Spring 5-15-2019

The Ontogeny of Complex Tool Use among Chimpanzees of the Goualougo Triangle, Republic of Congo

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Recommended Citation

Musgrave, Stephanie L., "The Ontogeny of Complex Tool Use among Chimpanzees of the Goualougo Triangle, Republic of Congo" (2019). *Arts & Sciences Electronic Theses and Dissertations*. 1859.
https://openscholarship.wustl.edu/art_sci_etds/1859

WASHINGTON UNIVERSITY IN ST. LOUIS

Department of Anthropology

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The Ontogeny of Complex Tool Use among Chimpanzees of the Goualougo Triangle, Republic of Congo

by
Stephanie L. Musgrave

A dissertation presented to
The Graduate School
of Washington University in
partial fulfillment of the
requirements for the degree
of Doctor of Philosophy

May 2019
St. Louis, Missouri

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Acknowledgements

Carrying out this dissertation research has been an immense privilege, and I am thankful to all those who have made it possible. The opportunity to work in the Goualougo Triangle has been made possible by the Ministry of Scientific Research and Technological Innovation in the Republic of Congo and by the Wildlife Conservation Society's Congo Program. I am grateful to J. M. Fay, B. Djoni, P. Elkan, S. Elkan, B. Curran, E. Arnhem, P. Telfer, M. Gately, E. Stokes, P. Ngouembe, D. Dos Santos, M. Ngangoue, J.R. Onononga, S.T. Ndolo Ebika, F. Maisels, T. Brncic, P. Tomlin, J. Ortega, and I. Kienast.

I would like to thank all of the members of the Goualougo Triangle Ape Project team. I am very grateful to Crepin Eyana-Ayina, Séverin Ndassoba Kialiema, Marcel Meguessa, and David Koni Boue for all they have done over the course of this research. I am also very appreciative to Jean Marie Massamba, Abel Nzeheke, Thierry Fabrice Ebombi, Juvey Marveric Wawa, Wen Aninate Rivard Mayoukou, Delon Ngoteni, Claude Abedine, Igor Singono, Gilbert Fils Bakombo, Pierre Moute, Francois Mombale, Gaston Loya, Aime Lembe, Samedi Massembo, David Bokili, Gregoire Mambeleme, Mangoussou Fils Alain, Ndombo Rock, Makassa, Mossaka, Herve Engo, Pouli Christian, Essouka Moise, Romain Mokole, Mokata, Jean Deli, Rene Ngoto, Kevin Makessa, Jean Bosco Mangoussou, Marcelin Mokoti, Giscar Dzambengo, Raymond Sombo, Heritier Ndjeka, Paulette Dzoukou, Massimo, Bokamou Cassette, Gbanzeze Pierre, Bote Pierre, Gervais Mandzebe, Mossimbo Eric, Senzoua Eugenie, Mbato Katy, Missambo Simond, Mangoussou Fils, Bedoua Michel, Baka Massonguet, Bossani, Bimba Japonais, Moussoungala Michael, Dzale Leon, Pembe Henri, Jeanne Mopeto, Eteko Lambert, Mondoume Michel, Makindo Albert, Lengo Gilbert, Mboula Elyse, Ndambio Justain, Deli Martine, and Makessa Fils. Thank you also to Catherine Manzele and Paul Zinguouata.

For their generous funding to support this research, I am grateful to the National Science Foundation, the Wenner-Gren Foundation, the Leakey Foundation, Lambda Alpha National Honor Society, and the John and Mary Pappajohn Scholarship Fund. I am also thankful to Washington University in St. Louis for the University Fellowship and the dissertation travel award, as well as for summer funding support.

It is not possible to adequately articulate my profound gratitude to my advisor, Dr. Crickette Sanz. I am so thankful for the myriad ways in which she has supported me and advanced my development and training. I have learned so much from her inspiring example. I am also very grateful to Dr. David Morgan for his generous mentorship, and I feel so fortunate to have benefitted from his incredible expertise. I have the greatest admiration for both Crickette and David and I will always be indebted to them for the opportunity to be part of the Goualougo Triangle Ape Project.

I owe many thanks as well to the other members of my committee. Dr. Rich Smith, Dr. E. A. Quinn, and Dr. Krista Milich have provided invaluable intellectual and professional mentorship. I am also grateful to Dr. Elizabeth Lonsdorf. I appreciate her generous guidance, and her pioneering work has been an inspiration. I also thank Dr. Bob Sussman, who was a member of my committee and provided an invaluable perspective. I appreciate all of the faculty in the Department of Anthropology at Washington University in St. Louis for contributing to my growth as an anthropologist and for being so willing to offer their help and advice.

I wish to also thank Dr. Katie MacKinnon for her mentorship and wonderful introduction to the experience of observing wild primates, and Dr. Barbara King for her support and for inspiring my interest in anthropology. My thanks are due to Dr. David Grove, who encouraged my pursuit of graduate education, and to Rhonda Pietsch, who taught me so much about working

with great apes. As I began my graduate work, Dr. Tab Rasmussen was a source of great encouragement. I am also indebted to Dr. Dorothy Fragaszy for her support. In various ways, all of the exceptional staff of the Washington University Anthropology department facilitated this research. I depended especially on the help of Kirsten Jacobsen, Jen Masterson, Calin Sterling, Abdul Ursani, and Karlee Kreikenkamp.

It was a joy to share the graduate experience with Effie Robakis and Crystal Riley Koenig, who provided unfailing support, insight, and wit. I am grateful to Kristena Cooksey, who is an incredible friend and colleague, and to Jake Funkhouser, for his willing collaboration and help. I also thank Elaine Kozma for all of her help. I appreciate the collegiality and friendship of the entire graduate student community in the Department of Anthropology at Washington University in St. Louis.

Throughout this work, I have been sustained by my family. My parents, Tony and Barbara, have made innumerable sacrifices, and the support they provide to me has always been my foundation. My brother, Jim, is brilliant, and his encouragement means the world. I am grateful to all of my extended family – grandparents, aunts, uncles, cousins, and in-laws. This dissertation is dedicated to my late grandmother, whose support I still feel. My family's unwavering presence, and their belief in the importance of this work, is an extraordinary gift.

Finally, I wish to thank Daniel, my husband and partner, for everything he has done to support me. I met him when he was working with great apes, and I was hoping to. He taught me so much about how to see, and how to listen, and he still does. Anything that I accomplish is a reflection of those beginnings, and of our ongoing efforts, together.

Stephanie L. Musgrave

Washington University in St. Louis
May 2019

Dedicated to Elaine Y. Avgerinos

Abstract of the Dissertation

The Ontogeny of Complex Tool Use among Chimpanzees of the Goualougo Triangle, Republic of Congo

by

Stephanie L. Musgrave

Doctor of Philosophy in Anthropology

Washington University in St. Louis, 2019

Professor Crickette Sanz, Chair

Various factors are hypothesized to have contributed to the flourishing of technology during human evolution, including high-fidelity social learning, a propensity for prosocial helping, and sex differences in foraging tool use. In this research, we examined the role of these factors on the development of complex tool-using skills among wild chimpanzees (*Pan troglodytes troglodytes*) in the Goualougo Triangle, Republic of Congo. These apes exhibit among the most complex tool behaviors of any nonhuman animal, including the flexible use of multiple tool types and the manufacture of tools from specific raw materials, according to a particular design. Specifically, we drew upon a 15-year, longitudinal dataset to assess the acquisition of termite-gathering skills among 25 immature chimpanzees and compare these results to those for chimpanzees (*Pan t. schweinfurthii*) at Gombe, Tanzania; test whether tool transfers from competent to less skilled conspecifics comprise a form of teaching; and compare tool transfer behavior among chimpanzees at Goualougo to those at Gombe. Results indicate that individuals learn single before multiple tool use, and in contrast to Gombe, tool use is learned before tool manufacture. We did not detect significant sex differences in skill acquisition, but females acquired most termite-gathering skills slightly before males do, and males on average manufactured tools slightly earlier than females. At Goualougo, skilled chimpanzees, typically mothers, sometimes transfer termite-gathering tools to their offspring, and these transfers comprise a functional form of teaching. The rate of tool transfers as well as the probability of tool transfer after request are higher at Goualougo, and transfer types are more prosocial. These findings suggest that the complexity of termite-gathering among chimpanzees in the Congo Basin may influence the sequence of skill acquisition and be associated with an enhanced role for social learning. Further research is necessary to determine what drives the manifestation of sex differences in skill acquisition, and how this relates to adult sex differences in tool use. Based on these findings, I conclude that high-fidelity social learning and prosocial helping intersect to promote the transmission of complex skills between individuals, supporting the hypothesis that these factors contributed to the emergence of cumulative cultural behavior in human evolution.

Chapter 1: Introduction

Investigating what led to the flourishing of technology during human evolution is an enduring and interdisciplinary effort. Technology in humans is a form of cumulative cultural behavior, whereby innovations build upon each other through the complementary forces of creativity and social transmission (Fuentes, 2017). Over time, the diversity, complexity and efficiency of cultural traits can "ratchet up" (Tomasello, 1999). There is evidence that cumulative cultural change may have characterized even early Oldowan technology (Stout, 2011), though rates of change accelerated by the Middle and Later Stone Ages (Ambrose, 2001; Powell, Shennan, & Thomas, 2009). While cumulative culture is widely agreed to be a transformative force in human evolution, the factors leading to its emergence, particularly the role of different social learning mechanisms, are debated (Boesch & Tomasello, 1998; Kempe, Lycett, & Mesoudi, 2014; Pradhan, Tennie, & van Schaik, 2012). Identifying what contributes to variation in the expression of tool behavior in extant taxa can help illuminate the adaptive basis of tool behaviors and assist in modeling the evolution of technology in the hominin lineage.

In this dissertation, I investigate the acquisition of complex tool skills in Central chimpanzees *(Pan troglodytes troglodytes*) of the Goualougo Triangle, Republic of Congo. These apes reside in an intact forest landscape (Morgan, Sanz, Ononongo, & Strindberg, 2006), and relative to other study sites, the Goualougo Triangle has the lowest level of human disturbance (Wilson et al., 2014). This has important implications for the endurance of ape cultures, as disturbance can interrupt the social transmission and maintenance of behaviors across the landscape (Kühl et al., 2019; van Schaik, 2002). This population has one of the most complex tool repertoires among nonhumans, comprising some of the best evidence for cumulative technology in the animal kingdom (Sanz & Morgan, 2007, 2010). Studying these apes thus provides a unique opportunity to examine what factors, including social learning, may facilitate cumulative cultural behavior. Together with my coauthors, I investigate how immature chimpanzees acquire tool skills, assess the role of teaching in skill transmission, and conduct a systematic comparison of the rate, probability and types of prosocial tool transfer between chimpanzees in the Goualougo Triangle and in Gombe, Tanzania.

This dissertation makes several novel contributions. First, many studies testing for social learning mechanisms are implemented in captive or provisioned settings, in order to control the levels of relevant variables (e.g., Reader & Biro, 2010; Vale, Davis, Lambeth, Schapiro, & Whiten, 2017). My research directly examines high-fidelity social learning in wild apes using novel, observational research methods, allowing insights into the role of these mechanisms in natural ecological contexts. I also investigate, for the first time, the acquisition of tool skills by known-age immature chimpanzees of the Central subspecies, which is understudied relative to chimpanzees in East and West Africa (Morgan & Sanz, 2003). In addition, my findings broaden our knowledge of sex differences in chimpanzee tool use (Goodall, 1968; McGrew, 1979; Pandolfi, van Schaik, & Pusey, 2003; Lonsdorf, 2005; Boesch & Boesch, 1984b, Pruetz & Bertolani, 2007) by examining this phenomenon for the first time from a longitudinal perspective in the context of a complex, sequential tool task. By systematically comparing tool transfers between two wild chimpanzee populations, we gain novel insights into the proximal factors supporting prosocial object transfer in apes, which to date has been principally examined in captivity (reviewed in Cronin, 2012; Marshall-Pescini et al., 2016) or using differing methods in the wild (reviewed in Pruetz & Lindshield, 2012). More broadly, a key contribution of the present work is the application of standardized methods to directly compare chimpanzee tool behavior at Goualougo to that at Gombe, the longest-running field study of wild chimpanzees.

Finally, we used camera traps to conduct longitudinal research on the development of tool skills in wild apes. This represents an important methodological advance in our ability to gather detailed behavioral data with minimal impact on wild primate communities. In addition, use of camera traps can advance a range of research and conservation aims by documenting key life history milestones and helping to monitor population demography (Galvis, Link, & Di Fiore, 2014).

This introduction chapter presents background information on topics that contextualize the subsequent chapters. First, I provide a brief summary of evidence for the evolution of complex tool use in the hominoid clade and discuss why high-fidelity social learning is implicated in the expansion of technology. I present an overview of animal tool behavior and describe key aspects of complexity, to establish important points of comparison between the tool behavior of early hominins and that of extant animal models. The subsequent sections review cognitive underpinnings of tool behavior and ecological hypotheses related to the evolution of tool use. Next I discuss the role of social learning and prosocial helping on tool behavior, before describing how an ontogenetic approach can provide unique insights into the role of social factors and sex differences on the development of tool use. I conclude by outlining my research methods and the structure of the subsequent chapters. Throughout, I discuss a range of variables relevant to tool use and include findings for other primate and non-primate taxa, in order to situate my research within a broader discussion of the ultimate and proximate influences on the evolution of tool behavior.

1.1 The Evolution of Complex Tool use in Hominoids

Tool use is defined here as the manipulation of an object, not part of the actor’s anatomical equipment and not attached to a substrate, to change the position, action, or condition of another object, either directly through the action of the tool on the object or of the object on the tool, or through action at a distance as in aimed throwing (Parker & Gibson, 1977). This definition has been selected over others (e.g., Shumaker, Walkup, & Beck, 2011; St Amant & Horton, 2008), because it permits broad comparison across taxa while also specifying that tools must be unattached objects. This is an important aspect of the definition for enabling comparisons with complex, human tool use, because unattached compared to attached objects can be more flexibly incorporated into complex sequences (Meulman, Sanz, Visalberghi, & van Schaik, 2012).

Tool behavior is relatively rare, documented in less than 1% of all animal genera, but it is taxonomically widespread (Biro, Haslam, & Rutz, 2013). It has evolved multiple times, as evidenced by its appearance across distantly related animal lineages. A variety of factors can influence whether tool behaviors evolve, such as the motivation and anatomical ability to dexterously manipulate objects; the cognitive abilities that enable the invention, learning, and implementation of tool skills; ecological and environmental factors that might necessitate dietary expansion and make foraging tool behaviors energetically profitable; and social variables that could support the acquisition and transmission of innovations, including the life history and demographic parameters that influence how behaviors persist over generations and across the landscape (Fig. 1.1).

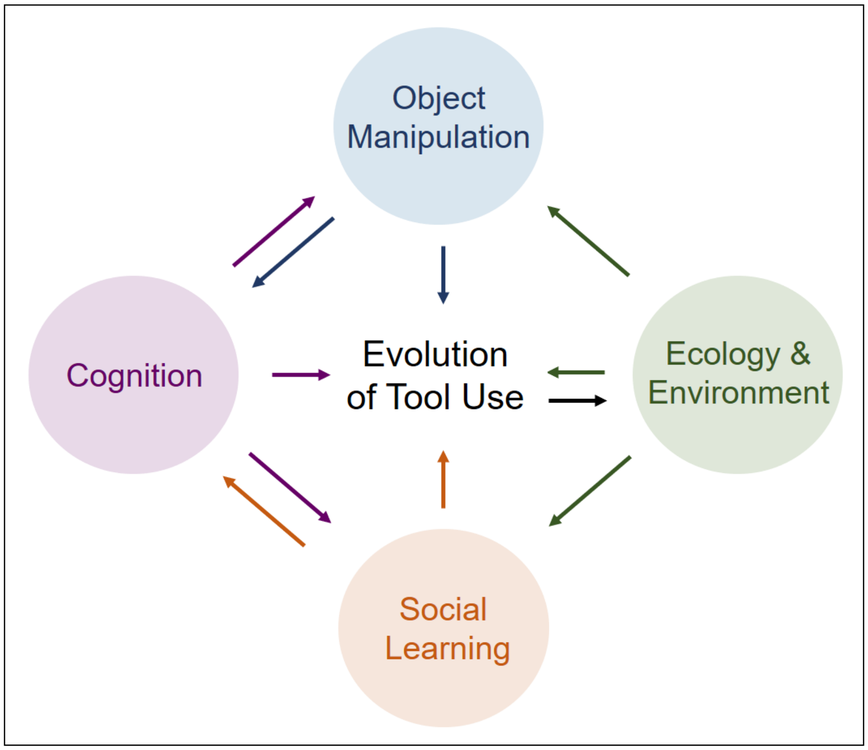

FIGURE 1.1. Factors influencing the evolution of tool use. Multiple factors influence the evolution of tool behavior, and these factors also interact with each other. In addition, tool users can affect their own environment, generating feedback loops whereby they construct their own niches.

The first possible direct evidence for stone tool use in the archaeological record dates to 3.3 Mya, at a site called Lomekwi 3 in Kenya (Harmand et al., 2015). Indirect evidence dating to 3.4 Mya has also been discovered at Dikika, Ethiopia, comprising cut marks on fossil mammal bones that are attributed to stone tool use (McPherron et al., 2010). Oldowan archaeological sites date back to at least 2.6-2.5 Mya (Semaw et al., 1997, 2003). These sites preserve several tool types associated with percussive technology, including cores, hammers, and flakes, and sometimes they also preserve faunal remains (Toth & Schick, 2018). Beginning as early as 1.76 Mya, Acheulean tools begin to appear alongside Oldowan artefacts, characterized by more diverse and sophisticated tool forms including hand-axes (Lepre et al., 2011).

While tool use was once considered the defining feature for the genus *Homo* (Oakley, 1949; Leakey et al., 1964) numerous other hominins including *Australopithecus* and *Paranthropus* were contemporaneous with and could potentially have used early stone tools at different localities across the African continent (Fig. 1.2).

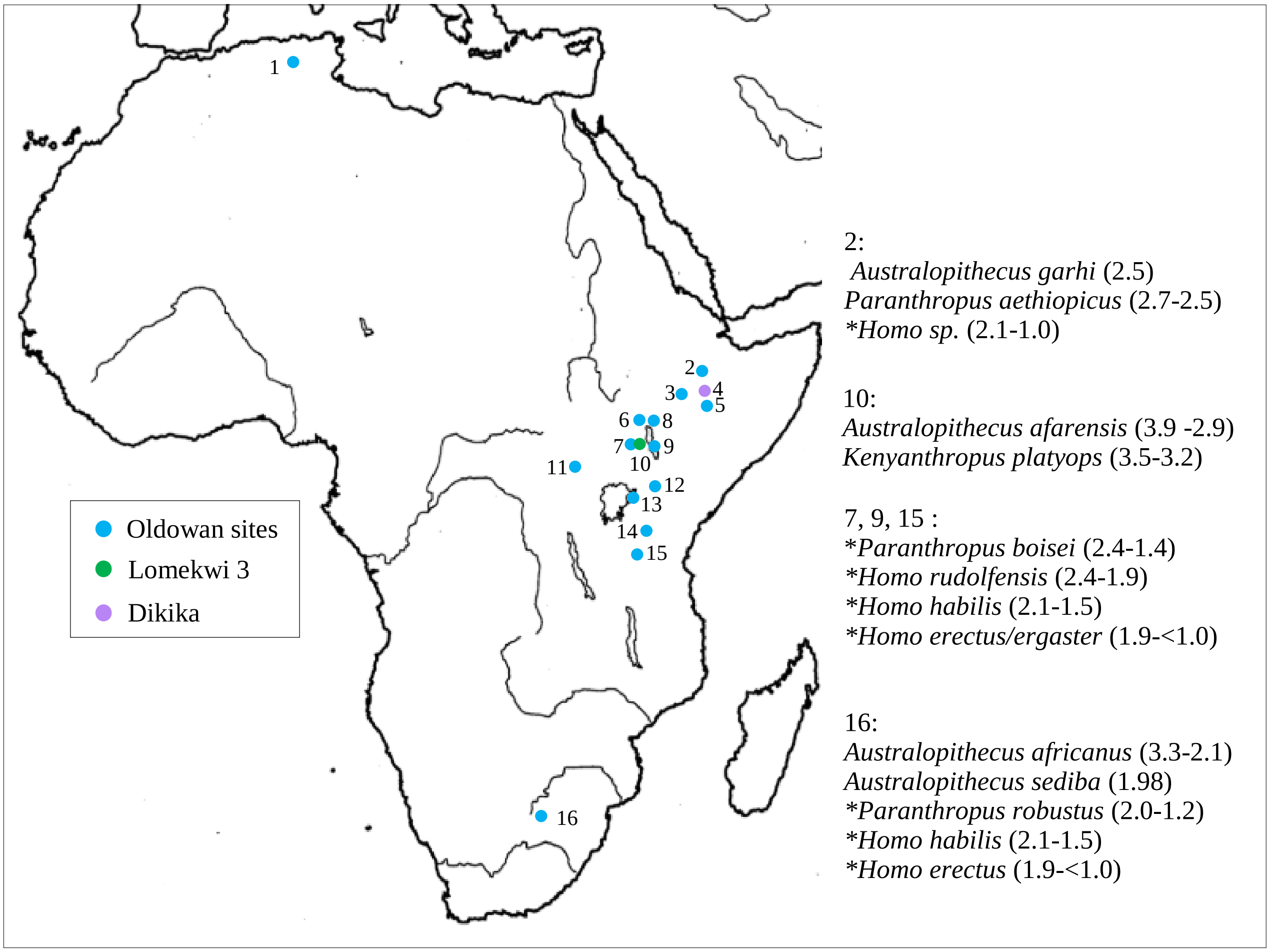

FIGURE 1.2. Distribution of localities with evidence for early stone tool use. 1. Ain Boucherit, Ain Hanech and El- Kherba, Algeria. 2. Gona and Hadar, Ethiopia; 3. Melka Kunturé, Ethiopia; 4. Dikika, Ethiopia; 5. Gadeb, Ethiopia; 6. Omo, Ethiopia; 7. West Turkana, Kenya; 8. Fejej, Ethiopia; 9. East Turkana (Koobi Fora), Kenya; 10. Lomekwi, Kenya; 11. Nyabusosi, Uganda; 12. Chesowanja, Kenya; 13. Kanjera, Kenya; 14. Peninj, Tanzania; 15. Olduvai Gorge, Tanzania; 16. Sterkfontein, Swartkrans and Kromdraai, South Africa. Hominin species that potentially overlap temporally with archaeological sites are listed, according to site(s) (e.g., 2 corresponds to Gona and Hadar). Approximate ages (Mya) are in parentheses; an asterisk indicates taxa where tools have been found in association or in nearby sediments of the same age (adapted from information in Toth & Schick, 2018, Tables 1 and 2 and Figure 1; McPherron et al., 2010; Harmand et al., 2015).

In addition, the tool-using behavior of extant apes suggests that the capacity for complex tool use did not arise *de novo* in the human lineage, and likely emerged earlier, in the common ancestor of humans and the other great apes (Panger, Brooks, Richmond, & Wood, 2002). At least one form of tool behavior occurs in all wild chimpanzee populations studied to date (Fowler & Sommer, 2007; McGrew, 1992; Sanz & Morgan, 2007). Some populations of wild orangutans also use a range of tool types (Meulman & van Schaik, 2013). In captivity, tool use is observed in all great ape species, even bonobos (Boose, White, & Meinelt, 2013; Gruber, Clay, & Zuberbühler, 2010) and gorillas (Lonsdorf, Ross, Linick, Milstein, & Melber, 2009), both of which do not routinely use tools in the wild.

Rather than comprising the first tools used by early hominins, stone tools were likely part of a tool repertoire that included perishable tools, evidence for which has not preserved in the archaeological record (Panger et al., 2002; Schick & Toth, 2000). The tool repertoire of Central chimpanzees includes the use of perishable tool sets to gather invertebrate resources (Bermejo & Illera, 1999; Boesch, Head, & Robbins, 2009; Estienne, Stephens, & Boesch, 2017; Fay & Carroll, 1994; Sanz & Morgan, 2007, 2009, 2010; Sanz, Morgan, & Gulick, 2004). A tool set is defined as the sequential use of two or more different tools (Brewer & McGrew, 1990). This rich, perishable tool repertoire may thus be of particular importance for reconstructing the skills of our last common ancestor with other apes, especially given that demographic declines are hypothesized to have led to tool trait loss in the other chimpanzee subspecies and in bonobos (Haslam, 2014).

The emergence of complex tool skills and associated, enhanced cognitive abilities in the hominoid clade are hypothesized to be the result of variability selection. According to the “fruit habitat hypothesis” (Potts, 2004), fluctuating climates and changing habitats selected for adaptability to environmental change, underpinned by flexible cognitive skills that enabled apes to find and specialize on ripe fruits despite spatial and temporal variability in the abundance of these resources. These cognitive skills may also have supported the ability to innovate means (i.e., tool use) of accessing fallback foods (Potts, 2004). The "Technical Intelligence" Hypothesis (Byrne, 1997) similarly highlights the cognitive skills of great apes, but with particular reference to their exceptional aptitude for skilled actions in foraging contexts. These include tool use as well as other behaviors, such as the sequential processing techniques gorillas use to process physically defended foods (Byrne & Byrne, 1993).

Specific social learning mechanisms are posited to have supported the elaboration of increasingly complex tool behaviors over time. In particular, high-fidelity social learning mechanisms, namely teaching and imitation, are hypothesized to have generated cumulative cultural capacities in the human lineage (Fogarty, Strimling, & Laland, 2011; Galef, 1992; Tennie, Call, & Tomasello, 2009). "High-fidelity" refers to the fact that these mechanisms support close behavioral matching between a model (e.g., a teacher) and a learner. This is important for ensuring faithful reproduction of the steps involved in complex tasks when the relationship between each step is opaque to a novice (Laland, 2004). High-fidelity social learning is expected to support the persistent transmission of behaviors over time as well as the progressive addition of new innovations, leading to the generation and inheritance of tools and behaviors more complex than any one individual could invent in a lifetime (Tomasello, 1999). In the human lineage, selection for social learning abilities in the context of an increasingly rich cultural matrix of learned behaviors likely contributed to the acceleration of selective pressure for these learning abilities. In turn, this could have augmented associated capacities to innovate new behaviors, further increasing the selective pressure for the ability to acquire this increasingly diverse portfolio of cultural skills – resulting in a remarkably enhanced capacity for, and reliance on culture (Boyd & Richerson, 1985; Fuentes, 2017; Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007; Laland, 2018; Richerson, Boyd, & Henrich, 2010).

It has been further suggested that the origins of complex tool behavior in hominoids could be related to sex differences in foraging strategies. While there is immense variation with respect to division of labor in modern humans, among foraging societies (defined as those with less than 10% dependence on animal husbandry or agriculture and engaging in minimal trade) men tend to more often target resources that are energy dense and riskier to acquire (e.g., large fauna), while women more often focus on gathering reliable items such as vegetal foods, insects, and small fauna (Marlowe, 2007). It has been suggested that sex differences related to complex food processing and tool use were present in the common ancestor of humans and chimpanzees (Hunt, 2006; McGrew, 1979). Dietary quality is known to limit reproductive success in female apes (Thompson & Wrangham, 2008). Female compared to male chimpanzees use tools more frequently to acquire termites (Goodall, 1968; McGrew, 1979; Pandolfi et al., 2003), crack nuts (Boesch & Boesch, 1984b) and disable vertebrate prey cached in tree holes (Pruetz & Bertolani, 2007). A female bias for tool use has also been documented for captive bonobos (Boose et al., 2013; Gruber et al., 2010; but see Herrmann, Hare, Call, & Tomasello, 2010). One possibility is that tool-assisted foraging offers safer, more consistent access to high-quality resources that males without dependent offspring might choose to access by hunting mobile vertebrate prey such as monkeys (McGrew, 1979). For example, depending on availability of other resources, gathering termites may be a reliable and profitable foraging strategy particularly for females because of termites' nutritional value and high collective biomass (Deblauwe & Janssens, 2008).

1.2 Complex Tool Behavior in Animals

When taking a comparative approach to understanding the evolution of technology in hominins, complex tool behaviors are of greatest interest. A range of methods have been used by researchers to assess and compare the complexity of tool behaviors (e.g., Boesch & Boesch, 1990; Hunt, Corballis, & Gray, 2006; Matsuzawa, 1996). Two essential criteria are flexibility and accumulation (Meulman et al., 2012). In addition, aspects of tool manufacture, including sophistication of tool design and raw material selectivity, also increase task complexity.

Flexibility and Accumulation

Flexibility involves the ability to deploy tools across multiple domains (e.g., foraging, social interactions, self-care), to attribute multiple functions to one tool, and to combine tools with each other to achieve goals (Call, 2013). This ability to apply knowledge from one setting to a different, analogous setting has been suggested to be an indicator of causal reasoning ability (Boesch, 2013; Tomasello & Call, 1997). Flexible tool users can also assess their progress and make adjustments during the tool-using sequence by adding, repeating, or omitting actions (Byrne, Sanz, & Morgan, 2013). Accumulation refers to the addition of an action to an existing one to create a new combination or sequence. Paradigmatic examples include the concurrent or sequential use of multiple different tools; the use of one tool to make another; and the addition of a step to an existing manufacture process, producing a more complex or efficient tool (Pradhan et al., 2012). Oldowan assemblages exhibit both flexibility and accumulation, as the hominins responsible produced multiple tool types and combined tools, including using one tool to make another (Schick & Toth, 2006; Toth & Schick, 2018).

In some taxa, tool behaviors are best understood as relatively inflexible behavioral specializations. For example, among invertebrates, tool use has been documented in ants, wasps, spiders, sea urchins, snails, crustaceans, and octopi (Shumaker et al., 2011). These tool behaviors typically involve a single type of action, and may have evolved from behavioral patterns already in the species' repertoires. Archerfish (*Toxotes*), for example, shoot streams of water from their mouths in order to knock insects down from branches hanging over the water's surface. One hypothesis is that this evolved from the tendency of this fish to leap out of the water, which has the side effect of throwing water onto an insect and knocking it down to the water (Hunt, Gray, & Taylor, 2013).

More flexible tool behaviors are observed among some species of birds and mammals, namely the Passeriformes and Primate orders (Smith & Bentley-Condit, 2010). New Caledonian crows (*Corvus moneduloides*), which range on the island of New Caledonia in the South Pacific, have the most impressive tool repertoire among wild birds, and populations throughout their range use stick and leaf tools to extract invertebrates such as wood-boring grubs (Hunt & Gray, 2002; Rutz & St. Clair, 2012). In addition, there is variation between populations in the tool variants that are included in their toolkits (Hunt & Gray, 2003; Hunt, 1996; Hunt & Gray, 2002). Woodpecker finches (*Camarhynchus pallidus*) living on the Galápagos Islands are also habitual tool users; they use various materials such as cactus spines, twigs, and leaf petioles to extract arthropods from tree holes (Tebbich, Taborsky, Fessl, & Dvorak, 2002).

Complex Tool Use in Primates

Habitual, flexible tool skills likely evolved at least three times in primates, in the lineages of capuchins, macaques, and great apes. While tool use is rare among platyrrhines generally, a few populations of bearded (*Sapajus libidinosus*) and yellow-breasted (*S. xanthosternos*) capuchins are exceptions. These monkeys, which inhabit seasonal caatinga and cerrado habitats in northeastern Brazil, use tools principally for foraging but also for social and investigative functions. Foraging tool behaviors typically involve using stone hammers and anvils to crack encased foods, primarily nuts as well as seeds and hard-shelled fruits (Ottoni & Izar, 2008; Visalberghi & Fragaszy, 2013). At Serra de Capivara, capuchins also use tools to dig for underground foods (Mannu & Ottoni, 2009; Moura & Lee, 2004), extract honey, and flush vertebrate prey (Falótico & Ottoni, 2014). In this population they have further been observed using one tool for two different functions and occasionally using two different types of tools in sequence (Falótico & Ottoni, 2014).

Among old world monkeys, there have been a few observations of tool use in baboons (*Papio*) as well as among Barbary macaques (*Macaca sylvanus)* and lion-tailed macaques (*M. silenus)* (Shumaker et al., 2011). The only habitual tool-using catarrhine monkeys are Burmese long-tailed macaques (*M. fascicularis aurea*) inhabiting coastal regions of Thailand (Malaivijitnond et al., 2007). They use stone hammers to access 47 different species of marine prey. Their tool actions cluster into three groups: "axe hammering" to break open oysters that are attached to rocks; "pound hammering" to open unattached prey such as crustaceans, sea almonds, and mollusks; and "edge hammering," in which the tool user uses the narrow edge of a stone tool to break open either an attached or an unattached resource (Tan, Tan, Vyas, Malaivijitnond, & Gumert, 2015).

Among the great apes, gorillas use tools the least; they have been observed using tools in the wild only a few times. For example, a female western lowland gorilla (*Gorilla gorilla*) used a stick to probe the depth of a waterway before she crossed it (Breuer, Ndoundou-Hockemba, & Fishlock, 2005), and a juvenile female mountain gorilla (*G. beringei beringei*) used a piece of wood to dip for ants (Kinani & Zimmerman, 2015). Thirteen types of tool use have been observed among bonobos, but it is not routine and does not occur in a foraging context. Instead, when bonobos do use tools, it is for social and self-care purposes, such as displaying, removing debris from teeth, or swatting away insects (Hohmann & Fruth, 2003). Despite the rarity of their tool use in the wild, both gorillas and bonobos are capable tool users in captivity. This phenomenon has been deemed the “captivity bias”; it refers to the fact that many more animal species use tools in captive compared to wild settings. Haslam (2013) posits that this could be related to having more freedom to discover tool behaviors, greater influence from humans, increased terrestriality, and increased opportunity to learn from conspecifics.

Orangutans living on the islands of Sumatra and Borneo use a variety of tools. Almost half of the 38 different tool variants documented for orangutans are directed toward physical comfort, for example to wipe fluids from the body (Meulman & van Schaik, 2013). Orangutans in all populations, including Bornean orangutans (*Pongo pygmaeus*), use branches or leaves to shield themselves from strong sun or rain. Only Sumatran orangutans (*P. abelii)* engage in regular foraging tool use, which could be related to increased reliance of extractive foraging, particularly for insects, in this subspecies (Meulman & van Schaik, 2013). At Suaq Balimbing, Sumatra, orangutans use sticks to remove seeds from *Neesia* fruits and also to extract insects and insect products from tree holes (Fox, Sitompul, & van Schaik, 1999; van Schaik, Fox, & Sitompul, 1996).

Chimpanzees exhibit the most diverse tool repertoire outside of humans, including a minimum of 43 different tool variants (Sanz & Morgan, 2007; Whiten et al., 2001). They use 22 different “modes” of tool use, such as hitting, probing, and absorbing, spanning a variety of foraging, self-care, and social contexts (Shumaker et al., 2011). In contrast to orangutans, chimpanzees focus much of their technological skill on foraging. Using leaves to soak up water is a universal chimpanzee behavior, and many populations also use probing technology to gather invertebrate resources such as ants, termites, and honey (McGrew, 1992; Sanz & Morgan, 2007).

The regional foraging traditions documented among chimpanzees include some of the most complex among nonhumans. In Taï Forest, Côte d'Ivoire, and in other areas of West Africa, chimpanzees (*P. t. verus)* use a hammer and anvil concurrently to crack nuts (Boesch, Marchesi, Marchesi, Fruth, & Joulian, 1994). At Bossou, Guinea, researchers have even observed metatool use, in which one tool is used on another; chimpanzees were observed to place a small stone as a wedge under an anvil in order to keep the anvil flat and stable during nut cracking (Matsuzawa, 1994). Researchers continue to discover new tool variants as they document the behavior of previously unstudied chimpanzee populations (e.g., Boesch et al., 2017).

These comparisons reveal a spectrum of complex tool use across birds and primates. The tool use of birds is principally focused on extractive foraging, while primates are distinguished by the diversity of contexts across which they use tools. In addition, some primate populations routinely use multiple tool types in a single task. Captive studies have confirmed that all great apes are capable tool users. Wild chimpanzees are exceptional in the number and complexity of tool variants they exhibit and are also unique in that every studied population both manufactures and uses tools in natural settings.

Complex Tool Manufacture

Tool manufacture may require additional skills beyond those needed for tool use, and the complexity of tool manufacture varies considerably across species and populations. Two important aspects of complexity with respect to tool manufacture are *tool design sophistication* and *selectivity for raw materials.* Tool manufacture is defined as actively modifying an object so that it serves, or serves more effectively, as a tool (Shumaker et al., 2011). For invertebrates, tool manufacture typically only involves detachment, such as crabs detaching anemones or sponges to protect their claws while foraging, or when ants detach a soil particle to drop onto a bee

(Shumaker et al., 2011). As with tool use, tool manufacture is more flexible and diverse in birds and primates. New Caledonian crows, in addition to detaching tools, sometimes modify these tools to make them more suitable for use. These crows manufacture two principal forms of foraging tools, stick tools and pandanus leaf tools, and both types can vary in terms of the steps involved in manufacture. Crows sometimes shape twig tools into hooks, and they are the only species besides humans that intentionally manufactures hook tools (Hunt, 1996; Hunt & Gray, 2004). Pandanus leaf tools take one of three forms: straight and narrow, straight and wide, or stepped. Stepped tools are manufactured when the bird makes a series of rips such that the tool becomes tapered down one side (Hunt, 2014; Hunt & Gray, 2003; Hunt, 1996). These three forms are not forced by the properties of these tools, suggesting that the crows could be following a mental template when manufacturing them (Hunt, 2000).

Chimpanzees have an exceptional propensity for manufacturing a diverse array of tool types, and they exhibit many different modes of tool manufacture, such as removal, addition, and reshaping (Shumaker et al., 2011). The ability to materially transform raw material is a strong indicator of flexibility. It enables tool users to tailor their actions to the demands of particular tasks and may promote more efficient tool use. In Fongoli, Senegal, chimpanzees spear bushbabies with tools that they produce by detaching branches, removing smaller side branches, stripping bark, and then using their teeth to sharpen the tip of the tool (Pruetz & Bertolani, 2007). In the Goualougo Triangle, chimpanzees manufacture brush-tips onto the ends of termite-fishing probes, an intentional modification that improves the efficiency of these tools at gathering insects (Sanz, Call, & Morgan, 2009). In addition, these chimpanzees are selective for the particular plant materials they use to manufacture tools (Sanz & Morgan, 2007). Both capuchins and chimpanzees show sensitivity to tool properties when selecting tools for nut-cracking. At

Fazenda Boa Vista, Brazil, capuchins select optimal anvil pits for placing nuts, and they select hammers on the basis of stone hardness and mass, the distance between the hammer and the nut-cracking locality, and nut resistance (Visalberghi, Sirianni, Fragaszy, & Boesch, 2015). Chimpanzees also select hammers of optimal size and weight (Carvalho, Cunha, Sousa, & Matsuzawa, 2008) and show conditional assessment of such variables when selecting nut-cracking hammers (Sirianni, Mundry, & Boesch, 2015). Compared to capuchins, chimpanzees also transport their tools over longer distances, and they occasionally intentionally modify wooden hammers. These interspecific differences could reflect a combination of factors such as body size relative to tool size, as well as cognitive differences (Visalberghi et al., 2015).

There is immense variation over time and between localities in complexity of hominin tool manufacture, and as both dating and analysis techniques have evolved, different categorization approaches have been proposed (de la Torre & Mora, 2005; Isaac, 1976; Leakey, 1971, 1975). While in general there is agreement that the complexity and pace of technological change increase over time, deciphering the contributions of particular variables to geographic and temporal variation among assemblages is challenging. For example, variation in the environment (e.g., availability of particular materials), the tool makers themselves (e.g., biomechanical constraints, cognitive ability, and cultural norms), as well as taphonomic processes can all contribute to the immense variation documented (Toth & Schick, 2018). Debate also persists about whether, and at what time, the complexity of tool manufacture by hominin tool makers required abilities and means of cultural transmission that go beyond those of extant apes (Davidson, 2016; Tennie, Braun, Premo, & McPherron, 2016; Wynn, Hernandez-Aguilar, Marchant, & Mcgrew, 2011; Wynn & McGrew, 1989).

To date, there is no evidence for material selectivity by Lomekwian tool makers at 3.3

Mya (Harmand et al., 2015). In contrast, at least some of the some of the earliest Oldowan tool-makers were likely selective for raw lithic materials, as their prevalence in archaeological assemblages exceeds their abundance on the landscape relative to other possible materials (Harmand, 2009; Stout, Quade, Semaw, Rogers, & Levin, 2005). There are also technique differences between Lomekwian and Oldowan tools. Lomekwian artefact features suggest that flakes were produced using passive hammer and bipolar techniques, in contrast to the direct freehand percussion of later, Oldowan assemblages; these simpler techniques require less control and understanding of fracture mechanics (Harmand et al., 2015). Within the Oldowan tradition, there is also evidence of temporal change with respect to complexity of manufacture techniques and final tool forms. For example, in Oldowan assemblages at Peninj, Tanzania, there is an increasing proportion over time of heavily flaked, bifacial, discoidal cores, which provide evidence that cores were carefully prepared to enable efficient removal of numerous, large, sharp flakes (de la Torre & Mora, 2005; de la Torre, Mora, Domínguez-Rodrigo, de Luque, & Alcalá, 2003). These bifacial discoids are likely precursors to later, large bifacial Acheulean tools (Toth & Schick, 2018). Another important marker of manufacture complexity is the presence of retouched flakes, which are flakes that have been secondarily modified after being detached. While there is some evidence for retouch at the earliest sites (i.e., Gona, Semaw et al., 2003), unambiguous cases of retouching are more easily identified in the Acheulean (summarized in Zaidner, 2013). The large cutting tools of the Acheulean, typically referred to as hand-axes, knives, and cleavers, show a number of other characteristics that differ markedly from earlier technologies, the most salient of which is shaping. While debates persist about the form of these tools (e.g., whether they were intentionally crafted to be symmetrical), they provide strong evidence that these tool makers possessed a mental template of tool form (McPherron, 2013).

1.3 Cognitive Underpinnings of Tool Use

Assessing the cognitive correlates of tool behaviors in living animals can provide insights for cognitive archaeologists and others seeking to better reconstruct the problem-solving abilities of past hominin tool makers (Toth & Schick, 2018). A key component of much of this research involves assessing the extent to which tool behaviors are based on the assimilation of sensorimotor, perceptual knowledge or result from the development of specific cognitive abilities. While not mutually exclusive, these perspectives highlight differing aspects of how the brain and the nervous system are involved in carrying out skilled tool actions. The perception-action model (Lockman, 2000), or manipulation-based approach, posits that tool use is based in exploratory motor behaviors exhibited in early life, through which sensorimotor skills become refined over time. Supporting evidence for this approach has been documented for both humans and nonhuman species (Fragaszy & Mangalam, 2018; see Chapter 2). Another perspective focuses more on the role of particular aspects of physical cognition (Call, 2013; Seed & Byrne, 2010; Visalberghi, Sabbatini, Taylor, & Hunt, 2017). This includes a range of abilities, two of the most important of which are causal reasoning and planning.

Causal Reasoning

Causal reasoning refers to the ability to understand the dynamic relationship between objects (Tomasello & Call, 1997). Here, causal reasoning is discussed as it applies to mechanical knowledge, an understanding of the physical processes by which a tool effects its outcome (Seed & Byrne, 2010:1034). This involves understanding the potential of tool properties to create effects, and how to create tools and apply forces with those tools to achieve the intended effects (Boesch & Boesch-Achermann, 2000). The manufacture sequences involved in hominin tool production suggest that flaking even relatively simple stone tools requires a flexible grasp of object properties and of the dynamic relationship between percussor and core tools. Tool makers must understand how particular materials will fracture and be able to perceive how individual flake removals will affect the overall shape of the core and the ability to remove subsequent flakes (Lewis & Harmand, 2016).

