Handedness during feeding in chimpanzees

(Pan troglodytes) at Chimfunshi Wildlife Orphanage, Zambia

by

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DEDICATION

This research and work is dedicated to Sheila Siddle, a woman with unfathomable patience,

courage, and kindness. Her life is my dream and my passion. And to Big Jane, who will be sorely missed.

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ABSTRACT

Humans are considered unique in their extreme population-level right handedness, seen in no other species to date. Certain behavioral asymmetries have been shown in other animals, especially in nonhuman primates, and these asymmetries are suspected to be closely tied to anatomical asymmetries in the brain and possibly correlated with language and complex thought. Studies of primate hand preference have searched for evidence of population-level handedness for certain tasks as a proxy for brain asymmetries and their potential intellectual correlates. My study examines the hand preference during feeding of 34 chimpanzees living at the Chimpanzee Project Area (CPA) at Chimfunshi Wildlife Orphanage in Zambia. Results indicate that 30 of the 34 subjects exhibit a significant hand preference for unimanual feeding, refuting the commonly held conception that less complex, everyday tasks will not be lateralized. Additionally, data indicate that age, sex, and the presence of family members at the sanctuary all have some effect on the handedness of the subject, though the direction of this effect could not be determined. While many of the chimpanzees at the CPA have diverse and unique backgrounds before entering the sanctuary, this did not appear to have an effect on the handedness of the subject, though a number of unique individuals and potentially influential factors had to be excluded from analyses. Additionally, I suggest standardizing and correcting methodological inconsistencies in studies of handedness by using statistical methods more appropriate to the type of data gathered in such studies. Finally, I review current findings in the field of primate handedness and revisit the significance of such findings in light of the current study.

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CHAPTER 1. INTRODUCTION AND BACKGROUND

1.1 Introduction

Humans have been interested in the puzzle of handedness for hundreds of years. The connection between the cerebral hemispheres and their correlated control of the opposite sides of the body has been known at least since Galen was a doctor to the gladiators during the Roman empire (Annett, 2002). That the left side of the brain is the major controller of speech has likely been known since its discovery by French physician, Marc Dax, but was only really recognized by neurologists in 1970 after the work of French physician, Paul Broca (Royal Anthropological Institute of Great Britain and Ireland, 1881). Broca conducted postmortem investigations on individuals with severe speech impediments and revealed consistent left frontal cerebral lobe brain lesions (Royal Anthropological Institute of Great Britain and Ireland, 1881). A few years later Austrian neurologist, Carl Wernicke, discovered another area of the brain that when damaged, had severe affects on speech capabilities again in the left cerebral hemisphere (Wernicke, 1970). After the realization that the left hemisphere controlled both the ability for speech as well as the preferred hand – the right hand in most people – it was deemed the "dominant" hemisphere by neurologists (Annett, 2002). Since that time neurologists, behaviorists, psychologists, and physiologists have studied the differences between left and right handed (and left and right brained) people (Zangwill, 1960; Hécaen and de Ajuriaguerra, 1964; Luria, 1970).

In the early 1900s researchers began to explore in depth the differences in hand, foot, and paw preferences in nonhuman animals (Friedmann and Davis, 1938; Finch, 1941; Hori, 1993). This endeavor led to many explanations of the function and importance of humans' species-wide right hand preference (Annett, 2002). Scientists have since been working to discover the timing of the emergence of this preference and its role shaping our evolution (MacNeilage et al., 1987). Much has been learned in this process, and many theories that help to explain this species-wide preference have emerged (see Annett,

2002 for review). To date, scientists continue to look at other animals, especially the great apes, our closest living relatives, to help us unravel this right handed "mystery".

1.2 Handedness as a Theme

Population level right handedness is a universal trait across all known human groups (Perelle and Ehrman, 1994; Raymond and Pontier, 2004). However, scientific studies of handedness have disagreed on the frequency of left handed people in modern human populations, with a range of 1 to 40% (Hécaen and de Ajuriaguerra, 1964). This variation tends to stem from people describing themselves as right or left handed based on hand preference for a single action. Assigning one action as deterministic regardless of the countless actions our hands perform and are capable of is misleading. Several different methods of taking the varying degrees of handedness into consideration have been used. Crovitz and Zener (1962) used a 1-5 scale for each of 14 actions and derived a laterality quotient (LQ) to determine the strength of preference for each individual. However, the LQ gives the same numerical value to actions requiring very different levels of skill, such as writing and sweeping. Bryden (1977) attempted to account for these varying degrees of required skill but still concluded that there was only a single dimension of hand preference. In an attempt to account for differences in skill due to different neural pathways, Annett developed a ranking system of skills required for various uni- and bimanual actions to give patterns of preference (Crovitz and Zener, 1962; Annett, 1970), which was used to identify seven subgroups of varying hand preference in the left-right spectrum (Annett, 2002). Therefore, although there is some variation on how to qualify overall hand preference, approximately 90% of humans identify as right handed (Perelle and Ehrman, 1994; Annett, 2002; Raymond and Pontier, 2004). This level of right handedness has not been recorded in any other species to date.

1.3 Asymmetry in Nonhuman Animals

Anatomical and behavioral asymmetry has been described in numerous nonhuman animal species. Evidence for what might be the earliest behavioral asymmetry can be found in the scars of trilobites living 500 million years ago (Babcock and Robison, 1989). Healed wounds on the carapace were more often located on the right side than on the left, suggesting that either the predators of the trilobites or the trilobites themselves moved asymmetrically (Babcock, 1993). The mouths of cichlids can open on either the right or left side, and the frequency with which this fluctuates indicates that it is likely governed by selection for feeding success (Hori, 1993). Shells of the water snail Limnaea usually coil to the right, though some coil to the left, in a mechanism following Mendelian rules of inheritance as expressed through the cytoplasm of the mother (Diver et al., 1925). Toads (Bufo sp.) have been reported to strike with their tongue at other toads in their left visual field more frequently (Robins et al., 1998), and several species of toads prefer to right themselves while lying upside down in water by flipping over on their right side (Bisazza et al., 1996). Chicks (Gallus gallus) show significant eye preference asymmetries during visual discrimination for different kinds of visual stimuli (McKenzie et al., 1998). Reports of parrots having foot preference for holding and manipulating food date back to the 17th century (Harris, 1989), with observations of 15 species of parrots and reanalysis of this same data 60 years later supporting the view that eight species appear to be right footed, six left footed, and eight without particular bias (Friedmann and Davis, 1938; Bradshaw and Rogers, 1993). Species level lateral asymmetries in birds and humans could have been driven by a similar pressure for vocal control of song and speech, in that the complexity of sounds produced for communication by birds and humans required cerebral control by one side (Friedmann and Davis, 1938; Bradshaw and Rogers, 1993). This argument is supported by evidence for behavioral asymmetries in the swimming, feeding, and echolocation of cetaceans (Palmer, 1996; Ridgway, 2002; Fahlke et al., 2011).

Several studies of Catarrhine monkeys concluded there was no hand preference in reaching gestures in either rhesus (*Macaca mulatta*) or Bonnett monkeys (*M. radiata*) (Warren, 1953; Lehman, 1978; Brooker et al., 1981). Passingham (1982) reanalyzed a study of different tasks in 81 immature and adult rhesus monkeys initially conducted by Warren t al. (1967), and showed that some animals were consistently right or left handed, but most preferred different hands for different tasks. This is similar to how mixed handedness has been described for humans (Annett, 2002). A compilation of *Cebus spp.* captive and wild population handedness studies (McGrew and Marchant, 1997) indicated that these species exhibit ambipreference for non-tool use activities, but individuals generally committed to one hand or the other for tool use activities. Numerous reviews of primate handedness (see Fagot and Vauclair, 1991; Papademetriou et al., 2005 and McGrew and Marchant, 1997) among captive and wild populations as well as between various tasks have revealed a split within monkey populations similar to that within great apes, with certain populations showing hand preference for specific activities and other populations not exhibiting hand preference for those same activities.

Given their close relatedness to humans, population-level lateralization in great apes has been and remains a topic of much debate (Warren, 1980; Bradshaw and Rogers, 1993; Crow, 2004; Hopkins, 2007). A number of studies have found population-specific hand preference (see Fagot and Vauclair, 1991 for review of primate studies of handedness during reaching; see Papademetriou et al., 2005 for review of primate studies of handedness; see Hopkins, 2006 for review of great ape handedness) while others have found none (see Fagot and Vauclair, 1991 for review of primate studies of handedness during reaching; see Papademetriou et al., 2005 for review of primate studies of handedness; see McGrew and Marchant, 1997 for review of *Cebus* and *Pan* captive and wild population handedness]. Researchers tend to agree that especially in great apes the handedness of the individual depends on the task performed, and that tasks requiring a more skilled manipulation of objects, such as object manipulation, are more likely to show a laterally-biased task performance (Warren, 1980; Bradshaw and

Nettleton, 1982; Marchant, 1996; Hopkins and Pearson, 2000; Hopkins, 2006). Unfortunately, there has been no standardization of methods between studies to assess the standardization of methods to assess task complexity and specificity (Hopkins and Cantalupo, 2005; Hopkins, 2006), making it difficult to get an understandable overview of manual laterality in great apes and other nonhuman primates, which complicates comparisons to studies of human handedness (Seltzer et al., 1990; Hopkins and Cantalupo, 2005). A more comprehensive overview of current findings on great ape hand preference will be discussed in section 1.6.

1.4 Why the Asymmetry?

In humans, hand preference and skill has been linked to the asymmetric lateralization of the cerebrum, specifically in that right handed people tend to be left brain dominant for important features of language and fine motor control. Over 95% of self-reported right-handed individuals show left hemisphere dominance for language, whereas only 70% of left-handed individuals show the same left hemisphere dominance (Rasmussen and Milner, 1977; Knecht et al., 2000). This lateralization is hypothesized to be partially under genetic control (Annett, 1985; Anon, 1996; Corballis, 1997), though evidence for such control has been scarce to date (DeLisi et al., 2003; Klar, 2003; Van Agtmael et al., 2003; Francks et al., 2007). Though there are argued to be several potential disadvantages to cerebral asymmetry such as schizophrenia (Johnstone et al., 1976; Crow, 1984; Frith, 1992; Crow, 1997a; b), autism (Frith, 1989; 1991; Rutter, 1991), and dyslexia (Brain, 1945; Rutter et al., 1970; Annett, 2002), there are also many advantages. Cerebral hemispheric specialization may help save neural space by avoiding replication of functions, allowing for simultaneous processing of different events, and helping to avoid hemispheric competition (Corballis, 1989; Rogers, 2002). It has also been suggested to improve cerebral abilities and behavioral efficiency (McGrew and Marchant, 1992; Crow et al., 1998; McGrew and Marchant, 1999; Vallortigara, 2000; Rogers et al., 2004; Sovrano et al., 2005; Vallortigara and

Rogers, 2005; Hopkins, 2007). The association of language lateralization and handedness has led many to hypothesize that right handedness and the evolution of language are linked in many fundamental ways (Corballis, 1992; Annett, 2002; Corballis, 2003; McManus, 2004). Fagot and Vauclair (1991) hypothesize that in humans, the brain must be lateralized for complex processes important for survival, and behavioral laterality should appear in such tasks. We see this in the lateralization of word and image processing, as well as fine motor control and the ability to process and perform hierarchical tasks (Byrne, 2005).

