non-human ape studies have rarely investigated laterality in natural behaviours. This is a big gap because natural behaviours are likely to be the conditions under which cerebral lateralization and motor biases evolved (e.g., Forrester et al., 2017). However, some studies have documented a group-level hand bias for certain behaviours in wild mountain gorillas (e.g., plant processing: Byrne and Byrne, 1991) and chimpanzees (tool-use: Boesch, 1991; Lonsdorf and Hopkins, 2005; Humle and Matsuzawa, 2009). However, these biases do not extend to all manipulative activities, nor do they reach the species-wide consistency seen in humans across all tasks including one-handed (unimanual) actions (McManus, 1985; Hopkins, 2006). Thus, more research is currently needed on behaviours under natural conditions to fully understand the factors that are likely to influence lateralization across individuals within a group and more cross-species comparisons are required of the same behaviour to understand specie-specific lateralized behaviour.

Understanding the origin and evolution of the manipulative abilities and handedness that characterises humans is a fundamental question in paleo-anthropology. Recent discoveries of the relatively complete hominin fossil hands of *Ardipithecus ramidus* (4.4 Ma; Lovejoy et al., 2009), *Australopithecus sediba* (1.98 Ma; Kivell et al., 2011) and *Homo naledi* (~250 Ka; Dirks et al., 2017) have made clear that the hand skeleton, like the postcranial skeleton overall, can include combinations of primitive and derived features that are not seen in living taxa and thus make functional interpretations challenging. Paleoanthropologists have different ideas about which features in the fossil hominin morphology are functionally important and reflect the behaviours that our ancestors were engaging in during their daily lives versus those features that might be primitive retentions and no longer functionally “useful” (e.g., Lovejoy et al., 1973; Stern, 1975; Latimer and Lovejoy, 1989; Rose, 1991; Stern and Susman, 1991; but see review in Kivell, 2016). The debate remains unsettled partly because hand use abilities are not well characterized under natural conditions in non-human apes and thus, we are limited in the functional interpretations that we can make from both external and internal bony morphology (e.g., Almecija and Alba, 2014; Tsegai et al., 2013; Kivell, 2015, 2016; Stephens et al., 2016). However, skeletal morphology alone does not explain the functional abilities of the hand; soft tissue morphology (i.e., muscles, ligaments), which is not preserved in the fossil record, can vary or be ‘plastic’, allowing for potentially a much greater range of behaviours than might be reconstructed from bony morphology alone (e.g., Hamrick et al., 1998; Marzke et al., 1998; Myatt et al., 2012). Thus, detailed investigations of how living apes use their hands, both for manipulation and locomotion, can provide greater insight into the potential range of behaviours that might be capable with a given bony morphology. Little is known as to which anatomical structures of the non-human ape hand are suited for complex manipulations as well as for arboreal locomotion, especially in natural environments.

As our closest living relatives, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) have been widely used as living models for reconstructing the behaviour of early hominins and identifying features either shared by humans and other apes or unique to humans (e.g., Washburn and Avis, 1958; Zihlmann and Cramer, 1978; Wrangham and Peterson, 1996; de Waal, 1997; Marzke, 1997; Marzke and Marzke, 2000). Chimpanzees have been studied extensively since the

1960s in both captivity and the wild with particular focus on their manipulative abilities (e.g., Napier, 1960; Marzke and Wullstein, 1962; Goodall, 1964; Boesch and Boesch, 1983; Inoue-Nakamura and Matsuzawa, 1997; see McGrew, 2016 for a recent list and map of all chimpanzee field sites). Long-term studies on several wild chimpanzee populations revealed manual preparation of plant foods, a diverse use of tools and methods of making tools from plants material (e.g., Goodall, 1986; Boesch and Boesch, 1990; McGrew, 1992; Nishida, 1986; Sugiyama, 1994; Stokes and Byrne, 2001; Marzke et al., 2015). A diverse repertoire of hand grips, in-hand movements, bimanual role differentiation, strong laterality and precise, visually-guided handling mark the chimpanzee's high manual skills when processing plants or using and making tools (e.g., Boesch and Boesch, 1993; Stokes and Byrne, 2001; Sanz et al., 2006; Marzke et al., 2015). The cracking of hard-shelled nuts using a pair of stones as hammer and anvil is one of the most complex tool-using skills found in the wild, which so far appears to be restricted to certain West African chimpanzee populations (e.g., Boesch et al., 1994; Matsuzawa, 1994; McGrew et al., 1997).

In contrast, little was known about the behaviour of wild bonobos until the 1970s and research on bonobos has remained more limited because data from fully habituated wild bonobos come from just three field sites (Wamba, Lui Kotale, Lomako; Badrian and Badrian, 1984; Badrian and Malenky, 1984; Kano, 1982, 1983; Hashimoto et al., 1998; Hohmann and Fruth, 2003). Although captive bonobos display equivalent tool-using capacities, tool use by wild bonobos is remarkably limited (Gruber et al., 2011; Furuichi et al., 2015) and their foraging and food processing skills have yet to be studied (Kano, 1982; Ingmanson, 1989, 1996; Hohmann and Fruth, 2003). Focusing primarily on chimpanzee manipulative abilities may underestimate or bias our interpretation of hand use and gripping ability in other apes, especially in bonobos and gorillas that do not engage in complex tool-use behaviours in the wild like chimpanzees do.

Gorillas also remain relatively understudied in terms of their arboreal locomotor and manipulative behaviours, especially in the wild. While gorillas lack a long powerful thumb, they have relatively shorter hands compared to arm length like humans and australopiths (Almécija et al., 2015). This suggests that gorillas could be important models for early human arboreal locomotion. Yet we know remarkably little about gorilla vertical climbing styles in the wild (Crompton, 2016). Although

wild gorillas use only rarely tools, their plant-processing behaviours reveal high manipulative skills (Byrne and Byrne, 1991; Byrne et al. 2001a, b; Breuer et al., 2005; Kinani and Zimmerman, 2015).

The different preferences for particular locomotor and manipulative behaviours in chimpanzees, bonobos and gorillas correlate highly with habitat structure and resource availability, not only at the level of species but also on the level of populations (chimpanzees: Reynolds, 2005; Watts, 2008; gorillas: Remis, 1998; bonobos: Hohmann and Fruth, 2003). For example, arboreality among gorillas is correlated with the amount of fruit in the diet. Lowland gorillas that eat a lot of fruit are more arboreal than mountain gorillas at Karisoke in the Virunga Mountains (Williamson et al., 1990; Remis, 1994). Virunga mountain gorillas have fewer motivations and opportunities to climb trees than do lowland gorillas as fruit trees are only rarely available in the high-altitude dwarf montane forest environment (Fossey, 1983; Watts, 1984). In contrast, the mountain gorillas of the Bwindi Impenetrable National Park, Uganda, live at lower altitude with a denser forest canopy and more fruit trees and thus, have greater opportunities to engage in arboreal behaviours (Robbins et al., 2006). Bwindi gorillas climb trees over several months and make use of arboreal fruit resources when they are seasonally available (Sarmiento et al., 1996; Ganas et al., 2004; Robbins, 2008). The ecological variation between Bwindi and the Virunga Mountains also leads to different foraging strategies, with Bwindi gorillas consuming more several plant parts (i.e., leaves, pith, peel or bark) of various abundant plant species than Virunga gorillas (e.g., Watts, 1984; Ganas et al., 2004). Differences in diet between both mountain gorilla populations may reveal different hand use and manipulation strategies. Without our understanding of the diversity in behaviour, both within and between species, there would be no starting point of reconstructing early human behaviours.

This dissertation aims to greatly improve our understanding of the link between hand morphology and behaviour in African apes by conducting detailed studies of hand/forelimb used during two complex manipulative behaviours (i.e., nut-cracking and food-processing) and arboreal locomotion (i.e., vertical climbing) under natural conditions. This focus will improve our understanding of the manual skills of non-human apes in the nut-cracking and feeding behaviours and allows us to understand where else these manual abilities occur, namely in arboreal locomotion.

Moreover, these new insights will provide a better functional reconstruction of fossil hominin hand morphology, both in terms of manipulative/tool-use abilities and arboreal locomotion. To achieve this aim, my dissertation has four main questions:

- 1) Bonobos and chimpanzees share similar hand proportions and joint morphology, but bonobos rarely use tools in the wild while chimpanzees are known as the most proficient tool-users across all primates. Are bonobos thus different from chimpanzees in their manual abilities?
- 2) Will Bwindi mountain gorillas perform complex manipulation, similar to that documented in other mountain gorillas, to process the specific foods in their environment, will they use similar grips during both locomotion and manipulation, and is there a functional link between food processing and hand morphology?
- 3) Do large-bodied mountain gorillas differ from smaller-bodied chimpanzees in their hand use and vertical climbing strategy, and what implications does that have for interpreting ape hand morphology?
- 4) What are the links across human arboreal locomotion, manipulation, stone tool use and tool-making?

My dissertation aims to shed light on the four main questions by using an interdisciplinary approach of behavioural studies, biomechanics and functional morphology. I will quantify and compare hand-preference, hand grips, and efficiency during the highly complex nut-cracking behaviour in semi-free-ranging bonobos compared with wild chimpanzees (Chapter 2). In Chapter 3, I investigate hand use, hand grips, laterality and behavioural complexity during plant processing in wild mountain gorillas. In Chapter 4, I analyse arboreal forelimb posture, hand grips and temporal gait characteristics during vertical climbing in mountain gorillas and chimpanzees. The general discussion (Chapter 5) synthesises ideas about the links across human arboreal locomotion, manipulation, using and making stone tools that will ultimately generate more informed reconstructions of fossil hominin locomotor and manipulative behaviours.

Chapter 2

Nut-cracking behaviour in wild-born rehabilitated bonobos (*Pan paniscus*): A comprehensive study of hand-preference, hand grips and efficiency

This chapter was published in 2017 in the *American Journal of Primatology* 79 (2), 1-16 (see *Appendix III*).

Abstract

There has been an enduring interest in primate tool-use and manipulative abilities, most often with the goal of providing insight into the evolution of human manual dexterity, right-hand preference, and what behaviours make humans unique. Chimpanzees (*Pan troglodytes*) are arguably the most well-studied tool-users among non-human primates, and are particularly well-known for their complex nut-cracking behaviour, which has been documented in several West African populations. However, their sister-taxon, the bonobos (*Pan paniscus*), rarely engage in even simple tool-use and are not known to nut-crack in the wild. Only a few studies have reported tool-use in captive bonobos, including their ability to crack nuts, but details of this complex tool-use behaviour have not been documented before. Here, I fill this gap with the first comprehensive analysis of bonobo nut-cracking in a natural environment at the Lola ya Bonobo sanctuary, Democratic Republic of the Congo. Eighteen bonobos were studied as they cracked oil palm nuts using stone hammers. Individual bonobos showed exclusive laterality for using the hammerstone and there was a significant group-level right-hand bias. The study revealed 15 hand grips for holding differently sized and weighted hammerstones, 10 of which had not been previously described in the literature. The findings also demonstrated that bonobos select the most effective hammerstones when nut-cracking. Bonobos are efficient nut-crackers and not that different from the renowned nut-cracking chimpanzees of Bossou, Guinea, which also crack oil palm nuts using stones.

2.1 Introduction

Tool use and the selective manipulation of objects are widespread across the animal kingdom (Beck, 1980; Bentley-Condit and Smith, 2010) but only a few species of primates use a variety of tools for multiple purposes and show a wide range of different manipulative behaviours in the wild. Wild bearded capuchins and long-tailed macaques are well-known for their regular tool-use, involving highly controlled sequences of percussive actions (e.g., Spagnoletti et al., 2011; Gumert and Malaivijitnond, 2013; Visalberghi et al., 2015). Orangutans and, to a lesser extent, western lowland gorillas also have been reported to use tools in the wild (Breuer et al., 2005; Meulman and van Schaik, 2013; Kinani and Zimmerman, 2015). However, among primates, chimpanzees are commonly regarded as the most skilled tool-users in the wild (McGrew, 1992) and their tool-use skills have been studied extensively since the 1960s (e.g., Goodall, 1964; Sugiyama, 1981; Boesch and Boesch, 1983; Inoue-Nakamura and Matsuzawa, 1997; Sanz and Morgan, 2013). Chimpanzees are particularly well-known for their nut-cracking tool-use behaviour, with different populations across West Africa using a variety of methods and materials (e.g. wood vs. stone hammers) (e.g., Boesch and Boesch, 1983; Hanna and McGrew, 1987; Biro et al., 2006).

In contrast to the relatively ubiquitous and culturally diverse tool-use behaviours of wild chimpanzees (*Pan troglodytes*), it is particularly interesting that their sister taxon, the bonobos (*Pan paniscus*), rarely use tools in the wild. Only a few observations of bonobo tool use have been made in the wild (e.g., Kano, 1982; Ingmanson, 1996; Hashimoto et al., 1998; Hohmann and Fruth, 2003) and most of these are rarely-documented instances of simple and occasional tool-use actions (Hohmann and Fruth, 2003; Furuichi et al., 2014). Unlike their chimpanzee cousins, nut-cracking, the most complex primate tool-use behaviour (Matsuzawa, 1994) ever recorded in the wild, has to date never been reported among wild bonobos. The simple tool-use actions in wild bonobos such as dragging branches, aimed stick throwing, leaf sponging or the use of leafy twigs to shield from rain (Kano, 1982;

Hohmann and Fruth, 2003; Furuichi et al., 2014), involve the use of one hand rather than two hands (MacNeilage et al., 1987; Hopkins, 1995), few sequential stages to realize the task (Marchant and McGrew, 1991) and a low level of precision of the required motor acts (e.g., Morris et al., 1993). In contrast, the nut-cracking behaviour in wild chimpanzees requires precise role-differentiated manipulation by both hands (Kano, 1982; Humle, 2003; Biro et al., 2006), the interface of three external objects (hammer, anvil and nut) at the same time, and a high level of motor control and cognitive ability (Matsuzawa, 1994).

Despite the general absence of tool-use in the wild, bonobos in captivity demonstrate an equally diverse and highly complex repertoire of tool-use behaviours compared with captive chimpanzees (Jordan, 1982; Takeshita and Walraven, 1996; Gruber et al., 2010; Roffman et al., 2015). The bonobo “Kanzi” is the best example illustrating this species’ capability to develop highly skilled tool-making and tool-using behaviours (e.g., Toth et al., 1993). Kanzi is able to produce stone flakes and selectively choose tools that are more useful than others (Schick et al., 1999). These findings suggest that bonobos have the same understanding of the functional properties of tools as other great apes (Hermann et al., 2008) and a cognitive ability for tool-related behaviours (Jordan, 1982; Gruber et al., 2010). Gruber et al. (2010) reported the nut-cracking ability in the bonobos of Lola ya Bonobo sanctuary, but details of this complex tool-use behaviour have not yet been documented. In addition, their shared hand and upper limb anatomy with chimpanzees (Susman, 1979; Diogo and Wood, 2011) suggests that bonobos have the same physical capability to perform equivalent manipulative tasks as seen in chimpanzees.

Several hypotheses have been put forth, such as variation in ecological constraints (Furuichi et al., 2014) or inherent differences between the species (Koops et al., 2015), which might explain the relative rarity of tool-use in wild bonobos. Alternatively, tool-use may be more common among bonobos but due to their small numbers in the wild and the limited number of habituated groups compared with chimpanzees, primatologists simply may not have yet witnessed their full tool-use repertoire. For example, data for chimpanzees comes from several field sites (Whiten et al., 2001), whereas long-term studies of bonobos are restricted to two populations (Wamba and Lomako, DRC) and the number of individuals observed at both sites is

relatively small (i.e., <25 individuals) (Hashimoto et al., 1998; Hohmann and Fruth, 2003). Moreover, some chimpanzee groups rarely use tools in the wild (Reynolds, 2005; Watts, 2008). Thus, the lack of data on bonobos may exaggerate their reported differences with chimpanzees. Nevertheless, the relative rarity of simple tool-use and the absence of complex tool-use in wild bonobos are in stark contrast to the well-documented and frequent complex tool-use observed among captive and wild chimpanzees (e.g., Boesch and Boesch, 1983, 1993; Biro et al., 2006; Hirata et al., 2008; Schrauf et al., 2012).

Many studies of primate tool-use and manipulative abilities aim to provide insights into the evolution of human manipulation, human hand-preference, and what gripping abilities make humans unique compared with other primates. Of the non-human primates that have been studied, most show dominant use of one hand at an individual-level for specific tasks (e.g., Collet et al., 1995; McGrew and Marchant, 1997; Papademetriou et al., 2005; Cashmore et al., 2008). A group-level bias has been occasionally reported in some non-human primate populations (e.g., Corps & Byrne, 2004; Spinozzi et al., 2004; Vauclair et al., 2005; Hopkins et al., 2007), but none has ever demonstrated species-wide consistency in hand-preference (i.e., ~90 % right-handed) typical of humans (e.g., Annett, 1972; Raymond and Pontier, 2004; McManus, 2009). Hand preference or laterality has been investigated in bonobos but almost exclusively in captive groups, and primarily involving unnatural objects and simple tasks such as reaching for food, gesturing or scratching (e.g., De Vleeschouwer et al., 1995; Hopkins and de Waal, 1995; Colell et al., 1995; Harrison and Nystrom, 2008). In all of these studies, most bonobo individuals were non-lateralized (i.e., used both hands interchangeably) for most of the actions studied. However, task complexity has been shown to be an important factor influencing manual laterality in primates (McGrew and Marchant, 1997a, 1999). The nut-cracking behaviour of chimpanzees is a particularly good example of a complex manual behaviour as the chimpanzee individuals exhibit more pronounced laterality of the dominant hand compared with simple unimanual tasks (Boesch, 1991; Sugiyama et al., 1993; Humle and Matsuzawa, 2009). Similar findings have been made for other tool use actions in wild chimpanzees or captive capuchin monkeys (Westergaard et al., 1998; McGrew and Marchant, 1997b; McGrew et al., 1999;

Londsorf and Hopkins, 2005). When bonobos are faced with artificial complex bimanual manipulative tasks, they show strong laterality at an individual-level but not at a group-level or population-level (Chapelain et al., 2011; Hopkins et al. 2011; Bardo et al., 2015). However, apart from these few studies, there are no published data on laterality during a natural complex bimanual task performance in bonobos.

Similarly little is known about the diversity of hand grips used by bonobos, especially when manipulating natural objects. Studies of bonobo (and chimpanzee) hand grips are done almost exclusively in captivity (Christel, 1993; Marzke and Wullstein, 1996; Christel et al., 1998; Pouydebat et al., 2011). These studies show that they are capable of precision grasping between the thumb and finger(s). However, because of their shorter thumb and smaller musculature (Marzke et al., 1999) they are generally considered to not be able to perform these grips as forcefully as humans (Marzke, 1997, 2013). Nevertheless, a recent study of wild chimpanzees suggests the use of forceful precision pinch grips - an ability traditional thought to be unique to humans (Marzke and Shackley, 1986; Marzke and Wullstein, 1996; Marzke et al., 1998) - during food-processing (Marzke et al., 2015). Long-tailed macaques show a similar ability during stone tool-use (Gumert and Malaivijitnond, 2009), suggesting more research on primate manipulative abilities is needed particularly in natural environments.

Here, I present the first detailed analysis of bonobo cracking oil palm nuts with stone hammers in the Lola ya Bonobo sanctuary, which is in a natural environment in the Democratic Republic of the Congo. The bonobos are known to show nut-cracking behaviour since the first nursery sanctuary was established in 1995. The rescued, wild-born bonobos are integrated into a social group where they can observe nut-cracking behaviour of more experienced individuals. The infants born there have ample opportunity to observe their mothers. This sanctuary population offers a unique opportunity to investigate a natural complex tool-use behaviour in bonobos and how this behaviour compares to the pervasive nut-cracking behaviour practiced by wild chimpanzees.

The aims of this study are to (1) investigate bonobo hand-preference (i.e., laterality) during a complex tool-use behaviour, (2) identify the full range of hand

grips during nut-cracking using various hammer stone weights, shapes, thicknesses and sizes, and (3) analyse the efficiency of bonobo nut-cracking relative to a chimpanzee population (Bossou, Guinea) using similar materials (i.e., oil palm nuts and stone hammers). Based on the high complexity of nut-cracking behaviour, I predict that bonobos will show a strong laterality similar to chimpanzees. Based on shared anatomy and results from studies in captivity, I further predict that bonobos will use a similar diversity of hand grips as documented during complex manipulative tasks in chimpanzees. However, given that wild populations of bonobos are not known to nut-crack and since this behaviour was only recently shown and disseminated among adult members of the first nursery sanctuary in 1995, I predict that they will be less efficient (i.e., require more hits to crack a nut, crack fewer nuts per minute) than their wild chimpanzee counterparts.

2.2 Materials and Methods

2.2.1 Species and study site

Lola ya Bonobo is a sanctuary, founded in 1995, for orphan bonobos rescued from the bush meat and pet trade. As of 2015 (when data were collected), the sanctuary housed 71 bonobos of wild-born (rescued, human-reared) and sanctuary-born (mother-reared) individuals. All but six bonobos that were born at the sanctuary were wild-born. Research on bonobos faces considerable challenges due to the political instability of the Democratic Republic of Congo and the difficulties in accessing the three field sites of wild bonobos deep in the Congo Basin. Therefore, the complex natural environment of the Lola ya Bonobo sanctuary provided a suitable alternative to study the manipulative actions of bonobos in a natural setting, and particularly behaviours that have not been observed in wild-habituated populations. Unlike in zoos, the sanctuary enclosures include a natural and complex environment, including high canopy forest areas with oil palm trees, swampy areas, freshwater ponds or river streams. The social groups are divided into three enclosures, which include a semi-natural forested environment in which the bonobos are allowed to range freely throughout the day. All three enclosures allow for nut-

cracking behaviour of oil-palm nuts (*Elaeis guineensis*) and the bonobos can be heard nut-cracking regularly in the forest. Nut-cracking in the open non-forested areas (i.e., near the sanctuary housing and feeding areas) is facilitated by the placement of anvil stones by humans that are embedded in the ground. Palm oil nuts attached to their branches were supplied by humans in the non-forested areas every morning, but there is also natural supply in forest enclosure. Hammerstones of different sizes and shapes (see below) were placed near the anvils and individuals were free to engage in nut-cracking when and as they wished.

2.2.2 Data collection

Data were collected at the ‘Lola ya Bonobo’ sanctuary in Kinshasa (DRC) during April and May 2015. The research protocols reported in this study were reviewed and approved by the ‘Les Amis des Bonobos du Congo’ Scientific Committee and its Scientific Coordinator and by the Ethics Committee of the School of Anthropology and Conservation at the University of Kent, UK. High-definition video was recorded at 50 HZ *ad libitum* (Altmann, 1974) at close range from several angles (anterior, side or posterior views) to capture dynamic hand movements, grip patterns and the particular digits involved (the thumb, which can often be opposed to the fingers and hidden from view) during nut-cracking on a sample of 18 individuals across all three bonobo groups, including 12 females and 6 males; 14 adults (>10 years old) and 4 adolescents (7-9 years old) (Badrian and Badrian, 1984). Nut-cracking behaviour for any given individual was divided into ‘**sessions**’ and ‘**bouts**’. Hand use and grip patterns for holding stone tools were recorded and analyzed for bouts. A ‘**session**’ was defined as a period in which one individual was engaged in nut-cracking. A **session** was considered continuous when the nut jumped away and was immediately picked up again; when the nut was changed; the stone broke apart and cracking continued with the same but smaller stone; or another individual interrupted shortly for sexual behaviour (a common occurrence in bonobos). In all of these instances, the individual did not leave the anvil site. A **session** was terminated when the individual stopped and walked away from the anvil, starting a new behaviour. A **session** was generally composed of multiple bouts. Hand use and grip

patterns for holding stone tools were recorded and analyzed for bouts. A ‘**bout**’ was defined as a continued period of nut-cracking behaviour, in which the hand used did not change (regardless of the number of hits) (Humle and Matsuzawa, 2009). A **bout** was considered terminated if there was a change in the hand(s) used (left vs. right), both hands vs. one hand/one foot, grip type, body posture, or when the nut was successfully or unsuccessfully cracked, or when nut-cracking was interrupted by another behaviour. Video data were analysed using The Observer XT12 (© Noldus Information Technology) to code hand-preference, hand grips and number of hits, frame by frame.

2.2.3 Data Analysis

2.2.3.1 Hand-preference

Similar to other studies, I considered the hand used for hammering to be the dominant hand for which aspects of hand use were recorded (Boesch, 1991; Humle, 2003). Hand-preference or laterality was recorded for bouts to ensure independence of data points (e.g., McGrew and Marchant, 1997; Humle and Matsuzawa, 2009; Chapelain et al., 2011). Only individuals for whom a minimum of 10 bouts or more were recorded were included in the analysis (Humle and Matsuzawa, 2009). I consequently investigated laterality in 15 individuals with a total number of 609 bouts. Laterality was investigated as the relative frequency of right (R) vs. left (L) hand use within and across individuals ($H_0: p_R = p_L$ vs. $H_1: p_R \neq p_L$). I used a binominal test for proportions to test the null hypothesis of a 50/50 distribution ($H_0: p_R = p_L$). I further tested the probability of success for the two proportions (R vs. L) in a Bernoulli trial (significance set at $p \leq 0.05$). I calculated a handedness index (HI) score ranging from -1 to +1 for each individual based on the total number of bouts: $HI = (R - L) / (R + L)$ (Humle and Matsuzawa, 2009; Chapelain et al., 2011). Negative values indicate a left hand bias and positive values indicate a right-hand bias. I further calculated the relative frequency of bouts using both hands (bimanual) and one-hand/one-foot in addition to the one handed hammering strategy. In addition, I explored whether right-hand or left-hand use has an effect on the efficiency of nut-cracking (number of hits per nut, nut-per-minute variable) (Boesch, 1991) via a

stepwise regression test. For the model presented here, age and sex were excluded as these factors had no effect.

2.2.3.2 Grip patterns when using hammerstones

2.2.3.2.1 Classification of hand grips

I investigated hand grips used to hold the hammerstone during nut-cracking in all 18 individuals. Different grips were first categorized broadly into palm (power) and precision grips (Napier, 1980; Marzke and Wullstein, 1996) and then into more detailed classification schemes with more specific focus on precision pinching such as the human three-jaw chuck ‘baseball grip’ and cradle grip (Marzke, 2003), and grip repertoire that have been identified in both wild and captive bonobos, chimpanzees, macaques and/or capuchin monkeys (Costello and Fragaszy, 1988; Christel, 1993, 1998; Boesch and Boesch, 1993; Jones-Engel and Bard, 1996; Marzke and Wullstein, 1996; Spinozzi et al., 2004; Pouydebat et al., 2009; Gumert and Malaivijitnond, 2009; Macfarlane, 2009; Marzke et al., 2015). My initial categorization centred on precision pinch, precision/passive palm, and power grips that have been previously identified in both wild and captive bonobos and chimpanzees. I further described how the thumb and fingers were used to grip hammerstones and how different grips related to the size, weight, shape and thickness of the hammerstone (see Results, Table 2.1).

2.2.3.2.2 Measurements and categorisation of hammerstones

A total of 28 potential hammerstones were placed next to the anvils of the enclosure. The maximum width (6-25 cm), maximum length (7-30 cm) and weight (0.10-4.48 kg) were measured and the general shape (e.g. oval, triangular) was recorded. Stone weight was categorised as light (0.10-0.38 kg), moderate (0.45-1.24 kg) and heavy (1.38-4.48 kg). An additional eight stones that the bonobo individuals had collected themselves from the forest were also used as hammerstones. Size and weight could only be inferred for these hammerstones and thus, a categorisation

scheme has been developed for reliable inferences about object size during grasping. Stone size was categorised by the diameter relative to hand size and by the length relative to hand length (Fig. 2.1): small, when ‘-smaller than the size of the palm-’ (i.e., small width; short length); medium, when ‘-roughly the size of the palm-’ (i.e., moderate width; moderate length) and large, when ‘-larger than the palm and fingers-’ (i.e., large width; long length). Stone shape (e.g., oval, rectangular) and thickness (narrow, medium, thick) were estimated and categorised by visual inspection. Patterns were compared across individuals using the same and different stones.

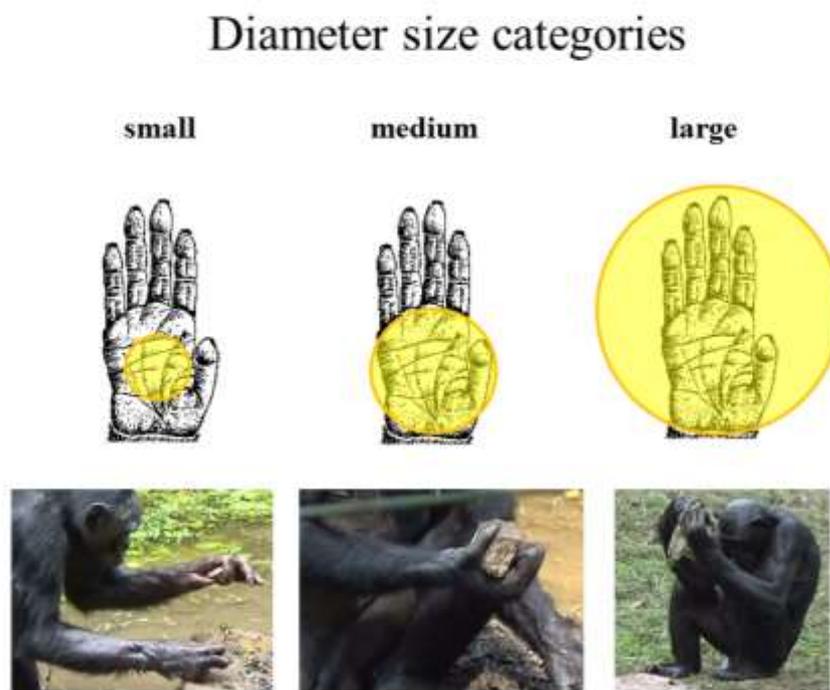


Figure 2.1: Diameter size categories for stone tools.

2.2.3.2.3 Analysis of hand grips and hammerstones

In the first analysis, I investigated the individual preference for specific hand grips used for 625 bouts and the diversity of grips across 18 bonobos. I recorded the use of each hand grip within a bout (as a bout is defined as the use of one grip only) for each individual and calculated the relative frequencies (Marzke et al., 2015). A stepwise regression analysis was used to test how the stone characteristics influenced the choice of a grip type for each individual. Since the grip types used to hold a stone were categorical, I needed to estimate the parameter of these regression models using a multinomial logistic regression. In this model, the probability of observing a particular hand grip was transformed using the logit function. Both the quantities of deviance and the Akaike information criteria (AIC) were used as indicators of how well the proposed regression model fits the data. A good model displayed a small deviance and AIC value.

2.2.3.4 Nut-cracking efficiency

Following previous studies, I calculated three measures of efficiency during episodes of nut-cracking for each stone per individual: (1) Hits per nut: average number of hits required per successfully cracked nut (Boesch and Boesch, 1981); (2) Nuts per minute: number of nuts (includes empty nuts and nuts yielding an edible kernel) cracked per minute (Boesch and Boesch, 1981); (3) Success rate: number of nuts yielding an edible kernel cracked per minute (Humle, 2003). I only considered sessions with a minimum of one minute duration of nut-cracking (Humle, 2003; Boesch and Boesch, 1981). Thus, I analysed a sample of 41 sessions and 30 different stones across 16 individuals. In the first analysis, I investigated the potential influence of several factors on the efficiency of nut-cracking in bonobos: (1) the dependency of stone size (width, length), weight, shape and thickness on the average number of hits and (2) the influence of each stone characteristic on the number of nuts cracked per minute. To test the different models, I used the backward elimination in a stepwise regression test to show the dependence of one variable on another. I do not report here on the influence of age and sex as these factors had no effect in the model.

I further used the results for hits per nut and success rate to run a comparable analysis with a Mann-Whitney U-test (significance level at $p \leq 0.05$), with the same data gathered from seven chimpanzees at Bossou, Guinea (Humle, 2003). Wild Bossou chimpanzees are a valuable comparison, because they use stone hammers (as opposed to wood, for example) and also crack solely oil palm nuts (as opposed to Panda and Coula nuts, for example) (e.g., Biro et al., 2006; Humle and Matsuzawa, 2009). The efficiency data were obtained through *ad libitum* behavioural sampling in the forest of Bossou.

2.3 Results

2.3.1 Laterality

When analysing the relative frequency of the dominant hand used for hammering with one hand, all 15 individuals used either the left or right hand exclusively (i.e., completely lateralised in 82 % of total 609 bouts across all individuals; $p < 0.0001$). Additionally, the handedness index, was always significantly different from 0 (either +1, right-handed or -1, left-handed), confirming a bias in hand use (Table 2.1). Taking the proportion of right versus left hand use, ten individuals (66 %; nine females, one male) used exclusively the right hand for hammering and five individuals (34 %; three females, two males) used exclusively the left hand. The overall right-hand bias across all individuals was highly significant ($N=15$, $p < 0.0001$). I additionally investigated how often the bonobos used another hand use strategy compared to exclusive right or left-handed hammering. Only five individuals, two right-handed females and three left-handed individuals (two females, one male), occasionally preferred both hands (15 % of total 609 bouts across all individuals) and three right-handed females rarely used the right hand/right foot (2.7 % of total 609 bouts across all individuals) hammering with larger stones. The combination of left hand/left foot was not observed.

Table 2.1: Summary of bout data and Handedness Index (HI) for each bonobo individual.

Individual	Sex	Age	Total time of nut-cracking (min)	Bouts of using both hands	Bouts of right hand / right foot	Bouts of exclusive hand use	HI	Category
Opala	F	20	34:35	0	0	66	1.00	RH
Semendwa	F	19	13:40	0	0	21	1.00	RH
Salonga	F	18	09:23	0	0	13	1.00	RH
Elikya	F	10	23:17	0	0	44	1.00	RH
Katako	F	11	20:18	0	0	55	1.00	RH
Pole	M	9	04:56	0	0	10	1.00	RH
Ilebo	M	14	18:33	0	0	24	- 1.00	LH
Malaika	F	8	54:45	35	1	50	1.00	RH
Masisi	F	10	17:54	0	5	34	1.00	RH
Muanda	F	12	38:48	22	0	40	- 1.00	LH
Lisala	F	14	14:30	0	10	16	1.00	RH
Mbandaka	M	14	26:56	3	0	46	- 1.00	LH
Isiro	F	18	19:55	10	0	23	1.00	RH
Kalina	F	17	16:58	23	0	40	- 1.00	LH
Likasi	F	14	06:22	0	0	18	- 1.00	LH
Bisengo	M	10	07:27	0	0	6	n/a	n/a
Yolo	M	12	04:40	0	0	6	n/a	n/a
Lomako	M	8	02:15	0	0	4	n/a	n/a

Sex: F, female; M, male; LH = left-handed individuals, RH = right-handed individuals. n/a: Individuals with less than 10 bouts were not included in the hand-preference analysis.

2.3.2 Hand grips used during nut-cracking

Fifteen different hand grips were observed across 18 bonobos (Table 2.2 and Fig. 2.2). I identified three precision (PC) grips (Pc1-Pc3), in which the object is held away from the palm by the thumb and fingers (Fig. 2.2a-c), as well as six power (Pw) grips (Pw1-Pw6) with active involvement of the entire palmar surface and fingers (Fig. 2.2j-o). I also observed six grips that could not be categorised as either precision or power grips that I thus consider to be novel and important for functional interpretations of hand anatomy (Fig. 2.2d-i). These grips are most similar to the precision finger/passive palm grips identified previously in chimpanzees when stabilising a food object in the hand as the teeth pulled against (Marzke et al., 2015), in long-tailed macaques when holding a stone to crack open oysters (Gumert and Malaivijitnond, 2009), and in humans when holding a core in the non-dominant hand during flake removal with the dominant hand (Marzke, 2006, 2013). However, in bonobos the same grip is dynamic rather than passive, such that the palm is contributing to the force of the strike as the hammerstone hits the object. Since the digits have most contact with the stone and only one part of the palm is in contact with the object, I call this category “precision finger/active palm grips” (PcApm4 – PcApm9).

This study revealed 10 new hand grips that had not been previously reported in the grip repertoire of either wild or captive bonobos, chimpanzees, capuchin monkeys and macaques (Costello and Frigaszy, 1988; Christel, 1993, 1998; Boesch and Boesch, 1993; Jones-Engel and Bard, 1996; Marzke and Wullstein, 1996; Spinozzi et al., 2004; Pouydebat et al., 2009; Gumert and Malaivijitnond, 2009; Macfarlane, 2009; Marzke et al., 2015). The remaining five grips (Pc1, Pc3, Pw1, Pw5 and Pw6) have either been reported or show interesting parallels to grips used in wild and captive chimpanzees (Pc1, Pw1, Pw5 and Pw6) (Boesch and Boesch, 1993; Jones-Engel and Bard, 1996; Marzke and Wullstein, 1996; Pouydebat et al., 2009; Marzke et al., 2015), macaques (Pc3, Pw6) (Gumert and Malaivijitnond, 2009) and studies of human manipulative behaviour (Pc1, Pc3, Pw6) (Marzke and Shakely, 1986; Marzke and Wullstein, 1996; Marzke, 2013; Bullock et al., 2013). The similarities will be discussed in more detail below.

Furthermore, the thumb was particularly important in holding and stabilising the hammerstone as has been recognized in wild nut-cracking chimpanzees and stone tool-using macaques (Boesch and Boesch, 1993; Gumert and Malaivijitnond, 2009). The thumb was involved in each grip type, either adducted to the index finger, or opposing it, and was always in contact with the surface of the hammerstone throughout a nut-cracking bout. In 10 grips (Pc1-Pc3; PcApm5; PcApm8; PcApm9; Pw1; Pw2; Pw3; Pw5) the stone was pinched between thumb and fingers, suggesting potential forceful loading of the thumb (Fig. 2.2).



Figure 2.2: Different hand grips used by the dominant hand during bonobo nut-cracking. Bonobo precision grips hold small and medium-sized hammerstones: (a) Pc1 grip; (b) Pc2 grip; (c) Pc3 grip. Novel precision finger/active palm grips typically used for small and medium-sized hammerstones: (d) PcApm4; (e) PcApm5; (f) PcApm6; (g) PcApm7; (h) PcApm8; (i) PcApm9. Power grips were most commonly used to hold all hammerstones: (j) Pw1; (k) Pw2; (l) Pw3; (m) Pw4; (n) Pw5; (o) Pw6.

Table 2.2: Bonobo hand grips used during nut-cracking.

Grasping category	Digit contact	Acronym	Description
Precision grip	1-2-3-4	Pc1	Stone held between the full thumb (including the region of the base of the thumb) and lateral aspect of distal and middle phalanges of flexed index finger, buttressed by the distal and middle phalanges of the flexed third and fourth finger. Thumb flexed at IP joint.
	1-2-3-4	Pc2	Stone held between thumb pad and dorsal aspect of distal phalanges of flexed digits 2-3-4, away from the palm. Thumb is opposed to Index finger.
	1-2-3-4-5	Pc3	Stone held between thumb at level of IP joint of ventral aspect of proximal phalanx and pads of flexed digits 2-3-4-5, without the palm. Thumb widely abducted and in opposition to the fingers.
Precision finger/ active palm grip	1-2	PcApm4	Stone held between lateral aspect of distal thumb and ventral aspect of index finger, supported by the distal palm. Thumb not flexed and adducted towards Index.
	1-5	PcApm5	Stone held between distal and proximal phalanges of the thumb and lateral aspect of distal phalanx of digit 5, supported by the hypothenar eminence of the extended palm. Thumb flexed at IP joint and abducted.
	1-2-3	PcApm6	Stone held between thumb pad and ventral proximal phalanges of digits 2-3, with support by the distal palm. Thumb is not flexed and adducted towards Index.
	1-2-3-4	PcApm7	Stone held between full thumb and flexed digits 2-3-4, supported by the distal palm. Thumb is not flexed and adducted towards Index.
	1-2-3-4	PcApm8	Stone held between thumb and dorsal aspect of distal & middle phalanges of the flexed digits 2-3 to the lateral aspect of digit 4, supported by the thenar eminence of the palm. Thumb can be flexed or extended.

	1-2-3-4-5	PcApm9	Stone held between lateral aspect of the thumb and dorsal aspect of distal phalanges of flexed digits 2-3-4-5, supported by the hypothenar eminence of the palm. Thumb flexed at MP and IP joints, held adducted towards Index.
Power grip	1-2	Pw1	Stone held between lateral aspect of proximal phalanx of thumb and flexed index finger, supported by the palm and the web at the V-shaped region between thumb and Index.
	1-2-3	Pw2	Stone held between full thumb and dorsal aspect of distal phalanges of flexed digits 2-3. Thumb flexed at IP joint.
	1-2-3-4	Pw3	Stone held between full thumb and dorsal distal phalanges of flexed digits 2-3-4, with support by the palm. Thumb slightly flexed.
	1-2-3-4-5	Pw4	Stone held between full thumb and dorsal aspect of distal phalanges of flexed digits 2-3-4-5, supported by the palm. Thumb adducted towards Index.
	1-2-3-4-5	Pw5	Stone held between thumb and flexed digits 2-3-4-5 at their ventral aspect of proximal phalanges and dorsal aspect of distal and middle phalanges. Stone lies in palm and in web at the V-shaped region between full thumb and index finger.
	1-2-3-4-5	Pw6	Stone held in the palm between the thumb and four fingers flexed at the MP or IP joints. Thumb either held opposed, abducted, inside or outside the grip. Hand wrist can adduct with this grip.

Hand grips previously described in literature are highlighted in light font. New observed hand grips are highlighted in dark font.

2.3.2.1 Relative Frequencies of Hand Grip Preference

I observed strong individual differences in hand grip preference and how often particular grips were used (Fig. 2.3). Precision grips were rarely used and only by two individuals. Precision finger/active palm grips occurred more often and across more individuals (N=7). In contrast, the power grips were much less variable, with the ‘Pw6’ (including all five digits, such that the stone is held between flexed fingers and the palm, with counter pressure from the thumb; Fig. 2.2o) being by far the most commonly used grip across all bouts and all individuals, regardless of stone weight and size (a multinomial logistic regression results found Residual Deviance: 20.05; AIC: 60.50). Table 2.3 represents the number of bouts a certain precision and power grip was used in relation to the hammerstone weight and size. These results also highlight the individual preferences for a particular hammerstone; moderate-weight and medium-sized stones were used in most bouts while small and light stones were rarely used.

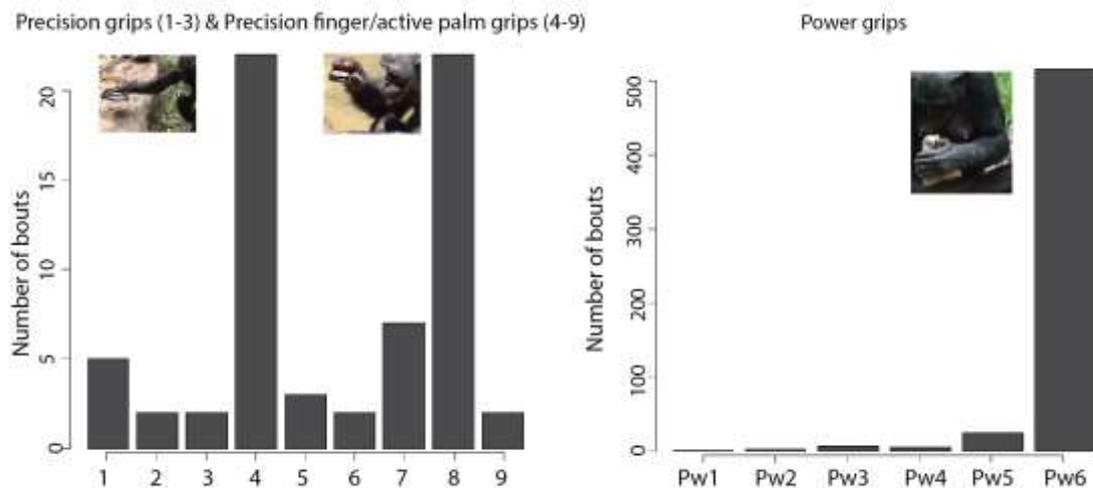


Figure. 2.3: Bar graph of relative frequency of hand grips used during nut-cracking. Precision grips (Pc1-Pc3) and precision finger/active palm grips (PcApm4-PcApm9) were used much more rarely and by fewer individuals than power grips (Pw1-Pw6). Note scales differ between graphs.

Table 2.3: Frequency of hand grips in relation to hammerstone weight and size.

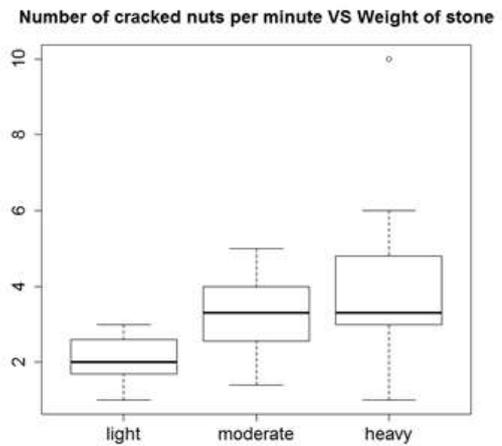
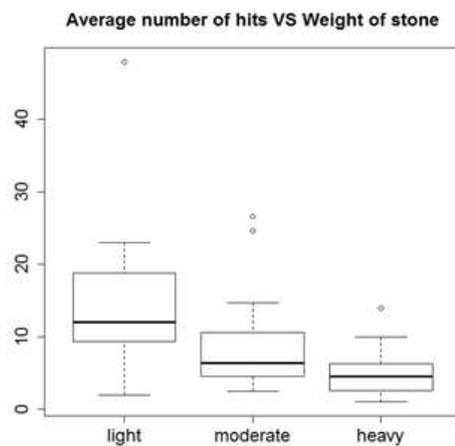
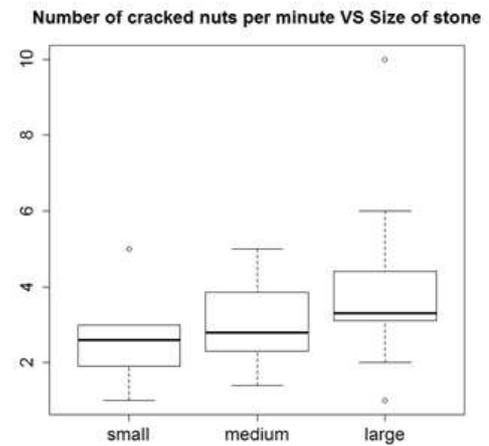
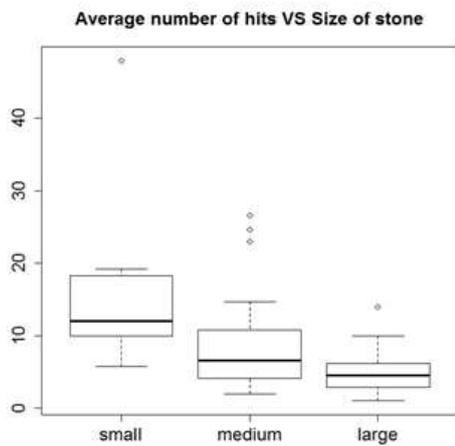
grip type	heavy stone	moderate stone	light stone	large stone	medium-sized stone	small stone
Pc1	-	-	5	-	-	5
Pc2	-	-	2	-	-	2
Pc3	-	2	-	2	-	-
Pc4	-	-	18	-	-	18
Pc5	-	-	3	-	-	3
Pc6	-	-	2	-	-	2
Pc7	-	4	-	-	-	4
Pc8	-	-	20	-	-	20
Pc9	-	-	2	-	-	2
Pw1	1	-	-	-	1	-
Pw2	-	-	4	-	-	4
Pw3	-	-	7	-	7	-
Pw4	-	5	-	-	5	-
Pw5	-	14	11	-0	23	2
Pw6	220	219	28	228	210	29

2.3.4 Nut-cracking Efficiency

Most individuals preferred moderate-weight and medium-sized stones while small and light stones were rarely used (Table 2.4 and Fig. 2.4). Two step-wise regression tests, showed that hammerstone size, weight, thickness and shape all had a strong and significant effect on both measures of efficiency: (1) the average number of hits required to crack a nut (N=41, $p < 0.0001$; R^2 values ranging from 0.87-0.96) and (2) the average number of nuts cracked per minute (N=41, $p < 0.0001$; R^2 values ranging from 0.87-0.88). Large and heavy stones were significantly more effective than small and light stones, while medium and moderate weighted stones were not significantly different from larger stones. Thicker stones required significantly fewer hits to crack a nut than thinner stones, but were similarly effective when it came to the number of cracked nuts per minute. Regarding stone shape, square-shaped stones were most efficient (Table 2.4 and Fig. 2.4).

Table 2.4: Effect of stone characteristics on nut-cracking efficiency.

	Mean # of hits per nut			Mean # of nuts per minute		
	F-stat.	p-value	R ²	F-stat.	p-value	R ²
Stone size	12.87	$p=1.265 \times 10^{-7}$	0.96	91.46	$p<0.0001$	0.87
Stone weight	130.5	$p<0.0001$	0.88	105.2	$p<0.0001$	0.88
Stone thickness	88.34	$p<0.0001$	0.87	95.4	$p<0.0001$	0.87
Stone shape	53.35	$p<0.0001$	0.87	59.23	$p<0.0001$	0.88



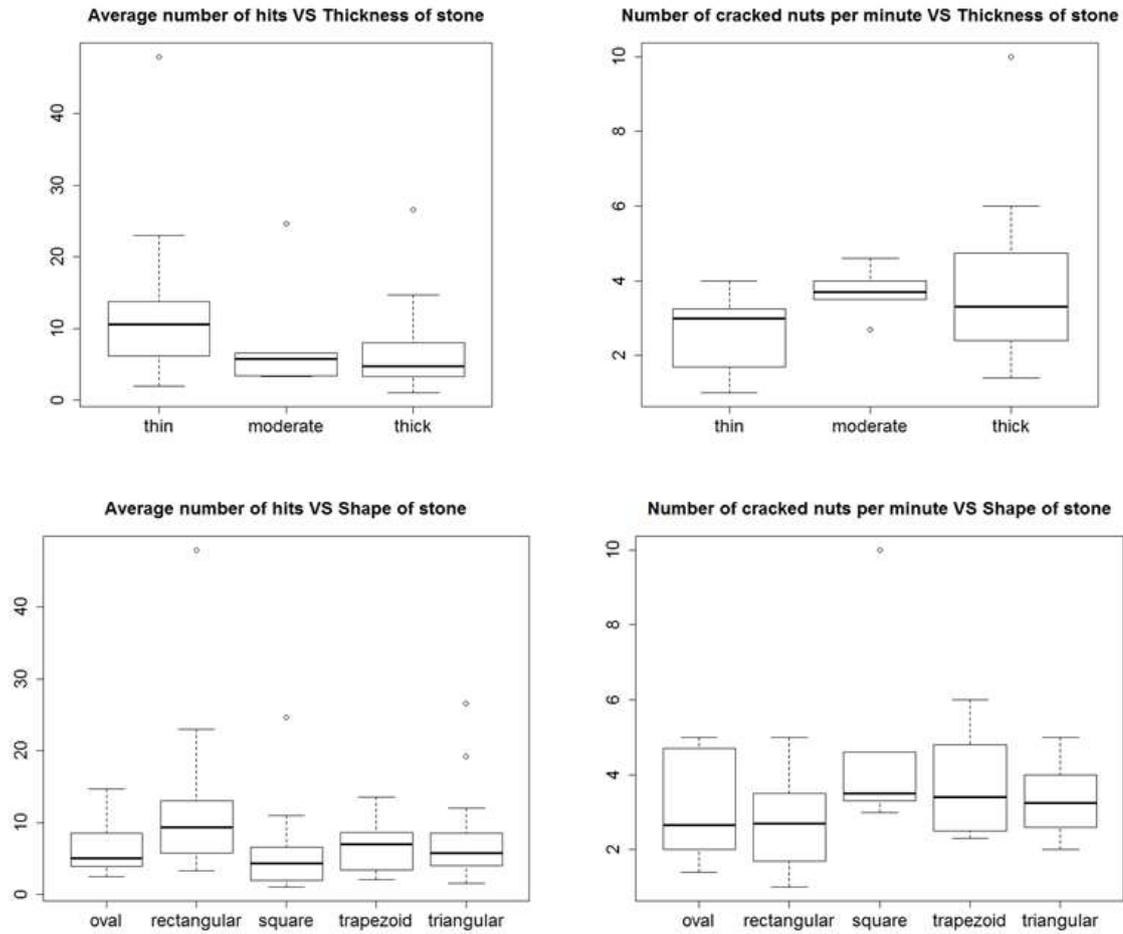


Figure 2.4: Nut-cracking efficiency relative to aspects of hammerstone characteristics. A simple linear regression test showed that the use of the right vs. left hand did not have a significant effect on (1) the average number of hits required to crack a nut (F-statistic: 133.3 on 2 and 49 DF, $p < 0.0001$, $R^2 = 0.8447$) and (2) the average number of nuts cracked per minute (F-statistic: 125.6 on 2 and 40 DF, $p < 0.0001$, $R^2 = 0.8624$). Left-handed individuals needed 4.75 (SD: 5.46; range: 20.94) hits to crack 3.5 nuts/minute and right-handed individuals required 6.56 (SD: 8.85; range: 47) hits to crack 3 nuts/minute. Across the sample, I found more variability across the right-handed individuals (**Figure 2.5**).

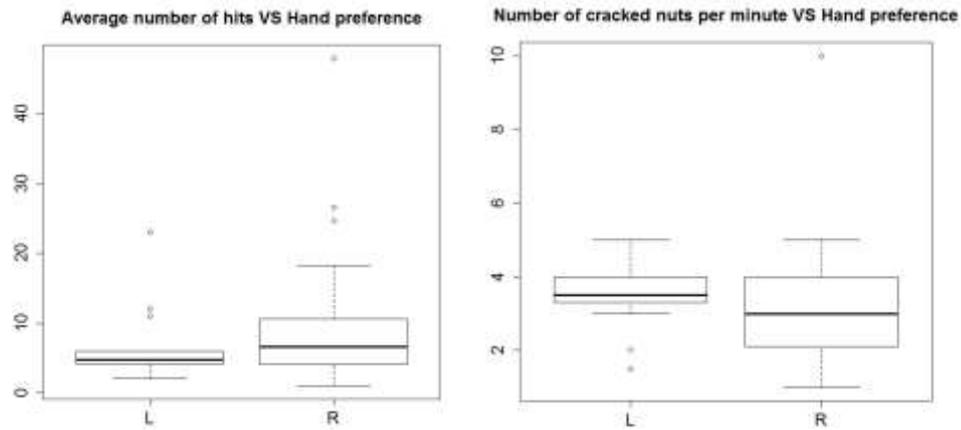


Figure 2.5: Effect of right (R) vs. left (L) hand on the efficiency of nut-cracking.