Studies of modern humans experiencing brain impairments highlight the role of mechanical knowledge in carrying out tool use. For example, *ideational apraxia* is a type of impairment in which individuals have difficulty conceptualizing and planning sequences of actions involving objects. These individuals can engage in a motor action (e.g., using a pencil to write), but they might select the wrong tool (e.g., a pair of scissors) if asked to initiate this task. This finding supports the interpretation that sensorimotor competence is necessary but not sufficient to complete tool tasks, and indicates a role for causal reasoning in skillful tool selection and tool use (Osiurak & Badets, 2016). Neuroimaging studies also support this view. In one experiment, macaques were trained to grip an object with pliers, which activated particular neurons in the ventral premotor cortex. The macaques were then trained to use “reverse pliers,” in which opening the hand, rather than closing it, caused the pliers to grip the object. The same neurons fired in this version of the task, indicating that neurologically, the macaques encoded the end goal (grip the object) of the tool task rather than any specific motor action (i.e., close versus open the hand) (Umilta et al., 2008).

A principal approach for investigating causal reasoning in captive settings has been the “trap-tube” paradigm, which requires animals to use a tool to extract a reward from an apparatus while avoiding an obstacle, the trap (Visalberghi & Limongelli, 1994). In one phase of the experiment, animals are trained to operate the apparatus, and in the test phase, aspects of the apparatus are changed to see whether subjects can transfer knowledge to the new version of the task. For example, researchers alter arbitrary features like color, while the underlying causal connections among component parts are maintained, to see if the animals are relying on simpler associative cues or using causal reasoning to problem solve. New Caledonian crows show mixed performance on these tests. In some cases, they can transfer knowledge from one version of the task to another, while in others, they do not, suggesting that there may be limitations to the extent to which they can apply abstract, causal principles (Taylor, Hunt, Medina, & Gray, 2009). Among tool-using primates, great apes generally show the most robust performance on trap tasks, though not all individuals show a consistent ability to solve them (Girndt, Meier, & Call, 2008; Martin-Ordas, Jaek, & Call, 2012). Some capuchins can also solve these tasks (e.g., Fujita et al., 2003). The inconsistent performance of both great apes and monkeys indicates that mechanical reasoning alone is not sufficient and suggests that compared to humans, other primates experience more difficulty managing multiple, dynamic spatial relations among objects (Fragaszy & Mangalam, 2018).

Studies of tool manufacture also provide insights into the cognitive underpinnings of tool behavior by revealing the extent to which animals are sensitive to how tools cause effects upon objects or substrates. All great ape species can successfully and spontaneously differentiate between nonfunctional and functional tools in captive experiments (Herrmann, Wobber, & Call, 2008). New Caledonian crows attend to the functionality of hook tools (St. Clair & Rutz, 2013), but are just as likely, when using pandanus leaf tools, to select tools with barbs facing downwards (nonfunctional) as upwards (functional) (Holzhaider, Hunt, Campbell, & Gray, 2008). Thus, even within species, there may be variation between tasks with respect to whether individuals are aware of or sensitive to the functional aspects of tools.

Planning

Planning is an important aspect of tool use because it can serve as an energy-saving strategy. It can enable more efficient procurement of raw materials, and maximize how raw materials are used, for example how many flakes can be removed from a stone cobble (Delagnes & Roche, 2005). The ability to plan tool behaviors has been inferred on the basis of manufacturing a tool in advance and transporting it to a tool site, for both wild chimpanzees (Boesch & Boesch, 1984a; Goodall, 1964; Sanz, Morgan, & Gulick, 2004) and capuchins (Visalberghi et al., 2015). These behaviors suggest that the tool users are able to conceive of a task and mentally represent the appropriate tool form when that task is not immediately in front of them. Analysis of the sequential structure of tool-using behaviors is also a fruitful approach for examining planning. In the Goualougo Triangle, chimpanzees repeat steps as necessary and omit unnecessary steps when using tools to gather subterranean termites, which is a strong indicator of hierarchical, goal-directed behavior (Byrne et al., 2013).

There is also compelling evidence for convergent evolution of planning abilities in corvids. Ravens (*Corvus corvax*), for example, can select and save a tool that they can use in the future to access a baited apparatus (Kabadayi & Osvath, 2017). New Caledonian crows can complete behavioral sequences to access a tool for a task that is out of view, while ignoring distractor items, suggesting that they can rely on mental representations of tool behaviors (Gruber et al., 2019).

Evidence for raw material sourcing and tool transport are of particular interest for examining whether hominin tool users could plan ahead. On some occasions, Oldowan tool makers may have transported stone from considerable distances. At Kanjera South, Kenya, tools were transported (either in successive bouts, or all at once) over 10 km (Braun et al., 2008). Application of *chaîne opératoire* techniques involving refitting of stone artefacts has also revealed missing pieces in core reduction sequences, which suggests that cores were tested at the site of acquisition before their planned transport to another location (Delagnes & Roche, 2005). The evidence for planning among Acheulean tool makers is even more pronounced. For example, raw materials were routinely transported longer distances (de la Torre & Mora, 2005). In addition, the consistent imposition of the hand-axe shape requires numerous sequential phases of manufacture, and management of multiple geometric and material variables (Gowlett, 2006). These tool forms thus suggest hierarchically planned sequences of significant time depth (de la Torre, 2016).

1.4 Ecological Influences on Tool Use

Several ecologically-based hypotheses have been proposed to help explain the evolution of tool behavior in particular taxa and to account for patterns of inter-and intraspecific variation, focusing on the likely origins of tool behaviors as they relate to foraging. Fox et al. (1999) proposed three, non-mutually exclusive hypotheses, the first of which is the "Necessity Hypothesis." This hypothesis posits that species or populations occupying more resource-scare environments will be more likely to innovate tool behaviors, and also that tool users will increase reliance on tool-assisted foraging when preferred resources are less available. On Santa Cruz Island of the Galápagos Archipelago, woodpecker finches living in a more arid, highly seasonal region used tools more than did finches living in zones where food was more abundant and accessible without tools (Tebbich et al., 2002). Tool use has also been proposed to be a principal strategy for accessing fallback foods (namely oil palm) for chimpanzees in Bossou, Guinea, during times of fruit scarcity (Yamakoshi, 1998). In contrast, among orangutans, ripe fruit availability does not correlate with use of tools to extract resources from tree holes (Koops, Visalberghi, & van Schaik, 2014), and in the Goualougo Triangle, termite gathering is not related to abundance of preferred resources (Sanz & Morgan, 2013a). Thus, scarcity in itself may not be sufficient to favor innovation and retention of tool traditions or to prompt increased rates of tool use in tool-using populations.

According to the “Opportunity Hypothesis,” abundance of target resources and tool raw materials prompts tool use by increasing rates of encounters with these items and thus the likelihood of tool use. For example, at Seringbara, Guinea, chimpanzees routinely use tools to gather army ants, which are abundant in their range, but rarely use tools to gather termites or nuts, which are less abundant (Koops, McGrew, & Matsuzawa, 2013). It also appears that for capuchins at Fazenda Boa Vista, monthly rates of nut cracking are correlated with availability of the nut species most often exploited (Spagnoletti, Visalberghi, Ottoni, Izar, & Fragaszy, 2011).

The “Relative Profitability” Hypothesis considers necessity and opportunity in tandem, and suggests that tool behaviors are a form of optimal foraging, emerging when they are more energetically profitable relative to other, non-tool assisted foraging methods (Rutz & St. Clair, 2012). For New Caledonian crows, just a few of the beetle larvae they routinely acquire with tools can nearly fulfill the daily energy needs for an adult crow. In addition, there is no direct competition for these embedded resources, and the crows face low predation risk; thus, tool use is likely a safe and profitable foraging method relative to alternative strategies (Rutz & St. Clair, 2012). The same is likely true for the subset of the dolphin population (*Tursiops sp.)* in Shark Bay, Australia, that carries marine sponges over their rostrum when foraging. This behavior improves the dolphins’ ability to detect or disturb fish burrowed in deep-water channels. As these fish are inaccessible without this tactic, spongers face no competition from non-spongers (Patterson & Mann, 2011). In the Goualougo Triangle, chimpanzees use tool sets that enable year-round access to termites, suggesting that this may be a profitable foraging strategy for maintaining access to a high-quality diet (Sanz & Morgan, 2013a). However, the Relative

Profitability Hypothesis has not yet been directly tested in primates.

Ecological constraints can also influence specific tool techniques used. In chimpanzees, for example, feeding techniques and tool dimensions when preying on insects in part reflect insect behavior and nest structure (Sanz, Deblauwe, Tagg, & Morgan, 2014; Schöning, Humle, Möbius, & McGrew, 2008). There are other cases where the forms of the tool behavior are not forced by detectable ecological features. There is a long history of examining the intraspecific variation of tool behavior in primates, particularly chimpanzees, via this "method of exclusion." This involves inferring that behaviors are culturally learned if ecological and genetic explanations for the variation can be excluded (e.g., Boesch et al., 1994; Goodall, 1973; McGrew, Tutin, & Baldwin, 1979; Whiten et al., 2001; Whiten et al., 1999). This method has also been applied to cetaceans (Rendell & Whitehead, 2001), capuchins (Perry et al., 2003) orangutans (van Schaik, 2003), and bonobos (Hohmann & Fruth, 2003). For example, neighboring communities of Western chimpanzees in the Taï Forest select different types of hammers for nut cracking, and these do not track ecological explanations such as abundance of different materials (Luncz, Mundry, & Boesch, 2012). As chimpanzee females immigrate to new groups at adolescence, the maintenance of between-group variation suggests that these females may be conforming to the techniques of the groups they enter. Alternately, female immigration between communities could be a pathway for the cultural diffusion of behavioral variants across broader regional scales over time (Lycett, Collard, & McGrew, 2010; Whiten, Schick, & Toth, 2009). For example, a female immigrant to the Kasekela community from the Mitumba community of Gombe chimpanzees was observed to be proficient at using tools to fish for *Camponotus* ants. In the years following her arrival, this behavior spread, and it is now common among Kasekela chimpanzees, suggesting this immigrant female introduced the behavior

(O’Malley, Wallauer, Murray, & Goodall, 2012).

The method of exclusion does not identify the actual mechanisms of social transmission. Further, if foraging tool behaviors are adaptive, it is expected that to some degree they will reflect local ecological conditions (Byrne, 2007). Thus, a role for ecological and environmental factors is not mutually exclusive with, and does not mitigate the potential importance of social learning in generating intraspecific variation in behavior (Koops et al., 2014).

1.5 Social Learning of Tool Use

Broadly defined, social learning is when the behavior of an observer, or learner, is influenced by observation of or interaction with a skilled individual or the results of an individual’s behavior (Galef, 1988; Heyes, 1994). An opportunity for social learning can occur when the behavior of two or more individuals is coordinated in space or in both space and time (Coussi-Korbel & Fragaszy, 1995). One approach for quantifying social learning opportunity has been to examine whether there is a relationship between gregariousness and diversity of behavioral repertoire. Recent studies suggest, however, that a larger average party size does not, in itself, predict the size of a population’s tool repeortire (Meulman & van Schaik, 2013). In the Goualougo Triangle, chimpanzees have a relatively large tool repertoire, but the average party size during tool use is relatively small (Sanz & Morgan, 2013b). This highlights the necessity of directly quantifying the types of social learning that occur and specific ways in which social interactions provide opportunity for learning.

Learning mechanisms are sometimes categorized as either “low-fidelity” or “high-fidelity.” Examples of low-fidelity mechanisms include stimulus or local enhancement, whereby a learner acquires information independently after being drawn to the object (stimulus) or locality of a model’s behavior (Thorpe, 1956). As described in Section 1.1, high-fidelity mechanisms including imitation or teaching are expected to ensure that a learner's behavior closely reproduces that of a model (Laland, 2004; Whiten & Ham, 1992). Emulation is considered somewhat intermediate, as it involves attending to the end goal of a behavior without precisely copying the actions to achieve it (Wood, 1989).

One leading hypothesis is that high-fidelity mechanisms underpin the transmission of cultural behaviors in humans, whereas low-fidelity mechanisms in concert with individual trial and error suffice to generate behavioral traditions in nonhumans (Tennie et al., 2009). Alternately, the deployment of particular learning mechanisms may depend on contextual factors. For example, social identification with a model may determine whether both humans and other apes show imitation and conformity (Whiten, Horner, & de Waal, 2005). In addition, task complexity can influence copying fidelity for apes and humans (Acerbi, Tennie, & Nunn, 2011; Chappell, Cutting, Apperly, & Beck, 2013; Hopper, Flynn, Wood, & Whiten, 2010). Tennie et al. (2016) suggest that Oldowan tool behaviors are not sufficiently complex to require high-fidelity learning such as imitation, and that, in contrast, these behaviors are well within the realm of what individuals could invent on their own. However, stone tool raw material procurement, manufacture and use involve multiple phases, and the sequence of even simple flake production itself is multi-step and removed from the eventual goal of using a flake to butcher meat. Thus, others have argued it is sufficiently "opaque" to have necessitated imitative learning (Caruana, D'Errico, & Backwell, 2013).

Low-fidelity social learning mechanisms also play an important role in the acquisition of tool skills for a wide range of species, including humans. Tool sites and artefacts comprise a constructed niche that is rich with information that may persist for weeks, months or longer (Fragaszy et al., 2013). Cross culturally, human children routinely interact with the tools made by older individuals (Lew-Levy, Reckin, Lavi, Cristóbal-Azkarate, & Ellis-Davies, 2017). From an evolutionary perspective, increasing terrestriality during the Pliocene (Foley & Gamble, 2009) is hypothesized to have increased technological complexity among hominins, one reason for which would have been the enhanced opportunity to encounter others' discarded tools (Meulman et al., 2012). In support of this hypothesis, tool use in monkeys occurs mostly in populations that are notably terrestrial; chimpanzees have more complex tool variants than the more arboreal orangutans; and chimpanzee tool variants are typically more complex in terrestrial versus arboreal settings (Meulman et al., 2012; Meulman & van Schaik, 2013).

Teaching occurs when a model actively facilitates another's learning. Teaching is considered foundational to human culture (Boyd & Richerson, 1985; Fogarty et al., 2011) but the role of teaching in the transfer of tool skills is debated (Garfield, Garfield, & Hewlett, 2016; Kline, 2015). Experimental approaches suggest that teaching is advantageous for information transfer, especially when accompanied by language (Morgan et al., 2015). Some perspectives emphasize aspects of teaching that are hypothesized to be unique to the human lineage, such as a teacher's use of ostensive cues to mark the onset of teaching behaviors, and adaptations in the learners to be sensitive to these cues (Csibra & Gergely, 2006). According to Caro and Hauser (1992), teaching can be identified according to several specific criteria: a teacher modifies its behavior in the presence of a naïve learner, and incurs a cost, or at least no benefit for doing so; and the learner acquires information or experience that otherwise would not have been available. This functional approach is compatible with complementary studies into the motivations or cognitive adaptations underlying teaching behavior, while having the benefit of identifying convergent forms of costly facilitation of skills across taxa.

1.6 Prosocial Helping during Tool Use

Prosocial motivation has also been recognized for its potential role in the evolution of cumulative culture. By sharing attention, intention, and motivation, individuals can more effectively cooperate to achieve goals, pooling their knowledge to discover more efficient solutions (Tomasello, 1999). Prosocial behavior has been shown to assist children in experimental, cumulative problem-solving tasks (Dean, Kendal, Schapiro, Thierry, & Laland, 2012). Often, studies of prosociality favor examining interactions between unrelated individuals, to examine how helpful behaviors might evolve in the absence of kin selection (Axelrod & Hamilton, 1981). However, a principal relationship in which information transmission occurs for primates, and many other animals, is between mothers and infants; this relationship is particularly critical for taxa such as great apes, which are characterized by extended periods of development and years of reliance on mothers for information (Lonsdorf, 2013). Prosocial helping in this context could confer fitness benefits, by more effectively advancing knowledge acquisition and foraging competence of dependent offspring than would occur simply by tolerance alone. Humans use a range of strategies to scaffold technological competence in children and adolescents, including routinely providing tools to novices who cannot yet manufacture these items on their own (Lew-Levy et al., 2017). However, the prevalence of this type of prosocial helping during tool use, and the contexts in which it occurs between and within species, have not been fully explored.

To date, prosociality has often been considered a derived characteristic in the human lineage. Narrowly defined, it is attributed only when *intent* to help another can be inferred (Jensen, 2016). Broader definitions focus on whether the behavior is a voluntary action that serves to help another individual (Warneken & Tomasello, 2009). Current debates reflect disagreement about to what extent nonhuman animals intentionally act to help other individuals (see Chapter 4). In addition to reflecting genuine species differences, variation in prosocial behavior can also result from differing experimental designs (Cronin, 2012; Marshall-Pescini, Dale, Quervel-Chaumette, & Range, 2016; Silk & House, 2011; Tennie, Jensen, & Call, 2016).

A principal area of debate has centered around the role of requesting behavior in eliciting prosocial actions. For chimpanzees, requests have been shown to both increase (e.g., Yamamoto, Humle, & Tanaka, 2009, 2012) or have no effect (e.g., Horner, Carter, Suchak, & de Waal, 2011; Vonk et al., 2008) on the likelihood that an actor behaves prosocially, whereas in tamarins, requests reduced prosocial responses (Cronin, Schroeder, Rothwell, Silk, & Snowdon, 2009). It remains unclear, however, how differences in experimental setup (e.g., the communicative options available to participants) interact with the actor's understanding of or willingness to help their partner and thus drive variation in prosocial response. For example, one possibility is that reaching actions are interpreted as an attempt to steal the reward from the possessor (summarized in Cronin, 2012). There is also debate about whether actor’s responses to requests are motivated by a desire not to help but to reduce costly harassment (Gilby, 2006). Thus, examining request behavior is helpful for understanding what might underlie an actor’s response.

1.7 Ontogenetic Approaches: Social Influences and Sex Differences in Learning

We adopt an ontogenetic approach to examining the complex tool behavior of wild chimpanzees, as this is a powerful method for illuminating the role of social factors on the maintenance of tool skills over generations. Ontogenetic studies on tool use have been conducted in several bird and primate taxa, and one of the key insights of these studies concerns the role of genetic influences versus the role of learning. Both woodpecker finches and New Caledonian crows acquire basic tool skills regardless of whether they have been exposed to a tool-using model, which suggests that there is a genetic component to their tool use (Hunt, Gray, &

Lambert, 2007; Kenward, Weir, Rutz, & Kacelnik, 2005; Tebbich et al., 2002). This does not, however, imply a complete absence of individual or social learning. For example, the presence of a human demonstrator can accelerate the tool use development of juvenile New Caledonian crows (Kenward, Rutz, Weir, & Kacelnik, 2006). In woodpecker finches, wild-caught birds tested in captivity show differing abilities to learn tool use depending on the ecological zone from which they were caught, suggesting that these skills do not emerge uniformly (Tebbich & Teschke, 2013). Access to the pandanus tools of parent birds is likely important for New Caledonian crows, as immature crows routinely interact with these during their first year of life (Tebbich & Teschke, 2013).

In primates, the flexible use of tools across different contexts suggests an evolved general capacity for skilled use of objects as tools, and there may also be a phylogenetic basis for the propensity of different species to engage in particular tools actions, such as percussing in capuchins, and probing in chimpanzees (discussed in Chapter 2). In addition, some inter-individual variation in tool skill and handedness are heritable in chimpanzees (Hopkins, Reamer, Mareno, & Schapiro, 2014). The extent of intraspecific and inter-individual variation in tool behaviors also indicates a significant role for social learning in the acquisition of these skills (Hunt et al., 2013). Chimpanzees, macaques, and capuchins all show intense interest in others' tools and tool sites (Fragaszy et al., 2013), and when young orangutans use tools, it is often those that have been left behind by their mothers in tree holes (van Noordwijk & van Schaik, 2005). This pattern suggests that artefacts are a consistent feature of the learning process. Another way in which skilled conspecifics can affect acquisition of tool skills by youngsters is through the amount of time invested in the activity. At Gombe and Bossou, the ages at which immature chimpanzees acquire tool skills for gathering termites and ants, respectively, is correlated with the amount of time mothers spend using tools (Humle, Snowdon, & Matsuzawa, 2009; Lonsdorf, 2006). In capuchins, nut cracking by conspecifics not only provides the materials for exploration by immature individuals but also stimulates higher rates of activities related to nut cracking. For example, immature capuchins are four times more likely to manipulate nuts when conspecifics are nut cracking compared to when they are engaging in other activities (Eshchar, Izar, Visalberghi, Resende, & Fragaszy, 2016). Further, capuchin infants selectively observe the most skilled nut crackers, which maximizes opportunities for both scavenging and learning (Ottoni, Resende, & Izar, 2005).

Traditionally, the social dynamic between chimpanzee mothers and offspring is defined as one of "master-apprenticeship" (Matsuzawa et al., 2001): chimpanzee mothers are very tolerant of the close proximity of their infants, who are highly motivated to observe their mothers; through this combination of their own initiative and their mothers' tolerance, immatures gain the necessary information to acquire complex skills. There is some evidence, however, that skilled models may play an even more active role through teaching in the context of difficult tasks. For example, at Taï Forest, on two occasions mothers were observed intervening when offspring were experiencing difficulty nut cracking, once to demonstrate the correct nut position and once to indicate the correct hand grip (Boesch, 1991). Given the critical role attributed to teaching in the evolution of human cultural capacities, however, the relative rarity of teaching in primates, particularly great apes, has been notable.

In addition to varying relative to task difficulty, social learning may also be moderated by the sex of the learner. At Taï, chimpanzee mothers volunteered more nuts and tools to sons than to daughters (Boesch & Boesch-Achermann, 2000). However, it does not appear that this leads to improved skill acquisition by males, as adult females show greater proficiency in nut cracking

(Boesch & Boesch, 1984b). One possible explanation for this is that females had to practice more as a result of reduced assistance during the learning process. Alternately, the sex difference in adults may result from the fact that at Taï, nut cracking is a somewhat solitary activity, such that males may prefer other activities that involve participation in larger social groups (Boesch & Boesch, 1984b). In contrast to Taï, differential treatment by mothers has not been detected during termite fishing at Gombe (Lonsdorf, 2005) or ant dipping at Bossou (Humle et al., 2009).

Another possibility is that male and female infants adopt differing social learning strategies. At Gombe, females observe mothers more than do males, and learn to termite fish earlier, suggesting they that rely more on imitation (Lonsdorf, 2005; see Chapter 2). At Bossou, no sex differences have been detected in observation and acquisition of ant dipping. One hypothesis proposed for these results is that the challenge of avoiding army ant bites generates relatively more interest for young males than does termite fishing, leading to similar levels of observation by both sexes during ant dipping (Humle et al., 2009). Another, non-mutually exclusive possibility is differences in motivation or skill for object manipulation. At Kalinzu, Uganda, immature male chimpanzees exhibit greater rates of object manipulation, but these actions are play-dominated; females exhibit a greater diversity of object manipulation types (Koops, Furuichi, Hashimoto, & van Schaik, 2015). At Gombe, there are infant sex differences in play, motor behavior and spatial proximity to conspecifics, with males showing greater independence before females (Lonsdorf et al., 2014). A variety of factors may thus influence whether there are sex differences in tool skill acquisition, and sex differences may vary across tasks.

1.8 Dissertation Methods

Study site

The Goualougo Triangle study site is located in the northern Republic of Congo, in the southern sector of the Nouabalé-Ndoki National Park (E 16°51′−16°56′; N 2°05′−3°03′). Created in 1993, the park protects 4000 km^2 of lowland rainforest and various populations of large mammals such as elephants (*Loxodonta cyclotis*), western lowland gorillas (*Gorilla gorilla gorilla*), leopards (*Panthera pardus*) and chimpanzees (*Pan troglodytes troglodytes*), as well as an array of other taxa. Both gorillas and chimpanzees occur at high densities in the northern Republic of Congo. Of the apes located within Western Equatorial Africa, 60% percent of the gorillas, and 43% of the chimpanzees are located within Republic of Congo (Strindberg et al., 2018). The Goualougo Triangle Ape Project (GTAP) was initiated by Dr. David Morgan in 1999. The study site is in a remote location, bordered from the west and the east by the Ndoki and Goualougo Rivers. Initial encounters with chimpanzees in this region between 1999-2001 involved a high proportion (69%) of naïve responses marked by curiosity on the part of the chimpanzees, indicating that these apes lacked previous experience with humans (Morgan & Sanz, 2003). As the first population habituated to human observation in the Congo Basin, the Goualougo Triangle chimpanzees offer singular insights into the behavior, ecology, and culture of apes in this region.

Remote Video Monitoring

The data for this dissertation research represent observational records of chimpanzees in the Goualougo Triangle spanning from 1999-2018. I undertook four field seasons between 2014-2018 focused on intensifying camera trapping of focal chimpanzees. This involved expanding an array of camera traps installed at termite nests in the chimpanzees’ home ranges. The use of camera networks was implemented by GTAP in 2003 (Sanz et al., 2004) and complements direct observations of chimpanzees. Camera traps are now being used widely as a cost-effective tool by researchers in a number of different settings, for gathering a range of data types, and for doing so while minimizing impact on the forest and the animals being studied (Burton et al., 2015; Caravaggi et al., 2017; McCarthy et al., 2018; Waldon, Miller, & Miller, 2011).

Over the course of the dissertation research, between 30 and 40 remote cameras were typically in operation, and observations were carried out at over 55 specific termite nest localities. Data were collected via monthly camera trap circuits in the Goualougo Triangle and were periodically transported data to Washington University in Saint Louis for archiving and screening. Between April 2014 and July 2018, remote cameras recorded approximately 96,000 clips, which we sorted according to broad species groups. Chimpanzee clips comprised approximately 22% of all camera triggers, totaling over 22,000 clips (approximately 367 hours of footage). We next linked videos to INTERACT video coding software (Mangold, 2015), identified focal chimpanzees from this footage, and coded it for relevant behaviors. In addition, we screened archived video footage for focal chimpanzees born beginning in 1999, such that data collection spans a nearly twenty-year period. Tool transfer data for use in Chapters 3 and 4 were also extracted from this archival footage.

Comparative Data Collection between the Goualougo Triangle and Gombe, Tanzania

A critical component of this dissertation involved comparing the behavior of Central chimpanzees at Goualougo to that of Eastern chimpanzees (*Pan t. schweinfurthii*) at Gombe, Tanzania. Chimpanzees at both Goualougo and Gombe gather *Macrotermes*, a genus of fungus-growing termites that are widely distributed throughout Africa and Asia (Eggleton, 2000). At Gombe, chimpanzee fish for *Macrotermes subhyalinus* (Collins & McGrew, 1987; Goodall, 1968; O’Malley & Power, 2012) and at Goualougo, for *M. lilljeborgi*, *M. muelleri*, and *M.*

nobilis (Sanz et al., 2014). Termite species in this genus build complex nest structures that encompass a network of below-ground chambers and in some species a towering, free standing mound reaching several meters high (Noirot & Darlington, 2000).

Tool manufacture and use are more complex at Goualougo compared to Gombe, and these population differences reflect broader regional patterns in tool techniques and characteristics for chimpanzee termite gathering. Populations across the chimpanzee range have been documented using tools to gather termites (Bogart & Pruetz, 2008; Goodall, 1986; McGrew & Collins, 1985; McGrew, Tutin, & Baldwin, 1979; Nishida & Uehara, 1980; Sanz, Morgan, & Gulick, 2004), but tool techniques and tool characteristics vary regionally (Sanz et al., 2014). In East and West Africa, termite gathering involves the use of a single tool type, a fishing probe, manufactured from a range of raw materials such as grass or bark (Goodall, 1968; McGrew et al., 1979). These behaviors contrast with the use of tool sets (Bermejo & Illera, 1999; Deblauwe, Guislain, Dupain, & Van Elsacker, 2006; Fay & Carroll, 1994; Muroyama, 1991; Sabater Pí, 1974; Sanz et al., 2004; Sugiyama, 1985; Suzuki, Kuroda, & Nishihara, 1995), and the manufacture of tools from specific raw materials (Sanz & Morgan, 2007) among chimpanzees in Central Africa. These differences allowed us to examine from a comparative perspective how complexity is linked to tool skill acquisition and relates to both high-fidelity social learning and prosocial helping.

The Gombe data assessed in the present study are based on the research conducted by Dr. Elizabeth Lonsdorf between 1999-2003 on the acquisition of termite-fishing skills by Gombe chimpanzees. Focal individuals for this research were immature individuals of the Kasekela community, which has been studied since the early 1960s (Goodall, 1968, 1986). The data collected by Dr. Lonsdorf comprise handheld video focal observations on five mothers and 14 offspring (8 males, 6 females) up to the age of 11 years old. Video focals were 15 minutes in length and total over 67 hours of video footage of termite-fishing sessions (Lonsdorf, 2005). Further details on the comparative aspects of this research are provided in Chapters 2 and 4.

1.9 Dissertation Structure

In order to better model the developmental and social processes underlying the intergenerational transmission of technology during human evolution, this dissertation examined the acquisition of complex tool skills in wild chimpanzees of the Goualougo Triangle, Republic of Congo. In Chapter 2, my co-authors and I examine the developmental trajectory of termite gathering and compare it to that for Gombe chimpanzees. We document the ages at which chimpanzees acquire termite-gathering critical elements and the sequence of skill acquisition. We establish that chimpanzees become proficient with single tools before multiple tools, and that in contrast to Gombe, chimpanzees learn to use tools before they learn to make them. We further document wide variation in the age range at which individuals begin to use perforating tool sets, and find that only subadults and adults can capably puncture subterranean nests. We did not detect significant sex differences in the sample of chimpanzees we studied, but we observed that females acquire most skills slightly before males do, while males manufacture tools slightly earlier than females do.

In Chapter 3, we examine the role of high-fidelity social learning on the acquisition of termite-gathering skills. We find that transfers of tools from skilled to less competent conspecifics in this context comprise a functional form of teaching. These transfers increase learning opportunity and provide knowledge to less competent tool users, while exacting a cost on the termite gathering of skilled tool users. We also describe potential strategies by which skilled tool users may buffer themselves from experiencing these costs (Musgrave, Morgan, Lonsdorf, Mundry, & Sanz, 2016).

In Chapter 4, we compare tool transfers in the Goualougo Triangle to those that occur at Gombe, Tanzania, from the perspective of prosociality. We examine how tool transfers fall along a continuum of prosocial response, what prompts prosocial tool transfer, and how these behaviors differ between these two populations. We find significant population differences in several indicators of prosociality. The rate of tool transfer is higher at Goualougo, and there is a significant interaction between population and request status, such that there is a higher probability of transfer upon request at Goualougo. Further, transfer types are more prosocial at Goualougo compared to Gombe. Finally, in Chapter 5, I summarize the results of this research and discusses the broader implications of these findings.

References

Acerbi, A., Tennie, C., & Nunn, C. (2011). Modeling imitation and emulation in constrained search spaces. *Learning and Behavior*, *39*(2), 104–114.

Ambrose, S. H. (2001). Paleolithic technology and human evolution. *Science, New Series, 291*(5509), 1748–1753.

Axelrod, R., & Hamilton, W. D. (1981). The evolution of cooperation. *Science, 211*(4489), 1390–1396.

Bermejo, M., & Illera, G. (1999). Tool-set for termite-fishing and honey extraction by wild chimpanzees in the Lossi Forest, Congo. *Primates*, *40*(4), 619–627.

Biro, D., Haslam, M., & Rutz, C. (2013). Tool use as adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences, 368*(1630), 20120408.

Boesch, C. (1991). Teaching among wild chimpanzees. *Animal Behaviour*, *41*(3), 530–532.

Boesch, C. (2013). Ecology and cognition of tool use in chimpanzees. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 21–47). Cambridge: Cambridge University Press.

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: Behavioural ecology and evolution.* Oxford: Oxford University Press.

Boesch, C., & Boesch, H. (1984a). Mental map in wild chimpanzees: An analysis of hammer transports for nut cracking. *Primates*, *25*(2), 160–170.

Boesch, C., & Boesch, H. (1984b). Possible causes of sex differences in the use of natural hammers by wild chimpanzees. *Journal of Human Evolution*, *13*(5), 415–440.

Boesch, C., & Boesch, H. (1990). Tool use and tool making in wild chimpanzees. *Folia Primatologica*, *54*(1–2), 86–99.

Boesch, C., Head, J., & Robbins, M. (2009). Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. *Journal of Human Evolution*, *56*(6), 560–569.

Boesch, C., Kalan, A. K., Agbor, A., Arandjelovic, M., Dieguez, P., Lapeyre, V., & Kühl, H. S. (2017). Chimpanzees routinely fish for algae with tools during the dry season in Bakoun, Guinea. *American Journal of Primatology, 79*(3), e22613.

Boesch, C., Marchesi, P., Marchesi, N., Fruth, B., & Joulian, F. (1994). Is nut cracking in wild chimpanzees a cultural behavior? *Journal of Human Evolution*, *26*(4), 325–338.

Boesch, C., & Tomasello, M. (1998). Chimpanzee and human cultures. *Current Anthropology*, *39*(5), 591–614.

Bogart, S., & Pruetz, J. (2008). Ecological context of savanna chimpanzee (*Pan troglodytes verus*) termite fishing at Fongoli, Senegal. *American Journal of Primatology, 70*(6), 605–612.

Boose, K. J., White, F. J., & Meinelt, A. (2013). Sex differences in tool use acquisition in bonobos (*Pan paniscus*). *American Journal of Primatology*, *75*(9), 917–926.

Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago: University of Chicago.

Braun, D. R., Plummer, T., Ditchfield, P., Ferraro, J. V., Maina, D., Bishop, L. C., & Potts, R. (2008). Oldowan behavior and raw material transport: Perspectives from the Kanjera Formation. *Journal of Archaeological Science, 35*(8), 2329–2345.

Breuer, T., Ndoundou-Hockemba, M., & Fishlock, V. (2005). First observation of tool use in wild gorillas. *PLoS Biology, 3*(11), 2041–2043.

Brewer, S. M., & McGrew, W. C. (1990). Chimpanzee use of a tool-set to get honey. *Folia Primatologica*, *54*(1–2), 100–104.

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., … Boutin, S. (2015). Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology, 52*(3), 675–685.

Byrne, R., Sanz, C., & Morgan, D. (2013). Chimpanzees plan their tool use. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 48–64). Cambridge: Cambridge University Press.

Byrne, R. W. (1997). The technical intelligence hypothesis: An additional evolutionary stimulus to intelligence? In A. Whiten & R. W. Byrne (Eds.), *Machiavellian intelligence II: Extensions and evaluations* (pp. 289-311). Cambridge: Cambridge University Press.

Byrne, R. W. (2007). Culture in great apes: Using intricate complexity in feeding skills to trace the evolutionary origin of human technical prowess. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1480), 577–585.

Byrne, R. W., & Byrne, J. (1993). Complex leaf-gathering skills of mountain gorillas (*Gorilla g. beringei)*: Variability and standardization. *American Journal of Primatology*, *31*, 241–261.

Call, J. (2013). Three ingredients for becoming a creative tool user. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 3–20). Cambridge: Cambridge University Press.

Caravaggi, A., Banks, P. B., Burton, A. C., Finlay, C. M. V., Haswell, P. M., Hayward, M. W., … Wood, M. D. (2017). A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation*, *3*(3), 109–122.

Caro, T. M., & Hauser, M. D. (1992). Is there teaching in nonhuman animals? *The Quarterly Review of Biology, 67*(2), 151–174.

Caruana, M. V., D'Errico, F., & Backwell, L. (2013). Early hominin social learning strategies underlying the use and production of bone and stone tools. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 242–285). Cambridge: Cambridge University Press.

Carvalho, S., Cunha, E., Sousa, C., & Matsuzawa, T. (2008). Chaînes opératoires and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *Journal of Human Evolution*, *55*(1), 148–163.

Chappell, J., Cutting, N., Apperly, I. A., & Beck, S. R. (2013). The development of tool manufacture in humans: What helps young children make innovative tools? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630), 20120409.

Collins, D., & McGrew, W. (1987). Termite fauna related to differences in tool-use between groups of chimpanzees (*Pan troglodytes*). *Primates*, *28*(4), 457–471.

Coussi-Korbel, S., & Fragaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour*, *50*(6), 1441–1453.

Cronin, K. A. (2012). Prosocial behaviour in animals: The influence of social relationships, communication and rewards. *Animal Behaviour*, *84*(5), 1085–1093.

Cronin, K. A., Schroeder, K. K. E., Rothwell, E. S., Silk, J. B., & Snowdon, C. T. (2009). Cooperatively breeding cottontop tamarins (*Saguinus oedipus*) do not donate rewards to their long-term mates. *Journal of Comparative Psychology*, *123*(3), 231–241.

Csibra, G., & Gergely, G. (2006). Social learning and social cognition: The case for pedagogy. In Y. Munakata & M. H. Johnson (Eds.), *Processes of change in brain and cognitive development. Attention and performance XXI*, *21* (pp. 249–274). Oxford: Oxford University Press.

Davidson, I. (2016). Stone tools: Evidence of something in between culture and cumulative culture. In M. Haidle, N. Conard, & M. Bolus (Eds.), *The nature of culture* (pp. 99–120). Dordrecht: Springer.

de la Torre, I. (2016). The origins of the Acheulean : Past and present perspectives on a major transition in human evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1698), 20150245

de la Torre, I., & Mora, R. (2005). *Technological strategies in the lower Pleistocene at Olduvai Beds I and II*. University of Liège Press.

de la Torre, I., Mora, R., Domínguez-Rodrigo, M., de Luque, L., & Alcalá, L. (2003). The Oldowan industry of Peninj and its bearing on the reconstruction of the technological skills of Lower Pleistocene hominids. *Journal of Human Evolution*, *44*(2), 203–224.

Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B., & Laland, K. N. (2012). Identification of the social and cognitive processes underlying human cumulative culture. *Science*, *335*(6072), 1114–1118.

Deblauwe, I., Guislain, P., Dupain, J., & Van Elsacker, L. (2006). Use of a tool-set by *Pan troglodytes troglodytes* to obtain termites (*Macrotermes*) in the periphery of the Dja Biosphere Reserve, southeast Cameroon. *American Journal of Primatology*, *68*(12), 1191–1196.

Deblauwe, I., & Janssens, G. P. J. (2008). New insights in insect prey choice by chimpanzees and gorillas in Southeast Cameroon: The role of nutritional value. *American Journal of Physical Anthropology*, *135*(1), 42–55.

Delagnes, A., & Roche, H. (2005). Late Pliocene hominid knapping skills: The case of Lokalalei 2C, West Turkana, Kenya. *Journal of Human Evolution*, *48*(5), 435–472.

Eggleton, P. (2000). Global patterns of termite diversity. In T. Abe, D. Bignell, & M. Higashi (Eds.), *Termites: Evolution, sociality, symbioses, ecology* (pp. 25–51). Dordrecht: Springer.

Eshchar, Y., Izar, P., Visalberghi, E., Resende, B., & Fragaszy, D. (2016). When and where to practice: Social influences on the development of nut-cracking in bearded capuchins (*Sapajus libidinosus*). *Animal Cognition*, *19*(3), 605–618.

Estienne, V., Stephens, C., & Boesch, C. (2017). Extraction of honey from underground bee nests by central African chimpanzees (*Pan troglodytes troglodytes*) in Loango National Park, Gabon: Techniques and individual differences. *American Journal of Primatology*, *79*(8), e22672.

Falótico, T., & Ottoni, E. B. (2014). Sexual bias in probe tool manufacture and use by wild bearded capuchin monkeys. *Behavioural Processes*, *108*, 117–122.

Fay, J. M., & Carroll, R. W. (1994). Chimpanzee tool use for honey and termite extraction in Central Africa. *American Journal of Primatology*, *34*(4), 309–317.

Fogarty, L., Strimling, P., & Laland, K. N. (2011). The evolution of teaching. *Evolution*, *65*(10), 2760–2770.

Foley, R., & Gamble, C. (2009). The ecology of social transitions in human evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1533), 3267–3279.

Fowler, A., & Sommer, V. (2007). Subsistence technology of Nigerian chimpanzees. *International Journal of Primatology*, *28*(5), 997–1023.

Fox, E., Sitompul, A. F., & van Schaik, C. (1999). Intelligent tool use in Sumatran orangutans. In S. T. Parker, R. W. Mitchell, & H. L. Miles (Eds.), *The mentalities of gorillas and orangutans* (pp. 99–116). Cambridge: Cambridge University Press.

Fragaszy, D., Biro, D., Eshchar, Y., Humle, T., Izar, P., Resende, B., & Elisabetta, V. (2013). The fourth dimension of tool use: Temporally enduring artefacts aid primates learning to use tools. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630), 20120410.

Fragaszy, D., & Mangalam, M. (2018). Tooling. In M. Naguib, L. Barrett, S. Healy, J. Podos, L. Simmons, & M. Zuk (Eds.), *Advances in the Study of Behavior* (Vol. 50, pp. 177–241). Elsevier.

Fuentes, A. (2017). Human niche, human behaviour, human nature. *Interface Focus, 7*.

Fujita, K., Kuroshima, H., & Asai, S. (2003). How do tufted capuchin monkeys (*Cebus apella*) understand causality involved in tool use? *Journal of Experimental Psychology: Animal Behavior Processes, 29*(3), 233–242.

Galef, B. G. (1988). Imitation in animals: History, definition, and interpretation of data from the psychological laboratory. In T. R. Zentall & B. G. Galef (Eds.), *Social learning: Psychological and biological perspectives* (pp. 3–28). Hillsdale: Lawrence Erlbaum Associates.

Galef, B. G. (1992). The question of animal culture. *Human Nature, 3*(2), 157–178.

Galvis, N., Link, A., & Di Fiore, A. (2014). A novel use of camera traps to study demography and life history in wild animals: A case study of spider monkeys (*Ateles belzebuth*). *International Journal of Primatology, 35*(5), 908–918.

Garfield, Z. H., Garfield, M. J., & Hewlett, B. S. (2016). A cross-cultural analysis of hunter-gatherer social learning. In H. Terashima & B. Hewlett (Eds.), *Social learning and innovation in contemporary hunter-gatherers* (pp. 19–34). Tokyo: Springer.

Gilby, I. C. (2006). Meat sharing among the Gombe chimpanzees: Harassment and reciprocal exchange. *Animal Behaviour, 71*(4), 953–963.

Girndt, A., Meier, T., & Call, J. (2008). Task constraints mask great apes’ ability to solve the trap-table task. *Journal of Experimental Psychology: Animal Behavior Processes, 34*(1), 54–62.

Goodall, J. (1964). Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature, 201*(4926), 1264–1266.

Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs, 1*, 161–311.

Goodall, J. (1973). Cultural elements in a chimpanzee community. In E. W. Menzel (Ed.), *Precultural primate behaviour*. Basel: Karger.

Goodall, J. (1986). *The chimpanzees of Gombe. Patterns of behavior* Cambridge: Belknap Press.

Gowlett, J. A. J. (2006). The elements of design form in Acheulian bifaces: Modes, modalities, rules and language. In N. Goren-Inbar & G. Sharon (Eds.), *Axe Age Acheulian toolmaking from quarry to discard* (pp. 203–221). London: Equinox.

Gruber, R., Schiestl, M., Boeckle, M., Frohnwieser, A., Miller, R., Gray, R., … Taylor, A. (2019). New Caledonian crows use mental representations to solve metatool problems. *Current Biology, 29*, 1–7.

Gruber, T., Clay, Z., & Zuberbühler, K. (2010). A comparison of bonobo and chimpanzee tool use: Evidence for a female bias in the *Pan* lineage. *Animal Behaviour*, *80*(6), 1023–1033.

Harmand, S. (2009). Variability in raw material selectivity at the Late Pliocene sites of Lokalalei, West Turkana, Kenya. In E. Hovers & D. R. Braun (Eds.), *Interdisciplinary approaches to the Oldowan. Vertebrate Paleobiology and Paleoanthropology*. (pp. 85–97). Springer.