1.5 Hand Bias in the Hominin Lineage

Current studies on the emergence of handedness in the hominin lineage look to brain size, manual dexterity, and handedness to help us understand when this feature, now universal in our species, first emerged. Brain size is likely indicative of complex social relationships as well as increased capacity for speech (Crow, 1998; Corballis, 2003; Steele and Uomini, 2009). Manual dexterity indicated both by the complexity of lithic items crafted as well as the physical capabilities of the hand (as reflected by skeletal morphology of the hand) shows the capacity for complex skills, and the use of an item indicates its importance to survival (McHenry and Coffing, 2000; Tocheri et al., 2008; Klein, 2009; Marzke, 2009). Additionally, the more complex a task was to do, or an item was to create, gives evidence for a deeper understanding and capacity for hierarchical thought as is commonly accepted as a fundamental human skill in the field of psychology (Chomsky, 1959; Miller et al., 1960; Newell and Simon, 1972).

We must also consider that many actions, simple and complex (both in humans and nonhuman primates), require bimanual action. While some bimanual actions may require the same ability and function from each hand, other bimanual actions require different things from each hand. These actions are typically referred to as asymmetric bimanual actions, and probably require neural flexibility. We can

characterize handedness by determining the use of each of the limbs in a task (Guiard, 1987). One performs movements of higher frequency, being more temporally and spatially precise, and the other performs movements of lower frequency, acting as a stabilizer or support and maintaining the spatial or temporal structure of the motion. Using this model, Guiard (1987) suggests that most modern humans perform the low frequency task with the left hand and the high frequency task with the right hand and are therefore classified as 'right handed'. This asymmetric bimanual action is only slightly less common in monkeys and has only been recently been tested (though see Blois-Heulin et al., 2006 and Boinski et al., 2000) yet is widely reported in apes [hammering in chimpanzees (Boesch and Boesch, 1993); plant processing in gorillas (Byrne et al., 2001); tool use in orangutans (Fox et al., 1999); stone tool use in chimpanzees (Inoue-Nakamura and Matsuzawa, 1997); and the TUBE test in chimpanzees (Hopkins, 1995)], though studies on hand preference remain controversial. Handedness can be assessed from tool productions requiring bimanual coordination, such as stone tool-making and flint-knapping, and other lateralized actions taken by our hominin ancestors like feeding and cave art (discussed below), and can also be used as a proxy for cerebral asymmetry (Corballis, 1989). Additionally, hand morphology gives an indication of the manual dexterity of an individual, which has implications for tool use and production capabilities.

Some of the earliest evidence we have of handedness in the hominin lineage is in Australopithecines. Although the use of tools by *Australopithecus afarensis* (3.7-2.8 mya) is contentious (Domínguez-Rodrigo, 2010; McPherron et al., 2010), their manual proportions suggest that they would have been capable of the pad-to-pad precision grip thought to have been necessary for stone tool production and use (Alba et al., 2003; Tocheri et al., 2008). Dart (1949) examined over 50 specimens of extinct baboon (*Parapapio broomi*) remains associated with *A. africanus* (3.1-2.0 mya). His findings, based on the location of injury to the baboon skulls, indicate that the baboons were most likely clubbed by a right handed individual.

Homo habilis (2.3-1.5 mya) is one of the earliest hominins with strong evidence of stone toolmaking and is associated with the comparatively primitive Oldowan tool complex (Napier, 1965; Marzke and Marzke, 2000; Tocheri et al., 2008). The hand morphology of *H. habilis* suggests a powerful grasp, similar to that of modern humans (Marzke and Marzke, 2000). Toth (1985) studied flakes from Oldowan tool production left by *H. habilis* at Koobi Fora dated to 1.4-1.9 mya and concluded that, based on strike pattern comparisons to modern stone tools created using the same methods, they were made by one or more right handed individual(s). In order to better understand the complexity, both mentally and manually, of creating Oldowan tools, Toth et al. (2006) attempted to get a bonobo (Pan paniscus) to reproduce Oldowan tools. The results of their efforts indicated that the bonobo, Kanzi, possessed an understanding of the overall action plan, but he was unable to adequately coordinate the actions necessary, likely due to the less flexible wrist morphology characterizing *Pan* (Schick et al., 1999). As early hominins such as *H. habilis* possessed a more flexible wrist, capable of the stone knapping patterns seen in the lithic record, this is an indication of increased manual dexterity, leading to the suggestion that selection for and on Oldowan tool making capabilities may have increased the elaboration of a manual ability that was also tied to the enhanced articulatory control required for more modern speech (Stout and Chaminade, 2009).

Though there are no hand bones positively identified as *H. erectus* or *H. ergaster* (1.8-1.0 mya) (McHenry and Coffing, 2000; Tocheri et al., 2008), these species are associated with the more complex bifacial tools that characterize the Acheulean tool industry as well as the Levallois technique, which is distinguished by core modification before flake production. These new techniques imply more complex thought and planning capabilities than previously seen in hominins and may have corresponded with a significant structural change in hand morphology (McHenry and Coffing, 2000; Tocheri et al., 2008; Klein, 2009). Examinations of the directionality of flakes removed in the making of Acheulean tools support the

conclusion that a right handed bias was present in *H. erectus/ergaster* (Toth, 1985; Steele and Uomini, 2005a; 2009).

Asymmetric striations on lithic remains associated with stone knapping from *Homo heidelbergensis* (1.3-0.25 mya) in Boxgrove, UK and Neanderthals (*Homo sapiens neanderthalensis*) across Europe indicate a right handed bias in stone tool production (Cornford, 1986; Roberts et al., 1999). More evidence of hominin handedness is taken from striations found on the anterior teeth of *H. heidelbergensis* and Neanderthals which are frequently interpreted as the result of a specific form of lateralized eating (Martin, 1923; Semenov, 1964; Trinkaus, 1983). Conclusions drawn from these patterns of striations indicate that *H. heidelbergensis* and Neanderthals were already as right handed as modern humans (Lozano et al., 2009). Studies of handedness as represented by cave art hand portrayals across Europe and the Middle East also support a right handed species-wide bias in Neanderthals and anatomically modern humans (AMH) (Delluc and Delluc, 1993; Steele and Uomini, 2005b). Overall, the paleoanthropological and archaeological evidence reveals that a right-handed bias may have been present in the hominin lineage as far back as Australopithecines and potentially as early as our lineage's split from *Pan*.

1.6 Handedness in Great Apes

We currently look to nonhuman primates, especially great apes, for evidence of cerebral asymmetry as seen through behavioral asymmetry to help us understand the importance of cerebral asymmetry both in their lives and in our own evolutionary history (Corballis, 1992; Crow, 1998; Hopkins, 2008). Behavioral preferences are likely to reflect brain lateralization, as seen in humans (Corballis, 1989). These behavioral preferences can be observed in great apes to assess brain asymmetry. Chimpanzees and bonobos (*Pan paniscus*) especially can give us a unique perspective on handedness and human evolution because they are our closest living relatives. Though, as neurophysiology is not

entirely understood (Hammond, 2002), is possible that hand preference developed two separate times in the Pan and in the Homo lineages. However, because we see hand preference at least at the individual level in great apes (see Hopkins 2006 for review), as well as numerous other primate species (Papademetriou et al., 2005), it is unlikely that brain lateralization appeared for the first time in humans. Therefore, precursors of the relatively increased brain lateralization may have been present earlier in the hominid lineage and may still characterize Pan. Additionally, the hands of great apes are similar to our own and are capable of the manufacture and use of tools (McGrew and Marchant, 1997; Byrne et al., 2001). They also are known to exhibit bipedal locomotion (Videan and McGrew, 2002; Susman and Badrian, 2005) as well as certain capacities for language (Savage-Rumbaugh et al., 1986; Miles, 1990), both of which have been proposed as mechanisms for the evolution of brain hemispheric specialization and handedness. Great ages also exhibit certain neuroanatomical brain asymmetries that are similar to those seen in humans, including leftward asymmetries of the planum temporale (Gannon et al., 1998; Hopkins et al., 1998; Cantalupo et al., 2003), inferior frontal gyrus (Cantalupo and Hopkins, 2001), and sylvian fissure length [injuries of which are associated with language impairment (Hopkins and Pilcher, 2001; Leonard, 2001)]. For these reasons, researchers continue to look to great apes as the best nonhuman model for clues to our asymmetrical origins.

Current studies on handedness in chimpanzees and other great apes have been inconclusive as to the presence of handedness in our closest living relatives (see Hopkins, 2006 and Papademetriou et al., 2005 for reviews). Population-level lateralization, specifically showing a right hand bias, has been reported in captivity (Hopkins and Cantalupo, 2005; Hopkins, 2008; Chapelain and Hogervorst, 2009), though some argue that this is due to imitation of humans' right handedness (McGrew and Marchant, 1997; Palmer, 2003). Captive chimpanzees, specifically, have shown strong evidence of population-level handedness for behaviors such as reaching (Olson et al., 1990; Hopkins, 1993; Colell et al., 1995a; Hopkins et al., 2005c), throwing (Hopkins et al., 2005b), bimanual feeding (Hopkins, 1994), manual

gestures (Hopkins et al., 2005a), and coordinated bimanual actions (Colell et al., 1995b). In contrast, reports of wild great apes fail to demonstrate population-level handedness bias in many of the same activities like scratching, reaching, or plucking at Gombe National Park (Marchant, 1996) and the Mahale Mountains, Tanzania (McGrew and Marchant, 2001; Corp and Byrne, 2004) or on various forms of tool use such as nut cracking at Bossou, Guinea (Biro et al., 2003; Humle and Matsuzawa, 2009), leaf sponging at Taï National Park, Côte d'Ivoire (Boesch, 1991) and Bossou, Guinea (Biro et al., 2003), ant dipping at the Mahale Mountains, Tanzania (Marchant and McGrew, 2007), and termite fishing at Gombe National Park, Tanzania (McGrew and Marchant, 1992; 1996). However, others question these claims (Hopkins and Cantalupo, 2005; Hopkins, 2006) and some have demonstrated a population level bias for several of the same activities, especially termite fishing in Gombe National Park, Tanzania (Lonsdorf et al., 2005) and Fongoli, Senegal (Bogart et al., 2012), but also for nut cracking and leaf sponging at Gombe National Park, Tanzania (Lonsdorf et al., 2005) and Bossou, Guinea (Humle and Matsuzawa, 2009) and bimanual feeding of Saba fruits and wild-growing lemons in the Mahale Mountains, Tanzania (Byrne and Byrne, 1991; Corp and Byrne, 2004). Captive bonobos have been shown to exhibit individual strong hand preference for complex bimanual tasks but not at the population level (Chapelain and Hogervorst, 2009).

An extensive review of research on handedness in great apes by Hopkins (2006) revealed several important findings, namely: (1) collectively, great apes exhibit right handedness, (2) bonobos and chimpanzees tend to show population-level right handedness, while gorillas (*Gorilla gorilla*) and orangutans (*Pongo spp.*) do not, (3) hand preferences in apes are task specific, (4) captive apes are more right handed than wild apes, though both are right handed, and (5) in the genus *Pan*, strength and direction of hand preferences are genetically inherited, with offspring handedness tending to follow the mother. However, evidence of group level bias is less common than not, and evidence for such a bias

remains contentious and disputed (Hopkins and Cantalupo, 2005; Papademetriou et al., 2005; Hopkins, 2006).