2.3.4.1 Nut-cracking Efficiency in Bonobos and Bossou Chimpanzees

I compared the (1) average number of hits per nut and (2) success rate (good nuts cracked per minute). A Mann-Whitney U test revealed that bonobos needed significantly ($U=99$, $N_1=16$, $N_2=7$, $p=0.003$) more hits per nut (median 7.3) than Bossou chimpanzees (median 3.8), but cracked significantly ($U=96.5$, $N_1=16$, $N_2=7$, $p=0.005$) more nuts per minute (median 2.8) compared with Bossou chimpanzees (median 1.9). Bonobos were also notably more variable across individuals in both efficiency measures (Fig. 2.6).

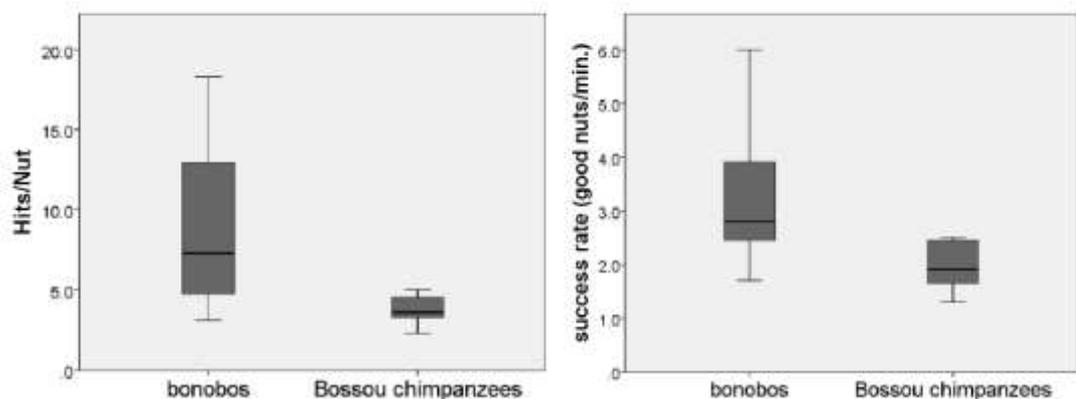


Figure 2.6: Box-and-whisker plots showing variation in nut-cracking efficiency between wild-born, rehabilitated bonobos and habituated, wild Bossou chimpanzees. Bonobos required significant more hits to crack a nut (left) but cracked significantly more good nuts per minute (right).

2.4 Discussion

I present here the first detailed study of hand laterality and hand grips used in bonobos at cracking palm nuts with stone tools. This is also the first analysis of nut-cracking efficiency in relation to qualities of the hammerstone, and how bonobo nut-cracking compares to that of Bossou chimpanzees.

2.4.1 Laterality

Most previous studies assessing hand preferences in bonobos have analysed simple tasks (e.g., spontaneous actions like reaching or feeding) in relatively small samples (2-10 individuals) (De Vleeschouwer et al., 1995; Hopkins and de Waal, 1995; Ingmanson, 1996). Although studies of more complex bimanual tasks found stronger individual hand preferences, no individuals were exclusively right- or left-handed (e.g., Chapelain et al., 2011; Hopkins et al., 2011; Bardo et al., 2015). In contrast to this previous work, the individual bonobos in this study were exclusively right- or left-handed and there was an overall significant right-hand bias at the group-level during nut-cracking. The determination of group-level hand preference is generally based on two factors: the strength of the individual hand preference (i.e., handedness index) and the number of individuals investigated (e.g., Papademetriou et al., 2005). Because bonobos (and other non-human primates) rarely exclusively use one hand for particular tasks (i.e., they have a relatively low handedness index), larger sample sizes are considered necessary to reliably detect a group-level bias (defined as >65 % of the individuals in the group) (Hopkins and Cantalupo, 2005; Hopkins et al., 2012; Hopkins 2013a, 2013b). In this study, the exclusive use of either the left- or right-hand (i.e., a high handedness index) by the 15 bonobo individuals suggests that use of the right-hand by 66 % of the individuals may reliably estimate a group-level right-hand bias for this particular complex manipulative behaviour. Although a future study of more individuals is needed to confirm this bias, these results are consistent with previous reports of nut-cracking in chimpanzees (Matsuzawa, 1996; Humle and Matsuzawa, 2009). Moreover, wild

chimpanzees of Gombe show exclusive use of one hand or the other when pounding hard-shelled fruits (*Strychnos* spp.) on anvils (McGrew et al., 1999). Wild western gorillas have been recently reported to demonstrate exclusive hand-preference and an overall right-hand bias during natural bimanual termite feeding (Salmi et al., 2016).

Hand use in relation to task complexity has been studied across four tool-using tasks in Bossou chimpanzees (Humle, 2003). Nut-cracking, the most cognitively complex of the four behaviours studied and the only one requiring complementary coordination of both hands, revealed the strongest degree on laterality in all adult individuals (N=7). Humle (2003) suggested that Bossou chimpanzees have a right-hand bias at the population-level, which was supported by Biro et al. (2006), reporting a high proportion of right-handed individuals (62 %) for nut-cracking in the same community. The Tai chimpanzees of Côte d'Ivoire show a hand-preference during nut-cracking at the individual-level, but the overall distribution was not biased to the left or right (Boesch, 1991). The study reported that 18 individuals were significantly, but not completely lateralized, while another 18 individuals were exclusively lateralized, with 10 chimpanzees being right-handed (Boesch, 1991). However, Tai chimpanzees typically use wooden hammers and more often use both hands and also the feet when the hammer is large.

In comparison to one-handed hammering, this study provides the first data on bonobos using a hand use strategy for different sized stone hammers. Most of the bonobos used one hand to hold small and medium-sized hammerstones. Five bonobo individuals occasionally preferred both hands (15 %) and three rarely their right-hand/right foot (2.7 %) when hammering with larger stones. For example, two females used both hands throughout a session when hammering with the same large and heavy stone (25 cm wide, 30 cm long, 3 kg). Two other females were observed to switch between one-hand and both hands for the same large and heavy stones (a: 13cm wide, 14 cm long, 3 kg; b: 15 cm wide, 23 cm long, 4.4 kg), while the bimanual action was clearly more preferred for a higher number of bouts. A male bonobo also occasionally tended to use his right-hand to support the dominant left-hand when hammering with a large and heavy stone (17 cm wide, 18 cm long, 4.48 kg). Three females used in addition to one-hand and both hands their right-hand/right-foot to handle large, heavy and large, moderate stones. One female

switched several times between one-hand, both hands and her right-hand/right food when pounding nuts with four different large and heavy stones. These results provide first evidence that bonobos do adapt an effective hand-use strategy in order to handle the different size and weight properties of their hammerstones.

2.4.2 Hand grips

This study revealed 10 new grips not previously reported in the literature and five grips that have either been previously reported or show interesting similarities to grips used by wild and captive chimpanzees and macaques, as well as in humans.

As Marzke and colleagues (1996) highlighted previously, the basic division of precision versus power grips as defined originally by Napier (1980) is not sufficient to describe and understand the complexity of manual manipulation in humans and other primates. Indeed, I observed three precision grips (Pc1-Pc3) between the fingers and thumb (i.e., without involvement of the palm), six power grips (Pw1-Pw6), with active contribution by the palm, and created a new category of grips called “precision finger/active palm” to accurately describe the manual manipulation of bonobo nut-cracking (Table 2.2 and Fig. 2.2). I also observed high variability across individuals in the use of precision grips and precision/active palm grips, showing the versatility of the bonobo hand in accommodating hammerstones of varying size and shape (Table 2.3 and Fig. 2.3). Overall, this display of manipulative flexibility was unexpected given that previous work on hand grips or object manipulation during tool-use in captive bonobos has not reported this degree of variability (Jordan, 1982; Christel, 1993; Christel et al., 1998, Bardo, 2016).

2.4.2.1 Precision Grips

Precision grips were only used by two bonobos, but to the best of my knowledge, none of the precision grips have been described in studies of captive bonobos (Christel, 1993; Christel et al., 1998) and capuchin monkeys (Costello and Fragaszy, 1988; Spinozzi et al., 2004) and wild nut-cracking chimpanzees (Boesch

and Boesch, 1993). The bonobos most often used precision grips when holding small hammerstones, which might explain why they have not been reported in wild chimpanzees that typically use much larger hammerstones (Boesch and Boesch, 1983). However, the grips used by the chimpanzees in nut-cracking have not yet been systematically described in the same detail as presented here for the bonobos and thus future studies may reveal greater overlap in grip types between the two sister taxa. The Pc2 grip (in which the stone is held between the thumb and dorsal aspect of the distal phalanges of the flexed digits 2-3-4, and the thumb is opposed to the index finger, Fig. 2.2b) has to the best of our knowledge not been reported in the literature before. The grip was used by one male bonobo after the hammerstone broke apart and he continued hammering with the smaller stone. The other two precision grips were used for five bouts (Pc1) and two bouts (Pc3) by one individual, and offer insight into the manipulative capabilities of the bonobo hand. The Pc1 grip (in which the stone is held between the full thumb and lateral aspect of the distal and middle phalanges of the index finger, buttressed by the distal and middle phalanges of the third and fourth finger; Fig. 2.2a) is similar to the ‘two-jaw chuck’ pad-to-side grip reported in captive and wild chimpanzees (Marzke and Wullstein, 1996; Jones-Engel and Bard, 1996; Marzke et al., 2015). While chimpanzees use only the thumb pad and side of the index finger when grasping different food objects, the bonobo recruits also the buttressed middle and fourth finger to stabilize the hammerstone. In humans, the buttressed pad-to-side grip is used when holding a flake and to pinch the tool tightly between the distal thumb pad and finger(s) (Marzke and Shackley, 1986; Marzke, 2006, 2013). The bonobo also used the region of the base of the thumb to stabilise the stone firmly enough against the index finger and buttressed middle and fourth fingers to resist displacement of the tool by the reaction force of the nut. The Pc3- precision grip shows interesting parallels to the human ‘four and five-jaw chuck’ precision grip, with opposed pads of the thumb, index, and fingers 3-4,5 used for holding hammerstones (Fig. 2.2c) (Marzke and Shackley, 1986). In bonobos the hand-sized stone is held between the thumb at level of the interphalangeal joint of the palmar aspect of the proximal phalanx and the pads of the four fingers, without contact to the palm. This grip appears to have a certain degree of finger-to-thumb pinching as the flexed fingers secure the stone and the widely abducted thumb serves as a prop. However, the grip is not as strong as in the human ‘four and five-jaw

chuck' grip to press objects firmly against the fingers, since the stone is held right above the nut and firm pressure by the thumb and fingers is not likely to be required. A similar form of finger-to-thumb pinching has been observed in wild long-tailed macaques for pound hammering and is described as a finger-to-thumb/passive palm grip (Gumert and Malaivijitnond, 2009). Although the use of precision grips were rare, in all instances, the bonobos were able to hold the stone firmly enough between the thumb and fingers (without the palm) to crack the nut successfully with enough force that a relatively low number of hits (mean: 7.2) were needed. This action during nut-cracking suggests forceful loading of the thumb in a manner that is more similar to the human and wild long-tailed macaques pinch grips than would be typically incurred during power grips (see below). Although, the relatively rare use of these grips suggests that they may not be as comfortable or effective given bonobo hand morphology.

2.4.2.2 Precision finger/ active Palm grips

During nut-cracking, bonobos grasped small and medium-sized hammerstones tightly between the thumb and fingers, with an additional force applied by the palm only at the moment of strike. Such grips have not been reported during nut-cracking in Tai chimpanzees (Boesch and Boesch, 1993) or feeding in Mahale chimpanzees (Marzke et al., 2015). When the bonobos used small hammerstones, something also not observed in nut-cracking chimpanzees (Boesch and Boesch, 1983, 1993), there is relatively little room to strike the nut without smashing the fingers. The bonobos grasped the stone precisely in such a way as to expose the hammering surface and allow the palm to contribute force, but so the fingers would not be crushed (Fig. 2.2d). Thus, these grips are best described as 'precision finger/active palm grip' (PcApm4-PcApm9), as they describe the change that occurs as the hand goes from a 'precision finger/passive palm grip' of the stone (Marzke and Wullstein, 1996) to a more active involvement of the palm (Fig. 2.2d-i). This grip is different from the cup grip reported in captive chimpanzees (Marzke and Wullstein, 1996) or the pinch grip with passive palm support seen in wild long-tailed macaques during stone hammering (Gumert and Malaivijitnond, 2009). Precision

finger/active palm grips were used by eight bonobos, with ‘PcApm4’ (stone held between the lateral aspect of the distal thumb and palmar aspects of the distal and middle phalanges of the index finger; Fig. 2.2d) and ‘PcApm8’ (stone held between the thumb and dorsal aspect of distal and middle phalanges of the flexed digits 2-3 to the lateral aspect of digit 4, supported by the thenar eminence of the palm; Fig. 2.2h) being the most common (Fig. 2.3).

2.4.2.3 Power Grips

The bonobos most often used power grips to hold the hammerstone during nut-cracking (Fig. 2.2j-o). Although six different power grips were used across all individuals, only three (Pw1, Pw5, Pw6) can be compared to studies on wild and captive chimpanzees and macaques. The Pw6-power grip was used among all individuals, in which the stone was held between all of the fingers and the palm with counter pressure from the thumb (Table 2.2) (Pw6; Fig.2.2o). This grip was used across different hammerstones, regardless of size, shape, thickness or weight, and appears to be the most effective grip for nut-cracking. A similar grip was also shown to be the most effective in humans during nut-cracking (Bril and Dietrich, 2015). For larger stones, the thumb was normally held in opposition (Fig. 2.2j) to or adducted to the fingers, while for smaller stones the thumb was held outside or inside the grip (Pw6; Fig.2.2o). A similar power grip has been observed in wild long-tailed macaques during one-handed pound hammering (Gumert and Malaivijitnond, 2009) and in captive chimpanzees when grasping larger food objects (Jones-Engel and Bards, 1996; Pouydebat, 2009). The bonobo power grip ‘Pw6’ appears also similar to the power grip typically used by the nut-cracking Tai chimpanzees (Boesch and Boesch, 1993). However, only juvenile Tai chimpanzees grasped small stones with the thumb held inside the grip, whereas adult bonobos frequently used this grip (Fig. 2.2o). This type of power grip involves adduction of the wrist rather than flexion, so that the stone is exposed at the ulnar side of the palm and strikes the nut (Fig. 2.2o). This action would have the advantage of avoiding smashing of the fingers that would occur with hammering by flexion of the wrist, while at the same time allowing a firm grip by the thumb and fingers. I observed less frequent use of two power grips (Pw1,

Pw5; Fig. 2.2j,n) involving the “V-shaped” region between the thumb and Index finger, first reported in Mahale chimpanzees during feeding (Marzke et al., 2015). The chimpanzee “V-pocket” grip is used to securely hold large fruits in the web between the full thumb and index finger, buttressed by the flexed third, fourth and fifth digits (Marzke et al., 2015). In bonobos, medium-sized hammerstones were rarely secured against the web of the palm either by the lateral aspect of the thumb and flexed index finger (Pw1; Fig. 2.2j) or more frequently by the thumb and the flexed four fingers at their ventral aspect of proximal phalanges and dorsal aspect of distal and middle phalanges (Pw5; Fig. 2.2n). Three new power grips (Pw2-Pw4) were also identified, typically used with small and medium-sized hammerstones and with relatively low frequency by four bonobos in this sample (Fig. 2.3). In most of these grips, the hammerstone was held between the palm, thumb and dorsal surface of the distal phalanges (i.e., fingers flexed) (Fig. 2.2k-m).

Bonobo hand grips (PcApm9, Pw5, Pw6; Fig. 2.2i, n, o) occasionally involved rotation of medium-sized hammerstones within the palm of one hand against the anvil surface, by movements at the carpometacarpal, metacarpophalangeal or interphalangeal joints of the thumb and finger(s). Repositioning of the stone helped to expose a different side of the hammering surface or to change the grip (e.g., Pw6 to Pw5). Additionally, medium-sized and large stones were grasped by the opposite hand, turned over by the hand via movement at the wrist, elbow and shoulder joints, and then placed back in the other hand to be regrasped in the desired orientation. Unlike in humans, I did not observe translation (object moved between the palm and fingertips) or precision handling (object moved by the digits alone) (e.g., Marzke and Shackley, 1986; Marzke and Wullstein, 1996), but found interesting parallels to a captive study of chimpanzee “in-hand movements” (Craet et al., 2009). Similar to the bonobo’s hand movements, chimpanzees perform in-hand movements for changing their grip on the object, sometimes use a surface when rotating an object and turn objects over in bimanual actions (Craet et al., 2009).

However, the high manual abilities of bonobos should actually come as no surprise given the shared similarities in hand proportions, joint morphology and muscular anatomy between bonobos and chimpanzees (e.g., Tuttle, 1969; Susman, 1979; Marzke et al., 2010; Myatt et al., 2012; Almécija et al., 2015; Liu et al., 2016; Patel and Maiolino, 2016). The observed flexion of the distal interphalangeal joint (DIP) and proximal interphalangeal joint (PIP) of the four fingers in this sample of bonobos and other great apes (including humans) are primarily due to the separate actions of two ventral forearm muscles, the *flexor digitorum profundus* and *flexor digitorum superficialis* (Tocheri et al., 2008; Lemelin and Diogo, 2016). The separate muscle actions allow bonobos to move the DIP joint independently from the PIP joint, such that the DIP joint could still move to accommodate to an irregularly shaped hammerstone when the middle phalanx had contacted the tool during a power grip (see: Pw1 in Figure 2.2j). Recently, a dissection on five adult bonobos revealed that the portion of the *flexor digitorum profundus* going to the thumb and index finger has a common muscle belly, separate from the *flexor digitorum profundus* portion going to digit 3, 4 and 5, (Vanhoof, 2016). In chimpanzees and other great apes, the tendon of the *flexor digitorum profundus* to the thumb is often either a very thin, vestigial structure or it is absent (Diogo et al., 2012). This structural configuration enables bonobos to move the thumb and index finger independently from the remaining digits, which might explain the bonobo's versatile grasping capability in securing the hammerstone firmly between the thumb and Index during various hand grips (Fig. 2.2).

2.4.3 Nut-cracking Efficiency

In this study of bonobo nut-cracking, I found that bonobos most often preferred the most efficient hammerstones. The weight, size, thickness and shape of a particular hammerstone had a significant effect on the number of hits required to crack a nut and on the number of nuts cracked per minute. The bonobos were significantly more efficient with larger and heavier stones, than with small and lighter (0.1-0.38 kg) stones. However, most individuals chose to use moderate-weight (0.45-1.24 kg) and medium-sized stones to crack open nuts, which appeared

easier to handle than larger, heavier (1.38-4.48 kg) stones and did not significantly differ in efficiency. Comparable studies on captive chimpanzees showed that, like bonobos, they preferred to use heavier hammers (1.2 kg, 1.4 kg) that required fewer hits and less time to crack open nuts (Schrauf et al., 2012). Wild Bossou chimpanzees differentiate stones by width, length and weight, choosing to use lighter stones as hammers and heavier stones as anvils during nut-cracking (Biro et al., 2006). Nut-cracking capuchin monkeys also actively select particular hammerstones based on the material and weight that is most appropriate to crack open palm nuts (Schrauf et al., 2008; Visalberghi et al., 2009).

Given that bonobos are not known to nut-crack in the wild, I found, not surprisingly, significant differences in nut-cracking efficiency between bonobos and Bossou chimpanzees. The bonobos needed on average almost twice as many hits to crack open a palm nut compared with Bossou chimpanzees. However, contrary to my predictions, bonobos were able to crack on average nearly one more nut per minute than their congeneric wild chimpanzee. These differences may result from two factors. First, there was a difference in the general strategy of collecting nuts (as collection time was included in the measure; see Methods); although both the bonobos and Bossou chimpanzees cracked nuts next to the palm nut source (i.e., 1-2 meters), the chimpanzees tended to spend more time collecting multiple nuts at one time to transport back to the anvil whereas the bonobos spent less time collecting because nuts were more readily available around their nut-cracking area. Second, the bonobos likely required a greater number of hits because, unlike Bossou chimpanzees (preferred hammers have an average weight of 1.0 kg; Bril et al., 2006), they also used lighter (0.10-0.38 kg) stones and were cracking fresher nuts that are much more challenging to crack than dry nuts. Regardless of these differences, these rehabilitated bonobos, which have only recently (i.e., last ~20 years) developed nut-cracking behaviour are surprisingly similar in efficiency to that of chimpanzees with a long history (i.e., 4.300 years; Mercader et al., 2002) of nut-cracking and other types of complex tool use.

The bonobo nut-cracking study made clear that more future studies on complex tool use behaviours in bonobos under natural conditions are necessary to explore the full range of their manipulative and tool use capabilities. It is interesting

that bonobos rarely use tools in the wild and yet they have highly skilled tool-using abilities that potentially place them on a par with chimpanzees in terms of efficiency. In this way, bonobos may also be appropriate models for reconstructing the tool use capabilities of our human ancestors, as studies of Kanzi have revealed (e.g., Toth et al., 2006; Toth and Schick, 2009; Roffman et al., 2012). It would be highly informative to quantify hand grips and postures as well as hand-use strategies in Kanzi and his conspecifics to test the repertoire of fine manipulations during various natural tool using tasks, given that Kanzi has engaged in regular skilled tool-use for almost 30 years.

This study of bonobo nut-cracking demonstrates that the relationship between morphology and behaviour may not always be clear. The bonobo hand is almost identical to that of chimpanzees, and thus it is not surprising that they are capable of a high degree of manipulative dexterity. However, unlike their chimpanzee cousins, they do not engage in complex tool-use behaviours in the wild, due likely to differences in the ecology, fruit availability, etc. that do not necessitate the complex tool-use behaviours to retrieve additional nutrients. Thus, although the morphology suggests the abilities for similar manipulative (and locomotor) behaviours in bonobos and chimpanzees, the actual behaviours are quite distinct (as they can be between different populations of chimpanzees as well). This has important implications for reconstructing behaviour in the fossil record and distinguishing between “potential” and “actual” behaviour.

2.5 Conclusion

This first detailed study of nut-cracking in bonobos revealed an unexpected manipulative versatility during stone tool-use, including 10 novel hand grips. This most complex tool-use behaviour showed 100 % lateralisation and a significant right-hand bias in most of the individuals studied, speaking to a group-level bias. Bonobos also have the ability, like nut-cracking capuchin monkeys (e.g., Schrauf et al., 2008) and chimpanzees (Boesch and Boesch, 1983; Biro et al., 2006) to select the most effective hammerstones. Moreover, bonobos can be efficient nut-crackers with a skill level not that different from wild chimpanzees. It is clear from this study, that more future studies on complex tool-use behaviour in bonobos under natural conditions are required, in order to explore the full range of their manipulative and tool-use capabilities.

Chapter 3

Manual skills in plant-processing of wild mountain gorillas

Abstract

Although gorillas rarely use tools in the wild, their manipulative skills (actions that are required to resolve particular problems of a task) during food processing may be similar to those of other tool-using great apes. Virunga mountain gorillas are known for the complexity in their methods of thistle plant preparation in the wild. Up to now, there is no comparable data of processing stem and leaf material of other plant species in other populations of wild mountain gorillas. Bwindi mountain gorillas eat plant foods that are identical to those eaten by Virunga gorillas, or at least appear similar in the degree of complexity needed to process them, as well as foods that are simple to process. Following on this work, it is predicted that Bwindi gorillas will demonstrate greater manipulative actions and greater strength of laterality (i.e., hand preference) when processing complex foods (e.g., defended plant foods) but lower manipulative actions and a lower laterality for less complex plant foods (e.g., without defenses). Here, I investigated the manual skills in processing three plant foods (peel, pith and leaves) in 11 wild, habituated mountain gorillas (*Gorilla beringei beringei*) in the Bwindi Impenetrable National Park, Uganda, using video records *ad libitum*. Similar to thistle feeding by Virunga gorillas, Bwindi gorillas used the greatest number of hand actions to process the most complex plant food (i.e., peel), the manipulative actions were ordered in several key stages and organised hierarchically. Similar to Virunga gorillas, Bwindi gorillas employed eight hand-use strategies that indicate their high manipulative skills. The demands of manipulating natural foods elicited 19 different hand grips and variable thumb postures, of which three grips were new and 16 grips have either been previously reported or show clear similarities to grips used by other wild and captive African apes and humans. A higher degree of lateralisation was elicited for the most complex behaviour of peel-processing but the strength of laterality was only moderate, suggesting that peel-processing is not as complex as thistle leaf-processing by Virunga gorillas.

3.1 Introduction

Various animal species have the capabilities to manipulate objects during extractive foraging, but there are few who regularly and flexibly use objects to achieve particular goals in the wild (Beck, 1980; Bentley-Condit and Smith, 2010). Chimpanzees (*Pan troglodytes*) are among the most consistent and prolific non-human tool users (McGrew, 1992), based on their frequent use of tools and diverse tool behaviours among study sites (e.g., Humle and Matsuzawa, 2001; Pruetz and Bertolani, 2007; but see Sanz and Morgan, 2010). The tool using repertoire of wild orangutans (*Pongo pygmaeus*, *Pongo abelii*) is also relatively large and diverse, but many of these tool behaviours are exhibited relatively infrequently (Meulman and van Schaik, 2013). Although gorillas rarely use tools in the wild (tool use has been documented only two times in western lowland gorillas and mountain gorillas; Breuer et al., 2005; Kinani and Zimmerman, 2015), they are arguable equally manipulative to tool-using great apes when it comes to retrieval and processing of plant foods. One possible explanation for the absence of observed tool use in wild gorillas is that they are less dependent on extractive foraging techniques that might require the use of tools, since they exploit food resources differently than chimpanzees (McGrew, 1989; van Schaik et al., 1999). Nevertheless, mountain gorillas (*Gorilla beringei beringei*) have been shown to possess food-processing skills (Byrne et al., 2001a) of comparable complexity and hierarchical organisation to chimpanzee termite fishing (McGrew and Marchant, 1996; Sanz and Morgan, 2011) and honey extraction (Estienne et al., 2017), which give them access to additional dietary resources in their habitat (Byrne and Byrne, 1993). Manipulative behaviours involve a specific repertoire of functionally-distinct actions that are required to reach a goal and are structurally organised in a hierarchical order (Byrne et al., 2001a). Both aspects have been used as indices of behavioural complexity (Byrne et al., 2001a). While western lowland gorillas (*Gorilla gorilla gorilla*) also process plant foods, such as swamp herbs, their diet has not yet revealed the same complex manipulative actions as documented in mountain gorillas when processing herbaceous foods (Parnell, 2001).

The work of Byrne and colleagues (e.g., Byrne and Byrne 1991, 1993; Byrne, 1994; Byrne et al., 2001a, b) in the Virunga Mountains, Rwanda, were the first to highlight the complex methods of plant preparation used by wild mountain gorillas. The herbaceous foods in the mountain gorilla diet (e.g., thistle leaves and stems, nettle leaves; Byrne and Byrne, 1991) require multi-stage processes of manual preparation before they can be eaten, because they often involve the need to first circumvent the physical defences of the plants such as stings, spines, minute hooks and hard casing. The hierarchical organisation of this manipulative behaviour is complex because it involves several unique functional hand actions ordered from the start to the end, precision grips, bimanual coordination of the hands and the mouth in performing an action, and elicits strong hand-preferences (Byrne et al., 2001a, b; Byrne, 2003). Indeed, patterns performed unimanually are found to be more straightforward for the brain to program than patterns performed bimanually as they require some degree of functional cerebral asymmetry to control (e.g., Elliott and Connolly, 1984; Hopkins and de Waal, 1995; Byrne, 2003). Processing thistle leaves is considered as the most complex task among wild mountain gorillas, involving the greatest hierarchical organisation (Byrne et al., 2001a). However, it appears that the complex skills elicited in the hierarchical structures of plant preparation, are only associated with the challenge of dealing with plant defences (Byrne et al., 2001a). Yet, we do not know whether plant stems of strong physical defenses, such as thistle stem, require more complex processing by gorillas than is typical for less defended woody stems, because they are harder to manipulate and thus, require more actions to complete the task. So far, there is no comparable data of processing stem and leaf material of other plant species in a different population of wild mountain gorillas.

The mountain gorillas of the Bwindi Impenetrable National Park, Uganda, provide an opportunity to investigate these questions. This population consumes a range of fibrous foods, including vines and stems defended by herbaceous or woody casings, as well as leaves that lack physical defenses (Ganas et al., 2004, 2008). The diet of Bwindi gorillas differs greatly from that of Virunga mountain gorillas, with more and different species of both arboreal fruits and terrestrial herbaceous vegetation (e.g., Watts, 1984; Ganas et al., 2004, 2008). Bwindi gorillas consume several plant parts (i.e., leaves, pith, peel or bark) of various abundant plant species but rarely eat thistle. This is in contrast to Virunga gorillas that most frequently

consume leaves and pith of the highly abundant thistle plant in the high altitude of the areas surrounding the Karisoke Research Center (e.g., Watts, 1984; Ganas et al., 2004). This ecological variation between Bwindi and the Virunga mountains leads to different adaptive foraging strategies between both mountain gorilla populations, which may reveal differences in the complexity of their food-processing behaviour.

3.1.1 Hand grips, object manipulation and complexity

Alongside tool-use, herbaceous food processing presents a good model of studying the demands of object manipulation on the non-human primate hand, and on the gorilla hand in particular. The range of manipulative actions used to procure and process available foods has been shown to elicit different grip patterns and hand movements in Virunga mountain gorillas, as well as in Mahale chimpanzees (e.g., Byrne et al., 2001b; Marzke et al., 2015). However, only six hand grips were described for gorilla thistle preparation based on broad grip categories and the number of digits involved (e.g., scissor precision grip, hook and power grips; Byrne et al., 2001b), which do not provide the detail needed for a comparative functional analysis of gorilla manipulation to that of other apes (including humans). To better understand what the hands of gorillas can do when they manipulate an object, systematic studies of the roles of each hand and their possible complementary roles are needed, in terms of bimanual hand-use, coordination, symmetry of actions, and repertoire of grips and hand movements (e.g., McGrew and Marchant, 1997a; Byrne et al., 2001a; Leca et al., 2011; Marzke et al., 2015; Heldstab et al., 2016). This present study provides a more detailed description of the areas of contact within the gorilla hand and quantifies the relative frequency of grips used during the manipulation of three different plant parts, which will reveal the repertoire of hand grips not previously examined. Processing plant parts such as peel, pith and leaves, may provide substantial challenges to the gorilla, as the hand has to adjust to varying sizes, shapes and toughness, including physical defenses (i.e., herbaceous and woody casings), and accommodate loadings exerted on the hand during retrieval and processing of the plants. Additionally, data on the functional role of the thumb during food processing are rare and exists only for Mahale chimpanzees (Marzke et al.,

2015). This research will fill the gap by examining how gorillas use their thumb when manipulating plant foods.

3.1.2 Laterality and complexity

The evolution and possible function of hand-preference or manual laterality in humans has been extensively studied, often through comparative studies with great apes (e.g., McGrew and Marchant, 1997a; Cashmore et al., 2008). Most studies of wild chimpanzees support this hypothesis, showing a significant right-hand or left-handed preference at the group-level when performing complex, bimanual tool-use activities such as nut-cracking (Boesch, 1991; Matsuzawa et al., 2001; Humle and Matsuzawa, 2009), termite-fishing (McGrew and Marchant, 1996; Lonsdorf and Hopkins, 2005), fruit-pounding (McGrew et al., 1999) and ant-fishing (Marchant and McGrew, 2007). These complex tool use behaviours are in contrast with most food manipulation behaviours that do not involve tool-use, where no significant lateral bias was found at the group level in chimpanzees (food-reaching/picking: Boesch, 1991; Sugiyama et al., 1993; food-plucking: Marchant and McGrew, 1996; McGrew and Marchant, 2001; eating: McGrew and Marchant, 2001; fruit-peeling: Corp and Byrne, 2004).

Relative to chimpanzees, gorilla laterality and task complexity remains understudied and the few studies that have been conducted report contrasting or inconclusive results. Most studies in captivity elicited a right-hand preference at the group-level for bimanual tasks but not unimanual tasks (e.g., Fagot and Vauclair, 1988; Annett and Annett, 1991; Hopkins et al., 2011; Meguerditchian et al., 2010; Tabiwo and Forrester, 2013; Forrester et al., 2011). However, other captive studies found no group-level hand preference in either task (Harrison and Nystrom, 2010; Lambert, 2012). To date only three studies have been conducted on wild gorillas. Byrne and Byrne (1991) found a significant right-hand bias at the group-level during thistle plant-processing in Virunga mountain gorillas. Similarly, Salmi and colleagues (2016) found a significant group-level right-hand preference during termite tapping (i.e., rhythmically shaking a piece of termite mound with the dominant hand) in western lowland gorillas. Both of these studies attributed the significant laterality to the complex motor actions and precise bimanual

asymmetrical coordinations needed to accomplish the task. The third study analysed more simple actions during feeding of swamp herbs in western lowland gorillas and reported a weak hand-preference with no significant bias at the group-level (Parnell, 2001). On the basis of the task-complexity model, and if we consider that precise bimanual coordinated asymmetrical strategies are more complex than one-handed strategies, then laterality should be stronger in the former than in the latter.

Plant-processing in Bwindi gorillas is a good candidate for the study of manual laterality because we know that Bwindi gorillas eat foods that are identical, or appear similar in the degree of complexity needed to process them, as well as foods that are simple to process, compared with Virunga mountain gorillas and western lowland gorillas (Byrne and Byrne, 1991; Parnell, 2001; Ganas et al., 2004, 2008; Sawyer and Robbins, 2008). Therefore, we can expect that Bwindi gorillas might show a similar strength of laterality for foods that are more complex to process (i.e., defended plant foods) and similarly low laterality for less complex plant foods (i.e., without defenses).

The aim of this study is to provide the first insights into the manual skills of wild Bwindi mountain gorillas by examining the techniques, hand-use strategies, hand grips and laterality used to process three different plants; two woody-stemmed plants for which the food is more challenging to access in comparison to leaves, that are relatively simple to process because of lacking physical defenses. This study investigates specifically (1) how the presence of plant defenses (i.e., hard outer casings) is associated with behavioural complexity, by comparing the manual processing of two woody plants and undefended leaves with what is known of processing the strong defended thistle plant in Virunga mountain gorillas, and (2) if the complexity of the food processing is positively correlated with strength of laterality. Here, I follow two behavioural complexity models, in which I assess complexity based on (1) the number of hand actions, or elements, that are employed in each bout of plant processing (Byrne and Byrne, 1991; Byrne et al., 2001a), and (2) the combinations of different hand-use strategies (e.g., coordinated use of both hands in different but complementary roles versus unimanual hand-use; Leca et al., 2011).

Based on these models, I test several predictions:

- 1) Plants with physical defenses (i.e., stems with herbaceous and woody casings) require a higher number of functionally-distinct elements and thus, are more complex to process than undefended plants (i.e., leaves).
- 2) Processing defended plants will show a greater number of different hand-use strategies and involves a higher proportion of actions performed asymmetrically by both hands (= bimanual role differentiation) than undefended plants.
- 3) Defended plants will elicit a greater number of hand grips as they require more behavioural elements of processing than undefended plants.
- 4) The degree of laterality at the individual-level and group-level will be greater for plants that are considered more complex.

3.2 *Materials and Methods*

3.2.1 *Species and study site*

Mountain gorillas (*Gorilla beringei beringei*) were observed in the Bwindi Impenetrable National Park (331 km²) in the southwest corner of Uganda (0° 53'1°08'N; 29°35'–29°50'E), with an altitude of 2100–2600 m (Robbins and McNeilage, 2003; Ganas et al., 2004; Wright et al., 2015). Data were collected on 11 individuals of one fully habituated group of gorillas (Kyagurilo) between February and March, 2015 (Table 3.1). The subjects included seven adult females and four males, which included one subadult (6-8 years), one blackback (8-12 years) and two silverbacks (≥ 12 years) (Czekala and Robbins, 2001; Robbins, 2001).

3.2.2 Plant foods

The three plant foods studied here are plant species that are a common part of the Bwindi mountain gorilla's diet (e.g., Ganas et al., 2004, 2008). The plant parts consumed are fibrous foods, including (1) the peel (outer casing of an herb's stem) of the woody and herbaceous vine *Urera hypselodendron*, (2) the pith of the woody stem *Mimulopsis arborescens*, and (3) the leaves of the climbing vine *Momordica foetida* (Fig. 3.1). The plant parts were generally eaten while the gorillas were in a seated posture. Only in one sequence was one male gorilla recorded to stand bipedally while feeding on leaves (and this was not found to change his style of food processing).



Figure 3.1: Plant species used in gorilla food-processing. Top, stripping of the green peel of *Urera hypselodendron* with an herbaceous stem (a) and woody stem (b). Middle, processing the stem of *Mimulopsis arborescens* to consume the pith, with a woody stem of relatively large diameter (c) and small diameter (d). Bottom, leaf-processing of the climbing vine *Momordica foetida*: (e, f).

3.2.3 Methods

The research protocols reported in this study were reviewed and approved by the Uganda Wildlife Authority, the Ugandan National Council for Science and Technology, and by the Ethics Committee of the School of Anthropology and Conservation at the University of Kent, UK.

The mountain gorillas were observed for an average of 4 hours/day, and a minimum of 7 m had to be maintained between the gorillas and the observer to reduce the risk of disease transmission. High-definition video filmed *ad libitum* at a frequency of 50Hz (HDR-CX240E, Sony, Japan). All processing sequences were recorded at relatively close range (7 m to ~20 m) and from multiple angles (i.e., frontal, lateral, back-view) during food-processing. Focal samples, periods in which specified information is collected from only one individual at a time (Altmann, 1974), were used to collect data from all individuals. The final focal sample total was 4 h 30 min, including 86 video sequences of stem-peel (*Urera hypselodendron*) processing and 45 sequences of stem-pith (*Mimulopsis arborescens*) processing in 11 individuals, and 45 sequences of leaf-processing (*Mormodica foetida*) in nine individuals. To analyse the details of food-processing and hand grips, stop-frame and slow-motion analyses were conducted, using the free software Sony Picture Motion Browser (Sony Europe Limited©).

3.2.4 Data analysis

3.2.4.1 Functional elements of plant-processing in Bwindi gorillas

The first aim of this study was to characterise the complexity of each plant-processing technique by looking at the behavioural repertoire size, in terms of the total number of elements (i.e., hand actions) employed, the individual variability (i.e., sex classes) of using functionally-distinct elements, and the frequencies of distinct elements across plants. I defined “technique” as the ordered sequence of discrete behavioural elements (Byrne and Byrne, 1993) performed by one individual.

Gorillas often accumulate edible items by the handful and eat then all at once, and thus the basic unit for the quantitative analyses was the '**handful**', following Byrne et al. (1991). Usually, gorillas process and eat several handfuls of a food type one after the other, before switching to a new food, or stopping feeding. Food processing behaviour for any given individual was divided into 'sessions' and 'bouts'. A '**session**' was defined as a period in which one individual was engaged in food-processing. A session was terminated when the individual stopped feeding and walked away, and/or started a new behaviour. A session was generally composed of multiple bouts. A '**bout**' was defined as a period of feeding on a single food type for 10 seconds or more, without interruption, and can include many separate handfuls of the same food object. A bout was considered terminated if there was a change of plant type (e.g., change from stem to leaf eating) or when food preparation was interrupted by another behaviour.

To assess complexity, plant-processing was divided into 'elements', following Byrne and colleagues (1993, 2001). An '**element**' of plant-processing is defined as a single, distinctive hand action that results in an observable change to an item of plant material and thus, is considered as an isolated act (Byrne and Byrne, 1991, 1993). Elements are described in terms of the hand grip, posture and/or movement, and they can be either manipulative (i.e., moving or processing the object) or 'supportive' (i.e., stabilising the object). A bout was composed of multiple isolated acts of functional elements of plant processing and could involve repetitions of the same element until each stage of processing was completed.

Following Byrne and colleagues (2001a), functional elements were scored in two ways: (1) elements were considered **functionally-similar** when the result achieved was the same, even when the hand action was different ('picking off' versus 'stripping up leaves') and (2) were considered **functionally-distinct** when the resulting changes are different (e.g., 'picking up' versus 'biting off' a portion of stem). The functionally-distinct elements within a bout are built-up in organisational key stages of an ordered and coordinated flow of processing (Byrne and Byrne, 1993). Among these elements of plant processing, there are '**obligate-elements**' that are required to resolve a task and consistently used across all individuals, and '**optional-elements**' that are more variably used across individuals.

The data did not meet the normality and homogeneity assumptions for parametric tests. Thus, a Mann-Whitney U-test was performed to compare individuals (i.e., sex classes) in their number of functionally-distinct elements used to process each plant. This analysis provides further insight into the potential variability of particular elements (i.e., hand actions) across different plants. The overall sample size was relatively small and thus, results of this statistical analysis should be interpreted with caution.

To analyse the frequency of distinct elements per plant, functionally similar elements were pooled into the same element (e.g., pull stem vs. yank stem, were considered as pulling, see Table 3.1 in *Appendix II*), following Byrne and colleagues (2001a). The frequency of each element was first tallied across the number of bouts for each individual to examine the individual frequency. Then a total mean frequency was calculated across all individuals for each element. Only those elements used with more than 25 % frequency across all individuals were considered frequent enough to be retained for this analysis.

3.2.4.2 Hand-use strategies for processing different plant parts

Following the behavioural complexity model by Leca and colleagues (2011), hand-use strategies were defined in the following ways: (1) **‘unimanual’**, with only one hand being active, (2) **‘bimanual’**, with both hands being involved, and (3) **‘mouth-hand’**, with the mouth and only one or both hands being involved in a manipulative activity. Bimanual hand-use was further classified by ‘coordination’ (uncoordinated versus coordinated) and ‘symmetry’ (symmetrical versus asymmetrical). **Uncoordinated** bimanual manipulation occurred when both hands performed actions independently of each other in space and/or time, whereas **coordinated** bimanual manipulation occurred when both hands performed actions dependent of each other in space and/or time, that is, they work together to achieve a unitary goal (Hopkins, 1995; Byrne et al., 2001; Leca et al., 2011). **Symmetrical** bimanual manipulation occurred when both hands performed the same action simultaneously or alternatively, whereas **asymmetrical** bimanual manipulation occurred when both hands performed simultaneously different actions (e.g., Takeshita and Walraven, 1996; Byrne, 2005; Macrae et al., 2008; Leca et al., 2011)

(Fig. 3.2). To ensure data point independence for statistical analysis, only one hand-use strategy was recorded per element. As hand-use strategies never changed during the repetition of the same element (i.e., 0 % of 1954 elements), hand-use strategy was assessed for its first occurrence within an element.

The data were analysed in the following ways:

- (1) Calculating the relative frequencies of hand-use strategies for the most frequent elements of processing across 11 individuals in peel- and pith-processing and for nine individuals in leaf-processing (Fig. 3.2).
- (2) Comparison of the total number of different hand-use strategies used by individuals across all three plants. To ensure independence of data points, each individual only contributed one data point within a particular hand-use strategy. Data was first tested for normality using the Kolmogorov-Smirnov test, followed by the non-parametric Kruskal-Wallis test to test for statistical significance between the plants. A Mann-Whitney U-test was applied for between-groups comparisons following a significant Kruskal-Wallis test.

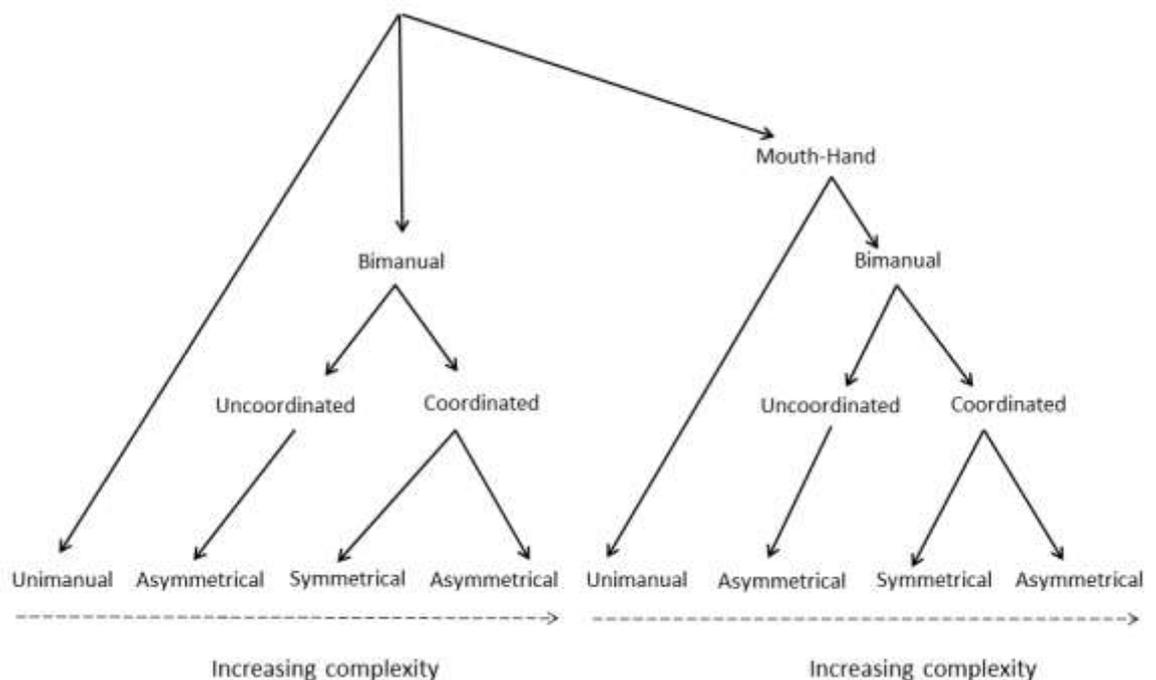


Figure 3.2: Flowchart modified after Leca et al. (2011), representing the different types of hand-use strategies in gorilla plant-processing.

3.2.4.3 Hand grips during plant-processing

The manual actions of mountain gorillas (N=11) were further assessed via a detailed examination of hand grips and hand movements to manipulate and support a food object during processing of all three plants.

As previously described, a bout was composed of multiple elements that are defined as either **functionally-similar** or **functionally-distinct** and each involving a pattern of grips and hand movements that serve to process the plant food. For each individual, the hand grips and movements were identified within a functional element of processing. For all three plants, a bout often involved repetitions of the same element with the same grip, and changes in grips occurred only rarely across repeated elements (i.e., 13 grip changes across 1954 elements). Thus, only the first grip was recorded during the first occurrence of an element to maintain data point independence required for statistical analyses.

Hand grips were classified as **(1) precision grips**, **(2) power (palm) grips**, **(3) hook grips** and **(4) compound grips** following previous studies that have identified these grips in both the wild and captivity (e.g., Napier, 1956; Marzke and Wullstein, 1996; MacFarlane, 2009; Pouydebat et al., 2011; Marzke et al., 2015, Bardo, 2016).

The first analysis examined the diversity of hand grips and hand movements for all elements (i.e., not just the most frequent, as in analyses above) used to process each of the three plants. Grip frequency was calculated in two ways: (1) by tallying the number of grip responses with the number of elements per individual to examine the individual frequency for each plant type, and (2) by calculating the total mean percentage from the individual frequencies per hand grip for each plant type. The comparison of grip use relative to plant type among individuals was assessed using Friedman rank sum tests (Q). If results were significant, pairwise comparisons were performed using the Wilcoxon signed rank test (Z) with continuity correction. Each individual only contributed one data point to ensure independence of data points.

The second analysis examined the frequency of grips relative to elements, to investigate the relationship between a particular grip and the hand action used across the three plant foods.

3.2.4.4 Laterality for processing different plant foods

I examined laterality for the most frequent elements of processing across the three plant species to test the prediction that the most complex plant shows the highest degree of lateralisation on individual- and group-level.

It is preferable to use either independent bouts or elements (=single, unique hand action) as the unit of analysis to assess hand-preference to ensure independence of data points (Vauclair and Fagot, 1987; Byrne and Byrne, 1991; Marchant and McGrew, 1991; McGrew and Marchant, 1997a). This study assessed laterality for elements within a bout. Hand-preference was only assessed for the most frequent (i.e., >25 % frequency across all individuals) functionally-distinct elements as they together built the hierarchical order of the plant processing common to most individuals in the group. Since the same element was often used repeatedly during processing, hand preference was only recorded for the first occurrence of the element or if the individual switched hands (a change in the dominant hand was considered a new element) to ensure that data points were independent of each other (e.g., Boesch, 1991; Westergaard and Suomi, 1996). Within these functionally-distinct elements, only those hand-use strategies that showed differentiation in hand use, i.e. unimanual and asymmetrical bimanual (including mouth-hand) hand-use, were assessed. In asymmetric hand-use, the hand used for manipulation is considered to be the dominant hand while the hand used for support is considered to be subordinate (e.g., Byrne and Byrne, 1991; Humle, 2003; Chaplain, 2010; Bardo, 2016). Hand preference was assessed at both the individual- and group-level.

The handedness index (HI) was calculated to examine the degree of preference for each individual using the formula: $HI = (R-L)/(R+L)$, where R and L are the number of times the right and left hands are used. HI ranges from -1.0 to +1.0, with negative values indicating a left-hand bias and positive values indicating a right hand bias (Hopkins, 1994). This index is informative for hand use but does not

tell whether the individual is lateralized or not. The absolute value of HI (ABS-HI) gives the overall strength of preference for each individual irrespective of direction and ranges from 0 (ambi-preferent) to 1.0 (extreme lateralisation in either direction) (Hopkins, 1994). The mean of ABS-HI was calculated to characterise laterality for the group in each elements (for bouts ≥ 2 including elements ≥ 4 ; e.g., Hopkins and Leavens, 1998; Hopkins and Wesley, 2002) and to determine if particular elements or particular plant-foods were more lateralized than others. Furthermore, the binominal z-score was calculated based on the total frequency of right-hand and left-hand use across all elements and plant foods to classify each individual as right-hand, left-handed or ambi-preferent. Binomial z-scores were calculated in Microsoft Excel using the formula $= (R - ((R+L)/2)) / (\text{SQRT}(\text{SUM}((R+L)/4)))$. Individuals with a z-score higher than 1.96 or less than -1.96 were classified as right- or left-handed, respectively, while individuals with a z-score between these values ($-1.96 < z < 1.96$) were considered ambi-preferent (e.g., Hopkins, 1999; Braccini et al., 2010). These three methods evaluating hand-preference are complementary and have been used separately or together in the majority of recent studies (e.g., Byrne and Byrne, 1991; Boesch, 1991; Papademetriou et al., 2005; Humle and Matsuzawa, 2009; Chapelain et al., 2011), allowing for comparisons with other apes.

Group-level laterality is recognised when “a significant majority of individuals display the same preference” (based on the two-tailed binomial test; Seagel and Castellan, 1988). Group-level laterality was tested based on binomial z-scores. Additionally, the percentage of lateralized and ambi-preferent individuals in the group was examined, and the number of lateralized and ambi-preferent individuals compared using a two-tailed binomial test for sample sizes from 6-10 (Seagel and Castellan, 1988) and a chi-square test for samples of 10 and above (Byrne and Byrne, 1991).

It was not always possible to video the starting moment of every food-processing session. Hence, a total of eight video sequences of four individuals (TW, MG, MK, HP; see Table 3.7 in *Appendix III*) were recorded shortly after the starting moment and contain only a small sample size of hand actions. Therefore, these four individuals were excluded from the analysis of laterality.

All statistical analyses were performed using the software SPSS (IBM SPSS Statistics for Windows, Version 24.0) and the level of significance was set at $p \leq 0.05$.

3.3 Results

3.3.1 Functional elements of plant-processing in Bwindi gorillas

Analysis of 345 bouts across 11 individuals (N=7 females; N=4 males) revealed 19 elements (i.e., a single, distinctive hand action that results in an observable change to the plant) for processing all three plant species, including 16 functionally-distinct elements and 3 functionally-similar elements (Table 3.1 in *Appendix II*). The functionally-distinct elements typically included obligate (i.e., used by 100 % of individuals) and optional elements of manipulative actions (see Table 3.2 for individual data). These elements happened typically in an ordered and coordinated sequence of key-stages within a bout that are described in Table 3.2.

- Peel-processing involved one obligate element and six optional elements, which occurred in four key stages (Table 3.3). A Mann-Whitney U-test revealed that female and male gorillas did not significantly differ in their number of functionally-distinct elements ($U=10$, $N=11$, $p=0.436$). The average number of distinct elements used by females was comparable to that used by males (range for females: 4-8 distinct actions; range for males: 5-8) (Table 3.2).
- Pith-processing involved two obligate elements and two optional elements, which occurred in three key stages (Table 3.3). Females and males were not significantly different in their number of functionally-distinct elements ($U=10.5$, $N=11$, $p=0.442$). Females performed on average a slightly lower number of different actions (range for females: 5-7) as compared to males (range for males: 5-8) (Table 3.2).

- Leaf-processing revealed one obligate element and three optional elements, which together occurred in four key stages (Table 3.3). There was no significant difference in the number of functionally-distinct elements ($U=10$, $N=9$; $p=0.260$) between females (range for females: 4-5) and males (range males: 5) (Table 3.2).

Across the tested individuals for pith-processing ($N=11$) and leaf-processing ($N=9$), the total mean frequency for each element (i.e., >25 % frequency across all individuals) showed that both plants most frequently involved four functionally-distinct elements, while peel-processing ($N=11$) required six functionally-distinct elements (Table 3.3).

Table 3.2: Summary of data for each gorilla individual.

Plant species	Individual ID	Sex/Age	Total no. of sessions	Total no. of bouts	Total no. of elements	No. of functionally-distinct elements
<i>Urera hypselodendron</i>						
(consuming peel)	JN	female/adult	3	7	36	7
	ST	female/adult	8	23	72	8
	KR	female/adult	3	3	15	5
	TN	female/adult	1	3	9	4
	TW	female/adult	2	2	11	6
	MG	female/adult	1	4	25	6
	BY	female/adult	3	7	46	7
	RC	male/silverback	13	24	157	7
	MK	male/silverback	2	2	33	8
	HP	male/subadult	2	2	9	5

	KA	male/blackback	8	20	116	7
TOTAL			45	101	529	
<i>Mimulopsis arborescens</i>						
(consuming pith)	JN	female/adult	2	6	37	5
	ST	female/adult	7	10	61	6
	KR	female/adult	6	18	119	7
	TN	female/adult	2	4	27	5
	TW	female/adult	3	5	42	5
	MG	female/adult	3	9	42	5
	BY	female/adult	4	13	41	5
	RC	male/silverback	5	12	115	8
	MK	male/silverback	4	9	55	6
	HP	male/subadult	6	10	51	5

	KA	male/blackback	2	7	23	5
TOTAL			44	103	613	
<i>Momordica foetida</i> (consuming leaf)	JN	female/adult	3	13	55	4
	ST	female/adult	2	7	25	5
	KR	female/adult	4	13	56	5
	TN	female/adult	2	5	23	4
	TW	female/adult	6	12	71	5
	BY	female/adult	9	26	117	5
	RC	male/adult	6	37	172	5
	HP	male/subadult	3	18	103	5
	KA	male/blackback	3	10	60	5
TOTAL			38	141	682	

Table 3.3: Functionally-distinct elements of plant-processing that were most frequently used (i.e. >25 % across all individuals) among the gorilla group (N=11). Obligate act(s) are labelled as**.