Harmand, S., Lewis, J. E., Feibel, C. S., Lepre, C. J., Prat, S., Lenoble, A., … Roche, H. (2015). 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature*, *521*(7552), 310–315.

Haslam, M. (2013). "Captivity bias" in animal tool use and its implications for the evolution of hominin technology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630), 20120421.

Haslam, M. (2014). On the tool use behavior of the bonobo-chimpanzee last common ancestor, and the origins of hominine stone tool use: Tool use in the bonobo-chimpanzee LCA. *American Journal of Primatology*, *76*(10), 910–918.

Herrmann, E., Call, J., Hernandez-Lloreda, M. V, Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science*, *317*(5843), 1360–1366.

Herrmann, E., Hare, B., Call, J., & Tomasello, M. (2010). Differences in the cognitive skills of bonobos and chimpanzees. *PLoS ONE*, *5*(8), 2–5.

Herrmann, E., Wobber, V., & Call, J. (2008). Great apes' (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, *Pongo pygmaeus*) understanding of tool functional properties after limited experience. *Journal of Comparative Psychology*, *122*(2), 220–230.

Heyes, C. (1994). Social learning in animals: Categories and mechanisms. *Biological Reviews*, *69*(2), 207–231.

Hohmann, G., & Fruth, B. (2003). Culture in bonobos? Between-species and within-species variation in behavior. *Current Anthropology*, *44*(4), 563–571.

Holzhaider, J., Hunt, G., Campbell, V. M., & Gray, R. D. (2008). Do wild New Caledonian crows (*Corvus moneduloides*) attend to the functional properties of their tools? *Animal Cognition*, *11*(2), 243–254.

Hopkins, W. D., Reamer, L., Mareno, M. C., & Schapiro, S. J. (2014). Genetic basis in motor skill and hand preference for tool use in chimpanzees (*Pan troglodytes*). *Proceedings of the Royal Society B: Biological Sciences*, *282*(1800).

Hopper, L. M., Flynn, E. G., Wood, L. A. N., & Whiten, A. (2010). Observational learning of tool use in children: Investigating cultural spread through diffusion chains and learning mechanisms through ghost displays. *Journal of Experimental Child Psychology*, *106*(1), 82–97.

Horner, V., Carter, J. D., Suchak, M., & de Waal, F. (2011). Spontaneous prosocial choice by chimpanzees. *Proceedings of the National Academy of Sciences, 108*(33), 13847–13851.

Humle, T., Snowdon, C. T., & Matsuzawa, T. (2009). Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Animal Cognition*, *12*(Suppl 1), 37–48.

Hunt, G. (1996). Manufacture and use of hook-tools by New Caledonian crows. *Nature*, *379*, 249–251.

Hunt, G. (2000). Human-like, population-level specialization in the manufacture of pandanus tools by New Caledonian crows *Corvus moneduloides*. *Proceedings of the Royal Society B: Biological Sciences*, *267*(1441), 403–413.

Hunt, G. (2014). New Caledonian Crows' (*Corvus moneduloides*) pandanus tool designs: Diversification or independent invention? *The Wilson Journal of Ornithology*, *126*(1), 133–139.

Hunt, G., Corballis, M., & Gray, R. (2006). Design complexity and strength of laterality are correlated in New Caledonian crows' pandanus tool manufacture. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1590), 1127–1133.

Hunt, G., & Gray, R. (2002). Species-wide manufacture of stick-type tools by New Caledonian Crows. *Emu - Austral Ornithology*, *102*(4), 349–353.

Hunt, G., & Gray, R. (2003). Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proceedings of the Royal Society B: Biological Sciences*, *270*(1517), 867–874.

Hunt, G., & Gray, R. (2004). Direct observations of pandanus-tool manufacture and use by a New Caledonian crow (*Corvus moneduloides*). *Animal Cognition*, *7*(2), 114–120.

Hunt, G., Gray, R., & Taylor, A. (2013). Why is tool use rare in animals? In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 89–118). Cambridge: Cambridge University Press.

Hunt, G. R., Gray, R. D., & Lambert, C. (2007). Cognitive requirements for tool use by New Caledonian crows (*Corvus moneduloides*). *New Zealand Journal of Zoology*, *34*(1), 1–7.

Hunt, K. (2006). Sex differences in chimpanzee foraging behavior and tool use: Implications for the Oldowan. In N. Toth & K. Schick (Eds.), *The Oldowan: Case studies into the earliest stone age* (pp. 243–266). Stone Age Institute Press.

Isaac, G. (1976). Stages of cultural elaboration in the Pleistocene. In S. Harnad, H. Stekelis, & J. Lancaster (Eds.), *Origins and evolution of language and speech* (pp. 275–288). New York: New York Academy of Science.

Izar, P., Humle, T., Resende, B., Fragaszy, D., Visalberghi, E., Biro, D., & Eshchar, Y. (2013). The fourth dimension of tool use: Temporally enduring artefacts aid primates learning to use tools. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630), 20120410.

Jensen, K. (2016). Prosociality. *Current Biology*, *26*(16), R748–R752.

Kabadayi, C., & Osvath, M. (2017). Ravens parallel great apes in flexible planning for tool-use and bartering. *Science*, *357*(6347), 202–204.

Kempe, M., Lycett, S. J., & Mesoudi, A. (2014). From cultural traditions to cumulative culture: Parameterizing the differences between human and nonhuman culture. *Journal of Theoretical Biology*, *359*, 29–36.

Kenward, B., Rutz, C., Weir, A. A. S., & Kacelnik, A. (2006). Development of tool use in New Caledonian crows: Inherited action patterns and social influences. *Animal Behaviour*, *72*(6), 1329–1343.

Kenward, B., Weir, A. A. S., Rutz, C., & Kacelnik, A. (2005). Tool manufacture by naive juvenile crows. *Nature*, *433*, 121.

Kinani, J. F., & Zimmerman, D. (2015). Tool use for food acquisition in a wild mountain gorilla (*Gorilla beringei beringei*). *American Journal of Primatology*, *77*(3), 353–357.

Kline, M. (2015). How to learn about teaching: An evolutionary framework for the study of teaching behavior in humans and other animals. *Behavioral and Brain Sciences*, *754*, 1–71.

Koops, K., Furuichi, T., Hashimoto, C., & van Schaik, C. (2015). Sex differences in object manipulation in wild immature chimpanzees (*Pan troglodytes schweinfurthii*) and bonobos (*Pan paniscus*): Preparation for tool use? *PLoS ONE*, *10*(10), 1–15.

Koops, K., McGrew, W., & Matsuzawa, T. (2013). Ecology of culture: Do environmental factors influence foraging tool use in wild chimpanzees, *Pan troglodytes verus*? *Animal Behaviour*, *85*(1), 175–185.

Koops, K., Visalberghi, E., & van Schaik, C. P. (2014). The ecology of primate material culture. *Biology Letters*, *10*(11), 20140508.

Kühl, H. S., Boesch, C., Kulik, L., Haas, F., Arandjelovic, M., Dieguez, P., … Kalan, A. K. (2019). Human impact erodes chimpanzee behavioral diversity. *Science*, *4532*.

Laland, K. (2004). Social learning strategies. *Learning & Behavior*, *32*(1), 4–14.

Laland, K. (2018). *Darwin's unfinished symphony: How culture made the human mind*. Princeton University Press.

Leakey, L., Tobias, P., & Napier, J. R. (1964). A new species of the genus *Homo* from Olduvai Gorge. *Nature*, *202*, 7–9.

Leakey, M. (1971). *Olduvai Gorge, volume 3: Excavations in beds I and II, 1960-1963*. Cambridge: Cambridge University Press.

Leakey, M. (1975). Cultural patterns in the Olduvai sequence. In K. W. Butzer & G. L. Isaac (Eds.), *After the Australopithecines: Stratigraphy, ecology, and culture change in the middle Pleistocene* (pp. 477–493). The Hague: Mouton Publishers.

Lepre, C. J., Roche, H., Kent, D. V., Harmand, S., Quinn, R. L., Brugal, J. P., … Feibel, C. S. (2011). An earlier origin for the Acheulian. *Nature*, *477*(7362), 82–85.

Lew-Levy, S., Reckin, R., Lavi, N., Cristóbal-Azkarate, J., & Ellis-Davies, K. (2017). How do hunter-gatherer children learn subsistence skills?: A meta-ethnographic review. *Human Nature*, *28*(4), 367–394.

Lewis, J. E., & Harmand, S. (2016). An earlier origin for stone tool making: Implications for cognitive evolution and the transition to *Homo*. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1698), 20150233.

Lockman, J. J. (2000). A perception-action perspective on tool use development. *Child Development*, *71*(1), 137–144.

Lonsdorf, E. (2005). Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Animal Behaviour*, *70*(3), 673–683.

Lonsdorf, E. (2006). What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Animal Cognition*, *9*(1), 36–46.

Lonsdorf, E. (2013). The role of mothers in the development of complex skills in chimpanzees. In K. B. H. Clancy, K. Hinde, & J. N. Rutherford (Eds.), *Building Babies* (pp. 303–318). New York, NY: Springer New York.

Lonsdorf, E., Markham, A. C., Heintz, M. R., Anderson, K. E., Ciuk, D. J., Goodall, J., & Murray, C. M. (2014). Sex differences in wild chimpanzee behavior emerge during infancy. *PLoS ONE*, *9*(6), e99099.

Lonsdorf, E., Ross, S. R., Linick, S. A., Milstein, M. S., & Melber, T. N. (2009). An experimental, comparative investigation of tool use in chimpanzees and gorillas. *Animal Behaviour*, *77*(5), 1119–1126.

Luncz, L. V., Mundry, R., & Boesch, C. (2012). Evidence for cultural differences between neighboring chimpanzee communities. *Current Biology*, *22*(10), 922–926.

Lycett, S. J., Collard, M., & McGrew, W. C. (2010). Are behavioral differences among wild chimpanzee communities genetic or cultural? An assessment using tool-use data and phylogenetic methods. *American Journal of Physical Anthropology*, *142*(3), 461–467.

Malaivijitnond, S., Lekprayoon, C., Tandavanittj, N., Panha, S., Cheewatham, C., & Hamada, Y. (2007). Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology*, *69*(2), 227-233.

Mangold. (2015). INTERACT 14 User guide. Mangold International GmbH.

Mannu, M., & Ottoni, E. B. (2009). The enhanced tool-kit of two groups of wild bearded capuchin monkeys in the Caatinga: Tool making, associative use, and secondary tools. *American Journal of Primatology*, *71*(3), 242–251.

Marlowe, F. W. (2007). Hunting and gathering: The human sexual division of foraging labor. *Cross-Cultural Research*, *41*(2), 170–195.

Marshall-Pescini, S., Dale, R., Quervel-Chaumette, M., & Range, F. (2016). Critical issues in experimental studies of prosociality in non-human species. *Animal Cognition*, *19*(4), 679–705.

Martin-Ordas, G., Jaek, F., & Call, J. (2012). Barriers and traps: Great apes' performance in two functionally equivalent tasks. *Animal Cognition*, *15*(5), 1007–1013.

Matsuzawa, T. (1994). Field experiments of tool-use. In R. Wrangham, W. McGrew, F. de Waal, & P. G. Heltne (Eds.), *Chimpanzee cultures* (pp. 157–164). Cambridge: Harvard University Press.

Matsuzawa, T. (1996). Chimpanzee intelligence in nature and captivity: Iso- morphism of symbol use and tool use. In W. McGrew, L. Marchant, & T. Nishida (Eds.), *Great Ape Societies* (pp. 196–209). Cambridge: Cambridge University Press.

Matsuzawa, T., Biro, D., Humle, T., Inoue-Nakamura, N., Tonooka, R., & Yamakoshi, G. (2001). Emergence of culture in wild chimpanzees: Education by master- apprenticeship. In T. Matsuzawa (Ed.), *Primate origins of human cognition and behavior* (pp. 557–574). Tokyo: Springer.

McCarthy, M. S., Després-Einspenner, M. L., Samuni, L., Mundry, R., Lemoine, S., Preis, A., … Kühl, H. S. (2018). An assessment of the efficacy of camera traps for studying demographic composition and variation in chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *80*(9), 1–10.

McGrew, W. (1979). Evolutionary implications of sex differences in chimpanzee predation and tool use. In D. A. Hamburg & E. R. McCown (Eds.), *The great apes* (pp. 441–463). Menlo Park: Benjamin/Cummings.

McGrew, W. (1992). *Chimpanzee material culture: Implications for human evolution*. Cambridge: Cambridge University Press.

McGrew, W. C., & Collins, D. A. (1985). Tool use by wild chimpanzees (*Pan troglodytes*) to obtain termites (*Macrotermes herus*) in the Mahale Mountains, Tanzania. *American Journal of Primatology*, *9*(1), 47–62.

McGrew, W., Tutin, C., & Baldwin, P. J. (1979). Chimpanzees, tools, and termites: Cross-cultural comparisons of Senegal, Tanzania, and Rio Muni. *Man*, *14*(2), 185–214.

McPherron, S. (2013). Perspectives on stone tools and cognition in the early Paleolithic record. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 286–309). Cambridge: Cambridge University Press.

McPherron, S. P., Alemseged, Z., Marean, C. W., Wynn, J. G., Reed, D., Geraads, D., … Béarat, H. A. (2010). Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature*, *466*(7308), 857–860.

Meulman, E., Sanz, C., Visalberghi, E., & van Schaik, C. P. (2012). The role of terrestriality in promoting primate technology. *Evolutionary Anthropology: Issues, News, and Reviews*, *21*(2), 58–68.

Meulman, E., & van Schaik, C. P. (2013). Orangutan tool use and the evolution of technology. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 176–202). Cambridge: Cambridge University Press.

Morgan, D., & Sanz, C. (2003). Naïve encounters with chimpanzees in the Goualougo Triangle, Republic of Congo. *International Journal of Primatology*, *24*(2), 369–381.

Morgan, D., Sanz, C., Onononga, J. R., & Strindberg, S. (2006). Ape abundance and habitat use in the Goualougo Triangle, Republic of Congo. *International Journal of Primatology* (Vol. 27).

Morgan, T. J. H., Uomini, N. T., Rendell, L. E., Chouinard-Thuly, L., Street, S. E., Lewis, H. M., … Laland, K. N. (2015). Experimental evidence for the co-evolution of hominin tool-making teaching and language. *Nature Communications*, *6*(6029), 1–8.

Moura, A. C. D. A., & Lee, P. C. (2004). Capuchin stone tool use in Caatinga dry forest. *Science*, *306*(5703), 1909.

Muroyama, Y. (1991). Chimpanzees' choices of prey between two sympatric species of *Macrotermes* in the Campo Animal Reserve, Cameroon. *Human Evolution*, *6*(2), 143–151.

Musgrave, S., Morgan, D., Lonsdorf, E., Mundry, R., & Sanz, C. (2016). Tool transfers are a form of teaching among chimpanzees. *Scientific Reports*, *6*, 34783.

Nishida, T. (1987). Local traditions and cultural transmission. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 462–474). Chicago: University of Chicago Press.

Nishida, T., & Uehara, S. (1980). Chimpanzees, tools, and termites: Another example from Tanzania. *Current Anthropology*, *21*(5), 671–672.

Noirot, C., & Darlington, J. (2000). Termite nests: Architecture, regulation and defence. In T. Abe, D. Bignell, & M. Higashi (Eds.), *Termites: Evolution, sociality, symbioses, ecology* (pp. 121–139). Dordrecht: Springer.

Oakley, K. P. (1949). Man the toolmaker. London: British Museum.

O'Malley, R. C., & Power, M. L. (2012). Nutritional composition of actual and potential insect prey for the Kasekela chimpanzees of Gombe National Park, Tanzania. *American Journal of Physical Anthropology*, *149*(4), 493-503.

O’Malley, R. C., Wallauer, W., Murray, C. M., & Goodall, J. (2012). The appearance and spread of ant fishing among the Kasekela chimpanzees of Gombe. *Current Anthropology*, *53*(5), 650–663.

Osiurak, F., & Badets, A. (2016). Tool use and affordance: Manipulation-based versus reasoning-based approaches. *Psychological Review*, *123*(5), 534–568.

Ottoni, E. B., & Izar, P. (2008). Capuchin monkey tool use: Overview and implications. *Evolutionary Anthropology: Issues, News, and Reviews*, *17*(4), 171–178.

Ottoni, E. B., de Resende, B. D., & Izar, P. (2005). Watching the best nutcrackers: What capuchin monkeys (*Cebus apella*) know about others’ tool-using skills. *Animal Cognition*, *8*(4), 215-219.

Pandolfi, S., van Schaik, C. P., & Pusey, A. (2003). Sex differences in termite fishing among Gombe chimpanzees. In F. B. M. de Waal & P. L. Tyack (Eds.), *Animal social complexity: Intelligence, culture and individualized societies* (pp. 414–418). Cambridge: Harvard University Press.

Panger, M. A., Brooks, A. S., Richmond, B. G., & Wood, B. (2002). Older than the Oldowan? Rethinking the emergence of hominin tool use. *Evolutionary Anthropology*, *11*(6), 235–245.

Parker, S. T., & Gibson, K. R. (1977). Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *Journal of Human Evolution*, *6*(7), 623–641.

Patterson, E. M., & Mann, J. (2011). The ecological conditions that favor tool use and innovation in wild bottlenose dolphins (*Tursiops sp.*). *PLoS ONE*, *6*(7).

Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., MacKinnon, K. C., … Rose, L. (2003). Social conventions in wild white-faced capuchin monkeys: Evidence for traditions in a Neotropical primate. *Current Anthropology*, *44*(2), 241–268.

Potts, R. (2004). Paleoenvironmental basis of cognitive evolution in great apes. *American Journal of Primatology*, *62*(3), 209–228.

Powell, A., Shennan, S., & Thomas, M. G. (2009). Late pleistocene demography and the appearance of modern human behavior. *Science*, *324*(5932), 1298–1301.

Pradhan, G. R., Tennie, C., & van Schaik, C. P. (2012). Social organization and the evolution of cumulative technology in apes and hominins. *Journal of Human Evolution*, *63*(1), 180–190.

Pruetz, J. D., & Bertolani, P. (2007). Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Current Biology*, *17*(5), 412–417.

Pruetz, J. D., & Lindshield, S. (2012). Plant-food and tool transfer among savanna chimpanzees at Fongoli, Senegal. *Primates*, *53*(2), 133–145.

Reader, S. M., & Biro, D. (2010). Experimental identification of social learning in wild animals. *Learning and Behavior*, *38*(3), 265–283.

Rendell, L., & Whitehead, H. (2001). Culture in whales and dolphins. *Behavioral and Brain Sciences*, *24*(3), 309–324.

Richerson, P. J., Boyd, R., & Henrich, J. (2010). Gene-culture coevolution in the age of genomics. *Proceedings of the National Academy of Sciences*, *107*(Suppl. 2), 8985–8992.

Rutz, C., & St. Clair, J. J. H. (2012). The evolutionary origins and ecological context of tool use in New Caledonian crows. *Behavioural Processes*, *89*(2), 153–165.

Sabater Pí, J. (1974). An elementary industry of the chimpanzees in the Okorobikó mountains, Rio Muni (Republic of Equatorial Guinea), West Africa. *Primates*, *15*(4), 351–364.

Sanz, C., Call, J., & Morgan, D. (2009). Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biology Letters*, *5*(3), 293–296.

Sanz, C., Deblauwe, I., Tagg, N., & Morgan, D. (2014). Insect prey characteristics affecting regional variation in chimpanzee tool use. *Journal of Human Evolution*, *71*, 28–37.

Sanz, C., & Morgan, D. (2007). Chimpanzee tool technology in the Goualougo Triangle, Republic of Congo. *Journal of Human Evolution*, *52*(4), 420–433.

Sanz, C., & Morgan, D. (2009). Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. *International Journal of Primatology*, *30*(3), 411–427.

Sanz, C., & Morgan, D. (2010). The complexity of chimpanzee tool-use behaviors. In E. Lonsdorf, S. R. Ross, & T. Matsuzawa (Eds.), *The mind of the chimpanzee: Ecological and experimental perspectives* (pp. 127–140). University of Chicago Press.

Sanz, C., & Morgan, D. (2013a). Ecological and social correlates of chimpanzee tool use. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630), 20120416.

Sanz, C., & Morgan, D. (2013b). The social context of chimpanzee tool use. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 161–175). Cambridge: Cambridge University Press.

Sanz, C., Morgan, D., & Gulick, S. (2004). New insights into chimpanzees, tools, and termites from the Congo Basin. *The American Naturalist*, *164*(5), 567–581.

Sanz, C., Schöning, C., & Morgan, D. (2010). Chimpanzees prey on army ants with specialized tool set. *American Journal of Primatology*, *72*(1), 17–24.

Schick, K., & Toth, N. (2000). Origin and development of tool-making behavior in Africa and Asia. *Human Evolution*, *15*(1–2), 121–128.

Schick, K., & Toth, N. (2006). An overview of the Oldowan industrial complex: The sites and the nature of their evidence. In N. Toth & K. Schick (Eds.), *The Oldowan: Case studies into the earliest stone age* (pp. 3–42). Stone Age Institute Press.

Schöning, C., Humle, T., Möbius, Y., & McGrew, W. C. (2008). The nature of culture: Technological variation in chimpanzee predation on army ants revisited. *Journal of Human Evolution*, *55*(1), 48–59.

Seed, A., & Byrne, R. (2010). Animal tool-use. *Current Biology*, *20*(23), R1032–R1039.

Semaw, S., Renne, P., Harris, J. W. K., Feibel, C. S., Bernor, R. L., Fesseha, N., & Mowbray, K. (1997). 2 .5-million-year-old stone tools from Gona, Ethiopia. *Nature*, *385*(6614), 333–336.

Semaw, S., Rogers, M. J., Quade, J., Renne, P. R., Butler, R. F., Dominguez-Rodrigo, M., … Simpson, S. W. (2003). 2.6-Million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. *Journal of Human Evolution*, *45*(2), 169–177.

Shumaker, R., Walkup, K., & Beck, B. B. (2011). *Animal tool behavior: The use and manufacture of tools by animals*. The Johns Hopkins University Press.

Silk, J. B., & House, B. R. (2011). Evolutionary foundations of human prosocial sentiments. *Proceedings of the National Academy of Sciences*, *108* (Supplement 2), 10910–10917.

Sirianni, G., Mundry, R., & Boesch, C. (2015). When to choose which tool: Multidimensional and conditional selection of nut-cracking hammers in wild chimpanzees. *Animal Behaviour*, *100*, 152–165.

Smith, & Bentley-Condit, V. (2010). Animal tool use: Current definitions and an updated comprehensive catalog. *Behaviour*, *147*(2), 185–32A.

Spagnoletti, N., Visalberghi, E., Ottoni, E., Izar, P., & Fragaszy, D. (2011). Stone tool use by adult wild bearded capuchin monkeys (*Cebus libidinosus*). Frequency, efficiency and tool selectivity. *Journal of Human Evolution*, *61*(1), 97–107.

St Amant, R., & Horton, T. E. (2008). Revisiting the definition of animal tool use. *Animal Behaviour*, *75*(4), 1199–1208.

St Clair, J. J. H., & Rutz, C. (2013). New Caledonian crows attend to multiple functional properties of complex tools. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630), 20120415.

Stout, D. (2011). Stone toolmaking and the evolution of human culture and cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1567), 1050–1059.

Stout, D., Quade, J., Semaw, S., Rogers, M. J., & Levin, N. E. (2005). Raw material selectivity of the earliest stone toolmakers at Gona, Afar, Ethiopia. *Journal of Human Evolution*, *48*(4), 365–380.

Strindberg, S., Maisels, F., Williamson, E. A., Blake, S., Stokes, E. J., Aba'a, R., … Wilkie, D. S. (2018). Guns, germs, and trees determine density and distribution of gorillas and chimpanzees in Western Equatorial Africa. *Science Advances*, *4*(4), eaar2964.

Sugiyama, Y. (1985). The brush-stick of chimpanzees found in south-west Cameroon and their cultural characteristics. *Primates*, *26*(4), 361–374.

Suzuki, S., Kuroda, S., & Nishihara, T. (1995). Tool-set for termite-fishing by chimpanzees in the Ndoki Forest, Congo. *Behaviour*, *132*(3/4), 219–235.

Tan, A., Tan, S. H., Vyas, D., Malaivijitnond, S., & Gumert, M. D. (2015). There is more than one way to crack an oyster: Identifying variation in burmese long-tailed macaque (*Macaca fascicularis aurea*) stone-tool use. *PLoS ONE*, *10*(5), 1–25.

Taylor, A. H., Hunt, G. R., Medina, F. S., & Gray, R. D. (2009). Do New Caledonian crows solve physical problems through causal reasoning? *Proceedings of the Royal Society B: Biological Sciences*, *276*(1655), 247–254.

Tebbich, S., Taborsky, M., Fessl, B., & Dvorak, M. (2002). The ecology of tool-use in the woodpecker finch (*Cactospiza pallida*). *Ecology Letters*, *5*, 656–664.

Tebbich, S., & Teschke, I. (2013). Why do woodpecker finches use tools? In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 134–158). Cambridge: Cambridge University Press.

Tennie, C., Braun, D., Premo, L. S., & McPherron, S. (2016). The island test for cumulative culture in the Paleolithic. In M. Haidle, N. Conard, & M. Bolus (Eds.), *The nature of culture* (pp. 121–133). Dordrecht: Springer.

Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: On the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1528), 2405–2415.

Tennie, C., Jensen, K., & Call, J. (2016). The nature of prosociality in chimpanzees. *Nature Communications*, *7*, 13915.

Thompson, M. E., & Wrangham, R. W. (2008). Diet and reproductive function in wild female chimpanzees (*Pan troglodytes schweinfurthii*) at Kibale National Park, Uganda. *American Journal of Physical Anthropology*, *135*(2), 171–181.

Thorpe, W. (1956). *Learning and instinct in animals*. London: Methuen.

Tomasello, M. (1999). The human adaptation for culture. *Annual Review of Anthropology*, *28*(1), 509–529.

Tomasello, M., & Call, J. (1997). *Primate cognition*. Oxford University Press.

Toth, N., & Schick, K. (2018). An overview of the cognitive implications of the Oldowan Industrial Complex. *Azania: Archaeological Research in Africa*, *53*(1), 3–39.

Umilta, M. A., Escola, L., Intskirveli, I., Grammont, F., Rochat, M., Caruana, F., … Rizzolatti, G. (2008). When pliers become fingers in the monkey motor system. *Proceedings of the National Academy of Sciences*, *105*(6), 2209–2213.

Vale, G. L., Davis, S. J., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2017). Acquisition of a socially learned tool use sequence in chimpanzees: Implications for cumulative culture. *Evolution and Human Behavior*, *38*(5), 635–644.

van Noordwijk, M. A., & van Schaik, C. P. (2005). Development of ecological competence in Sumatran orangutans. *American Journal of Physical Anthropology*, *127*(1), 79–94.

van Schaik, C. (2002). Fragility of traditions: The disturbance hypothesis for the loss of local traditions in orangutans. *International Journal of Primatology*, *23*(3), 527–538.

van Schaik, C., Fox, E., & Sitompul, A. F. (1996). Manufacture and use of tools in wild Sumatran orangutans: Implications for human evolution. *Naturwissenschaften*, *83*(4), 186–188.

van Schaik, C. P. (2003). Orangutan cultures and the evolution of material culture. *Science*, *299*(5603), 102–105.

Visalberghi, E., & Fragaszy, D. (2013). The etho-cebus project: Stone-tool use by wild capuchin monkeys. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 203–222). Cambridge: Cambridge University Press.

Visalberghi, E., & Limongelli, L. (1994). Lack of comprehension of cause-effect relations in tool-using capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, *108*, 15–22.

Visalberghi, E., Sabbatini, G., Taylor, A., & Hunt, G. (2017). Cognitive insights from tool use in nonhuman animals. In *APA Handbook of comparative psychology, 2* (pp. 673–701).

Visalberghi, E., Sirianni, G., Fragaszy, D., & Boesch, C. (2015). Percussive tool use by Taï Western chimpanzees and Fazenda Boa Vista bearded capuchin monkeys: A comparison. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1682), 20140351.

Vonk, J., Brosnan, S. F., Silk, J. B., Henrich, J., Richardson, A. S., Lambeth, S. P., … Povinelli, D. J. (2008). Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Animal Behaviour*, *75*(5), 1757–1770.

Waldon, J., Miller, B. W., & Miller, C. M. (2011). A model biodiversity monitoring protocol for REDD projects. *Tropical Conservation Science*, *4*(3), 254–260.

Warneken, F., & Tomasello, M. (2009). The roots of human altruism. *British Journal of Psychology*, *100*(3), 455–471.

Whiten, A., Goodall, J., McGrew, W., Nishida, T., Reynolds, V., Sugiyama, Y., … Boesch, C. (1999). Cultures in chimpanzees. *Nature*, *399*(6737), 682–685.

Whiten, A., Goodall, J., McGrew, W., Nishida, T., Reynolds, V., Sugiyama, Y., … Boesch, C. (2001). Charting cultural variation in chimpanzees. *Behaviour*, *138*(11–12), 1481–1516.

Whiten, A., & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: A reappraisal of a century of research. In P. J. B. Slater, J. S. Rosenblatt, C. Beer, & M. Milinki (Eds.), *Advances in the study of behavior* (pp. 239–283). San Diego: Academic Press.

Whiten, A., Horner, V., & de Waal, F. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature*, *437*(7059), 737–740.

Whiten, A., Schick, K., & Toth, N. (2009). The evolution and cultural transmission of percussive technology: Integrating evidence from palaeoanthropology and primatology. *Journal of Human Evolution*, *57*(4), 420–435.

Wilson, M. L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I. C., Hashimoto, C., … Wrangham, R. W. (2014). Lethal aggression in *Pan* is better explained by adaptive strategies than human impacts. *Nature*, *513*(7518), 414–417.

Wood, D. (1989). Social interaction as tutoring. In M. H. Bornstein & J. S. Bruner (Eds.), *Interaction in human development* (pp. 59–80). Hillsdale: Lawrence Erlbaum Associates.

Wynn, T., Hernandez-Aguilar, A., Marchant, L., & Mcgrew, W. (2011). "An ape's view of the Oldowan" revisited. *Evolutionary Anthropology: Issues, News, and Reviews*, *20*(5), 181–197.

Wynn, T., & McGrew, W. (1989). An ape 's view of the Oldowan. *Man*, *24*(3), 383–398.

Yamakoshi, G. (1998). Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use. *American Journal of Physical Anthropology*, *106*(3), 283–295.

Yamamoto, S., Humle, T., & Tanaka, M. (2009). Chimpanzees help each other upon request. *PLoS ONE*, *4*(10), e7416.

Yamamoto, S., Humle, T., & Tanaka, M. (2012). Chimpanzees' flexible targeted helping based on an understanding of conspecifics' goals. *Proceedings of the National Academy of Sciences*, *109*(9), 3588–3592.

Zaidner, Y. (2013). Adaptive flexibility of Oldowan hominins: Secondary use of flakes at Bizat Ruhama, Israel. *PLoS ONE*, *8*(6), e66851.

Chapter 2: The Ontogeny of Termite Gathering among Chimpanzees in the Goualougo Triangle, Republic of Congo

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2.1 Abstract

Much of the diverse, flexible tool repertoire of wild chimpanzees is directed toward gathering otherwise inaccessible food resources. Acquiring these tool skills can potentially improve dietary quality and increase fitness. In contrast to the use of a single tool type by chimpanzee populations in East and West Africa, chimpanzees in the Congo Basin use tool sets comprising multiple tool types to gather termites from above-ground and subterranean nests. They also modify herb stems to produce brush-tipped fishing probes. We investigated the acquisition of these termite-gathering skills by chimpanzees of the Goualougo Triangle, Republic of Congo, and compared it to the development of termite fishing for chimpanzees at Gombe, Tanzania. We predicted that chimpanzees would acquire simple tool behaviors and single tool use before more complex actions and sequential use of multiple tool types. Using a longitudinal approach, we documented the acquisition of termite-gathering critical elements for 25 immature chimpanzees at Goualougo. At Gombe, chimpanzees make fishing probes between ages 1.5-3.5, before or during the time they begin termite fishing. At Goualougo, all chimpanzees termite fished by 2.9 years but did not manufacture brush-tipped fishing probes until an average of 4.3 years. In contrast to Gombe, where all individuals acquire the termite-gathering task by age 5.5, at Goualougo the acquisition of tool sets extends further into juvenility and subadulthood. While we did not detect significant sex differences, most critical elements except tool manufacture were acquired slightly earlier by females. Differences between sites could reflect tool material selectivity and design complexity, the challenge of sequential tool behaviors, and strength

requirements of puncturing subterranean termite nests at Goualougo. These results expand our understanding of how task complexity influences the timing and sequence of skill acquisition, improving models of the ontogeny of tool behavior among early hominins who likely used complex, perishable technologies.

2.2 Introduction

Tool use has been documented in a range of animal species, but it is relatively rare. The habitual and flexible use of tools is most prevalent within the Primate and Passeriformes orders; among nonhuman primates, it occurs in all wild chimpanzee populations, and some populations of orangutans, macaques, and capuchins (Smith & Bentley-Condit, 2010; Shumaker, Walkup, & Beck, 2011). Multiple factors such as the assimilation of sensorimotor knowledge, the development of mechanical reasoning ability, and social and ecological influences intersect to support the emergence of tool skills. Studies into the ontogeny of tool behavior can help illuminate potential reasons for differences in tool behavior between and within taxa and add to our understanding of the adaptive basis for tool skills (Meulman, Seed, & Mann, 2013).

Perception-action theory (Lockman, 2000) posits that early exploratory actions with objects scaffold the maturation of tool behaviors. This theory predicts that over the course of development, simple actions involving single objects will precede combinatory actions involving multiple objects, or an object and a surface, and that an individual’s manipulative actions will become increasingly effective over time as individuals acquire experience with object properties. The specific tool behaviors that emerge across species may in part reflect phylogenetic biases for particular types of object manipulation. For example, from an early age, human and capuchin infants bang objects against substrates (Fragaszy & Adams-Curtis, 1991; Kahrs & Lockman, 2014), and these behaviors are later refined into percussive tool use for humans and some populations of capuchins (Resende, Ottoni, & Fragaszy, 2008). Stone handling emerges during infancy in several populations of macaques, which may scaffold the development of stone tool use under certain conditions (Tan, 2017). Chimpanzees are highly motivated to insert objects into holes or hollows (Hayashi & Matsuzawa, 2003), and stick tool use is prevalent across many wild chimpanzee populations (McGrew, 1992; Sanz & Morgan, 2007).

The development of mechanical reasoning skills may also be necessary for the acquisition of tool skills, particularly for complex tool tasks involving the flexible use of tools. Flexible tool use is characterized by the ability to use tools across contexts, to attribute multiple functions to a single tool, and to combine tools creatively (Call, 2013). Flexible tool users can adjust their behavior as needed during a tool-using sequence by including, repeating, or excluding actions in order to achieve a goal (Byrne, Sanz, & Morgan, 2013). Complex tool behaviors are also defined by the presence of cumulative elements, such as the use of multiple different objects concurrently or in sequence (Pradhan, Tennie, & van Schaik, 2012). Using two tools concurrently requires managing multiple, dynamic relations among objects (Visalberghi & Fragaszy, 2006). In addition, task components must be integrated into the correct order. Young capuchins and chimpanzees may be capable of picking up a nut, placing a nut on the anvil, holding the hammer stone, hitting a nut, picking up a kernel, and consuming it, but combining these actions to successfully crack nuts does not occur until after individual elements are mastered. This mastery occurs after age two for capuchins (Resende, Ottoni, & Fragaszy, 2008), and between ages three and four for chimpanzees at Bossou, Guinea, (Matsuzawa, 1994) and Taï Forest, Côte d’Ivoire (Boesch & Boesch-Achermann, 2000). In Loango, Gabon, chimpanzees use highly flexible action sequences to extract honey from underground nests (Estienne, Stephens, & Boesch, 2017), and immatures do not exhibit the complete, adult behavioral repertoire until age six or older (Estienne, Robira, Mundry, Deschner, & Boesch, 2019) (Table 2.1). The use of multiple tool types in sequence poses additional demands in that it requires a tool user to manage different causal relationships among objects in a specific order, often with a time delay between identifying a goal and achieving success (Boesch, 2013). In captive experiments with chimpanzees, sequential tasks are typically acquired after age three; at this age, chimpanzees may become more capable of socially learning sequential behaviors (Marshall-Pescini & Whiten, 2008).

TABLE 2.1 Developmental studies of different tool tasks observed in wild nonhuman primates

Taxon	Study Site	Task	Acquisition Age^a (yrs.)	Sample Size Male:Female
Chimpanzees	Bossou, Guinea	Leaf to drink water[1]	> 1.5	5:3
	Bossou, Guinea	Ant dip[2]	2-3	6:7^b
	Bossou, Guinea	Nut crack[1,3]	> 3.5	1:2
	Taï, Ivory Coast	Nut crack[4]	5-6	23:30^b
	Loango, Gabon	Honey extract[5]	≥6	10:6
	Gombe, Tanzania	Termite fish[6]	5.5	5:3^b
	Goualougo, Rep. Congo	Termite fish[7]	2.9	10:15^b
	Goualougo, Rep. Congo	Perforate + Fish[7]	10.5	4:3
Orangutans	Suaq Balimbing, Sumatra	Tree hole probe[8]	5	1:0
	Suaq Balimbing, Sumatra	*Neesia* seed extract[8]	9	2:3
Macaques	Koram Island, Thailand	Shellfish crack[9]	2.5-3.5	37:32^b
Capuchins	Fazenda Boa Vista, Brazil	Nut crack[10]	< 5	7:9^b
	Tietê Ecological Park, Brazil	Nut crack[11]	> 2	2:0

[1]Biro, Sousa, & Matsuzawa, 2006; [2]Humle, Snowdon, & Matsuzawa, 2009; [3]Inoue-Nakamura & Matsuzawa, 1997; [4]Boesch & Boesch-Achermann, 2000; [5]Estienne et al., 2019; [6]Lonsdorf, 2006; [7]This study; [8]Meulman, 2014; [9]Tan, 2017; [10]Eshchar, Izar, Visalberghi, Resende, & Fragaszy, 2016;[11]Resende et al., 2008.

a. Values are the age or age range by which most individuals acquire basic competency. b. Sample sizes reflect the entire data set; ages of acquisition are derived from a subset of these individuals for whom acquisition was documented.

Chimpanzees exhibit substantial intraspecific diversity in tool-assisted foraging behaviors, including the resources gathered and techniques used (McGrew, 1992; Sanz & Morgan, 2007; Whiten et al., 2001). Across their geographic range, chimpanzees use a variety of tool types to gather insects and insect products (McGrew, 2014). Termites and other social insects offer particular nutritional payoff because of their high collective biomass (Deblauwe &

Janssens, 2008), and termite fishing has been documented in multiple populations (Bogart & Pruetz, 2008; Goodall, 1986; McGrew & Collins, 1985; McGrew, Tutin, & Baldwin, 1979; Nishida & Uehara, 1980; Sanz, Morgan, & Gulick, 2004). In East and West Africa, chimpanzees use a single tool type, a fishing probe, to gather termites. These tools are manufactured from a range of materials such as grass, twigs, vines, bark, or palm fronds (Goodall, 1968; McGrew et al., 1979).

In Central Africa, in contrast, chimpanzees gather invertebrate resources with the use of tool sets (Bermejo & Illera, 1999; Boesch, Head, & Robbins, 2009; Deblauwe, Guislain, Dupain, & Van Elsacker, 2006; Fay & Carroll, 1994; Muroyama, 1991; Sabater Pí, 1974; Sanz, Schöning, & Morgan, 2010; Sanz et al., 2004; Sugiyama, 1985; Suzuki, Kuroda, & Nishihara, 1995). A tool set is defined as the use of two or more types of tools sequentially to achieve a goal (Brewer & McGrew, 1990). In the termite-gathering context, chimpanzees in this region use two tool sets to gather termites of the genus *Macrotermes* from epigeal (above-ground) and subterranean nests. The use and manufacture of these different tool types has been observed across different chimpanzee communities living in the Goualougo Triangle, Republic of Congo (Sanz & Morgan, 2007; Sanz et al., 2004). At epigeal nests, chimpanzees first use their fingers or a perforating twig to open sealed termite exit holes on the nest surface before using an herbaceous probe, the end of which chimpanzees have modified to a brush tip, to termite fish. In the subterranean nest setting, termites reside in underground chambers at an average depth of 50.6 cm from the nest surface (Sanz, Deblauwe, Tagg, & Morgan, 2014), and chimpanzees use a durable, woody puncturing stick to tunnel into these chambers before using a fishing probe to extract termites (Sanz et al., 2004). These chimpanzees are highly selective in plant species chosen to manufacture both puncturing sticks and fishing probes, and this is not an artifact of plant species abundance. Ninety-eight percent of puncturing sticks are manufactured from *Thomandersia hensii*, which has straight, rigid, and durable branches. Ninety-six percent of fishing probes are manufactured from *Sarcophyrnium* spp., which is smooth, pliable, and of ideal length and diameter for use as a probe; in addition, its fibers can be effectively frayed to a brush tip (Sanz & Morgan, 2007). The production of brush tips onto the herb stems is an intentional modification that improves the efficiency of the tool at gathering insects (Sanz, Call, & Morgan, 2009). The complex tool behaviors of chimpanzees in this region comprise some of the clearest evidence for cumulative technology in animals (Sanz et al., 2009), so examining how they are acquired offers unique comparative insights for understanding the emergence of cumulative culture during human evolution.

To master the termite-gathering task, young chimpanzees must acquire each of the components of tool manufacture and tool use and integrate them into the correct sequence. “Critical elements” are the individual, component steps that are necessary to extract termites and that characterize the adult form of this behavior (Lonsdorf, 2005). These steps differ between populations and between tasks depending on whether termite gathering involves fishing for termites with a single tool type versus using a perforating or a puncturing tool set (Fig. 2.1). For infants, manipulation of tools is another important critical element of tool skill acquisition. Developmentally, critical elements are acquired in the following order for all Gombe chimpanzees: identify a hole; manipulate tool; make a tool; insert a tool into the hole; and successfully extract termites. All individuals make tools in the same year, or in the year prior to when they first insert tools (Lonsdorf, 2005).

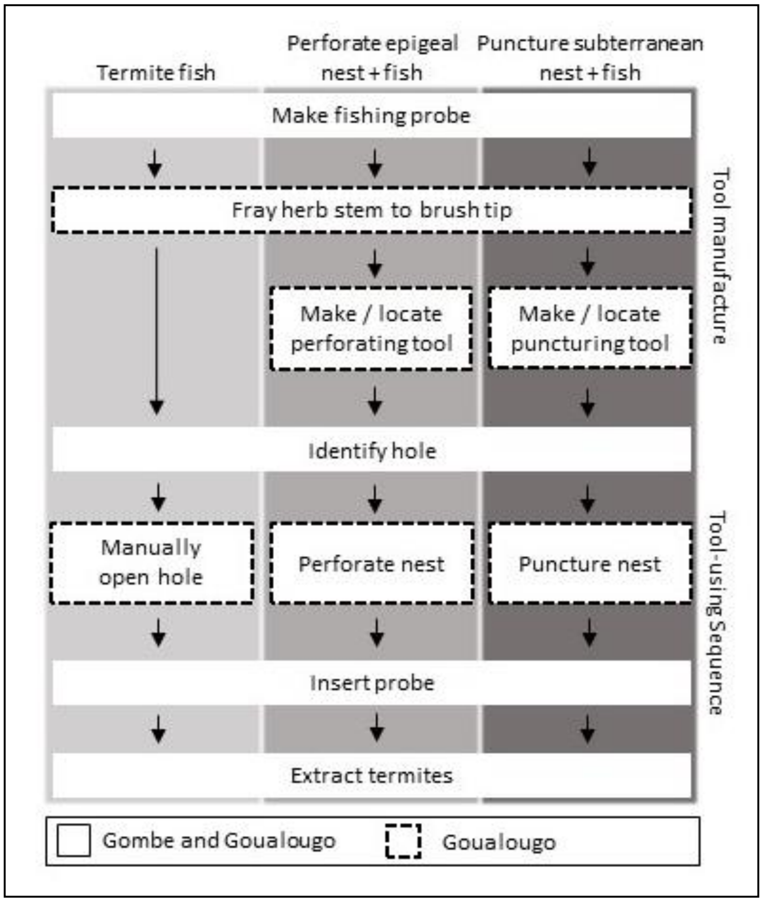

FIGURE 2.1 Termite-gathering critical elements**.** Elements are listed from top to bottom according to the typical sequence of tool manufacture and tool use. At both sites, identifying termite exit holes sometimes precedes tool manufacture, though at Goualougo chimpanzees often gather tools in advance of arriving at termite nests. Termite fishing occurs at both Goualougo and Gombe, while perforating and puncturing occur only at Goualougo.