Important to the discussion, there are a number of methodological issues with studying handedness in great apes. The most apparent is of task specificity and complexity. Studies have shown that handedness bias depends on the specific task and the complexity of that task (Warren, 1980; Bradshaw and Nettleton, 1982; Marchant, 1996; Hopkins and Pearson, 2000; Hopkins, 2006). This is an obvious flaw because the results of a study necessarily depend on the task used to assess laterality. Stronger hand preference is found more often in complicated tasks rather than less complicated, more spontaneous tasks (see above). This then leads to the conclusion that simple tasks with little object manipulation are less likely to be laterally biased within an individual, population, or species (Bradshaw and Nettleton, 1982; Arbib, 2006; Steele and Uomini, 2009), and can discourage researchers from examining such simple 'every day' tasks such as feeding, as is examined in this study. Additionally, it is also essential to standardize the methods used between studies to be able to make cross species comparisons. Currently there is no such consensus (Hopkins and Cantalupo, 2005; Hopkins, 2006). This problem is also apparent in comparisons between humans and nonhuman primates (Seltzer et al., 1990; Hopkins and Cantalupo, 2005; Hopkins et al., 2013).

1.7 Objectives and Hypotheses

The research conducted for this study was aimed at observing and identifying chimpanzee hand preference during feeding. This was accomplished by investigating the daily feeding habits of chimpanzees living at the Chimfunshi Wildlife Orphanage, specifically in the Chimpanzee Project Area (CPA), in north central Zambia. Analyzing these findings similarly to studies done elsewhere lends itself to a better overall understanding of chimpanzee hand preferences within this population and a more accurate comparison with other groups of chimpanzees. In doing so, two hypotheses were tested,

namely that subjects will use one hand preferentially for feeding, exhibiting an individual hand preference, and secondly that there will exist no population-level handedness of unimanual feeding of the chimpanzees living at the CPA. In contributing to current knowledge and assisting in the future direction of laterality studies, this research aims to promote a better and more complete understanding of both the evolutionary past of chimpanzees and other great apes, as well as the unique history and, potentially, the driving forces behind this aspect of human evolution.

CHAPTER 2. METHODS

2.1 Study Site and Subjects

Research for this study was carried out over the course of 43 days (May 20-July 11, 2012) at the Chimpanzee Project Area (CPA) of Chimfunshi Wildlife Orphanage (12°38′S, 27°51′E; elevation 1300m) in the Miombo woodland of northern Zambia. The Miombo woodland is a closed deciduous nonspinescent woodland and generally occurs in geologically old, nutrient-poor soil in the uni-modal rainfall zone where fires are a characteristic feature (Malaisse, 1978; Campbell, 1996). Spatial heterogeneity exists within the Miombo woodland, including areas defined as savanna (Huntley, 1982; White, 1983; Frost et al., 1986), woodland (White, 1983; Sokal and Rohlf, 1995), and forest (Malaisse, 1978; Hopkins et al., 2007). The study period occurred at the beginning of the dry season (May to October) where seasonal average high temperatures are 26°C, average low temperatures are 10°C, and average rainfall is 0mm (White, 1983; Hogan, 2012).

The Chimfunshi Project Area consists of four separate enclosures, which include the largest chimpanzee enclosures in the world, with variable numbers and ages of chimpanzees in each (see Appendix A). Enclosure 1 contains 23 chimpanzees: males and females, ranging from 6 months to 31 years of age (one female died during the period of study) in 190 acres. Enclosure 2 contains 46 chimpanzees: males and females, ranging from <1 month to 40 years of age (one female, Milla, lives in solitary confinement by choice, and 26 individuals are less than 12 years old) in 160 acres. Enclosure 3 contains 15 chimpanzees: males and females, ranging from 2 to 27 years of age in 47 acres (one female, Chrissy, is new to the group and was held in a separate enclosure during the duration of this study). Enclosure 4 contains 14 chimpanzees: males and females, ranging from 1 to 21 years of age, in 62 acres (one male, Chiffon, live in solitary confinement by choice).

Conditions at the CPA allow for the observation of chimpanzee feeding behaviors, as the chimpanzees are given food once each day in a series of interconnected observational chambers, with

restricted physical human interaction. This food is a supplement to what the apes eat from the local vegetation growing in their enclosures, though no formal survey of the vegetation and landscape within the enclosures has ever been conducted (Mark Bodamer, personal comm.). Additionally, chimpanzees are fed many kinds of foods that give them the opportunity to peel and break apart much of their diet bimanually. The chimpanzees are not fed meat, due to the expense, though wild chimpanzees regularly eat meat, and many of the individuals at Chimfunshi used to eat meat (Patrick Chambatu, personal comm.). A few times the chimpanzees were fed something in a container – chopped vegetables in plastic trays covered with wrap, crunchy vegetable crisps in foil bags. These were recorded as such, and though they are not a natural food for chimpanzees, they provide insight into the use of two hands for complementary tasks and therefore can be useful in assessing handedness.

2.2 Data Collection

To determine which of the four enclosures would be observed each day, from May 25 through June 10 enclosures were chosen by random sampling with replacement. From June 18 through July 12, I chose enclosures by random sampling without replacement, and during July two enclosures were observed each day by different groups of students. I had originally planned to choose chimpanzees randomly from those in the enclosure, but the feeding set-up did not allow this. The buildings were set up as a series of rooms interconnected by doors covered by metal plates. Each day around 1130 hours the keepers would call to the chimpanzees to come into their feeding rooms where they would be kept until all the food was finished or interest was lost; usually about 90 minutes. The intent was to always have the same groups of chimps eating together, in a way in which they had previously demonstrated they were able to safely eat in close proximity to one another. This usually meant that rooms would have the same one or two familiar groups of 3-9 chimpanzees in them each day, though the subjects were not always cooperative about going into their expected enclosures. Additionally, only the keepers

were allowed into the middle hall between the two sides of chimpanzee enclosures at Enclosures 1 and 2, and many of the enclosures could only be viewed from that middle hallway or from inside the multiacre outdoor chimpanzee enclosure, where other chimpanzees were still sitting and eating (see Appendix B for more detailed enclosure layouts). Because of this, many chimpanzees could not be observed (or were observed only once because they happened to be in a visible enclosure that day but usually were not) simply because they were in an inaccessible room. Additionally, each feeding room had several open windows covered by bars atop a counter where the keepers fed the chimpanzees. Through these windows we were able to observe the chimpanzees' behaviors, but because of this setup, the chimpanzees can and often did disappear out of sight during our observations – either jumping to another counter to eat, turning their backs on us, or sitting on the floor below the window. The time spent out of sight was recorded for each observation.

Given these restrictions on data collection, chimpanzee subjects were opportunistically, not randomly chosen. Instead of randomly choosing chimpanzees to observe, we waited until the keepers had finished handing out the food for that day and then noted which chimpanzees were eating within view. By comparing those we could see to the list of chimpanzees we had previously observed, we chose our focal subject in a way to try and maximize the total number of chimpanzees observed and to control for the amount of time spent observing each individual. Individuals less than five years of age and those kept in solitary confinement were not included in this study. To assess interobserver reliability, I paired up with one student every day of data collection (n=35) to gather data that could be directly compared, and the reliability of each student's data could be estimated for all days. I paired with each student at least once and with most students more than once over the course of the study period (see Table 1).

At the time of feeding (once each day), focal animal sampling data were collected from the feeding room for the duration of time the chimpanzees spent feeding in that enclosure, and after the focal subject had been identified – within the first minute of feeding. Data recording did not begin until

keepers had distributed all food to the apes, which typically lasted about five minutes The data recorded included: individual (by name, so data can be attached to each individual's unique past at a later time), time of day, food being eaten, and which hand and/or foot was used both in hand-to-mouth action as well as peeling vs. holding a food item. Distinction was made between grabbing a food item (e.g., from the floor, or another ape) and placing the item in the mouth. Each food item was listed separately, and if it could be determined that an individual went back to the same food item previously manipulated or fed on, this was also recorded, and these were considered single bouts. Food objects (typically scraps that were too small) that could not be identified were recorded as miscellaneous in a single category, but were later separated into individual pieces for analysis. If a subject left the viewing area or could not be reliably seen the individual was recorded as out of sight, and if a subject was out of sight for longer than five minutes, a new subject was chosen.

2.3 Data Summary and Analyses

More than 68 hours of data were collected, over 53 hours of which was independent (nonoverlapping, as I paired with one student each day to assess interobserver reliability – discussed below), over the course of 35 sampling days. For analyses, the data were considered as summaries of hand usage during hand to mouth motions of bouts. A bout was defined as the chronological consumption of a single food item (e.g., one fruit), regardless of what it was or how many bites were taken. Data were summed into three categories: right (every hand to mouth motion for that bout was performed with the right hand), left, and other (subject switched hands at least once during the bout, used both hands simultaneously, or a combination of using both hands and also a single hand or both hands and also switching hands). Hand used to grab the food item was not considered in the summary of a bout, as food items were many times taken from the keepers or from other apes and so were not consistently performed under the same context. To maximize data gathered, the records for each piece of food were

separated from long stretches of 'miscellaneous' feeding, and the uni- and bimanual actions were considered separately from one another. Since some students indicated if a piece of food was returned to and some did not, any return to a prior food item after the consumption of a different food item was treated as a separate data point. Though this could mean that certain data points are not independent from one another (if the chimpanzee continued to hold the food item or if he or she set it down and then picked it up again was not apparent in the data), the data were not clear enough to reliably pool returned-to items consistently across all observations. Additionally the amount of times that this occurred was quite low in comparison to the number of food items eaten as one complete bout (68 times out of 5618 bouts or 1.2% of total observations).

2.3.1 Interobserver Reliability

In order to assess interobserver reliability, the observations collected by each student, summed into hand preference of each bout (left, right or other), on the days that I was paired with that particular student (i.e. observing the same subject) were compared to the equivalent bout hand preference data that I gathered during the same time frame. The likelihood of the student recording the data he or she did, as summarized by frequencies of right handed, left handed, and 'other' bouts, given that my data were the expected values, was calculated using a G test of independence in which G=- $2(\Sigma obs*ln(exp/obs))$. The G test of independence is the log-likelihood ratio calculation from which chisquared tests and goodness of fit tests are based; it makes no assumptions of a normally distributed data set, and it has approximately a chi-squared distribution for assessing the significance of values (Sokal and Rohlf, 1995; Harrison and Nystrom, 2008). Students whose G score was greater than 5.99 (α =0.05, df=2) were considered significantly different from the expected observations (my own data) and were omitted from further analyses (Table 1). Similarly, chimpanzees with fewer than 40 recorded

feeding bouts were not included in further analyses, and so a total of 34 chimpanzees were analyzed in this study (Hopkins et al., 2007).