Plant part processed	Sequence of elements	Mean absolute frequency (%)	Order of key stages
peel-processing	pick up or pull stem	47	1. initial procurement of the plant
	brush-off leaves	29	2. remove unwanted parts with support of stem
	bite off length	34	
	peel-back outer casing	64	3. gather stripes of peel into hand
	tooth-strip peel**	100	
insert into mouth	77	4. insert edible peel into mouth	
pith-processing	pick up stem	49	1. initial procurement of the plant
	break off length	63	2. remove unwanted parts with support of stem
	snip-case: bite off hard case**	100	
	scrape-off edible pith**	100	3. consume edible pith
leaf-processing	pull into range	72	1. initial procurement of leaves
	pick leaves	65	2. leaf detachment with support
	accumulate handful of leaves	92	3. accumulation of items into hand
	put handful into mouth**	100	4. insert leaf bundle into mouth

3.3.2 Hand-use strategies for processing different plant foods

- Peel-processing involved seven hand-use strategies, in which bimanual-coordinated, asymmetrical hand-use was most frequent (23 %), followed by mouth-unimanual hand-use (20 %) and mouth-bimanual coordinated, symmetrical hand-use (18 %, Fig. 3.3). Uncoordinated bimanual hand-use was not used in peel-processing.
- Pith-processing showed six hand-use strategies, in which mouth-bimanual hand, coordinated asymmetrical hand-use (59 %) was by far the most frequent (Fig. 3.4). None of the individuals used bimanual-uncoordinated, asymmetrical and bimanual-coordinated, asymmetrical hand-use to process pith.
- Leaf-processing involved seven hand-use strategies, in which bimanual-coordinated, asymmetrical hand-use (31 %) and unimanual hand-use (26 %) occurred most frequently (Fig. 3.5). Mouth-bimanual hand, coordinated asymmetrical hand-use was not used by any individual.

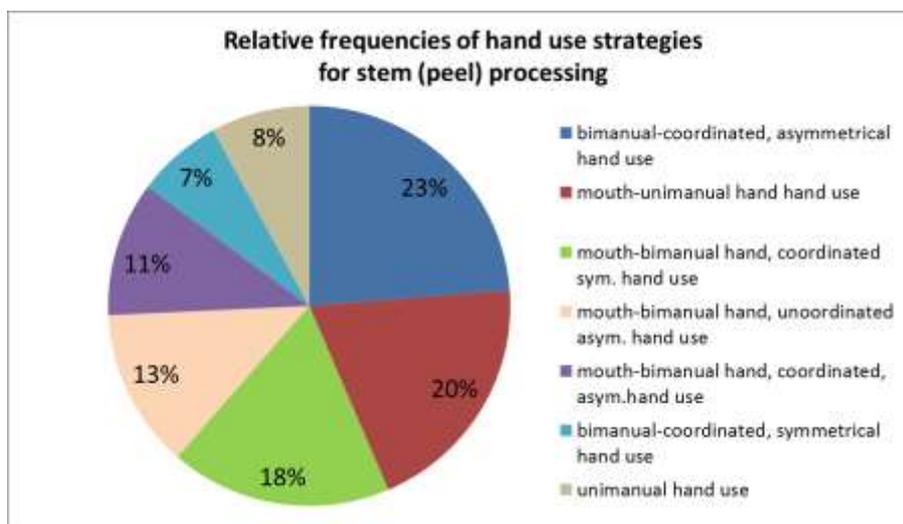


Figure 3.3: Relative frequencies of hand-use strategies for peel-processing.

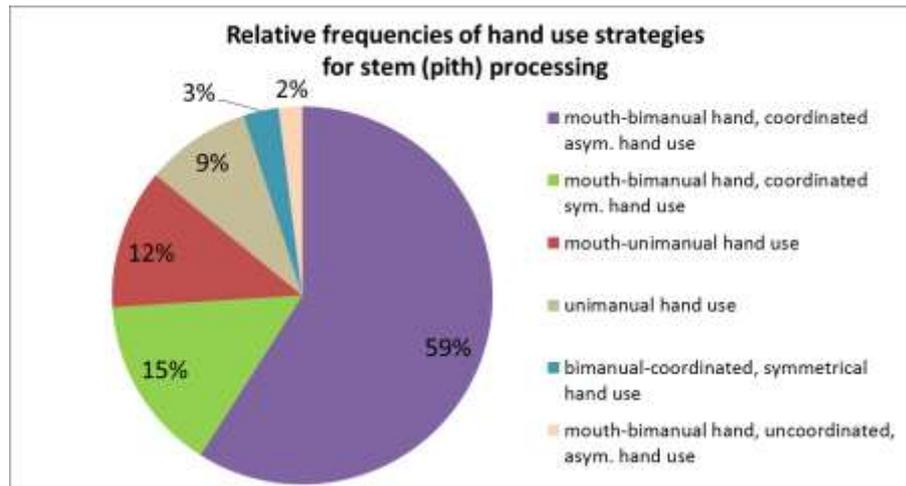


Figure 3.4: Relative frequencies of hand-use strategies for pith-processing.

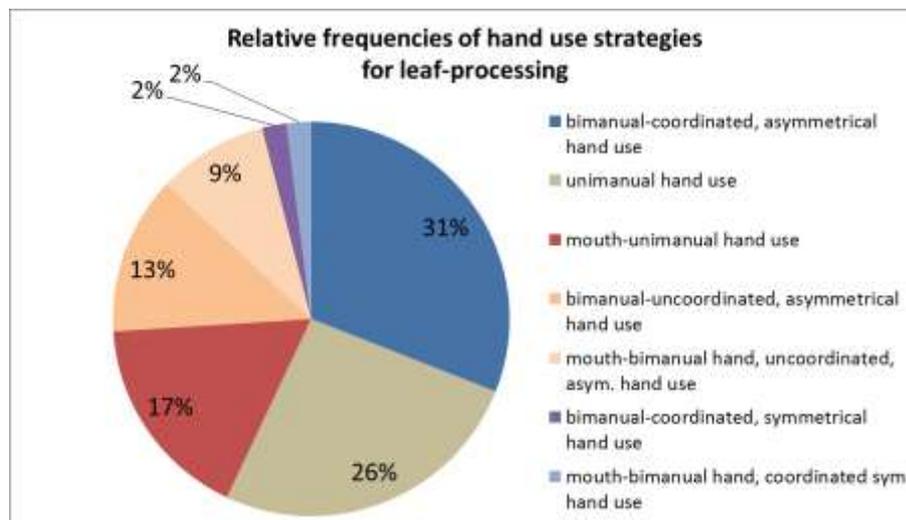


Figure 3.5: Relative frequencies of hand-use strategies for leaf-processing.

To test whether a particular hand-use strategy was used significantly more often for one plant over another plant, a non-parametric Kruskal-Wallis test was applied for seven hand-use strategies common to all three plants (apart from bimanual-uncoordinated, asymmetrical hand-use, which only occurred in leaf-processing). Five out of seven hand-use strategies were significantly different across the plants (Table 3.4).

Table 3.4: Kruskal-Wallis test for hand-use strategies of the three plant foods.

Hand-use strategy	Plant foods comparison	Statistical results
unimanual hand-use	peel vs. pith vs. leaf	H(2)= 14.6, N ₁ =N ₂ = 11, N ₃ = 9, p= 0.001
bimanual-coordinated, symmetrical hand-use	peel vs. pith vs. leaf	H(2)= 3.8, N ₁ =N ₂ = 11, N ₃ = 9, p= 0.147
bimanual-coordinated, asymmetrical hand-use	peel vs. leaf	H(1)= 11.54, N ₁ = 11, N ₂ = 9, p= 0.001
mouth-unimanual hand use	peel vs. pith vs. leaf	H(2)= 2.4, N ₁ =N ₂ = 11, N ₃ = 9, p= 0.303
mouth-bimanual hand, uncoordinated asymmetrical hand-use	peel vs. pith vs. leaf	H(2)= 14.79, N ₁ =N ₂ = 11, N ₃ = 9, p=0.001
mouth-bimanual hand, coordinated symmetrical hand-use	peel vs. pith vs. leaf	H(2)= 13.5, N ₁ =N ₂ = 11, N ₃ = 9, p= 0.001
mouth-bimanual hand, coordinated asymmetrical hand-use	pith vs. peel	H(1)= 7.9, N ₁ =N ₂ =11, p= 0.005

A Mann-Whitney U test for between-plant food comparisons returned varying results for the five hand-use strategies tested (Table 3.5). Unimanual hand-use was significantly more frequent in leaf-processing compared to peel-and pith-processing. Bimanual-coordinated asymmetrical hand-use was significantly more frequent in leaf-processing than in peel-processing. Mouth-bimanual hand, uncoordinated asymmetrical hand-use was significantly more often used in peel-and leaf-processing than in pith-processing. Mouth-bimanual hand, coordinated symmetrical hand-use occurred significantly more often in peel-and pith-processing compared to leaf-processing. Mouth-bimanual hand, coordinated asymmetrical hand-use was significantly higher in pith-processing than in peel-processing.

Table 3.5: Mann-Whitney U test for hand-use strategies of the three plant foods.

Hand-use strategy	Plant foods comparison	Statistical results
unimanual hand-use	peel vs. leaf	U=8, N ₁ =11, N ₂ =9, p= 0.002
	peel vs. pith	U=55, N ₁ =N ₂ =11, p= 0.712
bimanual-coordinated, asymmetrical hand-use	peel vs. leaf	U=5, N ₁ =11, N ₂ =9, p= 0.001
mouth-bimanual hand, uncoordinated asymmetrical hand-use	leaf vs. peel	U=25, N ₁ =11, N ₂ =9, p= 0.045
	leaf vs. pith	U=12, N ₁ =11, N ₂ =9, p= 0.003
	peel vs. pith	U=2, N ₁ =N ₂ =11, p<0.001
mouth-bimanual hand, coordinated symmetrical hand-use	peel vs. leaf	U=6, N ₁ =11, N ₂ =9, p= 0.001
	peel vs. pith	U=57, N ₁ =N ₂ =11, p= 0.817
	pith vs. leaf	U=11, N ₁ =11, N ₂ =9, p= 0.002
mouth-bimanual hand, coordinated asymmetrical hand-use	pith vs. peel	U=18, N ₁ =N ₂ =11, p= 0.005

The second set of analyses investigated whether plant processing evokes more bimanual-coordinated asymmetrical hand-use than bimanual-coordinated symmetrical hand-use by testing for a significant bias towards asymmetric processing (i.e., bimanual role differentiation) for all individuals during the most frequent elements of processing. A two-tailed binominal test of proportions showed that asymmetrical hand-use was highly significant for all three plant foods (peel, N=11, 65 %, p<0.001; pith, N=11, 76 %, p<0.001; leaf, N=9, 95 %, p<0.001).

3.3.3 Hand grips during plant-processing

Analysis of the hand grips during plant processing found a total of 19 different hand grips across the 19 elements of plant-processing (see Table 3.6). Mountain gorillas used eight precision grips, six hook grips, three power grips and two compound grips. This study revealed three hand grips (distal palm grip;

interdigital 2/3 brace - pad-to-side; power - pad-to-side; Table 3.6) that have not been previously reported in the literature and thus, are considered to be novel.

- **Peel-processing** elicited 15 hand grips and showed a significant preference within the group ($Q=29.04$, $N=11$, $df=3$, $p < 0.001$), using significantly more precision ($Z=2.94$, $p=0.003$) and hook ($Z=2.94$, $p=0.003$) grasping (Fig. 3.6) than power grasping.
- **Pith-processing** involved 12 hand grips with a significant preference within the group ($Q=26.32$, $N=11$, $df=3$, $p < 0.001$). Precision grasping was significantly more often used than hook ($Z=2.63$, $p=0.009$) and compound grasping ($Z=2.94$, $p=0.003$) (Fig. 3.6). Similarly, power grasping occurred significantly more often than hook ($Z=2.04$, $p=0.004$) and compound grasping ($Z=2.94$, $p=0.003$).
- **Leaf-processing** elicited 14 hand grips and showed a significant preference within the group ($Q=23.53$, $N=9$, $df=3$, $p < 0.001$), with precision grasping being significantly more often used than hook ($Z=2.55$, $p=0.011$), power ($Z=2.67$, $p=0.008$), and compound ($Z=2.67$, $p=0.008$) grasping (Fig. 3.6).

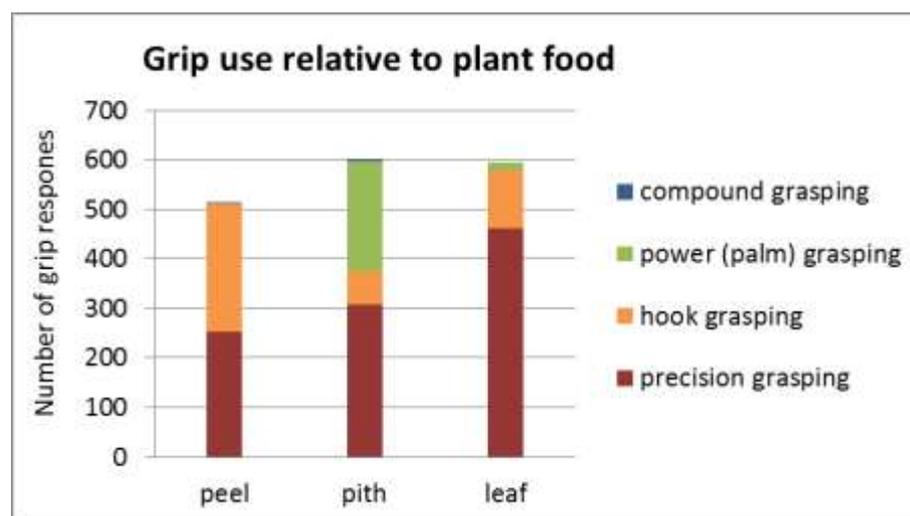


Figure 3.6: Number of grip responses relative to plant food.

The frequency of different grip types used by individuals for each plant food and how these relate to particular hand actions are presented in more detail below. Additionally, the typical processing sequence and associated hand grips are depicted for each plant below in Figures 3.8, 3.10, and 3.12.

3.3.3.1 Peel-processing

Grip use was recorded 513 times across the seven most frequent elements and for support (Table 3.6, Fig. 3.7). The **extended transverse hook grip** was the most frequent grip (mean frequency: 36 %, 159/513) and was used by all individuals (Table 3.6). This grip occurred in all manipulative elements and support (Fig. 3.7). The extended transverse hook grip was most frequently used (50 %, 79/159) for the obligate element, stripping off the peel. The **transverse hook grip** occurred relatively frequently (total mean 20 %, 103/513) and across all elements and support (Table 3.6, Fig. 3.7). The grip was most frequently used for picking up stems and peeling-back the outer casing (24 %, 25/103). The **two-jaw chuck pad-to-side precision grip** occurred with similar frequency (total mean 19 %, 99/513) and in six manipulative elements and support, with most frequent use for inserting the food bundle into the mouth (70 %, 69/99) (Table 3.6, Fig. 3.7). Finger hook grips, power grips and compound grips (i.e., I2-3B-PS, see Table 3.6) occurred only rarely (Table 3.6, Fig. 3.7).

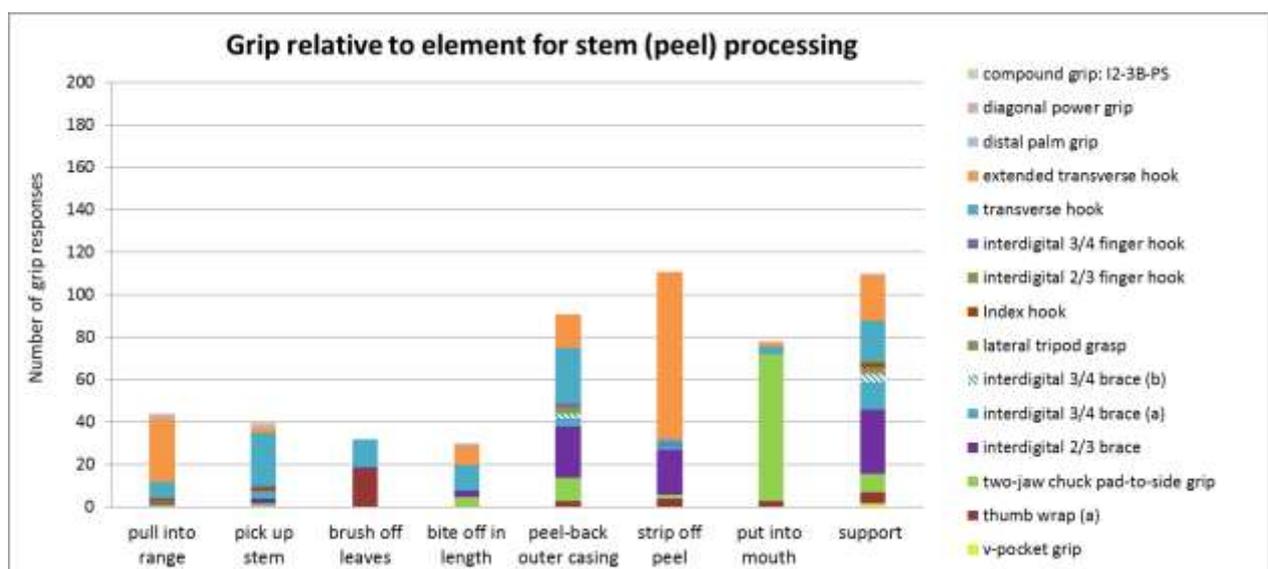


Figure 3.7: Relative frequencies of grips relative to most frequent elements for peel-processing.

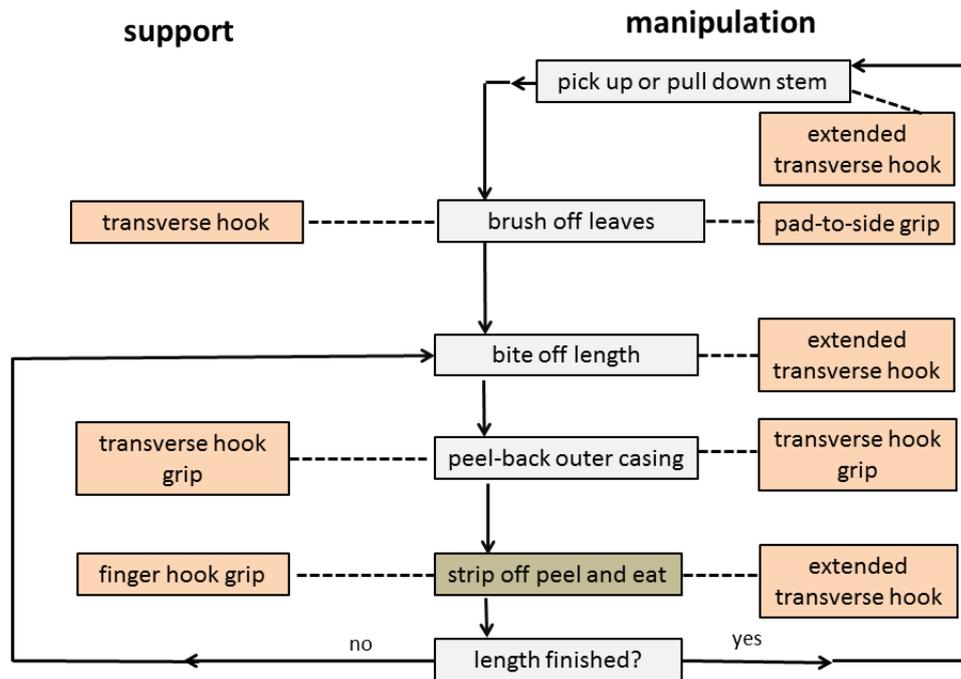
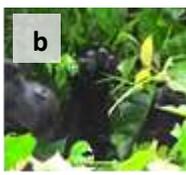


Figure 3.8: Typical sequence of peel-processing and associated hand grips used by all gorilla individuals. Chart is divided into hand functions (manipulation versus. support) to indicate elements with no significant laterality (see below). Optional elements are highlighted in grey and the obligate element is highlighted in tan. Dotted lines indicating most frequent grip.

Table 3.6: Hand grips used in mountain gorilla plant-processing.

Gripping category	Digit contact	Name (acronym)	Description	Mean absolute frequency (%) for each plant food	Illustrations
Precision grip	1,1-2	V-pocket grip ¹ (VPG)	Object held either in web between full thumb and side of flexed index finger or held only by the full thumb in web.	(peel): 5 % (pith): - (leaf): -	
	1-2	Thumb wrap ^{1,3} (TW)	Thumb and index cross over object and forming a “C” shape, thumb pad contacts side of middle phalanx of index finger, other fingers are flexed and either (a) not in contact with the object or (b) the third finger is involved and cross with the index over the object.	(peel): 8 % (a), - (b) (pith): 0.9 % (a, b) (leaf): 28 % (a), 6 % (b)	 
	1-2	Two-jaw chuck pad-to-side ^{1,2} (2JCPS)	Object held between thumb pad and side of index finger.	(peel): 19 % (pith): 18 % (leaf): 17 %	
	1-2	Two-jaw chuck pad-to-pad ¹ (2JCPP)	Object held between pad of the thumb and pad of index finger.	(peel): - (pith): 0.2% (leaf): -	

	2-3	Scissor hold ² (SH)	Object held between lateral side of second and third finger, excluding the thumb.	(peel): - (pith): - (leaf): 0.5 %	
	2-3	Interdigital 2/3 brace ⁴ (I2-3B)	Object is bracing in the webbing of the thumb and weaving under the index finger, exiting the hand between the proximal or middle phalanges of the second and third digits.	(peel): 16 % (pith): 27 % (leaf): 13 %	
	1-2-3-4	Interdigital 3/4 brace ⁴ (I3-4B)	Object held either (a) by strongly flexed digits 3-2 to side of digit 4 and side of distal or proximal phalanx of the thumb, or (b) by less flexed digits 3-2 to side of digit 4 and lying in web of the thumb. Wrist can be strongly flexed in this grip.	(peel): 14 % (a), 5 % (b) (pith): 8 % (a), 2 % (b) (leaf): 9 % (a), 0.5 % (b)	 
	1-2-3	Lateral tripod grasp ⁵ (LTG)	Object stabilized against radial side of third finger with index pulp on top of the object, and the thumb adducted and braced over or under anywhere along lateral side of index finger.	(peel): 3 % (pith): - (leaf): 0.2 %	
Hook grip	(1)-2,4-5	Finger hook ^{1,2} (FH)	Object stabilized either by flexed index finger only or by digits four and five. Thumb can be involved for stabilization.	(peel): 1 % (pith): - (leaf): 2 %	

	1-2-3	Interdigital 2-3 finger hook ⁶ (I2-3FH)	Object held by flexed index finger, exiting the hand between the middle phalanx of index and proximal phalanx of third finger. Thumb slightly flexed at interphalangeal (IP) joint contacting the dorsal side of distal phalanx of index finger and locking Index.	(peel): 4 % (pith): - (leaf): 0.5 %	
	2-3-4	Interdigital 3-4 finger hook ⁶ (I3-4FH)	Object held by flexed digits 2-3, exiting the hand between the side of middle phalanx of third and side or dorsal side of middle phalanx of fourth finger. Thumb is not involved.	(peel): 2 % (pith): - (leaf): 0.2 %	
	1-2-(3), 2-3, 2-3-4-(5)	Transverse hook ^{1,2} (TH)	Object held by fingers flexed at IP joint with the thumb either opposed or adducted in contact to side of index finger or without thumb. Distal part of palm is not involved.	(peel): 20 % (pith): 5 % (leaf): 9 %	
	(1)-2-3-4-(5)	Extended transverse hook ^{1,2} (ETH)	Object held between all four fingers flexed at all joints with the thumb either opposed, adducted and in contact to the side of index finger or not involved. Distal area of the palm can be partly involved.	(peel): 36 % (pith): 5 % (leaf): 9 %	
	1-2-3-4-5	Diagonal hook ⁷ (DH)	Object held diagonally across the fingers. Thumb is involved in this variant.	(peel): - (pith): - (leaf): 0.3 %	
Power grip	1-2-3-4-5	Power grip ² (PG)	An object is held between all five fingers and main part of the palm. The full power grip, in which the thumb is opposed and provides counter pressure, occurred in leaf-processing. A type was used in pith-processing, where the thumb is held adducted to the index finger and braces over the object at level of metacarpophalangeal (MCP) joint. Lower palm partially without contact, depending on object's diameter.	(peel): - (pith): 3 % (leaf): 3 %	

	1-2-3-4-5	Distal palm grip (DPM)	Type of power grip, where an object is held between all five fingers and only the distal area of the palm. Thumb either opposed and braced under the object at level of MCP joint or abducted to Index and held in line to the object. Counter pressure is applied by the thumb.	(peel): 1 % (pith): 34 % (leaf): -	
	1-2-3-4-5	Diagonal power grip ² (DPW)	Object held diagonally across the fingers and the palm. Typically used to pull vegetation into range.	(peel): 3 % (pith): 2 % (leaf): -	
Compound grip	1-2-3	Interdigital 2/3 brace - pad-to-side (I2-3B-PS)	Two objects are held in one hand using an interdigital 2/3 brace and pad-to-side grip.	(peel): 1 % (pith): 0.2 % (leaf): -	
	1-2-3-4-5	Power - pad-to-side (DPW-PS)	Two objects are held with power and pad-to-side grip.	(peel): - (pith): 0.3 % (leaf): -	

Hand grips are highlighted in light font that have been named and/or described previously in Marzke et al. (2015)¹, Marzke and Wullstein (1996)², Byrne et al. (2001b)³, Lesnik et al. (2015)⁴, Schneck (1987), cited in Schneck and Henderson (1990)⁵, Bardo (2016)⁶, Marzke et al. (1992)⁷. New observed hand grips are highlighted in dark font. "-" denotes absence of grip data.

3.3.3.2 Pith-processing

Grip use was recorded 572 times among the four most frequent elements and support (Table 3.6, Fig. 3.9). The **distal palm grip**, a type of power grip, was most frequently used (mean frequency: 34 %, 194/572) among the group (Table 3.6, Fig. 3.9). The grip occurred most frequently during support (relative frequency: 35 %, 68/194), followed by manipulation such as biting off the hard case (20 %, 39/194) and breaking the object in length (19 %, 37/194). The **interdigital 2/3 brace precision grip**, was frequently used (total mean 27 %, 157/572; Table 3.6) and associated with all four manipulative elements and support (Fig. 3.9). This grip was most often used for support (43 %, 57/157). The **two-jaw chuck pad-to-side grip precision grip** was relative frequently used (total mean 18 %, 105/572) in all four elements, including scraping-off the edible pith (46 %, 48/105) and biting off the hard case (32 %, 34/105) (Table 3.6, Fig. 3.9). Hook grips were less frequently used and compound grips only rarely used across all hand actions (Table 3.6, Fig. 3.9).

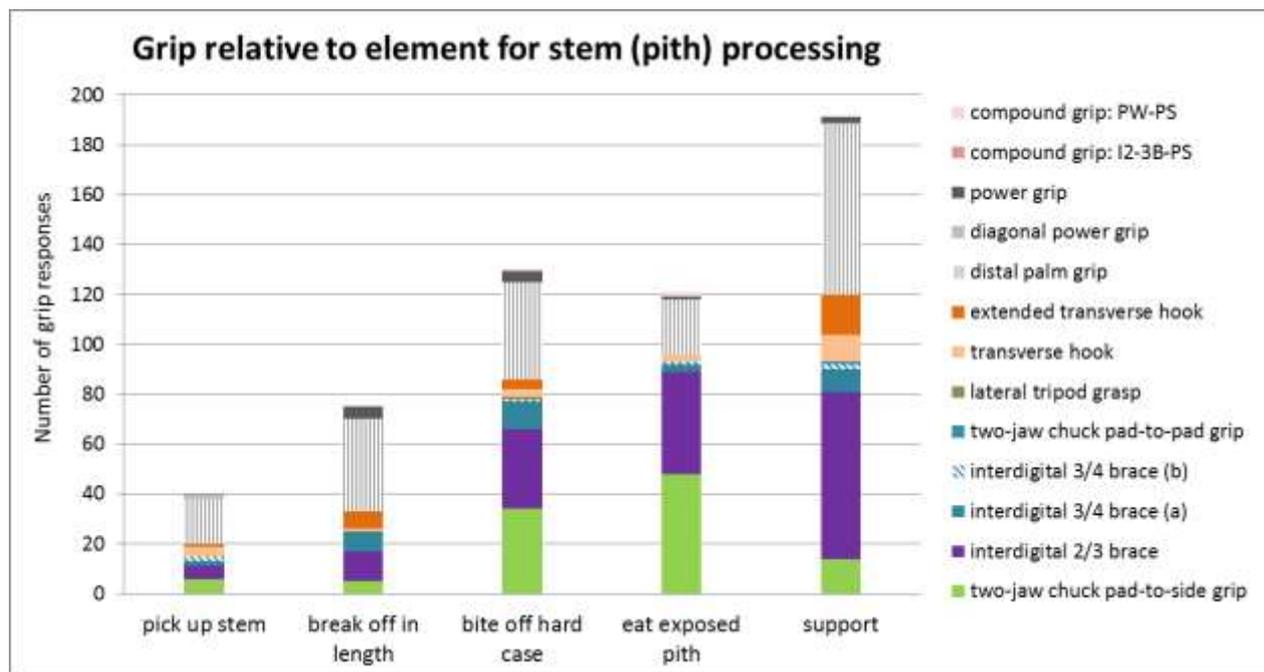


Figure 3.9: Relative frequencies of grips relative to most frequent elements for pith-processing.

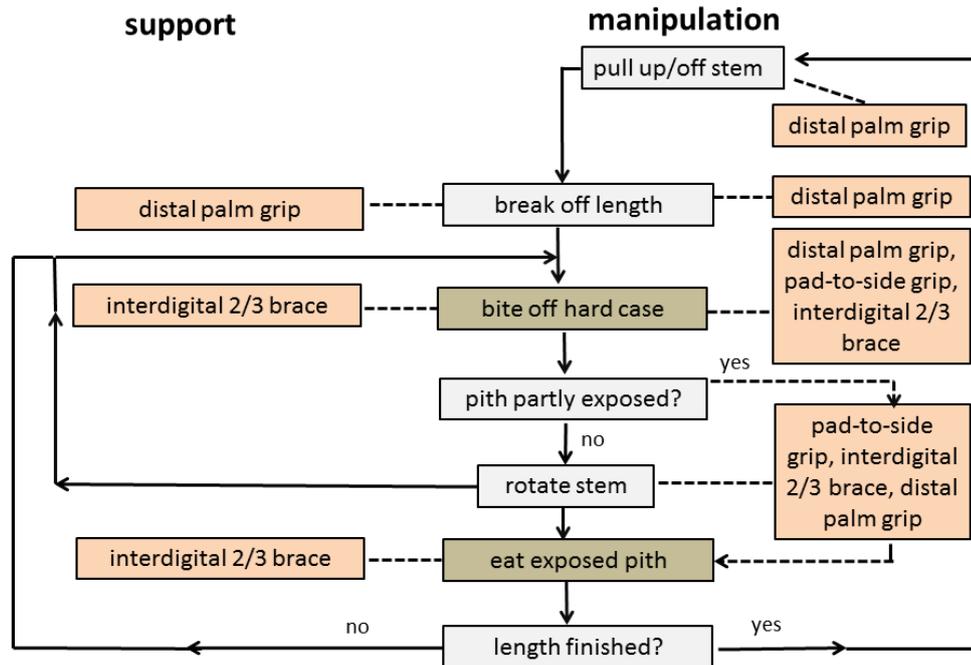


Figure 3.10: Typical sequence of pith-processing and associated hand grips used by all gorilla individuals. Chart is divided into hand functions (manipulation versus. support) to indicate elements with no significant laterality (see below). Optional elements are highlighted in grey and obligate elements are highlighted in tan. Dotted lines indicate most frequent grip.

3.3.3.3 Leaf-processing

Grip use was recorded 550 times during the four most frequent elements and for support (Table 3.6, Fig. 3.11). The **thumb wrap (type a) precision grip**, was the most frequent grip type (mean frequency: 28 %, 153/550) used among the group (Table 3.6). This grip type occurred only during manipulation (Fig. 3.11) and most frequently in the obligate element of inserting leaves into the mouth (relative frequency: 46 %, 71/153). The **two-jaw chuck pad-to-side precision grip** was frequently used (mean frequency: 17 %, 96/550) and associated with both manipulation and support (Table 3.6, Fig. 3.11). This grip was most often used for inserting leaves into the mouth (relative frequency: 34 %, 35/96). The **interdigital 2/3 brace precision grip** also occurred relatively frequently (mean frequency: 13 %, 73/550) and was used across all four elements and support, most often for both pulling the stem into range and support (relative frequency: 25 %, 18/73) (Table 3.6, Fig. 3.11). Power grips were less often and finger hook grips only rarely used. Compound grips were not observed during leaf-processing (Table 3.6, Fig. 3.11).

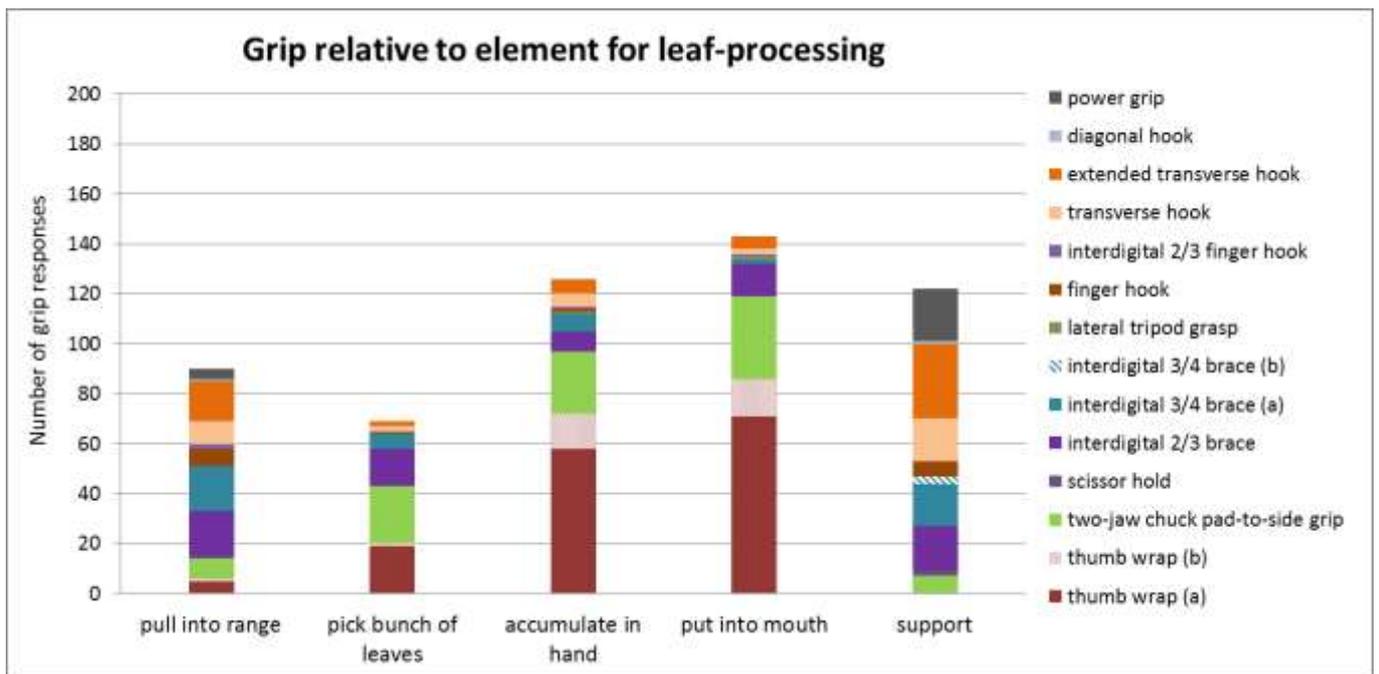


Figure 3.11: Relative frequencies of grips relative to most frequent elements for leaf-processing.

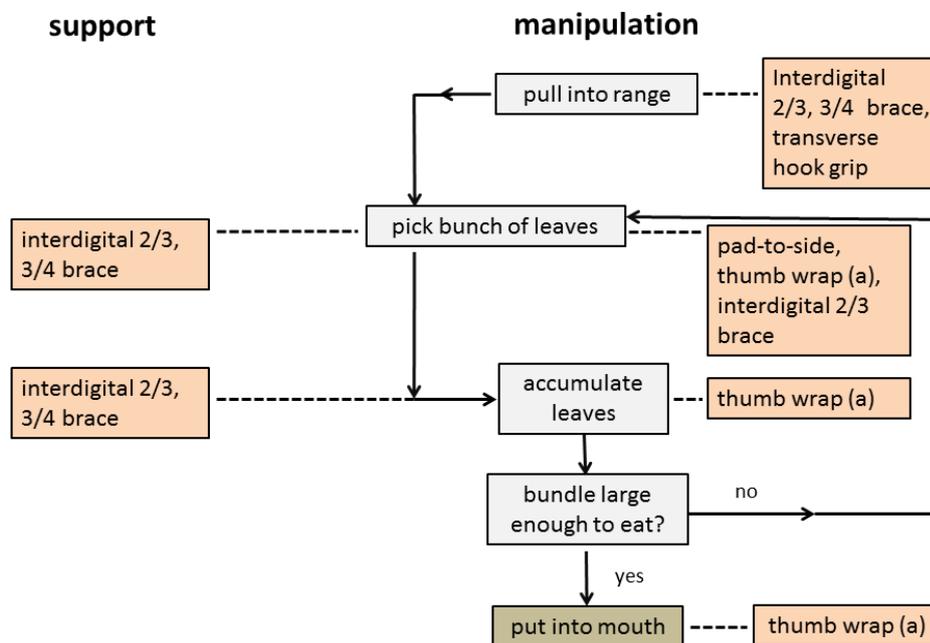


Figure 3.12: Typical sequence of leaf-processing and associated hand grips used by all gorilla individuals. Chart is divided into hand functions (manipulation versus. support) to indicate elements with no significant laterality (see below). Optional elements are highlighted in grey and the obligate element is highlighted in tan. Dotted lines indicate most frequent grip.

3.3.4 Laterality in hand-use during plant-processing

Laterality was assessed for unimanual and asymmetrical hand use during bimanual and mouth-hand strategies for the three plants at the individual- and group-level. At the individual-level, results showed an overall weak strength of laterality for most individuals for each plant food and there were no significant differences between the number of ambi-preferent and lateralized (i.e., right- or left-hand preference) individuals (see *Appendix III* for more details).

3.3.4.1 Strength of laterality among the three plants on group-level

To investigate the strength of hand-preference at the group-level, mean values of the individual handedness index (ABS-HI) were examined across all three plants (see Table 3.7 in *Appendix III*). The results indicate that the strength of laterality differs across the three plants at group-level. Laterality was strongest in peel-processing (mean: 0.46) but overall relatively weak among the group across all three plants (mean ABS-HI: < 0.5), indicating no group-level laterality for both unimanual and asymmetrical hand-use (Table 3.7 in *Appendix III*, Fig. 3.13). Based on the binomial z-scores, the overall high number of ambi-preferent individuals across all three plants indicates no lateral bias at the group-level (see Figures 3.14-3.16 in *Appendix III*). Thus, group-level laterality was not further statistically tested.

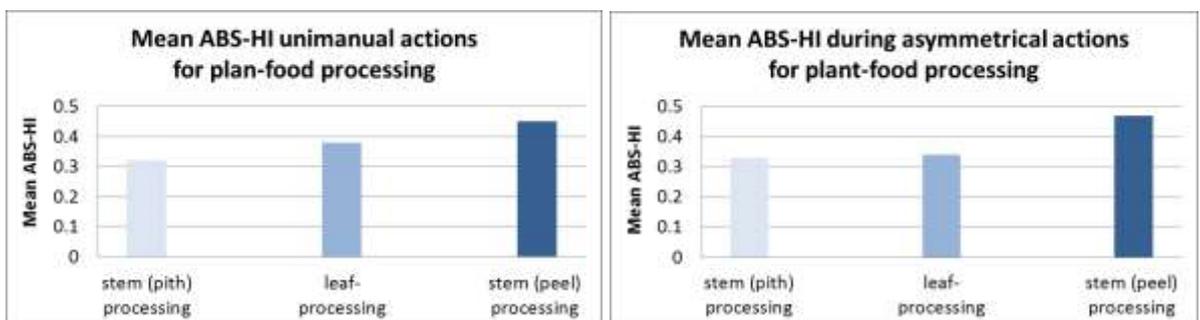


Figure 3.13: Mean values of individual handedness index (ABS-HI), with frequencies of unimanual and asymmetrical actions for all three plant foods.

3.4 Discussion

These new data on plant-processing in Bwindi mountain gorillas add to the sparse record of the manual skills and techniques used in the extractive foraging behaviour of wild gorillas and provide a broader comparative context in which to better understand the function of the primate hand as well as the variation in primate laterality during object manipulation. Previous studies on how primates use their hands to perform object manipulation defined manipulation complexity according to a variety of hierarchical criteria: First, bimanual hand use is considered more complex than unimanual hand use. Then, within bimanual hand use, asymmetrical manipulation is considered more complex than symmetrical manipulation, and coordinated is considered more complex than uncoordinated hand-use. Flexibility, which is characterised as the diversity of combinations of actions in a sequence and by the ability to apply one action to different contexts, is considered more complex than using one action repeatedly (Elliott and Connolly, 1984; van Schaik et al., 1999; Hopkins and de Waal, 1995; Byrne, 2003; Leca et al., 2011; Boesch, 2013). In this study, I add to this assessment of manipulation complexity by adding one new criterion: mouth-hand strategy, in which the use of both hands and the mouth is considered more complex than the use of one hand and the mouth.

In this study, I tested four hypotheses regarding differences in food processing of three different plants. Overall, I found only partial support for these hypotheses, the results of which are discussed below.

3.4.1 Functional elements of plant-processing in Bwindi gorillas

This study partially supports the hypothesis that plants with physical defences (i.e., stems with herbaceous and woody casing) require more behavioural elements of processing than undefended leaves.

Since the first studies by Byrne and colleagues (1991, 1993) on processing thistle stem and leaves (*Carduus nyassanus*) in Virunga mountain gorillas at Karisoke, Rwanda, there have been no comparable analyses of stem- or leaf-processing in a different population of wild mountain gorillas. Thus, we do not know

(1) whether thistle stem requires more complex processing techniques by gorillas than is typical for plant stems, and (2) whether processing thistle leaf is more complex compared to other plant foods commonly consumed by mountain gorillas in Virunga and Bwindi, as suggested by Byrne and colleagues (1991, 2001a, b). This study provides this much-needed comparative context in Bwindi mountain gorillas.

This study identified four key stages of peel- and leaf processing while three key stages were used when processing pith. To process peel, all gorillas followed the sequence of key stages: (1) procure plant, (2) remove inedible parts with support of the stem, (3) gather stripes of peel into hand, and (4) insert edible peel into the mouth. Although pith-processing showed only three key stages, all gorillas used similar key stages as for peel-processing: (1) procure plant, (2) remove inedible parts with support of stem, and (3) consume edible pith. In contrast, during leaf-processing all gorillas followed a different sequence of key stages and used only one element per key stage: (1) procure plant, (2) detach leaves with support, (3) accumulate leaves into hand, and (4) insert leaf bundle into the mouth. Both stem-and leaf-processing by Bwindi gorillas showed that the key stages of processing are routinely ordered and coordinated, which is a feature of hierarchical organisation (criteria outlined by Russon, 1998). Such an ordered and coordinated flow is also present in stem- and leaf-processing behaviours by Virunga gorillas, which they termed a ‘technique’ (Byrne and Byrne, 1993). Comparable research on wild chimpanzees (*Pan troglodytes schweinfurthii*) and long-tailed macaques (*Macaca fascicularis*) processing plant foods with physical defenses revealed similar evidence for the structural organisation of manipulative behaviours (Stokes and Byrne, 2001; Corp and Byrne, 2002; Tan et al., 2016) as documented in this sample of mountain gorillas. Rehabilitated orangutans (*Pongo pygmaeus*) have also demonstrated structural organisation during tool use and object manipulations (Russon and Galdikas, 1993; Russon, 1998).

Byrne and colleagues (2001a, b) described the processing of thistle stem as consisting of four key stages: (1) initial procurement of the stem, (2) support of the stem, (3) detachment of stem item, and (4) insertion of the stem into the mouth as being the only obligatory element. The processing of thistle leaves was broken down into six key stages: (1) procurement of the plant or leaf, (2) support of the plant, (3) leaf detachment, (4) accumulation of several items into a hand, (5) removing debris

from the leaf bundle and (6) inserting the leaf bundle into the mouth, with detachment of the leaf and insertion into the mouth as being obligatory elements. In contrast to the three plants prepared by Bwindi gorillas, processing thistle leaf involves a greater number of key stages while processing thistle stem is similar to other plant stems. Based on the data thus far, thistle leaf appears to require a more complex processing technique in Virunga mountain gorillas.

Bwindi gorillas use a repertoire of 19 elements to process three plant foods, including 11 functionally-distinct elements and 8 functionally-similar elements (see Table 3.1 in *Appendix II*). The second feature of hierarchical organisation found in this study is the presence of ‘optional’ behavioural components (Russon, 1998). Plant-processing by Bwindi gorillas involved obligate elements (used by 100 % of individuals) while others were optional and dependent on whether or not they were required by the task. Peel-processing required more functionally-distinct elements (N=6) across the four key stages than pith-and leaf-processing (N=4 each) and involved one obligate element but up to five optional elements. The greater number of elements and the greater flexibility of their use in different stages indicate that peel-processing - based on the definition of complexity used here (see above) - is a more complex and flexible technique than pith- or leaf-processing.

A comparably large repertoire of elements was recorded only for Virunga mountain gorillas processing leaves defended by stings or hooks, counting 20 elements (Byrne and Byrne, 1993). This number increases to include hundreds of different elements when the definition used to characterise unique elements accounts for the type of hand grip and fingers used while performing an action (222 elements for thistle processing, 78 for gallium and nettle leaves; Byrne et al., 2001). In contrast, the behavioural repertoire of extracting honey from underground bee nests by wild chimpanzees with 14 elements is comparatively much smaller (Estienne et al., 2017). The current study, thus, provides support that thistle processing shows a greater complexity and behavioural flexibility than processing other plant materials among wild mountain gorillas. However, this study found that the 19 elements performed by Bwindi gorillas were also used by Virunga gorillas (Byrne et al., 2001a), indicating that both mountain gorilla populations share the same techniques regardless of which plant food is being processed.

Bwindi gorillas demonstrated a third feature of hierarchical organisation seen in great apes' food-processing behaviours, which is repeating an element(s) within the key stages of processing (Russon, 1998). For example, the gorillas repeated elements involved in gathering leaves until a handful was obtained or stripped the peel off from the stem until the peel was fully removed. Similar observations have been made in leaf-processing by Virunga gorillas and wild chimpanzees (Byrne and Byrne, 1993; Stokes and Byrne, 2001). Thus, wild gorillas like other great apes, use behavioural routines that they repeat until the task is achieved or to maximise efficiency (Russon, 1998).

Processing thistle is also occasionally performed by Bwindi mountain gorillas (e.g., Ganas et al., 2004; Robbins et al., 2006). Although the repertoire of behavioural elements used to process thistle in Bwindi gorillas has not been systematically studied yet, the gorillas appear to use similar techniques and apply the same six key stages of processing to those of the Virunga gorillas (Robbins, pers. observation stated in Sawyer and Robbins, 2009). Moreover, one female gorilla in Bwindi showed a novel technique for thistle processing when tidying up the bundle before inserting it into the mouth. Her 'palm roll' technique (forming a tight ball of thistle leaves by rubbing the palms of both hands against one another) was distinctly different from all elements described for Virunga gorillas (Sawyer and Robbins, 2009). A similar 'rolling' technique and several other manipulative actions have been described for nettle feeding in western lowland gorillas in captivity (Tennie et al., 2008; Byrne et al., 2011), supporting the idea that gorillas are capable of using their hands in a flexible and diverse functional manner when processing various plant foods.

3.4.2 Hand-use strategies for processing different plant foods

This study investigated how gorillas use their hands to perform object manipulation by testing whether plants with physical defenses (1) will show a greater number of different hand-use strategies and (2) involve more complementary role differentiation between both hands (i.e., asymmetric hand-use) than undefended plants. However, the findings of this study do not clearly support these hypotheses.

The examination of different hand-use strategies for the most frequent elements (i.e., >25 % frequency) revealed a total of eight hand-use strategies, from which six were involved in pith-processing while peel- and leaf-processing involved seven hand-use strategies (Figs. 3.3-3.5). The prediction that defended plants will display more bimanual asymmetrical coordination was not supported because leaf-processing also involved a significantly more frequent use of bimanual asymmetrical coordination as well. However, gorillas used their hands in three different modes to manipulate plants, namely, (1) unimanual hand-use, (2) bimanual hand-use and (3) mouth-hand use. A clear link has been found between plant material and hand-use strategies, with peel- and pith-processing involving a significantly more frequent use of the mouth-hand strategy while leaf-processing involved a significant use of more bimanual and unimanual actions. However, the main effect of coordination was highly significant for bimanual hand use across all three plant foods while only the mouth-hand strategy used in leaf-processing involved a significant use of uncoordinated actions. In comparison, processing thistle by Virunga mountain gorillas also involved unimanual-, bimanual- and mouth-hand hand-use strategies, including coordinated symmetrical and asymmetrical strategies (Byrne and Byrne, 1991; Byrne et al., 2001b). Processing thistle evoked significantly more bimanual-coordinated asymmetrical hand-use (i.e., each hand doing a different role at the same time) than symmetrical hand-use (Byrne and Byrne, 1991), which is similar to the results of this study. Unlike to this study, however, uncoordinated hand-use strategies were not reported for processing thistle stem and leaves (Byrne and Byrne, 1991; Byrne et al., 2001b), although it is unclear whether Virunga gorillas did not perform uncoordinated hand-use strategies, or that this behaviour simply was not recorded. While thistle processing has not yet been studied in detail in Bwindi gorillas, preliminary observations indicate similar processing techniques, including asymmetrical, coordinated hand-use strategies that have been documented in the Virunga gorillas (Sawyer and Robbins, 2009).

3.4.3 Hand grips during plant-processing

The analysis of how gorillas grip the plant during processing revealed 19 different hand grips across the four main grip categories (i.e., precision grips, power grips, hook grips and compound grips), 16 of which have either been previously

reported or show clear similarities to grips used by wild and captive gorillas, chimpanzees, bonobos, and humans (Napier, 1956; Marzke, 1997; Byrne et al., 2001a; Marzke et al., 2015; Lesnik et al., 2015; Bardo, 2016). These include grips that are typically used for arboreal locomotion such as hook grips and power grips (e.g., Alexander, 1994; Marzke and Wullstein, 1996). The remaining three grips have not been previously reported in the literature. Although most of the grips described here have been reported in captivity, it is important to document that similar grips are also used in a more complex and variable natural environment. The greater range of hand actions and plant foods available in a natural context, generate new insights into both the function of particular manipulative strategies and possible morphological links between the gorilla's hand and these strategies.

I predicted that gorillas will show a greater number of hand grips when processing physically defended plants. This hypothesis was not supported; although the gorillas used the highest number of different hand grips (N=15) for processing peel, they used 14 grips during leaf-processing and 12 grips during pith-processing. This suggests that all three plant foods involve a range of specific hand actions of manipulation and support that elicit a diverse use of grips.

Precision handling and in-hand movements, which are typical of humans (Marzke, 1997) and have been documented in western lowland gorillas, chimpanzees and bonobos (Crast et al., 2009; Bardo et al., 2016, 2017), were never observed in the plant-processing activities of any mountain gorillas in this study and thus are not discussed.

3.4.3.1 New hand grips

This study revealed three hand grips that have not been previously described: two new types of compound grips and one new type of power grip, the distal palm grip (Table 3.5). Compound grips, where more than one object is held in one hand and two distinct grips are used at the same time, have been described by Napier (1956) for humans, by Macfarlane (2009) for captive macaques and by Jones and Fragaszy (2015) for captive capuchin monkeys. The compound grips used by Bwindi gorillas to process plant stems best resemble Napier's (1956) illustration of the human hand holding a smaller object with a precision grip as the dominant grip and

the three inner digits are free to be used in a supplementary role for holding a larger cylindrical object (see below Figure 3.17). However, while the human hand demonstrates a pad-to-pad precision grip and a diagonal power grip, gorillas combined a pad-to-side precision grip with a power grip involving four digits (DPW-PS, Table 3.6) or a interdigital 2/3 brace precision grip with a pad-to-side precision grip (I2-3B-PS, Table 3.6). Mountain gorillas are capable of using their digits asynchronously and grasp more than one food object in a single hand at a time (Table 3.6, Fig. 3.6). This type of grasping requires independent control of parts of the same hand used for separate purposes at the same time, indicating higher motor skills than do synchronous digits (e.g., Christel and Fragaszy, 2000; Byrne et al., 2001b, Heldstab et al., 2016). Compound grips were only observed during support while other grips were used for both manipulative and supportive hand actions. However, the rare frequency of these grips might be due to the small sample size in this study and thus, the effectiveness of compound grips for processing plants compared to non-compound grips requires further research.

In the distal palm grip, an object is held between all five digits and only the distal area of the palm with the thumb either opposed and braced under the object at the level of the metacarpophalangeal joint, or abducted to the index finger and held in line to the object (Table 3.6). The thumb provides counter pressure and appeared to enhance stability in both postures. This grip seemed to be most effective for pith-processing because it was frequently used across most individuals and used for all elements (Figure 3.9).



Figure 3.17: Napier's (1956) illustration of the human hand using a compound grip (left) compared with gorilla compound grips using (a) pad-to-side precision grip with a power grip, and (b) interdigital 2/3 brace precision grip with a pad-to-side precision grip.

3.4.3.2 Precision grips

This study revealed that precision grips were used to process all three plants but that leaf-processing involved the most frequent use of precision grasping (Fig. 3.6), with the thumb wrap (type a) being the most frequent used precision grip (Fig. 3.11). However, the two-jaw chuck pad-to-side precision grip occurred frequently across all the plant foods while the interdigital 2/3 brace precision grip was only used during leaf- and pith-processing (see Figs. 3.9, 3.11).

The results of precision grips have some interesting parallels to previous observations on grips used for processing thistle-leaf in Virunga gorillas (Byrne and Byrne, 1993), for feeding in the Mahale chimpanzees in Tanzania (Marzke et al., 2015) and for termite nest perforation in the Goualougo chimpanzees in the Republic of Congo (Lesnik et al., 2015). Similar to Virunga gorillas, gorillas in Bwindi used precision grips, hook grips, power grips and compound grips across the three plants (7 described grips; Byrne and Byrne, 1993). However, since Byrne's studies (1993, 2001a, b) did not describe most of the grips in more detail beyond these four main categories and did not quantify the relative frequency, the results here will be compared to the grasping strategies in wild chimpanzees and other captive primates that examined this detail.