Females at Gombe learned to termite fish at a mean age of 31±4 months, an average of 27 months earlier than males, who learned at a mean age of 58±6 months (Lonsdorf, Eberly, & Pusey, 2004). Females spent more time watching their mothers termite fish and were more likely to insert tools to similar depths as their mothers, suggesting that they relied more on imitative learning than did males (Lonsdorf, 2005). The socio-ecological model predicts that females will engage in behavior that maximizes food intake, and several studies have shown that among chimpanzees, adult females compared to adult males use tools more often to acquire termites (Goodall, 1986; McGrew, 1979), nuts (Boesch & Boesch, 1984) and vertebrates (Pruetz &

Bertolani, 2007). Tool use among captive bonobos is also female-biased (Boose, White, & Meinelt, 2013; Gruber, Clay, & Zuberbühler, 2010; but see Herrmann, Hare, Call, & Tomasello, 2010). No sex differences were detected for ant dipping at Bossou, however, for immatures or adults (Humle et al., 2009). Among macaques and capuchins, no sex differences have been reported in the acquisition of tool skills, but there are sex differences in adult tool use (Gumert, Hoong, & Malaivijitnond, 2011; Moura & Lee, 2010; Spagnoletti, Visalberghi, Ottoni, Izar, & Fragaszy, 2011). Long-tail macaque females use stone tools more often than males, and specialize slightly more on attached oysters, which could reflect female preference for a lower-risk foraging strategy. Males use larger tools than females, however, and are more successful than females at opening unattached shelled items such as snails or crabs (Gumert et al., 2011). In capuchins, where both sexes use hammers of comparable sizes, males compared to females use tools more often, and males more frequently use tools to crack high resistance nuts (Moura & Lee, 2010; Spagnoletti et al., 2011). For both macaques and capuchins, some of these observed sex differences are attributable to body size dimorphism, as percussive tool use is likely more energetically demanding for smaller-bodied females (Gumert et al., 2011; Spagnoletti et al., 2011; Visalberghi & Fragaszy, 2013). Outside of primates, sex differences have been reported for the practice of sponging for fish among dolphins. This behavior is strongly female-biased, and even though male offspring are equally exposed to the behavior, females adopt it preferentially. This could be because spongers tend to adopt more restricted ranges, and males prefer to range more broadly post weaning (Mann et al., 2008). By documenting when and how sex differences emerge, developmental studies of skill acquisition can help identify the contribution of ecological, morphological, and social factors that may contribute to the variable pattern of sex differences observed across tool-using taxa.

In the present study, we investigated how wild chimpanzees acquire a complex tool task involving the sequential use of different tool types, selectivity for raw materials, and tool design modifications. Using a longitudinal approach, we examined the age and sequence in which chimpanzees at Goualougo acquired critical elements of termite gathering. We predicted that chimpanzees would first perform simple manipulations of tools before manipulating tools in combination with the termite mound. We also predicted that chimpanzees would learn tool use before brush-tipped probe manufacture, due to the raw material selectivity and design complexity involved in probe manufacture. We further predicted that use of single tools would precede use of tool sets, and that puncturing tool use would be acquired last due to the physical difficulty of puncturing subterranean termite nests. We also examined whether there were sex differences in the acquisition of termite fishing. Finally, we compared the development of termite gathering among chimpanzees at Goualougo to those at Gombe.

2.3 Methods

2.3.1 Study Site and Subjects

Observations of chimpanzee were carried out in the Goualougo Triangle, which is located along the southern boundary of the Nouabalé-Ndoki National Park (N 2°05− 3°03; E 16°51−16°56) in the Republic of Congo. The study region encompasses 380 km^2 of evergreen and semi-deciduous lowland forest, with altitudes ranging between 330 and 600 meters. There is a primary rainy season from August to November and a short rainy season in May. Subjects included 25 immature chimpanzees of known birthdate (15 females, 10 males).

2.3.2 Data Collection

We placed remote video cameras with passive infrared sensors at termite nests to record chimpanzee visitation and tool-using behaviors (Sanz et al., 2004). All video footage was archived on hard drives and scored using INTERACT (Mangold, 2015). Approximately 662 hours of footage of chimpanzee visitation to termite nests collected between 2003-2018 were screened for the presence of focal chimpanzees. All footage of focal individuals was then screened and coded for the first observed occurrences of critical elements of termite gathering (Table 2.2) adapted for this study from Lonsdorf (2005) and Sanz & Morgan (2011). In addition to coding for the critical elements characterizing the adult form of these tasks, we also screened for first occurrences of “Manipulate fishing probe” and “Mound plus tool”, which aid in indexing the acquisition of tool competence. Remote cameras record the dates of observation, enabling calculation of the ages at which behaviors were first observed.

In order for an observation to be included in the data set, the focal individual must have been observed visiting a termite nest and have had the opportunity to engage in tool use at least once in the nine-month period prior to the visit in which they were first observed engaging in the behavior of interest. This ensured that individuals’ behaviors were detected with comparable precision to Gombe, where data were collected over four years during three-month termite-fishing seasons and individuals could have acquired skills in the nine-month period between field seasons. Differing sample sizes between elements reflect these selection criteria. Within-subjects analyses comparing acquisition of multiple elements included the subset of subjects for whom both of the relevant critical elements were observed in accordance with these criteria. For example, 12/25 subjects could be included for the within-subjects comparison of acquisition ages for manipulation of a fishing probe versus use of a fishing probe in combination with a termite mound.

TABLE 2.2 Critical elements of termite gathering

Critical Element	**Definition**
Identify hole*	Probes with finger, mops, sniffs, or looks into termite exit hole on nest.
Manually open termite exit hole*	Attempts to open termite exit hole by picking at soil with fingers.
Manipulate fishing probe*	Possesses tool with any body part and may hold, carry, or play with tool.
Mound plus tool*	Actively contacts termite nest with probe but does not insert tool.
Insert fishing probe*	Inserts probe into hole on surface of the termite nest.
Straighten brush fibers	Pulls tool through mouth, hands or fingers to straighten brush fibers.
Extract termites*	Acquires termites as a result of inserting fishing probe a minimum of three times during the same visit to a nest.
Fray end of tool to brush	Uses teeth or hand to fray the end of tool into a brush.
Manufacture brush-tipped fishing probe	Detaches raw material; uses teeth or hands to fray the end of the tool; and inserts or attempts to insert tool into termite nest.
Perforate epigeal nest	Presses the tip of a woody twig tool into the sealed tunnels of a termite nest, often rotating wrist to drill the tip into the nest.
Tool set: perforate + fish	Perforates termite nest, then inserts and extracts fishing probe.
Puncture subterranean nest	Pushes woody puncturing stick through the ground into a subterranean termite nest and successfully creates a new fishing tunnel.
Tool set: puncture + fish	Punctures subterranean termite nest, then inserts and extracts fishing probe.

* indicates that elements are also observed at Gombe

2.3.3 Analysis

We first examined whether the ages at which individuals first learned to insert probes and to extract termites were comparable between epigeal and subterranean nest types. We assessed a subset of individuals observed between both epigeal and subterranean settings during early infancy, using paired t-tests to compare their ages of acquisition of the critical elements “Insert fishing probe” and “Extract termites” in the epigeal versus subterranean settings. These two elements in particular were assessed because structural differences between nest types could place difference technical demands on the tool user.

To test our prediction that simple actions would precede combinatory manipulations, we compared ages at which chimpanzees exhibited the critical elements “Manipulate fishing probe” and “Mound plus tool”. To assess whether tool use would precede the manufacture of brush-tipped probes, we compared the ages of acquisition of “Extract termites” and “Manufacture brush-tipped fishing probe”. These tests were within-subjects and so we conducted paired T-tests or a Wilcoxon signed-rank test if the data were not normally distributed. We report descriptive statistics comparing the ages of acquisition of “Extract termites” to “Tool set: perforate + fish” to evaluate whether use of single tools would precede use of multiple tools.

To test for sex differences in the acquisition of termite fishing skills, we compared females and males with respect to ages of acquisition of “Extract termites” and “Manufacture brush-tipped fishing probe” using independent-samples t-tests.

Prior to conducting analyses, we visually inspected raw data and used Shapiro-Wilk tests to determine whether data were normally distributed. All tests were two-tailed and the significance threshold was set at .05. Analyses were conducted in R (version 3.4.4) (R Core Team, 2018).

2.4 Results

2.4.1 Comparison of Epigeal and Subterranean Nest Settings

We did not detect significant differences in the age at which chimpanzees learned to insert fishing probes in epigeal (*M*=2.2±0.7 years) versus subterranean (*M*=1.9±0.4 years) nest contexts (paired t-test, *t*(6)=1.05, *N*=7, *P*=0.33, 95% CI [-0.3, 0.7]. We also did not detect significant differences in the ages at which immature chimpanzees were successful extracting termites in epigeal (*M*=2.6±0.7 years) versus subterranean (*M*=2.3±0.7 years) nest contexts (paired t-test, *t*(4)=0.66, *N*=5, *P*=0.55, 95% CI [-0.9, 1.5]). However, for both elements, ages of acquisition were slightly earlier in the subterranean setting. We present subsequent results from both epigeal and subterranean contexts together but discuss the implications of this variation in the Discussion.

2.4.2 Simple versus Combinatory Actions

The majority of individuals (9/12) were observed manipulating tools at earlier visits than they were observed using a tool in combination with the mound, while three individuals were first observed manipulating a tool and using it in conjunction with the mound during the same visit. There was a significant difference in the age at which chimpanzees first began manipulating fishing probes (*M*=1.2±0.5 years) and the age at which they first used a fishing probe in combination with a termite mound (*M*=1.6±0.4 years) (paired t-test: *t*(11)=-4.01, *N*=12, *P*=0.002, 95% CI [-0.6, -0.2]).

2.4.3 Tool Use versus Tool Manufacture

All infants successfully fished for termites by age 2.9 (Table 2.3). At this age, infants typically used discarded tools, or they received tools from conspecifics. Most chimpanzees (10/12 infants) inserted fishing probes and also succeeded at acquiring termites (9/12 infants) before they detached any type of raw material themselves and attempted to use those materials as a tool. Three individuals were observed detaching leafy or twiggy material near the nest to fish, but they were not successful with these tools.

All individuals were observed successfully fishing for termites before they were observed independently gathering the specific herbaceous raw material adults typically select for this task and manufacturing brush-tipped fishing probes. Manufacture of brush-tipped fishing probes was first observed in chimpanzees of an average age of 4.3±1.1 years (*N*=10). There was a significant difference in the age of first successfully extracting termites (*M*=2.3±0.5 years) and brush-tipped probe manufacture (*M*=4±1 year) (Wilcoxon signed-rank test: *V*=36, *N*=8, *P*=0.008; 95% CI [1.1, 2.6]).

2.4.4 Use of Single versus Multiple tools

Eight individuals were observed using perforating tools at epigeal nests. The youngest individual was a female at 3.9 years old, while other chimpanzees were observed using perforating tools for the first time between ages four and 11. All individuals began using fishing probes and were successful extracting termites before first using a perforating tool set (the perforating twig plus the fishing probe in sequence). Relative to the similarity in ages at which fishing probe insertion and extraction of termites were first observed, the age at which individuals were first observed perforating was more variable between individuals (Fig. 2.2). One individual was also observed using his probe not only to fish but also to perforate. This involved reversing his fishing probe and using the unmodified end to clear a fishing tunnel, a behavior which has been observed among multiple individuals in this population (Sanz & Morgan, 2011). This was observed during the same visit where he was first observed using a perforating tool set, at age 10.5 years.

In the subterranean termite nest setting, infant and juvenile chimpanzees frequently manipulated puncturing sticks, inserted these tools into existing or partially cleared tunnels created by older conspecifics, and attempted to puncture new holes into subterranean nests. We observed five individuals (four females, one male) exhibit the sequence of puncturing tool set use (M=3.7±1.6 years). This involved inserting a puncturing tool into an existing hole and then fishing or attempting to fish from the tunnel with a fishing probe. All of these individuals were observed inserting fishing probes at earlier visits than they were observed engaging in the sequence of puncturing tool set use. Only two subadult individuals (one male, 11.7 years, and one female, 11 years) were observed successfully puncturing a new hole into a subterranean termite nest.

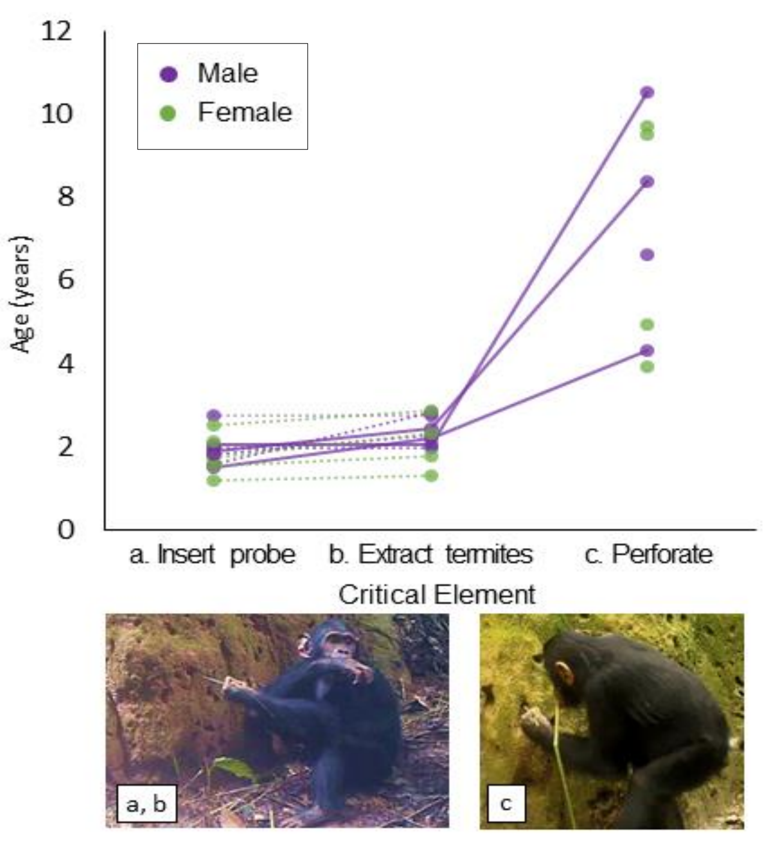

FIGURE 2.2. Variation in age of exhibiting perforating tool use. Dots represent individuals. Dotted lines connect observations for immature chimpanzees observed for both "Insert probe" and "Extract termites"; solid lines connect observations for three individuals for whom we could document ages for these elements as well as for the age at which they first exhibited perforating tool use. While all three of these individuals could extract termites by age 2.4, the ages at which they were first observed perforating (4.3, 8.4, and 10.5 years) varied widely. At left, a juvenile male inserts a fishing probe (a) and feeds on termites he has swept from the fishing probe after a successful extraction (b). At right (c), he uses a twig to perforate an epigeal nest, while holding a fishing probe in his mouth.

2.4.5 Sex Differences in Termite Gathering

The developmental trajectories of termite gathering were similar for female and male chimpanzees at Goualougo (Table 2.3; Fig. 2.3). We did not detect a significant difference in the age at which females (*M*=2.1±0.7 years, *N*=4) versus males (*M*=2.4±0.3 years, *N*=7) learned to extract termites (independent samples t-test: *t*(9)=-1.01, *P*=0.34; 95 % CI [-1.0, 0.4]). We also did not detect a significant difference between the ages at which females (*M*=4.6±1.5 years, *N*=4) versus males (*M*=4.1±0.8, *N*=6) first manufactured a brush-tipped probe (independent samples t-test: *t*(8)=0.67, *P*=0.52; 95% CI [-1.2, 2.2]). Females did acquire most critical elements, including the ability to fish, slightly before males on average (≈3.6 months earlier); the exception was tool manufacture, which males showed ≈6 months earlier (Fig. 2.4). The ages at which females and males first used tool sets were comparable and showed similar ranges (Table 2.3).

TABLE 2.3 Mean age of acquisition of critical elements for males and females at Goualougo

Critical Element	Female	Male
Termite Fishing		
Identify hole	0.8 (0.4 - 1.3), n=7	1.0 (0.6 - 1.7), n=5
Manipulate fishing probe	1.2 (0.3 - 1.7), n=7	1.2 (0.5 - 2.1), n=5
Manually open termite exit hole	1.3 (0.6 - 2.1), n=7	1.8 (0.8 - 2.5), n=8
Mound plus tool	1.6 (1.0 - 2.3), n=8	1.8 (1.0 - 2.7), n=8
Insert fishing probe	1.8 (1.2 - 2.5), n=5	1.9 (1.5 - 2.7), n=8
Straighten brush fibers	1.9 (1.2 - 2.3), n=5	2.1 (1.7 - 3.0), n=7
Extract termites	2.1 (1.3 - 2.9), n=4	2.4 (2.0 - 2.8), n=7
Fray end of tool to brush	3.4 (1.4 - 4.8), n=8	3.7 (2.4 - 4.7), n=7
Manufacture a brush-tipped fishing probe	4.6 (2.5 - 5.8), n=4	4.1 (3.3 - 5.5), n=6
Perforating at Epigeal Termite Nests		
Perforate	7.0 (3.9 - 9.7), n=4	7.5 (4.3 - 10.5), n=4
Tool set: perforate + fish	7.1 (3.9 - 9.8), n=4	9.0 (7.6 - 10.5), n=3
Puncturing at Subterranean Termite Nests		
Puncture	11.0, n=1	11.7, n=1
Tool set: puncture and fish	11.0, n=1	11.7, n=1

Values are the mean age of acquisition for the critical element. Age ranges of the earliest and latest appearances of the behaviors are listed in parentheses, followed by sample size of individuals (n).

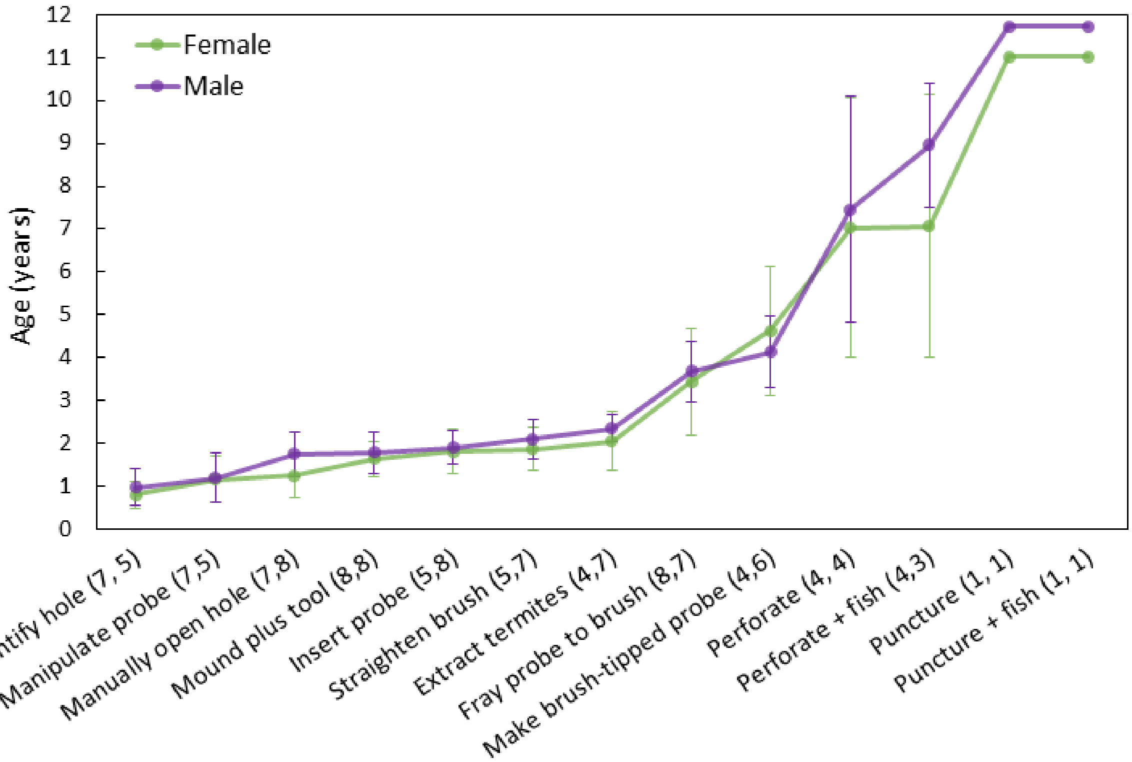

FIGURE 2.3. Ages of acquisition of critical elements for chimpanzees at Goualougo. Values are means and error bars represent standard deviation. Sample sizes are given for each sex in parentheses (female, male). Females and males acquired critical elements at comparable ages, though females acquired all critical elements except "Make brush-tipped fishing probe" before males. Compared to acquisition ages for single tool use, ages at which the use of tool sets were first observed were more variable.

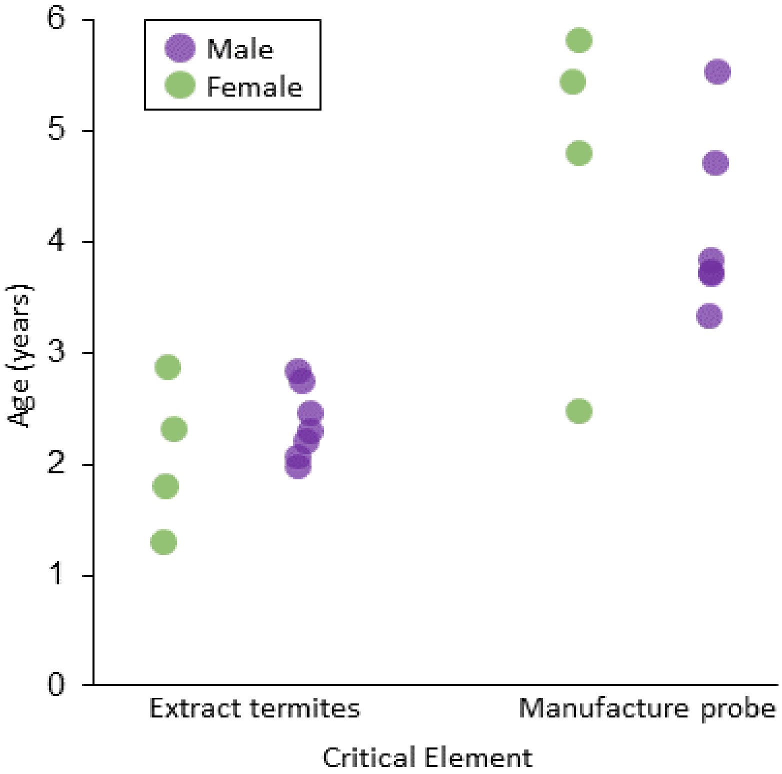

FIGURE 2.4. Ages of successful termite extraction versus tool manufacture for females and males. Dots represent individuals. The ages ranges for acquisition of both elements overlapped for males and females, though for both elements, the youngest observation was for a female. We observed that on average, females were observed successfully extracting termites at slightly younger ages than males, while males were observed making tools at younger ages than were females.

2.4.6 Development of Termite Gathering at Goualougo Compared to Gombe

Most infant chimpanzees at both Goualougo and Gombe begin interacting with tools and termite mounds within the first one to two years of life. There are differences, however, with respect to the timeframe in which infants first insert fishing probes, become capable of termite fishing, and independently manufacture tools (Table 2.4). In addition, the developmental period over which skills are acquired is longer at Goualougo. At Gombe, all individuals mastered the critical elements necessary for termite fishing by age 5.5. At Goualougo, individuals learned to termite fish during infancy, but several individuals were not observed perforating until they were juveniles or subadults. Only subadults were observed independently puncturing new tunnels into subterranean nests.

Table 2.4 Maximum ages of acquisition of termite-gathering critical elements in the Goualougo Triangle and at Gombe, Tanzania.

Critical Element	Goualougo	Gombe
Termite Fishing		
Identify hole	1.7 (0.4 - 1.7), n=12	1.5 (0.5 - 1.5), n=8
Manipulate fishing probe	2.1 (0.3 - 2.1), n=12	1.5; n=8
Insert fishing probe	2.7 (1.2 - 2.7), n=13	4.5 (2.5 - 4.5), n=8
Extract termites	2.9 (1.3 - 2.9), n=11	5.5 (2.5 - 5.5), n=6
Manufacture fishing probe without brush tip	3.0 (1.2 - 3.0), n=6	3.5 (1.5 - 3.5), n=6
Manufacture brush-tipped fishing probe	5.8 (2.5 - 5.8), n=10	-
Perforating at Epigeal Termite Nests		
Perforate	10.5 (3.9 - 10.5), n=8	-
Tool set: perforate + fish	10.5 (3.9 - 10.5), n=7	-
Puncturing at Subterranean Termite Nests		
Puncture	11.7 (11 - 11.7), n=2	-
Tool set: puncture and fish	11.7 (11 - 11.7), n=2	-

Values are the age in years by which all individuals in the sample acquired the critical element. Age ranges of the earliest and latest appearances of the behaviors are listed in parentheses, followed by sample size of individuals (n). "-" indicates that the behavior does not occur at Gombe.

2.5 Discussion

Tool-assisted foraging traditions may emerge when they are profitable relative to other feeding strategies (Rutz & St. Clair, 2012; Sanz & Morgan, 2013a), so learning these behaviors could have important adaptive benefits. Examining how novices acquire tool skills can provide insight into the perceptuo-motor and cognitive requisites of these skills as well the way ecological factors, social input, and task characteristics affect acquisition. In this study, we took a longitudinal approach to investigate the acquisition of termite-gathering critical elements among Goualougo Triangle chimpanzees. We found that these chimpanzees learn to termite fish before they manufacture brush-tipped probes and that they become competent with single tools before they use multiple tool types sequentially. We also documented differences in the developmental trajectory of termite gathering at Goualougo compared to Gombe. The sequence of skill acquisition, as well as the ages at which particular elements were acquired, differed between populations. In addition, in contrast to Gombe, we did not detect sex differences of a large magnitude in the ages at which chimpanzees at Goualougo learned to termite fish.

The onset of manipulative behaviors and tool use among chimpanzees at Goualougo is consistent with predictions of perception-action theory (Lockman, 2000), which anticipates that simpler behaviors and single tool use will be acquired before more complex sequences. Within the first year of life, most chimpanzees manipulated objects and investigated termite mounds. Between ages one and three, they progressed to goal-directed efforts to fish for termites, which involved locating a tool, manually opening a termite exit hole or using an exit hole opened by another chimpanzee, inserting a fishing probe, and successfully extracting termites. We did observe that probe insertion and fishing occurred at slightly earlier ages on average in the subterranean setting, and in future research we will examine whether there are differences in the specific skilled motor actions associated with the two nest types. For example, there could be subtle differences in the difficult of aligning a probe to a fishing tunnel in the epigeal versus subterranean setting. Nonetheless, once chimpanzees learned to use fishing probes in either the epigeal or subterranean context, they transferred their skills to the other setting. This ability to generalize skills from one context to another is a hallmark of flexible tool behavior. After becoming competent with single tools and learning to termite fish, chimpanzees then began manufacturing their own tools. Some individuals also began engaging in sequential tool use, involving a perforating twig plus a fishing probe in the epigeal context, and a puncturing stick plus a fishing probe in the subterranean context.

Our findings were also generally consistent with prior research from wild and captive settings that chimpanzees typically learn sequential behaviors after three years of age (Marshall-Pescini & Whiten, 2008). As with use of tool sets, the behavioral sequence associated with manufacture and use of brush-tipped fishing probes occurred on average after three years of age, and the component actions were acquired before they were combined into the correct order. Integration of actions into the correct sequence is hypothesized to be linked to the capacity for program-level imitation (Hayashi & Inoue-Nakamura, 2011; Marshall-Pescini & Whiten, 2008). This process involves an individual perceiving the hierarchical organization of a task that emerges from statistical regularities in a model's behavior and parsing that behavior into meaningful units, enabling reproduction of the structure of the behavior (Byrne, 1994; Byrne & Russon, 1998). It has also been hypothesized that there is a critical period during development for acquiring hierarchically structured, sequential behaviors, after which such acquisition cannot occur (Biro et al., 2003). While we documented general patterns in the acquisition of sequential behaviors after age three, there were two infants who exhibited the use of a puncturing stick and a fishing probe in sequence before age three. Additionally, only some individuals used perforating tool sets. Increased opportunity to practice tool-using skills and increased observation of conspecifics is associated with accelerated skill acquisition of termite fishing (Lonsdorf, 2006) and ant-dipping (Humle et al., 2009). Further research is required to identify how differing opportunity for social learning may contribute to inter-individual variation in the acquisition of complex, sequential skills at Goualougo.

As we predicted, puncturing subterranean nests was observed latest in development, though we did observe several infants and juveniles carry out the sequence of puncturing and fishing tool use. In addition to cognitive factors, physical strength and body size are important constraints on the use of puncturing tool sets. Subadult and adult chimpanzees often grip puncturing sticks with their hands and a foot, using the weight of their bodies to forcefully push puncturing sticks down through the ground. Despite repeated attempts, infants and juveniles were unable to create new fishing tunnels, as they could not push the puncturing stick through the soil. Nonetheless, young chimpanzees do attempt to puncture throughout the infant and juvenile period, sometimes focusing their efforts on existing or partially cleared tunnels that have been created by other chimpanzees. We are presently examining what contributes to the persistent efforts of young chimpanzees in this context.

We observed that both the timing and sequence of termite-gathering skill acquisition differed between Goualougo and Gombe chimpanzees. At Goualougo, infants inserted fishing probes and learned to extract termites at younger ages than at Gombe, particularly when compared to male infants at Gombe. One possibility for these differences is that year-round termite gathering at Goualougo (Sanz & Morgan, 2013a) provides greater opportunity for immature chimpanzees to develop skills relative to Gombe where termite-gathering efforts are concentrated during the rainy reason from October to December (Goodall, 1986; McGrew et al., 1979). The ages at which Goualougo chimpanzees began showing combinatory behaviors (“Mound plus tool” and “Insert fishing probe”) and learned to successfully extract termites appear more comparable to patterns of acquisition documented in some captive experiments, where combinatory manipulation was observed frequently by 21 months of age (Takeshita et al., 2005), and infants could successfully “fish” for honey at just under two years of age (Hirata & Celli, 2003). At Goualougo, several infants learned to successfully extract termites before or around two years of age. In the captive study of honey fishing, infants had monthly opportunities to develop these skills (Hirata & Celli, 2003). Thus, the opportunity to practice skills year round may result in faster acquisition than a shorter period of concentrated practice (Lonsdorf, 2006). An additional possibility is that opportunities for social learning differ between sites. At Gombe, the presence of multiple models does not accelerate offspring acquisition of skill (Lonsdorf, 2006), and at Goualougo, average party size at termite nests is relatively small, 2.23±1.57 individuals (Sanz & Morgan, 2013b). Thus, other aspects of social learning opportunity, such as tool sharing (Musgrave, Morgan, Lonsdorf, Mundry, & Sanz, 2016) may be more influential.

We also documented that there are differences between populations with respect to the sequence in which skills of tool use versus tool manufacture are acquired. At Gombe, infants learn to make tools at the same time or before they learn to use them (Lonsdorf, 2005). Similarly, at Bossou, chimpanzees manufacture tools before they gain the motor skill of tool use (Humle, 2006). At Goualougo, infants rarely attempted to manufacture their own tools before they were capable of fishing; instead, they appear to rely on discarded herb tools or tools that conspecifics, typically their mother, transfer to them. They learned to work effectively with these tools and to maintain the brush tip before moving on to gather herb stems independently and manufacture brush-tipped probes. Thus the manufacture of adult-like tools in this population always occurred after learning to termite fish. In other populations and species where tool characteristics and raw material impact tool performance, youngsters also tend to first rely on others' tools rather than manufacturing their own (e.g., leaf-folding to gather water in chimpanzees, Sousa, Biro, & Matsuzawa, 2009; Tonooka, 2001; or probing for insects by New Caledonian crows, Holzhaider et al., 2010)

These population differences could be related to cognitive challenges associated with identifying and locating suitable raw material in the environment, linking behaviors in the appropriate sequence, and producing a tool of suitable dimensions and with a functional brush tip at Goualougo. At Gombe, chimpanzees manufacture tools from varied materials rather than seeking out particular species, and they do not engage in the brush-tip modification, so tool manufacture is a simpler undertaking. The later age at which tool manufacture is acquired at

Goualougo may also be associated with the fact that mature chimpanzees often gather raw material in advance of arriving at a termite nest (Byrne et al., 2013; Sanz et al., 2004); if infants are traveling on their mother’s body, they may not dismount to independently acquire tool material on the way to the nest. Young chimpanzees continue to dorsally ride on their mothers through age 4-5 and remain in constant association through age 8-10 (Boesch & Boesch-Achermann, 2000; Goodall, 1968; Lonsdorf et al., 2014). After arrival at a nest, infants may be hesitant to depart the immediate vicinity of the nest to acquire raw material, as this could necessitate becoming separated from their mothers in order to travel to where suitable herb materials are located. Similar constraints as apply to fishing probes may help explain why we did not observe infants or juveniles manufacture puncturing sticks. In addition, these durable tools are conserved at subterranean termite nests over weeks or months, mitigating the need to manufacture a new tool. Given the inability of young individuals to puncture, there may also be little incentive to manufacture a new puncturing stick. We did observe youngsters manufacture perforating tools; unlike fishing probes and puncturing sticks, these tools were procured by detaching a twig in the immediate vicinity of the nest. Perforating twigs were also gathered from detached materials lying near the nest. The development of tool use and manufacture by immature chimpanzees in this population thus reflects the raw material demands and design features of the different tool types, and highlights the importance of access to others’ tools in enabling the opportunity to practice tool skills, particularly for fishing and puncturing.

With respect to sex differences, the youngest individual we observed exhibiting most critical elements was female, and on average, females acquired most critical elements of termite fishing slightly before males did. The exception to this was tool manufacture, which was observed on average 6 months earlier in males. We did not detect differences of a large magnitude such as have been documented for termite fishing at Gombe (Lonsdorf, 2005). The differences we observed could nonetheless reflect subtler variation between the sexes with respect to propensity for object manipulation (Koops, Furuichi, Hashimoto, & van Schaik, 2015), motor development (Lonsdorf et al., 2014), or social learning strategies (Lonsdorf, 2005). At Kalinzu, Uganda, immature male chimpanzees engage in higher rates of object manipulation than do female chimpanzees. However, their object manipulation is more play-dominated, suggesting that these behaviors provide preparation for gross motor behaviors (e.g., social displays, predator mobbing) in adulthood, rather than for tool use specifically. Females, in contrast, show more diverse types of object manipulation, potentially in preparation for adult tool use (Koops et al., 2015). At Gombe, male compared to female infant chimpanzees begin traveling independently at earlier ages than do females and show increased distance from their mothers by age three, indexing earlier gross motor development in males (Lonsdorf et al., 2014). The slightly younger ages of manufacture we observed in males could reflect earlier ages of spatial independence from mothers, which is necessary for raw material procurement. Relatively little is known about manual, fine motor control in great apes (Bardo, Cornette, Borel, & Pouydebat, 2017), though there is some evidence for superior performance by human female infants in fine motor tasks (e.g., Kokštejn, Musálek, & Tufano, 2017).

Despite these differences, it is still not immediately clear how sex differences in infancy relate to adult sex differences in tool use skill or frequency. At Gombe, the sex difference in how much time females versus males spent termite fishing when they were present at the mound disappeared after age 5.5, once all male infants had acquired the skill. Data for adult tool use are not yet available at Kalinzu. At Goualougo, adult females visit tool-using localities more frequently on average, though the average time spent using tools per day is similar between adult females and males (Ellison, Musgrave, Morgan, & Sanz, 2016). Females and males also do not differ in their mean dipping latencies, a measure of performance, when termite fishing (Sanz, Morgan, & Hopkins, 2016). Further research will help to discern whether immature males and females at Goualougo exhibit differing activity patterns or deploy different learning strategies (e.g., Lonsdorf, 2005); whether there are differences in how mothers treat female and male offspring (e.g., Boesch & Boesch-Achermann, 2000); and whether or how these factors foreshadow adult behavior. This will add to our understanding of how the ontogeny of tool skills is related to adult patterns of sexually differentiated foraging in this population and for chimpanzees more broadly.

Comparative investigations of the ontogeny of tool behavior across tool-using taxa, and within species between tasks, provide unique insights into the adaptive basis of tool skills and the factors supporting the maintenance of tool traditions over time. The present study offers the first assessment of the acquisition of termite gathering among chimpanzees in Central Africa. While the earliest stone tools date to 3.3 Mya (Harmand et al., 2015), indirect evidence suggests that the capacity for complex, flexible tool use likely evolved earlier, in the common ancestor of humans and the other great apes (Panger, Brooks, Richmond, & Wood, 2002). The rich, perishable tool repertoire of Central chimpanzees could provide clues to the tool skills of this common ancestor, evidence for which may not have been preserved in the archaeological record (Haslam, 2014). We suggest that in addition to influencing the timing and sequence of skill acquisition, the complexity of the termite-gathering task in this population is likely associated with an important role for social input in the acquisition of tool skills. Continued research on the ontogeny of complex elements in this context will further illuminate how the technology of chimpanzees in this region persists over generations.

2.6 Acknowledgements

We are deeply appreciative of the opportunity to work in the Nouabalé-Ndoki National Park and especially the Goualougo Triangle. This research would not be possible without the continued support of the Ministère de l'Economie Forestière et du Développement Durable (République du Congo), the Ministère de la Recherche Scientifique (République du Congo), and the Wildlife Conservation Society's Congo Program. Special thanks are due to J. M. Fay, P. Telfer, P. Elkan, S. Elkan, B. Curran, M. Gately, E. Stokes, T. Breuer, P. Ngouembe and D. Dos Santos. We would also like to recognize the tireless dedication of J. R. Onononga, C. Eyana-Ayina, S. Ndolo, A. Nzeheke, W. Mayoukou, S. Kialiema, J. Wawa, F. Ebombi, J. M. Massamba, J. Ortega, D. Koni, M. Meguessa, I. Singono, and the Goualougo tracking team. Grateful acknowledgment of funding is due to the National Science Foundation, the Wenner-Gren Foundation, the Leakey Foundation, Lambda Alpha, U.S. Fish and Wildlife Service, the National Geographic Society, and the Columbus Zoological Park. The authors declare no competing interests.

References

Bardo, A., Cornette, R., Borel, A., & Pouydebat, E. (2017). Manual function and performance in humans, gorillas, and orangutans during the same tool use task. *American Journal of Physical Anthropology*, *164*(4), 821–836.

Bermejo, M., & Illera, G. (1999). Tool-set for termite-fishing and honey extraction by wild chimpanzees in the Lossi Forest, Congo. *Primates*, *40*(4), 619–627.

Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: Evidence from field experiments. *Animal Cognition*, *6*(4), 213–223.

Biro, D., Sousa, C., & Matsuzawa, T. (2006). Ontogeny and cultural propagation of tool use by wild chimpanzees at Bossou, Guinea: Case studies in nut cracking and leaf folding. In T. Matsuzawa, M. Tomonaga, & M. Tanaka (Eds.), *Cognitive Development in Chimpanzees* (pp. 476–508). Tokyo: Springer-Verlag.

Boesch, C. (2013). Ecology and cognition of tool use in chimpanzees. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 21–47). Cambridge: Cambridge University Press.

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: Behavioural ecology and evolution.* Oxford: Oxford University Press.

Boesch, C., & Boesch, H. (1984). Possible causes of sex differences in the use of natural hammers by wild chimpanzees. *Journal of Human Evolution*, *13*(5), 415–440.

Boesch, C., Head, J., & Robbins, M. (2009). Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. *Journal of Human Evolution*, *56*(6), 560–569.

Bogart, S., & Pruetz, J. (2008). Ecological context of savanna chimpanzee (*Pan troglodytes verus*) termite fishing at Fongoli, Senegal. *American Journal of Primatology*, *70*(6), 605–612.

Boose, K. J., White, F. J., & Meinelt, A. (2013). Sex differences in tool use acquisition in bonobos (*Pan paniscus*). *American Journal of Primatology*, *75*(9), 917–926.

Brewer, S. M., & McGrew, W. C. (1990). Chimpanzee use of a tool-set to get honey. *Folia Primatologica*, *54*(1–2), 100–104.

Byrne, R. (1994). The evolution of intelligence. In P. J. B. Slater & T. R. Halliday (Eds.), *Behaviour and Evolution* (pp. 223–265). New York: Cambridge University Press.

Byrne, R., Sanz, C., & Morgan, D. (2013). Chimpanzees plan their tool use. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 48–64). Cambridge: Cambridge University Press.

Byrne, R. W., & Russon, A. E. (1998). Learning by imitation: A hierarchical approach. *Behavioral and Brain Sciences, 21*(5), 667–721.

Call, J. (2013). Three ingredients for becoming a creative tool user. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 3–20). Cambridge: Cambridge University Press.

Deblauwe, I., Guislain, P., Dupain, J., & Van Elsacker, L. (2006). Use of a tool-set by *Pan troglodytes troglodytes* to obtain termites (*Macrotermes*) in the periphery of the Dja Biosphere Reserve, southeast Cameroon. *American Journal of Primatology, 68*(12), 1191–1196.

Deblauwe, I., & Janssens, G. P. J. (2008). New insights in insect prey choice by chimpanzees and gorillas in Southeast Cameroon: The role of nutritional value. *American Journal of Physical Anthropology, 135*(1), 42–55.

Ellison, E., Musgrave, S., Morgan, D., & Sanz, C. (2016). Sex differences in tool use during termite gathering among chimpanzees (*Pan troglodytes troglodytes*) of the Goualougo Triangle, Republic of Congo. In *American Association of Physical Anthropology*.

Eshchar, Y., Izar, P., Visalberghi, E., Resende, B., & Fragaszy, D. (2016). When and where to practice: Social influences on the development of nut-cracking in bearded capuchins (*Sapajus libidinosus*). *Animal Cognition, 19*(3), 605–618.

Estienne, V., Robira, B., Mundry, R., Deschner, T., & Boesch, C. (2019). Acquisition of a complex extractive technique by the immature chimpanzees of Loango National Park, Gabon. *Animal Behaviour*, *147*, 61–76.

Estienne, V., Stephens, C., & Boesch, C. (2017). Extraction of honey from underground bee nests by central African chimpanzees (*Pan troglodytes troglodytes*) in Loango National Park, Gabon: Techniques and individual differences. *American Journal of Primatology, 79*(8), e22672.

Fay, J. M., & Carroll, R. W. (1994). Chimpanzee tool use for honey and termite extraction in Central Africa. *American Journal of Primatology*, *34*(4), 309–317.

Fragaszy, D. M., & Adams-Curtis, L. E. (1991). Generative aspects of manipulation in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology, 105*(4), 387–397.

Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs*, *1*, 161–311.