2.3.2 Individual Hand Preference

Many studies have called for a standardization of the methods used in primate handedness studies, but consensus within the field is lacking (Hopkins and Cantalupo, 2005; Hopkins, 2006; 2013). Current analytical methods in the field of primate handedness studies typically converge on HI scores (Hopkins et al., 2007; Marchant and McGrew, 2007; Papadatou-Pastou et al., 2008; Chapelain and Hogervorst, 2009; Hopkins et al., 2011) and z tests (Papademetriou et al., 2005; Hopkins et al., 2007; Chapelain and Hogervorst, 2009; Hopkins et al., 2011) to determine handedness of individuals in a way that is comparable to other studies in the field. HI is calculated as the difference in the number of right and left hand responses divided by the total number of right and left hand responses, or HI=(R-L)/(R+L)(Marchant and McGrew, 2007). While the HI score is admittedly arbitrary (Hopkins et al., 2007), it has the advantage over simple right hand ratios of inherently reflecting hand bias in the sign, making interpretations of HI scores that much simpler. However, the utility of the z score is less clear. Using a binomial z test on HI scores is not advisable, as a binomial distribution is by its nature, of discrete variables, not continuous variables, as the HI scores are (Lehmann and Romano, 2005), and yet many studies use this test (Hopkins, 2006; Hopkins et al., 2007; Chapelain and Hogervorst, 2009), as recommended by Michel et al. (2001). However, using a normal z test assumes a bell-shaped, normal distribution with probabilities found anywhere between two z values (Lehmann and Romano, 2005). That the data fit a normal distribution can be assumed with reasonably large sample sizes, but for small samples, that normality must be tested, rather than assumed (Lehmann and Romano, 2005). Many studies in primatology inherently have small sample sizes, due in part to relatively low numbers of study subjects, especially regarding wild individuals. Many tests exist to test the normality of a given data set,

including the Kolmogorov-Smirnov test, the Anderson-Darling test, and the Shapiro-Wilk test (Sokal and Rohlf, 1995; Razali and Wah, 2011). The Anderson-Darling test and Shapiro-Wilk tests are among the most powerful for assessing normality (Stephens, 1974). A handful of studies of primate handedness have used the Shapiro-Wilk test to help define the distribution of their data (Pellis and Iwaniuk, 2000; Stout and Chaminade, 2007; Harrison and Nystrom, 2008; Braccini et al., 2010), but many others make no test of normality of the data but still perform analyses, such as the z test, that assume a normal distribution (Colell et al., 1995a; Papademetriou et al., 2005; Fletcher, 2006; Hopkins, 2006; Hopkins et al., 2007; Chapelain and Hogervorst, 2009). While the normal z test can be used as an appropriate assessment of individual handedness (Michel et al., 2001), testing for the normality of data should be a precursor to analyzing data with statistical tests that assume normality.

In this study, the G test of independence was used to examine the handedness and significance of that preference for each individual. The G test is a likelihood-ratio, or maximum likelihood test, that is becoming increasingly used where chi-squared tests, such as Pearson's product-moment correlation, were previously used, as the G test is the more accurate logarithmic based function from which chisquared tests are derived (Sokal and Rohlf, 1995). With the advent of computers, it is no longer so laborious to calculate logarithmic functions, and so the approximations of the G test (i.e., chi-squared tests) are no longer the most accurate assessment of the data. Additionally, like chi-squared tests, likelihood-ratio tests make no assumption of a normally distributed population (Harrison and Nystrom, 2008) and therefore are a good fit for the field of primatology, where samples sizes are small and populations are not always normally distributed. While the G test does not inherently reflect the hand bias in the sign like the handedness index, it does have the added value of having approximately a chisquared distribution for assessing the significance of values. This is preferable in that no transformation of values is necessary to assess significance, as is needed when using the handedness index, which must be reassessed using a z test.

To determine if each subject exhibited a preference for using just one hand, rather than switching hands or using both hands – any response summarized as 'other' – the log likelihood ratio was calculated using a G test of independence, with the null hypothesis of equal preference for using one hand or 'other', or a frequency of 0.5 in either direction. This value was then compared to the critical value of 3.85 (α =0.05, df=1). Additionally, the same comparison of single hand preference and no single hand preference was demonstrated through a modification of the handedness index (HI) frequently used in other primate handedness studies (Marchant and McGrew, 2007; Papadatou-Pastou et al., 2008; Chapelain and Hogervorst, 2009; Hopkins et al., 2011). While HI is normally calculated as the difference in the number of right and left hand responses divided by the total number of right and left hand responses, or HI=(R-L)/(R+L) (Marchant and McGrew, 2007), in this case the equation was modified to indicate the strength of preference of using a single hand per feeding bout and so compared right and left hand responses together against 'other' responses using the equation of handedness preference (HP)=(R+L-O)/(R+L+O). Strength of preference was indicated by the directionality of the response, as -1≤HP≤1. Positive responses indicated a preference of using a single hand during feeding bouts, and negative responses indicated a preference toward not using a single hand during feeding bouts. A Shapiro-Wilk test of normality was performed on the resulting HP scores to see if the data fit a normal distribution (Harrison and Nystrom, 2008), and a two-tailed t-test was performed to see if the population average differed from the expected 0 (White, 1983; Campbell, 1996; Papademetriou et al., 2005).

In order to determine the hand preference (if there was one) of each individual chimpanzee, an HI score for each individual was calculated according to the previously discussed equation. After testing the data collected during this study for a normal distribution using the Shapiro-Wilk test and finding it normally distributed, z tests were then conducted to generate comparable values with other studies in the field. Individuals with z-scores \leq -1.96 were classified as left handed, those with z-scores \geq 1.96 were

classified as right handed, and responses in between were classified as no preference (NP) (Papademetriou et al., 2005; Hopkins et al., 2007; Chapelain and Hogervorst, 2009; Hopkins et al., 2011). These values, and their handedness classifications of the subjects of this study, were then compared directly to those classifications based on the likelihood ratio tests (G tests), again testing the null hypothesis of a lack of hand preference. The outcomes were then compared to the critical value of 3.85 (df=1) (see Table 3). In 33 of 34 subjects, both tests made the same conclusions on the handedness of the individual. On only one individual were their conclusions different – Commander – whose z-score classifies him as left handed (z=-1.9585, critical value -1.96) while his G score determined that he has no hand preference (G=3.6870, critical value 3.84). In both cases, the test statistic is very close to the critical value and, in the case of the z-score, he is only classified as left handed due to rounding and so could just as easily be classified as having no hand preference. Because these two tests yielded such similar results (nearly identical, depending on rounding interpretations), and the G test makes no assumptions of normality, I suggest scholars submit the G test as an alternative to the predominant z test as an easier, just as accurate method of calculating individual hand preference.

2.3.3 Population Level Handedness

Population level handedness was considered at many levels. Two-tailed t-tests were carried out to determine if population level handedness for feeding exists in each of the four enclosures at the Chimpanzee Project Area (CPA) of Chimfunshi Wildlife Orphanage (Papademetriou et al., 2005; Chapelain and Hogervorst, 2009). A two-tailed t-test was also used to indicate population level handedness, or lack thereof, for all chimpanzees surveyed at the CPA.

2.3.4 Bimanual Feeding

As the major focus of this study was unimanual feeding, student researchers were told that recordings of asymmetrical bimanual feeding (peeling food items, or opening containers of food) were considered 'extra' information and were not imperative to record. Because recordings then were inconsistent, and relatively few, interobserver reliability was not determined for bimanual feeding observations. Additionally, no ethogram or detailed explanation was given to the students before the study as to what constituted bimanual feeding and how to determine the directionality of dominance. What at first seemed like an obvious classification of bimanual action, later was realized to result in inconsistent recordings while observing subjects, due to the ambiguous nature of the bimanual actions. Observations of bimanual action were recorded as, for example, "hold L peel R", in which the food item was held with the left hand, and peeled with the right hand. However, what was realized later was that the hand peeling the food item was not always the manipulative, dominant hand or performing the higher frequency task. The immediately apparent scenario is when a food item - for example, an orange - is held passively by the supporting left hand, and actively peeled with the fingers on the manipulative right hand. However, what we observed was that in many cases the opposite was true – the orange (food item) was held in the left hand, and while the fingers of the right hand were separating the peel from the flesh of the fruit, they remained nearly stationary while the left hand manipulated the orange against the fingers of the right hand to remove the peel. Yet in each case, each observation recorded "hold L peel R". While this record is in each case correct, it does not give an accurate representation of the roles of each of the hands performing the task. Because of this ambiguity, these data were not analyzed statistically but rather are presented graphically in Figure 1.



Figure 1. Bimanual feeding observations (n=630); not used in statistical analyses *bars this size indicate 0 responses and are place holders only

2.3.5 Additional Factors

Because of the varied backgrounds of the chimpanzees living at the CPA, a linear regression model was run on the HI scores of the apes to see if other factors had any influence on the handedness of the individual in question. Factors considered included current age [not always known precisely, so analyses were run following Baldwin's age categories with slight modification (Pruetz and Bertolani, 2007)], as adults were estimated to be approximately >13 years of age, adolescents from 9-13 years, juveniles from 5-8 years, and infants \leq 4 years), sex, age at entry to the sanctuary (again, many were estimates, many were born at the sanctuary, and analyses were run on age class as a categorical variable), having known family members at the sanctuary (Y/N regarding presence of parents, offspring, or siblings), and the background of the individual prior to admission to the sanctuary (based on implied previous level of human interaction, and categorized as a house pet, captured from the wild shortly before entrance to the sanctuary, housed in a zoo, used by humans as direct and interactive entertainment (i.e. at a bar or restaurant, with no specific 'owner'), or born at the sanctuary). A linear regression model was chosen for this assessment over a correlation analysis, as regression models can show a one-way causal effect from the explanatory variables (such as age and sex) to the response variable (HI). A correlation analysis makes no assumptions about the relationship between variables, and therefore can only test the interdependence of the variables and not the dependence of one on another. In this way, linear regression can examine the dependence of individual handedness on the subject's sex or age, rather than a correlation analysis that can only investigate the interdependence between them. The data used for this analysis as well as certain additional information about the chimpanzees included in this study are summarized in Appendix C.

2.4 Results

A G test of independence to determine interobserver reliability showed that 3 of the 14 students collected feeding observational data that were significantly different from my own data (G score >5.99, α =0.05, df=2; results summarized in Table 1). These students were omitted from further analyses. Only chimpanzees with 40 or more recorded feeding bouts (n= 34 subjects) were included in handedness analyses (Hopkins et al., 2007).

Table 1. L	Table 1. Log likelihood and G score from interobserver reliability tests						
Student	Total Observations	Observation Overlap	logL	G	Conclusion		
	(minutes)*	(minutes)*		score**			
Carmen	344	143	-2.0164	4.0329	accept		
Kathryn	303	92	-2.2763	4.5526	accept		
Melissa	320	122	-4.3858	8.7716	reject		
Forrest	126	27	-1.8577	3.7155	accept		
Toby	94	38	-1.3398	2.6797	accept		
Ben	83	56	-0.3293	0.6587	accept		
Stephen	281	82	-3.6520	7.3040	reject		
lan	127	35	-4.5794	9.1589	reject		
Chris	368	45	-1.2376	2.4752	accept		
Joe	250	79	-2.9681	5.9362	accept		
Ashley	266	33	-2.3466	4.6933	accept		
Kate	250	35	-0.6752	1.3503	accept		
Cara	220	27	-0.8613	1.7228	accept		
Liz	185	94	-0.1925	0.3850	accept		
*additional information for interest only; not used in analyses							
**compared to a critical value of 5.99 (α =0.05, df=2)							

Two sets of statistical analyses were run to determine if each chimpanzee included in the study showed a preference using one hand per food item rather than switching hands or using both hands simultaneously ('other' category). A modified version of the handedness index (labeled HP scores) yielded the values in Table 2. A Shapiro-Wilk test of normality resulted in p<0.001, rejecting the null hypothesis that the values are normally distributed. Though the strong directionality of the scores leaves little doubt that the subjects all show a strong bias toward using just one hand during a single feeding bout, a two-tailed t-test of the HP scores then indicated a significant difference (t=47.0303, p=0.1708), therefore rejecting the null hypothesis that this population shows no preference for using a single hand during feeding bouts. Because of the slightly more arbitrary nature of the HP calculation (Hopkins et al., 2007), a second statistical analysis was conducted on the data to determine separately if the subjects exhibit a single hand preference during feeding bouts. The results of the G test of independence were classified as significant if >3.84 (df=1), and the direction of significance was inferred from the observed frequencies of left, right, and 'other' responses. The log likelihood and G-score as well as their conclusions are reported in Table 2.