Similar to Bwindi gorillas, Mahale chimpanzees used precision grips for feeding such as the two-jaw chuck pad-to-side grip, two-jaw chuck pad-to-pad grip, scissor hold and the V-pocket grip (Marzke et al., 2015). The grip between the thumb and the side of the index finger (two-jaw chuck pad-to-side grip, Marzke and Wullstein, 1996; Marzke et al., 2015) was the most frequent grip by Mahale chimpanzees and described as a strong grasp applied to pick-up and release food objects. One advantage of this grip is that it may help to place a food item in position where other parts of the hand do not get in the way during manipulation, and where wrist rotation is easy. This explanation applies well to gorilla manipulative strategies when shorter plant stems are held against pulling actions during feeding (peel and pith, Figs. 3.7, 3.9), leaves are picked off from stems and small food objects are inserted into the mouth (Fig. 3.11). This observation is also consistent with previous findings on herbaceous termite or ant fishing in wild chimpanzees and a food-extraction task in captive bonobos, where a fine stick has to be navigated precisely

through a small hole to retrieve food (e.g., Marzke et al., 2015; Lesnik et al., 2015; Bardo, 2016).

The interdigital 2/3 brace precision grip, where the object exits the hand between the proximal or middle phalanges of the second and third digits after bracing in the webbing of the thumb and weaving under the index finger, was first defined in wild chimpanzees that use twigs to forage for termites (Lesnik et al., 2015) and was recently found in captive bonobos during stick tool-use (Bardo, 2016). According to the ‘pencil grip’ categorized by Byrne as “accidental variant of power-grip” (1993, 2001b), where a plant stem is held in a closed-grip between a pair of digits (usually 2:3, 3:4 or 4:5) with support by the thumb, it can be reasonably assumed that Byrne also observed the ‘interdigital 2/3 brace’ in Virunga gorillas when processing thistle stem. In humans, this grip has been defined as an inefficient type of the pencil grip as it holds the pencil too tight and allows no finger movements needed for good handwriting (Selin, 2003). Lesnik and colleagues (2015) classified the interdigital 2/3 brace as being more powerful than the two-jaw chuck pad-to-side grip as the bracing of the tool against the hand gives the grip its greatest strength. This sounds reasonable in comparison with Bwindi gorillas, which used this grip frequently in each hand to process pith with bimanual asymmetrical coordination (Fig. 3.9). Additionally, this grip was relatively frequently used in leaf-processing when pulling vegetation into range, processing leaves and for support (Fig. 3.11).

There was not a single occurrence of thumb opposition to the tip of the index finger, and there was only one involving the distal pads of the thumb and index finger (i.e., two-jaw chuck pad-to-pad) in pith-processing. A thumb/index finger tip grip has been described for captive gorillas (Pouydebat et al., 2008) and some captive studies could successfully elicit these and other fine precision grips by offering small food items on flat surfaces (e.g., Napier, 1960; Christel, 1993; Jones-Engel and Bard, 1996; Macfarlane, 2009; Pouydebat et al., 2011) and on sticks (Butterworth and Itakura, 1998; Bardo, 2016). The Bwindi plant foods recorded in this study clearly did not elicit this level of fine precision. However, it remains open whether these fine precision grips might be involved when mountain gorillas prepare thistle and nettle plants as these herbs are typically defended by spines or hooks, and removal of these mechanical defences requires dexterity (Byrne and Byrne, 1991, 1993; Byrne et al., 2001a).

3.4.3.3 Hook grips

This study showed that mountain gorillas use hook grasping significantly more often to process peel than to process pith and leaves (Fig. 3.6), including two hook grips that are typical for ape arboreal locomotion and suspensory postures (extended transverse hook, transverse hook; Napier, 1960; Marzke et al., 1992; Marzke and Wullstein, 1996). These arboreal hook grips are essential for pulling vines into range, biting or breaking off stems in length, contributing strength to the removal of edible plant parts (peel, pith) and for counter support. While experimental studies in captivity tend to focus on precision grips in connection with simple feeding (e.g., Christel, 1993; Jones-Engel & Bard, 1996; Pouydebat et al., 2011), other studies successfully elicited similar locomotor hook grips in Virunga gorillas, wild chimpanzees and captive western lowland gorillas and bonobos during complex object manipulation (Byrne et al., 2001a; Marzke et al., 2015; Lesnik et al., 2015; Bardo et al., 2017).

3.4.3.4 Power grips

The mountain gorillas in this study used power grasping significantly more often for processing pith compared to the other plant foods (Fig. 3.6). However, similar to other primate studies the gorilla's opposed thumb involved in the full power grip and distal palm grip did not show the squeeze form of power grip as seen in humans when manipulating cylindrical wooden tools (e.g., humans: Marzke et al., 1992; Marzke, 2013; chimpanzees: Marzke and Wullstein, 1996; bonobos: Bardo, 2016). It is also important to note that the variable postures of the thumb in the power and distal palm grips (i.e., thumb adduction and abduction; Table 3.6) were associated with larger plants stems when processing pith. Counter pressure by the thumb was typically used in forceful hand actions that were coordinated between the mouth and both hands (i.e., mouth-bimanual hand, coordinated asymmetrical hand-use) such as breaking the stem off in length, biting off the hard outer casing and for support against resistance. Such food objects of cylindrical shape were not processed in wild chimpanzees and large food objects are rarely used in captive studies, and

that where large objects have been manipulated they have not elicited the variable thumb postures of these grips in both the wild and captivity (Pouydebat et al., 2009; Marzke et al., 2015).

This high diversity of hand grips elicited in gorilla plant-processing supports Tuttle's (1969) observation, made in his review of captive great ape manipulative behaviour, that more extensive comparative studies of wild apes in their natural environment would be needed because captive primates frequently have very different manipulative strategies.

3.4.3.5 Grip functions for gorilla hand morphology

Gorillas skeletal hand morphology differs somewhat from that of other great apes with a significantly longer thumb relative to the length of their fingers, such that their hand proportions (defined as thumb length relative to length of the fourth digit) are more similar to humans than those of all other great apes (Susman, 1979; Almécija et al., 2015). A relatively longer thumb is thought to enhance opposability to the fingers during grasping (e.g., Napier, 1993; Marzke, 1997) and is usually discussed within the context of human manipulation during the manufacture of stone tools (e.g., Marzke, 1997). Although gorillas have a longer thumb compared to other great apes, (e.g., Susman, 1979), it appears that the thumb is still too short and not able to generate together with the fingers a firm enough balanced pinch grip to resist more than moderate forces dislodging the food objects in stem-and leaf-processing. This probably explains why gorillas never processed plant foods with the thumb held opposed to the tip of the index finger but most frequently used the two-jaw chuck pad-to-side grip in precision grasping. Furthermore, the gorillas' thumb is not long enough to lock with its full length or stabilize against the index finger on larger plant stems as seen in humans when power squeeze gripping (e.g., Napier, 1960; Marzke et al., 1992).

However, the functional role of the thumb is found in the use of the thumb in the majority of grips and in the variable postures of the thumb (Table 3.6). Opposition of the thumb seemed to enhance the effectiveness of extended transverse hook grips during procurement and processing of plant foods. The opposed thumb provides leverage and appeared to enhance the ability to exert force by the hand on

the manipulated plants against resistance by the teeth when the peel is stripped off from stems or by the other hand when stems and vines are pulled into range (Figs. 3.8, 3.10). This cylindrical plant food is regularly lodged in the space between the base of the opposed thumb and the index finger metacarpophalangeal region. The gorilla's opposed thumb is long enough to bridge the space between the side of the index finger and the palm, where it acts as a fulcrum for breaking of the food that lies across the space. A relatively robust first metacarpal in mountain gorillas meets the demands of strong grasping involving the thumb (Hamrick and Inouye, 1995). The incorporation of the opposed thumb and the use of a strong extended transverse hook grip is also frequently used by Virunga gorillas and wild chimpanzees when processing plant food of tough, cylindrical shapes (Byrne, 1994 cited in Marzke et al. 2015; Marzke et al., 2015).

Gorillas and other apes share long and powerful digital flexors that enable strong grip strength (Myatt et al., 2012). Strong power grips and hook grips are important for moving safely within an arboreal environment (e.g., Marzke, 1992; Hunt, 1991; see Chapter 4) and arboreal hook grips also enable fine and forceful manipulation of objects, necessary for stick tool-use (e.g., Lesnik et al., 2015; Bardo, 2016) and elaborate preparation of various food types (e.g., Byrne and Byrne, 1993; Byrne et al., 2001a; Marzke et al., 2015). Therefore, it can be assumed that the powerful digital flexors in apes are associated with the functional versatility of the digits as they reflect the broad range of mechanical demands acting on the hand during arboreal locomotion and manipulative behaviours. This might explain why Bwindi gorillas and other apes use locomotor grips during manipulative behaviours.

The gorilla's thumb and fingers did not precisely maneuver food objects within one hand; reorientation of an object was effected primarily by movements at the wrist and forearm joints, or by transferring the object to the mouth and retrieving it again by the hand in the desired orientation. However, a captive study could recently show that gorillas can perform in-hand movements that involve the thumb and engage the palm when reorienting sticks in a complex tool-use task (i.e., maze-task; Bardo, 2016). Strikingly, in-hand movements were only associated with unimanual hand-use while bimanual coordination was not used at all by these gorillas (Bardo, 2016). It can thus be assumed that in-hand movements are more likely to occur when an individual is using only one hand to accomplish a specific

task. The Bwindi gorillas in this study confirm this suggestion by using a significantly high proportion of bimanual coordination during plant-processing (Table 3.5).

The gorilla's thumb indicates an apparent functional adaptation to variations in requirements for grasp strength, stabilisation and leverage of objects manipulated during plant-processing.

3.4.4 Laterality in hand use during plant-processing

This study provides new insight into laterality in hand use within and across three different plant processing behaviours to understand whether the degree of laterality at the individual-level and group-level will be greater for plants that are considered more complex. The results support this hypothesis by revealing a higher degree of lateralisation for peel-processing than for leaf-processing. These new data provide a comparative context to understand the variation in non-human primate lateralisation across different complex tasks in general, and particularly hand-preference in mountain gorilla plant-processing.

3.4.4.1 Strength of laterality in relation to task complexity

The findings of this study support partially the hypothesis based on the 'task complexity theory', in which complex tasks increase the strength of laterality among individuals and can induce a group-level bias for a right or left hand-preference in non-human primates (Fagot and Vauclair, 1991). Although the most complex behaviour of peel-processing showed the highest degree of lateralisation from all three plants (mean: ABS-HI: 0.46), most gorilla individuals were classified as ambipreferent for both unimanual and asymmetrical hand-use when hand-preference was assessed based on z-scores (see *Appendix III*). This suggests that hand-preference is inconsistent for most individuals as not all functionally-distinct elements of a processing sequence may evoke equal degree of lateral bias. A sequential variation in the degree of laterality could be elicited by simple elements that are more likely performed one-handed or symmetrically with both hands, and by complex elements that require a more frequent use of the dominant hand during bimanual asymmetrical

coordination. This hypothesis finds support in the thistle leaf-processing of Virunga gorillas, for which the degree of laterality increased as the sequence progressed and strongest lateralisation was found in those elements performed unimanually or asymmetrically (Byrne et al., 2001a).

The behaviour of peel-processing appears to be not sufficiently complex to elicit a strong hand-preference in Bwindi gorillas as the more complex task of thistle plant preparation does in Virunga gorillas (Byrne and Byrne, 1991). The majority of individuals were significantly lateralised and often showed exclusive hand-preference for either the right or left hand (i.e., 100 % right- or 100 % left-handed) (Byrne and Byrne, 1991). Most individuals were also lateralised for processing other plants with strong physical defenses such as nettle leaves, celery pith, *Galium* stems and leaves, and most of the gorillas used the dominant hand exclusively for three of the four foods (the exception was *Galium* stems; Byrne and Byrne, 1991). This was not the case for both defended plant stems studied here, which elicited only a moderate strength of laterality (mean ABS-HI: < 0.5 from a maximum of 1.0) and induced no lateral bias at the group level in Bwindi gorillas (Fig. 3.12, see *Appendix III*). This indicates that physical defenses such as herbaceous and woody casings are too weak to elicit strong hand-preferences in plant-processing.

Plant characteristics are likely to be an important factor in the difference between the strength of laterality at Bwindi and Virunga (Byrne and Byrne, 1991, 1993). While a positive correlation between task complexity and laterality (e.g., Fagot and Vauclair, 1988, 1991) was suggested for Virunga gorillas (Byrne and Byrne, 1991), another study on western lowland gorillas at Mbeli Bai, Republic of Congo, showed weak hand-preferences for processing plants without any defenses (Parnell, 2001). This finding confirms my result of a moderately strong laterality in woody plant stems while strong physical defenses (i.e., hooks, stings, spines) evoke strong lateralisation, and as such, their processing might be a suboptimal task for assessing strong hand preferences.

The lack of strong individual laterality may be also due to the relatively low number of hand responses for some subjects (see *Appendix III*) while the lack of group-level bias in all three plants might be due to the small number of subjects included in the study (N=11 gorillas, total of 345 bouts) compared with Virunga gorillas (N=38 gorillas, 720 bouts for thistle leaf alone; Byrne and Byrne, 1991).

Given that non-human primates rarely exclusively use one hand for particular tasks (i.e., relatively low handedness index), larger sample sizes are considered necessary to reliably detect a group-level bias (defined as >65 % of the individuals in the group) as they have substantially greater statistical power (e.g., Marchant and McGrew, 1991; McGrew and Marchant, 1997a; Hopkins and Cantalupo, 2005; Hopkins et al., 2012; Hopkins 2013a, 2013b). This highlights the need for more studies in wild populations of gorillas with a focus on larger sample sizes.

Numerous previous studies have shown that manual laterality depends on the task (e.g., Warren, 1980; Fagot and Vauclair, 1991; McGrew and Marchant, 1997a; Papademetrio et al., 2005). Task complexity has been consistently reported among wild and captive non-human primates and it is generally accepted that the degree and direction of laterality vary according to the task (e.g., Frigaszy and Mitchell, 1990; Byrne and Byrne, 1991; Marchant and McGrew, 1996; Spinozzi and Truppa, 1999; Hopkins and Cantalupo, 2005; Humle and Matsuzawa, 2009; Chapelain et al., 2011; Bardo et al., 2016). This raises important issues because the results thus depend on the task that is used to assess laterality. On the basis of the task-complexity model, precise actions with distinct complementary roles of both hands, such as stone tool-use or particular feeding behaviours, are considered to elicit a greater strength of laterality at the group level than simple one-handed reaching tasks (non-human primates: Byrne and Byrne, 1991; McGrew and Marchant, 1997a; Humle and Matsuzawa, 2009; Salmi et al., 2016; see Chapter 2; humans: Uomini, 2009). The plant-processing tasks studied here would not be considered as complex as nut-cracking in chimpanzees or thistle leaf-processing in Virunga gorillas, because not all hand actions may involve a more frequent use of bimanual asymmetrical coordination and thus, laterality may not as strong to elicit manual specialisation in the majority of individuals. Nevertheless, Bwindi gorillas meet most of the criteria of task complexity in object manipulation, that is to say the several different elements of hand actions organised into a multi-stage sequence of processing, precision grips, bimanual asymmetrical coordination and digit role differentiation.

3.5 Conclusion

This is the first quantitative analysis of hand use of Bwindi mountain gorillas during plant-food processing. Bwindi gorillas revealed a repertoire of 19 elements to process defended plant-stems and undefended leaves, including 11 functionally-distinct elements. Similar to plant feeding by Virunga gorillas, the manipulative actions of Bwindi gorillas were ordered in several key stages and their organisation was hierarchically structured, reflecting trial and error learning as well as a strong cognitive capacity (Byrne et al., 2001a). Foraging Bwindi gorillas employed eight hand-use strategies involving skilful bimanual techniques that are coordinated and asymmetrical. Moreover, the demands of manipulating natural food objects elicited a great variety of hand grips and variable thumb postures, which have not yet been documented in wild foraging gorillas (e.g., Byrne et al., 2001b; Parnell, 2001). A higher degree of lateralisation was elicited for the most complex behaviour of peel-processing but the strength of laterality was only moderate, suggesting that processing thistle plant is a more complex feeding task for wild mountain gorillas (Byrne and Byrne, 1991).

Chapter 4

Comparison of hand use and forelimb mechanics of
vertical climbing in mountain gorillas and chimpanzees

The first half of this chapter has been published in the *American Journal of Physical Anthropology* (see *Appendix IV*). The second half is currently under review in the *Journal of Zoology*.

Abstract

Biomechanical analyses of arboreal locomotion in great apes in their natural environment are scarce and thus, attempts to correlate behavioural and habitat differences with variations in skeletal morphology are limited. The aim of this study was to compare temporal gait characteristics of hand and forelimb use during vertical climbing in mountain gorillas (*Gorilla beringei beringei*) and chimpanzees (*Pan troglodytes* ssp.) to assess differences in the climbing styles that may relate to variation in hand or forelimb morphology and body mass. I investigated hand and forelimb posture coupled with temporal gait parameters and footfall sequences during vertical climbing (both ascent and descent) in 15 wild, habituated mountain gorillas and compared these data to those of eight semi-free-ranging chimpanzees, using video records obtained *ad libitum*. In both apes, forelimb posture was correlated with substrate size during both ascent and descent climbing. Both apes use power grips and a diagonal power grip, involving three different thumb postures. Mountain gorillas showed greater ulnar deviation of the wrist during vertical descent than chimpanzees, and the thumb played an important supportive role when gorillas vertically descended lianas. Both apes generally had the same grip preferences and used similar forelimb postures on supports of a similar size, which is consistent with their overall similarity in hard and soft tissue morphology of the hand and forelimb. However, some species-specific differences in morphology such as ulnocarpal articulation appear to elicit slightly different grasping strategies during vertical climbing between mountain gorillas and chimpanzees. Comparisons of temporal gait parameters revealed that large-bodied gorillas exhibited a longer cycle duration, lower stride frequency and generally a higher duty factor than chimpanzees. This study revealed that mountain gorillas adapt their climbing strategy to accommodate their large body mass in a similar manner previously found in captive western lowland gorillas, and that chimpanzees are less variable in their climbing strategy than has been documented in captive bonobos.

4.1 Introduction

Arboreal locomotor behaviours, although generally practiced infrequently compared to terrestrial locomotion, are critical to the daily life and survival of African apes. In particular, vertical climbing is used to access important food sources (e.g., Remis, 1995; Pilbeam, 2002; Robbins, 2008), to change levels within the forest canopy, to exploit safer substrates for horizontal travel, for safety from predators and for access to sleeping sites (e.g., Hunt, 1992b; Preuschoft, 2002; Thorpe and Crompton, 2006; Garber, 2007). Records of the frequency of arboreal (and terrestrial) locomotor behaviours in wild African apes vary depending on the species and population (e.g., Tuttle and Watts, 1985; Doran, 1993, 1996; Remis, 1995; Crompton et al., 2010). Most studies agree that gorillas are less arboreal than chimpanzees and bonobos (Hunt, 1991b; Crompton et al., 2010; Hunt, 2016). In particular, mountain gorillas (*Gorilla beringei beringei*) are typically considered the least arboreal of all the great apes and are thought to spend less than 1 % of total locomotor time engaging in vertical climbing (Tuttle and Watts, 1985).

Arboreal locomotor behaviours in mountain gorillas has to date only been broadly described and the frequency of arboreality is likely underestimated (Crompton, 2016). One possible explanation for the much lower reported frequency of arboreal locomotion in mountain gorillas compared with western lowland gorillas (e.g., Tutin et al., 1991; Nishihara, 1992; Remis, 1994, 1995; Tutin, 1996) may be differences in habitat structure and resource availability, as these have a substantial influence on gorilla locomotion (Remis, 1995). Most mountain gorilla locomotor data come from the Volcanoes National Park, Rwanda (Doran 1996, 1997). Remis (1999) suggested that the high frequency of terrestrial knuckle-walking exhibited by mountain gorillas at sites like Karisoke in the Virunga mountains represents an adaptation to a high-altitude dwarf forest environment, which likely limits their arboreality (average height climbed in trees <7 m; Fossey, 1983; Watts, 1984; Doran, 1996; Remis, 1998). However, little is known about gorilla arboreal locomotion in this type of environment and thus, the frequency of arboreal locomotor behaviours is generally based on estimates (e.g., Tuttle and Watts, 1985; Crompton et al., 2010).

The mountain gorillas of Bwindi Impenetrable National Park live at lower altitude (1,160-2,607 m; Robbins et al., 2006) with more trees and a denser forest canopy than that of Karisoke. Tree use by gorillas is relatively common at Bwindi when, for example, foraging for fruits (Sarmiento et al., 1996, Robbins, 2008). Studies of feeding behaviours have revealed that Bwindi mountain gorillas climb trees for several months of the year, making use of arboreal fruit resources when they are seasonally available (Ganas et al., 2004; Robbins, 2008; see methods). For example, Bwindi gorillas spent 95 days of 324 observation days eating fruit in trees (29.3 %), including 403 trees and 15 fruit species (Robbins, 2008), supporting recent assertion by Crompton (2016) that the <1 % frequency for vertical climbing reported in mountain gorillas is likely an underestimation. However, to date, vertical climbing in wild mountain gorillas has not been examined in detail.

Arboreal locomotion in chimpanzees, by contrast, is more frequent, spending up to half of their time in trees (Tuttle and Watts, 1985). Chimpanzee habitats are typically located in mid-altitude (e.g., 1500 m; Pontzer and Wrangham, 2004) thicket woodland or tropical montane rainforest habitats with tree heights >30 m (e.g., Stanford and O'Malley, 2008). While several studies investigated different arboreal locomotor behaviours in wild chimpanzees, they were mainly associated with body size effects, musculoskeletal adaptations of the upper body, or their daily energy cost (Hunt, 1991a,b, 1992b, 1994; Pontzer and Wrangham, 2004). The aim of this study is, therefore, to describe for the first time the biomechanics of vertical climbing in mountain gorillas in comparison to chimpanzees, focusing on the hand and forelimb posture coupled with temporal gait parameters.

During arboreal locomotion, and particularly vertical climbing, primates face several biomechanical challenges that often require changes in forelimb and hand posture. For example, the difficulty of maintaining stability increases as substrates get smaller and/or are more inclined because the risk of toppling backwards becomes higher when propulsive forces are placed on the hindlimbs (e.g., Cartmill, 1974; Preuschoft and Witte, 1991; Preuschoft, 2002). Our understanding of the ways in which primates cope with these challenges is largely based on small and medium-sized non-hominoid primates (e.g., mouse lemurs, cotton-top tamarins, lemurs or macaques; ranging from 0.06 to 11 kg; Hirasaki et al., 1993; Nyakatura et al., 2008;

Johnson et al. 2012; Shapiro et al., 2016) and theoretical models (e.g., Cartmill, 1974, 1979; Preuschoft and Witte, 1991; Preuschoft, 2002, 2004). However, the challenges of vertical climbing are amplified for larger-bodied primates, such that, both mechanical challenges and relative energetic costs of climbing increase in primates with a larger body size (Hanna et al., 2008). Larger-bodied primates appear to use their forelimbs mainly in tension and the hindlimbs mainly in compression, both when ascending and descending vertical substrates (Preuschoft, 2002; Hanna et al., 2017). When climbing on large substrates, wild chimpanzees have been observed to extend their elbows (“extended-elbow vertical climbing”) while the forelimbs assist in elevating the body through flexion of the elbow on small substrates (“flexed-elbow climbing”) (Hunt, 1992; Hunt et al., 1996). General similarity in elbow joint morphology among apes is interpreted as an adaptation for elbow stability in varied forelimb postures used during vertical climbing and other forms of arboreal locomotion (e.g., Jenkins, 1973; Rose, 1988, 1993; Drapeau, 2008). The hands are critically important to maintaining stability on differently-sized vertical substrates and providing a counterbalance to the feet (Hirasaki et al., 1993; Nakano, 2002; DeSilva, 2009; Johnson, 2012). Increased friction force between the prehensile hands (and feet) with the substrate (i.e., support phase) is needed when climbing upon vertical supports (Preuschoft, 2002). Although these previous studies demonstrate the importance of the primate forelimbs and hands during vertical climbing and the potential high loads that the hands may experience by gripping vertical substrates, they do not consider the actions that the hands are performing to facilitate this locomotion.

Detailed observations about how the hands grasp substrates during different arboreal locomotor behaviours have been reported in great apes, but these data were mainly obtained in captive settings and are limited, particularly in regards to the functional role of the thumb (Sarmiento, 1988, 1994; Marzke et al., 1992; Alexander, 1994; Marzke and Wullstein, 1996). The short thumb of African apes is not used during knuckle-walking (e.g., Tuttle, 1967; Wunderlich and Jungers, 2009) and its functional importance during arboreal behaviours, particularly during suspensory locomotion, has traditionally been downplayed (Ashely-Montagu, 1931; Straus, 1942; Tuttle, 1967; Rose, 1988; Sarmiento, 1988). However, a preliminary study of

orangutan arboreal locomotion revealed that they recruit the thumb much more often (i.e., more than 53 % of hand postures included thumb use) when grasping arboreal substrates than traditionally believed (McClure et al., 2012).

Among African apes, chimpanzee grips and hand postures have received the most attention. Chimpanzees use power grips, diagonal power grips and diagonal finger hook grips during vertical climbing as well as recruit their thumbs in different postures relative to differently sized substrates (Napier, 1960; Marzke et al., 1992; Alexander, 1994; Marzke & Wullstein, 1996). In contrast, arboreal hand use in gorillas has only once been broadly described in captivity, showing that western lowland gorillas use a more flexed wrist posture on smaller than on larger vertical supports to enable that the hand can wrap around the grasped support (Sarmiento, 1994).

Gorillas have a significantly longer thumb relative to the length of their fingers compared to other great apes (Susman, 1979), such that their hand proportions (defined as thumb length relative to length of the fourth digit) are more similar to humans than those of chimpanzees (Almécija et al., 2015a). A relatively longer thumb is thought to enhance opposability to the fingers during grasping (e.g., Napier, 1993; Marzke, 1997). Enhanced opposability is usually discussed within the context of manipulation (e.g., Marzke, 1997), but the variation in hand proportions, as well as differences in body size, between gorillas and chimpanzees, may also result in different grip and thumb use strategies during vertical climbing. However, there are no studies of which I am aware that have investigated mountain gorilla arboreal hand grips and thumb use, or how grasping posture might vary with forelimb posture during vertical climbing on a wide variety of differently sized natural substrates in gorillas compared with chimpanzees.

Attempts to correlate variations in African ape morphology (e.g., hand or limb proportions, body mass) with behavioural and habitat differences are limited because kinematics (e.g., movement of body segments, gait parameters) of arboreal locomotion, such as vertical climbing, are scarce especially in the wild. A few studies have investigated the spatio-temporal parameters and gait characteristics of vertical climbing in apes and other primates, all of which have been conducted in

captivity (Hirasaki, 2000; Isler 2002, 2003, 2005; Isler and Grueter, 2006; Schoonaert et al., 2016). Within great apes, there is only one naturalistic study that compared the gait parameters of vertical climbing in rehabilitated and wild Sumatran orangutans to captive individuals (Isler and Thorpe, 2003). Captive chimpanzee climbing patterns and limb joint kinematics have been briefly described in a preliminary study by Nakano and colleagues (2006), but gait parameters of fore- and hindlimbs have not been examined. Current knowledge about the spatio-temporal gait characteristics of gorilla vertical climbing stems solely from a captive study using a rope as locomotor support (Isler, 2002). Isler (2002) identified key differences in the gorilla climbing performance associated with the age and sex; vertical climbing in an adult male gorilla was characterised by higher duty factors (i.e., increased contact with the substrate), relatively shorter strides and more variable footfall patterns compared with adult female or juvenile gorillas. Isler (2002) interpreted these kinematic differences as evidence that vertical climbing on a rope was more challenging for adult male gorillas due to their larger body mass. Heavier animals will, in general, exhibit a prolonged support phase or higher duty factor, reflecting a higher energy expenditure relative to muscular strength (Cartmill, 1972, 1974; Taylor et al., 1972; Cartmill and Milton, 1977). However, the vertical climbing ‘characteristics’ in mountain gorillas and chimpanzees within a natural environment have never been investigated, and the potential differences in the climbing style between these two apes that differ significantly in body mass (e.g., Sarmiento, 1994; Smith and Jungers, 1997) are not yet known.

The aim of this study is to provide the first insights into the arboreal locomotor strategies of mountain gorillas and chimpanzees on natural substrates. I investigate hand and forelimb posture as well as gait characteristics during vertical climbing (both ascent and descent). Additionally, in an interspecific comparison with the vertical climbing ‘characteristics’ of other hominoids (Isler, 2002; Isler and Thorpe, 2003; Schoonaert et al., 2016), I explore how mountain gorilla morphology, as well as body mass, might influence their vertical climbing style. First, I predicted that shared features in forelimb morphology and body size within *Gorilla* (females 71.0-97.5 kg; males 162.5-175.2 kg across *G. beringei*, *G. gorilla*, *G. graueri*; Smith and Jungers, 1997) and within *Pan* (females 33.2-45.8 kg; males 42.7-59.7 kg across

P. paniscus and *P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus*; Smith and Jungers, 1997) will elicit similar forelimb postures during vertical climbing between (1) mountain gorillas and western lowland gorillas (Isler, 2002, 2003, 2005), and (2) between chimpanzees and bonobos (Isler, 2002, 2005). Second, I hypothesised that differences in hand and forelimb morphology, as well as body size, between mountain gorillas and chimpanzees will elicit different forelimb postures and grasping strategies on supports of a similar size. Third, I predicted that given the longer thumb length relative to the fingers in mountain gorillas, they will more often oppose their thumbs during grasping than chimpanzees. Fourthly, I hypothesised that vertical climbing of large-bodied mountain gorillas is characterised by longer cycle durations, higher duty factors, lower stride frequencies, a higher number of limbs used as support and less variable footfall patterns compared to smaller-bodied chimpanzees. More specifically, I predicted, following previous research across apes of varying body size (Isler, 2002, 2003, 2005), that mountain gorillas will adapt their climbing strategy to accommodate their large body mass in a similar manner to that documented in captive western lowland and, likewise, vertical climbing of smaller-bodied chimpanzees will be similar to bonobos given their generally similar body size.

4.2 Materials and Methods

4.2.1 Species and study site

Mountain gorillas (*Gorilla beringei beringei*) were observed in the Bwindi Impenetrable National Park (331 km²) in the southwest corner of Uganda (0° 53'1°08'N; 29°35'–29°50'E) and only 25 km away from the Virunga Conservation Area in Rwanda and Democratic Republic of Congo (DRC) (Sarmiento, 1996). Bwindi is an Afromontane forest characterised by a dense forest canopy, steep-sided hills, peaks, and narrow valleys throughout (331 km², elevation 1,160-2,607 m; Robbins et al., 2006). Bwindi has a higher mean annual temperature, greater plant diversity and a greater availability of arboreal fruits compared to the ecological extreme of mountain gorilla range at the Karisoke Research Centre, the best studied part of the Virunga Mountains (e.g., Butynski, 1984; Sarmiento et al., 1996; Robbins and McNeilage, 2003). Thus, the dense forest with fruiting trees make this location ideal for collecting much needed data on hand use during vertical climbing in mountain gorillas. Data were collected on two fully habituated groups of gorillas (Kyagurilo and Bitukura) between October-December 2014 and March-July 2015 during two fruiting seasons.

Chimpanzee (*Pan troglodytes* ssp.) vertical climbing data were collected between August-September 2014 on two colonies of semi-free-ranging chimpanzees at the Chimfunshi Wildlife Orphanage Trust (CWO), Zambia. Each colony was composed of a mixture of wild-born chimpanzees (e.g., from Tanzania, Uganda and Rwanda; Rawlings et al., 2014) and chimpanzees born at the CWO. All studied individuals were living within a natural setting in large outdoor enclosures (25-77 ha). The outdoor enclosures include dry woodland forest and floodplains with enough fruit groves and open grasslands suitable for chimpanzees to roam in a complex natural environment. Observations of chimpanzees were conducted for six hours per day from either outside the fence or from viewing platforms that overlook the forested habitats. Although the Chimfunshi chimpanzees are not wild, the sanctuary offers the ability to get within a much closer observation range within a forest environment than is possible with wild, habituated populations. Given that

hand use and forelimb mechanics during vertical climbing have not yet been studied in chimpanzees beyond preliminary studies in captivity, this location was ideal for collecting data on chimpanzee vertical climbing.

Research was conducted in accordance with guidelines of the Ethics Committee of the School of Anthropology and Conservation at the University of Kent, UK, and the national authorities where the work occurred. Approval and permission to conduct research was granted by the Uganda Wildlife Authority, the Uganda National Council of Science and Technology, and the Chimfunshi Wildlife Orphanage Trust, Zambia.

4.2.2 Data collection

Vertical climbing for any given individual was divided into ‘**sequences**’ and ‘**limb cycles**’. A **sequence** was defined as a continued period of climbing behaviour. A sequence started when the right hindlimb was initially placed in contact with the substrate and stopped if climbing was interrupted by a change of the substrate using another locomotor mode, or by a switch in behaviour such as sitting or feeding. A sequence was generally composed of multiple limb cycles. A **limb cycle** was defined as the interval between touchdown of one limb and the subsequent touchdown of the same limb (i.e., right foot/ hand to right foot/hand).

The mountain gorillas were observed for an average of 4 hours/day. To cope with the low-light conditions in the rainforest, high-definition video was filmed *ad libitum* at a frequency of 50 Hz (HDR-CX240E, Sony, Japan), allowing more light into the camera for high quality video footage. Gorillas (and chimpanzees), as large-bodied primates, tend to climb more slowly (i.e., longer cycle and stance phase durations) than smaller primates (e.g., Polk et al., 2006). As such, even slower video capture frequencies can exceed the minimum sampling rate (Nyquist frequency; Robertson et al., 2004) and prevent aliasing errors (e.g., 5 % as relative error of time-related factors at 30 Hz; Polk et al., 2006). Thus, the frame rate used in this study was sufficient to capture the moment of limb-substrate contact and accurately measure long intervals, such as stance phase duration.

All gorilla climbing sequences were recorded at relatively close range (7 m to ~20 m) during vertical ascent and descent on a sample of 15 individuals across the two study groups, including 10 adult females and five males, the latter including one subadult (6-8 years), one blackback (8-12 years) and three silverbacks (≥ 12 years) (Czekala and Robbins, 2001; Robbins, 2001). Video data also included a form of vertical descent in which the animal is sliding on vertical supports, where both forelimbs move alternately with a hand over hand movement to regulate velocity while both feet remain in contact with the substrate. This submode of vertical descent was classified as ‘fire-pole slide’ (Hunt et al., 1996). The gorillas had the opportunity to climb on various-sized substrates ranging from lianas to extremely large tree trunks. The limited accessibility of most climbing substrates made direct measurements of their circumference difficult. Thus, I grouped substrate size into three categories consistent with previous reports (Napier, 1960; Marzke et al., 1992; Alexander, 1994): (1) medium, when the diameter was approximately 6-10 cm (e.g., lianas, thin trees); (2) large, when the diameter was approximately 11-50 cm (e.g., tree trunks); (3) extra-large, when the diameter was >50 cm (e.g., tree trunks). Neither gorillas nor chimpanzees in this study climbed on small substrates less than 6 cm diameter (e.g., thin lianas, vertical branches). I recorded a total of 75 climbing sequences, containing 231 limb cycles (Table 4.2) on 31 medium, 13 large and 31 extra-large substrates.

It was often difficult to follow gorilla individuals for extended periods of time because the dense understory vegetation often limited visibility and maneuverability, and a minimum of 7 m had to be maintained between the gorillas and the observer to reduce the risk of disease transmission. As such, it was not always possible to video capture the starting moment of every climbing sequence. Hence, 34 sequences were recorded shortly after the starting moment and contain less than four limb cycles.

Similar to the mountain gorillas, the chimpanzees were recorded with high-definition video (50 Hz; HDR-CX240E, Sony, Japan) *ad libitum* at relatively close range (~10 m) from both the ground and viewing platforms. A total of 37 climbing sequences were collected, containing 111 limb cycles, in eight adult chimpanzees (six females, two males) (Table 4.2). Data were collected on substrates of varying sizes, but given that it was a natural environment within a sanctuary, substrates were

limited to tree trunks only. Data were collected on two medium-sized, 23 large and 12 extra-large substrates.

4.2.2 Data analysis

4.2.2.1 Forelimb posture in relation to substrate size during vertical climbing

I investigated the forelimb posture during vertical climbing in relation to the size of the substrate (N=75 sequences in 15 gorillas; N=37 sequences in eight chimpanzees). Hunt and colleagues (1996) described two types of vertical climbing in African apes in relation to substrate size: (1) when climbing on smaller substrates, flexion of the elbow helps to elevate the body ('flexed-elbow' vertical climbing); (2) on larger substrates, the elbow is typically extended throughout the motion cycle ('extended-elbow' vertical climbing). The same categories were used when scoring and analysing the data (Figs. 4.1a, c, 4.2a, c). To reduce the dependence of data points, findings were reduced by pooling sequential observations for each individual in which forelimb posture did not change along a particular substrate size category, following Hunt (1992b). The reduced data set contained N=36 pooled observations in 15 gorillas (N=10 medium-sized substrates; N=11 large substrates, N=15 extra-large substrates) and N=18 pooled observations in eight chimpanzees (N=2 medium-sized substrates, N=8 large substrates, N=8 extra-large substrates). Each individual only contributed one data point within a particular substrate size category. Individuals with missing data points were excluded from statistical analysis.

4.2.2.2 Hand grips and thumb use

Hand grips were investigated during vertical climbing in all 15 gorillas (N=231 limb cycles) and eight chimpanzees (N=111 limb cycles). Hand grips were categorised following previous descriptions in climbing chimpanzees (Napier, 1960; Hunt, 1991; Marzke et al., 1992; Alexander, 1994; Marzke and Wullstein, 1996). My initial categorisation centred on 1) the **power grip**, in which larger substrates are grasped by all five digits and against the entire palm of the hand, 2) the **diagonal**

power grip, in which smaller substrates lie diagonally across the fingers and the palm, and 3) the **diagonal finger hook grip** without the thumb and without active involvement of the palm (e.g., Napier, 1960; Hunt, 1991; Marzke et al., 1992) (see Figures 4.1, 4.2).

I further investigated in detail the role of the thumb during ascent and descent climbing, including different thumb positions in relation to substrate size. Three thumb positions were categorised following previously described climbing grips in chimpanzees (Marzke et al., 1992; Alexander, 1994; Marzke and Wullstein, 1996): (1) thumb held in adduction relative to index finger, (2) thumb held in abduction relative to index, (3) thumb held opposed to index finger, and was either wrapped around the substrate or held in line with the long-axis of the substrate (Figs. 4.1 and 4.2). Thumb posture was examined within a limb cycle for each individual and relative frequencies were calculated. As described above, dependence among data points was reduced by pooling limb cycles for each individual in which thumb posture did not change on a particular substrate size category. The reduced data set contained N=36 pooled observations for 15 gorillas (N=10 medium-sized substrates, N=11 large substrates, N=15 extra-large substrates) and N=18 pooled observations for eight chimpanzees (N=2 medium-sized substrates, N=8 large substrates, N=8 extra-large substrates). Each individual only contributed one data point within a particular substrate size category and individuals with missing data points were not included in the statistical analysis.

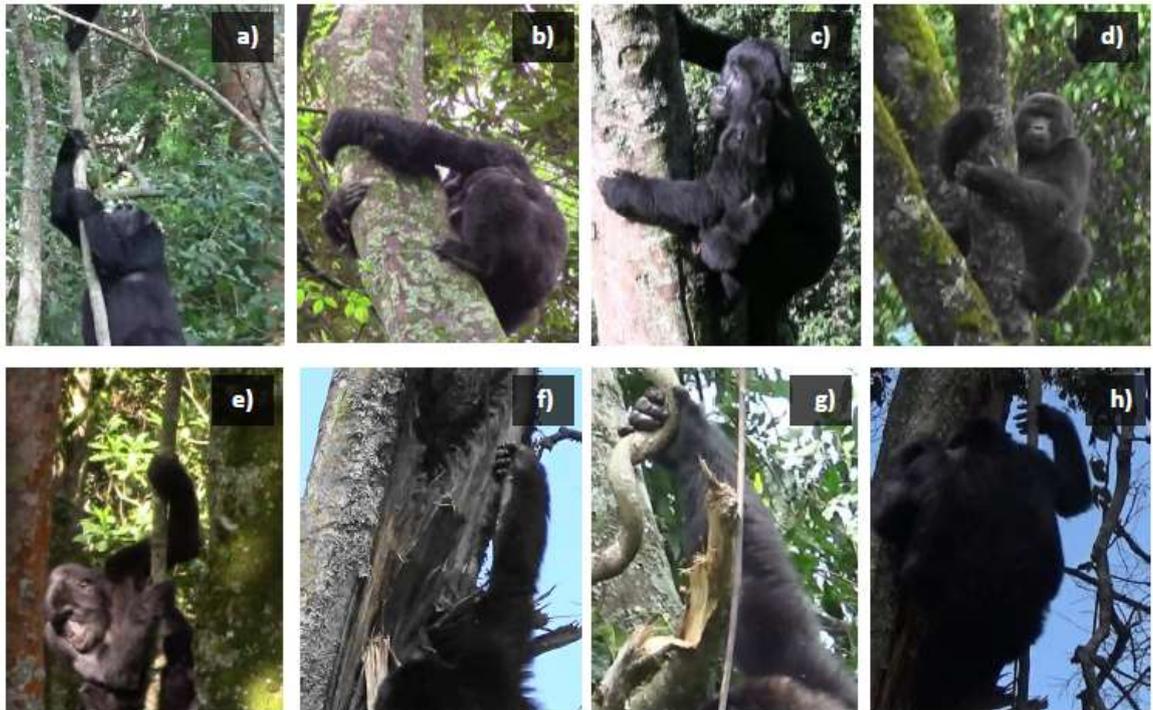


Figure 4.1: Forelimb (a-b) and hand (c-h) postures during vertical climbing in mountain gorillas. (a) Flexed-elbow climbing on medium-sized support and (b) a nearly extended-elbow posture during forelimb-only vertical descent on extra-large substrate in mountain gorillas. Hand grips and variable thumb postures in relation to supports of different size: (c) power grip with the thumb adducted to the index finger typically used on an extra-large substrate; (d) power grip with the thumb abducted from the index finger typically used on large substrates; (e) diagonal power grip with the thumb opposed to the index finger and held in line (right hand), exclusively used on medium-sized substrates; (f) the wrist is deviated in the ulna direction to an extreme degree, bringing the left hand's long axis in the plane of the support's cross section with the thumb held opposed and wrapped around the medium-sized substrate; (g) form of diagonal power grip adjusted to the curved substrate; (h) opposed thumb of the right hand making first contact with the substrate and secure the substrate within the V-shaped region between thumb and extended Index while climbing down the irregular support.



Figure 4.2: Forelimb postures (a-b) and hand grips (c-e) during vertical climbing in chimpanzees. (a) Flexed-elbow climbing on medium-sized support in chimpanzees and (b) extended-elbow climbing on large substrate during vertical descent. Hand grips and variable thumb postures in relation to supports of different diameter: (c) power grip with the thumb adducted to the index finger used on large substrate; (d) power grip with the thumb abducted from the index finger used on large substrate; (e) diagonal power grip with the thumb opposed to the index finger and held in line, exclusively used on medium-sized substrates (left hand).

4.2.2.3 Analysis of gait characteristics

Although the focus of this study is on the forelimb to provide a context for the potential variation in hand posture, I quantified gait characteristics based on both hindlimb and forelimb touchdowns during ascent and descent climbing such that the results were more readily comparable with previous literature. Only those climbing sequences that showed steady movement were retained for further analysis. In the end, analyses included N=120 limb cycles (ascent: 97; descent: 23) for 11 gorillas

and N=80 (ascent: 27; descent: 53) for all eight chimpanzees. In addition, 14 gorillas included N=98 forelimb cycles for forelimb-only vertical descent (Table 4.2).

The footfall sequence and gait parameters such as cycle duration, duty factor and stride frequency were determined by reviewing the video sequences in a slow-motion and frame by frame analyses using free motion software (Kinovea 0.8.15). **Cycle duration** (CD) is defined as the time between two initial contacts with the substrate (or ‘touchdowns’) by the same limb (e.g., Isler, 2002; Isler and Thorpe, 2003). The relative duration of the stance phase, or **duty factor** (S), is the fraction of the cycle duration that a particular limb contacts the substrate (Hildebrand, 1966). **Stride frequency** is the number of strides per unit of time, or $1/CD$ (Schoonaert et al., 2016). The limb cycles were classified as either symmetrical or asymmetrical gaits according to the timing of footfalls, following Hildebrand (1967). **Stride symmetry** was calculated as the percentage of cycle duration separating the time between touchdowns of the right and left hindlimbs (Hildebrand, 1966). A cycle was considered as symmetrical, if the opposing limb’s touchdown occurred between 40 % and 60 % of the cycle duration in order to allow comparison with Isler (2002, 2003, 2005) and Schoonaert et al. (2016). A cycle that was outside of this range (i.e., <40 % or >60 %) was considered as asymmetrical.

Symmetrical cycles were then further classified as being either diagonal sequence (DS) or lateral sequence (LS) gaits. In a **DS gait**, hindlimb touchdown is followed by the touchdown of the opposite forelimb (right hindlimb > left forelimb), whereas in a **LS gait** the ipsilateral forelimb follows (right hindlimb > right forelimb) (Hildebrand, 1966). **Limb phase** (D, also called diagonality) is a quantification of the timing of the footfalls and defined as the duration of time between hindlimb touchdown and touchdown of the ipsilateral forelimb, expressed as a percentage of the stride cycle (Hildebrand, 1966; Cartmill et al., 2002). Thus, LS gaits exhibit lower limb phase values because the ipsilateral forelimb will touch down sooner than in DS gaits. Intermediate between DS and LS gaits are gait sequence patterns in which a forelimb and hindlimb strike at nearly the same time. Thus, DS and LS strides can be further subdivided into five categories: diagonal couplets (DC), lateral couplets (LC), single foot (SF), pace and trot (Hildebrand, 1967) based on the relative timing of touchdown of the limbs (Table 4.1; Figure 4.3).

Finally, I investigated the average number of limbs supporting the animal's body during ascent and descent climbing (i.e., two-limb vs. three-limb support). Limb support was categorised as diagonal, lateral, tripedal or quadrupedal following Vilensky and Gankiewicz (1989) (Table 4.1).

Table 4.1: Definitions of gait sequence patterns and types of limb support.

Gait sequence pattern	Definition
diagonal couplets (DC)	diagonally opposite fore-and hindlimb touchdown at the same time
lateral couplets (LC)	the footfalls on the same body side are evenly spaced in time
single foot (SF)	the footfalls of all the limbs are evenly spaced
pace	the footfalls of the fore- and hindlimb on the same side are evenly spaced
trot	diagonally opposite limbs are evenly spaced in time
Types of limb support	Definition
diagonal pair	support by either combination of diagonal limbs
lateral pair	support by either pair of limbs on the same side
tripedal	support by any combination of three limbs
quadrupedal	support by all four limbs

Gait sequence patterns defined according to Hildebrand (1967) and type of limb support follow definitions by Vilensky and Gankiewicz (1989) and Isler (2002).

Because data were collected in a natural (wild and sanctuary) environment, there was no opportunity to control the location of reference points or the movement of individual subjects. The position of an individual relative to the camera angle varied substantially. Therefore, calibration during data collection was not possible and individual segment lengths could not be reliably estimated from digitized images. Thus, spatio-temporal gait parameters, such as stride length and climbing speed were not included in this study.

4.2.2.4 Statistics

All statistical analyses were run using SPSS (IBM SPSS Statistics for Windows, Version 24.0). An exact binomial test was applied to test the probability of using a particular forelimb posture (50/50 distribution) within each substrate size category. Similarly, we used an exact binomial test to determine the probability of observing a particular thumb posture (50/50 distribution) within each substrate size category. In chimpanzees, both flexed forelimb (N=2) and opposed thumb posture (N=2) used on medium-sized substrates were excluded from analysis due to small sample size. However, since one data point for the same individual may be included in all three substrate categories, the data are not fully independent. Gait parameters were analysed using mean values for all cycles/individual, so that each individual was contributing only a single observation within each condition to ensure independence of data points. A Kolmogorov-Smirnov test was used to check for normality and a Levene's test to assess the equality of variance. Differences in gait parameters between fore- and hindlimbs during vertical ascent vs. descent, including flexed- vs. extended-elbow climbing, were assessed with independent-samples t-tests. In gorillas, differences in forelimb gait parameters between "descent-climbing" vs. "fire-slide pole" were also analysed with independent-samples t-test. Following Isler (2002), significance of inter- and intraspecific (sex classes) differences in the gait parameters between gorillas and chimpanzees was tested using a one-way ANOVA and a *Scheffé's* post-hoc test. The overall sample size was too small to allow more sophisticated statistical tests that would take account for dependency within the data or species, sex, vertical climbing type etc. as fixed effects and the individual as a random effect. Therefore, results of these statistical analyses should be interpreted with caution. Results were considered significant at $p \leq 0.05$.

Table 4.2: Summary of vertical climbing in mountain gorillas and chimpanzees.

Species	Individual	Sex/Age	Total no. of climbing sequences	No. of hindlimb cycles for vertical ascent	No. of hindlimb cycles for vertical descent	No. of limb cycles for forelimb-only vertical descent
<i>G. b. beringei</i>	JN	female/adult	11	17	6	3
	ST	female/adult	11	13	6	2
	KR	female/adult	9	18	-	8
	TN	female/adult	5	10	-	13
	TW	female/adult	7	10	3	19
	MG	female/adult	8	2	8	10
	KG	female/adult	1	-	-	3
	BY	female/adult	5	3	-	6
	TD	female/adult	2	2	-	3
	BT	female/adult	1	-	-	10
	HP	male/subadult	2	-	-	8

	KA	male/blackback	4	7	-	5
	MK	male/silverback	6	12	-	-
	RC	male/silverback	2	3	-	3
	ND	male/silverback	1	-		5
TOTAL			75	97	23	98
<i>P. troglodytes</i> ssp.	RI	female/adult	2	-	6	-
	KB	female/adult	8	12	7	-
	MI	female/adult	11	9	15	-
	KY	female/adult	7	6	6	-
	JU	female/adult	3	-	8	-
	UN	female/adult	4	-	5	-
	TA	male/adult	1	-	4	-
	CO	male/adult	1	-	2	-
TOTAL			37	27	53	-

4.3 Results

4.3.1 Forelimb posture during vertical climbing

Mountain gorillas and chimpanzees employed both flexed-elbow and extended-elbow vertical climbing during ascent and descent. Gorillas always used a flexed-elbow posture on medium-sized substrates and an extended-elbow on large and extremely large substrates (Table 4.3). In gorillas, there was a significant use of a flexed elbow on medium-sized substrates (100 % of 10 sequences, $p=0.002$) (Fig. 4.1a, h) and a highly significant use of an extended elbow on large (100 % of 11 sequences, $p<0.001$) as well as on extra-large substrates (100 % of 15 sequences, $p<0.001$) (Fig. 4.1b).

Table 4.3: Frequency (no. of climbing sequences) of forelimb-posture in relation to total climbing sequences and substrate size.

Species	forelimb-posture	forelimb-posture relative to total climbing sequences	medium-sized substrate	large-sized substrate	extra-large substrate
mountain gorilla	extended-elbow	59 % of total 75	-	29.5 %	70.5 %
	flexed-elbow	41 % of total 75	100 %	-	-
chimpanzee	extended-elbow	92 % of total 37	-	65 %	35 %
	flexed-elbow	8 % of total 37	67 %	33 %	-

"-" denotes absence of forelimb data.

The detailed qualitative observations in the following sections were not possible to quantify and thus, are investigated using frequencies and are described below. During flexed-elbow climbing in mountain gorillas, which was only used on medium-sized substrates, the elbows were flexed and the torso was held nearly parallel to the support (Fig. 4.3a). Flexion of the elbow helped to elevate the body during the push of the hind limbs in ascent climbing, while the elbows were flexed

throughout the support phase until the mid-swing phase (unpooled data set: 100 % of 80 limb cycles), A strongly flexed position of the forelimb was occasionally used in late-swing phase until early-support phase during vertical descent (Fig. 4.1h). Strong horizontal abduction of the upper arm was obtained while reaching upward and at the very end of the support phase in flexed-elbow ascent (unpooled data set: 100 % of 33 limb cycles), when the elbow was already being lifted but the hand was still in contact with the substrate. The elbow was always elevated far above the shoulder (Fig. 4.3a).

During extended-elbow ascent climbing on large substrates, the torso was held roughly parallel to the substrate, while on extra-large substrates, the torso was angled forward such that the shoulders were closer than the hips to the support (Fig. 4.3b). The elbows were never fully extended throughout the motion cycle in both ascent and descent climbing (unpooled data set: 100 % of 151 limb cycles), but were clearly extended enough to allow both hands to control for friction while the feet appeared to experience more of the compressive load. When the hand lifted off the substrate, the humerus was slightly abducted and the elbow was most often elevated to shoulder level (unpooled data set: 81 % of 63 limb cycles) and less often slightly higher than the shoulder (Fig. 4.3b).

Gorillas most often descended trees by sliding downwards using only the forelimbs (14 individuals; 75 % of total descent sequences), in which the forearms were either flexed or extended throughout support and swing phase. The forearms moved alternately in lift-off and touchdown while both hindlimbs remained in contact with the substrate.

Chimpanzees always used a flexed-elbow posture on medium substrates. An extended-elbow posture was used on large and extremely large substrates but flexed-elbow postures were occasionally used on large trees (Table 4.3; Fig. 4.3c). In chimpanzees, there was a significant use of an extended elbow on extra-large substrates (100 % of 8 sequences, $p=0.008$), but the use of a flexed (25 % of 8 sequences) and extended-elbow (75 %) was not significantly different on large substrates ($p=0.289$).

When chimpanzees engaged in flexed-elbow climbing during vertical ascent, flexion of the elbow occurred during the early to mid-support phase until early swing phase (unpooled data set: 100 % of 7 limb cycles; Fig. 4.3c), whereas during extended-elbow climbing, the elbow was extended throughout the motion cycle (unpooled data set: 100 % of 19 limb cycles; Fig. 4.3d). In vertical descent, a flexed elbow posture was used during the mid-swing phase and throughout support phase (unpooled data set: 100 % of 4 limb cycles) while during extended-elbow climbing, extension of the elbow occurred throughout the motion cycle (unpooled data set: 100 % of 78 limb cycles),

Like mountain gorillas, chimpanzees never fully extended the elbow during ascent and descent climbing but (unpooled data set: 100 % of 98 limb cycles), the elbow was clearly extended enough to hold the body away from the support while the hindlimbs pushed-off from the substrate (Fig. 4.3d). Chimpanzees were not observed to slide down tree trunks using only the forelimbs as documented in gorillas.

During both flexed- and extended-elbow climbing, chimpanzees slightly abducted their humerus when the hand lifted off the substrate (Fig. 4.3c, d). Chimpanzees varied in their degree of elbow elevation during both flexed- and extended-elbow climbing on larger substrates; sometimes both elbows would be elevated to shoulder level while at other times, individuals showed asymmetry with one elbow would be elevated to shoulder level and the other reaching slightly above or far above the shoulder (Fig. 4.3c).