Goodall, J. (1986). *The chimpanzees of Gombe. Patterns of behavior.* Cambridge: Belknap Press.

Gruber, T., Clay, Z., & Zuberbühler, K. (2010). A comparison of bonobo and chimpanzee tool use: Evidence for a female bias in the *Pan* lineage. *Animal Behaviour, 80*(6), 1023–1033.

Gumert, M. D., Hoong, L. K., & Malaivijitnond, S. (2011). Sex differences in the stone tool-use behavior of a wild population of burmese long-tailed macaques (*Macaca fascicularis aurea*). *American Journal of Primatology*, *73*(12), 1239–1249.

Harmand, S., Lewis, J. E., Feibel, C. S., Lepre, C. J., Prat, S., Lenoble, A., … Roche, H. (2015). 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature*, *521*(7552), 310–315.

Haslam, M. (2014). On the tool use behavior of the bonobo-chimpanzee last common ancestor, and the origins of hominine stone tool use: Tool use in the bonobo-chimpanzee LCA. *American Journal of Primatology*, *76*(10), 910–918.

Hayashi, M., & Inoue-Nakamura, N. (2011). From handling stones and nuts to tool-use. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), *The Chimpanzees of Bossou and Nimba* (pp. 175–182). Tokyo: Springer Japan.

Hayashi, M., & Matsuzawa, T. (2003). Cognitive development in object manipulation by infant chimpanzees. *Animal Cognition*, *6*(4), 225–233.

Herrmann, E., Hare, B., Call, J., & Tomasello, M. (2010). Differences in the cognitive skills of bonobos and chimpanzees. *PLoS ONE*, *5*(8), 2–5.

Hirata, S., & Celli, M. L. (2003). Role of mothers in the acquisition of tool-use behaviours by captive infant chimpanzees. *Animal Cognition*, *6*(4), 235–244.

Holzhaider, J., Gray, R., & Hunt, G. (2010). The development of pandanus tool manufacture in wild New Caledonian crows. *Behaviour*, *147*(5), 553–586.

Humle, T. (2006). Ant dipping in chimpanzees: An example of how microecological variables, tool use, and culture reflect the cognitive abilities of chimpanzees. In T. Matsuzawa, M. Tomonaga, & M. Tanaka (Eds.), *Cognitive Development in Chimpanzees* (pp. 452–475). Springer Japan.

Humle, T., Snowdon, C. T., & Matsuzawa, T. (2009). Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Animal Cognition*, *12*(Suppl 1), 37–48.

Inoue-Nakamura, N., & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *111*(2), 159–173.

Kahrs, B. A., & Lockman, J. J. (2014). Building tool use from object manipulation: A perception–action perspective. *Ecological Psychology*, *26*(1–2), 88–97.

Kokštejn, J., Musálek, M., & Tufano, J. J. (2017). Are sex differences in fundamental motor skills uniform throughout the entire preschool period? *PLoS ONE*, *12*(4), 1–10.

Koops, K., Furuichi, T., Hashimoto, C., & van Schaik, C. (2015). Sex differences in object manipulation in wild immature chimpanzees (*Pan troglodytes schweinfurthii*) and bonobos (*Pan paniscus*): Preparation for tool use? *PLoS ONE*, *10*(10), 1–15.

Lockman, J. J. (2000). A perception-action perspective on tool use development. *Child Development*, *71*(1), 137–144.

Lonsdorf, E. (2005). Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Animal Behaviour*, *70*(3), 673–683.

Lonsdorf, E. (2006). What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Animal Cognition*, *9*(1), 36–46.

Lonsdorf, E., Eberly, L. E., & Pusey, A. E. (2004). Sex differences in learning in chimpanzees. *Nature*, *428*(6984), 715–716.

Lonsdorf, E., Markham, A. C., Heintz, M. R., Anderson, K. E., Ciuk, D. J., Goodall, J., & Murray, C. M. (2014). Sex differences in wild chimpanzee behavior emerge during infancy. *PLoS ONE*, *9*(6), e99099.

Mangold. (2015). INTERACT 14 User guide. Mangold International GmbH.

Mann, J., Sargeant, B. L., Watson-Capps, J. J., Gibson, Q. A., Heithaus, M. R., Connor, R. C., & Patterson, E. (2008). Why do dolphins carry sponges? *PLoS ONE*, *3*(12), e3868.

Marshall-Pescini, S., & Whiten, A. (2008). Social learning of nut-cracking behavior in East African sanctuary-living chimpanzees (*Pan troglodytes schweinfurthii*). *Journal of Comparative Psychology*, *122*(2), 186–194.

Matsuzawa, T. (1994). Field experiments of tool-use. In R. Wrangham, W. McGrew, F. B. M. de Waal, & P. Heltne (Eds.), *Chimpanzee Cultures* (pp. 351–370). Cambridge: Harvard University Press.

McGrew, W. (1979). Evolutionary implications of sex differences in chimpanzee predation and tool use. In D. A. Hamburg & E. R. McCown (Eds.), *The great apes* (pp. 441–463). Menlo Park: Benjamin/Cummings.

McGrew, W. (1992). *Chimpanzee material culture: Implications for human evolution*. Cambridge: Cambridge University Press.

McGrew, W. C. (2014). The “other faunivory” revisited: Insectivory in human and non-human primates and the evolution of human diet. *Journal of Human Evolution*, *71*, 4–11.

McGrew, W. C., & Collins, D. A. (1985). Tool use by wild chimpanzees (*Pan troglodytes*) to obtain termites (*Macrotermes herus*) in the Mahale Mountains, Tanzania. *American Journal of Primatology*, *9*(1), 47–62.

McGrew, W., Tutin, C., & Baldwin, P. J. (1979). Chimpanzees, tools, and termites: Cross-cultural comparisons of Senegal, Tanzania, and Rio Muni. *Man*, *14*(2), 185–214.

Meulman, E., Seed, A. M., & Mann, J. (2013). If at first you don't succeed... Studies of ontogeny shed light on the cognitive demands of habitual tool use. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630), 20130050.

Moura, A., & Lee, P. (2010). Wild capuchins show male-biased feeding tool use. *International Journal of Primatology*, *31*(3), 457–470.

Muroyama, Y. (1991). Chimpanzees' choices of prey between two sympatric species of *Macrotermes* in the Campo Animal Reserve, Cameroon. *Human Evolution*, *6*(2), 143–151.

Musgrave, S., Morgan, D., Lonsdorf, E., Mundry, R., & Sanz, C. (2016). Tool transfers are a form of teaching among chimpanzees. *Scientific Reports*, *6*, 34783.

Nishida, T., & Uehara, S. (1980). Chimpanzees, tools, and termites: Another example from Tanzania. *Current Anthropology*, *21*(5), 671–672.

Panger, M. A., Brooks, A. S., Richmond, B. G., & Wood, B. (2002). Older than the Oldowan? Rethinking the emergence of hominin tool use. *Evolutionary Anthropology*, *11*(6), 235–245.

Pradhan, G. R., Tennie, C., & van Schaik, C. P. (2012). Social organization and the evolution of cumulative technology in apes and hominins. *Journal of Human Evolution*, *63*(1), 180–190.

Pruetz, J. D., & Bertolani, P. (2007). Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Current Biology*, *17*(5), 412–417.

R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Resende, B. D., Ottoni, E., & Fragaszy, D. (2008). Ontogeny of manipulative behavior and nut-cracking in young tufted capuchin monkeys (*Cebus apella*): A perception-action perspective. *Developmental Science*, *11*(6), 828–840.

Rutz, C., & St. Clair, J. J. H. (2012). The evolutionary origins and ecological context of tool use in New Caledonian crows. *Behavioural Processes*, *89*(2), 153–165.

Sabater Pí, J. (1974). An elementary industry of the chimpanzees in the Okorobikó mountains, Rio Muni (Republic of Equatorial Guinea), West Africa. *Primates*, *15*(4), 351–364.

Sanz, C., Call, J., & Morgan, D. (2009). Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biology Letters*, *5*(3), 293–296.

Sanz, C., Deblauwe, I., Tagg, N., & Morgan, D. (2014). Insect prey characteristics affecting regional variation in chimpanzee tool use. *Journal of Human Evolution*, *71*, 28–37.

Sanz, C., & Morgan, D. (2007). Chimpanzee tool technology in the Goualougo Triangle, Republic of Congo. *Journal of Human Evolution*, *52*(4), 420–433.

Sanz, C., & Morgan, D. (2011). Elemental variation in the termite fishing of wild chimpanzees (*Pan troglodytes*). *Biology Letters*, *7*(4), 634–637.

Sanz, C., & Morgan, D. (2013a). Ecological and social correlates of chimpanzee tool use. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630), 20120416.

Sanz, C., & Morgan, D. (2013b). The social context of chimpanzee tool use. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 161–175). Cambridge: Cambridge University Press.

Sanz, C., Morgan, D., & Gulick, S. (2004). New insights into chimpanzees, tools, and termites from the Congo Basin. *The American Naturalist*, *164*(5), 567–581.

Sanz, C., Morgan, D., & Hopkins, W. (2016). Lateralization and performance asymmetries in the termite fishing of wild chimpanzees in the Goualougo Triangle, Republic of Congo: Handedness and performance in wild chimpanzees. *American Journal of Primatology*, *78*(11), 1190–1200.

Sanz, C., Schöning, C., & Morgan, D. (2010). Chimpanzees prey on army ants with specialized tool set. *American Journal of Primatology*, *72*(1), 17–24.

Shumaker, R., Walkup, K., & Beck, B. B. (2011). *Animal tool behavior: The use and manufacture of tools by animals*. The Johns Hopkins University Press.

Smith, & Bentley-Condit, V. (2010). Animal tool use: Current definitions and an updated comprehensive catalog. *Behaviour, 147*(2), 185–32A.

Sousa, C., Biro, D., & Matsuzawa, T. (2009). Leaf-tool use for drinking water by wild chimpanzees (*Pan troglodytes*): Acquisition patterns and handedness. *Animal Cognition*, *12*(S1), 115–125.

Spagnoletti, N., Visalberghi, E., Ottoni, E., Izar, P., & Fragaszy, D. (2011). Stone tool use by adult wild bearded capuchin monkeys (*Cebus libidinosus*). Frequency, efficiency and tool selectivity. *Journal of Human Evolution*, *61*(1), 97–107.

Sugiyama, Y. (1985). The brush-stick of chimpanzees found in south-west Cameroon and their cultural characteristics. *Primates, 26*(4), 361–374.

Suzuki, S., Kuroda, S., & Nishihara, T. (1995). Tool-set for termite-fishing by chimpanzees in the Ndoki Forest, Congo. *Behaviour*, *132*(3/4), 219–235.

Takeshita, H., Fragaszy, D., Mizuno, Y., Matsuzawa, T., Tomonaga, M., & Tanaka, M. (2005). Exploring by doing: How young chimpanzees discover surfaces through actions with objects. *Infant Behavior and Development*, *28*(3), 316–328.

Tan, A. W. Y. (2017). From play to proficiency: The ontogeny of stone-tool use in coastal-foraging long-tailed macaques (*Macaca fascicularis*) from a comparative perception-action perspective. *Journal of Comparative Psychology*, *131*(2), 89–114.

Tonooka, R. (2001). Leaf-folding behavior for drinking water by wild chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea. *Animal Cognition*, *4*(3–4), 325–334.

Visalberghi, E., & Fragaszy, D. (2006). What is challenging about tool use? The capuchin's perspective. In T. R. Zentall & E. A. Wasserman (Eds.), *Comparative Cognition: Experimental Explorations of Animal Intelligence* (pp. 777–799). Oxford University Press.

Visalberghi, E., & Fragaszy, D. (2013). The etho-cebus project: Stone-tool use by wild capuchin monkeys. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 203–222). Cambridge: Cambridge University Press.

Whiten, A., Goodall, J., McGrew, W., Nishida, T., Reynolds, V., Sugiyama, Y., … Boesch, C. (2001). Charting cultural variation in chimpanzees. *Behaviour*, *138*(11–12), 1481–1516.

Chapter 3: Tool Transfers are a Form of Teaching among Chimpanzees[1]

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Roger Mundry, and Crickette Sanz**

3.1 Abstract

Teaching is a form of high-fidelity social learning that promotes human cumulative culture. Although recently documented in several nonhuman animals, teaching is rare among primates. In this study, we show that wild chimpanzees (*Pan troglodytes troglodytes)* in the Goualougo Triangle teach tool skills by providing learners with termite fishing probes. Tool donors experienced significant reductions in tool use and feeding, while tool recipients significantly increased their tool use and feeding after tool transfers. These transfers meet functional criteria for teaching: they occur in a learner's presence, are costly to the teacher, and improve the learner's performance. Donors also showed sophisticated cognitive strategies that effectively buffered them against potential costs. Teaching is predicted when less costly learning mechanisms are insufficient. Given that these chimpanzees manufacture sophisticated, brush-tipped fishing probes from specific raw materials**,** teaching in this population may relate to the complexity of these termite-gathering tasks.

3.2 Introduction

Social learning facilitates the transfer of adaptive information within groups for a wide range of animal taxa and can generate group-specific behavior patterns (Fragaszy & Perry, 2003; Heyes & Galef, 1996; Thornton & Clutton-Brock, 2011). When these behaviors persist over generations and are transmitted through social learning, they are deemed cultural (Whiten, 2005).

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High-fidelity social learning is hypothesized to distinguish human from animal cultures by promoting cumulative culture (Boyd & Richerson, 1985; Dean, Kendal, Schapiro, Thierry, & Laland, 2012; Tennie, Call, & Tomasello, 2009); identifying what mechanisms underpin the social transmission of complex behaviors among animals is thus essential for comparative studies.

Of foremost interest is teaching. A functionalist approach identifies teaching when certain criteria are fulfilled (Caro & Hauser, 1992; Hoppitt et al., 2008; Thornton & Raihani, 2008) regardless of whether there is evidence of *intent* to facilitate another's learning (Fogarty, Strimling, & Laland, 2011; Kruger & Tomasello, 1998; Pearson, 1989; Premack & Premack, 1996). The most broadly applied criteria are that the behavior 1) occurs in the presence of a naïve learner, 2) at some cost or at least no benefit to the teacher, and 3) that it facilitates learning in another individual (Caro & Hauser, 1992). Using these criteria, strong experimental evidence for teaching has been found for meerkats (Thornton & McAuliffe, 2006), ants (Franks & Richardson, 2006), and pied babblers (Raihani & Ridley, 2008). Sensitivity to learner competence (Thornton & McAuliffe, 2006), or evaluation (Franks & Richardson, 2006), and ostensive cueing (Csibra & Gergely, 2009) have been suggested as further criteria. Linking functional criteria to cognitive correlates of candidate teaching behaviors can improve inferences about the evolutionary origins of teaching (Byrne & Rapaport, 2011; Kline, 2015) (see Table 3.1).

One such candidate behavior is the transfer of tools between individuals, which has been observed among wild chimpanzees in several tool-using contexts (Boesch & Boesch-Achermann, 2000; Fragaszy et al., 2013; Lonsdorf, 2006; Nishida & Hiraiwa, 1982; Pruetz & Lindshield, 2012). Chimpanzee tool repertoires vary between populations, and this can be attributed in part to social learning (Koops, Schöning, Isaji, & Hashimoto, 2015; Luncz & Boesch, 2015; Whiten et al., 2001). This variation could also be associated with differences in the types of social facilitation necessary to maintain behaviors that range in complexity from simple tasks, involving only a single tool and target, to more complex tasks involving the use of tool sets (Sanz & Morgan, 2010; Sanz, Morgan, & Gulick, 2004). For example, tool transfers have been documented during termite gathering among chimpanzees in the Goualougo Triangle, Republic of Congo (Sanz & Morgan, 2013b). There, chimpanzees are highly selective for plant species used to manufacture tools (Sanz & Morgan, 2007) and intentionally modify herb stems to fashion brush-tipped fishing probes (Sanz, Call, & Morgan, 2009). In addition, chimpanzees use two tool sets to gather termites from epigeal (above-ground) and subterranean nests. At epigeal nests, chimpanzees may use a perforating twig to open sealed termite exit holes on the nest surface before using an herbaceous probe to fish for termites. At subterranean nests, chimpanzees must breach underground nest chambers with a durable, woody puncturing stick before fishing (Sanz et al., 2004). Teaching is predicted to evolve when it is required to facilitate learning and when the fitness benefits accrued from a pupil's competence outweigh the costs of teaching (Thornton & Raihani, 2008). Given the complexity of these tool tasks, we hypothesized that tool transfers from skilled chimpanzees to less competent conspecifics constitute a form of teaching.

Using remote video footage of termite gathering, we scored behavior immediately before and after fishing probe transfers to test whether transfers impose costs on donors and confer benefits to recipients. We predicted that donors would spend proportionately less time termite gathering and exhibit reduced tool use and feeding after compared to before transfers, while recipients would spend more time using tools and exhibit increased tool use and feeding after compared to before transfers.

TABLE 3.1 Evidence for animal teaching

Defining Criteria		**Meerkats[2]**	**Ants[3]**	**Pied Babblers[6]**	**Macaques[7,8]**	**Callitrichids[10,11]**	**Felids[1]**	**Chimpanzees[12,13]**
Functional	Occurs in the presence of a naïve learner[1]	**E**	**E**	*E*	E	**N, E**	**N**	**N**
	At some cost or at least no benefit to teacher[1]	**E**	**E**	*E*	E	**?**	**N**	**N**
	Facilitates learning in another individual[1]	**E**	**E**	*E*	?	**?**	**E**	**N**
	Sensitivity to learner competence[2], evaluation[3]	**E**	**E**	*?*	?	**N, E**	**?**	**N**
	Ostensive cueing[4]	**-**	**-**	**-**	**-**	**-**	**-**	**?**
Cognitive	Ability to attribute knowledge to others[5]	**-**	**-**	**-**	?[9]	**-**	**-**	**N**, E[14]
	Deliberate intention to facilitate learning[11]	**-**	**-**	**-**	**-**	**-**	**-**	**N**, E[15,16]

Included are cases where evidence for satisfaction of teaching criteria is strong in either a captive or an experimental (E) or a natural (N) setting, or present but inconclusive (?); - indicates that there is presently no evidence for a criterion. The context of teaching behavior is indicated by; bold = foraging; italics = communication, and underlined = locomotion. Plain text indicates evidence derived from studies that did not specifically assess teaching criteria. More exhaustive coverage of evidence for possible cases of animal teaching is reviewed elsewhere (Caro & Hauser, 1992; Hoppitt et al., 2008; Thornton & Raihani, 2008; Kline, 2015). Chimpanzee data come from this study and the others referenced.

1. Caro & Hauser, 1992. 2. Thornton & McAuliffe, 2006 3. Franks & Richardson, 2006 4. Csibra & Gergely (2009). 5. Kruger & Tomasello, 1996 6. Raihani & Ridley, 2008 7. Maestripieri, 1995b. 8. Maestripieri, 1995a 9. Drayton & Santos (2014) 10. Rapaport & Brown (2008). 11. Humle & Snowdon (2008). 12 Boesch & Boesch-Achermann (2000). 13 Boesch (1991) 14. Call & Tomasello (2008). 15. Horner, Carter, Suchak & de Waal (2011). 16. Yamamoto, Humle, & Tanaka (2012).

3.3 Methods

3.3.1 Subjects

Chimpanzee observations were conducted in the Goualougo Triangle, located in the southern section of the Nouabalé-Ndoki National Park (E 16°51′−16°56′; N 2°05′−3°03′), Republic of Congo. The study area encompasses 380 km^2 of evergreen and semi-deciduous lowland forest, with altitudes ranging between 330 and 600 meter. Rainfall is bimodal, with a primary rainy season from August to November and a short rainy season in May.

3.3.2 Data Collection

We placed remote video-recording devices with passive infrared sensors at termite nests to record chimpanzee visitation and tool-using behaviors (Sanz et al., 2004). Video footage was archived on hard drives and converted to MPEG for review after which we coded videos using INTERACT Version 14 (Mangold, 2015). We screened 224 hours of footage and identified 96 fishing probe transfers, defined as the change of possession of a fishing probe from one individual to another. A subset of these transfers met criteria for inclusion in the present study. If multiple transfers occurred between the same individuals during the same visit to a termite nest, only the first transfer was included because subsequent transfers were considered nonindependent. On 4 separate visits, 2 transfers were coded in each and were included, because the transfers were separated by a minimum of approximately 10 minutes and by other intervening behaviors. Thus, we deemed each transfer event to be independent. Transfers were coded for age/sex class of donor and recipient. The resulting data set included 57 transfers of fishing probes from an older, more competent individual to an immature individual. There were two occasions in which there was a change of possession of a fishing probe between adults, four transfers from a subadult or older juvenile to an adult female, and two transfers between youngsters. These were not included in analyses due to their relative rarity.

Next we screened transfers for those in which the donor or recipient chimpanzee, or both, were continuously visible during the 30 seconds immediately before and after the transfer. We considered this time frame adequate for capturing representative behavior before and after transfers given the relatively short average duration (2.55 minutes) of termite nest visits by chimpanzees in this population (Sanz & Morgan, 2013a). In addition, because chimpanzees may go in and out of the camera field of view, coding clips continuously for the entire duration of chimpanzee presence at termite nests was not always feasible. For donors and recipients, respectively, 26 and 24 transfers allowed for determination of the proportion of time spent in active tool use. We coded behaviors including termite-gathering tool use (e.g., active insertion of fishing probes); and other behaviors such as play, inactivity, and locomotion. For a further subset of these clips, continuous visibility at a high degree of resolution for 30 seconds before and after the clips allowed for the coding of specific tool use and feeding behaviors. We further required that the donor must have initiated tool use by 30 seconds before the transfer. This was necessary in order to ensure that comparison of behavior before and after a transfer event was not systematically biased by a donor's latency to begin termite gathering upon arrival at a termite nest. This criterion was not applied to recipients, given that immature chimpanzees often engage in a range of behaviors other than termite gathering while present at termite nests and the purpose was to discern how their behavior changed, regardless of the behavior immediately preceding the transfer. For donors, we coded fishing probe insertions and feeding events for 17 and 15 transfers, respectively; and for recipients, we coded fishing probe insertions and feeding events for 15 and 14 transfers, respectively. Fishing probe insertions involved the insertion and extraction of an herbaceous probe into an exit hole on a termite mound. Feeding elements included sweeping termites from tools, eating termites directly from the tool, or gathering termites by hand, wrist or lips from the termite nest surface.

3.3.3 Analysis

In order to test whether the duration of tool use differed before and after the tool transfer we used exact (Mundry & Fischer, 1998; Siegel & Castellan Jr., 1988) Wilcoxon tests, applied separately for donors and recipients. In case individuals acted repeatedly as donor or recipient, respectively, we used the average duration per individual and time period (before or after, respectively). We did not use mixed models (see below) for the duration since it showed bottom and ceiling effects, making it impossible to find an appropriate error distribution.

For testing whether the number of feeding events and fishing probe insertions differed between before and after the tool transfer, we used Generalized Linear Mixed Models (GLMM) (Baayen, 2008), fitted separately for donors and recipients (see Appendix A, Tables A.1 and A.2). These included one fixed effect denoting whether the observation was made before or after the tool transfer ("time period"). As random intercepts we included the identity of the chimpanzee and also the particular transfer event. To keep Type I error rate at the nominal level of 0.05, we included the random slope of time period within chimpanzee identity whenever we had at least two tool transfer events for at least half of the individuals (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009); this random slope was included into the models for the number of fishing probe insertions of donors and the number of feeding events of donors. We did not include the correlation between the random intercept and slope to avoid overly complex models given the small sample sizes. We used either a Poisson error structure or, in case this revealed an overdispersed response, a negative binomial error structure. Specifically, we used a Poisson model for the number of fishing probe insertions for the donor (dispersion parameter=1.17) and negative binomial models for the other three (dispersion parameters, number fishing probe insertions, recipient: 1.48; number feeding events, donor: 1.10; number feeding events, recipient: 1.33). We tested the significance of time period using a likelihood ratio test comparing the full model with a respective null model lacking the effect (Barr et al., 2013; Dobson, 2002).

The models were fitted in R (R Core Team, 2016) using the functions glmer or glmer.nb of the package lme4 (Bates, Mächler, Bolker, & Walker, 2015) (version 1.1-10); and Wilcoxon tests were calculated using the function wilcox.exact of the package exactRankTests (Hothorn & Hornik, 2015).

3.4 Results

3.4.1 Transfers of Fishing Probes

We identified 96 transfers of fishing probes, all of which were initiated by the recipient. A subset of transfers met the criteria for analysis (see Methods). All transfers analyzed occurred between an adult female and her offspring; the one exception occurred between a sub-adult female and her infant sister. The results represent 13 unique donors and 13 unique recipients. Recipients were immature chimpanzees, including 5 females, 4 males, and 4 youngsters of unknown sex.

3.4.2 Time Spent using Tools to Gather Termites

As shown in Fig. 3.1a, donors' average time spent using tools to gather termites decreased substantially (an average of 10.6 seconds) during the 30 second interval after compared to before transfers in which donors relinquished their fishing probe to another individual (Wilcoxon signed-ranks test: T^{+}=45.00, N=13 donors, P=0.08). Conversely, tool recipients spent on average 15 seconds more using tools to gather termites after transfer events in which they received a fishing probe (T^+=85.5, N=13 recipients, P=0.003, Fig. 3.1b).

3.4.3 Fishing Probe Insertions

To test whether fishing probe insertions and feeding events differed between before and after the tool transfer, we used Generalized Linear Mixed Models (GLMM) (Baayen, 2008), fitted separately for donors and recipients (see Appendix A, Tables A.1 and A.2). As shown in Fig. 3.1c, donors (N=9) performed significantly fewer fishing probe insertions (an average of 1.8 fewer) per 30 seconds after the transfer of a fishing probe versus prior to the transfer (GLMM: estimate±SE=-0.49±0.18, χ^2=6.98, df=1, P=0.008). Of 9 donors, 5 showed an average decrease, 2 remained constant, and 2 showed increases. Those chimpanzees (N=11) who received a tool showed a significant increase (an average of 2.8 more) in the number of probe insertions after transfers compared to their performance before (1.24±0.35, χ^2=10.44, df=1, P=0.001, Fig. 3.1d).

3.4.4 Feeding Events

Donors (N=9) showed a reduction in the number of feeding events (on average 2.7 fewer) after the transfer of a fishing probe versus prior to the transfer (-0.69±0.24, χ^2=9.25, df=1, P=0.002; Fig. 3.1e). For recipients (N=10), there was a significant increase in the average number of feeding events (an average of 2.8 more) after transfers compared to before (1.46±0.43, χ^2=8.38, df=1, P=0.004; Fig. 3.1f).

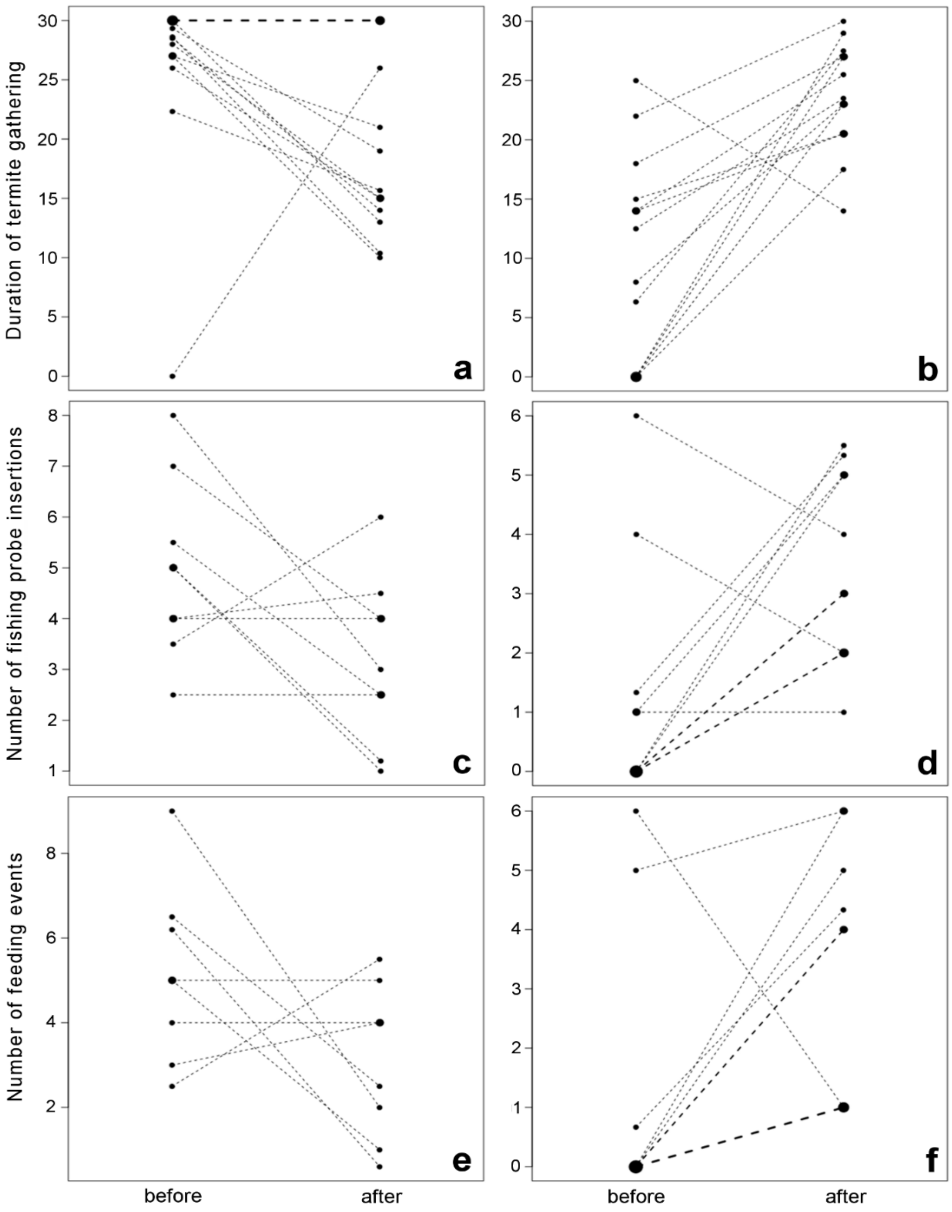

FIGURE 3.1 Changes in termite gathering from before to after tool transfer. The number of seconds spent using tools to gather termites *decreased* for the donor (n=26, Fig. 3.1a) after relinquishing a probe to another chimpanzee (recipient, n=24), whose time spent termite fishing *increased* (Fig. 3.1b). The number of fishing probe insertions also *decreased* for the donor (n=17, Fig. 3.1c) and *increased* for the recipient (n=15, Fig. 3.1d). Finally, the number of feeding events *decreased* for the donor (n=15, Fig. 3.1e) and *increased* for the recipient (n=14, Fig. 3.1f) after the transfers. Observations of the same individual or event, respectively, are denoted by a pair of points connected by a dashed line. Averages are shown for individuals with multiple observations. Tied observations (at least two individuals with the exact same value of the response) are denoted by larger points (whereby the area of the points codes the number of individuals; thicker lines have the corresponding meaning for the connections). n=number of transfers.

3.4.5 Donor Strategies Buffering Costs of Tool Transfers

Adult females occasionally transported multiple fishing probes to the termite nest in advance (n=4 occurrences) and used one of these additional probes after a transfer. In addition, adult females deployed a second strategy (see Supplementary Video 1) in which they divided their fishing probe lengthwise and then transferred half of their tool to their offspring while retaining the other half for their own use (n=11 occurrences). These strategies were observed in 3 and at least 6 different females, respectively. Use of a second tool or splitting of a tool lengthwise were deployed in 3 of the 6 occasions where donors' rate of tool use or feeding increased or showed no change following a transfer. These behaviors were thus effective in buffering against the costs of tool sharing, as they enabled individuals who transferred a tool to maintain or even show an increased rate of tool use in the post-transfer period.

3.5 Discussion

Of the functional criteria proposed to identify teaching (Caro & Hauser, 1992), the first is that the behavior occurs in the presence of a learner. Transfers are most common between adults and infants, principally mothers and offspring. In chimpanzees, mothers are the primary models for offspring (Lonsdorf, 2006; Matsuzawa, 2011) and are most likely to benefit from offspring acquisition of tool skills. Second, teaching behaviors are predicted to be costly to the teacher. In the present study, donors incurred costs in the form of reduced time spent termite gathering, fewer fishing probe insertions, and reduced termite consumption. Third, teaching should provide the learner with increased knowledge or opportunity to acquire a skill. Tool recipients increased their time spent termite gathering, and showed higher rates of fishing probe insertions and feeding events following transfers.

Changes of tool possession from older, more competent individuals to younger, less competent individuals are distinctive in several ways from tool transfers in the opposite direction or between peers (Pruetz & Lindshield, 2012), which were observed relatively rarely within this population. Active transfers in which adults move to facilitate a transfer in response to begging (Pruetz & Lindshield, 2012) (see Supplementary Video 2) have only been documented when a tool changed possession from a more to a less competent individual. Further, mothers showed evidence for anticipating transfers and devising strategies that buffer associated costs, while accommodating both their offspring's and their own need for a functional probe. Splitting a tool lengthwise is likely to be more effective for producing two viable tools than breaking the tool in half, which could result in loss of the brush tip or the tool being too short to insert to the appropriate depth. In addition, splitting a tool lengthwise or bringing a second tool in advance are both advantageous because they buffer the donor or recipient from having to locate tool material and manufacture a second tool after arrival. Tool manufacture requires identifying suitable raw material, and potentially departing from the vicinity of the nest and other conspecifics in order to do so, which increases vulnerability to predation.

An alternative interpretation of transfers, instead of teaching, is that adults relinquish tools to mitigate harassment (Boesch & Boesch, 1989), i.e., "sharing under pressure” (Gilby, 2006). However, costs to donors increased rather than decreased following tool transfers, which is the opposite effect than would be predicted by the sharing under pressure hypothesis. It is the relinquishing of a tool, rather than the proximity or harassment of offspring, that is costly.

With respect to the third functional criterion, tool recipients experienced an immediate benefit through the opportunity to manipulate and use appropriate tool materials, which resulted in their increased tool use and termite consumption. Consistent with past findings that mothers did not differentially facilitate termite fishing by male and female offspring at Gombe (Lonsdorf, 2006), transfers occurred to offspring of both sexes, and tool-using activity increased after transfers for 9 of the 10 recipients. Tool transfers included components both of transfer of declarative knowledge (Thornton & Raihani, 2008), i.e., what raw material is appropriate, as well as opportunity provisioning (Caro & Hauser, 1992) or providing (Hoppitt et al., 2008) to practice termite-gathering behaviors with a suitable tool. These tools were usually transferred with the modified brush tip facing the termite nest, further scaffolding appropriate tool use. At Tai, age and skill-related shifts have been documented in mother chimpanzees' facilitation of nut-cracking (Boesch & Boesch-Achermann, 2000). Given that the acquisition of some components of termite gathering may extend into juvenility and sub-adulthood in the Goualougo Triangle (Musgrave, Bell, Morgan, Lonsdorf, & Sanz, 2015), longitudinal studies will further illustrate how tool transfers impact skill acquisition as well as the extent to which tool donors are sensitive to learner competence (Franks & Richardson, 2006; Thornton & McAuliffe, 2006).

Teaching is hypothesized to evolve when it is optimal for transferring information that is otherwise too difficult or costly to acquire, and the limited evidence for nonhuman primate teaching comes from contexts which may fit this criterion (Boesch, 1991; Fouts & Fouts, 1989; Humle & Snowdon, 2008; Maestripieri, 1995b, 1995a; Rapaport & Brown, 2008). Teaching by active facilitation of complex behaviors could be beneficial, even if the overall rate of these behaviors is low. Given that teaching may appear absent in non-experimental settings because it is difficult to measure (Lonsdorf & Bonnie, 2010), developing rigorous methods for evaluating social learning mechanisms is necessary for comparative studies. In addition, captive research can help inform interpretation of possible cognitive correlates of teaching behaviors documented in natural settings. For example, the flexible use of coping strategies observed in this chimpanzee population indicates that donors are sensitive to and anticipate recipients' need for a functional tool; captive experiments demonstrated that chimpanzees can attribute knowledge to others (Call

& Tomasello, 2008) and can engage in prosocial helping under certain conditions (Horner, Carter, Suchak, & de Waal, 2011; Yamamoto, Humle, & Tanaka, 2012). Analyzing functional criteria alongside the potential cognitive underpinnings of social facilitation in the context of complex, learned tasks can advance our understanding of the evolution of teaching behavior across taxa and in our own lineage.

3.6 Acknowledgements

This research would not be possible without the continued support of the Ministère de l'Economie Forestière et du Développement Durable (République du Congo), the Ministère de la Recherche Scientifique (République du Congo), and the Wildlife Conservation Society's Congo Program. Special thanks are due to J. M. Fay, P. Telfer, P. Elkan, S. Elkan, B. Curran, M. Gately, E. Stokes, T. Breuer, P. Ngouembe and D. Dos Santos. We would also like to recognize the tireless dedication of J. R. Onononga, C. Eyana-Ayina, S. Ndolo, A. Nzeheke, W. Mayoukou, M. Meguessa, I. Singono, and the Goualougo tracking team. We thank Laura Kurtycz for screening video footage at the Goualougo Video Analysis Laboratory at Lincoln Park Zoo. Grateful acknowledgment of funding is due to the U.S. Fish and Wildlife Service, the National Geographic Society, and the Columbus Zoological Park.

References

Baayen, R. H. (2008). *Analyzing linguistic data: A practice introduction to statistics using R*. Cambridge: Cambridge University Press.

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*(3), 255–278.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48.

Boesch, C. (1991). Teaching among wild chimpanzees. *Animal Behaviour*, *41*(3), 530–532.

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: Behavioural ecology and evolution.* Oxford: Oxford University Press.

Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology*, *78*(4), 547–573.

Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago: University of Chicago.

Byrne, R. W., & Rapaport, L. G. (2011). What are we learning from teaching? *Animal Behaviour*, *82*(5), 1207–1211.

Call, J., & Tomasello, M. (2008). Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Sciences*, *12*(5), 187–192.

Caro, T. M., & Hauser, M. D. (1992). Is there teaching in nonhuman animals? *The Quarterly Review of Biology*, *67*(2), 151–174.

Csibra, G., & Gergely, G. (2009). Natural pedagogy. *Trends in Cognitive Sciences*, *13*(4), 148–153.

Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B., & Laland, K. N. (2012). Identification of the social and cognitive processes underlying human cumulative culture. *Science*, *335*(6072), 1114–1118.

Dobson, A. (2002). *An introduction to generalized linear models*. Chapman & Hall/CRC.

Fogarty, L., Strimling, P., & Laland, K. N. (2011). The evolution of teaching. *Evolution*, *65*(10), 2760–2770.

Fouts, R., & Fouts, D. (1989). Loulis in conversation with the cross-fostered chimpanzees. In R. A. Gardner, B. T. Gardner, & T. E. Van Cantfort (Eds.), *Teaching sign language to chimpanzees*. SUNY Press.

Fragaszy, D., Biro, D., Eshchar, Y., Humle, T., Izar, P., Resende, B., & Elisabetta, V. (2013). The fourth dimension of tool use: Temporally enduring artefacts aid primates learning to use tools. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630), 20120410.

Fragaszy, D., & Perry, S. (2003). *The biology of traditions: Models and evidence*. Cambridge: Cambridge University Press.

Franks, N. R., & Richardson, T. (2006). Teaching in tandem-running ants. *Nature*, *439*(7073), 153.

Gilby, I. C. (2006). Meat sharing among the Gombe chimpanzees: Harassment and reciprocal exchange. *Animal Behaviour*, *71*(4), 953–963.

Heyes, C., & Galef, Bennett Jr. (1996). *Social learning in animals: The roots of culture*. San Diego: Academic Press.

Hoppitt, W., Brown, G., Kendal, R., Rendell, L., Thornton, A., Webster, M., & Laland, K. (2008). Lessons from animal teaching. *Trends in Ecology & Evolution*, *23*(9), 486–493.

Horner, V., Carter, J. D., Suchak, M., & de Waal, F. B. M. (2011). Spontaneous prosocial choice by chimpanzees. *Proceedings of the National Academy of Sciences*, *108*(33), 13847–13851.

Hothorn, T., & Hornik, K. (2015). exactRankTests: Exact distributions for rank and permutation tests. R package version 0.8-28.

Humle, T., & Snowdon, C. T. (2008). Socially biased learning in the acquisition of a complex foraging task in juvenile cottontop tamarins, *Saguinus oedipus*. *Animal Behaviour*, *75*(1), 267–277.

Kline, M. (2015). How to learn about teaching: An evolutionary framework for the study of teaching behavior in humans and other animals. *Behavioral and Brain Sciences*, *754*, 1–71.

Koops, K., Schöning, C., Isaji, M., & Hashimoto, C. (2015). Cultural differences in ant-dipping tool length between neighbouring chimpanzee communities at Kalinzu, Uganda. *Scientific Reports*, *5*(1).

Kruger, A. C., & Tomasello, M. (1998). Cultural learning and learning culture. In D. Olson & N. Torrance (Eds.), *Handbook of education and human development: New models of learning, teaching, and schooling* (pp. 369–387). Blackwell.

Lonsdorf, E. (2006). What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Animal Cognition*, *9*(1), 36–46.

Lonsdorf, E., & Bonnie, K. E. (2010). Opportunities and constraints when studying social learning: Developmental approaches and social factors. *Learning & Behavior, 38*(3), 195–205.

Luncz, L. V, & Boesch, C. (2015). The extent of cultural variation between adjacent chimpanzee (*Pan troglodytes verus*) communities; A microecological approach. *American Journal of Physical Anthropology*, *156*(1), 67–75.

Maestripieri, D. (1995a). First steps in the macaque world: Do rhesus mothers encourage their infants' independent locomotion? *Animal Behaviour, 49*(6), 1541–1549.

Maestripieri, D. (1995b). Maternal encouragement in nonhuman primates and the question of animal teaching. *Human Nature*, *6*(4), 361–378.

Mangold. (2015). INTERACT 14 User guide. Mangold International GmbH.

Matsuzawa, T. (2011). Education by master-apprenticeship. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), *The Chimpanzees of Bossou and Nimba* (pp. 201–208). Tokyo: Springer Japan.

Mundry, R., & Fischer, J. (1998). Use of statistical programs for nonparametric tests of small samples often leads to incorrect P values: Examples from Animal Behaviour. *Animal Behaviour, 56*(1), 256–259.

Musgrave, S., Bell, E., Morgan, D., Lonsdorf, E., & Sanz, C. (2015). Preliminary report on the acquisition of tool-using elements during termite gathering among chimpanzees of the Goualougo Triangle, Republic of Congo. In *Supplement to the American Journal of Physical Anthropology,156 (Suppl. 60)* (pp. 232–232).

Nishida, T., & Hiraiwa, M. (1982). Natural history of a tool-using behavior by wild chimpanzees in feeding upon wood-boring ants. *Journal of Human Evolution*, *11*(1), 73–99.

Pearson, A. (1989). *The teacher: Theory and practice in teacher education*. New York: Routledge.

Premack, D., & Premack, A. (1996). Why animals lack pedagogy and some cultures have more of it than others. In D. Olson & N. Torrance (Eds.), *The handbook of education and human development: New models of learning, teaching and schooling* (pp. 302–323). Malden: Blackwell.

Pruetz, J. D., & Lindshield, S. (2012). Plant-food and tool transfer among savanna chimpanzees at Fongoli, Senegal. *Primates*, *53*(2), 133–145.

R Core Team. (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Raihani, N. J., & Ridley, A. R. (2008). Experimental evidence for teaching in wild pied babblers. *Animal Behaviour, 75*(1), 3–11.

Rapaport, L. G., & Brown, G. R. (2008). Social influences on foraging behavior in young nonhuman primates: Learning what, where, and how to eat. *Evolutionary Anthropology: Issues, News, and Reviews*, *17*(4), 189–201.