As all chimpanzees were shown to have a preference for using a single hand during each feeding bout, two separate analyses were performed to determine if each ape had a hand preference (left, right, or equal preference). Handedness index (HI) scores were calculated to make the data comparable to other primate studies (Marchant and McGrew, 2007; Papadatou-Pastou et al., 2008; Chapelain and Hogervorst, 2009; Hopkins et al., 2011) and are given in Table 3. A Shapiro-Wilk test of normality was performed on the HI scores, which indicated that the data were normally distributed (p=0.3188) and so normal z-scores were calculated for each individual. Apes with z-scores \leq -1.96 or \geq 1.96 were classified as left and right handed, respectively (Hopkins, 2006), and individuals with z-scores in between the two values were classified as having no hand preference (Table 3). A two-tailed t-test was performed on all HI scores, failing to reject the null hypothesis that the population mean was significantly different from zero (t=-1.4, p=0.1708), showing a slight overall trend towards left handedness, but not significantly so. Two-tailed t-tests were also performed to examine population level handedness for each enclosure, and no significant results were obtained. However, hand preference trended toward a left hand bias within enclosures 1 and 3 (t=-1.5083, p=0.1657, df=9 and t=-1.9485, p=0.0872, df=8 respectively), but only showed weak hand preference towards the left hand in enclosure 2 (t= -0.4164, p=0.6869, df=9)

and their respective conclusions					
Subject	HP	Conclusion*	logL	G score	Conclusion*
Barbie	0.8657	SHP	-119.7709	239.5417	SHP
Berta	0.8500	SHP	-17.0705	34.1410	SHP
Bob	0.7949	SHP	-56.5448	113.0896	SHP
Booboo	1.0000	SHP	-36.7368	73.4736	SHP
Brenda	0.7011	SHP	-23.6150	47.2299	SHP
Brian	0.9228	SHP	-178.5279	357.0558	SHP
Bussie	0.9487	SHP	-67.1463	134.2927	SHP
Clement	0.9030	SHP	-267.4910	534.9819	SHP
Commander	0.7363	SHP	-27.5934	55.1869	SHP
David	0.9821	SHP	-71.9185	143.8369	SHP
Debbie	0.9310	SHP	-31.5028	63.0057	SHP
Diane	0.8795	SHP	-38.6379	77.2758	SHP
Dolly	0.9512	SHP	-23.7178	47.4355	SHP
Donna	0.9300	SHP	-185.7280	371.4560	SHP
Erika	0.8333	SHP	-34.1301	68.2603	SHP
ET	0.8369	SHP	-191.3491	382.6982	SHP
Genny	0.7349	SHP	-25.0643	50.1285	SHP
Gerard	0.8051	SHP	-72.8783	145.7566	SHP
Girly	0.8376	SHP	-81.0482	162.0965	SHP
Ingrid	0.8701	SHP	-69.7329	139.4659	SHP
Innocentia	0.8033	SHP	-22.6726	45.3451	SHP
Julie	0.6471	SHP	-15.4461	30.8921	SHP
Junior	0.9439	SHP	-120.9731	241.9462	SHP
Kathy	0.9626	SHP	-128.4524	256.9048	SHP
Louise	0.9579	SHP	-56.1487	112.2974	SHP
Nikki	0.9625	SHP	-96.0022	192.0043	SHP
Nina	0.8712	SHP	-119.9238	239.8477	SHP
Noel	0.9219	SHP	-202.8265	405.6530	SHP
Pal	0.9286	SHP	-60.3760	120.7519	SHP
Sampie	0.8830	SHP	-80.4357	160.8713	SHP
Tara	0.8857	SHP	-49.7820	99.5641	SHP
Val	0.8868	SHP	-25.2083	50.4166	SHP
Vis	1.0000	SHP	-75.5530	151.1061	SHP
Zsabu	0.9808	SHP	-66.4477	132.8955	SHP
*SHP=single hand preference, OP='other' preference as defined in Chapter 2					

Table 2. Modified handedness index (HP) and G test of independence calculations and their respective conclusions

Table 3. Hand	edness ind	lex (HI) and	G test of in	depend	lence calculat	ions and the	ir respective	conclusio	ons
Subject	HI	Z score	р	HP*	logL	G score	р	HP**	
Barbie	0.5760	11.1412	< 0.0001	R	-44.1382	88.2763	<0.0001	R	
Berta	0.5135	3.6402	0.0003	R	-5.1192	10.2385	0.0014	R	
Bob	-0.8571	-19.6899	<0.0001	L	-61.0160	122.0320	<0.0001	L	
Booboo	-0.3962	-3.1417	0.0017	L	-4.2767	8.5534	0.0034	L	
Brenda	-0.2702	-2.4148	0.0157	L	-2.7366	5.4732	0.0193	L	
Brian	-0.4877	-10.0543	<0.0001	L	-40.2186	80.4372	<0.0001	L	
Bussie	-0.6491	-9.1112	<0.0001	L	-26.0765	52.1530	<0.0001	L	
Clement	-0.0235	-0.5315	0.5951	NP	-0.1412	0.2824	0.5951	NP	
Commander	-0.2152	<u>-1.9585</u>	0.0502	L	-1.8435	<u>3.6870</u>	0.0548	<u>NP</u>	
David	0.3694	4.1877	<0.0001	R	-7.7544	15.5088	0.0001	R	
Debbie	-0.2857	-2.2311	0.0257	L	-2.3179	4.6357	0.0313	L	
Diane	0.5128	5.2756	<0.0001	R	-10.7612	21.5225	<0.0001	R	
Dolly	0.5000	3.6515	0.0003	R	-5.2325	10.4650	0.0012	R	
Donna	-0.2931	-5.5764	<0.0001	L	-14.4238	28.8475	<0.0001	L	
Erika	-0.4545	-4.4780	<0.0001	L	-8.2540	16.5080	<0.0001	L	
ET	-0.1776	-3.7329	0.0002	L	-6.7836	13.5672	0.0002	L	
Genny	-0.8889	-16.4639	<0.0001	L	-34.4583	68.9167	<0.0001	L	
Gerard	0.1478	1.9816	0.0475	R	-1.9275	3.8550	0.0496	R	
Girly	0.2597	3.6176	0.0003	R	-6.1727	12.3454	0.0004	R	
Ingrid	0.1806	2.2029	0.0276	R	-2.3601	4.7203	0.0298	R	
Innocentia	-0.6000	-5.5621	<0.0001	L	-10.6010	21.2019	<0.0001	L	
Julie	-0.8571	-12.4530	<0.0001	L	-24.4064	48.8128	<0.0001	L	
Junior	-0.2692	-4.0318	0.0001	L	-7.6323	15.2646	0.0001	L	
Kathy	1.0000	51.9882	<0.0001	R	-145.5609	291.1218	<0.0001	R	
Louise	-0.0968	-0.9377	0.3484	NP	-0.4362	0.8723	0.3503	NP	
Nikki	0.6051	9.5231	<0.0001	R	-30.8186	61.6373	<0.0001	R	
Nina	-0.4089	-7.0421	<0.0001	L	-21.2676	42.5352	<0.0001	L	
Noel	-0.8103	-26.5612	<0.0001	L	-140.0456	280.0912	<0.0001	L	
Pal	0.1296	1.3586	0.1743	NP	-0.9100	1.8199	0.1773	NP	
Sampie	-0.9503	-38.7342	<0.0001	L	-92.8664	185.7327	<0.0001	L	
Tara	0.1515	1.5252	0.1272	NP	-1.1408	2.2815	0.1309	NP	
Val	0.6400	5.8897	<0.0001	R	-11.0877	22.1754	<0.0001	R	
Vis	0.0275	0.2875	1.2262	NP	-0.0413	0.0826	0.7738	NP	
Zsabu	-0.9612	-35.3466	< 0.0001	L	-61.5305	123.0611	<0.0001	L	

1. ٢. . . 1.1 -.

HP denotes statistically significant hand preference

*z-scores ≤-1.96 or ≥1.96 classified as R and L hand respectively; values in between classified as no preference (NP)

**G scores compared to a critical value of 3.85 (α =0.05, df=1); directionality inferred from frequency of left and right handed responses

Values underlined denote differing hand preference classification between the two tests on a single individual

and toward the right hand in enclosure 4 (t=0.6490, p=0.5517, df=4)(see Table 4). Additionally, a G test of independence was performed on the data to separately analyze the hand preference of each chimpanzee. G scores >3.84 (df=1) were classified as having a hand preference, the direction of which was taken from the observed frequencies of left and right handed responses. Log likelihood and G scores are reported in Table 3, along with their respective conclusions. Interestingly, the z score and G score classifications led to slightly different conclusions in only one individual, Commander. Commander's z score labels him as left handed (z=-1.9585) while the G score determined he has no handedness preference (G=3.6870).

Table 4. The results of two-tailed t-tests to examine evidence of population level handedness for each enclosure

Enclosure	Total # of	# Chimpanzees	Mean	t value	Critical	Direction of	р
	Chimpanzees	Sampled**	HI		Value	Handedness	
1	24*	10	-0.2143	-1.5083	2.62	L	0.1657
2	36	10	-0.0744	-0.4164	2.62	L	0.6869
3	15	9	-0.2814	-1.9485	2.31	L	0.0872
4	14	5	0.2162	0.6490	2.78	R	0.5517
ALL	89	34	-0.1276	-1.4000	2.04	L	0.1708
*including Rig Iana, who diad $\frac{6}{2}/12$; <10 bouts were recorded, but they were used in the							

*including Big Jane, who died 6/8/12; <40 bouts were recorded, but they were used in the interobserver reliability test

**this number minus 1 gives degrees of freedom used, α =0.05

Bimanual feeding bouts were not analyzed with statistical tests (see section 2.3.4 for discussion), but the responses recorded were summed into a single figure that is Figure 1. A linear regression model was run to examine effects of current age, age at entry into the sanctuary, sex, having related individuals at the CPA, and previous life history before being brought to the sanctuary (all categorical data; no numerical, as many were estimations or not known) on the handedness of each chimpanzee (the data used in these analyses can be found in Appendix C). The resulting F and p values (Table 5) indicate that for the 34 chimpanzees analyzed, current age, age at entry into the sanctuary, sex, and having related individuals at the CPA all had a significant effect on the handedness of the

Table 5. Results of filled	Table 5. Results of fillear regression modeling effects of external factors of					
individual hand preference						
Effect	Numerical df	F value	р			
Current Age	2	49.06	>0.0001*			
Age at Entry	2	72.96	>0.0001*			
Sex	1	133.58	>0.0001*			
Family at the CPA?	1	19.05	0.0002*			
Previous Life History	1	1.27	0.271			
*effect considered significant if P<0.05						

Table 5. Results of linear regression modeling effects of external factors on

individual (p<0.001). When models were run considering interactions between factors, the data were insufficient to detect any such interactions, though the existence of such connections could also not be ruled out. Additionally, several of the chimpanzees living at the CPA who have unique backgrounds (such as Milla, who was taken from the wild at <1 year old, and used as a tourist attraction, never seeing another chimpanzee for 17 years before being rescued and brought to Chimfunshi by Jane Goodall; Bobby, who was saved from a dilapidated zoo in Bangui and brought to Chimfunshi as an adolescent; or Chiffon, who was a pet to an Italian family who taught him to finger paint and use crayons when he was a juvenile) were not to be included in the linear regression analysis due to lack of sufficient data.