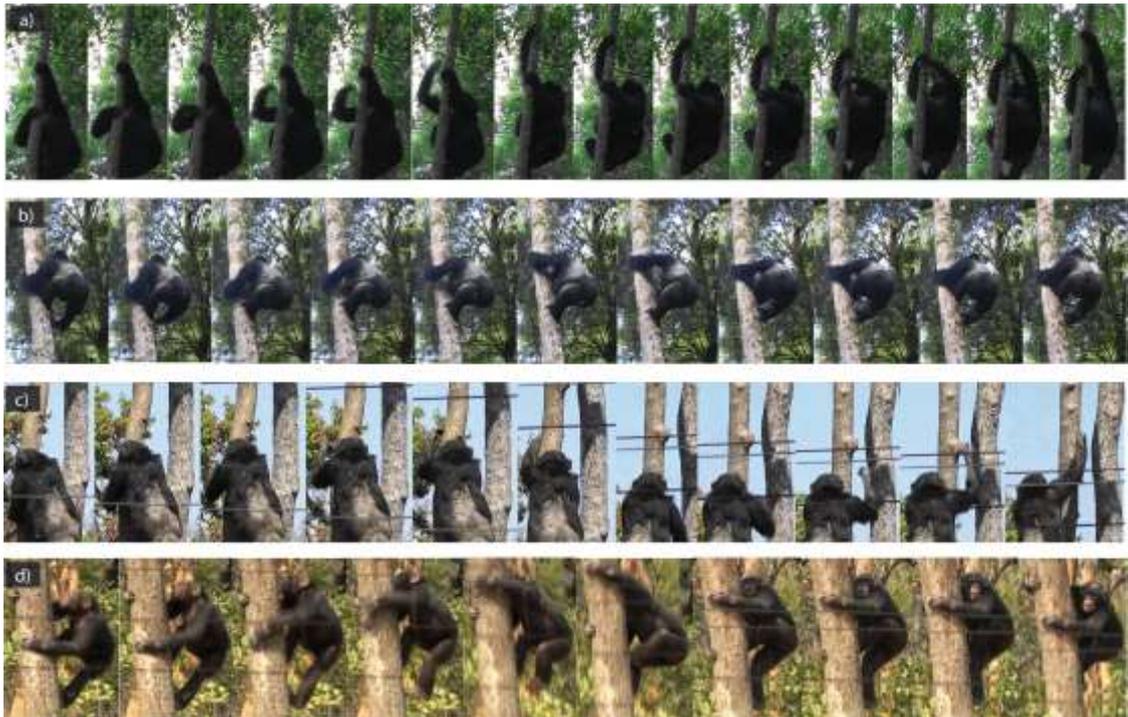


Figure 4.3: Typical vertical climbing sequences of mountain gorillas (a-b) and chimpanzees (c-d). (a) Female gorilla horizontally abducts the upper arm considerably and elevates the elbow far above the shoulder during flexed-elbow climbing on medium-sized support; (b) a silverback abducts the upper arm less of horizontal plane and elevates the elbow to shoulder level during extended-elbow climbing on a large substrate; (c) a female chimpanzee slightly abducts the upper arm and shows forelimb asymmetry in the degree of elbow elevation during flexed-elbow climbing on a large substrate; (d) a female chimpanzee slightly abducts the upper arm and elevates the elbow to shoulder level during extended-elbow climbing on an extra-large substrate.

4.3.2 Hand grips and thumb use

Both mountain gorillas and chimpanzees used a power grip as well as a diagonal power grip during vertical ascent and descent, regardless of whether the elbow joint was flexed or extended (Figures 4.1, 4.2). Gorillas used a power grip only during extended-elbow climbing, a diagonal power grip only during flexed-elbow climbing and both grips during ‘fire-pole slide’ (Fig. 4.1a-c). Chimpanzees used a power grip during both extended- and flexed-elbow climbing while a diagonal power grip was only used during flexed-elbow climbing (Fig. 4.2.a, b). Neither ape was observed to use the diagonal finger hook grip for climbing. Grip use depended upon the size of the substrate; both apes used the power grip only on large and extra-

large substrates and the diagonal power grip only on medium-sized substrates. A power grip was used at high frequency in both gorillas (63 % of total 231 limb cycles) and chimpanzees (95 % of total 111 limb cycles). A diagonal power grip was used relatively frequently in gorillas (37 % of total limb cycles) but rarely in our chimpanzee sample (5 % of total limb cycles) and only on medium-sized substrates (Figs. 4.1.a, 4.2a). Both apes showed significant differences in using a particular thumb posture on differently-sized substrates. Opposition of the thumb was only used when both apes grasped medium-sized substrates in a diagonal power grip and the thumb was most frequently held in line with the long axis of the substrate (Figs. 4.1a and 4.2e; Table 4.4). Gorillas used an opposed thumb significantly more on medium-sized substrates (100 % of 10 data points, $p=0.002$) and both gorillas (100 % of 15 data points, $p<0.001$) and chimpanzees (100 % of 8 data points, $p=0.008$) used an adducted thumb posture significantly more on extra-large substrates (Figs. 4.1c and 4.2b; Table 4.4). Neither ape showed a significant difference between thumb adduction and abduction on large substrates (gorillas: $N=11$, 23 % vs. 73 %, $p=0.227$; chimpanzees: $N=8$, 38 % vs. 63 %, $p=0.727$) (Figs. 4.1d and 4.2d; Table 4.4).

The detailed qualitative observations in the following section were not possible to quantify and thus, are described below. Both apes were observed to ulnarly deviate the wrist (tilting the wrist and hand towards the ulnar side of the forearm) such that the hand's long axis was orientated perpendicular to the substrate with the opposed thumb held either in line or wrapped around the substrate (Figs. 4.1a, 4.2e). Only mountain gorillas ulnarly deviated the wrist to an extreme degree during both vertical descent and 'fire-pole slide' on medium-sized substrates, bringing the hand perpendicular to the vertical substrate with the forelimb approaching a nearly parallel position with the substrate (Fig. 4.1f). Gorillas used two different grasping strategies when climbing lianas, neither of which were documented in the chimpanzees (although they were not observed climbing lianas). The first grasping strategy was used when the individual moved downward along the liana (Fig. 4.1h). During the swing phase of the opposing forelimb, strong ulnar deviation of the wrist allowed the individual to grasp the vertical support within the V-shaped region between the opposed thumb and extended index finger. When

descending lianas of irregular shape, the liana was grasped diagonally across all four fingers and mainly against the thenar area of the palm and proximal phalanx of the thumb (Fig. 4.1g).

Table 4.4: Frequency (no. of limb cycles) of thumb postures in relation to substrate size.

Species	Hand grip	Thumb posture	medium-sized substrate	large-sized substrate	extra-large substrate	total no. of limb cycles
mountain gorilla	Power grip	Thumb adducted to index	-	26 (19 %)	112 (81 %)	138
		Thumb abducted from index	-	10 (100 %)	-	10
	Diagonal power grip	Thumb opposed to index and held in line with long axis of substrate	59 (100 %)	-	-	59
		Thumb opposed to index and wrapped around substrate	24 (100 %)	-	-	24
chimpanzee	Power grip	Thumb adducted to index	-	26 (41 %)	37(59 %)	63
		Thumb abducted from index	-	41 (95 %)	2 (5 %)	43
	Diagonal power grip	Thumb opposed to index and held in line with long axis of substrate	5 (100 %)	-	-	5
		Thumb opposed to index and wrapped around substrate	-	-	-	-

The percentages of the total limb cycles are given in parentheses. "-" denotes absence of thumb data.

4.3.3 Gait characteristics of vertical climbing

I classified the type of gait used by both apes during (1) ascent and descent vertical climbing and (2) flexed-elbow and extended-elbow climbing, based on the timing of footfalls (i.e., including both feet and hands). Mountain gorillas used

diagonal sequence (DS) gaits more often than LS gaits and trot (see Table 4.5; Fig. 4.4) during both vertical ascent and descent, in which each hind footfall was followed by the diagonally opposite fore footfall (LH RF RH LF). Most of these DS gaits were further classified as diagonal couplets, followed by lateral couplets and diagonal sequence single. DS pace occurred less frequently while lateral couples and LS pace were not observed. Chimpanzees showed the opposite pattern, using LS gaits more often than DS gaits and trot (Table 4.5; Fig. 4.4) during both ascent and descent climbing, such that each hind footfall was followed by the ipsilateral fore footfall (LH LF RH RF). Most of these strides were diagonal couplets and single foot. LS pace was not observed in chimpanzees either (Fig. 4.4).

Table 4.5: Frequency of gait sequence patterns in mountain gorillas and chimpanzees.

	Diagonal Sequence Gaits						Lateral Sequence Gaits				
	DS	DC	SF	LC	Pace	Trot	LS	DC	SF	LC	Pace
Mountain gorillas	68 %	42 %	23 %	24 %	11 %	18 %	14 %	59 %	41 %	-	-
Chimpanzees	23 %	33 %	39 %	17 %	11 %	20 %	58 %	59 %	39 %	2 %	-

DS: diagonal sequence, LS: lateral sequence, DC: diagonal couplet, SF: single foot, LC: lateral couplet. Note that the total number of strides was N=120 in gorillas and N=80 in chimpanzees. In gorillas, the number of DS gait types was N=81, trot: N=22 and LS gaits: N=17. In chimpanzees, the number of DS gait types was N=18; trot: N=16 and LS gaits: N=46. Note that ‘**DS**’ and ‘**LS**’ in each category is the total % that both apes used diagonal sequence or lateral sequence gaits while the following categories are the subcategories of each. Same applies for ‘**Trot**’.

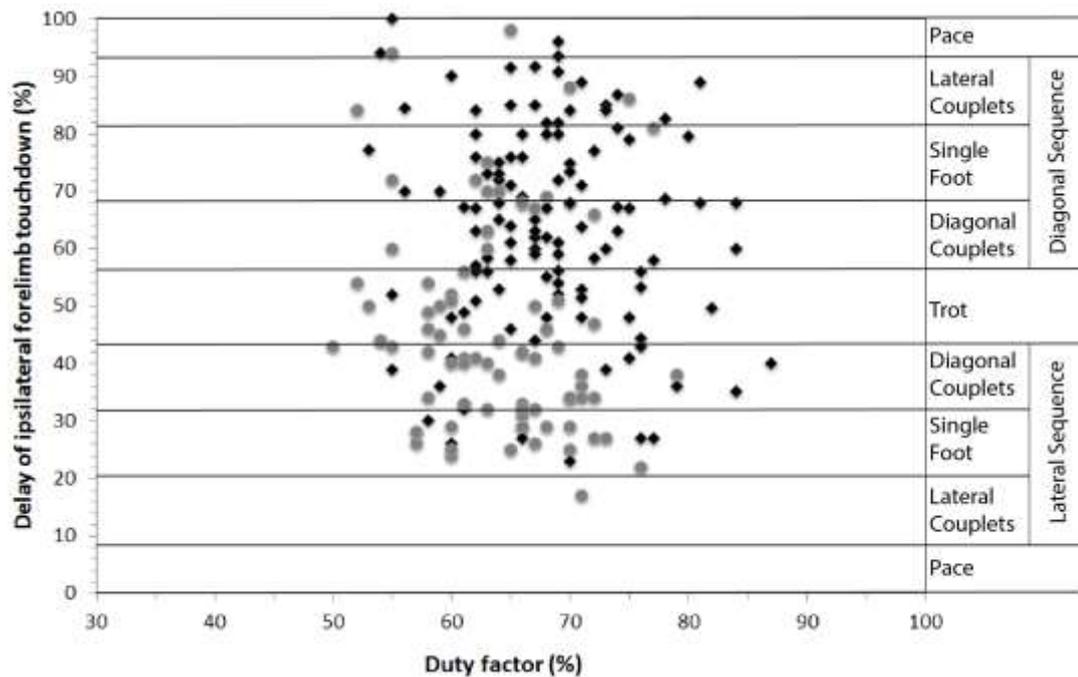


Figure 4.4: Classification of footfall patterns during symmetrical strides of vertical climbing in mountain gorillas (black diamonds) and chimpanzees (grey circles) following Hildebrand (1967). The x-axis shows the duty factor, or relative duration of the stance phase in percent of total cycle duration. The y-axis shows the delay of the ipsilateral forelimb following hindlimb touchdown, as a percentage of total cycle duration. Both mountain gorillas and chimpanzees used lateral and diagonal sequence gaits.

In mountain gorillas, limb phase (i.e., the duration of time between hindlimb touchdown and touchdown of the ipsilateral forelimb, expressed as a percentage of the stride cycle) was significantly higher ($N=11$; mean: 0.62, SD: 0.08; $t(17)=3.59$, $p=0.002$) for most limb cycles (20 cycles: 50-59 %, 30 cycles: 60-69 %, 18 cycles: 80-89 %) than in chimpanzees ($N=8$; mean: 0.46, SD: 0.12; 15 cycles: 20-29 %, 21 cycles: 40-49 %, 14 cycles: 30-39 %), which is consistent with the more frequent use of DS gaits in gorillas and LS gaits in chimpanzees.

In both gorillas and chimpanzees no significant difference in the gait parameters between fore- and hindlimbs during vertical ascent and descent, including flexed-elbow and extended elbow climbing was found (Table 4.6). Thus, all results were pooled for each species. Mean cycle duration and the relative duration of the

support phases (i.e., duty factor) of fore- and hindlimbs of gorillas and chimpanzees are summarized in Table 4.7.

Table 4.6: Independent-samples t-test of gait parameters between fore- (RF) and hindlimbs (RH) during vertical ascent and descent.

RF vs. RH during vertical ascent			
Species	cycle duration	stride frequency	duty factor
Mountain gorillas (N=10)	t(22)=0.21, p=0.834	t(22)=0.16, p=0.871	t(24)=-0.25, p=0.8
Chimpanzees (N=3)	t(4)=-1.71, p=0.873	t(4)=0.00, p=1.00	t(4)=1.98, p=0.119
RF vs. RH during vertical descent			
Species	cycle duration	stride frequency	duty factor
Mountain gorillas (N=4)	t(8)=-1.4, p=0.194	t(8)=-5.78, p=0.571	t(8)=0.51, p=0.63
Chimpanzees (N=8)	t(19)=0.35, p=0.728	t(18)=-0.2, p=0.82	t(14)=-1.53, p=0.88

Table 4.7: Cycle duration and duty factor of vertical ascent and descent in mountain gorillas and chimpanzees.

Species	Individual	Sex/ Age	No. of limb cycles (hind/fore)	Cycle duration Hindlimb (sec)	Cycle duration Forelimb (sec)	Duty factor Hindlimb (%)	Duty factor Forelimb (%)
<u>Vertical ascent</u> <u>extended-elbow climb</u>							
<i>G. b. beringei</i>	JN	Female adult	12/12	1.93 (0.20)	1.87 (0.32)	66 (0.04)	69 (0.04)
	ST	Female adult	13/11	2.76 (0.61)	2.49 (0.68)	70 (0.09)	69 (0.07)
	KR	Female adult	18/18	2.32 (0.54)	2.32 (0.52)	63 (0.04)	68 (0.05)
	TN	Female adult	10/10	2.04 (0.54)	2.45 (0.87)	71 (0.06)	72 (0.07)
	TW	Female adult	10/10	2.37 (0.38)	2.48 (0.58)	68 (0.09)	69 (0.06)
	BY	Female adult	3/3	2.22 (0.08)	2.10 (0.15)	68 (0.02)	71 (0.05)
	TD	Female adult	2/2	3.41 (0.53)	2.96 (0.74)	69 (0.09)	73 (0.08)
	KA	Male blackback	7/7	3.03 (0.53)	2.63 (0.16)	76 (0.06)	71 (0.05)
	MK	Male silverback	10/8	2.26 (0.71)	2.50 (1.65)	72 (0.04)	66 (0.05)
	RC	Male silverback	3/3	2.19 (0.35)	1.93 (0.13)	65 (0.05)	71 (0.03)
<i>P. troglodytes</i> ssp.	KB	Female adult	7/7	1.82 (0.38)	1.82 (0.21)	68 (0.05)	63 (0.07)
	MI	Female adult	9/8	1.73 (0.78)	1.73 (0.72)	65 (0.08)	59 (0.04)
	KY	Female adult	6/5	1.90 (0.47)	1.94 (0.67)	69 (0.07)	66 (0.09)
<u>flexed-elbow climb</u>							
<i>G. b. beringei</i>	JN	Female adult	5/5	2.35 (0.13)	2.35 (0.22)	64 (0.03)	64 (0.04)
	MG	Female adult	2/2	1.86 (0.14)	1.76 (0.21)	72 (0.03)	68 (0.00)
	MK	Male silverback	2/2	2.22 (0.30)	3.39 (0.72)	71 (0.03)	69 (0.01)
<u>Vertical descent</u> <u>extended-elbow climb</u>							
<i>G. b. beringei</i>	JN	Female adult	4/3	1.65 (0.24)	2.49 (1.40)	66 (0.03)	65 (0.05)
	KG	Female adult	0/3	n/a	3.35 (1.29)	n/a	69 (0.11)
	ST	Female adult	6/6	2.62 (0.76)	4.53 (0.93)	71 (0.04)	76 (0.04)

			0/2	n/a	1.24 (0.01)	n/a	61 (0.03)
	KR	Female adult	0/8	n/a	1.75 (0.52)	n/a	58 (0.11)
	TN	Female adult	0/13	n/a	1.98 (1.08)	n/a	58 (0.13)
	TW	Female adult	3/3	4.34 (3.02)	3.35 (1.91)	69 (0.07)	71 (0.08)
			0/19	n/a	2.74 (1.79)	n/a	68 (0.11)
	MG	Female adult	8/8	2.40 (0.70)	3.50 (1.59)	66 (0.06)	65 (0.11)
			0/10	n/a	3.38 (1.47)	n/a	69 (0.10)
	BY	Female adult	0/6	n/a	3.13 (1.31)	n/a	74 (0.07)
	TD	Female adult	0/3	n/a	2.21 (0.86)	n/a	57 (0.11)
	BT	Female adult	0/10	n/a	2.31 (0.34)	n/a	75 (0.07)
	HP	Male subadult	0/8	n/a	1.14 (0.16)	n/a	52 (0.06)
	KA	Male blackback	0/5	n/a	1.25 (0.21)	n/a	65 (0.08)
	RC	Male silverback	0/3	n/a	1.93 (0.13)	n/a	71 (0.03)
	ND	Male silverback	0/5	n/a	2.32 (0.79)	n/a	60 (0.10)
<i>P. troglodytes</i> ssp.	RI	Female adult	6/6	1.43 (0.38)	1.56 (0.55)	61 (0.09)	61 (0.08)
	KB	Female adult	12/12	1.83 (0.71)	1.78 (0.43)	66 (0.11)	62 (0.08)
	MI	Female adult	15/15	1.40 (0.31)	1.48 (0.34)	64 (0.06)	67 (0.07)
	KY	Female adult	6/6	1.60 (0.32)	1.71 (0.33)	65 (0.04)	65 (0.08)
	JU	Female adult	8/6	1.38 (0.20)	1.40 (0.15)	62 (0.03)	63 (0.07)
	UN	Female adult	5/5	1.81 (0.33)	1.55 (1.60)	68 (0.02)	68 (0.03)
	TA	Male adult	4/4	1.34 (0.14)	1.45 (0.18)	61 (0.02)	58 (0.03)
	CO	Male adult	2/2	1.23 (0.00)	0.94 (0.04)	62 (0.17)	58 (0.05)
<u>flexed-elbow climb</u>							
<i>G. b. beringei</i>	JN	Female adult	2/2	2.42 (0.52)	4.75 (0.47)	73 (0.00)	71 (0.01)
<i>P. troglodytes</i> ssp.	JU	Female adult	2/2	1.28 (0.18)	1.22 (0.47)	68 (0.06)	66 (0.16)
	UN	Female adult	2/2	1.62 (0.30)	1.87 (0.08)	55 (0.04)	68 (0.02)

There were no significant differences in forelimb (and hindlimb) cycle duration, duty factor and stride frequency between males and females within both gorillas and chimpanzees (Table 4.8). Interspecifically, however, significant variation was found across all gait parameters (Fig. 4.5). Overall, gorillas (i.e., sexes pooled) showed a significantly longer cycle duration (N=11, mean: 2.7, SD: 0.8; ANOVA, $F(3)=9.52$, $MSE=1.45$, $p=0.001$) than chimpanzees (N=8, mean: 1.6, SD: 0.3) (Fig. 4.5). Cycle duration was significantly longer in female gorillas (mean: 2.7, SD: 0.9) than in female (mean: 1.6, SD: 0.2) and male (mean: 1.3, SD: 0.4) chimpanzees (Table 4.8). In contrast, male gorillas had a significantly longer cycle duration (mean: 2.4, SD: 0.4) than male chimpanzees but not compared to female chimpanzees (Table 4.8).

The duty factor was significantly higher in gorillas overall (N=11, mean: 69 %, SD: 3; ANOVA, $F(3)=5.71$, $MSE=53.16$, $p=0.009$) than in chimpanzees (N=8, mean: 63 %, SD: 3.6) (Fig. 4.5). The duty factor was significantly different between female gorillas (mean: 70 %, SD: 3) and female (mean: 63 %, SD: 3) and male (mean: 58 %, SD: 0) chimpanzees (Table 4.8). Similarly, male gorillas showed a significantly higher duty factor (mean: 69 %, SD: 2.9) than female and male chimpanzees (Table 4.8). In both apes, the duty factor was most frequently between 60-69 % (gorillas: 65 limb cycles; chimpanzees: 42 limb cycles), but in gorillas the duty factor was higher for more limb cycles (36 limb cycles: 70-79 %, 8 cycles: 80-89 %) than in chimpanzees (18 limb cycles: 70-79 %) (Fig. 4.4).

The stride frequency was significantly lower in gorillas overall (N=11, mean: 0.40, SD: 0.11; ANOVA, $F(3)=22.16$, $MSE=0.12$, $p<0.001$) compared to chimpanzees (N=8, mean: 0.65, SD: 0.13) (Fig. 4.5). Interspecific differences showed that female gorillas exhibited a significantly lower stride frequency (mean: 0.38, SD: 0.12) than female (mean: 0.62, SD: 0.14) and male chimpanzees (mean: 0.78, SD: 0.04) (Table 4.8). Male gorillas similarly had a significantly lower stride frequency (mean: 0.43, SD: 0.03) than female and male chimpanzees (Table 4.8).

Table 4.8: *Scheffé's* post-hoc tests of gait parameters in mountain gorillas and chimpanzees.

Intraspecific	cycle duration	stride frequency	duty factor
female vs. male gorillas (N=10)	p=1.000	p=0.999	p=0.566
female vs. male chimpanzees (N=8)	p= 0.888	p=0.287	p=0.811
Interspecific	cycle duration	stride frequency	duty factor
female gorillas vs. female chimpanzees	p<0.001	p=0.001	p=0.002
female gorillas vs. male chimpanzees	p=0.003	p<0.001	p<0.001
male gorillas vs. female chimpanzees	p=0.075	p=0.004	p=0.040
male gorillas vs. male chimpanzees	p=0.005	p=0.001	p=0.003

The results show a significant difference in cycle duration between “vertical descent climbing” (N=6) using both forelimbs and hindlimbs, and the “fire-pole slide” (N=11) used by gorillas. Forelimb cycle duration was significantly longer ($t(15)= 4.07$, $p=0.001$) in descent climbing (mean: 3.4, SD: 0.83) than fire-pole slide (mean: 2.1, SD: 0.75). The duty factor ($t(15)= 1.68$, $p=0.112$) was similarly high between both modes (vertical descent climbing, mean: 69 %, SD: 5.3; fire-pole slide, mean: 65 %, SD: 7.5) and stride frequency ($t(15)= -1.5$, $p= 0.151$) was also not significantly different between vertical descent climbing (mean 0.4, SD: 0.18) and fire-pole slide (mean: 0.5, SD: 0.19).

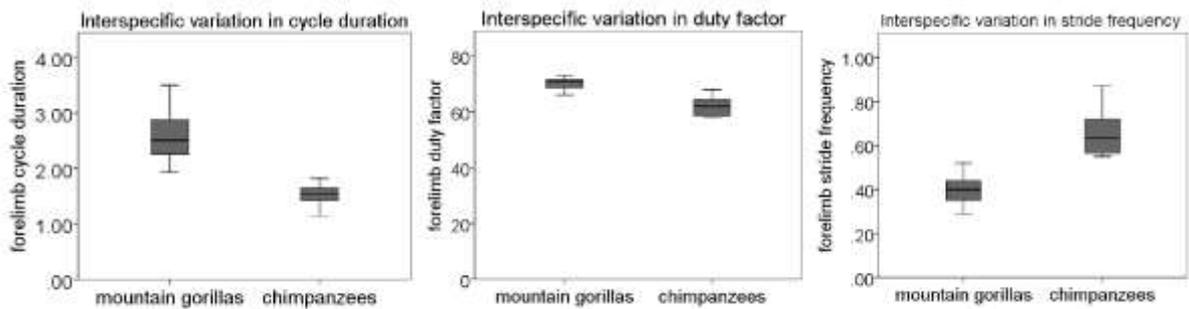


Figure 4.5: Box-and-whisker plots of interspecific variation in forelimb cycle duration, duty factor and stride frequency between mountain gorillas and chimpanzees. These differences were significant.

The types of limb support used during both vertical ascent and descent in gorillas and chimpanzees are summarized in Table 4.9. The average number of supporting limbs was not significantly different between mountain gorillas (N=4, limbs: 2.7, SD: 0.4) and chimpanzees (N=8, limbs: 2.6, SD: 0.3) for vertical ascent ($t(10) = -0.29$, $p=0.774$) as well as for vertical descent (gorillas: N=11, limbs: 2.4, SD: 0.05; chimpanzees: N=3, limbs: 2.4, SD: 0.1; $t(12) = 0.46$, $p=0.809$). Both apes used on average three limbs as support more frequently during vertical ascent than during descent.

Table 4.9: Limb support during vertical ascent and descent in mountain gorillas and chimpanzees.

Species	Individual	Sex/Age	Total no. of hindlimb cycles (100%)	D	L	T	Q	Mean no. of supp. limbs
<u>Vertical ascent</u> <i>Gorilla beringei b.</i>	JN	Female adult	17	3 (17.6%)	1 (5.9%)	12 (70.6%)	1 (5.9%)	2.8
	ST	Female adult	13	3 (23.1%)	4 (30.8%)	6 (46.2%)	0 (0.0%)	2.5
	KR	Female adult	18	3 (16.7%)	0 (0.0%)	15 (83.3%)	0 (0.0%)	2.8
	TN	Female adult	10	2 (20.0%)	1 (10.0%)	7 (70.0%)	0 (0.0%)	2.7
	TW	Female adult	10	0 (0.0%)	0 (0.0%)	60 (60%)	40 (40%)	3.4
	MG	Female adult	2	0 (0.0%)	0 (0.0%)	2 (100%)	0 (0.0%)	2.0
	TD	Female adult	2	2 (100%)	0 (0.0%)	0 (0%)	0 (0.0%)	2.0
	BY	Female adult	3	2 (66.7%)	0 (0.0%)	1 (33.3%)	0 (0.0%)	2.3
	KA	Male subadult	7	0 (0.0%)	0 (0.0%)	7 (0.0%)	0 (0.0%)	3.0
	MK	Male silverback	12	0 (0.0%)	2 (16.7%)	10 (83.3%)	0 (0.0%)	2.8
	RC	Male silverback	3	0 (0.0%)	0 (0.0%)	3 (100%)	0 (0.0%)	3.0

<i>Pan troglodytes ssp.</i>	KB	Female adult	7	2 (28.6%)	1 (14.3%)	4 (57.2%)	0 (0.0%)	2.6
	MI	Female adult	12	1 (8.3%)	5 (41.6%)	6 (50.0%)	0 (0.0%)	2.5
	KY	Female adult	6	0 (0.0%)	2 (33.3%)	4 (66%)	0 (0.0%)	2.7
<u>Vertical descent</u>								
<i>Gorilla beringei b.</i>	JN	Female adult	6	1 (16.7%)	2 (33.3%)	3 (50.0%)	0 (0.0%)	2.4
	ST	Female adult	6	4 (66.7%)	1 (16.7%)	1 (16.7%)	0 (0.0%)	2.4
	TW	Female adult	3	0 (0.0%)	2 (66.7%)	1 (33.3%)	0 (0%)	2.3
	MG	Female adult	8	5 (62.5%)	0 (0.0%)	3 (37.5%)	0 (0%)	2.4
<i>Pan troglodytes ssp.</i>	RI	Female adult	8	3 (37.5%)	2 (25%)	3 (37.5%)	0 (0%)	2.4
	KB	Female adult	7	0 (0%)	3 (42.8%)	4 (57.2%)	0 (0%)	2.6
	MI	Female adult	16	1 (6.3%)	5 (31.3%)	10 (62.5%)	0 (0%)	2.6
	KY	Female adult	5	0 (0%)	0 (0%)	5 (100%)	0 (0%)	3.0
	JU	Female adult	8	5 (62.5%)	0 (0%)	3 (37.5%)	0 (0%)	2.4
	UN	Female adult	5	2 (40%)	1 (20%)	2 (40%)	0 (0%)	2.4
	TA	Male adult	4	2 (50%)	2 (50%)	0 (0%)	0 (0%)	2
	CO	Male adult	2	0 (0%)	2 (100%)	0 (0%)	0 (0%)	2

4.4 Discussion

This study provides the first insights into mountain gorilla and chimpanzee hand use, forelimb mechanics and temporal gait characteristics during both ascent and descent vertical climbing in a natural environment. These new data, although sample sizes are small, provide greater insight into the potential range of grasping strategies that are capable with a given bony and muscular morphology in African apes, and generally provides a better understanding of the postural and biomechanical adaptations for vertical climbing in large-bodied primates.

4.4.1 Forelimb posture during vertical climbing

Mountain gorillas have the largest body mass among living primates (e.g., Sarmiento, 1994; Smith and Jungers, 1997) and thus locomotion and maintaining stability in a complex three-dimensional arboreal environment poses considerable challenges. I found partial support for the first prediction that similar forelimb morphology and body size within *Gorilla* and *Pan* would elicit similar forelimb postures (1) between mountain gorillas and western lowland gorillas and (2) between chimpanzees and bonobos (Isler 2002, 2003, 2005).

Although mountain gorillas used extended-elbow climbing more often (59 % of total 75 sequences) on both extra-large and large tree trunks than on medium-sized substrates, they relatively frequently (41 % of total sequences) engaged in flexed-elbow climbing, exclusively on medium-sized tree trunks (Fig. 4a,e). The mountain gorillas commonly entered and left large trees by climbing on medium-sized vertical substrates (69 % of total 26 instances). When ascending vertical supports, flexion of the elbow joint appears to help pull the body upwards during the mid-support phase, and keeps the body positioned close to the substrate throughout the support phase, while the gorilla's strong muscular hindlimbs (Zihlman et al., 2011) provide most of the propulsive power and push against the substrate in the mid-support phase. Similar to previous reports, the flexed forelimb posture stabilizes the upper body against backward rotation caused by the propulsive force of the hindlimbs (Hunt, 1991,

1992). As the demands are particularly high in flexed-elbow vertical climbing (Isler, 2005), mountain gorillas likely show, like all other apes, adaptations for large force production in the elbow flexors for pulling-up (Myatt et al., 2012) and have forearm flexor muscles that are nearly four times as large as in cursorial mammals (Alexander et al., 1981). Therefore, differences in the elbow joint morphology between mountain and lowland gorillas (Inouye, 2003) does not appear to inhibit the mountain gorilla's ability to climb safely upon medium-sized substrates. Western lowland gorillas in captivity also used flexion of the elbow to help elevate and stabilize the body when climbing up a vertical rope (see Figs. 3 and 4 in Isler, 2003). The mountain gorillas in our study occasionally used a stronger flexed forelimb posture when descending lianas (Fig. 4.1h) compared with ascent on smaller-diameter trees (Fig. 4.1a,e), bringing the torso even closer to the compliant support and providing greater stability against the potentially high gravitational pull of the heavy body.

Furthermore, I observed that mountain gorillas abduct the humerus considerably during the process of reaching upward for the next grip during flexed-elbow climbing, elevating the elbow far above the shoulder. Isler (2002, 2003, 2005) noted a similar forelimb posture in captive western lowland gorillas. The abduction of the forelimb during climbing is consistent with interpretations of the gorilla's forelimb anatomy to accommodate shoulder joint mobility for vertical climbing and reaching while maintaining joint stability during terrestrial quadrupedal locomotion (Zihlman et al., 2011).

The semi-free-ranging chimpanzees in this study used a flexed-elbow posture on smaller substrates, similar to that previously described in captive bonobos (Isler, 2005). However, unlike bonobos ascending a vertical rope, the chimpanzees did not abduct their humerus at the very end of the forelimb's support phase and varied in their degree of elbow elevation when ascending larger substrates (Fig. 4.3c,d). Similar to my observations, wild and captive chimpanzees have been observed to elevate the arm only slightly higher above shoulder level (Hunt, 1991b, 1992; Nakano et al., 2006) while humeral abduction has been documented in a study on scapulohumeral muscle function in captive chimpanzees during vertical climbing (Larson and Stern, 1986). Variations in the degree of elbow elevation in this chimpanzee sample may be related to speed modulation, if the speed increase were to

be achieved more through an increase in forelimb stride length than through an increase in stride frequency (Isler, 2005). Comparisons to captive bonobo vertical climbing suggest that chimpanzees may abduct their humerus less of horizontal plane, which may reflect a slower climbing speed as found in male bonobos (Isler, 2002). However, chimpanzees are adapted for highly abducted arm postures just like all other arboreal apes, based on shared features in joint morphology and muscular anatomy of the shoulder (for circumduction), elbow (rotation), and wrist (adduction) (e.g., Tuttle, 1969; Larson, 1998; Chan, 2008; Preuschoft et al., 2010; Zihlman et al., 2011; Myatt et al., 2012). Whether forelimb joint excursions increase with climbing speed in chimpanzees and other apes requires further testing as, at present, there are insufficient data on spatio-temporal gait parameters in primates to clarify this issue.

The prediction that, due to differences in forelimb morphology and body mass, there will be differences in forelimb posture on similarly-sized substrates between mountain gorillas and chimpanzees was only partially supported. Mountain gorillas only used flexed-elbow climbing on smaller substrates, while chimpanzees flexed their elbows on both smaller and larger substrates (Fig. 4.3). However, the chimpanzees in this sample climbed on trees of a lower diameter range (11-50 cm; see Methods), while Hunt and colleagues (1996) suggested that a substrate diameter larger than 20 cm is more likely to evoke extended-elbow climbing in chimpanzees. Similarly, both apes abducted the humerus less of horizontal plane and showed a lower degree of elbow elevation during ascent on larger-sized substrates (Fig. 4.3b,d). Finally, mountain gorillas commonly slid down vertical supports while this strategy of descending trees was not observed in the chimpanzees of this sample and appears not to be used in other adult chimpanzee populations either (Table 3 in Sarringhaus, 2014).

The variation documented here in mountain gorilla and chimpanzee forelimb postures on different sized substrates, as well as differences in forelimb joint excursions, needs to be tested on a larger comparative data set including more individuals and substrate types to see if these patterns still hold. Furthermore, 3D kinematic analyses in a natural environment, although challenging, would provide more detailed insight into the biomechanical strategies used by large-bodied apes.

4.4.2 *Hand use and the role of the thumb during vertical climbing*

Both mountain gorillas and chimpanzees most frequently used a power grip only on larger substrates and less often a diagonal power grip, which was used only on medium-sized substrates during ascent and descent climbing. This result is consistent with previous reports on chimpanzees grasping locomotor supports of different sizes (Napier, 1960; Hunt, 1991a; Marzke et al., 1992; Alexander, 1994; Marzke and Wullstein, 1996). In both apes, the power grip was used during extended-elbow climbing while a diagonal power grip was used during flexed-elbow climbing. Gorillas also used both grips when sliding down tree trunks (which was not documented in chimpanzees). Neither ape was documented using a diagonal finger hook grip for climbing, although this grip has been reported in climbing chimpanzees to be typically used on smaller substrates, which were not used in this study (e.g., Marzke et al., 1992). Mountain and lowland gorillas use hook grips during food processing and stick tool-use (Byrne et al., 2001; Bardo, 2016; Chapter 3) but whether they are capable of using this hand posture during arboreal locomotion to support their large body mass is not yet known. Their large body mass typically limits the gorilla's substrate choice to larger and more robust substrates (Reynolds, 1969; Remis, 1998), which also limits their arboreal grip repertoire. Lowland gorilla phalanges are shorter and straighter than those of chimpanzees (Stern et al., 1995; Patel and Mailino, 2016) and assuming mountain gorillas are the same (Matarazzo, 2008), this morphology may place greater restrictions on the grasping postures that can be used on smaller substrates (i.e., vines, thin branches), especially for large-bodied mountain gorillas. Further investigation of grasping on smaller natural substrates is needed, in all species of gorillas, to understand the full repertoire of available hand postures in an arboreal environment.

However, as Alba and colleagues (2003) pointed out, although non-human primate locomotor patterns and manual dexterity are not necessarily functionally exclusive behaviours, the selective pressures they place on hand morphology are frequently in opposition. On one hand, highly specialised locomotor modes such as forelimb-dominated climbing and ricochetal brachiation of gibbons favours long hand proportions functioning as a grasping hook during suspension and/or climbing that is considered to be less suitable for manipulative functions (Susman, 1979;

Inouye, 1992). On the other hand, hand morphology can also represent a compromise between diverse locomotor and manipulative functions as seen in African apes (Preuschoft and Chivers, 1993). This becomes particularly apparent in the less curved finger phalanges of the gorilla hand, which appear to allow only power and diagonal power grips to accommodate the higher forelimb mechanics of climbing compared to chimpanzees but enable gorillas to use hook grips for the weaker demands of plant-processing (Chapter 3). The present results, thus, only partly support a functional link between diet and hand morphology than has been previously hypothesized (Marzke, 2006; Moya-Sola et al., 2008; Marzke et al., 2015). The external forces of vertical climbing are considered to be much higher compared to feeding behaviours (Preuschoft and Chivers, 1993; Jouffroy et al., 1991) and thus, likely place greater selective pressures on hand anatomy that might have laid the basis for forceful manipulations during processing food and stone tool-use.

Although the frequency of vertical climbing is lower in mountain gorillas than in chimpanzees and other hominoids, all hominoids retain arboreal features in their hand and forelimb due to the selective advantage of being able to ascent and descent arboreal substrates of variable size and compliance effectively and safely (gorillas: Taylor, 1997; hominoids: Larson, 1998). Indeed, while species-specific differences in morphology between gorillas and chimpanzees appear to elicit slightly different grasping strategies during vertical climbing (e.g., loss of ulnocarpal articulation of the wrist in gorillas vs. reduction in chimpanzees; Tuttle, 1969; Lewis 1989), general similarity in hard and soft tissue morphology of the hand and forelimb (i.e., long and powerful digital flexors; Schultz, 1969; Myatt et al., 2012) allow both apes to use the same grip preferences and similar forelimb postures on supports of a similar size. Despite gorillas phalanges being less curved than that of chimpanzees, they are more curved on average than the straight phalanges of humans and thus, their morphology would still reduce strain when grasping medium-sized substrates (Deane and Begun, 2008; Patel & Maiolino, 2016; Richmond, 2007; Nguyen et al. 2014). However, the mountain gorilla's ability to ulnarly deviate the wrist to an extreme degree (Tuttle, 1969) appears to be particularly valuable when descending medium-sized supports, as the hand can fully wrap around the vertical support in a firm diagonal-power grip (Fig. 4.1f). Although this high range of ulnar deviation was

not observed in this sample of climbing chimpanzees, ulnar deviation of the wrist is also used by chimpanzees on smaller-diameter vertical supports (e.g., Sarmiento, 1988; Marzke et al., 1992). Furthermore, chimpanzees (mean: 71 degrees) are capable of a similar degree of wrist adduction as western lowland gorillas (mean: 70 degrees; Tuttle, 1969), and potentially mountain gorillas. The ulnar side of the hand appears to provide the strongest friction against the downward pull of gravitational force, which is consistent with Susman's (1979) observations of ape hand posture during vertical climbing.

I predicted that gorillas would oppose their relatively longer thumb when grasping arboreal substrates more frequently than chimpanzees. I found partial support for this hypothesis. The functional role of the thumb during vertical ascent and descent climbing, as well as during flexed-elbow and extended-elbow climbing, revealed the use of three different thumb postures relative to different sized substrates in both gorillas and chimpanzees. Both apes significantly used an adducted thumb in a power grip on extra-large substrates (Figs. 4.1c, 4.2c) and opposed their thumb to the index finger in a diagonal power grip on medium-sized substrates only (Figs. 4.1e, 4.2e). Both apes generally held the opposed thumb in line with the substrate, which is consistent with previous studies of chimpanzees (Napier, 1960; Marzke et al., 1992; Alexander, 1994). Only mountain gorillas wrapped the thumb around the support during diagonal power grasping, supporting my prediction. However, the absence of this thumb posture in the chimpanzee sample is likely due to the limited size on the smaller-diameter substrates, as it has been reported previously in chimpanzees (e.g., Napier, 1960; Marzke et al., 1992; Alexander, 1994). Furthermore, in mountain gorillas the opposed thumb appeared particularly important when grasping lianas whereas the chimpanzees were not observed to climb on lianas (Fig. 4.1g). When gorillas grasped lianas, the downward pull of the body appeared to be resisted mostly by the second, third and fourth fingers, while the thenar region of the palm and the proximal phalanx of the thumb counter stabilized the grip. The observations of a relative frequent use of grasping with an opposed thumb (36 % of total 231 limb cycles) together with the gorilla's need to resist the downward pull of its large body mass during descent climbing, suggest that the gorilla thumb may experience large loading during this arboreal behaviour. This

hypothesis is consistent with the robust first metacarpal in mountain gorillas (Hamrick and Inouye, 1995), suggesting that the mountain gorilla's thumb is adapted to meet the potentially high forces during vertical ascent and descent, that occur due to their great body mass. Finally, mountain gorillas and chimpanzees occasionally abducted the thumb at roughly a right angle to the index finger, typically in a power grip on large substrates (Figs. 4.1d, 4.2d). In this abducted posture, the thenar area of the palm is recruited for counter pressure and thus, the thumb may potentially experience forceful loading at the metacarpal region (Fig. 4.2).

Although the gorilla's hand proportions are closer to humans than those of other hominoids (Almécija et al., 2015), their thumb is still too short to lock with or stabilize against the index finger on medium-sized supports as seen in humans when power squeeze gripping (e.g., Napier, 1960; Marzke et al., 1992; but see illustrations in Sarmiento, 1988 and Hasley et al., 2017 for human arboreal behaviours). Nevertheless, the high range of ulnar deviation of the wrist that was elicited in vertical descent enabled mountain gorillas to use the opposed thumb as an additional point of contact on lianas if needed, so that the support can be grasped quickly and firmly in case of slipping off from the irregular main support. The extremely ulnarly-deviated wrist posture allowed the liana to be held securely in the web at the V-shaped region (Marzke et al., 2015) between the opposed thumb and extended index finger while the gorilla's forelimb moved downward along the substrate (Fig. 4.1h). This important supportive role of the thumb was not observed in this chimpanzee sample and it has not been reported in other chimpanzees (e.g., Marzke et al., 1992; Hunt, 1991a, 1992; Alexander, 1994; Hunt et al., 1996). However, since the chimpanzees in this sample did not exhibit such an extreme degree of ulnar deviation (although they are anatomically capable of it; Tuttle, 1969) as compared with mountain gorillas during descent climbing, it needs to be further investigated whether chimpanzees use the same grasping strategy to overcome substrate irregularities.

This comparative study provides much needed data on how the hand and forelimb are used during vertical climbing in a natural environment that can, in turn, help interpret differences in both external and internal bony morphology. However, this study also makes clear that there is a complex relationship between species-

specific morphology and the range of potential postures that may be used in a natural environment. Although recent work found clear differences in foot morphology between more arboreal western gorillas and less arboreal eastern gorillas that correlate well with differences in arboreality, slight differences between eastern gorilla subspecies (i.e., lowland gorillas vs. mountain gorillas) did not follow the functional predictions (Tocheri et al., 2011, 2016). Furthermore, previous work examining African ape hand and foot morphology in relation to frequencies of arboreality and terrestriality, did not find strong concordance between functional predictions and the observed morphology across species and subspecies (Jabbour, 2008). Together, these findings underline both the difficulty and critical importance of identifying skeletal features that have a clear functional and adaptive signal to “potential” and “actual” behaviors.

4.4.3 Gait characteristics of vertical climbing

This study found clear support for the hypothesis that, due to variation in body size, larger-bodied mountain gorillas will differ in their gait characteristics (i.e., temporal gait parameters, footfall sequences and limb support pattern) during vertical climbing compared to smaller-bodied chimpanzees.

Firstly, I found no intraspecific sex differences within the temporal gait parameters in gorillas and chimpanzees (Table 4.8). Male and female gorillas showed similar high duty factors when their hands contact the substrate and both forelimbs are loaded in tension (female mean: 70 %; male mean: 69 %), suggesting that ascent and descent climbing as well as flexed-elbow and extended-elbow climbing are similarly demanding for both sexes, despite their large variation in body mass (e.g., Schultz, 1934; Sarmiento, 1994; Smith and Jungers, 1997). However, a larger sample size on male individuals is needed to clarify whether mountain gorillas differ more between the sexes during vertical climbing compared to this study.

As predicted, mountain gorillas and chimpanzees show striking differences in their temporal gait parameters with gorillas having significantly longer cycle duration, higher duty factor and lower stride frequency than chimpanzees (Table

4.8). The higher duty factor of the mountain gorilla's forelimb indicates that the gorilla's hand is held in contact with the substrate for longer and thus, would experience tensile forces for longer phases compared to chimpanzees. Forceful hand grips and the use of variable thumb postures relative to substrate size are, therefore, likely particularly important in large-bodied mountain gorillas, as they face greater biomechanical challenges during vertical climbing than smaller-bodied chimpanzees. The lower cycle duration and stride frequency combined with longer contact times, represents a more cautious and stable climbing style, which would increase safety when traversing unfamiliar or irregular substrates in an arboreal environment (Pontzer and Wrangham, 2004), as well as likely reduce energetic costs as found in other climbing primates (e.g., Isler, 2003; Isler and Thorpe, 2003; Hanna, 2005, Hanna and Schmitt, 2011). Indeed, several studies have indicated that arboreal great apes display energy-saving adaptations in their locomotion to cope with their large body mass in an energetically challenging environment (Thorpe et al., 2007; Pontzer et al., 2010). An interspecific comparison between western lowland gorillas and bonobos, as well as between juvenile and adult gorillas and orang-utans, supports both suggestions on climbing safety and energy-saving adaptations (Isler, 2002, 2005). A further investigation of the spatio-temporal gait parameters will show whether mountain gorillas also use relative long strides and climb at low speed similar to western lowland gorillas (Isler, 2005).

I also predicted that mountain gorillas would adapt their climbing strategy to accommodate their large body mass in a similar manner to that previously described in western lowland gorillas (Isler 2002, 2003) and, likewise, that smaller-bodied chimpanzees would show a similar climbing style to that of bonobos (Isler, 2002). This prediction was only partially supported.

Similar to mountain gorillas, Isler (2002) found high duty factors in captive western lowland gorillas, although she attributed this in part to their difficulty in climbing up a vertical rope (Isler, 2002, 2003). Although all of the chimpanzees in this study exhibited comparatively lower mean duty factors like that of bonobos, Isler (2002) found that female and male bonobos differed considerably in their gait parameters, with females showing a shorter cycle duration and lower duty factor than males. Female bonobos could climb at a faster speed while the male bonobos would

typically climb more slowly, combining long strides with a long cycle duration (Isler, 2002). However, a recent study of bonobos climbing a pole found similar gait parameters between the sexes (Schoonaert et al., 2016), suggesting that a flexible rope poses a higher locomotor challenge for bonobos than climbing on a rigid support. This is in contrast to climbing in gorillas, where a compliant rope or liana might become stiffer in line of action while a gorilla climbs up, using their large body mass against the substrate. However, since the sample size for male chimpanzees in this study and for female bonobos (Schoonaert et al., 2016) were rather small, a more comprehensive analysis of the spatio-temporal gait parameters in a larger sample on different substrate types will clarify whether chimpanzees also show the same level of intraspecific variation reported in bonobos (Isler, 2002).

This study also found that the climbing performance of mountain gorillas is not less versatile than that of chimpanzees in the natural environment, but that gorilla individuals most often use a different footfall sequence pattern, the diagonal sequence (DS) gait, compared to chimpanzees (Fig. 4.4; Table 4.5). However, at a given duty factor, mountain gorillas used a significantly higher limb phase on vertical supports than that of chimpanzees, likely leading to an increase in the frequency of simultaneous footfalls of diagonally opposite limbs (DSDC) to improve the balancing abilities (e.g., Cartmill et al., 2002; Stevens, 2003, 2006). By using DSDC gaits, the gorilla hindlimb can touch down before the contralateral forelimb to secure a firm foothold on the substrate and both limbs can provide body support for part of the gait cycle. Changes in duty factor and gait sequence patterns result in a higher proportion of strides with support by more limbs at one time on substrates that challenge stability (Stevens, 2003, 2006). This holds true for this sample of mountain gorillas, which used mainly three limbs as body support during vertical ascent (Table 4.8). This is consistent with the climbing strategy documented in western lowland gorillas in captivity, in which they also used mainly three-limb support and mostly engaged in trot or DSDC gaits (Isler, 2002). However, my sample size on individuals descending substrates was rather small and thus, results on limb support pattern during vertical descent should be interpreted with caution (Table 4.9). More data on vertical descent climbing will clarify whether mountain gorillas also support their body mainly by three limbs as during vertical ascent.

In contrast, smaller-bodied chimpanzees appear to climb effectively in a lateral sequence/diagonal couplet gait, in which the hind foot touches down slightly later than the contralateral forelimb and the body is balanced on two diagonally opposite limbs. This is perhaps not surprising as it has long been acknowledged that either DS or LS gaits can be used in combination with diagonal limb couplet support patterns (e.g., Muybridge, 1887; Hildebrand, 1966, 1976, 1985). This support pattern is also equally true of trots, which are defined by near simultaneous contact by diagonal limb couplets and were frequently used by both apes during vertical climbing (Fig. 4.4, Table 4.5). The diagonal couplet support enables primates to arrange the limbs as a widely splayed diagonal bipod and allows the center of mass to be contained within the base of support, reducing the risk of slipping and falling off the support during climbing (Cartmill et al., 2002). Similar to this sample of chimpanzees, bonobos also used LS gaits more often than lowland gorillas during rope climbing but used two-limb, rather than three-limb, supports (Isler, 2002). Bonobo pole climbing showed a similar pattern with a more frequent use of LS gaits than DS gaits (Schoonaert et al., 2016). However, the variation in footfall sequences between gorillas and chimpanzees suggests that hypotheses (i.e., avoiding limb interference: Hildebrand, 1980; stability: Cartmill et al., 2002; energetic benefit: Griffin et al., 2004) of primate-specific DS gait adaptations for arboreal locomotion may require further investigation. A computer simulation of chimpanzee quadrupedal locomotion also found a partial preference for LS/lateral couplet gaits (Sellers et al., 2013). Furthermore, Stevens (2006) showed that primates could readily switch between DS and LS gaits on different arboreal supports likely because of differences in relative stance and swing phase durations. These results suggest that neither DS nor LS gaits offer a particular advantage for stability on horizontal (e.g., Shapiro & Raichlen, 2005; Stevens, 2006, 2008) and potentially vertical supports. This may reflect the need for most primates to use both arboreal and terrestrial substrates and thus, gait flexibility is the key feature of primate locomotion rather than the choice of a specific footfall sequence (Stevens, 2006; Higurashi, Hirasaki & Kumakura, 2009).

4.5 Conclusion

This quantitative analysis demonstrates the importance of powerful grasping and the use of variable thumb postures relative to substrate size in both ape species, and particularly in large-bodied mountain gorillas as they face greater biomechanical challenges during vertical climbing than smaller-bodied chimpanzees. Moreover, this study reveals the supportive role of the gorilla's thumb during vertical descent. Additionally, the interspecific comparison of the temporal gait parameters between mountain gorillas and chimpanzees and other great apes provides further insight into the locomotor strategies required of large-bodied arboreal primates. However, more field studies and additional laboratory studies on more challenging (i.e., differently sized, less stable, irregular surface) supports are needed to clarify if captive studies are adequately representative for the patterns found in natural environments. Likewise, more work is needed to further characterise arboreal kinematic variability and gait choice among a wider range of primates (body proportions, body size) during vertical ascent and descent.

Chapter 5

General Discussion, Conclusion and Future Directions

The aim of this doctoral dissertation was to greatly improve our understanding of the functional link between hand morphology and behaviour in African apes by conducting detailed studies of different complex manipulative behaviours and hand/forelimb biomechanics during arboreal locomotion (i.e., vertical climbing) under natural conditions. In this general discussion, I will summarize results of my dissertation and synthesize how these results shed light on human arboreal locomotion, manipulation, tool-use and tool-making to generate more informed reconstructions of fossil hominin locomotor and manipulative behaviours.

Chapter 2 investigated the potential differences in manual abilities between bonobos and chimpanzees during a complex tool-use behaviour. This first comprehensive analysis of bonobo nut-cracking revealed an exclusive laterality for using the hammerstone and a significant right-hand bias in most of the individuals studied, suggesting a group-level bias (although sample size was not large enough to confirm this). The bonobos demonstrated an unexpected manipulative versatility during stone tool-use, including 10 novel hand grips. Moreover, bonobos can be efficient nut-crackers with a skill level not that different from the renowned nut-cracking chimpanzees of Bossou, Guinea.

Chapter 3 examined whether Bwindi mountain gorillas perform complex manipulation, similar to that documented in other mountain gorillas, to process the specific foods in their environment. Two of these plants are woody-stemmed plants for which the food is more challenging to access in comparison to leaves, lacking physical defenses that are relatively simple to process. Similar to thistle feeding by Virunga gorillas, Bwindi gorillas used the greatest number of hand actions to process the most complex plant food (i.e., peel), the manipulative actions were ordered in several key stages and organised hierarchically. Similar to Virunga gorillas, Bwindi gorillas employed eight hand-use strategies that indicate their high manipulative skills. The demands of manipulating natural foods elicited 19 different hand grips and variable thumb postures, of which three grips have not been previously described in the literature. A higher degree of lateralisation was elicited for the most complex behaviour of peel-processing but the strength of laterality was only moderate, suggesting that peel-processing is not as complex as thistle leaf-processing by Virunga gorillas.

Chapter 4 addressed the question whether large-bodied mountain gorillas differ from smaller-bodied chimpanzees in their hand use and vertical climbing strategy. This research revealed that both apes used power grips and a diagonal power grip, involving three different thumb postures. Mountain gorillas showed greater ulnar deviation of the wrist during vertical descent than chimpanzees, and the thumb played an important supportive role when gorillas vertically descended lianas. Comparisons of temporal gait parameters revealed that large-bodied gorillas exhibited a longer cycle duration, lower stride frequency and generally a higher duty factor than chimpanzees. This study revealed that mountain gorillas adapt their climbing strategy to accommodate their large body mass in a similar manner previously found in captive western lowland gorillas, and that chimpanzees are less variable in their climbing strategy than has been documented in captive bonobos.