Sanz, C., Call, J., & Morgan, D. (2009). Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biology Letters*, *5*(3), 293–296.

Sanz, C., & Morgan, D. (2007). Chimpanzee tool technology in the Goualougo Triangle, Republic of Congo. *Journal of Human Evolution*, *52*(4), 420–433.

Sanz, C., & Morgan, D. (2010). The complexity of chimpanzee tool-use behaviors. In E. Lonsdorf, S. R. Ross, & T. Matsuzawa (Eds.), *The mind of the chimpanzee: Ecological and experimental perspectives* (pp. 127–140). Chicago: University of Chicago Press.

Sanz, C., & Morgan, D. (2013a). Ecological and social correlates of chimpanzee tool use. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630), 20120416.

Sanz, C., & Morgan, D. (2013b). The social context of chimpanzee tool use. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 161–175). Cambridge: Cambridge University Press.

Sanz, C., Morgan, D., & Gulick, S. (2004). New insights into chimpanzees, tools, and termites from the Congo Basin. *The American Naturalist*, *164*(5), 567–581.

Schielzeth, H., & Forstmeier, W. (2009). Conclusions beyond support: Overconfident estimates in mixed models. *Behavioral Ecology*, *20*(2), 416–420.

Siegel, S., & Castellan Jr., N. J. (1988). Measures of association and their tests of significance. In *Nonparametric statistics for the behavioral sciences* (pp. 190–222). New York: McGraw-Hill.

Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: On the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1528), 2405–2415.

Thornton, A., & Clutton-Brock, T. (2011). Social learning and the development of individual and group behaviour in mammal societies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1567), 978–987.

Thornton, A., & McAuliffe, K. (2006). Teaching in wild meerkats. *Science*, *313*(5784), 227–229.

Thornton, A., & Raihani, N. J. (2008). The evolution of teaching. *Animal Behaviour*, *75*(6), 1823–1836.

Whiten, A. (2005). The second inheritance system of chimpanzees and humans. *Nature*, *437*(7055), 52–55.

Whiten, A., Goodall, J., McGrew, W., Nishida, T., Reynolds, V., Sugiyama, Y., … Boesch, C. (2001). Charting cultural variation in chimpanzees. *Behaviour*, *138*(11–12), 1481–1516.

Yamamoto, S., Humle, T., & Tanaka, M. (2012). Chimpanzees' flexible targeted helping based on an understanding of conspecifics' goals. *Proceedings of the National Academy of Sciences*, *109*(9), 3588–3592.

Chapter 4: Differences in Prosociality between Wild Chimpanzee Populations

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4.1 Abstract

Prosociality is hypothesized to have contributed to the evolution of cumulative culture, including technology. The transfer of tools is common in humans and is a type of prosocial helping through which skilled practitioners facilitate skill development in less competent tool users. The occurrence of object transfer is variable in other taxa, both between and within species and across natural and captive settings. Applying a standardized method, we compared the tool transfer behavior of chimpanzees in the Goualougo Triangle, Republic of Congo, and in Gombe, Tanzania. Multiple measures indicated population differences in prosociality. The rate of tool transfers as well as the probability of tool transfer upon request were significantly higher at Goualougo, while resistance to tool transfers was significantly higher at Gombe. Active transfers of tools in which possessors moved to facilitate possession change were the most common transfer type at Goualougo, but were not observed at Gombe. In contrast, requests for tools were typically refused in the Gombe population. These differences in the rate, probability, and types of tool transfer may relate to task complexity and tool characteristics. At Goualougo, chimpanzee tools show several aspects of design complexity including manufacture from specific raw materials and modifications that improve tool efficiency, which could make it challenging for novices to independently manufacture suitable tools. We suggest that wild chimpanzees have a flexible capacity for prosocial helping and that prosociality may promote the social transmission of complex technological skills.

4.2 Introduction

The emergence of cumulative technology is a defining aspect of human evolution. Identifying the social factors that facilitate the transfer of complex skills in humans and other animals is essential for modeling the pedagogical settings that may have accompanied the inception of hominin tool technologies (Boyd & Richerson, 1985; Dean, Kendal, Schapiro, Thierry, & Laland, 2012; Tennie, Call, & Tomasello, 2009). Among modern humans, competent tool users scaffold the development of technological skills in novices with a range of strategies, one of which is the provisioning of tools (Lew-Levy, Reckin, Lavi, Cristóbal-Azkarate, & Ellis-Davies, 2017). For example, Aka mothers in the Congo Basin provide children with artefacts such as axes, digging sticks, or baskets, sometimes even producing child-sized versions (Hewlett, Fouts, Boyette, & Hewlett, 2011). In West Papua New Guinea, young boys are gifted bows and arrows long before they can themselves manufacture these tools (Nishiaki, 2013). Konso women living in southern Ethiopia pass lithic expertise to daughters and granddaughters, whose early apprenticeship involves using tools produced by experienced practitioners (Arthur, 2010). Novices typically spend many years learning to manipulate specific raw materials and honing the skills to craft high-quality tools (Lew-Levy et al., 2017). Access to skilled individuals' tools provides novices with information and experience they cannot yet acquire on their own.

Access to experts' tools can also aid in skill development in other taxa, particularly when choosing or manufacturing tools involves selectivity for raw material or design complexity (Meulman, Seed, & Mann, 2013). For example, both capuchins (Spagnoletti, Visalberghi, Ottoni, Izar, & Fragaszy, 2011) and chimpanzees (Boesch & Boesch-Achermann, 2000; Luncz, Mundry, & Boesch, 2012; Matsuzawa, 1994) consider nut resistance when selecting percussive tools for nut-cracking. *Tool reuse* is one way in which novices can acquire an expert's tool. This involves an individual recovering another's discarded tool, regardless of whether the original possessor is still in proximity to the tool or has abandoned it (Izar et al., 2013). Tool reuse has been documented in chimpanzees, macaques, capuchins, and New Caledonian crows (Biro et al., 2003; Boesch & Boesch-Achermann, 2000; Fragaszy et al., 2013; Hirata & Celli, 2003; Holzhaider, Gray, & Hunt, 2010; Holzhaider, Hunt, & Gray, 2010; Meulman et al., 2013; Tan, 2016). Novices can also acquire experts' tools via *tool transfer:* a transfer occurs when an individual takes possession or is given a tool by the original owner, when the original owner still has the tool in their possession or vicinity immediately before the change of possession. Tool transfers can be associated with multiple costs to the original possessor (Musgrave, Morgan, Lonsdorf, Mundry, & Sanz, 2016), and there are potential differences between tool reuse and tool transfer from the perspective of investment.

There is substantial variation across species in the prevalence of object transfer. Chimpanzees and capuchins actively transfer objects in captive settings (e.g., Barnes, Hill, Langer, Martinez, & Santos, 2008; Drayton & Santos, 2014; Melis & Tomasello, 2013; Rosati, DiNicola, & Buckholtz, 2018; Warneken & Tomasello, 2006; Yamamoto, Humle, & Tanaka, 2009, 2012), while this is rare or undocumented in other tool-using taxa and in captive bonobos. In addition, wild chimpanzees routinely transfer tools in different tool contexts (Boesch, 1991; Inoue-Nakamura & Matsuzawa, 1997; Lonsdorf, 2006; Matsuzawa et al., 2001; Musgrave et al., 2016; Nishida & Hiraiwa, 1982; Pruetz & Lindshield, 2012; Sanz & Morgan, 2013b). These findings suggest that the capacity for tool transfer may also be flexible within particular species, according to context.

Broadly, prosocial behaviors are a form of cooperative behavior in which an individual performs an action that benefits another. Humans show proactive prosocial behavior across multiple contexts, and these behaviors are prevalent across societies (Fehr & Fischbacher, 2003;

Henrich et al., 2001). Prosocial behavior does vary, however, between and within cultures (Gurven & Winking, 2008; Gurven, Zanolini, & Schniter, 2008; House et al., 2013; Richerson et al., 2016; Schäfer, Haun, & Tomasello, 2015). In addition, while children help flexibly and spontaneously from a young age on (Melis & Warneken, 2016), the emergence of prosocial behaviors over development is sensitive to variation in socialization practices (Callaghan & Corbit, 2018). Complex interactions of biological, social, and cultural factors thus shape the expression of human prosocial behavior across contexts and over the lifetime (Hepach & Warneken, 2018).

Prosocial acts are also widespread in other animals (Bartal, Decety, & Mason, 2011; Clutton-Brock, 2002; Dugatkin, 1997; Nakahara et al., 2017; Schwab, Swoboda, Kotrschal, & Bugnyar, 2012) including nonhuman primates (Cronin, 2012; de Waal & Suchak, 2010; Jaeggi, Burkart, et al., 2010; Marshall-Pescini, Dale, Quervel-Chaumette, & Range, 2016; Yamamoto & Takimoto, 2012). Evidence of prosociality in wild chimpanzees includes social grooming, assisting each other in conflicts, jointly patrolling territory borders, and adopting orphaned infants (Boesch & Boesch-Achermann, 2000; Boesch, Bolé, Eckhardt, & Boesch, 2010; Goodall, 1986; Mitani, Merriwether, & Zhang, 2000; Watts, 2002), and in certain circumstances, food sharing (de Waal, 1989; Gilby, 2006; Samuni, Preis, et al., 2018; Silk, Brosnan, Henrich, Lambeth, & Shapiro, 2013). Transferring a tool is a type of helping behavior that may involve varying degrees of prosociality (Jaeggi, Burkart, & van Schaik, 2010) ranging from proactive to reactive to passive (Fig. 1).

From one perspective, prosocial actions in humans can be considered qualitatively different than those shown by other animals. Proactive prosociality in particular is hypothesized to be a derived and uniquely human trait (Jensen, 2016; Silk et al., 2005). The evolutionary origins of human prosociality have been linked to the adoption of cooperative breeding practices (Burkart et al., 2014; Burkart, Fehr, Efferson, & van Schaik, 2007; Burkart, Hrdy, & van Schaik, 2009; Burkart & van Schaik, 2016; Hrdy, 2009); elaborated theory of mind skills (Silk et al., 2005); increased sensitivity to an audience, internalized as a "conscience" (Jaeggi, Burkart, et al., 2010); and costly signaling, whereby males in particular advertise their value as a future mate or cooperative partner (Hockings et al., 2007; Jaeggi, Burkart, et al., 2010).

From another perspective, prosocial behavior in humans builds on a common foundation of skills and motivations that are shared with other taxa and it is the scope and flexibility of prosocial behaviors that differ (Melis, 2018; Melis & Warneken, 2016; Tan & Hare, 2013; Warneken & Tomasello, 2009). The "versatile prosociality hypothesis" suggests that nonhuman great apes as well as humans are capable of direct transfers, defined as handing over items in one's possession, but that the contexts that elicit these transfers differ among species. Examining prosocial actions in the context of direct transfers is ideal for facilitating comparisons of prosocial responses between humans and other taxa, as this is what characterizes much of humans' sharing of food and non-food items (Krupenye, Tan, & Hare, 2018).

In line with the "versatile prosociality hypothesis", bonobos and chimpanzees exhibit differing prosociality profiles. Bonobos willingly share food, even with strangers, but rarely toys or tools (Hare & Kwetuenda, 2010; Hare, Melis, Woods, Hastings, & Wrangham, 2007; Krupenye et al., 2018; Tan & Hare, 2013; Yamamoto, 2015; but see Cronin, De Groot, & Stevens, 2015; Jaeggi, Stevens, & van Schaik, 2010). The high prosocial tendencies of bonobos in feeding contexts are attributed to selection for tolerance and against aggression in this species (Hare, 2017; Hare, Wobber, & Wrangham, 2012; Wrangham & Pilbeam, 2002). Particularly in captive settings, chimpanzees, compared to bonobos, show more limited evidence for prosocial food sharing (Amici, Visalberghi, & Call, 2014; Jensen, Hare, Call, & Tomasello, 2006; Silk et al., 2005; Vonk et al., 2008; but see Horner, Carter, Suchak, & de Waal, 2011; Melis et al., 2011), which could be due to a more competitive preoccupation with food (Boysen & Berntson, 1995; Cronin, 2012; Hirata, 2007). However, hunting and resource sharing do have a cooperative basis in some wild chimpanzee populations (Boesch, 1994; Samuni, Deschner, Crockford, Wittig, & Preis, 2018; Samuni, Preis, et al., 2018), suggesting that the occurrence of these behaviors are sensitive to contextual, ecological, and social factors (Boesch, 1994; Gilby, Eberly, Pintea, & Pusey, 2006; Jaeggi & van Schaik, 2011; Samuni, Preis, et al., 2018; Watts & Mitani, 2002). In contrast to bonobos, chimpanzees routinely share objects and show prosocial helping in captive experiments (Warneken & Tomasello, 2006; Warneken et al., 2007; Hare et al., 2007; Yamamoto et al., 2009). Chimpanzees will even transfer the specific tool a conspecific requires, indicating that they are capable of understanding others' goals (Yamamoto et al., 2012). The reasons for these species differences in prosocial object transfer are not immediately apparent, but could be related to differing intrinsic propensities toward object manipulation (Koops, Furuichi, & Hashimoto, 2015).

Species differences in the presence and strength of prosocial helping could thus result from differences both in intrinsic motivations and in sensitivity to extrinsic factors (Jaeggi, Burkart, et al., 2010). In addition, ecological settings or task features, including task complexity, could be associated with inter- and intraspecific variation in prosocial helping. In humans, success at solving tasks of increasing difficulty levels varies with the number of prosocial acts received, indicating that prosocial helping facilitates the social transmission of complex tasks (Dean et al., 2012). Investigating tool transfer behaviors across tool tasks of differing complexity in wild chimpanzee populations can help us identify which factors prompt these behaviors and understand the evolutionary contexts that favor prosocial helping.

Using a standardized method, we compared tool transfers in the context of termite gathering by chimpanzees in the Goualougo Triangle, Republic of Congo, with those in Gombe, Tanzania. Both of these chimpanzee populations exhibit a minimum of 22 different types of tool use, comprising some of the largest tool repertoires of any nonhuman tool-user (Sanz & Morgan, 2007). There are differences in termite-gathering behavior between Goualougo and Gombe populations that reflect broader regional patterns for chimpanzees in Central and East Africa, respectively. In Central Africa, chimpanzees gather invertebrate resources with the aid of tool sets, which involve the sequential use of two or more different tools (Brewer & McGrew, 1990). These behaviors differ from the use of single tools by chimpanzee populations in East and West Africa (Sanz, Morgan, & Gulick, 2004). There are also regional differences in tool selection and manufacture. In the Goualougo Triangle, chimpanzees manufacture fishing probes and puncturing sticks from selected raw plant materials (Sanz & Morgan, 2007). They also intentionally modify herb probes to fashion brush tips, a design feature which has been shown to be more efficient than an unmodified probe for gathering insects (Sanz, Call, & Morgan, 2009). At Gombe, individuals use one tool type, fishing probes, to acquire termites, and probes can be manufactured from various materials such as grass, twigs, or bark (Goodall, 1968; McGrew, Tutin, & Baldwin, 1979).

Given the specific requirements of tool manufacture at Goualougo, we hypothesized that there would be greater need and benefit associated with transferring tools to youngsters during termite gathering in this population relative to termite fishing at Gombe. Indeed, immature chimpanzees at Goualougo obtain significant increases in tool use and feeding after being transferred a fishing probe (Musgrave et al., 2016). We thus predicted that there would be a higher overall rate of tool transfer at Goualougo compared to Gombe, that requests or attempts to take tools would more often result in a change of possession at Goualougo compared to Gombe, and that rates of resistance by tool possessors would be lower at Goualougo compared to Gombe. We predicted that population differences would be strongest for reactive transfers, as response to request is considered a more precise index of prosocial motivation relative to a possessor simply tolerating another's action (Cronin, 2012; Jaeggi, Burkart, et al., 2010). We also predicted that at Goualougo there would be a shorter latency between requesting behavior and transfers, as shorter latencies correspond to more prosocial responses (Rosati et al., 2018).

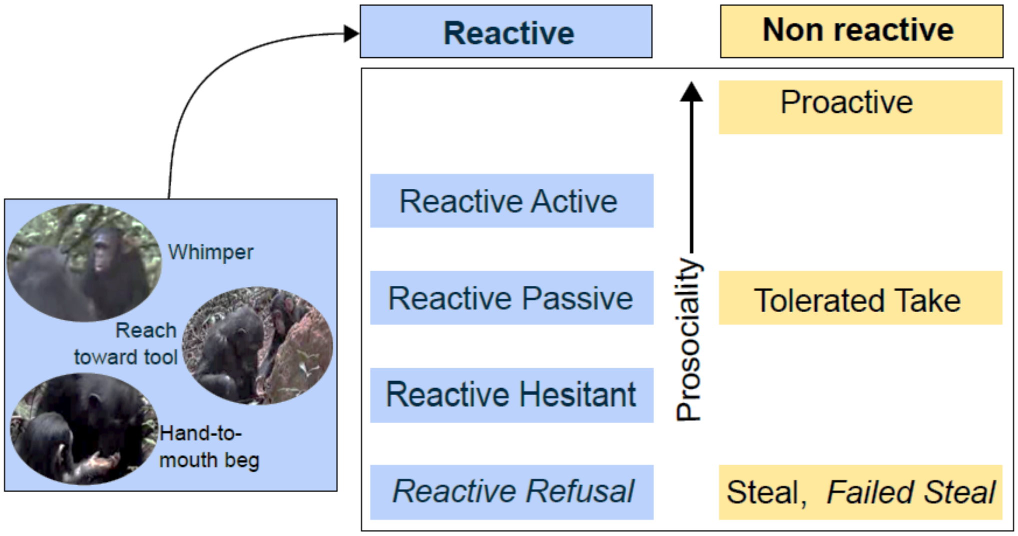

FIGURE 4.1. Categorization of transfer types according to the level of prosociality. Transfer types are arranged vertically from most (top) to least (bottom) prosocial. Transfers are grouped into two categories: reactive (blue) in which the potential recipient first requests the tool by whimpering and/or reaching toward the tool, or (rarely, at Gombe only) by making hand-to-mouth gestures; and non-reactive (yellow) in which the recipient receives, takes or attempts to take the tool without first requesting it. While reactive and non-reactive transfer types are presented together, note that Reactive Active, Reactive Passive and Reactive Hesitant transfers may more clearly index prosocial behavior, as they inherently involve a possessor physically relinquishing a tool, while non-reactive transfers are more ambiguous (Jaeggi, Burkart, et al., 2010). Reactive Refusal transfers, and Steal / Failed Steal transfers, are ranked comparably because for each of these, the possessor does not, or does not willingly, relinquish a tool; thus these are not considered prosocial. Italics indicate that no possession change occurs.

4.3 Methods

4.3.1 Study Sites

Goualougo Triangle, Republic of Congo: The Goualougo Triangle is located in the southern section of the Nouabalé-Ndoki National Park (E 16°51′−16°56′; N 2°05′−3°03′). The study area includes 380 km^2 of evergreen and semi-deciduous lowland forest, and altitudes range between 330 and 600 meters. There is a primary rainy season from August to November and a short rainy season in May. Termite gathering occurs year-round and is not related to seasonally varying resource abundance (Sanz & Morgan, 2013a).

Gombe, Tanzania: Gombe National Park is located on the shore of Lake Tanganyika, at the western border of Tanzania. The park comprises 35 km^2 of woodland, grassland, and riverine forest (Clutton-Brock & Gillet, 1979). Chimpanzees termite fish year round, but particularly during the rainy season from October to December (Goodall, 1986; McGrew et al., 1979).

4.3.2 Data Collection

Data collection was undertaken in the Goualougo Triangle using remote cameras with passive infrared sensors to record chimpanzee tool behavior at termite nests. These data were archived on hard drives and converted to MPEG for review. We screened 224 hours of video footage recorded between 2003 and 2011 and analyzed video footage using INTERACT 15 (Mangold, 2015).

At Gombe, all day focal follows (Altmann, 1974) on mothers with immature (under age 11) offspring were performed over the course of four termite-fishing seasons between 1998 and 2001. Once termite fishing commenced, 15-minute, video-taped follows were conducted, during which the observer narrated information on tool use, apparent success, and social interactions at the mound (Lonsdorf, 2005).

Using a standardized protocol applied to videos from Goualougo and Gombe, we coded footage for all instances of immature chimpanzees requesting or attempting to take tools, type of tool transfer event, requesting behavior, and any instance of resistance by tool possessors. We included age, sex, and identity of individuals involved in transfers in our analyses, given the potential influence of these variables in the context of tool skill acquisition among young chimpanzees (Boesch & Boesch-Achermann, 2000; Inoue-Nakamura & Matsuzawa, 1997; Lonsdorf, 2005).

Transfer rate: We coded the duration of time individuals were present at a termite nest during which there was an opportunity for a tool transfer. This was defined as another individual being present and in possession of a termite-gathering tool. We calculated the rate of tool transfer for each individual by dividing the number of transfer events observed by the total duration of transfer opportunity scored in minutes.

Fishing Probe Transfer Type: We classified all fishing probe tool transfer events according to transfer event type. Transfer event types were defined on the basis of several criteria: whether or not they were preceded by a request (reactive versus non-reactive, respectively); whether or not the tool changed possession from one individual to another; and whether at the time preceding the transfer event the possessor was in physical possession (tool held in mouth, hand or foot) or spatial possession (tool must be either within one meter of possessor or in passive contact with possessor's body, *and* tool can be readily identified as a previous tool of the individual). Transfer event types were further differentiated according to whether the tool possessor protested against the transfer (Table 1).

Requests: We coded all request behavior after first scoring video clips for whether or not audio was sufficient to detect vocalizations and whether visibility of the individuals involved in the transfer was sufficient to allow for coding of manual gestures. In contrast to Gilby's (2006) definition with respect to begging for meat, merely sitting and staring within three meters of a tool possessor was not sufficient to be considered begging in this study. This approach is justified given the well-known practice of young chimpanzees to observe tool use at close proximity (Lonsdorf, 2006). As such, to be classified as begging, *both* close proximity (within three meters) and orientation to a tool possessor had to be present *and* accompanied by either a whimper vocalization (Goodall, 1989; Nishida, Kano, Goodall, McGrew, & Nakamura, 1999; Plooij, 1984), a whimper face (Parr, Waller, Vick, & Bard, 2007), or a manual gesture. For example, if a whimper vocalization was detected, it was not scored as begging unless the individual was also in the possessor's proximity and oriented towards the possessor. Whimpering often occurred as an ongoing sequence and so was scored once per transfer event, while all manual gestures were coded and categorized as follows: manual gestures included reaches towards the fishing probe, where the individual extends a hand towards, or touches (but does not grasp), the tool in a slow manner indicative of a request, as well as hand-to-mouth begging gestures (Goodall, 1989; Plooij, 1984). If an individual first grasped a probe without a preceding request, this was considered an attempt to take, rather than to request the tool, and the classification of the transfer automatically diverted to the non-reactive transfer types.

<u>Request Latency:</u> We determined the amount of time in seconds that elapsed between the first request for a fishing probe and a change of possession. In the case of manual gestures, the time of the request was coded at the initiation of movement.

<u>Resistance:</u> We identified all occurrences of a possessor exhibiting a negative reaction in response to requests or attempts to take tools. This could include instrumental actions to prevent an individual from reaching for or getting a tool, for example extending a hand or foot to hold an

individual off or push an individual’s hand away. Resistance also included actions such as threatening the individual who requests or attempts to take a tool by baring teeth, lunging, or barking.

4.3.3 Analyses

We first compared the rate of transfers of termite-gathering tools between sites for 14 individuals at Goualougo and 9 at Gombe with a Wilcoxon-Mann-Whitney U-test (Siegel & Castellan, 1988), using the wmwTest function in the asht R package (Fay & Malinovsky, 2018; R Core Team, 2018). Alpha level was set at 0.05 for all analyses. Next we compared transfers of fishing probes to immature individuals between populations as well as resistance to transfers by tool possessors. We observed 112 fishing probe tool transfer events at Goualougo and 106 at Gombe. When analyzing tool transfers, we excluded Steals (n=8 at both sites), as the negative reaction from the possessor precludes them from being prosocial. We then excluded any remaining transfers for which individual identity or sex could not be assigned (n=13 transfers at Goualougo) or when it was not clear whether there was a request (n=2 at Goualougo). Steals were retained for analyses of resistance.

While it would be ideal to use precise ages to compare populations, these were not available for all individuals in the Goualougo Triangle study (initiated in 1999, compared to research at Gombe, which was initiated in 1960) and dramatically reduced our sample size. Therefore, we adopted Estienne, Robira, Mundry, Deschner, & Boesch's (2019) approach of classifying chimpanzee ages from camera trap footage into three age class bins (0-5 years, 5-10 years, and 10-15 years).

We used Generalized Linear Mixed Models (GLMMs) (Baayen, 2008) with binomial error structure and logit link function (McCullagh & Nelder, 1989) to test our first prediction that at Goualougo, compared to Gombe, chimpanzees would be more successful gaining possession of another's tool. The key terms with fixed effects in this model were *population* and its interaction with *request status* (i.e., whether the potential recipient requested a tool transfer). We further included fixed effects for the main effect of *request status, recipient age,* and *recipient sex*. The identity of the possessor, the recipient, and the dyad (unique possessor-recipient combination) were included as random effects. We also examined the probability of tool transfer for the reactive transfers only, since these are considered a stronger indicator of prosocial motivation (Cronin, 2012; Jaeggi, Burkart, et al., 2010). As this model included only the subset of transfers that involved a request, it lacked the effects *request status* and the interaction of *population* and *request status*. Finally, we tested whether the tool possessor showed signs of resisting tool transfers. This model was identical to the tool transfer model. Sample sizes for these models were 187 observations (89 transfers) of 29 possessors and 28 recipients forming 42 dyads (tool transfer model); 101 observations (49 transfers) of 22 possessors and 23 recipients, forming 31 dyads (reactive tool transfer model); and 201 observations (with 43 cases of resistance) of 31 possessors and 30 recipients forming 44 dyads (resistance model).

Of the reactive transfers at Goualougo with known outcome, a subset of 38 both met the criteria for measuring latency and involved a change of tool possession; of the reactive transfer events at Gombe, a subset of 7 met criteria for measuring latency and involved a change of tool possession. However, we were unable to fit a model for assessing latency to transfer tools, largely because of the small number of data available for Gombe.

In order to avoid cryptic multiple testing, we first compared each full model with a respective null model lacking population and the interactions it was involved in (if there was one in the respective full model) but was otherwise identical to the full model (Forstmeier &

Schielzeth, 2011). This comparison was based on a likelihood ratio test (Dobson 2002).

All analyses were conducted in R (version 3.4.4) (R Core Team, 2018). We fitted all GLMMs using the function glmer of the lme4 package (version 1.1-17; Bates, Mächler, Bolker, & Walker, 2015). We checked for absence of collinearity (Field, 2005) among predictor variables using the function vif of the package car (Fox & Weisberg, 2011) applied to a standard linear model lacking the random effects. Collinearity was not an issue in any of the models (Maximum Generalized VIF (squares of the n^{th} root of GVIF, with n being twice the degrees of freedom of the respective predictor): tool transfer model: 1.249; reactive tool transfer model: 1.26; resistance model: 1.228; Fox & Monette, 1992).

We assessed model stability by excluding levels of the random effects one at a time, fitting the respective full model to the subsets, and comparing the estimates derived with those obtained from the model for the whole data set. We tested the significance of the individual predictors using likelihood ratio tests comparing the full models with respective reduced models lacking the effect in question (Barr, Levy, Scheepers, & Tily, 2013; Dobson, 2002). To obtain confidence intervals of model coefficients we used a parametric bootstrap using the function bootMer of the package lme4 (Bates et al., 2015).

4.4 Results

4.4.1 Tool Transfers

Transfer Rate

We detected a significant difference between populations in the rate of tool transfer behavior (Mann-Whitney estimate=0.21, 95% CI=0.04-0.46, *P*=0.026). Transfer rate for immature chimpanzees was an average of 0.06 transfers/minute at Goualougo (14 individuals, n=45 transfers) and 0.02 transfers/minute at Gombe (9 individuals, n=33 transfers). Transfer rate at Goualougo ranged from 0–0.12/minute, and at Gombe from 0–0.09/minute. At both sites, there were several immatures who experienced multiple transfers on the same day (Goualougo, 6/14 individuals; Gombe, 3/9 individuals).

Possession Change of Fishing Probes

Tool transfer probability clearly differed between the two populations (full null model comparison: χ^2=16.195, *df*=2, *P*<0.001), whereby we found a significant interaction between population and request status (χ^2=9.687, *df*=1, *P*=0.002). In fact, while the probability of a transfer was similar in Gombe and Goualougo when the tool was not requested, the probability of a transfer after a request was considerably higher in Goualougo as compared to Gombe (Fig. 4.2; Appendix C, Table C.1). We also detected significant effects of the two control predictors recipient age (1.915±1.144, χ^2=7.260, *df*=2, *P*=0.027) and sex (-1.489±0.746, χ^2=4.064, *df*=1, *P*=0.044) whereby the probability of a transfer was higher in the 5-10 year age class relative to the 0-5 year age class, and was higher for females.

The reactive tool transfer model, including only the subset of transfer events preceded by request, also revealed a clear difference between populations, with a higher probability of transfer following a request at Goualougo compared to Gombe (full null model comparison: χ^2=7.400, *df*=1, *P*=0.007; Fig. 4.3; Appendix C, Table C.2).

Fishing Probe Transfer Event Types

With respect to types of tool transfer events, 63/110 (57.3%) at Goualougo and 47/106 (44.3%) at Gombe were reactive (preceded by a request). At Goualougo, 48/63 of these requests (76.2%) resulted in a change of tool possession, compared to 7/47 requests (14.9%) at Gombe. The most common type of reactive transfer at Goualougo was Reactive Active (n=22, 19.6%), and this was also the most frequently observed transfer type at Goualougo overall (Table 4.1).

No Reactive Active transfer events occurred at Gombe. In contrast, the most numerous transfer event type was Reactive Refusal (n=40, 85%), consisting of a request followed by the possessor's refusal to transfer the tool.

In both populations, immature chimpanzees also attempted to take tools without first requesting them. At Goualougo, novices were sometimes permitted to take tools without a reaction (Tolerated Take, n=15); novices also stole (Steal, n=8) or attempted to steal (Failed Steal, n=16) tools. At Gombe, chimpanzees were also permitted to take tools without a reaction (Tolerated Take, n=26), and, as at Goualougo, novices occasionally also stole (Steal, n=8) or attempted to steal (Failed Steal, n=15) tools.

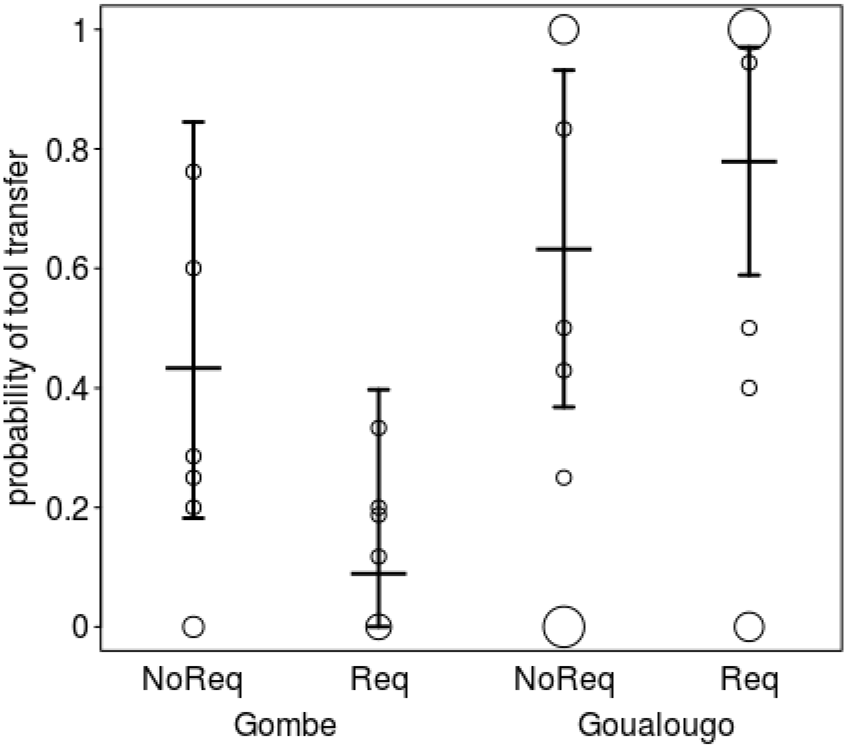

FIGURE 4.2. Tool transfer probability and how it depended on tool request status and population. Indicated are the fitted model and its confidence limits (horizontal lines with error bars), and the observed transfer probabilities per possessor. The area of the symbols depicts the number of possessors per population and request status with the same transfer probability, such that larger symbols correspond to a greater number of possessors at that value (range: 1 to 8).

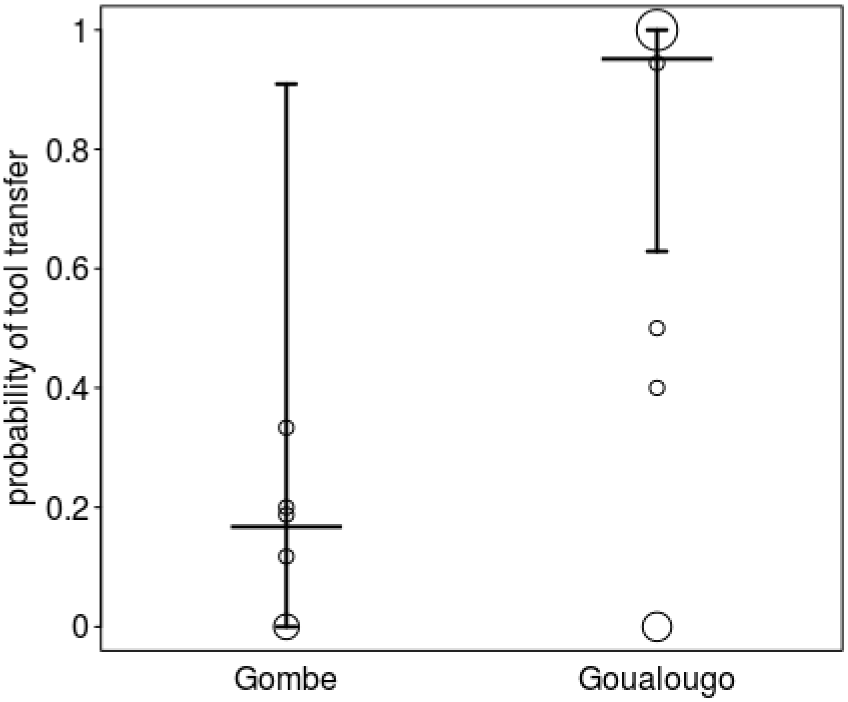

FIGURE 4.3. Probability of reactive tool transfer and how it differed between populations. Indicated are the fitted model and its confidence limits (horizontal lines with error bars), and the observed transfer probabilities per possessor. The area of the symbols depicts the number of possessors per population with the same transfer probability, such that larger symbols correspond to a greater number of possessors at that value (range: 1 to 8).

TABLE 4.1 Definition of transfer types as well as counts and percentages of fishing probe transfer types for each population. n= number of transfers.

Transfer Type[a]	Definition	Goualougo (n=110)		Gombe (n=106)	
		n	%	n	%
Preceded by request					
Reactive Active	Possessor moves to facilitate the transfer or divides the tool so that the recipient can take a portion[b] (U,	22	20%	0	0%
Reactive Passive	Possessor allows the recipient to take tool. Possessor shows neither facilitation nor hesitation[c] (U, P).	10	9.1%	2	1.9%
Reactive Hesitant	The recipient begs, then grasps the tool; the possessor transfers the tool only after delaying or resisting the transfer (U, P, S[d]).	12	10.9%	5	4.6%
Reactive Refusal	Possessor does not transfer tool despite begging; refusal can involve actively resisting transfer such as pulling away (U, P).	14	12.7%	40	37.0%
Reactive, Possession change	Tool changes possession after a beg but the possessor's reaction is not visible, preventing further categorization (U, P).	4	3.6%	0	0%
Reactive, unknown possession change	It cannot be discerned whether tool changes possession after a beg, and the possessor's reaction is not visible, preventing further categorization (U, P).	1	0.9%	0	0%
	Total number of requests	63	57.3%	47	44.3%
Not preceded by request					
Proactive	Possessor initiates transfer and tool changes possession (U, P).	0	0	0	0%
Tolerated Take	Possessor allows recipient to take tool. Possessor shows neither facilitation nor hesitation[e] (U, P, S).	15	13.6%	26	24.5%
Steal	Recipient takes tool from possessor, who reacts negatively (e.g., attempts to keep tool or threatens the stealer[f,g]) (U, P, S).	8	7.1%	8	7.4%
Failed Steal	Recipient tries unsuccessfully to take the possessor's tool. The possessor exhibits a negative reaction, as in "Steal" (U, P, S).	16[h]	14.3%	15	13.9%
Failed Attempt	Recipient tries unsuccessfully to take the possessor's tool. The possessor does not react (U, P, S).	8	7.1%	10	9.3%
	Total number of take attempts	47	42%	59	54.6%

a. Transfer types were categorized according to whether or not they were preceded by a request, whether a possession change occurred, whether the tool possessor protested the transfer, and whether at the time of transfer the tool was in use (U), Physical Possession (P) or Spatial Possession (S). The table excludes the 2 transfers for which it could not be discerned whether or not there was a request. b. *Sensu* Pruetz & Lindshield (2012), “active-passive” and “active” transfer. c. *Sensu* Pruetz & Lindshield (2012), “passive”. d. Transfers could be classified as a Reactive Hesitant transfer if a tool was in the possessor’s spatial possession at the time of possession change only if the tool was *initially* in use or physical possession. For example, a Reactive Hesitant was coded if there was a request after which the possessor dropped the tool on the ground, and the recipient took possession. e. If tool was in use or in physical possession, this is equivalent to "passive" *if* there is no begging; if tool was in spatial possession, this is equivalent to "recovery" (Pruetz & Lindshield, 2012). f. Adapted from Gilby (2006). g. For similar approaches see Gilby (2006); Boesch & Boesch (1989); de Waal (1989, 1997b, 1997a); Stevens & Gilby (2004); and Pruetz & Lindshield (2012), “theft”. h. Includes one transfer that occurred in a play context.

4.4.2 Resistance

The probability of resistance differed between populations (full null model comparison: χ^2=7.211, *df*=2, *P*=0.027), and we again found a significant interaction between population and request status (χ^2=4.688, *df*=1, *P*=0.030; Appendix C, Table C.3). In fact, while resistance probability was generally low in Goualougo and also in Gombe when there was no request, this probability more than doubled in Gombe following a request (Fig. 4.4).

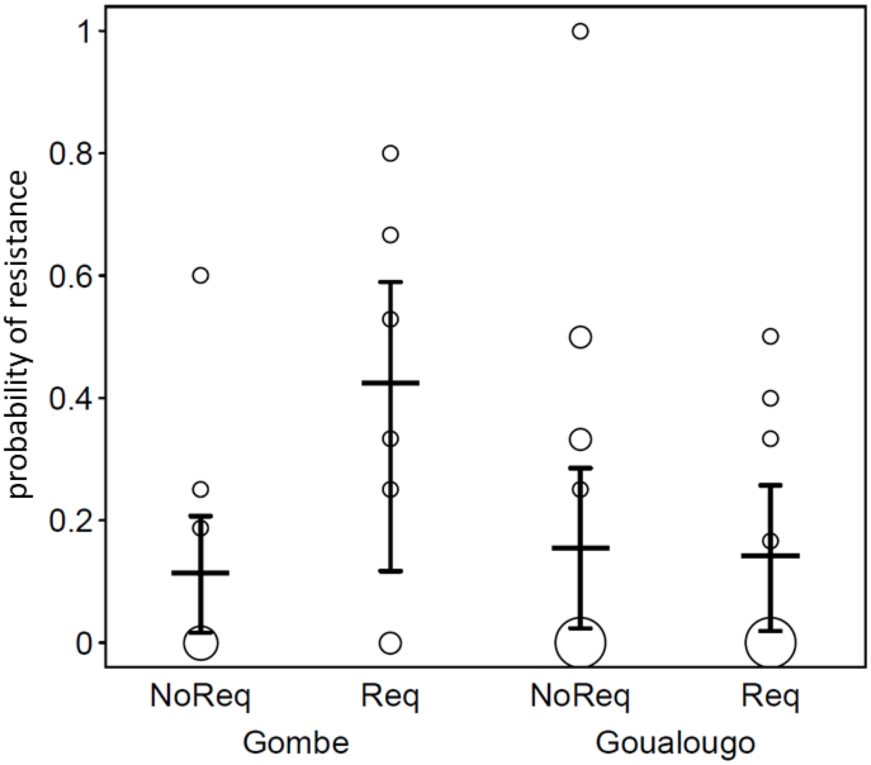

FIGURE 4.4. Resistance probability and how it depended on tool request status and population. Indicated are the fitted model and its confidence limits (horizontal lines with error bars), and the observed transfer probabilities per possessor. The area of the symbols depicts the number of possessors per population and request status with the same transfer probability, such that larger symbols correspond to a greater number of possessors at that value (range: 1 to 11).

4.4.3 Request Behavior and Latency to Transfer

Request behavior could be assessed for 31 transfers at Goualougo and 42 at Gombe. At Goualougo, requesting behavior most often involved a combination of reaching and whimpering together (n=17 transfers), followed by just reaching (n=10 transfers), or occasionally just whimpering (n=5 transfers). At Gombe, reaching (n=22 transfers) and reaching and whimpering (n=17) were observed, while only whimpering was not. At Gombe but not Goualougo, hand-to-mouth gestures were observed (n=3 transfers), twice along with reaches toward the tool and once in conjunction with whimpering.

At Goualougo, the mean latency in seconds between an immature chimpanzee begging for a tool and a possessor relinquishing it was 11 seconds (SD=7, n=38 transfers). At Gombe, the mean latency to tool transfer was 15.8 seconds (SD=18.3, n=7 transfers).

4.5 Discussion

Tool transfers are a common way in which humans scaffold the acquisition of skilled, tool-assisted foraging in novices, and these transfers exemplify the human propensity for prosocial helping. In this study, we systematically compared tool transfer behavior between two chimpanzee populations that use tools to gather termites. We found significant population differences in several indicators of prosociality, showing that prosocial helping was greater at Goualougo than at Gombe. First, we found that tool transfers occurred approximately three times as often at Goualougo as at Gombe. Second, we found that there was there was a higher probability of tool transfer following request at Goualougo. Request behavior makes an individual’s goals highly salient and so the possessor’s response to a request is a strong index of prosocial motivation (Cronin, 2012). Third, we found that requests were more likely to be met with resistance at Gombe than at Goualougo. Resistance behaviors provide a clear indicator that an individual is attempting to prevent tool transfer and are consistent with the differences found in prosocial response between Goualougo and Gombe. We further found population differences with respect to transfer types. We observed Reactive Active transfers only at Goualougo, and this active donation was the most common response by tool possessors at Goualougo. In contrast, at Gombe, we did not observe any Reactive Active transfers.

Active transfers are common in humans but had not previously been quantified in other animal tool users in natural settings. In captivity, chimpanzees help flexibly according to a recipient's needs (Yamamoto et al., 2012), and this behavior does not appear to be motivated by rewards (Warneken & Tomasello, 2008); nor does a desire to reduce harassment explain helping in captivity (e.g., Melis & Tomasello, 2013; Yamamoto, Humle, & Tanaka, 2009; Yamamoto et al., 2012) or among Goualougo chimpanzees (Musgrave et al., 2016). Thus, the voluntary, active transfers in this context provide a compelling indicator of prosociality (Jaeggi, Burkart, et al., 2010).