CHAPTER 3. DISCUSSION AND CONCLUSIONS

3.1 Population Level Handedness

Studies of handedness in great apes have been widely inconsistent as to the presence of hand preference in our closest living relatives (Warren, 1980; MacNeilage et al., 1987; Fagot and Vauclair, 1991; Lehman, 1993; McGrew and Marchant, 1998; Palmer, 2002; Hopkins and Cantalupo, 2005; Papademetriou et al., 2005; Hopkins, 2006)(see Table 6 for review). Population-level lateralization, specifically showing a right bias, has been reported in captivity in gorillas (Heestand, 1986; Olson et al., 1990; Shafer, 1993), chimpanzees (Heestand, 1986; Colell et al., 1995a), orangutans (Olson et al., 1990), and bonobos (Shafer, 1993; Ingmanson, 1996; 1998). Captive chimpanzees, specifically, have shown good evidence of population-level handedness for behaviors such as reaching (Olson et al., 1990; Hopkins, 1993; Colell et al., 1995a; Hopkins et al., 2005c), throwing (Hopkins et al., 2005b), bimanual feeding (Hopkins, 1994), manual gestures (Hopkins et al., 2005a), and coordinated bimanual actions (Colell et al., 1995b). Population-level left handedness had been found for self-directed touching in rehabilitated orangutans (Rogers and Kaplan, 1996) and in spontaneous, every day actions in captive chimpanzees (Toback, 1999). However, many reports fail to demonstrate population-level hand preference in chimpanzees for spontaneous every day activities like scratching, reaching, and plucking (Marchant, 1996; McGrew and Marchant, 2001; Corp and Byrne, 2004). Studies of many other everyday activities such as scratching, grooming, picking up, eating, and holding have been inconsistent in their findings of hand bias in both captive and wild chimpanzees (see Table 7 for summary). Even studies of humans have failed to show population level hand preference for similar spontaneous hand use (Marchant et al., 1995; Eaton et al., 1998). Population-level handedness has also not been demonstrated in various forms of tool use by chimpanzees such as nut cracking at Bossou, Guinea (Biro et al., 2003; Humle and Matsuzawa, 2009), leaf sponging at Tai National Park, Cote d'Ivoire (Boesch, 1991) and Bossou, Guinea (Biro et al., 2003), and ant dipping (Marchant and McGrew, 2007) and termite fishing

Table 6. Distribution of handedness as a function of species and rearing history								
		Hand Preference Classification						
	Strong Left	Strong Left Mild Left Ambipreferent Mild Right Strong Right						
Species								
Bonobo	5	4	22	21	40			
Chimpanzee	281	68	171	71	375			
Gorilla	70	14	46	11	100			
Orangutan	31	6	14	4	33			

Adapted from Hopkins 2006

(McGrew and Marchant, 1992; 1996) in the Mahale Mountains, Tanzania. However, not all researchers

agree with these claims (Hopkins and Cantalupo, 2005; Hopkins, 2006) and some have concluded a

population level bias for several of the same activities, especially termite fishing at Gombe National

Park, Tanzania (Lonsdorf et al., 2005), and Fongoli, Senegal (Bogart et al., 2012), but also for nut

cracking, leaf sponging, grooming at Bossou, Guinea (Humle and Matsuzawa, 2009) (see Hopkins and

Table 7. Distribution of hand preference for five behaviors recorded in captive and fi	ield
studies of chimpanzees	

	_	C	aptive			Wild		
	# Left	# Right	# No Preference		# Left	# Right	# No Preference	
Scratch ¹	2	5	1		14	23	44	
Groom ²	4	4	24		16	29	40	
Eat ³	15	9	36		21	14	44	
Pick-up ⁴	51	52	86		27	17	29	
Hold⁵	36	6	81		19	25	11	

¹ Data from Marchant & McGrew, 1996; McGrew & Marchant, 2001; Leavens, Aureli, Hopkins, & Hyatt, 2001.

² Data from Boesch, 1991; Marchant & McGrew, 1996; McGrew & Marchant, 2001; Marchant, 1983; Steiner, 1990.

³ Data from Marchant & McGrew, 1996; McGrew & Marchant, 2001; Marchant, 1983; Stiener, 1990.

⁴ Data from Boesch, 1991: Marchant & McGrew, 1996; McGrew & Marchant, 2001; Sugiyama et al., 1993; Hopkins, 1993 (quadrupedal only); Marchant, 1983 (non-social reach only); Heestand, 1986; Steiner, 1990; Tonooka & Matsuzawa, 1995; Colell et al., 1995a.

⁵ Data from Marchant & McGrew, 1996; McGrew & Marchant, 2001; Marchant, 1983; Steiner, 1990, Toback, 2000.

Adapted from Hopkins & Cantalupo, 2005.

Table 8. Reports of population level handedness from studies of wild chimpanzees					
Site	Activity	Hand Bias	Source		
Bossou, Guinea	algae scooping	Right	Humle & Matsuzawa 2009		
Bossou, Guinea	ant dipping	Right	Humle & Matsuzawa 2009		
Bossou, Guinea	leaf sponging	Ambipreferent	Biro et al. 2003		
Bossou, Guinea	leaf sponging	Right	Biro et al. 2006		
Bossou, Guinea	nut cracking	Ambipreferent	Biro et al. 2003		
Bossou, Guinea	nut cracking	Ambipreferent	Humle & Matsuzawa 2009		
Bossou, Guinea	nut cracking	Ambipreferent	Humle & Matsuzawa 2011		
Bossou, Guinea	nut cracking	Right	Biro et al. 2006		
Bossou, Guinea	pestle pounding	Ambipreferent	Humle & Matsuzawa 2010		
Fongoli, Senegal	termite fishing	Left	Bogart et al. 2012		
Gombe National Park, Tanzania	leaf sponging	Right	Lonsdorf et al. 2005		
Gombe National Park, Tanzania	nut cracking	Right	Lonsdorf et al. 2005		
Gombe National Park, Tanzania	scratching, reaching, plucking	Ambipreferent	Marchant 1996		
Gombe National Park, Tanzania	scratching, reaching, plucking	Ambipreferent	McGrew & Marchant 2001		
Gombe National Park, Tanzania	termite fishing	Left	Lonsdorf et al. 2005		
Gombe National Park, Tanzania	termite fishing	Ambipreferent	McGrew & Marchant 1992		
Gombe National Park, Tanzania	termite fishing	Ambipreferent	McGrew & Marchant 1996		
Mahale Mountains, Tanzania	ant dipping	Right tendency	Hopkins et al. 2011		
Mahale Mountains, Tanzania	ant dipping	Ambipreferent	Marchant & McGrew 2007		
		Left (males) and			
Mahale Mountains, Tanzania	bimanual feeding of Saba fruits and lemons	Right (females)	Corp & Byrne 2004		
Mahale Mountains, Tanzania	scratching, reaching, plucking	Ambipreferent	Corp & Byrne 2004		
Mahale Mountains, Tanzania	termite fishing	Ambipreferent	Marchant & McGrew 1992		
Mahale Mountains, Tanzania	termite fishing	Ambipreferent	Marchant & McGrew 1996		
Taï National Park, Cote d'Ivoire	leaf sponging	Ambipreferent	Boesch 1991		
Taï National Park, Cote d'Ivoire	nut cracking	Right	Boesch 1991		

Cantalupo 2005 for review), and bimanual feeding of *Saba* fruits and lemons in the Mahale Mountains, Tanzania (Corp and Byrne, 2004)(see Table 8 for summary of population level hand bias in wild chimpanzees). Additionally, many studies show a strong hand preference during tool use only at the individual level (Marchant, 1983; Boesch, 1991; McGrew and Marchant, 1992; Hopkins et al., 1993; Sugiyama et al., 1993; Matsuzawa, 1994; Hopkins and Rabinowitz, 1997; McGrew et al., 1999).

Although this study failed to find population-level handedness within any of the four enclosures or at Chimfunshi as a whole, it does demonstrate an overall trend of left hand preference for unimanual feeding at Chimfunshi, specifically within enclosures 1 and 3 and a weak hand preference towards the left hand in enclosure 2 and a weak right hand preference in enclosure 4. It has been argued that hand preference depends on the specific task being performed and on the complexity of that task (Warren, 1980; Bradshaw and Nettleton, 1982; Marchant, 1996; Hopkins and Pearson, 2000; Hopkins, 2006). Stronger hand preference has been suggested as seen more when performing more complicated tasks rather than less complicated, spontaneous tasks (Hopkins and Cantalupo, 2005). This then leads to the conclusion that simple tasks with less object manipulation are less likely to be laterally biased within an individual, population, or species (Bradshaw and Nettleton, 1982; Hopkins and Cantalupo, 2005; Arbib, 2006; Steele and Uomini, 2009). However, out of the 34 individuals included in this study, 30 were shown to have significant hand preference (using the G test), 22 of whom still exhibit a hand bias even when the alpha level of probability is changed from the usual 0.95 to 0.999 (critical value becomes 10.83 rather than 3.84), and 16 of the 34 still show a hand preference even when alpha becomes 0.99999 (critical value of 19.51) (see Table 3). While the number of subjects used in this study is not as large as in some meta-analyses (Hopkins and Fernándes-Carriba, 2000; Hopkins, 2006; Hopkins et al., 2011), it was conducted on a total of over 5600 feeding bouts, with each subject averaging 165 bouts. The relative strength of these analyses, and the finding of strong hand preference for a task as commonplace as feeding suggests that perhaps less complicated, but frequently exhibited actions – such as grooming and

feeding – may tell us just as much (if not more, since larger numbers of observations can be recorded of more frequent actions) about primate hand preference as the more specialized, complicated tasks that are currently given research and literature preference.

3.2 Social Influences on Handedness

Primates are in part characterized by their increased social affiliations and bonds compared to those of most other mammals (Pough et al., 2012). The degree to which handedness or hand preference is influenced by genetics or culture is still a topic under much debate, as some advocate more for the genetics of handedness (Hopkins et al., 2001) and others more for a social influence (Lycett et al., 2010), as primates learn mostly by emulation, or perhaps imitation, especially from their mothers (Biro et al., 2003; Lonsdorf, 2005b; a). It has been demonstrated that humans have a hand preference before 12 months of age (Michel et al., 2001), but while chimpanzees have acquired complex skill sets such as termite fishing by 5.5 years, the strength of their hand preference in such tasks is not as strong as when they reach adulthood (Biro et al., 2003; Lonsdorf, 2005a; b). Additionally in chimpanzees, for many activities, the sexes show a difference in acquisition speed and relative skill (Lonsdorf, 2005a; Pruetz and Bertolani, 2007).