What are the links across human arboreal locomotion, manipulation, stone tool-use and tool-making?

5.1 African ape manipulative abilities and the evolution of the human hand

When compared to African apes, our closest living relatives, and to all other primates, humans are distinctive in exhibiting a combination of “-unique-” features, including habitual bipedalism locomotion, highly dexterous hands and a species-level bias to use the right hand for most tasks.

Traditionally, human bipedalism and their extraordinary manipulative abilities are thought to have evolved when our early ancestors left the trees for more open grassland, where they exploited the savannah as persistent endurance hunters and upright bipedal walking 'freed the hands' to make tools (e.g., Washburn, 1960; Lovejoy, 1981; Shipman, 1986; Sinclair et al., 1986; Carrier, 1984, or see review in Harcourt-Smith, 2013). This argument is underscored by the rationale that the mechanical and manipulative adaptations that facilitate locomotion on the savannah and making tools are fundamentally incompatible with those of climbing trees. However, more recent palaeontological and archaeological evidence contradicts this

traditional view and demonstrates that a rapid and absolute transition from arboreal to terrestrial environments is not a likely scenario in hominin evolution. Skeletal evidence of bipedal locomotion predates the earliest evidence of stone tools (3.3 Ma; Harmand et al., 2015) and stone tool use (3.4 Ma; McPherron et al., 2010) by up to 3.5 million years (Senut et al., 2001; Brunet et al., 2002). More recent fossil hominin discoveries reveal mosaic postcranial morphologies that show features indicative of bipedal locomotion as well as a functionally significant degree of arborealism, and enhanced manipulative abilities (e.g., Berger et al., 2010, 2015; Harmand et al., 2015; Skinner et al., 2015a). For example, many australopith species, including *Australopithecus afarensis* (3.9-2.9 Ma), *Australopithecus africanus* (3-2 Ma) and *Australopithecus sediba* (2 Ma), had relatively short fingers but retained curved phalanges, a relatively long forelimb and a mobile and cranially-oriented shoulder joint, that together suggest they were actively climbing in the woodland environment in which they lived (e.g., Bush et al., 1982; Ricklan, 1987; Sellers et al., 2005; Berger et al., 2010; Churchill et al., 2013; Kivell, 2015; Feuerriegel et al., 2016). Furthermore, *Homo naledi*, although surprisingly recent (~250 Ka; Dirks et al., 2017) also has more curved phalanges than many australopiths and cranially-oriented shoulder joints, suggesting climbing was still a significant component of its locomotor repertoire (Kivell et al., 2015; Feuerriegel et al., 2016). In contrast, *H. naledi* foot morphology is remarkably human-like (Harcourt-Smith et al., 2015) and the wrist shows human and Neanderthal-like morphological features commonly considered adaptations to committed tool use (Kivell et al., 2015). Other analyses indicate that modern human-like hand proportions evolved prior the advent of systematic flaked stone tool culture in human evolution and are more similar to those of Miocene apes (Alba et al., 2003; Almécija et al., 2010, 2015b). Together, these findings imply that human-like features of the hand and advanced manipulative skills do not necessarily exclude an arboreal lifestyle (e.g., Kivell et al., 2011; Kivell et al., 2015; Skinner et al., 2015b). Recently, some researchers have highlighted the similarities between the australopith and gorilla - rather than chimpanzee - hand and forelimb morphology, suggesting that chimpanzees have diverged more in their morphology since the last common ancestor than gorillas may have (e.g., Drapeau and Ward, 2007; Almécija et al., 2015b, see review in Crompton, 2016). Thus, palaeontological and archaeological evidence presents a more complex and mosaic evolution of the hominin locomotor and manipulative behaviours than traditionally

thought, and brings into question the utility of using chimpanzees as the sole “living model” of *Pan*-hominin last common ancestor (LCA).

The results of this dissertation provide additional support to the hypothesis that enhanced manipulative abilities are not mutually exclusive to arboreal locomotion (i.e., vertical climbing) and, in particular, that gorillas may be an equally, if not more, informative living model for the LCA. In Chapter 3, I demonstrated that a diverse repertoire of hand grips, variable thumb postures, bimanual role differentiation, and precise, forceful handling mark the Bwindi mountain gorilla’s high manual skills when processing technically difficult plant foods. Chapter 4 showed that Bwindi mountain gorillas use powerful grips, variable thumb positions and an extreme degree of wrist adduction to grasp, stabilize, and accommodate variation in substrate size during vertical climbing. The gorilla’s hand morphology, although generally similar to other African apes in having relatively long fingers and a short, weak thumb, is capable of both effective vertical climbing and fine, forceful manipulation. The gorilla’s hand can be distinguished from *Pan* and other hominoids by several features, including less curved finger phalanges, a more mobile wrist, a relatively longer thumb, and a more robust first metacarpal (Tuttle, 1969; Susman, 1979; Hamrick and Inouye, 1995; Alméjija et al., 2015a). Together, perhaps these relatively subtle differences in hand morphology compared with *Pan* represent a compromise between diverse locomotor (e.g., knuckle-walking, vertical climbing) and the dexterous and forceful manipulative functions required for food processing (Preuschoft and Chivers, 1993).

Likewise, the bonobo hand possesses a high potential on manual ability to perform efficient stone-tool use behaviour and precision grasping (see Chapter 2), despite their lack of known habitual tool-use in the wild (Hohmann and Fruth, 2003; Furuichi et al., 2015) and hand proportions (i.e., relatively long fingers and a short thumb) that suggest a low degree of dexterity and a poor potential of using forceful precision grips to hold small objects or perform precision handling (Feix et al., 2015; Liu et al., 2016). Like gorillas, bonobos and chimpanzees, have a saddle-shaped trapeziometacarpal (TMC) joint allowing abduction and opposition of the thumb while the curvature permits distribution of axial loadings associated with forceful gripping (Marzke et al., 2010). This is evident by the variable thumb postures used in bonobos to accommodate hammerstones of varying size and shape when crack open

oil palm nuts (Chapter 2). Nevertheless, the amount of force that the bonobo thumb can apply in the three precision grips observed (see Pc1-Pc3 in Figure 2.1, Chapter 2) is probably lower than in humans, primarily because, like chimpanzees, bonobos have fewer and less powerful (i.e., shorter muscle moment arms) thumb muscles (Marzke et al., 1999).

However, although the functional importance of the short thumb during arboreal behaviours has traditionally been downplayed in non-human apes (Ashely-Montagu, 1931; Straus, 1942; Tuttle, 1967; Rose, 1988; Sarmiento, 1988), results of this study (Chapters 2 and 3) and other research (Marzke et al., 2015; Bardo, 2016) have revealed that African apes recruit their thumb not only in complex manipulation but also in vertical climbing (Chapter 4). Despite the relatively low frequency of arboreal behaviours (even if frequencies are underestimated; Crompton et al., 2010) compared with terrestrial locomotion in mountain gorillas, the amount of arboreality and/or selective pressures within an arboreal environment (e.g., injuries from falling), are sufficient to maintain a finger and forelimb morphology that able to meet the high mechanical demands of vertical climbing (Larson, 1998; Tuttle, 1969). The same can now be said of gorilla thumb morphology; the thumb plays an important supportive role during vertical climbing and its morphology is capable of coping with these high mechanical demands. At the same time, the gorilla thumb is able to provide the dexterity (and cope with comparatively weaker forces) required for complex plant processing. Together, these results have significant consequences for the functional interpretation of thumb morphology in non-human apes and how the human thumb may have evolved. Importantly, our human ability to use and make tools may not have required the extensive morphological changes from a generalised arboreal hand as had already been suggested elsewhere (e.g., Lovejoy et al., 2009; White et al., 2009; Hashimoto et al., 2013).

Altogether, the biomechanical and manual adaptations in the African ape hand that facilitate arboreal locomotion (i.e., vertical climbing) appear to be fundamentally compatible with adaptations that facilitate complex and precise manipulations. This hypothesis is further supported by the fact that this dissertation only partly supports a functional link between diet and hand morphology in mountain gorillas. The external forces of vertical climbing are considered to be much higher compared to feeding behaviours (Preuschoft and Chivers, 1993; Jouffroy et al., 1991)

and thus, likely place greater selective pressures on hand anatomy. It is this foundation of arboreally-selected morphological features of the hand that might allow for effective manipulative actions to process food and use stone tools. For example, strong recruitment of the digits and base of the thumb during power (palm) grasping and hook grasping in gorilla plant-processing recruit the powerful digital flexors and thumb joint (i.e., trapeziometacarpal) features that were likely already adapted to high external forces incurred during the use of arboreal climbing grips (i.e., power and diagonal power grasping).

5.2 Human hand morphology and arboreal locomotion

This dissertation has provided further support for the highly dextrous abilities of African apes, particularly those of mountain gorillas and bonobos, despite having a hand morphology that is considered largely adaptive for terrestrial (gorillas) and arboreal (bonobos) locomotion (Schultz, 1930; Tuttle, 1969; Rose, 1988; Sarmiento, 1988). Inversely, recent research has shown that human hand morphology, characterised by derived features considered adaptive for manipulation, is capable of competent and effective arboreal locomotion (Venkataraman et al., 2013; Kraft et al. 2014; Hasley et al., 2017). However, humans and African ape hand morphology differs considerably from each other, with consequential effects in precision grasping capabilities (Marzke, 1997). The bony morphology and musculature of the human thumb reflects its importance in our highly dexterous manual behaviours, allowing the hand to secure objects firmly or to rotate them using the distal thumb and finger pads. All but one of the muscles of the human thumb have a significantly longer moment arm length than that of chimpanzees, permitting better mechanical advantage or leverage (Marzke et al., 1998, 1999). The human hand has an independent and well-developed *flexor pollicis longus* (FPL) muscle, which allows flexing and stabilising the tip of the thumb (Marzke, 1997; Almecija et al., 2010). Although this muscle is important for precise control and manipulation, it is particularly active during power squeeze grips, rather than precision pinch grips (Marzke et al., 1998; Hamrick et al., 1998). Some other apes have an independent FPL (i.e., hylobatids) or a similar attachment on the distal phalanx of the thumb (i.e., orangutans), but the presence of a well-developed and independent FPL in humans

fulfils the specific functional requirements of the thumb to be able to make and use tools (Marzke et al., 1998, 1999). Distinctive changes in carpal bone morphology and the orientation of their articulations (e.g., a flatter and broader trapeziometacarpal joint and boot-shaped trapezoid) in the human wrist compared to chimpanzees helps to better accommodate large axial loadings from the thumb associated with manipulative gripping but also facilitate full opposition to the fingers and maximal stabilisation during thumb/index finger pinch grips (Tocheri, 2007; Marzke and Marzke, 2000; Marzke et al., 2010; Liu et al., 2016). The shape of the human trapeziometacarpal complex appears to allow more complex in-hand movements compared to other hominoids (Craet et al., 2009; Bardo, 2016). This highly dexterous manual ability is thought to favour highly complex manipulations required for the use of flaked-stone cutting tools and production (Marzke et al., 2010). The human wrist joint (i.e., features enabling greater wrist extension) permits an efficient knapping strategy while flake production appears to be one of the most likely behaviours to have influenced our hand's anatomical and functional evolution (Williams et al., 2010, Williams-Hatala, 2016). Ape-like hands, on the contrary, are presumed to be less effective at generating high forces between the thumb and fingers, and appear to be less able to tolerate the presumed high bone and joint stresses associated with the repeated use of hard-hammer percussion for removing flakes (Marzke and Shackley, 1986; Susman, 1994; Marzke, 1997; Rolian et al., 2011). Together, a large suite of derived hard and soft tissue features of the human hand are thought to be responsible for the “unique” dexterity that separates humans from all other primates and is suggested to have been selected at least in part for the performance of stone tool behaviour.

Human intrinsic hand proportions are certainly important to facilitate refined and forceful manipulations but are just as important to provide a firm hold on arboreal substrates (Sarmiento, 1988). New research has demonstrated that many human populations remain adept at arboreal locomotion, despite being committed terrestrial bipeds (Venkataraman et al., 2013; Kraft et al., 2014). Irrespective of differences in hand morphology, tree climbing humans exhibit thumb postures and grips to accommodate variation in substrate size similar to those described for mountain gorillas and chimpanzees in this dissertation. For example, humans use power grips and positioning the thumb in adduction or abduction on large vertical

supports while opposing the thumb and adduct the wrist on smaller supports (Sarmiento, 1988). However, in humans, the degree of ulnar deviation is limited by the wrist joint compared to the extensive adduction at the wrist in mountain gorillas, leading to slightly different hand postures on vertical supports between these hominids (Sarmiento, 1988; Chapter 4). Furthermore, a recent experimental study has shown that humans employ a ‘light fingertip touch’ strategy to maintain bipedal balance in a simulated forest canopy environment, indicating that some adaptations in the hominin hand that facilitated continued access to forest canopies may have complemented, rather than opposed, adaptations that facilitated precise and forceful manipulation and tool use (Johannsen et al., 2017). Furthermore, modern humans still share with the other hominoids a suite of adaptations to below-branch, orthograde arboreal behaviours, such as long, strong forelimbs, a broad, shallow thorax and scapulae positioned dorsally that allow an extensive range of motion in the shoulders (Ward, 2007; Crompton et al., 2008). This allows many rainforest hunter-gatherer communities to routinely obtain arboreal food resources (Venkataraman et al., 2013; Kraft et al., 2014). Humans’ climbing ability is also used in sports, particularly by rock climbers and parkour athletes. These involve the hands and limbs in a wide range of joint positions, in tension and compression, much like the arboreal locomotion of other apes (Hunt et al., 1996; Thorpe and Crompton, 2006, Hasley et al., 2017). Recent studies have shown that humans adapt to the mechanical demands involved and become habituated to these specific types of locomotion. For example, the practice of rock climbing not only increases muscle strength but also results in adaptations among specific hand muscles, leading to a greater hand performance during prehensile activities (Vigouroux et al., 2015). Parkour athletes are able to optimise their performance and reduce their energy expenditure as they become more familiar with an arboreal locomotor task (Halsey et al., 2017).

Climbing-related changes in muscle tendon and skeletal architecture of the hand could be particularly pronounced in climbing populations of hunter and gatherers, who demonstrate that significant amounts of arboreal behaviours, particularly vertical climbing, are possible with a ‘modern’ human-like morphology (Venkataraman et al., 2013). Tree climbing begins at a young age in hunter-gatherers (Hill and Hawkes, 1983; Lye, 2004; cited in Venkataraman et al., 2013) and may be reflected in ontogenetically plastic traits, such as phalangeal curvature and trabecular

bone structure, which respond to the mechanical loading of habitual locomotor behaviours during life (Richmond, 1998; Tsegai et al., 2013; Chirchir et al., 2016). Skeletal signals of vertical climbing in modern hunter-gatherers could, thus, provide us an important comparative context for functional interpretations of early hominin morphology. Form-function inferences of the hand in early hominins demand, therefore, consideration of the different arboreal locomotor strategies of both extant apes and modern humans. In comparison with apes and other primates, the diverse locomotor repertoire of humans has received little attention (Watanabe, 1971; Devine, 1985) and thus, more field studies on human arboreal behaviours are needed to gain better insight into the locomotor performances of facultative arboreal modern humans. It is also important to further investigate whether human arboreal locomotion is associated with forceful hand grips and large axial loadings on the thumb like tool-related behaviours (e.g., Tocheri et al., 2008, Marzke et al., 2010). Such data will elucidate whether some adaptations in the human hand and forelimb that allow us to facilitate arboreal behaviours may have complemented adaptations or been exacted to facilitate tool-use and eventually the emergence of tool production.

5.3 African ape motor and cognitive abilities as implications for the evolution of human stone tool-use and tool-making

In spite of their distinct hand morphologies, this dissertation has provided further support to previous studies (e.g., Boesch and Boesch, 1993; Byrne et al., 2001; Marzke et al., 2015) showing that African apes and humans are capable of dexterous manipulation, complex extractive foraging, and stone tool-use (see Chapters 2 and 3). Moreover, new findings increasingly reveal Oldowan-like cognitive and manual capacities in our closest living relatives and other primates (e.g., capuchin monkeys and macaques), in terms of showing routine forms of tool use that involve the combination of multiple elements simultaneously or sequentially, transport, accidental stone flake production through percussive technology, and even (albeit rarely) the use of fracturing tools (e.g., Toth et al., 2006; Gumert et al., 2009; Spagnoletti et al., 2009; Whiten et al., 2009; McGrew, 2010; Roffman et al., 2015; Proffitt et al., 2016). Together this research suggests that tool-making is no longer unique to the human lineage and that a human-like hand morphology is not required

for or potentially responsible for the emergence of stone tool making. More comparative research, such as “primate archaeology” (e.g., Haslam et al., 2017), will add further support to an ongoing paradigm shift in our understanding of the early stages of stone tool production and the uniqueness of hominin technology.

That being said, the archaeological and palaeontological record provides compelling evidence about evolutionary shifts toward enhanced manual dexterity of the modern human hand and advanced forms of lithic stone tool manufacture (e.g., Moyà-Solà et al., 2008; Kivell et al., 2011; Almécija et al., 2010; Almécija and Alba, 2014). Together, this suggests that the derived hands of modern humans may indicate that more terrestrial bipedalism and the consequential relaxation of arboreal locomotor demands of the hand (i.e., hand proportions, wrist and thumb morphology) provided an opportunity and selective environment for using our hands primarily for dexterous manipulations; eventually leading to a morphological commitment to tool-related behaviours (e.g., Alba et al., 2003; Tocheri et al., 2005, Marzke, 2013, Almécija and Sherwood, 2017). Besides manual anatomy and locomotion, several other conditions have been proposed to play a role in promoting hominin stone tool innovation. Various scientists have hinted at a positive effect of an increase in brain size, brain structure, social transmission and terrestriality on the likelihood of a complex and widespread stone tool culture (e.g., McPherron et al., 2010; Meulman et al., 2012 Harmand et al., 2015; Heldstab et al., 2016; Almécija and Sherwood, 2017). A recent study by Heldstab and colleagues (2016) found that, among non-human primates, those using their hands for more complex manipulations, also exhibit larger brains and higher amounts of terrestrial behaviours. Terrestriality seems to promote the acquisition and maintenance of complex tool-using skills among several primate species, such as chimpanzees, capuchin monkeys and long-tailed macaques (Visalberghi et al., 2005; Gumert et al., 2009; Mannu and Ottoni, 2009; Meulman et al., 2012; Falótico et al., 2017). Indeed, laterality in hand use has been observed for terrestrial but not yet for arboreal tool use (Marchant and McGrew, 2007; Humle and Matsuzawa, 2009). Thus, it would seem that humans represent an extension along this primate trend. This increase in tool complexity documented in the hominin clade may be due to opportunities closely associated with a primarily terrestrial lifestyle, such as affecting the availability of diverse materials to be used as tools as well as enhancing hand use behaviours and hand specialisation compared to the constraints

on hand use and posture in the trees (Visalberghi et al., 2005; Meulman et al., 2012, see Chapter 4).

Results of this dissertation lend further support to the idea that humans and other primates may have developed high manual skills in respect to the demands of their foraging niche, and that manipulation complexity and cognitive complexity would have coevolved with brain size and terrestriality (Meulman et al., 2012; Heldstab et al., 2016). Mountain gorillas, for example, demonstrate high manual dexterity and complex bimanual coordination in processing tough, fibrous plant foods of their terrestrial foraging niche (Chapter 3) while they seem to use predominately simple reaching and picking actions for retrieving arboreal fruits from tree crowns (Neufuss *pes. observ.*). These data also adds support that terrestrial foraging would have had a relevant role in the evolution of technological abilities and associated cognitive traits during human evolution. Technically difficult foods are thought to be key selection pressures for the evolution of intelligence (Russon, 1998), supporting abilities to solve extractive foraging problems, and organise multi-step processing techniques efficiently (Parker and Gibson, 1979). Hierarchical organisation of behavioural programs is currently known to be a shared capability between great apes, humans, capuchins and long-tailed macaques (Russon 1998; Stokes and Byrne 2001; Byrne 2005, Sabbatini et al., 2014; Tan et al., 2016; Estienne et al., 2017). Additionally, the pattern of bimanual feeding on woody plant stems appears to have interesting implications for the evolution of hominin perceptual-motor processes relevant to tool making. This is a coordinated pattern in which one hand supports and stabilises the plant stem while the other hand facilitates forceful manipulation (Chapter 3). The pattern of bimanual role differentiation between both hands appears to be an example of a perceptual-motor skill for food acquisition activities that Rein and colleagues (2013) suggest may have underlain stone knapping capabilities.

Likewise, the study of bonobo nut cracking (see Chapter 2) supports the hypothesis proposed by Meulman and colleagues (2012), that terrestriality may have been a crucial factor for the acquisition of complex tool-use and the maintenance of high manipulative skills in primates. Similar to other studies in the wild, Chapter 2 demonstrates how semi-free-ranging bonobos were able to crack palm oil nuts on the ground, reuse multiple tools such as anvil and stone hammers, involve both hands in complex bimanual coordination, as well as indicate hand specialisation (Visalberghi

et al., 2005; Biro et al., 2006; Gumert et al., 2009). However, observations by Boesch and colleagues (1984, 1990) partially contradict the terrestriality hypothesis as Tai chimpanzees crack nuts at the beginning of the season directly in the branches of the trees with both hands in complementary roles, which allows them to expand the nut-cracking season by a whole month. This aspect emphasises the need to consider the possible individual variation in a behaviour (Kappeler and Kraus, 2010) and presents a good example of the adaptability of motor processes to easier access to obtain food across different foraging niches.

One suggested precursor for hominin stone tool manufacture has been the behaviour of nut cracking (Marchant and McGrew, 2005; Haslam et al., 2009). Nut cracking also represents a crucial model with which to infer the evolution of higher cognitive abilities in our lineage (e.g., Byrne, 2007; Kruetzen, et al., 2011; Wynn et al., 2011). It has been argued that great apes in principle demonstrate all necessary cultural requirements for successful stone knapping (Davidson, 2010) except the motor skills to precisely aim forceful blows and to control manipulative actions of both hands (Byrne, 2004; Toth and Schick, 2009). Thus, research investigating the limitations in striking precision or control of the supporting hand in nut cracking and stone flaking primates seems warranted. Assuming that the last common ancestor of African apes and humans possessed similar features like extant great apes (McGrew, 2010), this suggests a special development of motor skills supporting the development of stone knapping (Bril and Roux, 2005; Stout and Chaminade, 2007; Faisal et al., 2010).

Human right-handedness as a population-level bias is a defining feature of our species (review in Llaurens et al., 2009). Traditional definitions of human 'handedness' consider it as resulting from unimanual actions and tend to describe the right hand as dominant, such as the most common methods of measuring handedness in humans by noting the writing hand (Oldfield, 1971; Bryden, 1977). Humans appear to show degrees of hand preference according to the type of task being tested, while lateralisation increases with skilled manipulations (e.g., Annett, 1972; Steenhuis and Bryden, 1989; Fagard and Corroyer, 2003). However, as Steele and Uomini (2009) pointed out, an exclusive focus on the preference for a single dominant hand diverts attention from the bimanual asymmetrical coordination required in most tool-using tasks and daily activities. In fact, complementary role

differentiation between both hands characterises prehistoric object manipulations (Eshed et al., 2004), and it is most pronounced in tool-use manufacture where the dominant hand (mostly the right hand) acts more frequently and precisely while the opposite hand (mostly the left hand) moves less frequently as support (Guiard, 1987).

Manual specialisation is also found in the Bwindi mountain gorillas of this dissertation (Chapter 3) as well as in other non-human primates during bimanual asymmetrical coordinated tool-use and feeding behaviours, but often found only strong individual preferences (e.g., Byrne and Byrne, 1991; Hopkins et al., 2011; Chapelein et al., 2011; Bardo et al., 2016). A more direct comparison to human manual specialisation at the group-level can be made with the highly complex tool-use task of nut-cracking in wild chimpanzees and the semi-free-ranging bonobos of this study, eliciting exclusive hand use with a significant right-hand bias at the group-level (Matsuzawa, 1996; Humle and Matsuzawa, 2009; see Chapter 2). When individual hand-preferences are compared between humans and other apes, lateralisation strength appears to be similarly influenced by the effects of task complexity and different complementary roles of both hands (chimpanzee nut-cracking: Boesch, 1991; Sugiyama et al., 1993; Biro et al., 2003; human nut-cracking: Uomini, 2009). It is, thus, possible that the behaviour of using stones to crack open nuts played a role during the evolution of hemispheric asymmetries needed for the manufacture of lithic stone tools (Bril et al., 2012). It further appears that the more complex the tasks, the less common they are in the spontaneous behaviour of an individual. For example, one-handed object manipulations with synchron digits were found to be the most common tasks among non-human primates, followed by bimanual asymmetrical manipulations of one object, while complementary bimanual tasks involving multiple objects are the most seldom performed actions (Heldstab et al., 2016). However, practicing increasingly complex hand actions on a daily basis may differentiate humans from other apes as most of their daily manipulations are proposed to be not complex enough to elicit hand preference (Corballis, 1998). As the nut-cracking data show, the highly complex tool using skills of chimpanzees and bonobos may be related to their stronger laterality compared to other non-tool using primates (see Chapter 2).

Based on the high manipulative abilities of non-human primates, it is likely that prior to stone tool use and manufacture the earliest hominins made use of perishable materials, such as sticks and branches, or non-modified bones and stones as tools (Panger et al., 2002). It is possible that the first lithic morphotypes resulted from stones being used as hard hammers to crack open nuts on anvils, which may have led to unintentional flaking as documented in the chimpanzees of Gombe and Bossou (Mercader et al., 2002; Carvalho et al., 2009), and more recently in capuchin monkeys breaking stones (Proffitt et al., 2016). Some of the sharp-edged flakes and cores may have remained as passive stone tools until our early human ancestors used them to accomplish more complex activities according to the demands of their foraging niche. With the evidence that human right-handedness may have emerged through the social transmission of increasingly complex tool use involving complementary role differentiation (see Uomini, 2009), more comparative research is needed on non-human primate stone tool-use in natural environments as it seems to be an important factor for the evolutionary history of human handedness.

Conclusion

This dissertation provided new insight into the functional link between hand morphology and behaviour in African apes that may ultimately generate more informed reconstructions of fossil hominin locomotor and manipulative behaviours. My results demonstrate that the morphological requirements of high manipulative skills in African apes may be fewer than previously considered, and that those precise manipulative abilities (i.e., nut-cracking and plant-processing) can be effectively balanced with those of arboreal locomotion (i.e., vertical climbing). Bonobo nut-cracking demonstrated that lateralisation strength is influenced by the effects of task complexity and different complementary roles of both hands similar to human stone tool-use. Moreover, *Gorilla* and *Pan* were likely loading their thumbs forcefully during some hand actions involved in manipulation and arboreal locomotion, which has been thought to be not possible. However, although humans are characterised by pad-to-pad forceful precision pinch grips and precision handlings, the suite of “unique human grips” or “unique human manipulative

abilities” is getting much smaller the more we learn about African apes - especially in their complex natural environment where the hand has to adjust to varying foods and arboreal substrates, and where individuals have ample opportunity to learn and develop high manipulative skills. But most importantly, the interdisciplinary approach of this dissertation supports new ideas about the evolutionary shift in human hand use from locomotion to manipulation. Further comparative research on both non-human apes and modern human climbing populations in natural environments is now needed to answer the fundamental question of whether our ancestors needed to completely abandon the trees to be dedicated tool-users and tool-makers.

Future Directions

This dissertation demonstrated that African apes provide us with examples of possible morphological adaptations of their locomotor system to different ecological conditions, their locomotor performance related to their body mass in their natural habitat, manipulative and cognitive abilities during complex terrestrial feeding and tool-use behaviours. This comprehensive study also showed that new questions are continually arising to which constructive answers have to be found.

Findings of unintentional stone flaking in wild chimpanzees and capuchin monkeys (Mercader et al., 2002; Carvalho et al., 2009; Proffitt et al., 2016) contradict the current paleoanthropological paradigm that human-like thumb/hand proportions would be diagnostic of stone tool-making capacities (Susman, 1994, 1995, 1998). Therefore, close up-video recordings and detailed descriptions of thumb/index activity of these behaviours can throw interesting new light on functions and manipulative capabilities of this region of the hand that might have not yet been noted in captive non-human primates.

Since the grips used by nut-cracking Tai chimpanzees have not yet been systematically described in the same detail as for bonobos, future field work may reveal a greater similarity in grip types between these two closely related species. Furthermore, a greater sample of bonobo individuals during nut-cracking is needed

to confirm the right-handed bias at the group-level, as this highly complex tool-use behaviour seems to be an important factor for the evolutionary history of human handedness.

Bwindi gorillas also occasionally process thistle-leaf as the most complex plant food (e.g., Ganas et al., 2004; Robbins et al., 2006), but hand-use strategies, grips and hand-preference have not yet been systematically studied. Thus, comparative research is needed to test whether Bwindi and Virunga mountain gorillas display similar skills for thistle leaf-processing.

The implications of the temporal gait parameters found between climbing mountain gorillas and chimpanzees can be further examined by quantifying joint movements using 3D kinematic analyses in their natural habitat. This will provide more detailed insight into the biomechanical strategies used by each ape and help interpret the functional implications of variations in morphology between gorillas and chimpanzees. Furthermore, a more comprehensive analysis of the spatio-temporal gait parameters and gait choice pattern in a larger sample of chimpanzees will clarify whether chimpanzees also show the same level of intraspecific variation reported in bonobos (Isler, 2002) and if captive studies are representative for the patterns found in natural environments. Since many hunter-gather communities also continue to climb trees routinely, they are highly relevant for understanding potential anatomical constraints on hominin arboreality and thus, kinematic studies on human climbing are needed to gain better insight into their arboreal locomotor performances.

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Appendices

Appendix I

Coding Scheme established for Bonobo nut-cracking

	A	B	C	D	E	F
	MASTER FILES	Code	MODIFIER (1)	Code	MODIFIER (2)	Code
1						
2						
3	LOCATION					
4	anvil	an				
5	tree trunk	tr				
6	ground	gr				
7	NOT VISIBLE	lrw				
8						
9	MATERIAL of HAMMER					
10	stone	st				
11	wood	wo				
12						
13	MATERIAL gets cracked					
14	palm nut	pn				
15	coala nut	cn				
16	panda nut	pa				
17	NOT VISIBLE	mnw				
18						
19	Postural Behaviour					
20	sit	si				
21	squat	sg				
22	stand	sa				
23						
24	Bimanual coordination or unimanual action					
25	bimanual coordination	bi				
26	unimanual action	un				
27						
28	What hand is ACTIVE for hammering					
29	right hand	rh				
30	left hand	lh				
31	both hands	bh				
32	right hand & foot	rhf				
33	left hand & foot	lhf				
34	both hands & foot	bhf				
35						
36	What TYPE of hand grip in the RIGHT hand					
37	Precision grip					
38	1-2 contact area not visible	1r				
39	1-2 pad	2r				
40	1-2 tip	3r				
41	1-2 side	4r				
42	1-5 side	5r				
43	Palm grip					
44	1--2--3--4--5	6r				
45	1--2--3--4	7r				
46	1--2--3	8r				
47	1--2	9r				
48	1--4	10r				
49	1--5	11r				
50	NO HAND GRIP	12r				when not active: unimanual left
51	NOT VISIBLE	hnvr				
52						
53	What TYPE of hand grip in the LEFT hand					
54	Precision grip					
55	1-2 contact area not visible	1l				
56	1-2 pad	2l				
57	1-2 tip	3l				
58	1-2 side	4l				
59	1-5 side	5r				
60	Palm grip					
61	1--2--3--4--5	6l				
62	1--2--3--4	7l				
63	1--2--3	8l				
64	1--2	9l				
65	1--4	10l				
66	1--5	11l				
67	NO HAND GRIP	12l				when not active: unimanual right
68	NOT VISIBLE	hnvl				
69						
70	THUMB POSITION to Index for right hand being active					
71	Thumb straight and next to Index on object	ar				
72	Thumb flexed and next to Index on object	br				
73	Thumb splayed to Index on object	er				
74	Thumb opposed to Index and straight IP joint on object	dr				
75	Thumb opposed to Index and flexed IP joint on object	fr				
76	Thumb with flexed MP joint and hold inside the grip	gr				
77	Thumb has contact on lateral side of Index	hr				
78	Thumb opposed and has contact on dorsal side of Index finger	ir				
79	NOT hammering. Hand is placing the nut or non-active	jr				
80	NOT VISIBLE	thrv				
81						
82	THUMB POSITION to Index for left hand being active					
83	Thumb straight and next to Index on object	al				
84	Thumb flexed and next to Index on object	bl				
85	Thumb splayed to Index on object	cl				
86	Thumb opposed to Index and straight IP joint on object	dl				
87	Thumb opposed to Index and flexed IP joint on object	fl				
88	Thumb with flexed MP joint and hold inside the grip	gl				
89	Thumb has contact on lateral side of Index	hl				
90	Thumb opposed and has contact on dorsal side of Index finger	il				
91	NOT hammering. Hand is placing the nut or non-active	jl				
92	NOT VISIBLE	tpnv				
93						
94	SIZE of STONE relative to hand size for RIGHT hand					
95	small - short	ssr				
96	small - medium long	smr				
97	small - long	slr				
98	medium - short	msr				
99	medium - medium long	mmr				
100	medium - long	mlr				

101	large - short	lsr			
102	large - medium long	lmr			
103	large - long	llr			
104	NOT VISIBLE	nvr			
105					
106	SIZE of STONE relative to hand size for LEFT hand				
107	small - short	ssl			
108	small - medium long	sml			
109	small - long	sll			
110	medium - short	msl			
111	medium - medium long	mm1			
112	medium - long	mll			
113	large - short	lsl			
114	large - medium long	lml			
115	large - long	lll			
116	NOT VISIBLE	nvl			
117					
118	visible joint movements		Type of strike		
119	hand wrist	hw	small strike	sa	
120	elbow joint	ej	medium strike	ms	
121	shoulder joint	sj	large strike	ls	
122					
123	stone SHAPE			FLAT or THICK	
124	square-shaped	squ		flat	fl
125	triangular-shaped	tri		thick	th
126	trapezoid-shaped	tra			
127	rectangular-shaped	rec			
128	oval-shaped	ova			
129	NOT VISIBLE	nvs			
130					
131	ORIENTATION of stone in the hand				
132	vertically	ver			
133	horizontally	hor			
134	NOT VISIBLE	nvo			
135					
136	No. of hits per nut				
137		1			1
138		2			2
139		3			3
140		4			4
141		5			5
142		6			6
143		7			7
144		8			8
145		9			9
146		10			10
147		11			11
148		12			12
149		13			13
150		14			14
151		15			15
152		16			16
153		17			17
154		18			18
155		19			19
156		20			20
157		21			21
158		22			22
159		23			23
160		24			24
161		25			25
162		26			26
163		27			27
164		28			28
165		29			29
166		30			30
167					
168	Successful in cracking nut: YES or NO				
169	nut cracked successfully	Y			
170	nut not cracked	N			
171	NOT VISIBLE	nvc			
172					
173	is nut edible: YES or NO				
174	nut is edible	Ja			
175	nut is not edible	Ne			
176	NOT VISIBLE	nve			
177					

Appendix II

Table 3.1: Elements used across all three plant foods. Functionally-distinct elements are highlighted in bold. Elements are labelled as optional* and as obligate** (terminology equivalent and follows that of Byrne and Byrne, 1993; Byrne et al., 2001a,b). Elements are labelled for peel-^(a), pith-^(b) and leaf-processing^(c).

Element	Description
bite-off ^{*(a)}	Use teeth to cut off portion of naturally attached or hand-supported object; hands resist pull of teeth.
break-off ^{*(b)}	Both hands pull stem away from teeth to break it apart; teeth resist pull of hands.
brush-off ^{***(a), (c)}	Using flexed index and thumb crossed over (held in “C” shape) to gently brush along stem, midrib or bundle in order to dislodge debris.
accumulate ^{***(c)}	Accumulate food items in hand and move for feeding towards mouth. Typically used for handful of leaves.
knuckle-push ^{*(b)}	Fist held as is in knuckle-walking to apply force to break naturally attached object, supported by opposite hand.
peel-back ^{*(a)}	One or both hands are used to pull stem away from teeth while teeth detach outer casing. Occasionally opposite hand is used as support.
pick-up ^{*(a), (b)}	Pinch-grip used to lift stem from ground.
pick-off, pick-out ^{*(c)}	Pinch grip on small item that is pulled off an object held in other hand or picked out from among a mass of items.
pull-off, pull-down ^{*(a), (b)}	Holding a naturally attached object with one hand and pull into range, thus applying force to detach item; effect as yank.
rotate-push ^{*(b)}	Turn or twist long stem held in firm hand grip (e.g., power grip) and pushed against to break and detach from its natural attachment, supported by opposite hand.
sausage-feed ^{*(a)}	Repeated loosening grip and re-grasping lower down an approximately sausage-shaped food bundle, in order to insert it into the mouth as a whole (without the bundle coming apart).
scrape-off ^{***(b)}	Incisor teeth are used to scrape off soft pith while object is supported with hand(s); hand(s) move up and down.
snip-case ^{***(b)}	Use incisor teeth to clip off outer casing in order to discard the casing and expose edible pith.

spaghetti-feed ^{*(a)}	With peel held in mouth without use of the hands, lips used to feed in rest of its length – similar to eating spaghetti.
strip-up ^{*(c)}	Flexed index and thumb held in “C” shape around leafy stem or midrib of leaf, sliding the hand upwards against force of detachment or the other hand’s supporting grip, ending up with holding a bundle of leaves in the hand.
swap-hand ^{*(a), (b), (c)}	Transfer object or handful from one hand to other.
tooth-strip ^{***(a)}	Hand(s) pull stem through partially closed incisors; hand(s) pull stem either sideways or frontal away from teeth. Typically used for stripping off peel.
twist-off ^{*(c)}	Holding a naturally attached object in one hand and twisting, thus applying force to detach object. Occasionally used when picking off leaves.
yank ^{*(a), (b)}	Hand(s) used to apply force on object which is pulled against natural attachment (often to detach the object), or to part of object supported by other hand.

Appendix III

Laterality of peel-processing on individual-level

When the strength of hand-preference at the individual-level was assessed based on the absolute handedness index (ABS-HI) (N=9 individuals). Individual ABS-HI values ranged from 0.08 to 1.00 for both unimanual (mean: 0.45, SD: 0.34) and asymmetrical (mean: 0.47, SD: 0.5) hand-use, indicating a moderate strength of laterality in peel-processing (see Table 3.6 and Fig. 3.14 in *Appendix III*). Concerning the *z*-scores, two gorillas were classified as left-handed, two were classified as right-handed and five were classified as ambi-preferent for unimanual hand-use. One gorilla was classified as left-handed, two as right-handed and six as ambi-preferent for asymmetrical hand-use (see Table 3.6 and Fig. 3.14 in *Appendix III*). Overall, the number of ambi-preferent individuals was not significantly different from the number of lateralized individuals for both unimanual (56 %, N=5/9, $p=1.00$) and asymmetrical hand-use (67 %, N=6/9, $p=0.508$).

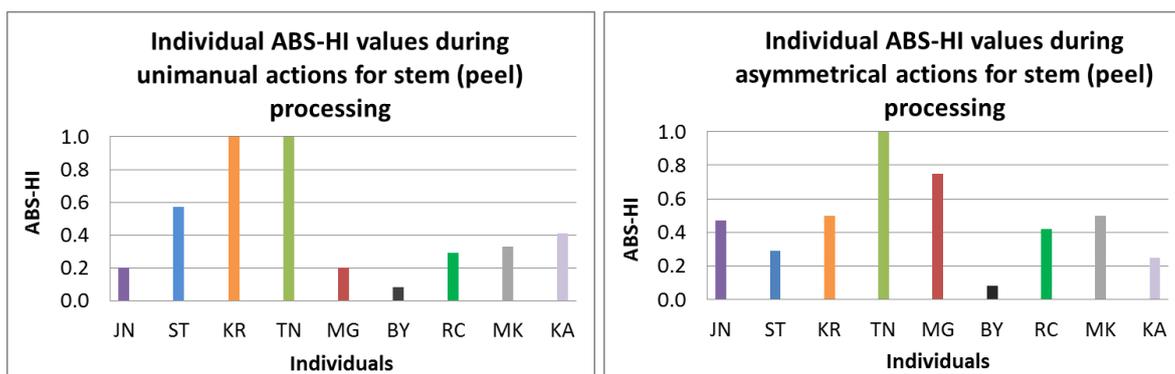


Figure 3.14: Mean values of individual absolute handedness index (ABS-HI), with frequencies for the unimanual and asymmetrical actions in peel-processing (N=9).

Laterality of pith-processing on individual-level

Individual ABS-HI values ranged from 0.0 to 1.0 in unimanual hand-use (mean: 0.32, SD: 0.3) and from 0.14 to 0.76 for asymmetrical hand-use (mean: 0.33, SD: 0.2), indicating a relatively weak strength of laterality in pith-processing (see Table 3.6 and Fig. 3.15 in *Appendix III*). When hand-preference was assessed based

on z -scores, two gorillas were classified as left-handed and nine as ambi-preferent for unimanual hand-use. No individual was classified as right-handed. For asymmetrical hand-use, three gorillas were classified as right-handed and eight as ambi-preferent, while no individual was classified as left-handed. Overall, significantly more individuals were ambi-preferent for unimanual hand-use (82 %, $X^2(1, N=11) = 4.5$, $p=0.035$) while asymmetrical hand-use showed no significant difference (73 %, $X^2(1, N=11) = 2.3$, $p=0.32$)

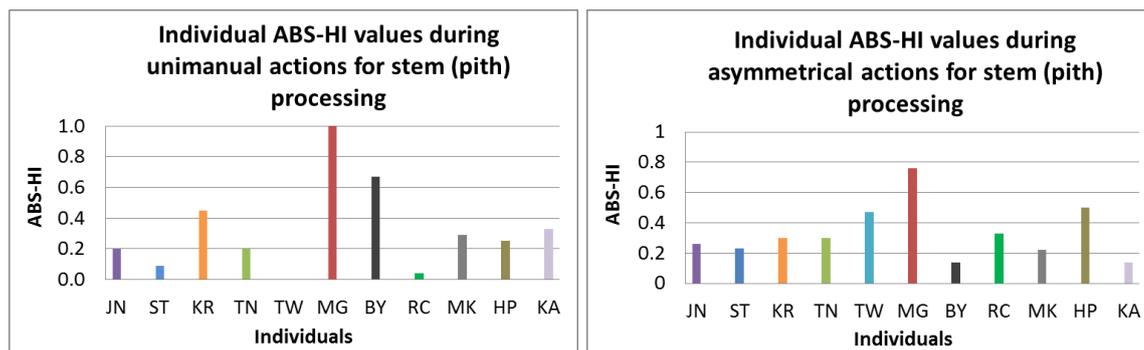


Figure 3.15: Mean values of individual absolute handedness index (ABS-HI), with frequencies for the unimanual and asymmetrical actions in pith-processing (N=11).

Laterality in leaf-processing on individual-level

Individual ABS-HI values (N=9) ranged from 0.2 to 0.59 for unimanual hand-use (mean: 0.38, SD: 0.1) and from 0.14 to 0.57 for asymmetrical hand-use (mean: 0.34, SD: 0.16), indicating a relatively weak strength of laterality in leaf-processing (see Table 3.6 and Fig. 3.16 in *Appendix III*). Based on z -scores, five gorillas were classified as left-handed and four as ambi-preferent for unimanual hand-use. For asymmetrical hand-use, three gorillas were classified as left-handed and six as ambi-preferent. Individuals were not classified as right-handed in either hand-use strategy. Overall, the number of ambi-preferent individuals was not significantly different from the number of lateralized individuals for both unimanual (56 %, N=5/9, $p= 1.00$) and asymmetrical hand-use (70 %, N=7/9, $p= 0.344$).

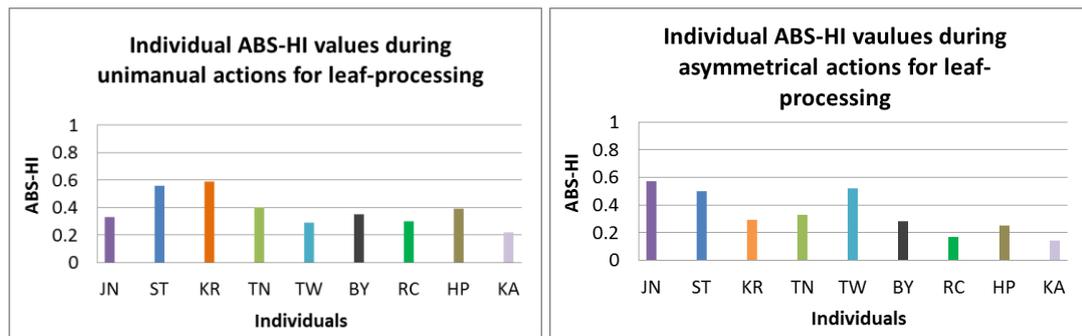


Figure 3.16: Mean values of individual absolute handedness index (ABS-HI), with frequencies for the unimanual and asymmetrical actions in leaf-processing (N=9).

Table 3.6: Data on hand-responses for unimanual and asymmetrical hand-use strategies, and results for laterality studied in three plant foods.^a

Plant food	Individuals	Unimanual hand-use					Asymmetrical hand-use				
		Freq R/L	HI	ABS-HI	Z	Category	Freq R/L	HI	ABS-HI	Z	Category
peel	JN	3/2	0.20	0.20	0.45	A	14/5	0.47	0.47	2.06	RH
	ST	5/18	-0.57	0.57	-2.71	LH	6/11	-0.29	0.29	-1.21	A
	KR	0/6	-1.00	1.00	-2.45	LH	3/1	0.50	0.50	1.00	A
	TN	5/0	1.00	1.00	2.24	RH	0/3	-1.00	1.00	-1.73	A
	TW*	1/1	n/a	n/a	n/a	-	0/1	n/a	n/a	n/a	-
	MG	3/2	0.20	0.20	0.45	A	7/1	0.75	0.75	2.12	RH
	BY	6/7	-0.08	0.08	-0.28	A	7/6	0.08	0.08	0.28	A
	RC	12/22	-0.29	0.29	-1.71	A	11/27	-0.42	0.42	-2.60	LH
	MK	4/8	-0.33	0.33	-1.15	A	3/1	0.50	0.50	1.00	A
	HP*	1/0	n/a	n/a	n/a	-	0/1	n/a	n/a	n/a	-
	KA	19/6	0.41	0.41	2.12	RH	15/9	0.25	0.25	1.22	A
<i>Mean:</i>		5.4/7	-0.45	0.45	-0.34		6.1/6	0.47	0.47	1.69	
<i>SD:</i>		1.7/2.2	0.34	0.34	1.72		5.4/7.8	0.50	0.50	1.24	
pith	JN	3/2	0.20	0.20	0.45	A	4/10	-0.26	0.26	-1.60	A
	ST	5/6	-0.09	0.09	-0.30	A	7/13	-0.23	0.23	-1.34	A
	KR	8/21	-0.45	0.45	-2.41	LH	13/19	-0.30	0.30	-1.06	A
	TN	3/2	0.20	0.20	0.45	A	5/2	0.30	0.30	1.13	A
	TW	2/2	0.00	0.00	0.00	A	12/3	0.47	0.47	2.32	RH
	MG	0/26	-1.00	1.00	-5.10	LH	4/3	-0.76	0.76	0.38	A

	BY	5/1	0.67	0.67	1.63	A		3/5	0.14	0.14	-0.71	A
	RC	13/14	-0.04	0.04	-0.19	A		29/7	0.33	0.33	3.67	RH
	MK	5/9	-0.29	0.29	-1.07	A		11/7	0.22	0.22	0.94	A
	HP	3/5	-0.25	0.25	-0.71	A		15/1	0.50	0.50	3.50	RH
	KA	1/2	-0.33	0.33	-0.58	A		4/3	0.14	0.14	0.38	A
	<i>Mean:</i>	4/8	-0.32	0.32	-1.77			10/7	0.33	0.33	1.80	
	<i>SD:</i>	3.6/8.5	0.30	0.30	0.71			8/5	0.20	0.20	0.69	
leaf	JN	9/18	-0.33	0.33	-1.73	A		3/11	-0.57	0.57	-2.14	LH
	ST	4/14	-0.56	0.56	-2.36	LH		3/1	0.50	0.50	1.00	A
	KR	6/23	-0.59	0.59	-3.16	LH		9/5	0.29	0.29	1.07	A
	TN	7/3	0.40	0.40	1.26	A		3/6	-0.33	0.33	-1.00	A
	TW	12/22	-0.29	0.29	-1.71	A		6/19	-0.52	0.52	-2.60	LH
	MG*	0/1	n/a	n/a	n/a	-		0/1	n/a	n/a	n/a	-
	BY	17/35	-0.35	0.35	-2.50	LH		13/23	-0.28	0.28	-1.67	A
	RC	31/57	-0.30	0.30	-2.77	LH		22/18	0.10	0.10	0.63	A
	MK*	0/1	n/a	n/a	n/a	-		0/1	n/a	n/a	n/a	-
	HP	7/16	-0.39	0.39	-1.88	A		12/20	-0.25	0.25	-1.41	A
	KA	11/7	0.22	0.22	0.94	A		12/9	0.14	0.14	0.65	A
	<i>Mean:</i>	12/21.6	-0.38	0.38	-1.54			9/12	-0.34	0.34	-1.44	
	<i>SD:</i>	8/16	0.1	0.1	1.57			6.3/7.7	-0.16	0.16	0.67	

^a R= number of right-hand responses, L= Number of left-hand responses, HI = Handedness Index. ABS-HI = Absolute value of HI. z = z-scores. Category (based on z-scores): LH = left-handed individuals, RH = right-handed individuals, A = ambi-preferent individuals, mean values and standard-deviation (SD) in italics. Individuals* were excluded from analysis.

Appendix IV

Nut-cracking behaviour in wild-born, rehabilitated bonobos (*Pan paniscus*): a comprehensive study of hand-preference, hand grips and efficiency

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There has been an enduring interest in primate tool-use and manipulative abilities, most often with the goal of providing insight into the evolution of human manual dexterity, right-hand preference, and what behaviours make humans unique. Chimpanzees (*Pan troglodytes*) are arguably the most well-studied tool-users amongst non-human primates, and are particularly well-known for their complex nut-cracking behaviour, which has been documented in several West African populations. However, their sister-taxon, the bonobos (*Pan paniscus*), rarely engage in even simple tool-use and are not known to nut-crack in the wild. Only a few studies have reported tool-use in captive bonobos, including their ability to crack nuts, but details of this complex tool-use behaviour have not been documented before. Here, we fill this gap with the first comprehensive analysis of bonobo nut-cracking in a natural environment at the Lola ya Bonobo sanctuary, Democratic Republic of the Congo. Eighteen bonobos were studied as they cracked oil palm nuts using stone hammers. Individual bonobos showed exclusive laterality for using the hammerstone and there was a significant group-level right-hand bias. The study revealed 15 hand grips for holding differently sized and weighted hammerstones, 10 of which had not been previously described in the literature. Our findings also demonstrated that bonobos select the most effective hammerstones when nut-cracking. Bonobos are efficient nut-crackers and not that different from the renowned nut-cracking chimpanzees of Bossou, Guinea, which also crack oil palm nuts using stones.

KEYWORDS

hand grips, laterality, manual dexterity, nut-cracking, tool-use

1 | INTRODUCTION

Tool use and the selective manipulation of objects are widespread across the animal kingdom (Beck, 1980; Bentley-Condit & Smith, 2010) but only a few species of primates use a variety of tools for multiple purposes and show a wide range of different manipulative behaviours in the wild. Wild bearded capuchins and long-tailed macaques are well-known for their regular tool-use, involving highly controlled sequences of percussive actions (e.g. Gumert & Malaivijitnond, 2013; Spagnoletti, Visalberghi, Ottoni, Izar, & Frigaszy, 2011; Visalberghi, Sirianni, Frigaszy, & Boesch, 2015). Orangutans and, to a lesser extent, western lowland gorillas also

have been reported to use tools in the wild (Breuer, Ndongou-Hockemba, & Fishlock, 2005; Meulman & Van Schaik, 2013). However, amongst primates, chimpanzees are commonly regarded as the most skilled tool-users in the wild (McGrew, 1992) and their tool-use skills have been studied extensively since the 1960s (e.g. Boesch & Boesch, 1983; Goodall, 1964; Inoue-Nakamura & Matsuzawa, 1997; Sanz & Morgan, 2013; Sugiyama, 1981). Chimpanzees are particularly well-known for their nut-cracking tool-use behaviour, with different populations across West Africa using a variety of methods and materials (e.g. wood vs. stone hammers) (e.g., Biro, Sousa, & Matsuzawa, 2006; Boesch & Boesch, 1983; Hannah & McGrew, 1987).

In contrast to the relatively ubiquitous and culturally diverse tool-use behaviours of wild chimpanzees (*Pan troglodytes*), it is particularly interesting that their sister taxon, the bonobos (*Pan paniscus*), rarely use tools in the wild. Only a few observations of bonobo tool use have been made in the wild (e.g. Hashimoto et al., 1998; Hohmann & Fruth, 2003; Ingmanson, 1996; Kano, 1982) and most of these are rarely documented instances of simple and occasional tool-use actions (Furuichi et al., 2014; Hohmann & Fruth, 2003). Unlike their chimpanzee cousins, nut-cracking, the most complex primate tool-use behaviour (Matsuzawa, 1994) ever recorded in the wild, has to date never been reported amongst wild bonobos. The simple tool-use actions in wild bonobos such as dragging branches, aimed stick throwing, leaf sponging or the use of leafy twigs to shield from rain (Furuichi et al., 2014; Hohmann and Fruth, 2003; Kano, 1982), involve the use of one hand rather than two hands (MacNeilage, Studdert-Kennedy, & Lindblom, 1987; Hopkins, 1995), few sequential stages to realize the task (Marchant & McGrew, 1991) and a low level of precision of the required motor acts (e.g. Morris, Hopkins, & Bolser-Gilmore, 1993). In contrast, the nut-cracking behaviour in wild chimpanzees requires precise role-differentiated manipulation by both hands (Biro et al., 2006; Humle, 2003; Kano, 1982), the interface of three external objects (hammer, anvil and nut) at the same time, and a high level of motor control and cognitive ability (Matsuzawa, 1994).

Despite the general absence of tool-use in the wild, bonobos in captivity demonstrate an equally diverse and highly complex repertoire of tool-use behaviours compared with captive chimpanzees (Gruber, Clay, & Zuberbuehler, 2010; Jordan, 1982; Roffman et al., 2015; Takeshita & Walraven, 1996). The bonobo 'Kanzi' is the best example illustrating this species' capability to develop highly skilled tool-making and tool-using behaviours (e.g. Toth, Schick, Savage-Rumbaugh, Sevcik, & Rumbaugh, 1993). Kanzi is able to produce stone flakes and selectively choose tools that are more useful than others (Schick, Toth, & Garufi, 1999). These findings suggest that bonobos have the same understanding of the functional properties of tools as other great apes (Herrmann, Wobber, & Call, 2008) and a cognitive ability for tool-related behaviours (Gruber et al., 2010; Jordan, 1982). Gruber et al. (2010) reported the nut-cracking ability in the bonobos of Lola ya Bonobo sanctuary, but details of this complex tool-use behaviour have not yet been documented. In addition, their shared hand and upper limb anatomy with chimpanzees (Diogo & Wood, 2011; Susman, 1979) suggests that bonobos have the same physical capability to perform equivalent manipulative tasks as seen in chimpanzees.