Chimpanzees in captive settings have further been observed to proactively transfer objects, without a preceding request, and we have also documented this at Goualougo. For example, we observed a tool transfer in which a juvenile male approached his mother while self-scratching but without gesturing or vocalizing, at which point his mother divided her fishing probe and provided him with one of the resulting tools (Supplementary Video). On another occasion, the same juvenile experienced difficulty inserting his fishing probe, at which point his mother handed her tool to him. While not included in the present analyses because they fell outside of the sample of video footage systematically screened for transfers, these interactions indicate that under certain circumstances chimpanzees can be sensitive not only to overt signals, but also to subtler signs of need (Jaeggi, Burkart, et al., 2010).

We detected significant population differences in fishing probe transfers between Goualougo and Gombe despite comparability of factors that are proposed to be important proximate regulators of prosocial response (Cronin, 2012; Jaeggi, Burkart, et al., 2010). These include intrinsic motivation and physical capabilities (same species), social distance between individuals (at both sites, transfers occurred principally between mothers and infants), proximity to food (the tool task involves extraction of embedded *Macrotermes* termites), and opportunity for a potential recipient to signal their need by making a direct request (both tasks occur in terrestrial contexts where chimpanzees can approach and make gestural and vocal requests in close proximity). Indeed, in both populations we observed requests for tools in the form of manual gestures and/or vocalizations, after which the requestor was sometimes either given (Goualougo) or was allowed to take (Goualougo and Gombe) a fishing probe. Requests for tools have previously been documented for chimpanzees and in a few cases for orangutans, but not for other primate species (Cronin, 2012). Our findings further underscore this potential difference between species in how signals of need prompt prosocial helping (Table 4.2). Further, the similarity of requests at Goualougo and Gombe indicates that population differences did not result from differences in the requestor's initiative, but from differences in the response of the tool possessors.

We suggest that these population differences in prosociality during tool use could reflect the differing complexity of the tool tasks between populations, particularly the material and design demands associated with production of tool sets at Goualougo. Transfers of fishing probes as well as other tool types in this context provides information about tool material and design and also provides an opportunity to practice with an appropriate tool. This may be particularly critical in cases where raw material and form influence tool effectiveness (e.g., Sousa, 2011; Sousa, Biro, & Matsuzawa, 2009; Tonooka, Tomonaga, & Matsuzawa, 1997), as is the case for brush-tipped fishing probes (Sanz et al., 2009) and likely also puncturing sticks. We have previously documented that tool transfers at Goualougo function as a form of teaching

(Musgrave et al., 2016). The present results thus highlight the intersection of high-fidelity social learning and prosocial helping in the context of this complex task, where it could be challenging for novices to acquire tools, and thus to develop tool skills, without assistance.

TABLE 4.2. The proximate regulation of instrumental helping in the best-studied primate species. Table is adapted from (Jaeggi, Burkart, et al., 2010, Table 2). ++ = observed in experimental and natural contexts; + = observed in at least 1 context; - = absent in both contexts; (-) possibly absent or not yet documented.

	Humans	**Chimpanzees**	**Bonobos**	**Capuchins**
Need[a]	++ (signals and signs) [b]	++ (signals and signs)	-	+ (signals)
Social distance[c]	++	+	(-)	(-)
Reward[d]	-	-	(-)	+
Audience[e]	++	(-)	(-)	(-)
Proactive[f]	++	++	-	-

a. Does helping vary according to recipient need?
b. *Signals* of need comprise direct requests such as whimpering or gesturing toward a desired object, while *signs* of need are not directed toward the actor, but indicate that the recipient needs assistance (e.g., struggling with a task).
c. Do aspects of social relationship, such as kinship or dominance relationship influence helping?
d. Does the possibility of being rewarded increase the probability of prosocial helping?
e. Is prosocial helping adjusted to the perceived presence or size of an audience?
f. Do actors help in the absence of any soliciting stimuli?

The demands of tool manufacture at Goualougo may also help to explain the significance of age as a predictor of tool transfer. Tool transfer probability was higher for individuals between the ages of 5-10 relative to those aged 0-5. At Goualougo, chimpanzees do not manufacture brush-tipped probes until, on average, after 4 years of age, with some individuals not observed independently making a tool until after age 5 (Chapter 2). They may continue to refine tool manufacture skills during the juvenile period and to use tools manufactured by skilled conspecifics even after they have begun manufacturing tools independently. Mothers appear to remain willing to transfer tools even to adolescent offspring, as we observed that 94% of transfer attempts involving recipients that were 10-15 years old (n=16, with 14 of these including a request) resulted in a change of possession. The age effect is principally the result of differences within the Goualougo data set, as individuals at Gombe rarely attempt to take or request tools after age 5. At Gombe, infants begin making fishing probes between the ages of 1.5-3.5 (Lonsdorf, 2005). During the juvenile period, there may be less incentive to take or request conspecifics' tools because of the comparative ease of tool manufacture.

The results regarding age are similar to patterns among chimpanzees in Taï Forest, Côte d'Ivoire; at both sites, social facilitation shows flexibility across development. Peak ages of facilitation during nut-cracking at Taï occur during late infancy and juvenility. Mothers and infants sometimes share a hammer between them, and mothers allow offspring to use their high-quality hammers while settling for poorer quality hammers themselves (Boesch & Boesch-Achermann, 2000; Boesch, Bombjaková, Meier, & Mundry, 2019). Identifying whether these interactions involve request and active movement on the part of tool possessors could clarify whether active transfers also occur in this tool task.

We also detected potential subtle variation in maternal responses to female versus male offspring's attempts to take tools. In contrast to Taï, where male offspring receive more nuts and tools from mothers (Boesch & Boesch-Achermann, 2000), we observed that females in both populations were more successful at acquiring tools, and there was a significant effect of sex on likelihood of tool transfer, including both reactive and nonreactive transfers. At Gombe, female infants spent more time watching their mothers (Lonsdorf, 2005), so the observed difference could also be associated with females' increased interest in or identification of opportunities to retrieve discarded tools. At Goualougo, further research will be required to help identify whether, like at Gombe, there are sex differences in activity patterns or social learning strategies that may help to account for this difference.

Continued data collection will also help to illuminate how age and sex influence success upon request at Goualougo. Although we did not detect significant effects of age or sex in the model containing only reactive transfers, success upon request was 93% for females (26/28 requests) and 62% for males (16/26 requests). In addition, the requests of older individuals were rarely refused. Stealing or attempting to steal tools was more characteristic of young infants, and individuals may increasingly adopt this more successful request strategy as they get older. At Gombe, transfers in response to requests are rare and typically unsuccessful regardless of requestor characteristics.

Despite the differences we observed between populations, our findings contribute to an increasing body of evidence that chimpanzees possess a robust and varied capacity for prosocial helping. In this context, we observed that chimpanzees at both Goualougo and Gombe were permitted to take possession of others' tools, and at Goualougo, skilled individuals actively handed tools to others. While such active transfers do not appear to be prevalent among other species, tolerated taking may occur in macaques (Tan, 2016), capuchins (Eshchar, 2015; Eshchar, Izar, Visalberghi, Resende, & Fragaszy, 2016), New Caledonian crows (Holzhaider, Gray, et al., 2010) and possibly sea otters (Sandegren, Chu, & Vandevere, 1973). The lack of tool transfers in orangutans (Meulman, 2014) may be related to their arboreality, as terrestrial settings could increase opportunity for observation and retrieval of discarded tools (Meulman, Sanz, Visalberghi, & van Schaik, 2012). In future studies, documenting whether skilled tool users are still in proximity to tools they have set down and their reactions at the time these tools are procured by novices, could help to clarify the scope of tool transfer behavior across different species.

4.6 Conclusion

In the present study we employed standardized methods to compare prosociality in the tool-using context between two populations of wild chimpanzees. We found several indications of differences in prosocial helping between chimpanzees at Goualougo and Gombe during termite gathering, which could be related to the complexity of tool tasks between sites. Future study of other species, additional tool tasks, and on specific prosocial actions during tool use will add to our understanding of the types of social facilitation that promote the spread of technology, the extent to which such facilitation is flexible within species, and the potential relationship between task complexity and prosocial helping. The roles of prosociality and of particular social learning mechanisms such as teaching in the accumulation of technological complexity in humans are debated (Ambrose, 2001; Dean et al., 2012; Morgan et al., 2015; Tennie et al., 2009; Wynn, Hernandez-Aguilar, Marchant, & Mcgrew, 2011). We suggest that a propensity for prosocial helping may be shared between humans and chimpanzees and that prosociality may be an essential prerequisite of the cultural transmission of complex skills.

4.7 Acknowledgements

We are deeply appreciative of the opportunity to work in the Nouabalé-Ndoki National Park and especially the Goualougo Triangle. This research would not have been possible without the continued support of the Ministère de l'Economie Forestière et du Développement Durable (République du Congo), the Ministère de la Recherche Scientifique (République du Congo), and the Wildlife Conservation Society's Congo Program. Special thanks are due to J. M. Fay, P. Telfer, P. Elkan, S. Elkan, B. Curran, M. Gately, E. Stokes, T. Breuer, P. Ngouembe and D. Dos Santos. We would also like to recognize the tireless dedication of J. R. Onononga, C. Eyana-Ayina, S. Ndolo, A. Nzeheke, W. Mayoukou, M. Meguessa, I. Singono, and the Goualougo tracking team. Grateful acknowledgment of funding is due to the U.S. Fish and Wildlife Service, the National Geographic Society, and the Columbus Zoological Park. The authors declare no competing interests.

References

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*(3–4), 227–266.

Ambrose, S. H. (2001). Paleolithic technology and human evolution. *Science, New Series*, *291*(5509), 1748–1753.

Amici, F., Visalberghi, E., & Call, J. (2014). Lack of prosociality in great apes, capuchin monkeys and spider monkeys: Convergent evidence from two different food distribution tasks. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1793), 20141699.

Arthur, K. W. (2010). Feminine knowledge and skill reconsidered: Women and flaked stone tools. *American Anthropologist*, *112*(2), 228–243.

Baayen, R. H. (2008). *Analyzing linguistic data: A practical introduction to statistics using R*. Cambridge: Cambridge University Press.

Barnes, J. L., Hill, T., Langer, M., Martinez, M., & Santos, L. R. (2008). Helping behaviour and regard for others in capuchin monkeys (*Cebus apella*). *Biology Letters*, *4*(6), 638–640.

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*(3), 255–278.

Bartal, I. B.-A., Decety, J., & Mason, P. (2011). Empathy and pro-social behavior in rats. *Science*, *334*(6061), 1427–1430.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48.

Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: Evidence from field experiments. *Animal Cognition*, *6*(4), 213–223.

Boesch, C. (1991). Teaching among wild chimpanzees. *Animal Behaviour*, *41*(3), 530–532.

Boesch, C. (1994). Cooperative hunting in wild chimpanzees. *Animal Behaviour*, *48*(3), 653–667.

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: Behavioural ecology and evolution.* Oxford: Oxford University Press.

Boesch, C., Bolé, C., Eckhardt, N., & Boesch, H. (2010). Altruism in forest chimpanzees: The case of adoption. *PLoS ONE*, *5*(1), e8901.

Boesch, C., Bombjaková, D., Meier, A., & Mundry, R. (2019). Learning curves and teaching when acquiring nut-cracking in humans and chimpanzees. *Scientific Reports*, *9*(1), 1515.

Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago: University of Chicago.

Boysen, S. T., & Berntson, G. G. (1995). Responses to quantity: Perceptual versus cognitive mechanisms in chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior Processes*, *21*(1), 82–86.

Brewer, S. M., & McGrew, W. C. (1990). Chimpanzee use of a tool-set to get honey. *Folia Primatologica*, *54*(1–2), 100–104.

Burkart, J., Allon, O., Amici, F., Fichtel, C., Finkenwirth, C., Heschl, A., … van Schaik, C. (2014). The evolutionary origin of human hyper-cooperation. *Nature Communications*, *5*, 4747.

Burkart, J., Fehr, E., Efferson, C., & van Schaik, C. P. (2007). Other-regarding preferences in a non-human primate: Common marmosets provision food altruistically. *Proceedings of the National Academy of Sciences*, *104*(50), 19762–19766.

Burkart, J., Hrdy, S., & van Schaik, C. (2009). Cooperative breeding and human cognitive evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, *18*(5), 175–186.

Burkart, J., & van Schaik, C. (2016). Revisiting the consequences of cooperative breeding. *Journal of Zoology*, *299*(2), 77–83.

Callaghan, T., & Corbit, J. (2018). Early prosocial development across cultures. *Current Opinion in Psychology*, *20*, 102–106.

Clutton-Brock, T. (2002). Breeding together: Kin selection and mutualism in cooperative vertebrates. *Science*, *296*(5565), 69–72.

Clutton-Brock, T., & Gillet, J. B. (1979). A survey of forest composition in the Gombe National Park, Tanzania. *African Journal of Ecology*, *17*(3), 131–158.

Cronin, K. A. (2012). Prosocial behaviour in animals: The influence of social relationships, communication and rewards. *Animal Behaviour*, *84*(5), 1085–1093.

Cronin, K. A., De Groot, E., & Stevens, J. M. G. (2015). Bonobos show limited social tolerance in a group setting: A comparison with chimpanzees and a test of the relational model. *Folia Primatologica*, *86*(3), 164–177.

de Waal, F. (1989). Food sharing and reciprocal obligations among chimpanzees. *Journal of Human Evolution*, *18*(5), 433–459.

de Waal, F. (1997a). Food transfers through mesh in brown capuchins. *Journal of Comparative Psychology*, *111*(4), 370–378.

de Waal, F. (1997b). The chimpanzee's service economy: Food for grooming. *Evolution and Human Behavior*, *18*(6), 375–386.

de Waal, F., & Suchak, M. (2010). Prosocial primates: Selfish and unselfish motivations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1553), 2711–2722.

Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B., & Laland, K. N. (2012). Identification of the social and cognitive processes underlying human cumulative culture. *Science*, *335*(6072), 1114–1118.

Dobson, A. (2002). *An introduction to generalized linear models*. Chapman & Hall/CRC.

Drayton, L. A., & Santos, L. R. (2014). Capuchins' (*Cebus apella*) sensitivity to others' goal-directed actions in a helping context. *Animal Cognition*, *17*(3), 689–700.

Dugatkin, L. A. (1997). *Cooperation among animals: An evolutionary perspective*. *Oxford series in ecology and evolution*. New York: Oxford University Press.

Eshchar, Y. (2015). *Development of tool-use behavior in a social context – nut-cracking in wild bearded capuchin monkeys (Sapajus libidinosus).* Doctoral dissertation, University of Georgia.

Eshchar, Y., Izar, P., Visalberghi, E., Resende, B., & Fragaszy, D. (2016). When and where to practice: Social influences on the development of nut-cracking in bearded capuchins (*Sapajus libidinosus*). *Animal Cognition*, *19*(3), 605–618.

Estienne, V., Robira, B., Mundry, R., Deschner, T., & Boesch, C. (2019). Acquisition of a complex extractive technique by the immature chimpanzees of Loango National Park, Gabon. *Animal Behaviour, 147*, 61–76.

Fay, M. P., & Malinovsky, Y. (2018). Confidence intervals of the Mann-Whitney parameter that are compatible with the Wilcoxon-Mann-Whitney test. *Statistics in Medicine*, *37*(27), 3991–4006.

Fehr, E., & Fischbacher, U. (2003). The nature of human altruism. *Nature*, *425*(6960), 785–791.

Field, A. (2005). *Discovering statistics using SPSS*. London: Sage Publications.

Forstmeier, W. & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: Overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology*, *65*(1), 47–55.

Fox, J., & Monette, G. (1992). Generalized collinearity diagnostics. *Journal of the American Statistical Association*, *87*(417), 178–183.

Fox, J., & Weisberg, S. (2011). *An {R} companion to applied regression. Second edition.* Los Angeles: Sage Publications.

Fragaszy, D., Biro, D., Eshchar, Y., Humle, T., Izar, P., Resende, B., & Elisabetta, V. (2013). The fourth dimension of tool use: Temporally enduring artefacts aid primates learning to use tools. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630), 20120410.

Gilby, I. C. (2006). Meat sharing among the Gombe chimpanzees: Harassment and reciprocal exchange. *Animal Behaviour*, *71*(4), 953–963.

Gilby, I. C., Eberly, L. E., Pintea, L., & Pusey, A. E. (2006). Ecological and social influences on the hunting behaviour of wild chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour*, *72*(1), 169–180.

Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs, 1*, 161–311.

Goodall, J. (1986). *The chimpanzees of Gombe. Patterns of behavior.* Cambridge: Belknap Press.

Goodall, J. (1989). Glossary of chimpanzee behaviors. Jane Goodall Institute.

Gurven, M., & Winking, J. (2008). Collective action in action: Prosocial behavior in and out of the laboratory. *American Anthropologist*, *110*(2), 179–190.

Gurven, M., Zanolini, A., & Schniter, E. (2008). Culture sometimes matters: Intra-cultural variation in pro-social behavior among Tsimane Amerindians. *Journal of Economic Behavior and Organization*, *67*(3–4), 587–607.

Hare, B. (2017). Survival of the friendliest: *Homo sapiens* evolved via selection for prosociality. *Annual Review of Pyschology*, *68*, 155–186.

Hare, B., & Kwetuenda, S. (2010). Bonobos voluntarily share their own food with others. *Current Biology*, *20*(5), R230–R231.

Hare, B., Melis, A., Woods, V., Hastings, S., & Wrangham, R. (2007). Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology, 17*(7), 619–623.

Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour, 83*(3), 573–585.

Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., & McElreath, R. (2001). In search of *Homo economicus*: Behavioral experiments in 15 smale-scale societies. *American Economic Review*, *91*(2), 73–78.

Hepach, R., & Warneken, F. (2018). Editorial overview: Early development of prosocial behavior: Revealing the foundation of human prosociality. *Current Opinion in Psychology, 20*, iv–viii.

Hewlett, B. S., Fouts, H. N., Boyette, A. H., & Hewlett, B. L. (2011). Social learning among Congo Basin hunter-gatherers. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1567), 1168–1178.

Hirata, S. (2007). Competitive and cooperative aspects of social intelligence in chimpanzees. *Japanese Journal of Animal Psychology*, *57*(1), 29–40.

Hirata, S., & Celli, M. L. (2003). Role of mothers in the acquisition of tool-use behaviours by captive infant chimpanzees. *Animal Cognition*, *6*(4), 235–244.

Hockings, K. J., Humle, T., Anderson, J. R., Biro, D., Sousa, C., Ohashi, G., & Matsuzawa, T. (2007). Chimpanzees share forbidden fruit. *PLoS ONE*, *2*(9), e886.

Holzhaider, J., Gray, R., & Hunt, G. (2010). The development of pandanus tool manufacture in wild New Caledonian crows. *Behaviour*, *147*(5), 553–586.

Holzhaider, J., Hunt, G. R., & Gray, R. D. (2010). Social learning in New Caledonian crows. *Learning & Behavior*, *38*(3), 206–219.

Horner, V., Carter, J. D., Suchak, M., & de Waal, F. (2011). Spontaneous prosocial choice by chimpanzees. *Proceedings of the National Academy of Sciences*, *108*(33), 13847–13851.

House, B. R., Silk, J. B., Henrich, J., Barrett, H. C., Scelza, B. A., Boyette, A. H., … Laurence, S. (2013). Ontogeny of prosocial behavior across diverse societies. *Proceedings of the National Academy of Sciences*, *110*(36), 14586–14591.

Hrdy, S. B. (2009). *Mothers and others: The evolutionary origins of mutual understanding* (Vol. 112). Cambridge: Harvard University Press.

Inoue-Nakamura, N., & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *111*(2), 159–173.

Izar, P., Humle, T., Resende, B., Fragaszy, D., Visalberghi, E., Biro, D., & Eshchar, Y. (2013). The fourth dimension of tool use: Temporally enduring artefacts aid primates learning to use tools. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630), 20120410.

Jaeggi, A., Burkart, J., & van Schaik, C. P. (2010). On the psychology of cooperation in humans and other primates: Combining the natural history and experimental evidence of prosociality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1553), 2723–2735.

Jaeggi, A., Stevens, J., & van Schaik, C. (2010). Tolerant food sharing and reciprocity is precluded by despotism among bonobos but not chimpanzees. *American Journal of Physical Anthropology*, *143*(1), 41–51.

Jaeggi, A., & van Schaik, C. (2011). The evolution of food sharing in primates. *Behavioral Ecology and Sociobiology*, *65*(11), 2125–2140.

Jensen, K. (2016). Prosociality. *Current Biology*, *26*(16), R748–R752.

Jensen, K., Hare, B., Call, J., & Tomasello, M. (2006). What’s in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1589), 1013–1021.

Koops, K., Furuichi, T., & Hashimoto, C. (2015). Chimpanzees and bonobos differ in intrinsic motivation for tool use. *Scientific Reports*, *5*(1), 11356.

Krupenye, C., Tan, J., & Hare, B. (2018). Bonobos voluntarily hand food to others but not toys or tools. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *285*(1886), 20181536.

Lew-Levy, S., Reckin, R., Lavi, N., Cristóbal-Azkarate, J., & Ellis-Davies, K. (2017). How do hunter-gatherer children learn subsistence skills?: A meta-ethnographic review. *Human Nature*, *28*(4), 367–394.

Lonsdorf, E. (2005). Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii,* of Gombe National Park, Tanzania. *Animal Behaviour*, *70*(3), 673–683.

Lonsdorf, E. (2006). What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Animal Cognition*, *9*(1), 36–46.

Luncz, L. V., Mundry, R., & Boesch, C. (2012). Evidence for cultural differences between neighboring chimpanzee communities. *Current Biology*, *22*(10), 922–926.

Mangold. (2015). INTERACT 14 User guide. Mangold International GmbH.

Marshall-Pescini, S., Dale, R., Quervel-Chaumette, M., & Range, F. (2016). Critical issues in experimental studies of prosociality in non-human species. *Animal Cognition*, *19*(4), 679–705.

Matsuzawa, T. (1994). Field experiments of tool-use. In R. Wrangham, W. McGrew, F. de Waal, & P. G. Heltne (Eds.), *Chimpanzee cultures* (pp. 157–164). Cambridge: Harvard University Press.

Matsuzawa, T., Biro, D., Humle, T., Inoue-Nakamura, N., Tonooka, R., & Yamakoshi, G. (2001). Emergence of culture in wild chimpanzees: Education by master- apprenticeship. In T. Matsuzawa (Ed.), *Primate origins of human cognition and behavior* (pp. 557–574). Tokyo: Springer.

McCullagh, P., & Nelder, J. (1989). *Generalized linear models*. London: Chapman & Hall.

McGrew, W., Tutin, C., & Baldwin, P. J. (1979). Chimpanzees, tools, and termites: Cross-cultural comparisons of Senegal, Tanzania, and Rio Muni. *Man*, *14*(2), 185–214.

Melis, A. (2018). The evolutionary roots of prosociality: The case of instrumental helping. *Current Opinion in Psychology, 20,* 82–86.

Melis, A., & Tomasello, M. (2013). Chimpanzees' (*Pan troglodytes*) strategic helping in a collaborative task. *Biology Letters*, *9*(2), 20130009.

Melis, A., & Warneken, F. (2016). The psychology of cooperation: Insights from chimpanzees and children. *Evolutionary Anthropology: Issues, News, and Reviews*, *25*(6), 297–305.

Melis, A., Warneken, F., Jensen, K., Schneider, A. C., Call, J., & Tomasello, M. (2011). Chimpanzees help conspecifics obtain food and non-food items. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1710), 1405–1413.

Meulman, E. (2014). *Wild orangutan tool use: New insights for human evolution*. Doctoral dissertation, University of Zürich.

Meulman, E., Sanz, C., Visalberghi, E., & van Schaik, C. P. (2012). The role of terrestriality in promoting primate technology. *Evolutionary Anthropology: Issues, News, and Reviews*, *21*(2), 58–68.

Meulman, E., Seed, A. M., & Mann, J. (2013). If at first you don't succeed... Studies of ontogeny shed light on the cognitive demands of habitual tool use. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630), 20130050.

Mitani, J. C., Merriwether, D. A., & Zhang, C. (2000). Male affiliation, cooperation and kinship in wild chimpanzees. *Animal Behaviour*, *59*(4), 885–893.

Morgan, T. J. H., Uomini, N. T., Rendell, L. E., Chouinard-Thuly, L., Street, S. E., Lewis, H. M., … Laland, K. N. (2015). Experimental evidence for the co-evolution of hominin tool-making teaching and language. *Nature Communications*, *6*(6029), 1–8.

Musgrave, S., Morgan, D., Lonsdorf, E., Mundry, R., & Sanz, C. (2016). Tool transfers are a form of teaching among chimpanzees. *Scientific Reports*, *6*, 34783.

Nakahara, F., Komaba, M., Sato, R., Ikeda, H., Komaba, K., & Kawakubo, A. (2017). Spontaneous prosocial choice by captive bottlenose dolphins, *Tursiops truncatus*. *Behavioural Processes*, *135*, 8–11.

Nishiaki, Y. (2013). "Gifting" as a means of cultural Transmission: The archaeological implications of bow and arrow technology in Papua New Guinea. In T. Akazawa, Y. Nishiaki, & K. Aoki (Eds.), *Dynamics of learning in Neanderthals and modern humans (Vol. 1)* (pp. 173–185). Tokyo: Springer.

Nishida, T., & Hiraiwa, M. (1982). Natural history of a tool-using behavior by wild chimpanzees in feeding upon wood-boring ants. *Journal of Human Evolution*, *11*(1), 73–99.

Nishida, T., Kano, T., Goodall, J., McGrew, W., & Nakamura, M. (1999). Ethogram and ethnography of Mahale chimpanzees. *Anthropological Science*, *107*(2), 141–188.

Parr, L. A., Waller, B. M., Vick, S. J., & Bard, K. A. (2007). Classifying chimpanzee facial expressions using muscle action. *Emotion*, *7*(1), 172–181.

Plooij, F. X. (1984). *The behavioral development of free-living chimpanzee babies and infants*. Ablex Publishing Corporation.

Pruetz, J. D., & Lindshield, S. (2012). Plant-food and tool transfer among savanna chimpanzees at Fongoli, Senegal. *Primates*, *53*(2), 133–145.

R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Richerson, P., Baldini, R., Bell, A. V, Demps, K., Frost, K., Hillis, V., … Zefferman, M. (2016). Cultural group selection plays an essential role in explaining human cooperation: A sketch of the evidence. *Behavioral and Brain Sciences*, *39*, e30.

Rosati, A. G., DiNicola, L. M., & Buckholtz, J. W. (2018). Chimpanzee cooperation is fast and independent from self-control. *Psychological Science, 29*(11), 1832–1845.

Samuni, L., Deschner, T., Crockford, C., Wittig, R., & Preis, A. (2018). Reward of labor coordination and hunting success in wild chimpanzees. *Communications Biology, 1*, 1–9.

Samuni, L., Preis, A., Mielke, A., Deschner, T., Wittig, R. M., & Crockford, C. (2018). Social bonds facilitate cooperative resource sharing in wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences, 285*, 20181643.

Sandegren, F. E., Chu, E. W., & Vandevere, J. E. (1973). Maternal behavior in the California sea otter. *Journal of Mammalogy*, *54*(3), 668.

Sanz, C., Call, J., & Morgan, D. (2009). Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biology Letters*, *5*(3), 293–296.

Sanz, C., & Morgan, D. (2007). Chimpanzee tool technology in the Goualougo Triangle, Republic of Congo. *Journal of Human Evolution*, *52*(4), 420–433.

Sanz, C., & Morgan, D. (2013a). Ecological and social correlates of chimpanzee tool use. *Philosophical Transactions of the Royal Society B: Biological Sciences, 368*(1630), 20120416.

Sanz, C., & Morgan, D. (2013b). The social context of chimpanzee tool use. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 161–175). Cambridge: Cambridge University Press.

Sanz, C., Morgan, D., & Gulick, S. (2004). New insights into chimpanzees, tools, and termites from the Congo Basin. *The American Naturalist*, *164*(5), 567–581.

Schäfer, M., Haun, D. B. M., & Tomasello, M. (2015). Fair is not fair everywhere. *Psychological Science, 26*(8), 1252–1260.

Schwab, C., Swoboda, R., Kotrschal, K., & Bugnyar, T. (2012). Recipients affect prosocial and altruistic choices in jackdaws, *Corvus monedula*. *PloS One*, *7*(4), e34922.

Siegel, S., & Castellan Jr., N. J. (1988). *Nonparametric statistics for the behavioral sciences*. New York: McGraw-Hill.

Silk, J. B., Brosnan, S. F., Henrich, J., Lambeth, S. P., & Shapiro, S. (2013). Chimpanzees share food for many reasons: The role of kinship, reciprocity, social bonds and harassment on food transfers. *Animal Behaviour*, *85*(5), 941–947.

Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S., … Schapiro, S. J. (2005). Chimpanzees are indifferent to the welfare of unrelated group members. *Nature, 437*(7063), 1357–1359.

Sousa, C. (2011). Use of leaves for drinking water. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), *The Chimpanzees of Bossou and Nimba* (pp. 85–96). Tokyo: Springer Japan.

Sousa, C., Biro, D., & Matsuzawa, T. (2009). Leaf-tool use for drinking water by wild chimpanzees (*Pan troglodytes*): Acquisition patterns and handedness. *Animal Cognition*, *12*(S1), 115–125.

Spagnoletti, N., Visalberghi, E., Ottoni, E., Izar, P., & Fragaszy, D. (2011). Stone tool use by adult wild bearded capuchin monkeys (*Cebus libidinosus*). Frequency, efficiency and tool selectivity. *Journal of Human Evolution*, *61*(1), 97–107.

Stevens, J. R., & Gilby, I. C. (2004). A conceptual framework for nonkin food sharing: Timing and currency of benefits. *Animal Behaviour*, *67*(4), 603–614.

Tan, A. (2016). *Behavioral processes and social influences on the development of stone-tool use in long-tailed macaques.* Doctoral dissertation, Nanyang Technological University.

Tan, J., & Hare, B. (2013). Bonobos share with strangers. *PLoS ONE*, *8*(1), e51922.

Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: On the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1528), 2405–2415.

Tonooka, R., Tomonaga, M., & Matsuzawa, T. (1997). Acquisition and transmission of tool making and use for drinking juice in a group of captive chimpanzees (*Pan troglodytes*). *Japanese Psychological Research*, *39*(3), 253–265.

Vonk, J., Brosnan, S. F., Silk, J. B., Henrich, J., Richardson, A. S., Lambeth, S. P., … Povinelli, D. J. (2008). Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Animal Behaviour*, *75*(5), 1757–1770.

Warneken, F., & Tomasello, M. (2006). Altruistic helping in human infants and young chimpanzees. *Science, 311*(5765), 1301–1303.

Warneken, F., & Tomasello, M. (2008). Extrinsic rewards undermine altruistic tendencies in 20-month-olds. *Developmental Psychology*, *44*(6), 1785–1788.

Warneken, F., & Tomasello, M. (2009). The roots of human altruism. *British Journal of Psychology*, *100*(3), 455–471.

Watts, D. (2002). Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour*, *139*(2), 343–370.

Watts, D., & Mitani, J. (2002). Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, *23*(1), 1–28.

Wrangham, R., & Pilbeam, D. (2002). African apes as time machines. In B. Galdikas, N. Erickson Briggs, L. Sheeran, G. Shapiro, & J. Goodall (Eds.), *All apes great and small* (pp. 5–17). Boston: Springer.

Wynn, T., Hernandez-Aguilar, A., Marchant, L., & Mcgrew, W. (2011). “An ape’s view of the Oldowan” revisited. *Evolutionary Anthropology: Issues, News, and Reviews*, *20*(5), 181–197.

Yamamoto, S. (2015). Non-reciprocal but peaceful fruit sharing in wild bonobos in Wamba. *Behaviour*, *152*(3–4), 335–357.

Yamamoto, S., Humle, T., & Tanaka, M. (2009). Chimpanzees help each other upon request. *PLoS ONE*, *4*(10), e7416.

Yamamoto, S., Humle, T., & Tanaka, M. (2012). Chimpanzees’ flexible targeted helping based on an understanding of conspecifics’ goals. *Proceedings of the National Academy of Sciences*, *109*(9), 3588–3592.

Yamamoto, S., & Takimoto, A. (2012). Empathy and fairness: Psychological mechanisms for eliciting and maintaining prosociality and cooperation in primates. *Social Justice Research*, *25*(3), 233–255.

Chapter 5: Conclusion

The flourishing of technology is a hallmark of human evolution. High-fidelity social learning mechanisms, such as teaching and imitation (Fogarty, Strimling, & Laland, 2011; Galef, 1992; Tennie, Call, & Tomasello, 2009), as well as prosocial helping (Dean, Kendal, Schapiro, Thierry, & Laland, 2012), are hypothesized to have been important for this process. In addition, sex differences in foraging tool use have been linked to the emergence of complex tool use in hominoids (Hunt, 2006; McGrew, 1979; Zihlman, 2012). In this research, our goal was to examine the influence of these factors on the acquisition of tool skills in chimpanzees of the Goualougo Triangle, Republic of Congo, and to compare the developmental trajectory of termite gathering to that for chimpanzees at Gombe, Tanzania. We employed ontogenetic methods because how young primates learn tool skills is key to understanding how behavioral traditions persist over time and across the landscape. In addition, comparing two populations enabled us to generate novel insights into how social facilitation may relate to task complexity.

Prior to this research, the acquisition of tool sets by wild chimpanzees had not been documented, and it was unknown how individuals of the Central subspecies learned to use tools to gather invertebrates. In addition, it has been widely held that the social transmission of tool skills among wild chimpanzees occurs largely through low-fidelity mechanisms and that teaching, in particular, is rare or absent in chimpanzees (Dean et al., 2012; Fogarty et al., 2011; Tennie et al., 2009). There has also been extensive debate regarding the degree to which chimpanzees are capable of or motivated to provide prosocial assistance, both in tool-using and other contexts (e.g., Horner, Carter, Suchak, & de Waal, 2011; Melis et al., 2011; Silk, Brosnan, Henrich, Lambeth, & Shapiro, 2013; Silk et al., 2005; Tennie, Jensen, & Call, 2016; Yamamoto, Humle, & Tanaka, 2012; Yamamoto, Humle, & Tanaka, 2009). Finally, to date there have been varying results with respect to the detection of sex differences in object manipulation and tool use among immature chimpanzees (e.g., Boesch & Boesch-Achermann, 2000; Humle, Snowdon, & Matsuzawa, 2009; Koops, Furuichi, Hashimoto, & van Schaik, 2015; Lonsdorf, 2005). In this chapter, I summarize our main results, and I discuss plans for future research that could build upon particular findings. I then consider the broader implications of this research for modeling the pedagogical settings accompanying the tool behavior of early hominins.

5.1 The Acquisition of Tool Sets

In Chapter 2, my co-authors and I examined the acquisition of termite-gathering critical elements. The use of a longitudinal dataset proved critical. As predicted based on pilot data (Musgrave, Bell, Morgan, Lonsdorf, & Sanz, 2015), we found that the process of gaining technical competence extends into subadulthood. Chimpanzees performed simple manipulations before using tools in combination with the termite mound and became proficient at using single tools (fishing probes) before using perforating and puncturing tool sets. The ages at which individuals were first detected using perforating tool sets varied widely relative to the ages at which they were first documented successfully extracting termites. Puncturing competency was acquired last. These findings aligned with predictions of the Perception-Action model (Lockman, 2000) and with results for other species that the development of flexible tool skills reflects maturation of particular sensorimotor skills. In addition, the later development, on average, of sequential behaviors – both in terms of the correct integration of ordered steps for termite fishing, and in the deployment of multiple tools in sequence – suggests that managing different, causal relationships in serial order draws upon cognitive skills including causal reasoning and planning. We will expand upon the present work by examining the ages at which individuals acquire adult-like efficiency, as well as the types of errors made by infant and juvenile chimpanzees, to further clarify how sensorimotor and cognitive demands constrain tool actions at different ages. This would also help us to better understand the differing challenges of concurrent versus sequential tool use for primates (Fragaszy & Mangalam, 2018).

Perforating at Epigeal Nests

The variation in ages at which individuals were first observed using perforating tool sets in the epigeal nest setting was striking. One contributing factor is likely that termite exit holes are routinely opened manually, rather than with a tool. Perforating activity may also relate to season. Termites maintain the nest surface to maintain precise climatic conditions within the mound, and this could vary seasonally, affecting the relative difficulty chimpanzees encounter piercing the external crust. However, it is not clear why there are differences in whether and when young tool users begin perforating. Adults in this population show variation in their tool repertoires, including their use of perforating tools (Sanz & Morgan, 2011), so future work will examine whether young chimpanzees' use of perforating tools is correlated with perforating tool use by mothers or other social associates. Another possibility is that individual mothers vary in their willingness to share tool sites. A greater willingness by mothers to provide access to opened exit holes could reduce the likelihood that an infant initiates perforating tool use. One possibility for future research would be to score all transfers of tool sites to examine whether there is variation in this behavior by skilled associates.

Puncturing at Subterranean Nests

In the subterranean nest context, we routinely observed young chimpanzees attempting, unsuccessfully, to create new fishing tunnels; inserting puncturing tools into tunnels just created by older specifics; or, particularly as they began to increase in body mass during later juvenility, using puncturing tools to clear tunnels partially created by older conspecifics. Young chimpanzees' efforts to create new tunnels with puncturing tools do not result in access to subterranean nest chambers, and even efforts in partially cleared tunnels are often unsuccessful. This raises questions of what stimulates or reinforces their efforts in this context, and whether successful puncturing of a new tunnel is principally a function of body mass or also varies depending on practice and knowledge of where and to what depth to puncture. The practice of conspecifics is known to stimulate nut-cracking activity in novice capuchins (Eshchar, Izar, Elisabetta, Resende, & Fragaszy, 2016), but it is not yet clear to what extent nonhuman primates are sensitive to variable effort and success in models. Human infants are more persistent in experimental tasks when adult models show more persistent efforts to achieve goals versus when models succeed easily (Leonard, Lee, & Schulz, 2017). In addition, persistence is a critical predictor of a variety of life outcome measures, such as academic performance, in humans (Martin, Ryan, & Brooks-Gunn, 2013). To examine persistence in chimpanzees, we have undertaken a longitudinal study of puncturing during termite gathering at subterranean nests. We are investigating whether chimpanzee infants differ in the time and effort they use attempting to puncture termite nests, how this varies with age and between the sexes, and whether proximity to persistent models – those who exhibit greater puncturing effort – impacts the persistence of novice tool users.

5.2 Sex Differences in Tool Skill Acquisition

The overall trajectory of skill acquisition for termite gathering was similar for males and females at Goualougo. This contrasts with Gombe, where males learned to termite fish over two years later than did females. We did find that females at Goualougo acquired most critical elements before males did and learned to fish several months earlier. Males, in contrast, were observed making tools on average 6 months earlier than females. These results nonetheless highlight the possibility that sex differences of large magnitude, such as those at Gombe

(Lonsdorf, 2005; Lonsdorf, Eberly, & Pusey, 2004), may not be a ubiquitous feature of tool skill acquisition in chimpanzees. Whether or not sex differences are detected, for tool use or other behaviors, likely reflects dynamic interactions among many factors (Lonsdorf, 2017; Meredith, 2015). For tool use, this may include social learning strategies (Lonsdorf, 2005); nature of the task, such as level of risk (Humle et al., 2009); the precise sensorimotor demands (Fragaszy & Mangalam, 2018); treatment by mothers (Boesch & Boesch-Achermann, 2000); as well as potential biological differences in disposition towards or skill in object manipulation (Koops et al., 2015).

It is also essential to consider that the relatively small sample sizes that often characterize developmental studies (Chapter 2, Table 2.1) affect the ability to detect sex differences. Differences that are not statistically significant may represent meaningful variation in biology and behavior that merits further study. A synthetic understanding of sex differences in chimpanzee tool use will require additional studies to elucidate the various potentially relevant factors and how they interact in different ecological and social settings. A next step in this research will be to examine whether females and males at Goualougo show comparable activity patterns (e.g., time spent in goal-directed termite-gathering activity versus playing) and comparable observation of conspecifics, or whether, like at Gombe, there are sex differences in these behaviors that can help to explain the differing ages at which males and females learn to termite fish (Lonsdorf, 2005).

At Gombe, male and female chimpanzees spent similar amounts of time termite fishing once they reached juvenility – i.e., once all males had acquired the task by age 5.5, the differences in time spent fishing that were evident in infancy, disappeared (Lonsdorf, 2005). Thus, it is not immediately clear whether or how sex differences in infancy foreshadow adult sex differences in foraging strategies, including termite fishing (Goodall, 1968; McGrew, 1979). Continued research is necessary to clarify what the potential links are between sex differences in infant tool use and adult tool use. This will require attention to the nature of any observed differences (e.g., proficiency, frequency of visits, duration of visits, diversity of tool repertoire), as this has implications for understanding the possible adaptive basis. It would also be instructive to examine this in the broader context of variation in dietary strategies between the sexes and according to female reproductive status.

5.3 The Role of Artefacts and Tool Transfers

One of the most notable differences we discovered between Goualougo and Gombe relates to the pattern of acquiring tool use versus tool manufacture. At Gombe, chimpanzees learned to make tools at or before the time they learned to fish, while at Goualougo, chimpanzees learned to fish before they learned to make tools. We suggest that the opposite pattern observed could be related to the differing requirements associated with tool manufacture. We further observed that it was rare for infants at Goualougo to detach raw material (such as a leaf) and to attempt, unsuccessfully, to use this as a tool. Instead, infants learning to fish typically used discarded tools, or they received tools from more skilled conspecifics. These findings accord with the increasing appreciation for the critical role artefacts play in scaffolding technical competence across taxa (Fragaszy et al., 2013). Tool sites, including the tools and debitage of past tool users, are constructed niches that can influence learning and scaffold the tool-using behavior of the individuals who visit. At the same time, our observations of direct tool transfers in this setting represent a notable departure from what has been documented in most other species. This indicates that there may be species differences with respect to awareness of or willingness to act in response to a novice’s need for a tool.

Tool Transfers as Teaching

Given the potential pedagogical benefits of tool transfers, in Chapter 3 we investigated whether tool transfers in the termite-gathering context at Goualougo comprised a functional form of teaching. We adopted the teaching criteria proposed by Caro and Hauser (1992), and using three different measures (time spent termite gathering, fishing rate, and feeding rate), we found that transfers satisfy functional criteria for teaching: transfers occur principally between mothers and infants, are costly to tool donors, and provide knowledge and learning opportunity for tool recipients. We further documented “buffering strategies”, whereby tool donors reduced the cost of tool transfers by bringing multiple tools in advance or splitting their tools lengthwise and relinquishing half to the recipient (Musgrave et al., 2016). A natural follow-up study to increase our understanding of planning in this context will be to examine whether there are differences among individuals – for example, females with and without offspring – in transport of multiple tools. Multiple tool transport would have obvious potential advantages for any individual, but particularly for those with infant or juvenile offspring who do not yet manufacture their own tools.

Costly facilitation such as tool transfers is predicted when it would be difficult for the receiver of the help or information to acquire it another way. Further, it is expected to be ubiquitous if it is necessary (Thornton & Raihani, 2008). We documented tool transfers across 13 different donors, principally mothers, over a multi-year period, and we continue to observe these behaviors. Thus, tool transfer appears to be a widespread behavior. Given the differences in when young chimpanzees manufacture versus use tools in this population, the provisioning of tools in this context could be related to the challenges tool manufacture poses to young chimpanzees.