Given the evidence of social factors influencing hand preference and task performance skill, it is hardly surprising that a linear regression model of the data presented in this study showed that the sex, age (both at entry into the sanctuary as well as age during the study), and confirmed presence of relatives had a significant effect on the handedness of the subjects. Interaction models could not confirm or deny the existence of interactions between the variables, in part due to a relatively small sample size with few input variables. However, the chimpanzees with some of the most unique backgrounds were not used in statistical analyses due to lack of an adequate number of observational bouts. Notable chimpanzees who did not make the analysis include Milla, who was captured from the wild at <1 year old, and lived inside of a bar as a tourist attraction, becoming addicted to cigarettes and alcohol and was only weaned off of them at the age of 18, when she was brought to Chimfunshi. Bobby, who was also excluded, was saved from a run down zoo in Bangui, at which several other chimpanzees had recently died and was brought to Chimfunshi as an adolescent in such poor condition he was not expected to live. There is also Chiffon, who was a pet (along with Berta) to an Italian family who taught him to finger paint and use crayons when he was a juvenile, and to this day he still chooses to live in solitary confinement, not interacting with the other chimpanzees. Several other individuals that were not included in the study had unusual interactions and experiences with offspring, such as Roxy and Noel who did not know how to care for their first infants, which died shortly after birth. There is also Miracle (also unable to be included in analyses), whose mother, Maggie, so neglected her that keepers were forced to remove Miracle from Maggie's care and nurse her to health in human hands. Several chimpanzees also have physical disabilities that may have an effect on their eating behavior, such as Pal who is missing many of his teeth, which were brutally knocked out during his capture, or ET who is missing the 3rd, 4th, and 5th fingers on her right hand (she has been shown to be left handed, though whether this is a preference or simply a side effect of her handicap, we may never know). Perhaps because this study was unable to look into some of the more (tragic but) diverse personal histories of the chimpanzees at Chimfunshi, it failed to detect any significant effect of individuals' pre-sanctuary life history (what is known about that history, at least) on hand preference during feeding. Additional information obtained in further studies on those individuals not born within the sanctuary may be of use in shedding light on those personal effects on hand preference.

Alternatively, it is possible that the length of time spent at the sanctuary, after whatever each individual experienced, has a more profound effect on the hand preference of each individual. The most accurate way to test that would be to observe the hand preference of an individual immediately after arriving at the sanctuary and see if and how that changed over the amount of time the individual spent

in the sanctuary. However, Chimfunshi is currently at capacity and can no longer accept new chimpanzees, though perhaps a study such as this might be done elsewhere. Additionally, studies of the hand preference during different activities of those individuals who previously experience high levels of human interaction (such as Milla, Berta, and Chiffon) could be informative as to the effect of culture, learning style, and genetics on hand preference. If, for example, Chiffon, who was taught to paint, used the same hand to paint as the person(s) who taught him, that would lend support for learning via imitation, though it would not rule out the possibility of Chiffon having an inherent preference for that hand. However, if further studies of Chiffon were conducted on different activities – some that he learned from humans and some that he learned from other chimpanzees or came up with on his own, it could help shed light on the differential effects of culture (learning) and any potentially genetic component. To date, no such studies on chimpanzees of these types of unique backgrounds have been done, but Chimfunshi would be an excellent place to conduct such a study.

3.3 Bimanual Feeding and Postural Effects

MacNeilage, Studdert-Kennedy, and Lindblom (1987) posed the postural origins theory (POT) of primate handedness, suggesting that ancestrally the left hand was used for reaching while the right hand was mainly used for postural support (holding onto trees). They further proposed that as terrestriality evolved, the left hand was still used for reaching, meaning that as the left hand grasped the object initially, the right hand was free to manipulate that object, and was actually pre-adapted for such manipulation due to increased grasping abilities (MacNeilage et al., 1987). Thus, it was proposed that the right hand came to dominate bimanual actions. However, a major criticism of this study is that it does not offer a testable model as to why the left hand should be preferred over the right hand for reaching and not for hanging rather than the other way around, or why then the predominantly gripping right hand would be better suited than the left for manipulative actions (McGrew and Marchant, 1998).

In fact, the gripping support actions of the left hand are essential for the effective and efficient bimanual manipulations seen in humans where the right hand is typically preferred for manipulative actions (Guiard, 1987; Michel, 1998), meaning the left hand grips or supports an object while the right hand manipulates it. Guiard also (1987) characterizes these asymmetric bimanual actions by determining the use of each of the hands (or limbs) in a given task. One hand performs movements of higher frequency, being more temporally and spatially precise (the manipulative motions), and the other performs movements of lower frequency, acting as a stabilizer or support. This categorization of coordinated bimanual action is used in studies of primate handedness to classify individuals as right or left handed (Papademetriou et al., 2005; Fletcher, 2006; Hopkins et al., 2007; Zhao et al., 2008; Chapelain and Hogervorst, 2009; Zhao et al., 2010; Hopkins et al., 2011; Lambert, 2012). Confusingly, what at first seemed like an obvious classification of just such bimanual action during this study, was later realized to result in inconsistent recordings while observing subjects, due to the ambiguous nature of the bimanual actions. This ambiguity was previously discussed in greater detail in Chapter 2.3.4.

Additionally, for a majority of the 'bimanual' observations in this study (531 out of 630 total) peeling was done with the mouth in conjunction with one or both hands. To date, few studies have examined the use of the mouth to aid tasks done by the hands although it is widely acknowledged that chimpanzees have prehensile lips, which are used in complex manipulative tasks. Zhao, Gao, and Li (2010) discuss the use of the mouth for grooming in Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) but conclude that a larger sample size is necessary to determine if the use of the mouth has an effect on the handedness of the individual during grooming. In a similar study of grooming in chimpanzees, Hopkins et al. (2007b) found that the use of the mouth did not affect the hand preference of the individual. Whether the use of the mouth for peeling a food item has any effect on the handedness of the individual is a topic of interest but lies outside the scope of this study, largely because each subject was recorded using his or her mouth to peel a food item only an average of 18

times over the course of the study period, in addition to the previously discussed ambiguous nature of dominant hand (or mouth) use determination from recordings.

Numerous studies have demonstrated postural and situational effects on the hand preference of nonhuman primates (MacNeilage et al., 1987; Lehman, 1993; Ward and Cantalupo, 1997; Hopkins and Fernándes-Carriba, 2000; Braccini et al., 2010). Specifically, chimpanzees were demonstrated to actively alter hand use to eat a food item with their preferred hand, even when postural biases (such as side experimenter approached from and which hand – or mouth – food was placed in) were randomized (Hopkins and Fernándes-Carriba, 2000). Chimpanzees have also been shown to exhibit a stronger hand preference during bipedal tool use than while seated (Braccini et al., 2010). Although posture was recorded during this study, it was not systematically recorded, not recorded by all observers, and not standardized by the use of an ethogram. Therefore, I could not look specifically at the influence of posture on hand preference of the subjects. However, I frequently observed that subjects changed positions to block other individuals from their personal pile of food, or alternatively, moved to a different position to snatch food from the pile, hand, or mouth of another chimpanzee. Additionally, it was often observed that subjects would place the hand not being used for feeding on the bars of the observational enclosures, or that they would lie down on one arm and pick up and consume scraps from the surface they were lying on with the opposite arm.

3.4 Handedness Revisited

One universal trait of humans is their population-level right handedness (Perelle and Ehrman, 1994; Raymond and Pontier, 2004). Though there are differences in the proportion of people identifying as left handed among all cultures studied to date, 85-90% of humans classify themselves as right handed (Porac and Coren, 1981; Perelle and Ehrman, 1994). Archaeological evidence from stone tool production and wear suggest a population-level right hand bias as early as 2 mya (Cashmore et al., 2008; Uomini,

2009). Furthermore, right handed bias for motor function is associated with a left hemispheric specialization for language: 96% of individuals who report themselves as left handed show a left hemisphere dominance for language, while only 70% of left handed individuals show the same left hemisphere dominance (Rasmussen and Milner, 1977; Knecht et al., 2000). This association between handedness and language, although relatively weak, has lead to the hypothesis that the evolution of language and right hand bias are linked in fundamental ways (Corballis, 1992; Annett, 2002; Corballis, 2003). The benefits of brain lateralization include improved efficiency by avoiding hemispheric competition and replication of functions (Corballis, 1989; Vallortigara, 2000; Rogers, 2002; Vallortigara and Rogers, 2005). Because of these advantages, the brain should be lateralized for the processes that are important for survival, and we would expect behavioral laterality to appear in such tasks (Fagot and Vauclair, 1991). Therefore, hand preference is used as an indicator of brain hemispheric lateralization (Corballis, 1989). It has been well documented that individual apes may show hand preference for a certain task (Marchant, 1983; Boesch, 1991; McGrew and Marchant, 1992; Hopkins et al., 1993; Sugiyama et al., 1993; Matsuzawa, 1994; Hopkins and Rabinowitz, 1997; McGrew et al., 1999), but the extent to which a significant majority exhibit the same preference for a given task has been a topic of considerable debate (Warren, 1980; MacNeilage et al., 1987; Fagot and Vauclair, 1991; Lehman, 1993; McGrew and Marchant, 1998; Palmer, 2002; Hopkins and Cantalupo, 2005; Papademetriou et al., 2005; Hopkins, 2006). Although there may not be total agreement across studies as to the degree of handedness bias seen within nonhuman individuals, populations, or species, no study to date has shown the extreme level of handedness bias seen in the human species.

Though the neurobiology and evolution of handedness is not wholly understood (Hammond, 2002), many have reported associations between hand use and brain asymmetries in humans in cortical areas implicated in linguistic functions, especially the inferior frontal gyrus (Broca's area) and planum temporale (Wernicke's area) (Habib, 1989; Beaton, 1997; Moffat et al., 1998; Shapleske et al., 1999).

However, recent studies using voxel-based morphometry (neuroimaging analysis of differential brain anatomy using statistical parametric mapping of volume of various regions of interest) have not shown those associations of handedness and asymmetry in either inferior frontal or posterior temporal regions (Good et al., 2001). Additionally, hand preferences have been associated with brain asymmetries located outside the classically defined language areas (Foundas et al., 1995; Amunts et al., 1996; Hammond, 2002), raising questions of the causal relationship between handedness and hemispheric specialization for language.

Hemispheric leftward asymmetries have been found in great apes in the planum temporale (Gannon et al., 1998; Hopkins et al., 1998; Cantalupo et al., 2003), inferior frontal gyrus (Cantalupo and Hopkins, 2001), and sylvian fissure length (injuries of which are associated with language impairment (Leonard, 2001)) (Hopkins and Pilcher, 2001). In squirrel monkeys (*Saimiri sciureus*), greater neural activity in the motor cortex is found in the cerebral hemisphere opposite the preferred hand (Nudo et al., 1992). In capuchin monkeys (*Cebus apella*), asymmetries of the precentral gyrus (lesions of which are associated with paralysis of the contralateral side of the body) are correlated with hand preferences for bimanual actions (Phillips and Sherwood, 2005). Additionally, in chimpanzees, hand preference is associated with asymmetries in the "knob" region of the precentral gyrus, but *not* with asymmetries in either the inferior frontal gyrus or the planum temporale (Hopkins and Cantalupo, 2004). Combined, these data challenge the belief that brain asymmetries are unique to the hominin lineage.

The current state of the field challenges many things we thought we knew about handedness both in nonhuman animals and ourselves, and sheds new light on our own uniqueness. The traditional view of the association of hand preference with the evolution of language is no longer as well supported as it once was. As research continues to find brain asymmetries and hand or limb preference in nonhuman animals, the uniqueness of what it makes us human is again called into question. In order to productively continue research on handedness and behavioral and anatomical asymmetries, we must

also continue our search for the significance of handedness to be able to understand what it means (and meant) for the survival and evolution of species including ourselves. Though we may not currently have a complete picture of neurobiology and the evolution of handedness, it is through these studies of handedness bias, behavioral unevenness, brain asymmetry, and the discovery of their importance that we stand to gain a deeper understanding of and insight into the human condition.