Several hypotheses have been put forth, such as variation in ecological constraints (Furuichi et al., 2014) or inherent differences between the species (Koops, Furuichi, & Hashimoto, 2015), which might explain the relative rarity of tool-use in wild bonobos. Alternatively, tool-use may be more common amongst bonobos but due to their small numbers in the wild and the limited number of habituated groups compared with chimpanzees, primatologists simply may not have yet witnessed their full tool-use repertoire. For example, data for chimpanzees comes from several field sites (Whiten et al., 2001), whereas long-term studies of bonobos are restricted to two populations (Wamba and Lomako, DRC) and the number of individuals

observed at both sites is relatively small (i.e. <25 individuals) (Hashimoto et al., 1998; Hohmann & Fruth, 2003). Moreover, some chimpanzee groups rarely use tools in the wild (Reynolds, 2005; Watts, 2008). Thus, the lack of data on bonobos may exaggerate their reported differences with chimpanzees. Nevertheless, the relative rarity of simple tool-use and the absence of complex tool-use in wild bonobos are in stark contrast to the well-documented and frequent complex tool-use observed amongst captive and wild chimpanzees (e.g. Boesch & Boesch, 1983, Boesch-Achermann & Boesch, 1993; Biro et al., 2006; Hirata, Morimura, & Houki, 2009; Schrauf, Call, Fuwa, & Hirata, 2012).

Many studies of primate tool-use and manipulative abilities aim to provide insights into the evolution of human manipulation, human hand-preference and what gripping abilities make humans unique compared with other primates. Of the non-human primates that have been studied, most show dominant use of one hand at an individual-level for specific tasks (e.g. Cashmore, Uomini, & Chapelain, 2008; Collel, Segarra, & Sabater, 1995; McGrew & Marchant, 1997a; Papademetriou, Sheu, & Michel, 2005). A group-level bias has been occasionally reported in some non-human primate populations (e.g. Corp & Byrne, 2004; Hopkins, Russell, Remkus, Freeman, & Schapiro, 2007; Spinozzi, Truppa, & Lagana, 2004; Vaclair, Meguerditchian, & Hopkins, 2005), but none has ever demonstrated species-wide consistency in hand-preference (i.e. ~90% right-handed) typical of humans (e.g. Annett, 1972; McManus, 2009; Raymond & Pontier, 2004). Hand preference or laterality has been investigated in bonobos but almost exclusively in captive groups, and primarily involving unnatural objects and simple tasks such as reaching for food, gesturing or scratching (e.g. Costello & Frigaszy, 1988; De Vleeschouwer et al., 1995; Harrison & Nystrom, 2008; Hopkins & de Waal, 1995). In all of these studies, most bonobo individuals were non-lateralised (i.e. used both hands interchangeably) for most of the actions studied. However, task complexity has been shown to be an important factor influencing manual laterality in primates (McGrew & Marchant, 1997a; McGrew, Marchant, Wrangham, & Klein, 1999). The nut-cracking behaviour of chimpanzees is a particularly good example of a complex manual behaviour as the chimpanzee individuals exhibit more pronounced laterality of the dominant hand compared with simple unimanual tasks (Boesch, 1991; Humle & Matsuzawa, 2009; Sugiyama, Fushimi, Sakura, & Matsuzawa, 1993). Similar findings have been made for other tool use actions in wild chimpanzees or captive capuchin monkeys (Lonsdorf & Hopkins, 2005; McGrew & Marchant, 1997b; McGrew et al., 1999; Westergaard, Kuhn, & Suomi, 1998). When bonobos are faced with artificial complex bimanual manipulative tasks, they show strong laterality at an individual-level but not at a group-level or population-level (Bardo, Pouydebat, & Meunier, 2015; Chapelain, Hogervorst, Mbonzo, & Hopkins, 2011; Hopkins et al., 2011). However, apart from these few studies, there are no published data on laterality during a natural complex bimanual task performance in bonobos.

Similarly little is known about the diversity of hand grips used by bonobos, especially when manipulating natural objects. Studies of bonobo (and chimpanzee) hand grips are done almost exclusively in captivity (Christel, 1993; Christel, Kitzel, & Niemitz, 1998; Marzke &

Wullstein, 1996; Pouydebat, Reghem, Borel, & Gorce, 2011). These studies show that they are capable of precision grasping between the thumb and finger(s). However, because of their shorter thumb and smaller musculature (Marzke, Marzke, Linscheid, & Smutz, 1999), they are generally considered to not be able to perform these grips as forcefully as humans (Marzke, 1997, 2013). Nevertheless, a recent study of wild chimpanzees suggests the use of forceful precision pinch grips—an ability traditional thought to be unique to humans (Marzke & Shackley, 1986; Marzke & Wullstein, 1996; Marzke et al., 1998)—during food-processing (Marzke, Marchant, McGrew, & Reece, 2015). Long-tailed macaques show a similar ability during stone tool-use (Gumert & Malaivijitnond, 2009), suggesting more research on primate manipulative abilities is needed particularly in natural environments.

Here, we present the first detailed analysis of bonobos cracking oil palm nuts with stone hammers in the Lola ya Bonobo sanctuary, which is in a natural environment in the Democratic Republic of the Congo. The bonobos are known to show nut-cracking behaviour since the first nursery sanctuary was established in 1995. The rescued, wild-born bonobos are integrated into a social group where they can observe nut-cracking behaviour of more experienced individuals. The infants born there have ample opportunity to observe their mothers. This sanctuary population offers a unique opportunity to investigate a natural complex tool-use behaviour in bonobos and how this behaviour compares to the pervasive nut-cracking behaviour practiced by wild chimpanzees.

The aims of this study were to: (1) investigate bonobo hand-preference (i.e. laterality) during a complex tool-use behaviour; (2) identify the full range of hand grips during nut-cracking using various hammer stone weights, shapes, thicknesses and sizes and (3) analyse the efficiency of bonobo nut-cracking relative to a chimpanzee population (Bossou, Guinea) using similar materials (i.e. oil palm nuts and stone hammers). Based on shared anatomy and results from studies in captivity, we predicted that bonobos would use a similar diversity of hand grips as documented during complex manipulative tasks in chimpanzees. However, given that wild populations of bonobos are not known to nut-crack and since this behaviour was only recently shown and disseminated amongst adult members of the first nursery sanctuary in 1995, we predicted that they would be less efficient (i.e. require more hits to crack a nut, crack fewer nuts per minute) than their wild chimpanzee counterparts.

2 | METHODS

2.1 | Species and study site

Lola ya Bonobo is a sanctuary for orphan bonobos rescued from the bush meat and pet trade. Unlike in zoos, the sanctuary enclosures include a natural and complex environment, including high canopy forest areas with oil palm trees, swampy areas, freshwater ponds or river streams. The social groups are divided into three enclosures, which include a semi-natural forested environment in which the bonobos are allowed to range freely throughout the day. All three enclosures allow for nut-cracking behaviour of oil-palm nuts (*Elaeis*

guineensis) and the bonobos can be heard nut-cracking regularly in the forest. Nut-cracking in the open non-forested areas (i.e.: near the sanctuary housing and feeding areas) is facilitated by the placement of anvil stones by humans that are embedded in the ground. Palm oil nuts attached to their branches were supplied by humans in the non-forested areas every morning, but there is also natural supply in forest enclosure. Hammerstones of different sizes and shapes (see below) were placed near the anvils and individuals were free to engage in nut-cracking when and as they wished.

2.2 | Data collection

Data were collected at the Lola ya Bonobo sanctuary during April and May 2015. The research protocols reported in this manuscript were reviewed and approved by the Les Amis des Bonobos du Congo Scientific Committee and its Scientific Coordinator and by the Ethics Committee of the School of Anthropology and Conservation at the University of Kent, UK. The methods used in this research adhered to the American Society of Primatologists principles for the ethical treatment of primates. High-definition video was recorded *ad libitum* at close range from multiple angles during nut-cracking on a sample of 18 individuals across all three bonobo groups, including 12 females and 6 males; 14 adults (>10 years old) and 4 adolescents (7–9 years old) (Badrian & Badrian, 1984). Nut-cracking behaviour for any given individual was divided into 'sessions' and 'bouts'. Hand use and grip patterns for holding stone tools were recorded and analysed for bouts. A 'session' was defined as a period in which one individual was engaged in nut-cracking. A session was considered continuous when the nut jumped away and was immediately picked up again; when the nut was changed; the stone broke apart and cracking continued with the same but smaller stone; or another individual interrupted shortly for sexual behaviour (a common occurrence in bonobos). In all of these instances, the individual did not leave the anvil site. A session was terminated when the individual stopped and walked away from the anvil, starting a new behaviour. A session was generally composed of multiple bouts. Hand use and grip patterns for holding stone tools were recorded and analysed for bouts. A 'bout' was defined as a continued period of nut-cracking behaviour, in which the hand used did not change (regardless of the number of hits) (Humble & Matsuzawa, 2009). A bout was considered terminated if there was a change in the hand(s) used (left vs. right), both hands versus one hand/one foot, grip type, body posture, when the nut was successfully or unsuccessfully cracked, or when nut-cracking was interrupted by another behaviour. Video data were analysed using The Observer XT12 (© Noldus Information Technology, Wageningen, Netherlands) to code hand-preference, hand grips and number of hits, frame by frame.

2.3 | Hand preference

Similar to other studies, we considered the hand used for hammering to be the dominant hand for which aspects of hand use were recorded (Boesch, 1991; Humle, 2003). Hand-preference or laterality was recorded for bouts to ensure independence of data points (e.g. Chapelain et al., 2011; Humle & Matsuzawa, 2009; McGrew &

Marchant, 1996). Only individuals for whom a minimum of 10 bouts or more were recorded were included in the analysis (Humble & Matsuzawa, 2009). We consequently investigated laterality in 15 individuals with a total number of 609 bouts. Laterality was investigated as the relative frequency of right (R) versus left (L) hand use within and across individuals ($H_0: pR = pL$ vs. $H_1: pR \neq pL$). We used a binomial test for proportions to test the null hypothesis of a 50/50 distribution ($H_0: pR = pL$). We further tested the probability of success for the two proportions (R vs. L) in a Bernoulli trial (significance set at $p = 0.05$). We calculated a handedness index (HI) score ranging from -1 to $+1$ for each individual based on the total number of bouts: $HI = (R-L)/(R+L)$ (Chapelain et al., 2011; Humle & Matsuzawa, 2009). Negative values indicate a left hand bias and positive values indicate a right-hand bias. We further calculated the relative frequency of bouts using both hands (bimanual) and one-hand/one-foot in addition to the one handed hammering strategy. In addition, we explored whether right- or left-hand use has an effect on the efficiency of nut-cracking (number of hits per nut, nut-per-minute variable) (Boesch, 1991) via a stepwise regression test. For the model presented here, we excluded age and sex as these factors had no effect.

2.4 | Grip patterns when using hammerstones

2.4.1 | Classification of hand grip types

We investigated hand grips used to hold the hammerstone during nut-cracking in all 18 individuals. Different grips were first categorised broadly into palm (power) and precision grips (Marzke & Wullstein, 1996; Napier, 1993) and then into more detailed classification schemes with more specific focus on precision pinching such as the human three-jaw chuck 'baseball grip' and cradle grip (Marzke, 2013), and grip repertoire that have been identified in both wild and captive bonobos, chimpanzees, macaques and/or capuchin monkeys (Boesch-Achermann & Boesch, 1993; Christel, 1993; Christel et al., 1998; Costello & Fragaszy, 1988; Gumert & Malaivijitnond, 2009; Jones-Engel & Bard, 1996; Macfarlane & Graziano, 2009; Marzke & Wullstein, 1996; Marzke et al., 2015; Pouydebat, Gorce, & Bels, 2009; Spinozzi et al., 2004). Our initial categorization centred on precision pinch, precision/passive palm and power grips that have been previously identified in both wild and captive bonobos and chimpanzees. We further described how the thumb and fingers were used to grip hammerstones and how different grips related to the size, weight, shape and thickness of the hammerstone (see results, Table 1).

2.5 | Measurements and categorization of hammerstones

A total of 28 potential hammerstones were placed next to the anvils of the enclosure. The maximum width (6–25 cm), maximum length (7–30 cm) and weight (0.10–4.48 kg) were measured and the general shape (e.g. oval, triangular) was recorded. Stone weight was categorised as light (0.10–0.38 kg), moderate (0.45–1.24 kg) and heavy (1.38–4.48 kg). An additional eight stones that the bonobo individuals had collected themselves from the forest were also used as

hammerstones. Size and weight could only be inferred for these hammerstones. Stone size was categorised relative to the individual's hand size: small, when '-smaller than the size of the palm-' (i.e. small width; short length); medium, when roughly the size of the palm (i.e. moderate width; moderate length) and large, when '-larger than the palm and fingers-' (i.e. large width; long length). Stone shape and thickness (narrow, medium, thick) were estimated and categorised by visual inspection. Patterns were compared across individuals using the same and different stones.

2.6 | Analysis of hand grips and hammerstones

In our first analysis, we investigated the individual preference for specific hand grips used for 625 bouts and the diversity of grips across 18 bonobos. We recorded the use of each hand grip within a bout (as a bout is defined as the use of one grip only) for each individual and calculated the relative frequencies (Marzke et al., 2015). A step-wise regression analysis was used to test how the stone characteristics influenced the choice of a grip type for each individual. Since the grip types used to hold a stone were categorical, we needed to estimate the parameter of these regression models using a multinomial logistic regression. In this model, the probability of observing a particular hand grip was transformed using the logit function. Both the quantities of deviance and the Akaike information criteria (AIC) were used as indicators of how well the proposed regression model fits the data. A good model displayed a small deviance and AIC value.

2.7 | Nut-cracking efficiency

Following previous studies, we calculated three measures of efficiency during episodes of nut-cracking for each stone per individual: (1) hits per nut: average number of hits required per successfully cracked nut (Boesch & Boesch, 1981); (2) nuts per minute: number of nuts (includes empty nuts and nuts yielding an edible kernel) cracked per minute (Boesch & Boesch, 1981) and (3) success rate: number of nuts yielding an edible kernel cracked per minute (Humble, 2003). We only considered sessions with a minimum of one minute duration of nut-cracking (Boesch & Boesch, 1981; Humle, 2003). Thus, we analysed a sample of 41 sessions and 30 different stones across 16 individuals. In our first analysis, we investigated the potential influence of several factors on the efficiency of nut-cracking in bonobos: (1) the dependency of stone size (width, length), weight, shape and thickness on the average number of hits and (2) the influence of each stone characteristic on the number of nuts cracked per minute. To test our different models, we used the backward elimination in a step-wise regression test to show the dependence of one variable on another. We do not report here on the influence of age and sex as these factors had no effect in our model.

We further used our results for hits per nut and success rate to run a comparable analysis with a Mann-Whitney *U*-test (significance level at $p < 0.05$), with the same data gathered from seven chimpanzees at Bossou, Guinea (Humble, 2003). Wild Bossou chimpanzees are a valuable comparison, because they use stone hammers (as opposed to wood, for example) and also crack solely oil

TABLE 1 Summary of bout data and handedness index (HI) for each bonobo individual

Individual	Sex	Age	Total time of nut-cracking (min)	Bouts of using both hands	Bouts of right hand/right foot	Bouts of exclusive hand use	HI	Category
Opala	F	20	34:35	0	0	66	1.00	RH
Semendwa	F	19	13:40	0	0	21	1.00	RH
Salonga	F	18	09:23	0	0	13	1.00	RH
Elikya	F	10	23:17	0	0	44	1.00	RH
Katako	F	11	20:18	0	0	55	1.00	RH
Pole	M	9	04:56	0	0	10	1.00	RH
Ilebo	M	14	18:33	0	0	24	-1.00	LH
Malaika	F	8	54:45	35	1	50	1.00	RH
Masisi	F	10	17:54	0	5	34	1.00	RH
Muanda	F	12	38:48	22	0	40	-1.00	LH
Lisala	F	14	14:30	0	10	16	1.00	RH
Mbandaka	M	14	26:56	3	0	46	-1.00	LH
Isiro	F	18	19:55	10	0	23	1.00	RH
Kalina	F	17	16:58	23	0	40	-1.00	LH
Likasi	F	14	06:22	0	0	18	-1.00	LH
Bisengo	M	10	07:27	0	0	6	n/a	n/a
Yolo	M	12	04:40	0	0	6	n/a	n/a
Lomako	M	8	02:15	0	0	4	n/a	n/a

Sex: F, female; M, male; LH, left-handed individuals; RH, right-handed individuals. n/a: Individuals with less than 10 bouts were not included in the hand-preference analysis.

palm nuts (as opposed to Panda and Coula nuts, for example) (e.g. Biro et al., 2006; Humle & Matsuzawa, 2009). The efficiency data were obtained through *ad libitum* behavioural sampling in the forest of Bossou.

3 | RESULTS

3.1 | Laterality

When analysing the relative frequency of the dominant hand used for hammering with one hand, all 15 individuals used either the left or right hand exclusively (i.e. completely lateralised in 82% of total 609 bouts across all individuals; $p = 0.000$). Additionally, the handedness index, was always significantly different from 0 (either +1, right-handed or -1, left-handed), confirming a bias in hand use (Table 1). Taking the proportion of right versus left hand use, 10 individuals (66%; nine females, one male) used exclusively the right hand for hammering and five individuals (34%; three females, two males) used exclusively the left hand. The overall right-hand bias across all individuals was highly significant ($p < 0.0001$). We additionally investigated how often the bonobos used another hand use strategy compared to exclusive right or left-handed hammering. Only five individuals—two right-handed females and three left-handed individuals (two females, one male)—occasionally preferred both hands (15% of total 609 bouts across all individuals) and three right-handed females rarely used the right hand/right foot (2.7% of total 609 bouts across all individuals) hammering with

larger stones. The combination of left hand/left foot was not observed.

3.2 | Hand grips used during nut-cracking

Fifteen different hand grips were observed across 18 bonobos (Table 2 and Figure 1). We identified three precision (PC) grips (Pc1-Pc3), in which the object is held away from the palm by the thumb and fingers (Figure 1a-c), as well as six power (Pw) grips (Pw1-Pw6) with active involvement of the entire palmar surface and fingers (Figure 1j-o). We also observed six grips that could not be categorised as either precision or power grips that we thus consider to be novel and important for functional interpretations of hand anatomy (Figure 1d-i). These grips are most similar to the precision finger/passive palm grips identified previously in chimpanzees when stabilising a food object in the hand as the teeth pulled against (Marzke et al., 2015), in long-tailed macaques when holding a stone to crack open oysters (Gumert & Malaivijitnond, 2009), and in humans when holding a core in the non-dominant hand during flake removal with the dominant hand (Marzke, 2006, 2013). However, in bonobos the same grip is dynamic rather than passive, such that the palm is contributing to the force of the strike as the hammerstone hits the object. Since the digits have most contact with the stone and only one part of the palm is in contact with the object, we call this category 'precision finger/active palm grips' (PcApm4-PcApm9).

This study revealed 10 new hand grips that had not been previously reported in the grip repertoire of either wild or captive bonobos, chimpanzees, capuchin monkeys and macaques

TABLE 2 Bonobo hand grips used during nut-cracking.

Grasping category	Digit contact	Acronym	Description	
Precision grip	1-2-3-4	Pc1	Stone held between the full thumb (including the region of the base of the thumb) and lateral aspect of distal and middle phalanges of flexed index finger, buttressed by the distal and middle phalanges of the flexed third and fourth finger. Thumb flexed at interphalangeal (IP) joint	
	1-2-3-4	Pc2	Stone held between thumb pad and dorsal aspect of distal phalanges of flexed digits 2-3-4, away from the palm. Thumb is opposed to Index finger	
	1-2-3-4-5	Pc3	Stone held between thumb at level of IP joint of ventral aspect of proximal phalanx and pads of flexed digits 2-3-4-5, without the palm. Thumb widely abducted and in opposition to the fingers	
Precision finger/ active palm grip	1-2	PcApm4	Stone held between lateral aspect of distal thumb and ventral aspect of index finger, supported by the distal palm. Thumb not flexed and adducted towards Index	
	1-5	PcApm5	Stone held between distal and proximal phalanges of the thumb and lateral aspect of distal phalanx of digit 5, supported by the hypothenar eminence of the extended palm. Thumb flexed at IP joint and abducted	
	1-2-3	PcApm6	Stone held between thumb pad and ventral proximal phalanges of digits 2-3, with support by the distal palm. Thumb is not flexed and adducted towards index	
	1-2-3-4	PcApm7	Stone held between full thumb and flexed digits 2-3-4, supported by the distal palm. Thumb is not flexed and adducted towards index	
	1-2-3-4	PcApm8	Stone held between thumb and dorsal aspect of distal & middle phalanges of the flexed digits 2-3 to the lateral aspect of digit 4, supported by the thenar eminence of the palm. Thumb can be flexed or extended	
	1-2-3-4-5	PcApm9	Stone held between lateral aspect of the thumb and dorsal aspect of distal phalanges of flexed digits 2-3-4-5, supported by the hypothenar eminence of the palm. Thumb flexed at metacarpophalangeal (MP) and IP joints, held adducted towards index	
	Power grip	1-2	Pw1	Stone held between lateral aspect of proximal phalanx of thumb and flexed index finger, supported by the palm and the web at the V-shaped region between thumb and index
		1-2-3	Pw2	Stone held between full thumb and dorsal aspect of distal phalanges of flexed digits 2-3. Thumb flexed at IP joint
		1-2-3-4	Pw3	Stone held between full thumb and dorsal distal phalanges of flexed digits 2-3-4, with support by the palm. Thumb slightly flexed
1-2-3-4-5		Pw4	Stone held between full thumb and dorsal aspect of distal phalanges of flexed digits 2-3-4-5, supported by the palm. Thumb adducted towards Index	
1-2-3-4-5		Pw5	Stone held between thumb and flexed digits 2-3-4-5 at their ventral aspect of proximal phalanges and dorsal aspect of distal and middle phalanges. Stone lies in palm and in web at the V-shaped region between full thumb and index finger	
1-2-3-4-5		Pw6	Stone held in the palm between the thumb and four fingers flexed at the MP or IP joints. Thumb either held opposed, abducted, inside or outside the grip. Hand wrist can adduct with this grip	

(Boesch-Achermann & Boesch, 1993; Christel, 1993; Christel et al., 1998; Costello & Frigaszy, 1988; Gumert & Malaivijitnond, 2009; Jones-Engel & Bard, 1996; Macfarlane and Graziano, 2009; Marzke & Wullstein, 1996; Marzke et al., 2015; Pouydebat et al., 2009; Spinozzi et al., 2004). The remaining five grips (Pc1, Pc3, Pw1, Pw5 and Pw6) have either been reported or show interesting parallels to grips used in wild and captive chimpanzees (Pc1, Pw1, Pw5 and Pw6) (Boesch-Achermann & Boesch, 1993; Jones-Engel & Bard, 1996; Marzke & Wullstein, 1996; Marzke et al., 2015; Pouydebat et al., 2009), macaques (Pc3, Pw6) (Gumert & Malaivijitnond, 2009) and studies of human manipulative behaviour (Pc1, Pc3, Pw6) (Bullock, Zheng, De

La Rosa, Guertler, & Dollar, 2013; Marzke, 2013; Marzke & Shackley, 1986; Marzke & Wullstein, 1996). The similarities will be discussed in more detail below.

Furthermore, the thumb was particularly important in holding and stabilising the hammerstone as has been recognised in wild nut-cracking chimpanzees and stone tool-using macaques (Boesch-Achermann & Boesch, 1993; Gumert & Malaivijitnond, 2009). The thumb was involved in each grip type, either adducted to the index finger, or opposing it, and was always in contact with the surface of the hammerstone throughout a nut-cracking bout. In 10 grips (Pc1-Pc3; PcApm5; PcApm8; PcApm9; Pw1; Pw2; Pw3; Pw5) the stone was

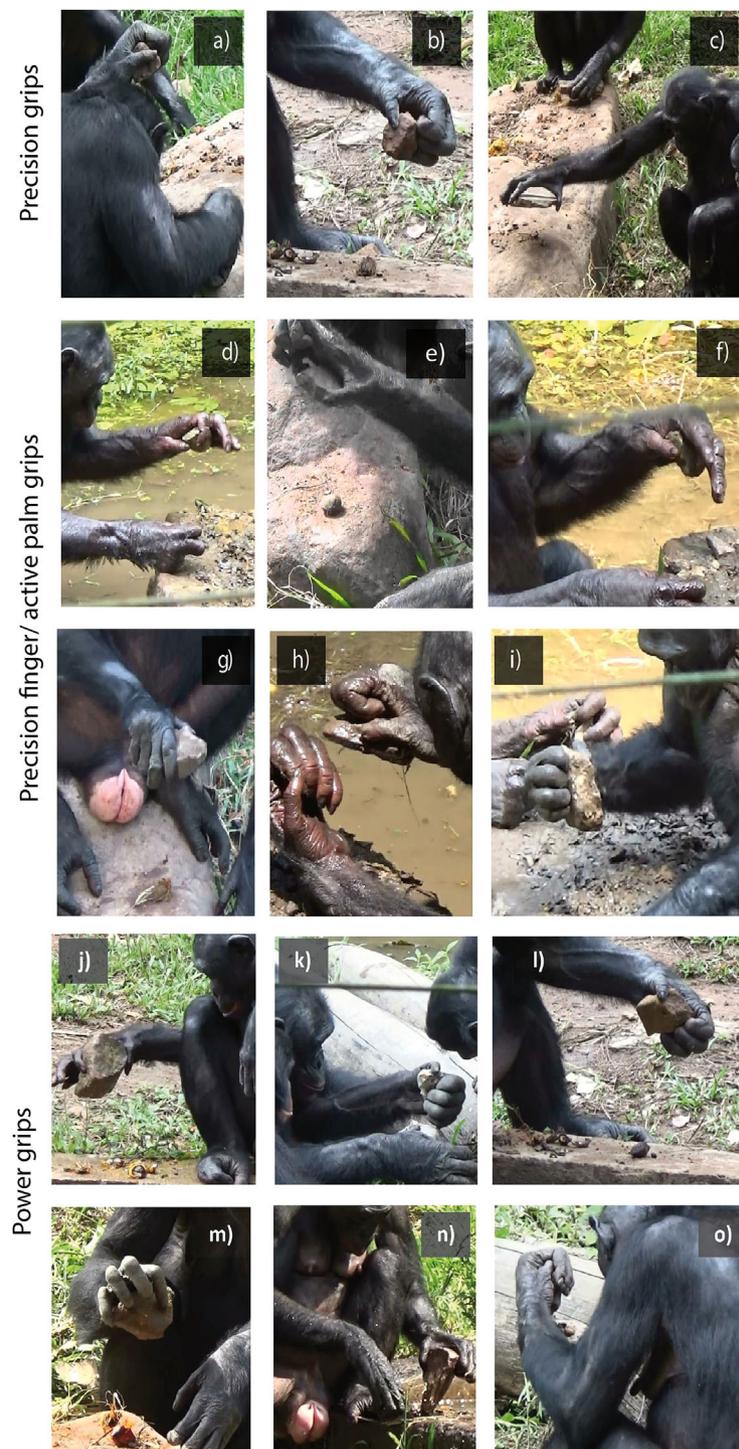


FIGURE 1 Different hand grips used by the dominant hand during bonobo nut-cracking. Bonobo precision grips hold small and medium-sized hammerstones: (a) Pc1 grip; (b) Pc2 grip; (c) Pc3 grip. Novel precision finger/active palm grips typically used for small and medium-sized hammerstones: (d) PcApm4; (e) PcApm5; (f) PcApm6; (g) PcApm7; (h) PcApm8; (i) PcApm9. Power grips were most commonly used to hold all hammerstones: (j) Pw1; (k) Pw2; (l) Pw3; (m) Pw4; (n) Pw5; (o) Pw6 (photographs by J. Neufuss)

pinched between thumb and fingers, suggesting potential forceful loading of the thumb (Figure 1).

3.3 | Relative frequencies of hand grip preference

We observed strong individual differences in hand grip preference and how often particular grips were used (Figure 2). Precision grips were

rarely used and only by two individuals. Precision finger/active palm grips occurred more often and across more individuals ($n = 7$). In contrast, the power grips were much less variable, with the 'Pw6' (including all five digits, such that the stone is held between flexed fingers and the palm, with counter pressure from the thumb; Figure 1o) being by far the most commonly used grip across all bouts and all individuals, regardless of stone weight and size (a multinomial logistic

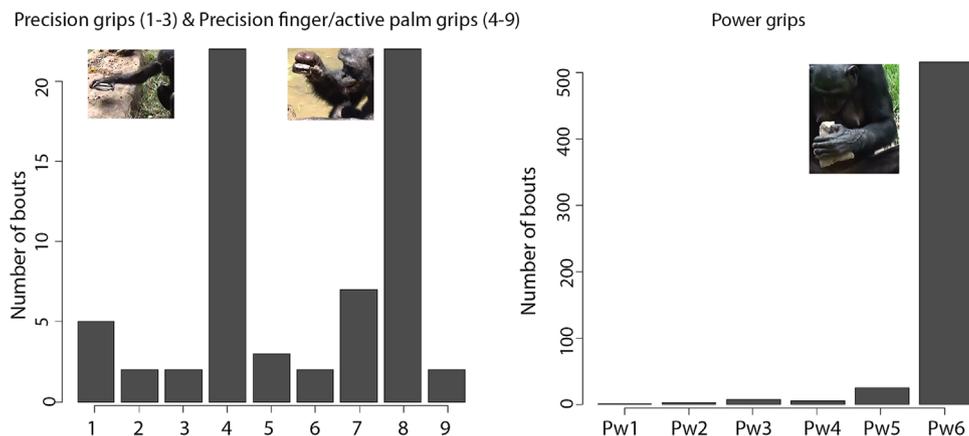


FIGURE 2 Bar graph of relative frequency of hand grips used during nut-cracking. Precision grips (Pc1–Pc3) and precision finger/active palm grips (PcApm4–PcApm9) were used much more rarely and by fewer individuals than power grips (Pw1–Pw6). Note scales differ between graphs. See also Figure 1

regression results found Residual Deviance: 20.05; AIC: 60.50). Table 3 represents the number of bouts a certain precision and power grip was used in relation to the hammerstone weight and size. These results also highlight the individual preferences for a particular hammerstone; moderate-weight and medium-sized stones were used in most bouts while small and light stones were rarely used.

3.4 | Nut-cracking efficiency

Two step-wise regression tests, showed that hammerstone size, weight, thickness and shape all had a strong and significant effect on both measures of efficiency: (1) the average number of hits required to crack a nut ($p < 0.0001$; R^2 values ranging from 0.87–0.96) and (2) the average number of nuts cracked per minute ($p < 0.0001$; R^2 values ranging from 0.87–0.88). Large and heavy stones were significantly more effective than small and light stones, while medium

and moderate weighted stones were not significantly different from larger stones. Thicker stones required significantly fewer hits to crack a nut than thinner stones, but were similarly effective when it came to the number of cracked nuts per minute. Regarding stone shape, square-shaped stones were most efficient (Table 4 and Figure 3).

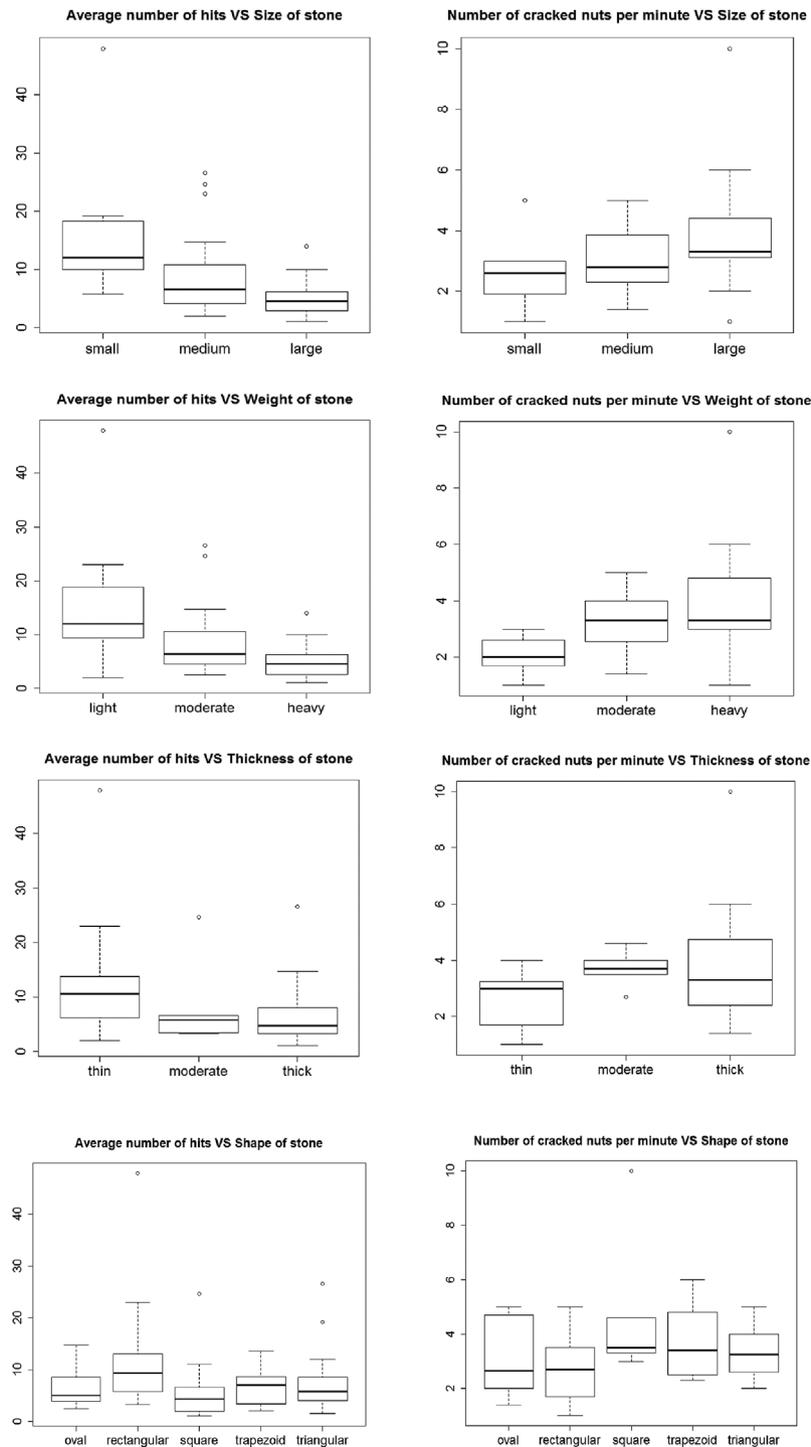
A simple linear regression test showed that the use of the right versus left hand did not have a significant effect on (1) the average number of hits required to crack a nut (F -statistic: 133.3 on 2 and 49 DF, $p < 0.0001$, $R^2 = 0.8447$) and (2) the average number of nuts cracked per minute (F -statistic: 125.6 on 2 and 40 DF, $p < 0.0001$, $R^2 = 0.8624$). Left-handed individuals needed 4.75 (SD: 5.46; range: 20.94) hits to crack 3.5 nuts/minute and right-handed individuals required 6.56 (SD: 8.85; range: 47) hits to crack 3 nuts/minute. Across our sample, we found more variability across the right-handed individuals (Figure 4).

TABLE 3 Frequency of hand grips in relation to hammerstone weight and size

Grip type	Heavy stone	Moderate stone	Light stone	Large stone	Medium-sized stone	Small stone
Pc1	–	–	5	–	–	5
Pc2	–	–	2	–	–	2
Pc3	–	2	–	2	–	–
Pc4	–	–	18	–	–	18
Pc5	–	–	3	–	–	3
Pc6	–	–	2	–	–	2
Pc7	–	4	–	–	–	4
Pc8	–	–	20	–	–	20
Pc9	–	–	2	–	–	2
Pw1	1	–	–	–	1	–
Pw2	–	–	4	–	–	4
Pw3	–	–	7	–	7	–
Pw4	–	5	–	–	5	–
Pw5	–	14	11	0	23	2
Pw6	220	219	28	228	210	29

TABLE 4 Effect of stone characteristics on nut-cracking efficiency

	Mean # of hits per nut			Mean # of nuts per minute		
	F-stat.	p-value	R ²	F-stat.	p-value	R ²
Stone size	12.87	$1.265 \times 10^{(-7)}$	0.96	91.46	≈0	0.87
Stone weight	130.5	≈0	0.88	105.2	≈0	0.88
Stone thickness	88.34	≈0	0.87	95.4	≈0	0.87
Stone shape	53.35	≈0	0.87	59.23	≈0	0.88

**FIGURE 3** Nut-cracking efficiency relative to aspects of hammerstone characteristics

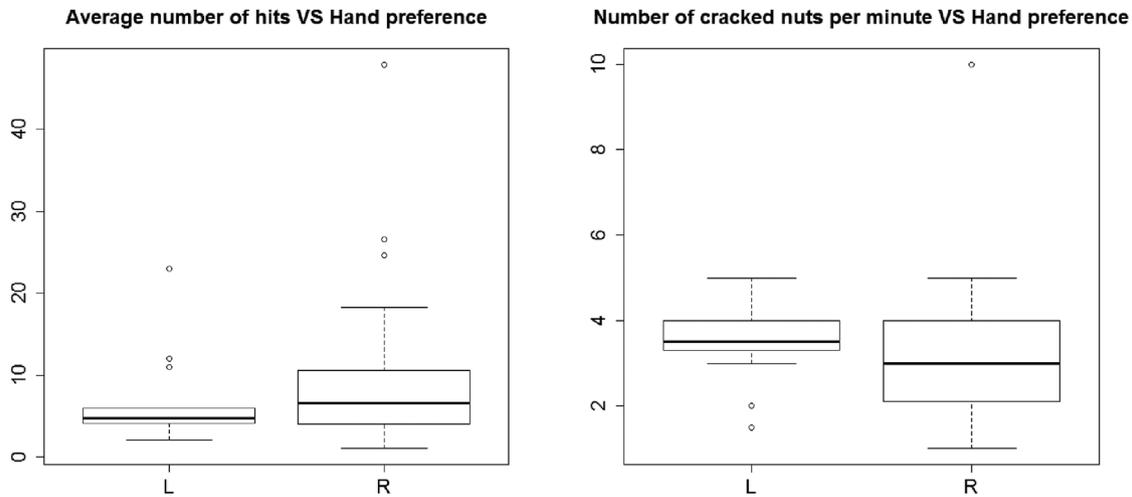


FIGURE 4 Effect of right (R) versus left (L) hand on the efficiency of nut-cracking

3.5 | Nut-cracking efficiency in bonobos and Bossou chimpanzees

We compared the (1) average number of hits per nut and (2) success rate (good nuts cracked per minute). A Mann–Whitney *U*-test revealed that bonobos needed significantly ($p = 0.003$) more hits per nut (median 7.3) than Bossou chimpanzees (median 3.8), but cracked significantly ($p = 0.005$) more nuts per minute (median 2.8) compared with Bossou chimpanzees (median 1.9). Bonobos were also notably more variable across individuals in both efficiency measures (Figure 5).

4 | DISCUSSION

We present here the first detailed study of hand laterality and hand grips used in bonobos at cracking palm nuts with stone tools. We also present the first analysis of nut-cracking efficiency in relation to

qualities of the hammerstone, and how bonobo nut-cracking compares to that of Bossou chimpanzees.

4.1 | Laterality

Most previous studies assessing hand preferences in bonobos have analysed simple tasks (e.g. spontaneous actions like reaching or feeding) in relatively small samples (2–10 individuals) (De Vleeschouwer et al., 1995; Hopkins & de Waal, 1995; Ingmanson, 1996). Although studies of more complex bimanual tasks found stronger individual hand preferences, no individuals were exclusively right- or left-handed (e.g. Bardo et al., 2015; Chapelain et al., 2011; Hopkins et al., 2011). In contrast to this previous work, the individual bonobos in this study were exclusively right- or left-handed and there was an overall significant right-hand bias at the group-level during nut-cracking. The determination of group-level hand preference is generally based on two factors: the strength of the individual hand preference (i.e. handedness index) and the number of individuals

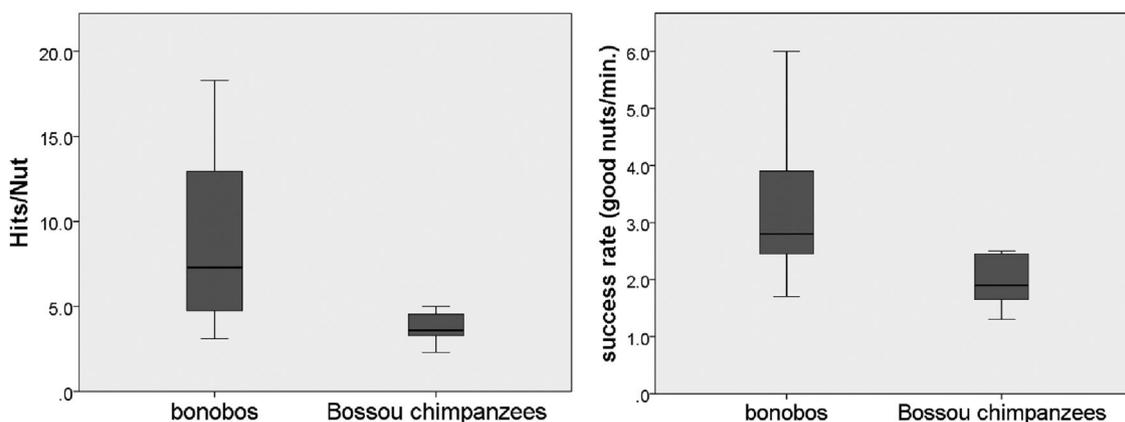


FIGURE 5 Box-and-whisker plots showing variation in nut-cracking efficiency between wild-born, rehabilitated bonobos and habituated, wild Bossou chimpanzees. Bonobos required significant more hits to crack a nut (left) but cracked significantly more good nuts per minute (right)

investigated (e.g. Papademetriou et al., 2005). Because bonobos (and other non-human primates) rarely exclusively use one hand for particular tasks (i.e. they have a relatively low handedness index), larger sample sizes are considered necessary to reliably detect a group-level bias (defined as >65% of the individuals in the group) (Hopkins 2013a, 2013b; Hopkins & Cantalupo, 2005; Hopkins et al., 2012). In this study, the exclusive use of either the left- or right-hand (i.e. a high handedness index) by the 15 bonobo individuals suggests that use of the right-hand by 66% of the individuals may reliably estimate a group-level right-hand bias for this particular complex manipulative behaviour. Although a future study of more individuals is needed to confirm this bias, these results are consistent with previous reports of nut-cracking in chimpanzees (Humble & Matsuzawa, 2009; Matsuzawa, 1996). Moreover, wild chimpanzees of Gombe show exclusive use of one hand or the other when pounding hard-shelled fruits (*Strychnos* spp.) on anvils (McGrew et al., 1999). Wild western gorillas have been recently reported to demonstrate exclusive hand-preference and an overall right-hand bias during natural bimanual termite feeding (Salmi, Rahman, & Doran-Sheehy, 2016).

Hand use in relation to task complexity has been studied across four tool-using tasks in Bossou chimpanzees (Humble, 2003). Nut-cracking, the most cognitively complex of the four behaviours studied and the only one requiring complementary coordination of both hands, revealed the strongest degree on laterality in all adult individuals ($n = 7$). Humle (2003) suggested that Bossou chimpanzees have a right-hand bias at the population-level, which was supported by Biro et al. (2006), reporting a high proportion of right-handed individuals (62%) for nut-cracking in the same community. The Taï chimpanzees of Côte d'Ivoire show a hand-preference during nut-cracking at the individual-level, but the overall distribution was not biased to the left or right (Boesch, 1991). The study reported that 18 individuals were significantly, but not completely lateralised, while another 18 individuals were exclusively lateralised, with 10 chimpanzees being right-handed (Boesch, 1991). However, Taï chimpanzees typically use wooden hammers and more often use both hands and also the feet when the hammer is large (Boesch, 1991).

In comparison to one-handed hammering, our study provides the first data on bonobos using a hand use strategy for different sized stone hammers. Most of the bonobos used one hand to hold small and medium-sized hammerstones. Five bonobo individuals occasionally preferred both hands (15% of total bouts) and three rarely their right-hand/right foot (2.7%) when hammering with larger stones. For example, two females used both hands throughout a session when hammering with the same large and heavy stone (25 cm wide, 30 cm long, 3 kg). Two other females were observed to switch between one-hand and both hands for the same large and heavy stones (a: 13 cm wide, 14 cm long, 3 kg; b: 15 cm wide, 23 cm long, 4.4 kg), while the bimanual action was clearly more preferred for a higher number of bouts. A male bonobo also occasionally tended to use his right-hand to support the dominant left-hand when hammering with a large and heavy stone (17 cm wide, 18 cm long, 4.48 kg). Three females used in addition to one-hand and both hands their right-foot to handle large, heavy and large, moderate stones. One female switched several times between one-hand, both hands and her right-hand/right foot when

pounding nuts with four different large and heavy stones. Our results provide first evidence that bonobos do adapt an effective hand-use strategy to handle the different size and weight properties of their hammerstones.

4.2 | Hand grips

This study revealed 10 new grips not previously reported in the literature and five grips that have either been previously reported or show interesting similarities to grips used by wild and captive chimpanzees and macaques, as well as in humans.

As Marzke & Wullstein (1996) highlighted previously, the basic division of precision versus power grips as defined originally by Napier (1956) is not sufficient to describe and understand the complexity of manual manipulation in humans and other primates. Indeed, we observed three precision grips (Pc1-Pc3) between the fingers and thumb (i.e. without involvement of the palm), six power grips (Pw1-Pw6), with active contribution by the palm, and created a new category of grips called 'precision finger/active palm' to accurately describe the manual manipulation of bonobo nut-cracking (Table 2 and Figure 1). We also observed high variability across individuals in the use of precision grips and precision/active palm grips, showing the versatility of the bonobo hand in accommodating hammerstones of varying size and shape (Table 3 and Figure 2). Overall, this display of manipulative flexibility was unexpected given that previous work on hand grips or object manipulation during tool-use in captive bonobos has not reported this degree of variability (Christel, 1993; Christel et al., 1998; Jordan 1982).

4.2.1 | Precision grips

Precision grips were only used by two bonobos, but to the best of our knowledge, none of the precision grips has been described in studies of captive bonobos (Christel, 1993; Christel et al., 1998) and capuchin monkeys (Costello & Fragaszy, 1988; Spinozzi et al., 2004) and wild nut-cracking chimpanzees (Boesch-Achermann & Boesch, 1993). The bonobos most often used precision grips when holding small hammerstones, which might explain why they have not been reported in wild chimpanzees that typically use much larger hammerstones (Boesch & Boesch, 1983). However, the grips used by the chimpanzees in nut-cracking have not yet been systematically described in the same detail as presented here for the bonobos and thus future studies may reveal greater overlap in grip types between the two sister taxa. The Pc2 grip (in which the stone is held between the thumb and dorsal aspect of the distal phalanges of the flexed digits 2-3-4, and the thumb is opposed to the index finger, Figure 1b) has to the best of our knowledge not been reported in the literature before. The grip was used by one male bonobo after the hammerstone broke apart and he continued hammering with the smaller stone. The other two precision grips were used for five bouts (Pc1) and two bouts (Pc3) by one individual, and offer insight into the manipulative capabilities of the bonobo hand. The Pc1 grip (in which the stone is held between the full thumb and lateral aspect of the distal and middle phalanges of the index finger, buttressed by the distal and middle phalanges of the third and fourth finger; Figure 1a) is similar to the 'two-jaw chuck'

pad-to-side grip reported in captive and wild chimpanzees (Jones-Engel & Bard, 1996; Marzke & Wullstein, 1996; Marzke et al., 2015). While chimpanzees use only the thumb pad and side of the index finger when grasping different food objects, the bonobos also recruit the buttressed middle and fourth finger to stabilise the hammerstone. In humans, the buttressed pad-to-side grip is used when holding a flake and to pinch the tool tightly between the distal thumb pad and finger(s) (Marzke, 2006, 2013; Marzke & Shackley, 1986). The bonobo also used the region of the base of the thumb to stabilise the stone firmly enough against the index finger and buttressed middle and fourth fingers to resist displacement of the tool by the reaction force of the nut. The Pc3-precision grip shows interesting parallels to the human 'four and five-jaw chuck' precision grip, with opposed pads of the thumb, index, and fingers 3–4, 5 used for holding hammerstones (Figure 1c) (Marzke & Shackley, 1986). In bonobos, the hand-sized stone is held between the thumb at level of the interphalangeal joint of the palmar aspect of the proximal phalanx and the pads of the four fingers, without contact to the palm. This grip appears to have a certain degree of finger-to-thumb pinching as the flexed fingers secure the stone and the widely abducted thumb serves as a prop. However, the grip is not as strong as in the human 'four and five-jaw chuck' grip to press objects firmly against the fingers, since the stone is held right above the nut and firm pressure by the thumb and fingers is not likely to be required. A similar form of finger-to-thumb pinching has been observed in wild long-tailed macaques for pound hammering and is described as a finger-to-thumb/passive palm grip (Gumert & Malaivijitnond, 2009). Although the use of precision grips were rare, in all instances, the bonobos were able to hold the stone firmly enough between the thumb and fingers (without the palm) to crack the nut successfully and with enough force that a relatively low number of hits (mean: 7.2) were needed. This action during nut-cracking suggests forceful loading of the thumb in a manner that is more similar to the human and wild long-tailed macaques pinch grips than would be typically incurred during power grips (see below Section 4.2.2). Although, the relatively rare use of these grips suggests that they may not be as comfortable or effective given bonobo hand morphology.

4.2.2 | Precision finger/active palm grips

During nut-cracking, bonobos grasped small and medium-sized hammerstones tightly between the thumb and fingers, with an additional force applied by the palm only at the moment of strike. Such grips have not been reported during nut-cracking in Taï chimpanzees (Boesch-Achermann & Boesch, 1993) or feeding in Mahale chimpanzees (Marzke et al., 2015). When the bonobos used small hammerstones, something also not observed in nut-cracking chimpanzees (Boesch & Boesch, 1983, Boesch-Achermann & Boesch, 1993), there is relatively little room to strike the nut without smashing the fingers. The bonobos grasped the stone precisely in such a way as to expose the hammering surface and allow the palm to contribute force, but so the fingers would not be crushed (Figure 1d). Thus, these grips are best described as 'precision finger/active palm grip' (PcApm4–PcApm9), as they describe the change that occurs as the

hand goes from a 'precision finger/passive palm grip' of the stone (Marzke & Wullstein, 1996) to a more active involvement of the palm (Figure 1d–i). This grip is different from the cup grip reported in captive chimpanzees (Marzke & Wullstein, 1996) or the pinch grip with passive palm support seen in wild long-tailed macaques during stone hammering (Gumert & Malaivijitnond, 2009). Precision finger/active palm grips were used by eight bonobos, with 'PcApm4' (stone held between the lateral aspect of the distal thumb and palmar aspects of the distal and middle phalanges of the index finger; Figure 1d) and 'PcApm8' (stone held between the thumb and dorsal aspect of distal and middle phalanges of the flexed digits 2–3 to the lateral aspect of digit 4, supported by the thenar eminence of the palm; Figure 1h) being the most common (Figure 2).

4.2.3 | Power grips

The bonobos most often used power grips to hold the hammerstone during nut-cracking (Figure 1j–o). Although six different power grips were used across all individuals, only three (Pw1, Pw5, Pw6) can be compared to studies on wild and captive chimpanzees and macaques. The Pw6-power grip was used amongst all individuals, in which the stone was held between all of the fingers and the palm with counter pressure from the thumb (Table 2) (Pw6; Figure 1o). This grip was used across different hammerstones, regardless of size, shape, thickness or weight, and appears to be the most effective grip for nut-cracking. A similar grip was also shown to be the most effective in humans during nut-cracking (Bril et al., 2015). For larger stones, the thumb was normally held in opposition (Figure 1j) to or adducted to the fingers, while for smaller stones the thumb was held outside or inside the grip (Pw6; Figure 1o). A similar power grip has been observed in wild long-tailed macaques during one-handed pound hammering (Gumert & Malaivijitnond, 2009) and in captive chimpanzees when grasping larger food objects (Jones-Engel & Bard, 1996; Pouydebat et al., 2009). The bonobo power grip 'Pw6' appears also similar to the power grip typically used by the nut-cracking Taï chimpanzees (Boesch-Achermann & Boesch, 1993). However, only juvenile Taï chimpanzees grasped small stones with the thumb held inside the grip, whereas adult bonobos frequently used this grip (Figure 1o). This type of power grip involves adduction of the wrist rather than flexion, so that the stone is exposed at the ulnar side of the palm and strikes the nut (Figure 1o). This action would have the advantage of avoiding smashing of the fingers that would occur when hammering with a flexed wrist, while at the same time allowing a firm grip by the thumb and fingers. We observed less frequent use of two power grips (Pw1, Pw5; Figure 2) involving the 'V-shaped' region between the thumb and index finger, first reported in Mahale chimpanzees during feeding (Marzke et al., 2015). The chimpanzee 'V-pocket' grip is used to securely hold large fruits in the web between the full thumb and index finger, buttressed by the flexed third, fourth and fifth digits (Marzke et al., 2015). In bonobos, medium-sized hammerstones were rarely secured against the web of the palm either by the lateral aspect of the thumb and flexed index finger (Pw1; Figure 1j) or more frequently by the thumb and the flexed four fingers at their ventral aspect of proximal phalanges and dorsal aspect of distal and middle phalanges

(Pw5; Figure 1n). Three new power grips (Pw2–Pw4) were also identified, typically used with small and medium-sized hammerstones and with relatively low frequency by four bonobos in our sample (Figure 2). In most of these grips, the hammerstone was held between the palm, thumb and dorsal surface of the distal phalanges (i.e. fingers flexed) (Figure 1k–m).

Bonobo hand grips (PcApm9, Pw5, Pw6; Figure 1i, n and o) occasionally involved rotation of medium-sized hammerstones within the palm of one hand against the anvil surface, by movements at the carpometacarpal, metacarpophalangeal or interphalangeal joints of the thumb and finger(s). Re-positioning of the stone helped to expose a different side of the hammering surface or to change the grip (e.g., Pw6 to Pw5). Additionally, medium- and large-sized stones were grasped by the opposite hand, turned over by the hand via movement at the wrist, elbow and shoulder joints, and then placed back in the other hand to be regrasped in the desired orientation. Unlike in humans, we did not observe translation (object moved between the palm and fingertips) or precision handling (object moved by the digits alone) (e.g. Marzke & Shackley, 1986; Marzke & Wullstein, 1996), but found interesting parallels to a captive study of chimpanzee 'in-hand movements' (Craet, Frigaszy, Hayashi, & Matsuzawa, 2009). Similar to the bonobo's hand movements, chimpanzees perform in-hand movements for changing their grip on the object, sometimes using a surface when rotating an object, and turning objects over in bimanual actions (Craet et al., 2009).

4.3 | Nut-cracking efficiency

In this study of bonobo nut-cracking, we found that bonobos most often preferred the most efficient hammerstones. The weight, size, thickness and shape of a particular hammerstone had a significant effect on the number of hits required to crack a nut and on the number of nuts cracked per minute. The bonobos were significantly more efficient with larger and heavier stones, than with small and lighter (0.1–0.38 kg) stones. However, most individuals chose to use moderate-weight (0.45–1.24 kg) and medium-sized stones to crack open nuts, which appeared easier to handle than larger, heavier (1.38–4.48 kg) stones and did not significantly differ in efficiency. Comparable studies on captive chimpanzees showed that, like bonobos, they preferred to use heavier hammers (1.2 kg, 1.4 kg) that required fewer hits and less time to crack open nuts (Schrauf et al., 2012). Wild Bossou chimpanzees differentiate stones by width, length and weight, choosing to use lighter stones as hammers and heavier stones as anvils during nut-cracking (Biro et al., 2006). Nut-cracking capuchin monkeys also actively select particular hammerstones based on the material and weight that is most appropriate to crack open palm nuts (Schrauf, Huber, & Visalberghi, 2008; Visalberghi et al., 2009).

Given that bonobos are not known to nut-crack in the wild, we found, not surprisingly, significant differences in nut-cracking efficiency between bonobos and Bossou chimpanzees. The bonobos needed on average almost twice as many hits to crack open a palm nut compared with Bossou chimpanzees. However, contrary to our predictions, bonobos were able to crack on average nearly one more

nut per minute than their congeneric wild chimpanzee. These differences may result from two factors. First, there was a difference in the general strategy of collecting nuts (as collection time was included in the measure; see Section 2); although both the bonobos and Bossou chimpanzees cracked nuts next to the palm nut source (i.e. 1–2 m), the chimpanzees tended to spend more time collecting multiple nuts at one time to transport back to the anvil whereas the bonobos spent less time collecting because nuts were more readily available around their nut-cracking area. Second, the bonobos likely required a greater number of hits because, unlike Bossou chimpanzees (preferred hammers have an average weight of 1.0 kg; Biro et al., 2006), they also used lighter (0.10–0.38 kg) stones and were cracking fresher nuts that are much more challenging to crack than dry nuts. Regardless of these differences, these rehabilitated bonobos, which have only recently (i.e. last ~20 years) developed nut-cracking behaviour are surprisingly similar in efficiency to that of chimpanzees with a long history (i.e. 4.300 years; Mercader et al., 2007) of nut-cracking and other types of complex tool use.

5 | CONCLUSION

This first detailed study of nut-cracking in bonobos revealed an unexpected manipulative versatility during stone tool-use, including 10 novel hand grips. This most complex tool-use behaviour showed 100% lateralisation and a significant right-hand bias in most of the individuals studied, speaking to a group-level bias. Bonobos also have the ability, like nut-cracking capuchin monkeys (e.g. Schrauf et al., 2008) and chimpanzees (Boesch & Boesch, 1983; Biro et al., 2006) to select the most effective hammerstones. Moreover, bonobos can be efficient nut-crackers with a skill level not that different from wild chimpanzees. It is clear from this study, that more future studies on complex tool-use behaviour in bonobos under natural conditions are required, in order to explore the full range of their manipulative and tool-use capabilities.

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CONFLICT OF INTEREST

The authors acknowledge no conflict of interest in the submission.

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RESEARCH ARTICLE

Comparison of hand use and forelimb posture during vertical climbing in mountain gorillas (*Gorilla beringei beringei*) and chimpanzees (*Pan troglodytes*)

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Abstract

Objectives: Studies on grasping and limb posture during arboreal locomotion in great apes in their natural environment are scarce and thus, attempts to correlate behavioral and habitat differences with variation in morphology are limited. The aim of this study is to compare hand use and forelimb posture during vertical climbing in wild, habituated mountain gorillas (*Gorilla beringei beringei*) and semi-free-ranging chimpanzees (*Pan troglodytes*) to assess differences in the climbing styles that may relate to variation in hand or forelimb morphology and body size.

Materials and methods: We investigated hand use and forelimb posture during both ascent and descent vertical climbing in 15 wild mountain gorillas and eight semi-free-ranging chimpanzees, using video records obtained *ad libitum*.

Results: In both apes, forelimb posture was correlated with substrate size during both ascent and descent climbing. While climbing, both apes used power grips and diagonal power grips, including three different thumb postures. Mountain gorillas showed greater ulnar deviation of the wrist during vertical descent than chimpanzees, and the thumb played an important supportive role when gorillas vertically descended lianas.

Discussion: We found that both apes generally had the same grip preferences and used similar forelimb postures on supports of a similar size, which is consistent with their overall similarity in hard and soft tissue morphology of the hand and forelimb. However, some species-specific differences in morphology appear to elicit slightly different grasping strategies during vertical climbing between mountain gorillas and chimpanzees.

KEYWORDS

African apes, forelimb, hand grip, thumb, vertical climbing

1 | INTRODUCTION

Arboreal locomotor behaviors, although generally practiced infrequently compared to terrestrial locomotion, are critical to the daily life and survival of African apes. In particular, vertical climbing is used to access important food sources (e.g., Pilbeam, 2002; Remis, 1995; Robbins,

2008), to change levels within the forest canopy, to exploit safer substrates for horizontal travel, for safety from predators and for access to sleeping sites (e.g., Garber, 2007; Hunt, 1992a; Preuschoft, 2002; Thorpe & Crompton, 2006). Records of the frequency of arboreal locomotion in wild African apes varies depending on the species and population (e.g., Crompton, Sellers, & Thorpe, 2010; Doran, 1993, 1996;

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Remis, 1995; Tuttle & Watts, 1985). Most studies agree that gorillas are less arboreal than chimpanzees and bonobos (Tuttle & Watts, 1985; Doran, 1996; Crompton et al., 2010; Hunt, 2016). In particular, mountain gorillas (*Gorilla beringei beringei*) are typically considered the least arboreal of all the great apes and are thought to spend less than 1% of total locomotor time engaging in vertical climbing (Tuttle & Watts, 1985).

Arboreal locomotor behaviors in mountain gorillas have to date only been broadly described (e.g., Doran, 1996; Schaller, 1963) and the frequency is likely underestimated (Crompton, 2016). One possible explanation for the much lower reported frequency of arboreal locomotion in mountain gorillas compared with western lowland gorillas (e.g., Nishihara, 1992; Remis, 1994, 1995; Tutin, 1996; Tutin, Fernandez, Rogers, Williamson, & McGrew, 1991) may be differences in habitat structure and resource availability, as these have a substantial influence on gorilla locomotion (Remis, 1995). Most mountain gorilla locomotor data come from the Volcanoes National Park, Rwanda (e.g., Doran, 1996, 1997). Remis (1999) suggested that the high frequency of terrestrial knuckle-walking exhibited by mountain gorillas at sites like Karisoke in the Virunga mountains represents an adaptation to a high-altitude dwarf forest environment, which likely limits their arboreality (average height climbed in trees <7 m; Doran, 1996; Fossey, 1983; Remis, 1998; Watts, 1984). However, little is known about gorilla arboreal locomotion in this type of environment and thus, the frequency of arboreal locomotor behaviors is generally based on estimates (e.g., Crompton et al., 2010; Tuttle & Watts, 1985).

The mountain gorillas of Bwindi Impenetrable Forest live at lower altitude (1,160–2,607 m; Robbins et al., 2006) with more trees and a denser forest canopy than that of Karisoke (canopy height ranges between 10 and 35 m; Shaw & Shewry, 2001). Tree use by gorillas is relatively common at Bwindi when, for example, foraging for fruits (Robbins, 2008; Sarmiento, Butynski, & Kalina, 1996). Studies of feeding behaviors have revealed that Bwindi mountain gorillas climb trees for several months of the year, making use of arboreal fruit resources when they are seasonally available (Ganas, Robbins, Nkurunungi, Kaplin, & McNeilage, 2004; Robbins, 2008; see methods). For example, Bwindi gorillas spent 95 days of 324 observation days eating fruit in trees (29.3%), including 403 trees and 15 fruit species (Robbins, 2008), supporting recent assertion by Crompton (2016) that the <1% frequency for vertical climbing reported in mountain gorillas is likely an underestimation. However, to date, vertical climbing in wild mountain gorillas has not been examined in detail.

Arboreal locomotion in chimpanzees, by contrast, is more frequent (spending up to half of their time in trees; Tuttle & Watts, 1985). Chimpanzee habitats are typically located in mid-altitude (e.g., 1500 m; Pontzer & Wrangham, 2004) thicket woodland or tropical montane rainforest habitats with tree heights >30 m (e.g., Stanford & O'Malley, 2008). While several studies investigated different arboreal locomotor behaviors in wild chimpanzees, they were mainly associated with body size effects, musculoskeletal adaptations of the upper body, or their daily energy cost (Hunt, 1991a, 1992b, 1994; Pontzer & Wrangham, 2004).

During arboreal locomotion, and particularly vertical climbing, primates face several biomechanical challenges that often require changes

in forelimb and hand posture. For example, the difficulty of maintaining stability increases as substrates get smaller and/or are more inclined because the risk of toppling backwards becomes higher when propulsive forces in the hindlimbs increase (e.g., Cartmill, 1974; Preuschoft, 2002; Preuschoft & Witte, 1991). Our understanding of the ways in which primates cope with these challenges is largely based on small and medium-sized non-hominoid primates (e.g., mouse lemurs, cotton-top tamarins, lemurs or macaques; ranging from 0.06 to 11 kg; Hirasaki, Kumakura, & Matano, 1993; Johnson, 2012; Nayakatura, Fischer, & Schmidt, 2008; Shapiro, Kemp, & Young, 2016) and theoretical models (e.g., Cartmill, 1974, 1979; Preuschoft, 2002, 2004; Preuschoft & Witte, 1991). However, the challenges of vertical climbing are amplified for larger-bodied primates, such that, both mechanical challenges and relative energetic costs of climbing increase in primates with a larger body size (Hanna, Schmitt, & Griffin, 2008). Larger-bodied primates appear to use their forelimbs mainly in tension and the hindlimbs mainly in compression, both when ascending and descending vertical substrates (Hanna, Granatosky, Rana, & Schmitt, 2017; Preuschoft, 2002). When climbing on large substrates, wild chimpanzees have been observed to extend their elbows ("extended-elbow vertical climbing") while the forelimbs assist in elevating the body through flexion of the elbow on small substrates ("flexed-elbow climbing") (Hunt, 1991b, 1992; Hunt, Cant, Gebo, Rose, & Walker, 1996). General similarity in elbow joint morphology among apes is interpreted as an adaptation for elbow stability in varied forelimb postures used during climbing and other forms of arboreal locomotion (e.g., Drapeau, 2008; Jenkins, 1973; Rose, 1988, 1993). The hands are critically important to maintaining stability on differently-sized vertical substrates and providing a counterbalance to the feet (DeSilva, 2009; Hirasaki et al., 1993; Johnson, 2012; Nakano, 2002). Increased friction force between the prehensile hands (and feet) with the substrate (i.e., support phase) is needed when climbing upon vertical supports (Preuschoft, 2002).

Although previous studies demonstrate the importance of the primate forelimbs and hands during vertical climbing and the potential high loads that the hands may experience by gripping vertical substrates, they do not consider the actions that the hands are performing to facilitate this locomotion.

Detailed observations about how the hands grasp substrates during different arboreal locomotor behaviors have been reported in great apes, but these data were mainly obtained in captive settings and are limited, particularly in regards to the functional role of the thumb (Alexander, 1994; Hunt, 1991a; Marzke & Wullstein, 1996; Marzke, Wullstein, & Viegas, 1992; Sarmiento, 1988, 1994).

The short thumb of African apes is not used during knuckle-walking (e.g., Tuttle, 1967; Wunderlich & Jungers, 2009) and its functional importance during arboreal behaviors, particularly during suspensory locomotion, has traditionally been downplayed (Ashely-Montagu, 1931; Rose, 1988; Sarmiento, 1988; Straus, 1942; Tuttle, 1967). However, a preliminary study of orangutan arboreal locomotion revealed that they recruit the thumb much more often (i.e., more than 53% of hand postures included thumb use) when grasping arboreal substrates than traditionally believed (McClure, Phillips, Vogel, & Tocheri, 2012).

Among African apes, chimpanzee grips and hand postures have received the most attention. Chimpanzees use power grips, diagonal power grips and diagonal finger hook grips during vertical climbing as well as recruit their thumbs in different postures relative to differently sized substrates (Alexander, 1994; Marzke & Wullstein, 1996; Marzke et al., 1992; Napier, 1960). In contrast, arboreal hand use in gorillas has only once been broadly described in captivity, showing that western lowland gorillas use a more flexed wrist posture on smaller than on larger vertical supports to enable that the hand can wrap around the grasped support (Sarmiento, 1994).

Gorillas have a significantly longer thumb relative to the length of their fingers compared to other great apes (Susman, 1979), such that their hand proportions (defined as thumb length relative to length of the fourth digit) are more similar to humans than those of chimpanzees (Almécija, Smaers, & Jungers, 2015). A relatively longer thumb is thought to enhance opposability to the fingers during grasping (e.g., Marzke, 1997; Napier, 1993). Enhanced opposability is usually discussed within the context of manipulation (e.g., Marzke, 1997), but the variation in hand proportions, as well as differences in body size, between gorillas and chimpanzees may also result in different grip and thumb use strategies during vertical climbing. However, there are no studies of which we are aware that have investigated mountain gorilla arboreal hand use, or how grasping posture might vary with forelimb posture during vertical climbing on natural substrates in gorillas compared with chimpanzees.

The aim of this study was to provide the first insights into the hand use and forelimb posture of mountain gorillas and free-ranging chimpanzees used during vertical climbing (both ascent and descent) on natural substrates. First, we predict that shared features in forelimb morphology and body size within *Gorilla* (females 71.0–97.5 kg; males 162.5–175.2 kg across *G. beringei*, *G. gorilla*, *G. graueri*; Smith & Jungers, 1997) and within *Pan* (females 33.2–45.8 kg; males 42.7–59.7 kg across *P. paniscus* and *P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus*; Smith & Jungers, 1997) will elicit similar forelimb postures during vertical climbing between (1) mountain gorillas and western lowland gorillas (Isler, 2002, 2003, 2005), and (2) between chimpanzees and bonobos (Isler, 2002, 2005). Second, we hypothesize that differences in hand and forelimb morphology, as well as body size, between mountain gorillas and chimpanzees will elicit different forelimb postures and grasping strategies on supports of a similar size. Third, we predict that given the relatively longer thumb length of mountain gorillas, they will more often oppose their thumbs during grasping than chimpanzees.

2 | MATERIALS AND METHODS

2.1 | Species and study sites

Mountain gorillas (*Gorilla beringei beringei*) were observed in the Bwindi Impenetrable National Park (331 km²) in the southwest corner of Uganda (0° 53'1"08"N; 29°35'–29°50'E), with an altitude of 2,100–2,600 m (Ganas et al., 2004; Robbins & McNeilage, 2003; Wright et al., 2015). Data were collected on two fully habituated groups of gorillas

(Kyagurilo and Bitukura) between October–December 2014 and March–July 2015 during two fruiting seasons.

Chimpanzee (*Pan troglodytes* ssp.) vertical climbing data were collected between August–September 2014 on two colonies of semi-free-ranging chimpanzees at the Chimfunshi Wildlife Orphanage Trust (CWO), Zambia. Each colony was composed of a mixture of wild-born chimpanzees (e.g., from Tanzania, Uganda and Rwanda; Rawlings, Davila-Ross, & Boyson, 2014) and chimpanzees born at the CWO. All individuals in our study were living within a dry woodland natural environment in large outdoor enclosures (25–77 ha).

2.2 | Data collection

Vertical climbing for any given individual was divided into 'sequences' and 'limb cycles'. A 'sequence' was defined as a continued period of climbing behavior. A sequence started when the right hindlimb was initially placed in contact with the substrate and stopped if climbing was interrupted by a change of the substrate using another locomotor mode, or by a switch in behavior, such as sitting or feeding. A sequence was generally composed of multiple limb cycles. A limb cycle was defined as the interval between touchdown of one limb and the subsequent touchdown of the same limb (i.e., right foot/hand to right foot/hand).

The mountain gorillas were observed for an average of 4 hours/day. A minimum of 7 m had to be maintained between the gorillas and the observer to reduce the risk of disease transmission. High-definition video was filmed *ad libitum* at a frequency of 50Hz (HDR-CX240E, Sony, Japan).

All gorilla climbing sequences were recorded at relatively close range (7 m to ~20 m) during vertical ascent and descent on a sample of 15 individuals across the two study groups, including 10 adult females and five males, the latter including one subadult (6–8 years), one blackback (8–12 years) and three silverbacks (≥ 12 years) (Czekala & Robbins, 2001; Robbins, 2001). Video data also included a form of vertical descent in which the animal is sliding on vertical supports, where both forelimbs move alternately with a hand over hand movement to regulate velocity while both feet remain in contact with the substrate. This sub-mode of vertical descent was classified as 'fire-pole slide' (Hunt et al., 1996). The gorillas had the opportunity to climb on various-sized substrates ranging from lianas to extremely large tree trunks. The dense understorey vegetation often limited access to climbing substrates, making direct measurements of their circumference difficult. Thus, we grouped substrate size into three categories consistent with previous reports (Alexander, 1994; Marzke et al., 1992; Napier, 1960): (1) medium, when the diameter was approximately 6–10 cm (e.g., lianas, thin trees); (2) large, when the diameter was approximately 11–50 cm (e.g., tree trunks); (3) extra-large, when the diameter was > 50 cm (e.g., tree trunks). Neither gorillas nor chimpanzees in our study climbed on small substrates less than 6 cm diameter (e.g. thin lianas, vertical branches). We recorded a total of 75 climbing sequences, containing 231 limb cycles (Table 1) on 31 medium, 13 large and 31 extra-large substrates.

Similar to the mountain gorillas, the free-ranging chimpanzees were recorded with high-definition video (50Hz; HDR-CX240E, Sony, Japan) *ad libitum* at relatively close range (~10 m) from both the

TABLE 1 Summary of vertical climbing in Bwindi mountain gorillas and Chimfunshi chimpanzees

Species	Individual	Sex/Age	Total no. of climbing sequences	No. of forelimb cycles for vertical ascent	No. of forelimb cycles for vertical descent	No. of limb cycles for fire-pole slide	
<i>G. b. beringei</i>	JN	female/adult	11	17	6	3	
	ST	female/adult	11	13	6	2	
	KR	female/adult	9	18	-	8	
	TN	female/adult	5	10	-	13	
	TW	female/adult	7	12	3	19	
	MG	female/adult	8	2	9	10	
	KG	female/adult	1	-	-	3	
	BY	female/adult	5	3	4	6	
	TD	female/adult	2	2	-	4	
	BT	female/adult	1	-	-	10	
	HP	male/subadult	2	-	-	9	
	KA	male/blackback	4	7	2	5	
	MK	male/silverback	6	13	-	3	
	RC	male/silverback	2	3	-	3	
	ND	male/silverback	1	-	-	6	
	Total			75	100	30	101
	<i>P. troglodytes</i> ssp.	RI	female/adult	2	-	7	-
KB		female/adult	8	7	19	-	
MI		female/adult	11	12	20	-	
KY		female/adult	7	6	13	-	
JU		female/adult	3	3	8	-	
UN		female/adult	4	-	10	-	
TA		male/adult	1	-	4	-	
CO		male/adult	1	-	2	-	
Total			37	28	83	-	

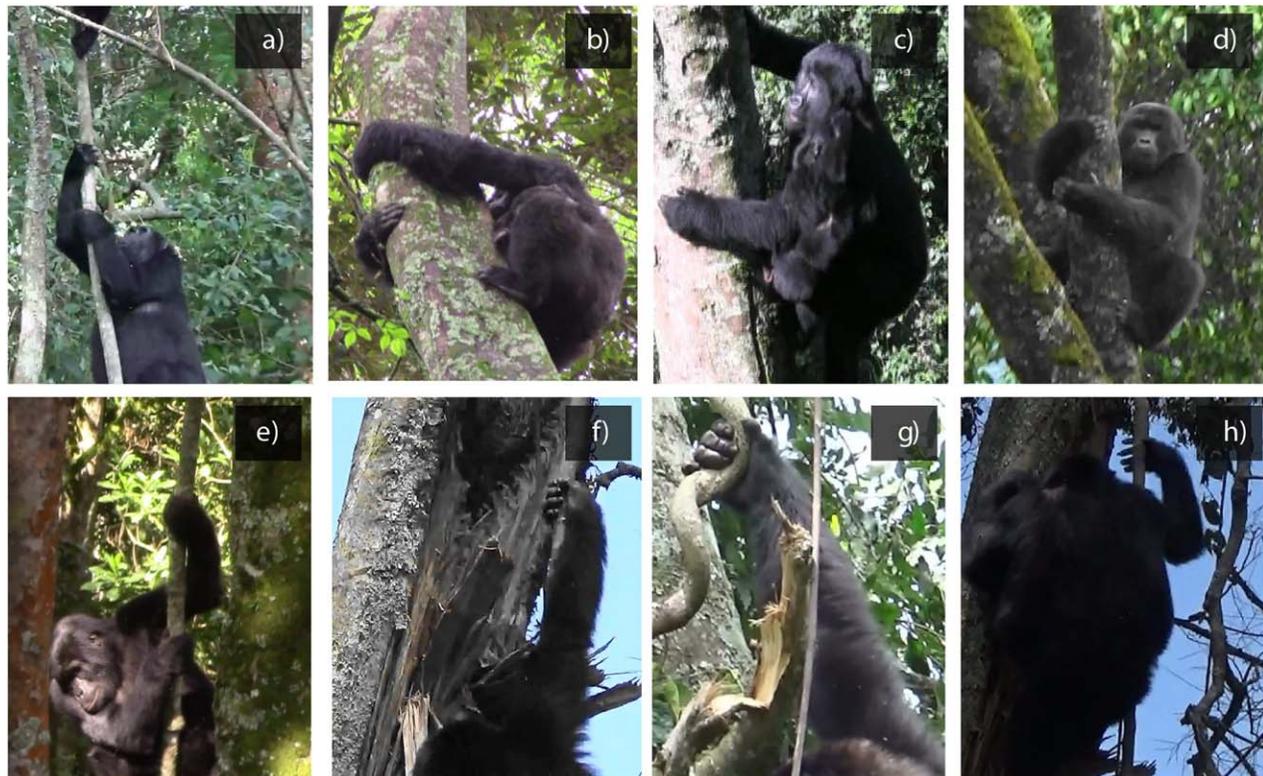


FIGURE 1 Forelimb (a-b) and hand (c-h) postures during vertical climbing in mountain gorillas. (a) Flexed-elbow climbing on medium-sized support and (b) a nearly extended-elbow posture during fire-pole slide on extra-large substrate in mountain gorillas. Hand grips and variable thumb postures in relation to supports of different size: (c) power grip with the thumb adducted to the index finger typically used on an extra-large substrate; (d) power grip with the thumb abducted from the index finger typically used on large substrates; (e) diagonal power grip with the thumb opposed to the index finger and held in line (right hand), exclusively used on medium-sized substrates; (f) the wrist is deviated in the ulna direction to an extreme degree, bringing the right hand's long axis relatively in the plane of the support's cross section with the thumb held opposed and wrapped around the medium-sized substrate; (g) form of diagonal power grip adjusted to the curved liana; (h) showing that opposed thumb of the right hand making first contact with the substrate and secure the substrate within the V-shaped region between thumb and extended Index while climbing down the irregular support

ground and viewing platforms. We collected a total of 37 climbing sequences, containing 111 limb cycles, in eight adult chimpanzees (six females, two males) (Table 1). Data were collected on substrates of varying sizes, but given that it was a natural environment within a sanctuary, substrates were limited to tree trunks only. Data were collected on two medium-sized, 23 large and 12 extra-large substrates.

2.3 | Forelimb posture in relation to substrate size during vertical climbing

We investigated the hand and forelimb posture during vertical climbing in relation to the size of the substrate ($N = 75$ sequences in 15 gorillas; $N = 37$ sequences in eight chimpanzees). Hunt and colleagues (1996) described two types of vertical climbing in African apes in relation to substrate size: (1) when climbing on smaller substrates, flexion of the elbow helps to elevate the body ('flexed-elbow' vertical climbing); (2) on larger substrates, the elbow is typically extended throughout the motion cycle ('extended-elbow' vertical climbing). We used these same categories when scoring and analyzing our data (Figures 1a,c and 2a,c). To reduce the dependence of data points, findings were reduced by pooling sequential observations for each individual in which forelimb

posture did not change along a particular substrate size category, following Hunt (1992b). The reduced data set contained $N = 36$ pooled observations in 15 gorillas ($N = 10$ medium-sized substrates; $N = 11$ large substrates, $N = 15$ extra-large substrates) and $N = 18$ pooled observations in eight chimpanzees ($N = 2$ medium-sized substrates, $N = 8$ large substrates, $N = 8$ extra-large substrates). Each individual only contributed one data point within a particular substrate size category. Individuals with missing data points were excluded from statistical analysis.

2.4 | Hand grips and thumb use

We investigated hand use and grip types during vertical climbing in all 15 gorillas ($N = 231$ limb cycles) and eight chimpanzees ($N = 111$ limb cycles). We classified each hand grip within a limb cycle (as a limb cycle is defined as the use of one grip only between the two touchdowns by the same forelimb) for each individual and calculated the relative frequencies. Hand grips were categorized following previous descriptions of hand use and grips during climbing in chimpanzees (Alexander, 1994; Hunt, 1991a; Marzke & Wullstein, 1996; Marzke et al., 1992; Napier, 1960; Sarmiento, 1988). Our initial categorization centered on



FIGURE 2 Forelimb (a-b) and hand (c-e) postures during vertical climbing in chimpanzees. (a) Flexed-elbow climbing on medium-sized support in chimpanzees and (b) extended-elbow climbing on large substrate during vertical descent. Hand grips and variable thumb postures in relation to supports of different diameter: (c) power grip with the thumb adducted to the index finger used on large substrate; (d) power grip with the thumb abducted from the index finger used on large substrate; (e) diagonal power grip with the thumb opposed to the index finger and held in line, exclusively used on medium-sized substrates (left hand)

the **power grip**, in which larger substrates are grasped by all five digits and the entire palm of the hand, the **diagonal power grip**, in which smaller substrates lie diagonally across the fingers and the palm, and the **diagonal finger hook grip** without the thumb and without active involvement of the palm (e.g., Hunt, 1991a; Marzke et al., 1992; Napier, 1960) (Figures 1a,c and 2a,c).

We further investigated in detail the role of the thumb during ascent and descent climbing, including different thumb postures in relation to substrate size ($N = 231$ limb cycles for 15 gorillas; $N = 111$ limb cycles for eight chimpanzees). Three thumb positions were categorized following previously described climbing grips in chimpanzees (Alexander, 1994; Marzke & Wullstein, 1996; Marzke et al., 1992): (1) thumb held in adduction relative to index finger, (2) thumb held in abduction relative to index, (3) thumb held opposed to index finger, and was either wrapped around the substrate or held in line with the long-axis of the substrate (Figures 1 and 2). Thumb posture was

examined within a limb cycle for each individual and relative frequencies were calculated. As described above, dependence among data points was reduced by pooling limb cycles for each individual in which thumb posture did not change on a particular substrate size category. The reduced data set contained $N = 36$ pooled observations for 15 gorillas ($N = 10$ medium-sized substrates, $N = 11$ large substrates, $N = 15$ extra-large substrates) and $N = 18$ pooled observations for eight chimpanzees ($N = 2$ medium-sized substrates, $N = 8$ large substrates, $N = 8$ extra-large substrates). Each individual only contributed one data point within a particular substrate size category and individuals with missing data points were not included in the statistical analysis.

2.5 | Statistics

All statistical analyses were run in SPSS (IBM SPSS Statistics for Windows, Version 24.0). An exact binomial test was applied to test the

TABLE 2 Frequency (no. of climbing sequences) of forelimb-posture in relation to total climbing sequences and substrate size

Species	Forelimb-posture	Forelimb-posture relative to total climbing sequences	Medium-sized substrate	Large-sized substrate	Extra-large substrate
mountain gorilla	extended-elbow	59% of total 75	-	29.5%	70.5%
	flexed-elbow	41% of total 75	100%	-	-
chimpanzee	extended-elbow	92% of total 37	-	65%	35%
	flexed-elbow	8% of total 37	67%	33%	-

“-” denotes absence of forelimb data.

probability of using a particular forelimb posture (50/50 distribution) within each substrate size category. Similarly, we used an exact binomial test to determine the probability of observing a particular thumb posture (50/50 distribution) within each substrate size category. In chimpanzees, both flexed forelimb ($N = 2$) and opposed thumb posture ($N = 2$) used on medium-sized substrates were excluded from analysis due to small sample size. The significance threshold was set at $p = .05$. However, since one data point for the same individual may be included in all three substrate categories, the data are not fully independent. The overall sample size was too small to allow more sophisticated statistical tests that could take into account dependency within the data. Therefore, results of these statistical analyses are interpreted with caution.

3 | RESULTS

3.1 | Forelimb posture during vertical climbing

We observed both flexed-elbow and extended-elbow vertical climbing during ascent and descent in mountain gorillas and chimpanzees. Gorillas always used a flexed-elbow posture on medium-sized substrates and an extended-elbow on large and extremely large substrates (Table 2). In gorillas, there was a significant use of a flexed elbow on medium-sized substrates (100% of 10 sequences, $p = .002$) (Figure 1a,h) and a highly significant use of an extended elbow on large (100% of 11 sequences, $p < .001$) as well as on extra-large substrates (100% of 15 sequences, $p < .001$) (Figure 1b).

During flexed-elbow climbing in mountain gorillas, which was only used on medium-sized substrates, the elbows were flexed and the torso was held nearly parallel to the support. Flexion of the elbow helped to elevate the body during the push of the hind limbs in ascent climbing, while the elbows were flexed throughout the support phase until the mid-swing phase. A strongly flexed position of the forelimb was occasionally used in late-swing phase until early-support phase during descent climbing (Figure 1h). Strong horizontal abduction of the upper arm was obtained while reaching upward and at the very end of the support phase in flexed-elbow ascent (unpooled data set: 100% of 33 limb cycles), when the elbow was already being lifted but the hand was still in contact with the substrate. The elbow was always elevated far above the shoulder (Figure 3a).

During extended-elbow ascent climbing on large substrates, the torso was held roughly parallel to the substrate, while on extra-large substrates, the torso was angled forward such that the shoulders were

closer than the hips to the support. The elbows were never fully extended throughout the motion cycle in both ascent and descent climbing, but were clearly extended enough to allow both hands to control for friction while the feet appeared to experience more of the compressive load. When the hand lifted off the substrate, the humerus was slightly abducted and the elbow was most often elevated to shoulder level (unpooled data set: 81% of 63 limb cycles) and less often slightly higher than the shoulder (Figure 3b).

Gorillas most often descended trees by sliding downwards using only the forelimbs (14 individuals; 75% of total descent sequences), in which the forearms were either flexed or extended throughout support and swing phase. The forearms moved alternately in lift-off and touchdown while both hindlimbs remained in contact with the substrate.

Chimpanzees always used a flexed-elbow posture on medium substrates. An extended-elbow posture was used on large and extremely large substrates but flexed-elbow postures were occasionally used on large trees (Table 2). In chimpanzees, there was a significant use of an extended elbow on extra-large substrates (100% of 8 sequences, $p = .008$), but the use of a flexed (25% of 8 sequences) and extended-elbow (75%) was not significantly different on large substrates ($p = .289$).

When chimpanzees engaged in flexed-elbow climbing during vertical ascent, we observed that flexion of the elbow occurred during the early to mid-support phase until early swing phase whereas during extended-elbow climbing, the elbow was extended throughout the motion cycle. In vertical descent, a flexed elbow posture was used during the mid-swing phase and throughout support phase while during extended-elbow climbing, extension of the elbow occurred throughout the motion cycle.

Like mountain gorillas, chimpanzees never fully extended the elbow during ascent and descent climbing but, the elbow was clearly extended enough to hold the body away from the support while the hindlimbs pushed-off from the substrate. Chimpanzees were not observed to slide down tree trunks using only the forelimbs as documented in gorillas.

During both flexed- and extended-elbow climbing, chimpanzees slightly abducted their humerus when the hand lifted off the substrate (Figure 3c,d). Chimpanzees varied in their degree of elbow elevation during both flexed- and extended-elbow climbing on larger substrates; sometimes both elbows would be elevated to shoulder level while at other times, individuals showed asymmetry with one elbow would

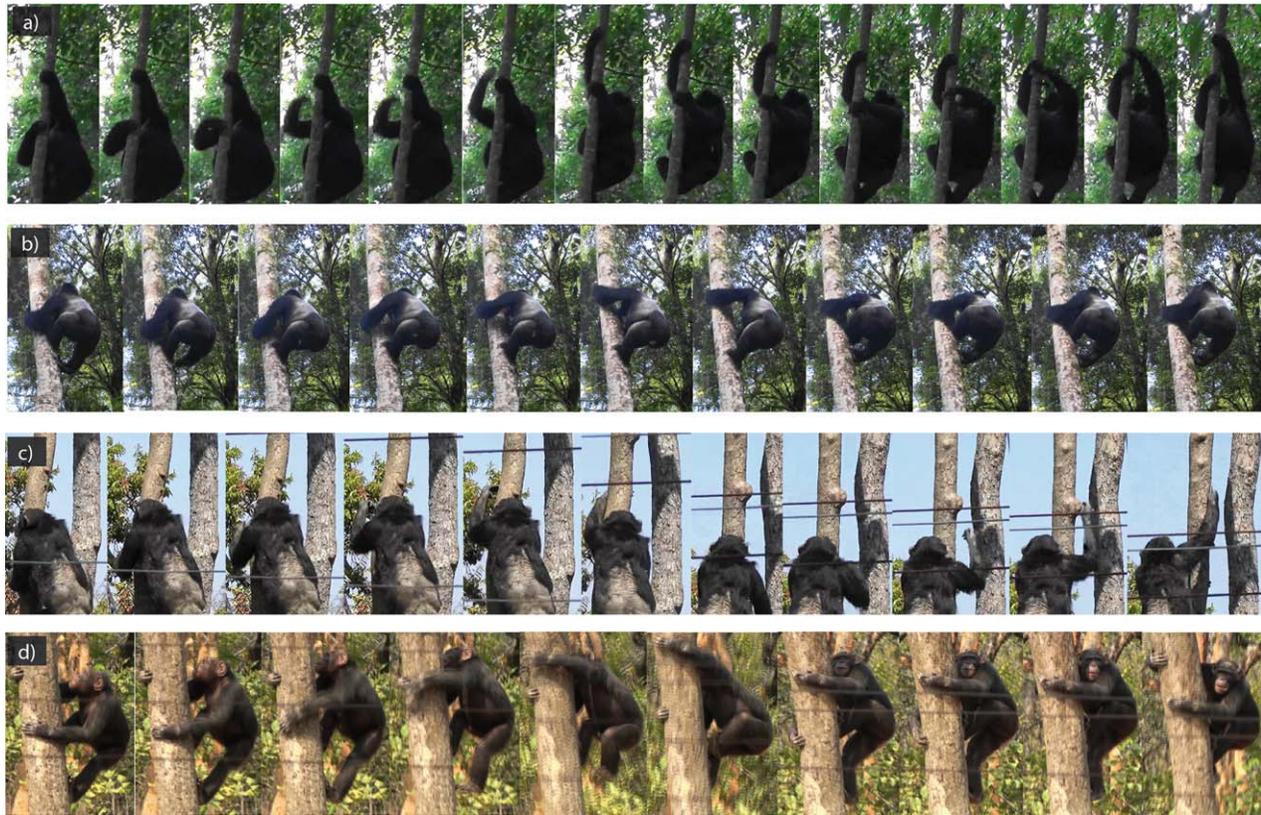


FIGURE 3 Typical vertical climbing sequences of mountain gorillas (a-b) and chimpanzees (c-d). (a) Female gorilla horizontally abducts the upper arm considerably and elevates the elbow far above the shoulder during flexed-elbow climbing on medium-sized support; (b) a silver-back abducts the upper arm less of horizontal plane and elevates the elbow to shoulder level during extended-elbow climbing on a large substrate; (c) a female chimpanzee slightly abducts the upper arm and shows forelimb asymmetry in the degree of elbow elevation during flexed-elbow climbing on a large substrate; (d) a female chimpanzee slightly abducts the upper arm and elevates the elbow to shoulder level during extended-elbow climbing on an extra-large substrate

elevated to shoulder level and the other reaching slightly above or far above the shoulder (Figure 3c).

3.2 | Hand grips and thumb use

Both mountain gorillas and chimpanzees used a power grip and a diagonal power grip during ascent and descent climbing (Figures 1 and 2). Gorillas used a power grip only during extended-elbow climbing, a diagonal power grip only during flexed-elbow climbing and both grips during forelimb-only descent. Chimpanzees used a power grip during both extended- and flexed-elbow climbing while a diagonal power grip was only used during flexed-elbow climbing. Neither ape was observed to use the diagonal finger hook grip for climbing. Grip use depended upon the size of the substrate; both apes used the power grip only on large and extra-large substrates and the diagonal power grip only on medium-sized substrates. A power grip was used at high frequency in both gorillas (63% of total 231 limb cycles) and chimpanzees (95% of total 111 limb cycles). A diagonal power grip was used relatively frequently in gorillas (37% of total limb cycles) but rarely in our chimpanzee sample (5% of total limb cycles) and only on medium-sized substrates (Figure 1e). Both apes showed significant differences in using a particular thumb posture on differently-sized substrates.

Opposition of the thumb was only used when both apes grasped medium-sized substrates in a diagonal power grip and the thumb was most frequently held in line with the long axis of the substrate (Table 3; Figures 1a and 2e). Gorillas used an opposed thumb significantly more on medium-sized substrates (100% of 10 data points, $p = .002$) and both gorillas (100% of 15 data points, $p < .001$) and chimpanzees (100% of 8 data points, $p = .008$) used an adducted thumb posture significantly more on extra-large substrates (Table 3; Figures 1c and 2b). Neither ape showed a significant difference between thumb adduction and abduction on large substrates (gorillas: $N = 11$, 23% vs. 73%, $p = .227$; chimpanzees: $N = 8$, 38% vs. 63%, $p = .727$) (Table 3; Figures 1d and 2d).

Both apes were observed to ulnarly deviate the wrist (tilting the wrist and hand towards the ulnar side of the forearm) such that the hand's long axis was orientated perpendicular to the substrate with the opposed thumb held either in line or wrapped around the substrate (Figures 1a and 2e). Only mountain gorillas ulnarly deviated the wrist to an extreme degree during both vertical descent and fire-pole slide on medium-sized substrates, bringing the hand perpendicular to the vertical substrate with the forelimb approaching a nearly parallel position with the substrate (Figure 1f). Gorillas used two different grasping strategies when climbing lianas, neither of which were documented in

TABLE 3 Frequency (no. of limb cycles) of thumb postures in relation to substrate size

Species	Hand grip	Thumb posture	medium-sized substrate	large-sized substrate	extra-large substrate	total no. of limb cycles
mountain gorilla	Power grip	Thumb adducted to index	-	26 (19%)	112 (81%)	138
		Thumb abducted from index	-	10 (100%)	-	10
	Diagonal power grip	Thumb opposed to index and held in line with long axis of substrate	59 (100%)	-	-	59
		Thumb opposed to index and wrapped around substrate	24 (100%)	-	-	24
chimpanzee	Power grip	Thumb adducted to index	-	26 (41%)	37 (59%)	63
		Thumb abducted from index	-	41 (95%)	2 (5%)	43
	Diagonal power grip	Thumb opposed to index and held in line with long axis of substrate	5 (100%)	-	-	5
		Thumb opposed to index and wrapped around substrate	-	-	-	-

The percentages of the total limb cycles are given in parentheses. "-" denotes absence of thumb data.

the chimpanzees (although they were not observed climbing lianas). The first grasping strategy was used when the individual moved downward along the liana (Figure 1h). During the swing phase of the opposing forelimb, strong ulnar deviation of the wrist allowed the individual to grasp the vertical support within the V-shaped region between the opposed thumb and extended index finger. When descending lianas of irregular shape, the liana was grasped diagonally across all four fingers and mainly against the thenar area of the palm and proximal phalanx of the thumb (Figure 1g). The different postures of the flexed fingers conformed to the irregular shape of the liana and firmly maintain the grip against the downward pull of the body during vertical descent. The pull appeared to be resisted mostly by the second, third and fourth fingers while the shorter fifth finger was not able to flex as much at the metacarpophalangeal joint to fully contribute to the grasp (Figure 1g).

4 | DISCUSSION

This study provides the first comparative study of wild mountain gorilla and free-ranging chimpanzee hand use and forelimb posture during both ascent and descent vertical climbing in natural environments. These new data, although sample sizes are small, provide greater insight into the potential range of grasping strategies that are capable with a given bony and muscular morphology in African apes, and generally provides a better understanding of the postural adaptations for vertical climbing in large-bodied primates.

4.1 | Forelimb posture during vertical climbing

Mountain gorillas have the largest body mass among living primates (e.g., Sarmiento, 1994; Smith & Jungers, 1997) and thus locomotion and maintaining stability in a complex, three-dimensional arboreal environment poses considerable challenges. We found partial support for our first prediction that similar forelimb morphology and body size within *Gorilla* and *Pan* would elicit similar forelimb postures (1) between

mountain gorillas and western lowland gorillas and (2) between chimpanzees and bonobos (Isler 2002, 2003, 2005).

Our sample of mountain gorillas most often engaged in extended-elbow climbing (59% of total 75 sequences), both on extra-large and large substrates, and also frequently used flexed-elbow climbing (41% of total sequences), exclusively on medium-sized substrates (Figure 1a,e).

The mountain gorillas commonly entered and left large trees by climbing on medium-sized vertical substrates (69% of total 26 instances). When ascending medium-sized substrates, flexion of the elbow joint appears to help pull the body upwards during the mid-support phase, and keeps the body positioned close to the substrate throughout the support phase, while the gorilla's strong muscular hindlimbs (Zihlman, McFarland, & Underwood, 2011) provide most of the propulsive power and push against the substrate in the mid-support phase. Similar to previous reports on vertical climbing in chimpanzees (Hunt, 1991b, 1992), the flexed-elbow posture stabilizes the upper body against backward rotation caused by the propulsive force of the hindlimbs. As the demands are particularly high in flexed-elbow vertical climbing (Isler, 2005), mountain gorillas likely show, like all other apes, adaptations for large force production in the elbow flexors for pulling-up (Myatt et al., 2012) and have forearm flexor muscles that are nearly four times as large as in cursorial mammals (Alexander, Jayes, Maloiy, & Wathuta, 1981). Therefore, differences in the elbow joint morphology between mountain and lowland gorillas (Inouye, 2003) does not appear to inhibit the mountain gorilla's ability to climb safely upon medium-sized substrates. Western lowland gorillas in captivity also used flexed-elbow climbing on smaller-sized substrates, which helped to elevate and stabilize the body when climbing up a vertical rope (see Figures 3 and 4 in Isler, 2003). The mountain gorillas in our study occasionally used a stronger flexed forelimb posture when descending lianas (Figure 1h) compared with ascent on smaller-diameter trees (Figure 1a,e), bringing the torso even closer to the compliant support and providing greater stability against the potentially high gravitational pull of the heavy body.

We also observed that mountain gorillas abduct the humerus considerably during the process of reaching upward for the next grip during flexed-elbow climbing, elevating the elbow far above the shoulder. Isler (2002, 2003, 2005) noted a similar forelimb posture in captive western lowland gorillas. The abduction of the forelimb during climbing is consistent with interpretations of the gorilla's forelimb anatomy to accommodate shoulder joint mobility for vertical climbing and reaching while maintaining joint stability during terrestrial quadrupedal locomotion (Zihlman et al., 2011).

The semi-free-ranging chimpanzees in our sample used a flexed-elbow posture on smaller substrates, similar to that previously described in captive bonobos (Isler, 2005). However, unlike bonobos ascending a vertical rope, the chimpanzees did not abduct their humerus at the very end of the forelimb's support phase and varied in their degree of elbow elevation when ascending larger substrates (Figure 3c). Similar to our observations, wild and captive chimpanzees have been observed to elevate the arm only slightly higher above shoulder level (Hunt, 1991a, 1992; Nakano, Hirasaki, & Kumakura, 2006) while humeral abduction has been documented in a study on scapulohumeral muscle function in captive chimpanzees during vertical climbing (Larson & Stern, 1986). Variations in the degree of elbow elevation across our chimpanzee individuals may be related to speed modulation, if the speed increase were to be achieved more through an increase in forelimb stride length than through an increase in stride frequency (Isler, 2005). Comparisons to captive bonobo vertical climbing suggest that chimpanzees abduct their humerus less of horizontal plane, which may reflect a slower climbing speed as found in male bonobos (Isler, 2002). However, chimpanzees are adapted for highly abducted arm postures just like all other arboreal apes, based on shared features in joint morphology and muscular anatomy of the shoulder (for circumduction), elbow (rotation), and wrist (adduction) (e.g., Chan, 2008; Larson, 1998; Myatt et al., 2012; Preuschoft et al., 2010; Tuttle, 1969; Zihlman et al., 2011). Whether forelimb joint excursions increase with climbing speed in chimpanzees and other apes requires further testing as, at present, there are insufficient data on spatio-temporal gait parameters in primates to clarify this issue.

Our prediction that, due to differences in forelimb morphology and body mass, we would see differences in forelimb posture on similarly-sized substrates between mountain gorillas and chimpanzees was only partially supported. Mountain gorillas only used flexed-elbow climbing on smaller substrates, while chimpanzees flexed their elbows on both smaller and larger substrates (Figure 2a,d). However, the chimpanzees in our sample climbed on trees of a lower diameter range (11–50 cm; see Methods), while Hunt and colleagues (1996) suggested that a substrate diameter larger than 20 cm is more likely to evoke extended-elbow climbing in chimpanzees. Similarly, both apes abducted the humerus less of horizontal plane and showed a lower degree of elbow elevation during ascent on larger-sized substrates (Figure 3b,c). Finally, mountain gorillas commonly slid down vertical supports while this strategy of descending trees was not observed in the chimpanzees of our sample and appears not to be used in other adult chimpanzees either (Table 3 in Sarringhaus, 2014).

The variation documented here in mountain gorilla and chimpanzee forelimb postures on different sized substrates, as well as differences in forelimb joint excursions, needs to be tested on a larger comparative data set including more individuals and substrate types to see if these patterns still hold. Furthermore, 3D kinematic analyses in a natural environment, although challenging, would provide more detailed insight into the biomechanical strategies used by large-bodied apes.

4.2 | Hand use and the role of the thumb during vertical climbing

Both mountain gorillas and chimpanzees most frequently used a power grip only on larger substrates and less often a diagonal power grip, which was used only on medium-sized substrates during ascent and descent climbing. This result is consistent with previous reports on chimpanzees grasping locomotor supports of different sizes (Alexander, 1994; Hunt, 1991a; Marzke et al., 1992; Marzke & Wullstein, 1996; Napier, 1960). In contrast to chimpanzees, gorillas used a power grip only during extended-elbow climbing while a diagonal power grip was used only during flexed-elbow climbing. Mountain gorillas also used both grips when sliding down tree trunks (which was not documented in chimpanzees). Neither ape was documented using a diagonal finger hook grip for climbing, although this grip has been reported in climbing chimpanzees to be typically used on smaller substrates, which were not used in this study (e.g., Marzke et al., 1992). Mountain and lowland gorillas use hook grips during food processing and stick tool-use (Bardo, 2016; Byrne, Corp, & Byrne, 2001) but whether they are capable of using this hand grip to support their large body mass during vertical climbing is not yet known. Their large body mass typically limits the gorilla's substrate choice to larger and more robust substrates (Remis, 1998; Reynolds, 1969), which in turn limits their grip repertoire for climbing. Lowland gorilla phalanges are shorter and straighter than those of chimpanzees (Patel & Mailino, 2016; Stern, Jungers, & Susman, 1995) and assuming mountain gorillas are the same (Matarazzo, 2008), this morphology may place greater restrictions on the grasping postures that can be used on smaller substrates, especially for large-bodied mountain gorillas. Further investigation of grasping smaller natural substrates is needed, in all species of gorillas, to understand the full repertoire of available hand grips in an arboreal environment.

Although the frequency of vertical climbing is lower in mountain gorillas than in chimpanzees and other hominoids, all hominoids retain arboreal features in their hand and forelimb due to the selective advantage of being able to ascent and descent arboreal substrates of variable size and compliance effectively and safely (gorillas: Taylor, 1997; hominoids: Larson, 1998). Indeed, while species-specific differences in bony morphology of the hand between gorillas and chimpanzees appear to elicit slightly different grasping strategies during vertical climbing (e.g., loss of ulnocarpal articulation of the wrist in gorillas; Tuttle, 1969; Lewis 1989), general similarity in hard and soft tissue morphology of the hand and forelimb (i.e., long and powerful digital flexors; Myatt et al., 2012; Schultz, 1969) allow both apes to use the same grip preferences and similar forelimb postures on supports of a similar size. Grip strength is critical when climbing safely and both hand grips exert

contact pressure for strong friction between the palmar surface of the hands and the support (Cartmill, 1979, 1985; Preuschoft, 2002). However, the mountain gorilla's ability to ulnarly deviate the wrist to an extreme degree appears to be particularly valuable when descending medium-sized supports, as the hand can fully wrap around the vertical support in a firm diagonal-power grip (Figure 1f). Although we did not observe this high range of ulnar deviation in our sample of climbing chimpanzees, ulnar deviation of the wrist is also used by chimpanzees on smaller-diameter vertical supports (e.g., Marzke et al., 1992; Sarmiento, 1988). Furthermore, chimpanzees are capable of a similar degree of wrist adduction as western lowland gorillas (Tuttle, 1969), and potentially mountain gorillas. The ulnar side of the hand appears to provide the strongest friction against the downward pull of gravitational force, which is consistent with Susman's (1979) observations of ape hand posture during vertical climbing.

We predicted that gorillas would oppose their relatively longer thumb when grasping arboreal substrates more frequently than chimpanzees. We found partial support for this hypothesis. The functional role of the thumb during vertical ascent and descent climbing, as well as during flexed-elbow and extended-elbow climbing, revealed the use of three different thumb postures relative to differently sized substrates in both mountain gorillas and chimpanzees. Both apes significantly used an adducted thumb in a power grip on extra-large substrates (Figures 1c and 2c) and opposed their thumb to the index finger in a diagonal power grip on medium-sized substrates only (Figures 1e and 2e). Both apes generally held the opposed thumb in line with the substrate, which is consistent with previous studies of chimpanzees (Alexander, 1994; Marzke et al., 1992; Napier, 1960). Only mountain gorillas wrapped their opposed thumb around the support during diagonal power grasping, supporting our prediction. However, the absence of this thumb posture in our chimpanzee sample is likely due to our limited sample size on the smaller-diameter substrates, as it has been reported previously in chimpanzees (e.g., Alexander, 1994; Marzke et al., 1992; Napier, 1960). Furthermore, in mountain gorillas the opposed thumb appeared particularly important when grasping lianas whereas the chimpanzees were not observed to climb on lianas (Figure 1g). When gorillas grasped lianas, the downward pull of the body appeared to be resisted mostly by the second, third and fourth fingers, while the thenar region of the palm and the proximal phalanx of the thumb counter stabilized the grip. Our observations of a relative frequent use of grasping with an opposed thumb (36% of total 231 limb cycles) together with the gorilla's need to resist the downward pull of its large body mass during descent climbing, suggest that the gorilla thumb may experience large loading during this arboreal behavior. This hypothesis is consistent with the robust first metacarpal in mountain gorillas (Hamrick & Inouye, 1995), suggesting that the mountain gorilla's thumb is adapted to meet the potentially high forces during vertical ascent and descent, that occur due to their great body mass. Finally, mountain gorillas and chimpanzees occasionally abducted the thumb at roughly a right angle to the index finger, typically in a power grip on large substrates (Figures 1d and 2d). In this abducted posture, the thenar area of the palm is recruited for counter pressure

and thus, the thumb may potentially experience forceful loading at the metacarpal region (Figure 2).

Although the gorilla's hand proportions are closer to humans than those of other hominoids (Almécija et al., 2015), their thumb is still too short to lock with or stabilize against the index finger on medium-sized supports as seen in humans when power squeeze gripping (e.g., Marzke et al., 1992; Napier, 1960; but see illustrations in Sarmiento, 1988 and Hasley, Coward, Crompton, & Thorpe, 2017 for human arboreal behaviours). Nevertheless, the great range of ulnar deviation at the wrist that was used during vertical descent enabled mountain gorillas to use the opposed thumb as an additional point of contact on lianas if needed, so that the support can be grasped quickly and firmly in case of slipping off, especially when the substrate surface was uneven. The extremely ulnarly-deviated wrist posture allowed the liana to be held securely in the web at the V-shaped region (Marzke et al., 2015) between the opposed thumb and extended index finger while the gorilla's forelimb moved downward along the substrate (Figure 1h). We did not observe this important supportive role of the thumb in our chimpanzee sample and it has not been reported in other chimpanzees (e.g., Alexander, 1994; Hunt et al., 1996; Hunt, 1991a, 1992; Marzke et al., 1992). However, since the chimpanzees in our sample did not exhibit such an extreme degree of ulnar deviation (although they are anatomically capable of it; Tuttle, 1969) as compared with mountain gorillas during descent climbing, it needs to be further investigated whether chimpanzees use the same grasping strategy to overcome substrate irregularities.

This comparative study provides much needed data on how the hand and forelimb are used during vertical climbing in a natural environment that can, in turn, help interpret differences in both external and internal bony morphology. However, this study also makes clear that there is a complex relationship between species-specific morphology and the range of potential postures that may be used in a natural environment. Although recent work found clear differences in foot morphology between more arboreal western gorillas and less arboreal eastern gorillas that correlate well with differences in arboreality, slight differences between eastern gorilla subspecies (i.e., lowland gorillas vs. mountain gorillas) did not follow the functional predictions (Tocheri et al., 2011, 2016). Furthermore, previous work examining African ape hand and foot morphology in relation to frequencies of arboreality and terrestriality, did not find strong concordance between functional predictions and the observed morphology across species and subspecies (Jabbour, 2008). Together, these findings underline both the difficulty and critical importance of identifying skeletal features that have a clear functional and adaptive signal to "potential" and "actual" behaviors.

5 | CONCLUSION

This is the first comparative study on hand use and forelimb posture in mountain gorillas and chimpanzees during vertical climbing. This study demonstrates the importance of powerful grasping and the use of variable thumb postures relative to substrate size in both ape species. Moreover, our study reveals for the first time the supportive role of

the gorilla's thumb during vertical descent. However, this study shows that more work is needed to characterize the potential range of grasping and postural strategies that might be used by African apes in their natural environments.

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