3.5 Conclusions

While the original aim of this study was to examine the potential individual and population level hand preference during feeding of the chimpanzees at Chimfunshi Wildlife Orphanage, Zambia, the conclusions from this study are more apt to provoke critical thought within primatology and other behavioral asymmetry studies. The analyses of the data collected for this study lend strong support for the use of the G test rather than the z test for determining individual hand preference, as the G test can be used on populations not falling within a normal distribution and gives a more accurate representation of the relative strength of individual hand preference. Additionally, while several factors such as posture, bimanual action, and social influence could not be examined in this study, or could only be examined on a very elementary level, Chimfunshi Wildlife Orphanage is well poised among sites used within the field of primatology to examine such factors, specifically posture and personal history, and their effects on hand preference. While bimanual actions could also be examined more thoroughly at this site, this study discusses how traditional definitions of dominant hand use during bimanual behaviors may not always account for the variation seen among the actions performed. Although no population-level hand preference was found at Chimfunshi in this study, many individuals showed high levels of significance of hand preference, suggesting that the study of every day activities – such as feeding – can give us important insights into handedness bias and should not be consistently passed over or ignored in favor of complex tasks. Finally, the significance of handedness bias as a unique

feature is becoming less clear as more studies of brain asymmetry are performed, showing that while animals may not have a population-wide handedness bias of the levels seen in humans, they do exhibit brain asymmetry in many of the same areas previously thought to be unique to humans' language ability. As the association between hand preference and language is seen as less clear cut than we once thought, we must reassess our new knowledge and attempt to recognize the significance of hand preference and brain asymmetry, in order to fully understand what the results of such studies mean for the past and future developments and survival of species.

APPENDIX A

An alphabetical list of chimpanzees (and their ages during the summer of 2012 – estimated or exact) living at the Chimpanzee Project Area of Chimfunshi Wildlife Orphanage.

ENCLOSURE 1 – 190 acres			acres
<u>Subject</u>	<u>Age (yrs)</u>	<u>Sex</u>	Known Relationships
Big Jane*	~31	F	mother of Bob and BJ *died 6/8/12
BJ	5	Μ	son of Big Jane
Bob	11	Μ	son of Big Jane
Booboo	~30	М	-
Brandon	6	Μ	son of Brenda
Brenda	~17	F	mother of Brandon
Girly	~30	F	mother of Genny, Goliath, and Gerard, grandmother of Gonzaga
Genny	15	F	daughter of Girly, mother of Gonzaga
Goliath	21	Μ	son of Girly
Gerard	10	М	son of Girly
Ingrid	~21	F	sister of Lionel, mother of Ilse, Innocentia, and Irene, daughter of Liza (deceased)
llse	10	F	daughter of Ingrid
Innocentia	5	F	daughter of Ingrid
Irene	6 mos.	F	daughter of Ingrid
Josephine	~29	F	-
Lionel	12	М	brother of Ingrid, son of Liza (deceased)
Pal	~31	Μ	-
Regina	6	F	daughter of Renata
Renata	15	F	daughter of Rita, mother of Regina
Rita	~29	F	mother of Renata and Rusty, grandmother of Regina
Rusty	6	Μ	son of Rita
Tara	~29	Μ	-
Tobar	~30	Μ	-

ENCLOSURE 2 - 160 acres

<u>Subject</u>	<u>Age (yrs)</u>	<u>Sex</u>	Known Relationships
Carol	16	F	daughter of Coco, mother of Charity and newborn (NB)
Charity	4	F	daughter of Carol
Claire	10	F	daughter of Coco
Сосо	~27	F	mother of Carol and Claire, grandmother of Charity and NB
Daisey	8	F	daughter of Diana
Darwin	5	Μ	son of Dora
David	11	Μ	son of Diana
Debbie	11	F	daughter of Donna
Diana	~21	F	mother of David, Daisey, and Dizzy
Dizzy	4	F	daughter of Diana
Dolly	16	F	daughter of Dora
Donna	~28	F	mother of Debbie
Dora	~23	F	mother of Dolly, Doug, Darwin, and NB
Doug	9	Μ	son of Dora
Little Jane	~27	F	mother of Little Judy, Little Jenkins, Little Jones, and LJ, grandmother of Little John and NB
Little Jenkins	5	F	daughter of Little Jane
Little John	6	Μ	son of Little Judy

(Enclosure 2 cont.)		
<u>Subject</u>	<u>Age (yrs)</u>	<u>Sex</u>	Known Relationships
Little Jones	2	F	daughter of Little Jane
Little Judy	17	F	daughter of Little Jane, mother of Little John and NB
IJ	11	Μ	son of Little Jane
Maggie	~26	F	mother of Miracle and Moyo
Mary	7	F	daughter of Masya
Masya	~21	F	mother of Mary
Max	6	Μ	son of Misha
Maxine	11	F	daughter of Misha
Mikey	14	Μ	-
Milla	~40	F	-
Misha	~24	F	mother of Maxine, Max, and NB
Моуо	5	Μ	son of Maggie
Nikkie	15	F	daughter of Noel
Nina	9	F	daughter of Noel
Noel	~35	F	mother of Nikkie and Nina
Pan	~23	Μ	-
Pippa	~23	F	-
Taylor	8	F	daughter of Trixie
Tess	14	F	daughter of Tina (deceased)
Tilly	11	F	daughter of Trixie
Trixie	~22	F	mother of Tilly and Taylor
Violet	~21	F	mother of Vis
Vis	8	М	son of Violet
Zsabu	~22	Μ	-

ENCLOSURE 3 – 47 acres

<u>Subject</u>	<u>Age (yrs)</u>	<u>Sex</u>	<u>Known Relationships</u>
Barbie	~17	F	mother of Bussie and Bruce
Brian	~18	Μ	-
Bruce	3	Μ	son of Barbie
Buffy	~27	F	-
Bussie	8	Μ	son of Barbie
Chrissy	6	F	daughter of Cleo
Clement	~19	Μ	-
E.T.	~17	F	mother of Erika
Erika	6	F	daughter of E.T.
Junior	~17	Μ	-
Lods	2	F	daughter of Lori
Lori	~17	F	mother of Lods
Louise	~25	F	-
Sampie	~20	Μ	-
Roxy	~17	F	-

ENCLOSURE 4 – 62 acres

<u>Subject</u>	<u>Age (yrs)</u>	<u>Sex</u>	Known Relationships
Berta	~12	F	-
Bobby	~19	Μ	-
Chiffon	~12	Μ	-
Commander	~21	Μ	-
Jack	4	М	son of Julie

(Enclosure 4	cont.)		
<u>Subject</u>	<u>Age (yrs)</u>	<u>Sex</u>	Known Relationships
Julie	~18	F	mother of Jack
Kambo	~16	F	mother of Kit and Ken
Kathy	~13	F	-
Ken	1	Μ	son of Kambo
Kit	7	Μ	son of Kambo
Miracle	12	F	daughter of Maggie
Nicky	~21	Μ	-
Sinkie	~18	Μ	-
Val	~12	М	-



<-- VIEWING AREA -->



	Hand		Current	Age at	Previous			
Chimpanzee	Preference*	Sex	Age	Entry	Life	Family at the CPA?	Additional Information**	_
Barbie	R	F	adult	infant	pet	Y (offspring)**	came with ET and Roxy; mother of Bussie and Bruce	-
Berta	R	F	adolescent	juvenile	pet	Ν	lived as a pet for several years; came with Chiffon (who	
							paints); makes kissy noises with lips	=
Bob	L	Μ	adolescent	born	born	Y (mother)	son of Big Jane	ndi
Booboo	L	Μ	adult	infant	pet	Ν	purchased from hunters, kept as pet for 6 mo.,	vid
							voluntarily brought to Chimfunshi	ua
Brenda	L	F	adult	born	born	Y (offspring)	mother of Brandon	l ha
Brian	L	Μ	adult	infant	capture	Ν	possibly father of several young chimpanzees; came with Clement - inseparable from - and Doreen (died 2006)	d put
Bussie	L	Μ	adolescent	born	born	Y (mother)	son of Barbie	ref
Clement	NP	Μ	adult	infant	capture	Ν	possibly father of several young chimpanzees; came with	ere
							Brian - inseparable from - and Doreen (died 2006)	enc
Commander	NP	Μ	adult	infant	capture	Ν	orphaned by bushmeat trade; alpha male of enclosure 4;	as
							possibly father of young chimpanzees	cha
David	R	Μ	adolescent	born	born	Y (mother)	son of David	ed
Debbie	L	F	adolescent	born	born	Y (mother)	daughter of Donna	in
Diane	R	F	adult	infant	capture	Y (offspring)	smuggled from Zaire; mother of David, Daisy and Dizzy	AF rist
Dolly	R	F	adult	born	born	Y (mother)	daughter of Dora; mother of Dominique (deceased)	ppE ear
Donna	L	F	adult	infant	capture	Y (offspring)	mother of Debbie	re ^{s,} a NE
Erika	L	F	juvenile	born	born	Y (mother)	daugher of ET	olX nd
ET	L	F	adult	infant	pet	Y (offspring)	came with Barbie and Roxy; mother of Erika; missing fingers 3,4&5 on R hand	C life ł essio
Genny	L	F	adult	born	born	Y (mother)	daughter of Girly	n rr
Gerard	R	М	adolescent	born	born	Y (mother)	son of Girly	
Girly	R	F	adult	infant	capture	Y (offspring and	mother of Geny, Goliath and Gerard; grandmother of	lel
						grandchild)	Gonzaga	ç
Ingrid	R	F	adult	born	born	Y (offspring and	mother of Ilse, Innocentia and Irene; sister of Lionel;	lin
						brother)	daughter of Liza (deceased)	ıfuı
Innocentia	L	F	juvenile	born	born	Y (mother)	daughter of Ingrid	nsh
Julie	L	F	adult	?	?	Y (offspring)	mother of Jack	ii cl
Junior	L	Μ	adult	juvenile	pet	Ν	possibly father of young chimpanzees	him
Kathy	R	F	adolescent	infant	capture	Ν	missing L pinky; found stuffed in a box in Qatar airport with Val	npanz
Louise	NP	F	adult	infant	capture	Ν	came with Stephan; smuggled into Russia; drugged with alcohol and stuffed into a taped up shoe box	lees
Nikki	R	F	adult	born	born	Y (mother)	daughter of Noel	
Nina	L	F	adolescent	born	born	Y (mother)	daughter of Noel	
Noel	L	F	adult	adult	pet	Y (offspring)	pet in Zaire for 12 years but chained to a tree for 8 years; mother of Nikki and Nina	

Individual hand preference,	characteristics, and life histo	v of Chimfunshi chim	ipanzees as used in line	ear regression model

(cont.) Individual hand preference, characteristics, and life history of Chimfunshi chimpanzees; used in linear regression

	Hand		Current	Age at	Previous		
Chimpanzee	Preference*	Sex	Age	Entry	Life	Family at the CPA?	Additional Information**
Pal	NP	Μ	adult	infant	capture	Ν	horrible trauma from capture; first chimp at Chimfunshi
Sampie	L	Μ	adult	infant	capture	Ν	sold by members of the Zairian Consulate in 1995; alpha
							male of enclosure 3; possibly father of young
							chimpanzees
Tara	NP	Μ	adult	infant	capture	Ν	from Ndola, twice appeared in court as 'exhibit number
							one'
Val	R	Μ	adolescent	infant	capture	Ν	found stuffed in a box in Qatar airport with Kathy
Vis	NP	Μ	adolescent	born	born	Y (mother)	son of Violet
Zsabu	L	Μ	adult	infant	capture	Ν	alpha male of enclosure 2; probably father of many
							young chimpanzees

*as determined using log likelihood ratio **additional information for interest only; not used in analyses

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