A recent comparison of the acquisition of *Panda* nut cracking between Mbendjele foragers from the Republic of Congo and the Taï chimpanzees from Côte d'Ivoire found evidence for teaching by both species in this context. There was a greater diversity of teaching intervention types, as well as more intensive interventions, by humans (Boesch, Bombjaková, Meier, & Mundry, 2019). The authors defined teaching broadly to encompass behaviors such as leaving collected nuts on an anvil for novices to crack, and relinquishing hammers to novices (Boesch, 1991; Boesch & Boesch-Achermann, 2000). The Technical Intelligence Hypothesis (Byrne, 1997) would predict that among the great apes, humans will be quickest to acquire technical skills due to having the most sophisticated skills of physical cognition. However, according to the same efficiency measures, chimpanzees learned to crack the hard-shelled *Panda* nuts more quickly than did humans (Boesch et al., 2019). The Life History Hypothesis (Kaplan, Hill, Lancaster, & Hurtado, 2000; Kaplan & Robson, 2002) would predict humans to acquire nut-cracking skills more slowly, but to be more skilled once they did. However, adult efficiencies were comparable between species. These counterintuitive findings could be related to the fact that in humans, nut-cracking sometimes involves use of the sharp edge of a blade as an anvil, which may be more difficult to learn. In addition, humans typically acquire a much broader array of technical behaviors between ages 2 and 7, whereas chimpanzee can concentrate the development of technical skills on a smaller number of tasks (Boesch et al., 2019). This highlights the importance of considering the acquisition of a skill not in isolation, but relative to the broader ecological and social context, including the other skills an individual must acquire.

We plan to expand upon the present research on the development of tool-using skills in the termite-gathering context in several ways in order to help achieve this. We are presently working with collaborators to assess skilled actions in the termite-gathering context (Ortiz et al., 2018). By assessing proficiency measures ontogenetically in infants and juveniles, we could provide results for comparison to the nut-cracking context, as well as to tool use in other species. In addition, we have plans to examine when chimpanzees in this population develop competence at other technical skills, such as leaf sponging and honey gathering in the arboreal context. This will provide an even more complete picture of how sensorimotor skill, technical intelligence, and life history variables influence the "learning curves" (Boesch et al., 2019) of different tasks within and between species. Examining arboreal tool behaviors will also enable us to assess how arboreal versus terrestrial setting might affect learning opportunity (Meulman, Sanz, Visalberghi, & van Schaik, 2012; Meulman & van Schaik, 2013). Leaf sponging is relatively simple compared to honey gathering, which involves the flexible use of multiple tool types in sequence. Investigating the acquisition of these behaviors could thus provide further insight into whether and how learning mechanisms vary between tasks of differing complexity.

5.4 Insights from a Functional Approach to Teaching

As discussed in Chapters 1 and 3, high-fidelity social learning can facilitate the transmission of skills or information too "opaque" to be transferred by lower-fidelity mechanisms. The capacity for and reliance on these mechanisms are hypothesized to have conferred evolutionary advantages by enabling the flourishing of cumulative culture (Boyd & Richerson, 1996; Kempe, Lycett, & Mesoudi, 2014; Tennie et al., 2009). Some researchers have suggested that only humans truly show teaching because only humans possess adequate faculties for joint attention and theory of mind (Kruger & Tomasello, 1998; Tomasello, Kruger, & Ratner, 1993). This cognitive or "mentalistic" perspective (Kline, 2015) emphasizes the ubiquity of *intentional* teaching in humans, and some have proposed that humans have evolved particular psychological adaptations for teaching (Csibra & Gergely, 2009).

However, there is no consensus on the prevalence of intentional teaching cross-culturally despite a long history of anthropological inquiry into this question (e.g., Mead, 1970). From one perspective, intentional teaching of children is considered principally a characteristic of "WEIRD" - Western, Educated, Industrialized, Rich, Democratic (Henrich, Heine, & Norenzayan, 2010) societies (Lancy & Grove, 2010). When intentional teaching is reported outside of WEIRD societies, such as among Fijians on the Yasawa Islands (Kline, Boyd, & Henrich, 2013), it has been criticized on the basis of response bias from the interview setting. For example, Little and Lancy (2016) suggest that as a result of exposure to missionary influence and Western schooling, respondents were inclined to report didactic pedagogical techniques when in fact such practices did not occur. Others have argued that reports of the absence of teaching outside of WEIRD societies may be exaggerated, particularly when more informal methods are considered. For example, among Aka and Bofi hunter-gatherers, mothers have been observed demonstrating use of tools (Hewlett, Fouts, Boyette, & Hewlett, 2011). On the basis of a review of 982 ethnographic texts from the Human Relations Area Files, teaching was found to be the most common social learning method among hunter-gatherers (Garfield, Garfield, & Hewlett, 2016). However, the authors note that extensive focus on teaching by researchers may have biased how frequently this is reported.

A range of theoretical-definitional issues as well as methodological variation may thus lead researchers to come to differing conclusions about the extent to which humans across societies rely on teaching to transmit skills to novices. Further, the diversity of results may reflect the reality that the occurrence of teaching - including teaching through more informal, less didactic interactions – likely varies considerably cross-culturally, historically, ontogenetically, as well as according to task difficulty (Kline, 2015, and peer commentaries). For humans, as well as for other taxa, there is still much to investigate and understand about this topic, including the best way(s) to operationally define teaching (Eshchar & Fragaszy, 2015), the relationship between causal opacity and teaching (Hernik & Gergely, 2015; Moore & Tennie, 2015) and the importance of teaching relative to other social learning mechanisms (Garfield et al., 2016). A functional approach has the advantage of being fully compatible with complementary inquiry into what biological, cultural, or cognitive factors support teaching behaviors. In adopting a functional approach to assess teaching in Chapter 3, we identified a context in which skilled chimpanzees, at a cost to themselves, provided less skilled tool users with information and an opportunity to practice their skills. This laid a foundation for examining tool transfers in Chapter 4 in broader perspective.

5.5 Population Differences in Prosociality

In Chapter 4, we examined tool transfers from the theoretical framework of prosociality. This helped to link our functional results for teaching to discussions about what abilities or propensities might support this form of high-fidelity social learning among Goualougo Triangle chimpanzees. More broadly, this approach allowed us to gain insights about inter and intraspecific variation in prosocial helping during tool use. Like teaching, prosociality has been proposed to be an important factor enabling cumulative culture (Dean et al., 2012; Tomasello, 1999). We undertook a direct comparison of tool transfer between Goualougo and Gombe, in order to see whether the rate and spectrum of prosocial helping varied between two settings where task complexity differed.

Broadly, the willingness of chimpanzees at both Goualougo and Gombe to allow chimpanzees to take tools suggests that the transfer of tools is an important way in which experts scaffold skill development in chimpanzees and in humans. This was notable with respect to the relative lack of transfers reported for other taxa. However, more explicit investigation of the prevalence of "tolerated taking" transfers in other taxa will be fruitful. Specifically, further clarification is needed regarding whether some instances of youngsters retrieving discarded tools (e.g., New Caledonian crows picking up tools that had previously been used by parent birds) would comprise transfers according to our definition.

Despite the comparable occurrence of tolerated-taking transfers between chimpanzee populations, we found significant population differences in the rate, probability, and types of tool transfer that occurred at Goualougo versus Gombe. We suggest that these multiple indicators comprise robust evidence for population differences in prosociality in the tool-using context. Chimpanzees at Goualougo transferred tools at three times a higher rate than did chimpanzees at Gombe. The average rate (0.06 transfers/minute) of tool transfer for individuals that we documented at Goualougo was similar to that (0.05 times/minute) reported by Boesch et al. (2019) for humans in the nut-cracking context. We further found that there were population differences in the probability of tool transfer upon request, which is a more precise indicator of prosocial motivation than passive tolerance of a transfer that occurs without a preceding request. Further, the frequency of active tool transfers upon request, and the complete absence of active transfers at Gombe, was emblematic of the striking population differences. This is the first study to employ identical methods to compare and document differences in prosociality during tool use among wild chimpanzees.

The Role of Request in Tool Transfer

We scored requests for tools in order to better understand what prompted tool transfers and whether or how this differed between populations. Captive studies have reported varying results regarding the impact of request on likelihood of tool transfer (summarized in Cronin, 2012; Marshall-Pescini, Dale, Quervel-Chaumette, & Range, 2016). In Chapter 3, we noted that the “sharing under pressure” or harassment-reduction model does not appear to explain tool transfers among Goualougo chimpanzees, as costs to tool donors went up rather than down after relinquishing tools (Musgrave et al., 2016). Captive chimpanzees will transfer specific items a conspecific requires even when they are physically separated from the other individual (e.g., Yamamoto et al., 2012), which also suggests that motivation to ward off harassment is not what leads to sharing. We found that begging durations at Goualougo were relatively short and were shorter on average than begging durations at Gombe. This faster response time is consistent with the interpretation that tool transfer is not only more common but has a more prosocial basis at Goualougo than at Gombe (Rosati, DiNicola, & Buckholtz, 2018).

There may be a similar population difference between Gombe and Taï with respect to the basis for food sharing, including meat sharing after hunting. At Gombe, chimpanzees’ requests for meat comprise a form of costly harassment such that meat possessors are motivated to share by a desire to reduce the energy costs associated with defending food from beggars (Gilby, 2006). Among Taï chimpanzees, however, sharing of food including meat is most strongly predicted by enduring social bonds, not harassment. Begging durations were shorter between more closely bonded individuals, and retaliation in response to begging was rare (Samuni et al., 2018). In addition, increased oxytocinergic activity while engaging in hunting behavior supports a cooperative interpretation of group hunting activities (Samuni, Deschner, Crockford, Wittig, & Preis, 2018). Together with our results, these findings provide complementary evidence that helping and sharing, and the proximate motivators of these behaviors, can differ substantially between populations.

Another possible interpretation of our results for active sharing is that *past* instances of harassment have stimulated increasingly active tool transfer behavior among Goualougo chimpanzees, i.e., that individuals have learned that relinquishing a tool, though costly, is less costly than refusing a request or withstanding prolonged begging. It is not clear why, however, if reducing harassment is the primary motivator, this would apply to mothers at Goualougo but not at Gombe. Infants in both populations make requests, and at Gombe, these begging bouts sometimes involved persistent gesturing and whimpering. There was no indication that begging was more disruptive at Goualougo than at Gombe. Given that mothers at Gombe could more easily manufacture a suitable replacement, it is particularly striking that they would be less willing to relinquish their tools. Thus, even if harassment reduction plays some role in either or both populations, it does not fully account for the transfer of tools or for population differences.

Tolerance versus Prosociality

We also examined rates of resistance in order to further contextualize any observed population differences in prosociality. In both populations, mothers were extremely tolerant and severe reactions were extremely rare. Infants routinely peered in close proximity, climbed on their mothers’ bodies, and were permitted to touch her arms and hands during tool use. However, despite being generally tolerant, mothers at Gombe were twice as likely to show resistance specifically after request for a tool - further highlighting that prosociality is not simply a byproduct of tolerance. Related to this, we do not have evidence at present that there is an ecological basis for mothers at Gombe to be more likely than those at Goualougo to perceive infant tool use as a form of competition – i.e., we have no evidence that there is a greater perceived scarcity of locations to use tools that might be mitigating willingness to transfer tools. However, in future research we could attempt to quantify the density of available potential tool-using localities relative to the number of individuals typically present.

Given that chimpanzees in both populations make requests, the differential responses by mothers indicate flexibility within species regarding sensitivity to requests. It is unknown to what extent mothers' differential willingness to transfer tools reflects understanding of the relative challenges of the manufacture process in each population. In further research, we could follow up on whether there are subtle differences in request that cue increased or decreased sharing. For example, in meerkats, changes in pups' begging calls cue changes in how mothers and helpers facilitate foraging competence (Thornton & McAuliffe, 2006).

Linking High-Fidelity Social Learning and Prosociality

While there has been some discussion of the relevance of prosociality for understanding the evolution of cumulative culture (e.g., Dean et al., 2012) research endeavors focused on teaching and high-fidelity social learning are often undertaken separately from those examining the evolution of prosociality, the latter focusing more on the implications of prosociality for fairness, altruism and cooperation among unrelated individuals (e.g., Horner et al., 2011; Jaeggi, Burkart, & Van Schaik, 2010; Silk et al., 2005) than for information transfer specifically. As mentioned in Chapter 1, however, many aspects of mother-infant interactions are highly cooperative. Regardless of whether foraging or technical skill acquisition were primary selective contexts for the skills and motivations underlying prosocial helping, prosociality provides an effective framework for examining the spectrum of helping behaviors between skilled individuals and novices during tool use. Taking this approach allowed us to examine tool transfer more synthetically – both from the functional perspective of how it serves as teaching in the Goualougo Triangle, and to better understand whether and how helping behavior varies between tasks of differing complexity. Examining tool transfers from the perspective of prosociality also provided insights that might not have been as evident if we worked exclusively from existing theoretical schemas. For example, while both active transfers and tolerated-taking transfers could be defined as “opportunity provisioning” (Hoppitt et al., 2008; Kline, 2015), examining the varying prosocial basis of transfers allowed further, standardized investigation of *how* opportunity provisioning was accomplished in each population.

A next step in this research will be to relate milestones of skill acquisition documented in Chapter 2 to measures of social learning, including teaching, enhancement and observational learning, to examine to what extent social facilitation is related to skill over a longer time period. It is also of interest to assess whether these differences persist into adulthood, in order to further examine potential fitness implications of social facilitation. An additional intriguing possibility would be to examine whether variation in tool transfer behavior across mothers predicts variation in this behavior among offspring as they mature, in order to gain insights into the ontogenetic origins of prosocial behavior in wild chimpanzees.

5.6 Broader Implications for the Study of Human Evolution

The “Island Test” (Tennie, Braun, Premo, & McPherron, 2016; Tomasello, 1999) is a thought experiment for considering the role and importance of social learning in the transmission and maintenance of a behavior. It asks whether an individual alone on an island, with the appropriate materials and target resources, could invent the behavior in question, or whether social learning, particularly high-fidelity mechanisms including teaching and imitation, would be necessary for the behavior to persist in a population. Tennie et al. (2016) posit that the archaeological record for Oldowan and potentially even Acheulean tool behavior does not exhibit compelling evidence of tool use of sufficient complexity, or of geographic or temporal variation at high enough levels, to indicate high-fidelity social learning and cumulative culture.

One of the principal arguments made in support of this position is that early hominin tool behavior is comparable to that of great apes, for which there is posited to be a lack of evidence for teaching or imitation (Tennie et al., 2009). Others have also made the argument that the technical capacity of Oldowan hominins was no greater (was within the “adaptive grade”) than that of extant apes – but have focused on the shared presence, not absence, of diverse, variable, complex tool behaviors in both groups (e.g., Wynn & McGrew, 1989; Wynn, Hernandez-Aguilar, Marchant, & Mcgrew, 2011). These debates highlight that along with the archaeological record itself, experimental archaeology, and brain imaging studies, the complex tool behaviors of living apes are key to how we think about and attempt to reconstruct the evolution of hominin culture and cognition (Toth & Schick, 2018).

We established that high-fidelity social learning occurs in the context of termite gathering among chimpanzees, and that these interactions are supported by a flexible propensity for prosocial helping. We examined just one type of social learning and one type of interaction. In future research, we will further explore what strategies govern chimpanzees’ use of different social learning strategies, and whether there is evidence for imitation in these tool-using contexts. Many researchers would argue that there is, in fact, already compelling evidence for ape imitative capacity (e.g., Horner & Whiten, 2005; Lonsdorf, 2005). At this time, it is not possible to differentiate with certainty which if any of the skills involved in the termite-gathering tasks examined here could be invented independently, or with the support of only low-fidelity social learning. However, considering the example of termite gathering in the subterranean context is instructive. For a naïve individual, engaging in this behavior would require first finding an underground nest; these can often be cryptic, as termites can exit the nest to forage via tunnels that extend far from the nest chambers themselves. Suitable raw materials for both the puncturing and the fishing tasks must be chosen and located from among the myriad plant species present. Rather than simply use detached herb materials to fish, individuals manufacture brush tips onto the ends of tools. Fishing for termites at subterranean mounds also requires that a tunnel first be punctured through the ground. It is difficult to imagine that individuals would independently and consistently converge not only upon the practice of termite gathering, but upon sequential use of these two tools, identical raw material choices, and brush-tipped probe manufacture.

It is also not clear whether on the basis of low-fidelity social learning alone individuals could acquire this knowledge and learn to integrate these different actions into the same sequences so as to maintain these behaviors at the population level. Undoubtedly, stimulus and local enhancement play a critical role in skill acquisition, and the importance of these mechanisms for many taxa has likely been underemphasized until recently (e.g., Fragaszy et al., 2013). In fact, there is no evidence that cumulative culture *cannot* develop via these mechanisms alone, though high-fidelity mechanisms can provide very significant benefits (Morgan, 2017). Despite the likely importance of low-fidelity mechanisms, however, the occurrence of teaching among Goualougo Triangle chimpanzees indicates that at least in some contexts, high-fidelity social learning occurs: it comprises part of the repertoire of mechanisms by which behaviors are passed on between individuals.

Oldowan tool use appears at least as complex as what is observed in extant apes. For example, unlike extant apes, with the exception of apes in captivity who learned to do so (Schick et al., 1999; Toth & Schick, 2009; Toth, Schick, Savage-Rumbaugh, Sevcik, & Rumbaugh, 1993) the hominins who produced Oldowan tools routinely used one tool to make another, suggesting comparable abilities of causal reasoning and planning, as well as sensorimotor skill (Toth & Schick, 2018; Wynn et al., 2011). It is also important to remember that while hominin tool skills are manifest in the archaeological record principally through stone tools, these were likely but a fraction of the broader tool kits (Toth & Schick, 2009) and total technological systems (de la Torre, 2017) that characterized hominin lifeways. It thus seems parsimonious that these hominins would have had social learning capacities comparable to or greater than those of extant apes. Given evidence for both teaching and imitation in chimpanzees, it also seems likely that the capacity for high-fidelity social learning would have been part of the suite of factors – e.g., postural/locomotor, cognitive, social, dietary, morphological, neurological – that accompanied the flourishing of technical skills and practices in human evolution. Further, rather than think of high-fidelity social learning as emerging only once, it is also possible that it emerged multiple times, being variably lost and retained across different populations of hominins (Luncz & Haslam, 2017).

Our results also lend support to the perspective that the ability and propensity for prosocial helping may be shared among humans, bonobos, and chimpanzees (Krupenye, Tan, & Hare, 2018; Melis, 2018; Melis & Warneken, 2016; Tan & Hare, 2013; Warneken & Tomasello, 2009), rather than represent strictly a derived capacity that emerged with the adoption of cooperative breeding (Burkart, Hrdy, & van Schaik, 2009; Hrdy, 2009). The flexible, targeted helping chimpanzees offer in captive settings (Yamamoto et al., 2012) and our observations that at least sometimes, help is offered in the absence of a direct request (Chapter 4), indicate that nonhuman apes do, if rarely, even offer help proactively. Our results nonetheless align with prior findings suggesting the general importance of request in eliciting prosocial helping in chimpanzees. Among apes, humans appear distinctive in the flexibility and scope with which they offer assistance to related and unrelated individuals both with and without request (Jaeggi et al., 2010). It is plausible that selection to enhance intrinsic sensitivity not only to signals of need (e.g., a novice making a begging gesture), but to subtler signs of need (e.g., a novice lacking a needed tool) (Jaeggi et al., 2010) could have accelerated learning in tool contexts during hominin evolution. The striking differences in prosociality we observed between Goualougo and Gombe in the termite-gathering context suggest an enhanced role for prosocial helping during difficult tasks. This is one context among many others – e.g., care of offspring, food sharing, territory or resource defense – in which enhanced initiative for cooperative acts could have conferred fitness benefits.

It is unequivocal that humans possess distinctly rich technologies that are unparalleled in complexity and that highly specific cultural practices govern the learning of technical skills. As discussed by Ingold (1997) and highlighted by Stout (2002:694), "Technology itself is an inherently social phenomenon". To some extent, this statement is also helpful when considering the "Island Test" for the tool behaviors of our closest living relatives in evolutionary perspective. Under normal circumstances, infant chimpanzees are rarely if ever alone; they experiment in tool-using environments that are structured by the past actions of other tool users; they often use tools that were previously selected and modified by others, including tools that have been actively provided to them; and they routinely observe others' tool use. Further, the group into which young chimpanzees are born exerts a substantial effect on the behaviors they will come to learn – both with respect to tool use as well as other domains such as courtship and communication (Boesch, 2012; McGrew, 1992; Whiten et al., 2001). It seems increasingly clear that social factors thus contribute to the canalizing of behavior within groups, even as broader-scale regional patterns may emerge due to overlapping ranges or immigration of individuals between groups confronting similar ecological challenges. This is compatible with the interpretation that tool repertoire diversity in the Oldowan is related at least in part to social factors (Stout, Semaw, Rogers, & Cauche, 2010).

Over time, and in association with many other changes to our bodies, brains, and behavior, technology has come to pervade human lifeways. Our ability to transform our environment shapes our own lives and also exerts profound influence on the health, behavior and evolution of the other animals with whom we share the planet. Like many other long-lived, slowly reproducing animals, all of the world’s apes are threatened with extinction. Apes and other large-bodied animals play critical roles in ecosystems, for example as seed dispersers (Abernethy, Coad, Taylor, Lee, & Maisels, 2013). Thus, their decline has far-reaching implications not only for their own survival but for that of other plant and animal species. Even if populations are able to persist amidst the range of threats they face, human disturbance can erode primate cultures (Gumert, Hamada, & Malaivijitnond, 2013; van Schaik, 2002). Human impact is already implicated in substantial losses of chimpanzee behavioral diversity (Kühl et al., 2019). In Central Africa, large areas of viable great ape habitat remain (Strindberg et al., 2018). This provides hope that conservation efforts drawing upon understanding of great ape behavior and ecology (Morgan et al., 2018, 2013; Morgan & Sanz, 2010) can help to safeguard these ape populations for generations to come. Studying the technical behaviors of our closest living relatives is one of the most important tools we have for reconstructing human evolutionary processes. This privilege depends on conserving great apes and their vulnerable homes.

References

Abernethy, K. A., Coad, L., Taylor, G., Lee, M. E., & Maisels, F. (2013). Extent and ecological consequences of hunting in Central African rainforests in the twenty-first century. *Philosophical Transactions of the Royal Society B: Biological Sciences, 368*(1631), 20130494.

Boesch, C. (1991). Teaching among wild chimpanzees. *Animal Behaviour, 41*(3), 530–532.

Boesch, C. (2012). *Wild cultures: A comparison between chimpanzee and human cultures*. Cambridge: Cambridge University Press.

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: Behavioural ecology and evolution.* Oxford: Oxford University Press.

Boesch, C., Bombjaková, D., Meier, A., & Mundry, R. (2019). Learning curves and teaching when acquiring nut-cracking in humans and chimpanzees. *Scientific Reports, 9*(1), 1515.

Boyd, R., & Richerson, P. J. (1996). Why culture is common, but cultural evolution is rare. *Proceedings of the British Academy*, *88*, 77–93.

Burkart, J., Hrdy, S., & van Schaik, C. (2009). Cooperative breeding and human cognitive evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, *18*(5), 175–186.

Byrne, R. (1997). The technical intelligence hypothesis: An additional evolutionary stimulus to intelligence. In A. Whiten & R. Byrne (Eds.), *Machiavellian intelligence II* (pp. 289–311). Cambridge University Press.

Caro, T. M., & Hauser, M. D. (1992). Is there teaching in nonhuman animals? *The Quarterly Review of Biology*, *67*(2), 151–174.

Cronin, K. A. (2012). Prosocial behaviour in animals: The influence of social relationships, communication and rewards. *Animal Behaviour*, *84*(5), 1085–1093.

Csibra, G., & Gergely, G. (2009). Natural pedagogy. *Trends in Cognitive Sciences, 13*(4), 148–153.

de la Torre, I. (2017). Peer commentary on “Early stone tools and cultural transmission: Resetting the null hypothesis” by Claudio Tennie, L. S. Premo, David Braun, and Shannon McPherron. *Current Anthropology*, *58*(5), 662–663.

Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B., & Laland, K. N. (2012). Identification of the social and cognitive processes underlying human cumulative culture. *Science, 335*(6072), 1114–1118.

Eshchar, Y., & Fragaszy, D. (2015). What is teaching? A clear, integrative, operational definition for teaching is still needed. [Peer commentary on “How to learn about teaching: An evolutionary framework for the study of teaching behavior in humans and other animals,” by Michelle Kline]. *Behavioral and Brain Sciences, 754,* 23–24.

Eshchar, Y., Izar, P., Elisabetta, V., Resende, B., & Fragaszy, D. (2016). When and where to practice: Social influences on the development of nut-cracking in bearded capuchins (*Sapajus libidinosus*). *Animal Cognition*, *19*(3), 605–618.

Fogarty, L., Strimling, P., & Laland, K. N. (2011). The evolution of teaching. *Evolution, 65*(10), 2760–2770.

Forstmeier, W. & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: Overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology*, *65*(1), 47–55.

Fragaszy, D., Biro, D., Eshchar, Y., Humle, T., Izar, P., Resende, B., & Elisabetta, V. (2013). The fourth dimension of tool use: Temporally enduring artefacts aid primates learning to use tools. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630), 20120410.

Fragaszy, D., & Mangalam, M. (2018). Tooling. In M. Naguib, L. Barrett, S. Healy, J. Podos, L. Simmons, & M. Zuk (Eds.), *Advances in the Study of Behavior* (Vol. 50, pp. 177–241). Elsevier.

Galef, B. G. (1992). The question of animal culture. *Human Nature, 3*(2), 157–178.

Garfield, Z. H., Garfield, M. J., & Hewlett, B. S. (2016). A cross-cultural analysis of hunter-gatherer social learning. In H. Terashima & B. Hewlett (Eds.), *Social learning and innovation in contemporary hunter-gatherers* (pp. 19–34). Tokyo: Springer.

Gilby, I. C. (2006). Meat sharing among the Gombe chimpanzees: Harassment and reciprocal exchange. *Animal Behaviour*, *71*(4), 953–963.

Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs, 1,* 161–311.

Gumert, M. D., Hamada, Y., & Malaivijitnond, S. (2013). Human activity negatively affects stone tool-using Burmese long-tailed macaques *Macaca fascicularis aurea* in Laem Son National Park, Thailand. *Oryx, 47*(4), 535–543.

Henrich, J., Heine, S. J., & Norenzayan, A. (2010). The weirdest people in the world? *Behavioral and Brain Sciences*, *33*(2–3), 61–83.

Hernik, M., & Gergely, G. (2015). To what adaptive problems is human teaching a solution? [Peer commentary on "How to learn about teaching: An evolutionary framework for the study of teaching behavior in humans and other animals," by Michelle Kline]. *Behavioral and Brain Sciences, 754,* 26–27.

Hewlett, B. S., Fouts, H. N., Boyette, A. H., & Hewlett, B. L. (2011). Social learning among Congo Basin hunter-gatherers. *Philosophical Transactions of the Royal Society B: Biological Sciences, 366*(1567), 1168–1178.

Hoppitt, W., Brown, G., Kendal, R., Rendell, L., Thornton, A., Webster, M., & Laland, K. (2008). Lessons from animal teaching. *Trends in Ecology & Evolution*, *23*(9), 486–493.

Horner, V., Carter, J. D., Suchak, M., & de Waal, F. B. M. (2011). Spontaneous prosocial choice by chimpanzees. *Proceedings of the National Academy of Sciences, 108*(33), 13847–13851.

Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Animal Cognition*, *8*(3), 164–181.

Hrdy, S. B. (2009). *Mothers and others: The evolutionary origins of mutual understanding* (Vol. 112). Cambridge: Harvard University Press.

Humle, T., Snowdon, C. T., & Matsuzawa, T. (2009). Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Animal Cognition*, *12*(Suppl 1), 37–48.

Hunt, K. (2006). Sex differences in chimpanzee foraging behavior and tool use: Implications for the Oldowan. In N. Toth & K. Schick (Eds.), *The Oldowan: Case studies into the earliest stone age* (pp. 243–266). Stone Age Institute Press.

Ingold, T. (1997). Eight themes in the anthropology of technology. *Social Analysis: The International Journal of Social and Cultural Practice*, *41*(1), 106–138.

Jaeggi, A. V, Burkart, J. M., & Van Schaik, C. P. (2010). On the psychology of cooperation in humans and other primates: Combining the natural history and experimental evidence of prosociality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1553), 2723–2735.

Kaplan, H., Hill, K., Lancaster, J., & Hurtado, M. (2000). A theory of human life history evolution: Diet,intelligence, and longevity. *Evolutionary Anthropology*, *9*, 156–185.

Kaplan, H., & Robson, A. J. (2002). The emergence of humans: The coevolution of intelligence and longevity with intergenerational transfers. *Proceedings of the National Academy of Sciences*, *99*(15), 10221–10226.

Kempe, M., Lycett, S. J., & Mesoudi, A. (2014). From cultural traditions to cumulative culture: Parameterizing the differences between human and nonhuman culture. *Journal of Theoretical Biology*, *359*, 29–36.

Kline, M. (2015). How to learn about teaching: An evolutionary framework for the study of teaching behavior in humans and other animals. *Behavioral and Brain Sciences*, *754*, 1–71.

Kline, M., Boyd, R., & Henrich, J. (2013). Teaching and the life history of cultural transmission in Fijian villages. *Human Nature*, *24*(4), 351–374.

Koops, K., Furuichi, T., Hashimoto, C., & van Schaik, C. (2015). Sex differences in object manipulation in wild immature chimpanzees (*Pan troglodytes schweinfurthii*) and bonobos (*Pan paniscus*): Preparation for tool use? *PLoS ONE*, *10*(10), 1–15.

Kruger, A. C., & Tomasello, M. (1998). Cultural learning and learning culture. In D. Olson & N. Torrance (Eds.), *Handbook of education and human development: New models of learning, teaching, and schooling* (pp. 369–387). Blackwell.

Krupenye, C., Tan, J., & Hare, B. (2018). Bonobos voluntarily hand food to others but not toys or tools. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *285*(1886), 20181536.

Kühl, H. S., Boesch, C., Kulik, L., Haas, F., Arandjelovic, M., Dieguez, P., … Kalan, A. K. (2019). Human impact erodes chimpanzee behavioral diversity. *Science*, *4532*.

Lancy, D., & Grove, A. (2010). The role of adults in children's learning. In D. Lancy, J. Bock, & S. Gaskins (Eds.), *The anthropology of learning in childhood* (pp. 145–180). AltaMira Press.

Leonard, J. A., Lee, Y., & Schulz, L. E. (2017). Infants make more attempts to achieve a goal when they see adults persist. *Science*, *357*(6357), 1290–1294.

Little, C., & Lancy, D. (2016). How do children become workers? Making sense of conflicting accounts of cultural transmission in Anthropology and Psychology. *Ethos*, *44*(3), 269–288.

Lockman, J. J. (2000). A perception-action perspective on tool use development. *Child Development*, *71*(1), 137–144.

Lonsdorf, E. V. (2005). Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Animal Behaviour*, *70*(3), 673–683.

Lonsdorf, E. V. (2017). Sex differences in nonhuman primate behavioral development. *Journal of Neuroscience Research*, *95*(1–2), 213–221.

Lonsdorf, E. V, Eberly, L. E., & Pusey, A. E. (2004). Sex differences in learning in chimpanzees. *Nature*, *428*(6984), 715–716.

Luncz, L., & Haslam, M. (2017). Peer commentary on "Early stone tools and cultural transmission: Resetting the null hypothesis" by Claudio Tennie, L. S. Premo, David Braun, and Shannon McPherron. *Current Anthropology*, *58*(5), 656–557.

Marshall-Pescini, S., Dale, R., Quervel-Chaumette, M., & Range, F. (2016). Critical issues in experimental studies of prosociality in non-human species. *Animal Cognition*, *19*(4), 679–705.

Martin, A., Ryan, R. M., & Brooks-Gunn, J. (2013). Longitudinal associations among interest, persistence, supportive parenting, and achievement in early childhood. *Early Childhood Research Quarterly*, *28*(4), 658–667.

McGrew, W. (1979). Evolutionary implications of sex differences in chimpanzee predation and tool use. In D. A. Hamburg & E. R. McCown (Eds.), *The great apes* (pp. 441–463). Menlo Park: Benjamin/Cummings.

McGrew, W. (1992). *Chimpanzee material culture: Implications for human evolution*. Cambridge: Cambridge University Press.

Mead, M. (1970). Our educational emphases in primitive perspective. In J. Middleton (Ed.), *From child to adult: Studies in the anthropology of education, Vol. 12* (pp. 1–13). The Natural History Press.

Melis, A. P. (2018). The evolutionary roots of prosociality: The case of instrumental helping. *Current Opinion in Psychology, 20*, 82–86.

Melis, A. P., & Warneken, F. (2016). The psychology of cooperation: Insights from chimpanzees and children. *Evolutionary Anthropology: Issues, News, and Reviews*, *25*(6), 297–305.

Melis, A. P., Warneken, F., Jensen, K., Schneider, A. C., Call, J., & Tomasello, M. (2011). Chimpanzees help conspecifics obtain food and non-food items. *Proceedings of the Royal Society B: Biological Sciences, 278*(1710), 1405–1413.

Meredith, S. L. (2015). Comparative perspectives on human gender development and evolution: Comparative perspectives on gender. *American Journal of Physical Anthropology*, *156*, 72–97.

Meulman, E. J. M., Sanz, C., Visalberghi, E., & van Schaik, C. P. (2012). The role of terrestriality in promoting primate technology. *Evolutionary Anthropology: Issues, News, and Reviews*, *21*(2), 58–68.

Meulman, E. J. M., & van Schaik, C. P. (2013). Orangutan tool use and the evolution of technology. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 176–202). Cambridge: Cambridge University Press.

Moore, R., & Tennie, C. (2015). Cognitive mechanisms matter – but they do not explain the absence of teaching in chimpanzees. [Peer commentary on "How to learn about teaching: An evolutionary framework for the study of teaching behavior in humans and other animals," by Michelle Kline]. *Behavioral and Brain Sciences*, *754*, 32–33.

Morgan, D., Mundry, R., Sanz, C., Ayina, C. E., Strindberg, S., Lonsdorf, E., & Kühl, H. S. (2018). African apes coexisting with logging: Comparing chimpanzee (*Pan troglodytes troglodytes*) and gorilla (*Gorilla gorilla gorilla*) resource needs and responses to forestry activities. *Biological Conservation*, *218*, 277–286.

Morgan, D., & Sanz, C. (2010). Best practice guidelines for reducing the impact of commercial logging on great apes in Western Equatorial Africa. *IUCN SSC Primate Specialist Group*.

Morgan, D., Sanz, C., Greer, D., Rayden, T., Maisels, F., & Williamson, E. A. (2013). Great apes and FSC: Implementing "ape friendly" practices in Central Africa's logging concessions. *Occasional Papers of the IUCN Species Survival Commission*.

Morgan, T. (2017). Peer commentary on "Early stone tools and cultural transmission: Resetting the null hypothesis" by Claudio Tennie, L. S. Premo, David Braun, and Shannon McPherron. *Current Anthropology*, *58*(5), 658–659.

Musgrave, S., Bell, E., Morgan, D., Lonsdorf, E., & Sanz, C. (2015). Preliminary report on the acquisition of tool-using elements during termite gathering among chimpanzees of the Goualougo Triangle, Republic of Congo. In *American Journal of Physical Anthropology, Vol. 156 (Suppl. 60)* (pp. 232–232).

Musgrave, S., Morgan, D., Lonsdorf, E., Mundry, R., & Sanz, C. (2016). Tool transfers are a form of teaching among chimpanzees. *Scientific Reports*, *6*, 34783.

Ortiz, M., Osuna-Mascaró, A., Stolz, E., Sanz, C., Morgan, D., Musgrave, S., & Fragaszy, D. (2018). Dexterity and flexibility in termite fishing by adult female chimpanzees (*Pan troglodytes troglodytes*) in the Goualougo Triangle, Republic of Congo. Presented at the meeting of the American Society of Primatologists, San Antonio, Texas.

Rosati, A. G., DiNicola, L. M., & Buckholtz, J. W. (2018). Chimpanzee cooperation is fast and independent from self-control. *Psychological Science, 29*(11), 1832–1845.

Samuni, L., Deschner, T., Crockford, C., Wittig, R. M., & Preis, A. (2018). Reward of labor coordination and hunting success in wild chimpanzees. *Communications Biology*, *1*(1), 1–9.

Samuni, L., Preis, A., Mielke, A., Deschner, T., Wittig, R. M., & Crockford, C. (2018). Social bonds facilitate cooperative resource sharing in wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences, 285*, 20181643.

Sanz, C., & Morgan, D. (2011). Elemental variation in the termite fishing of wild chimpanzees (*Pan troglodytes*). *Biology Letters, 7*(4), 634–637.

Schick, K. D., Toth, N., Garufi, G., Savage-Rumbaugh, E. S., Rumbaugh, D., & Sevcik, R. (1999). Continuing investigations into the stone tool-making and tool-using capabilities of a bonobo (*Pan paniscus*). *Journal of Archaeological Science*, *26*(7), 821–832.

Silk, J. B., Brosnan, S. F., Henrich, J., Lambeth, S. P., & Shapiro, S. (2013). Chimpanzees share food for many reasons: The role of kinship, reciprocity, social bonds and harassment on food transfers. *Animal Behaviour, 85*, 941–947.

Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S., … Schapiro, S. J. (2005). Chimpanzees are indifferent to the welfare of unrelated group members. *Nature*, *437*(7063), 1357–1359.

Stout, D. (2002). Skill and cognition in stone tool production. *Current Anthropology, 43*(5), 693–722.

Stout, D., Semaw, S., Rogers, M. J., & Cauche, D. (2010). Technological variation in the earliest Oldowan from Gona, Afar, Ethiopia. *Journal of Human Evolution, 58*(6), 474–491.

Tan, J., & Hare, B. (2013). Bonobos share with strangers. *PLoS ONE, 8*(1), e51922.

Tennie, C., Braun, D., Premo, L. S., & McPherron, S. (2016). The island test for cumulative culture in the Paleolithic. In M. Haidle, N. Conard, & M. Bolus (Eds.), *The nature of culture* (pp. 121–133). Dordrecht: Springer.

Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: On the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1528), 2405–2415.

Tennie, C., Jensen, K., & Call, J. (2016). The nature of prosociality in chimpanzees. *Nature Communications*, *7*, 13915.

Thornton, A., & McAuliffe, K. (2006). Teaching in wild meerkats. *Science*, *313*(5784), 227–229.

Thornton, A., & Raihani, N. J. (2008). The evolution of teaching. *Animal Behaviour*, *75*(6), 1823–1836.

Tomasello, M. (1999). *The cultural origins of human cognition*. Cambridge: Harvard University Press.

Tomasello, M., Kruger, A. C., & Ratner, H. H. (1993). Cultural learning. *Behavioral and Brain Sciences*, *16*, 495–552.

Toth, N., & Schick, K. (2009). The Oldowan: The tool making of early hominins and chimpanzees compared. *Annual Review of Anthropology*, *38*(1), 289–305.

Toth, N., & Schick, K. (2018). An overview of the cognitive implications of the Oldowan Industrial Complex. *Azania: Archaeological Research in Africa*, *53*(1), 3–39.

Toth, N., Schick, K., Savage-Rumbaugh, E. S., Sevcik, R., & Rumbaugh, D. (1993). Pan the tool-maker: Investigations into the stone tool-making and tool-using capabilities of a bonobo (*Pan paniscus*). *Journal of Archaeological Science*, *20*, 81–91.

van Schaik, C. (2002). Fragility of traditions: The disturbance hypothesis for the loss of local traditions in orangutans. *International Journal of Primatology*, *23*(3), 527–538.

Warneken, F., & Tomasello, M. (2009). Varieties of altruism in children and chimpanzees. *Trends in Cognitive Sciences*, *13*(9), 397–402.

Whiten, A., Goodall, J., McGrew, W., Nishida, T., Reynolds, V., Sugiyama, Y., … Boesch, C. (2001). Charting cultural variation in chimpanzees. *Behaviour*, *138*(11–12), 1481–1516.

Wynn, T., Hernandez-Aguilar, A., Marchant, L., & Mcgrew, W. (2011). “An ape’s view of the Oldowan” revisited. *Evolutionary Anthropology: Issues, News, and Reviews*, *20*(5), 181–197.

Wynn, T., & McGrew, W. (1989). An ape’s view of the Oldowan. *Man*, *24*(3), 383.

Yamamoto, S., Humle, T., & Tanaka, M. (2009). Chimpanzees help each other upon request. *PLoS ONE*, *4*(10), e7416.

Yamamoto, S., Humle, T., & Tanaka, M. (2012). Chimpanzees’ flexible targeted helping based on an understanding of conspecifics’ goals. *Proceedings of the National Academy of Sciences*, *109*(9), 3588–3592.

Zihlman, A. L. (2012). The real females of human evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, *21*(6), 270–276.

Appendix A: Chapter 3 Results of GLMMs

TABLE A.1 Fixed Effects

	Estimate	SE	Lower CL	Upper CL	Min	Max
Fishing probe insertion, donor:						
Intercept	1.059	0.143	0.722	1.309	0.000	1.099
Time period	0.490	0.181	0.128	0.887	0.000	0.680
Fishing probe insertion, recipient:						
Intercept	1.369	0.197	0.890	1.699	0.000	1.421
Time period	-1.244	0.346	-2.032	-0.582	-1.609	0.001
Feeding events, donor:						
Intercept	0.981	0.190	0.627	1.260	0.802	1.308
Time Period	0.693	0.244	0.328	1.087	0.275	0.950
Feeding events, recipient:						
Intercept	1.273	0.262	0.571	1.712	1.146	1.350
Time period	-1.464	0.433	-2.519	-0.620	-1.988	-1.227

Indicated are the estimated coefficients for the fixed effects together with their standard errors (SE) confidence intervals (lower CL, upper CL) and estimations of model stability (columns headed min and max, which indicate the range of estimates derived from excluding levels of the random effects one at a time).

TABLE A.2 Random Effects

Fishing probe insertion, donor:	grp	Term	vcov	sdcor	min	max
	Transfer	event ID	0.000	0.000	0.000	0.004
	(chimpanzee)	Time period	0.000	0.000	0.000	0.003
	Chimpanzee	donor ID	0.000	0.000	0.000	0.234
Fishing probe insertion, recipient:	grp	var1	vcov	sdcor	min	max
	Transfer	event ID	0.000	0.000	0.000	0.004
	Chimpanzee	recipient ID	0.000	0.000	0.000	0.003
Feeding events, donor:	grp	Term	vcov	sdcor	min	max
	Transfer	event ID	0.000	0.000	0.000	0.001
	(chimpanzee)	Time period	0.000	0.000	0.000	0.353
	Chimpanzee	donor ID	0.000	0.000	0.000	0.002
Feeding events, recipient:	grp	Term	vcov	sdcor	min	max
	Transfer	event ID	0.111	0.333	0.002	0.688
	Chimpanzee	recipient ID	0.000	0.000	0.000	0.636

Indicated are the estimated variance (vcov) and corresponding standard deviation (sdcor) for the random intercept of donor or recipient identity and the random slope of time period within donor or recipient, respectively, together with estimations of model stability (columns headed min and max, which indicate the range of standard deviations derived from excluding levels of the random effects one at a time).

Appendix B: Chapter 3 Supplementary Video Clip Descriptions

Supplementary Video Clip 1
Title: Adult female chimpanzee divides a fishing probe lengthwise
Description: An adult female chimpanzee at an above-ground termite nest divides her fishing probe lengthwise. She provides one half of her tool to her offspring, who uses it to successfully fish for termites, and retains the other half for her own use. This strategy produces two viable tools, which helps to buffer tool donors against the cost of transferring a tool.

Supplementary Video Clip 2
Title: Adult female chimpanzee actively transfers a fishing probe
Description: An adult female chimpanzee at an above-ground termite nest performs an active transfer of a fishing probe to her offspring, who uses it to successfully fish for termites. Active transfers involve moving to facilitate a transfer in response to begging.

Appendix C: Chapter 4 Results of GLMMs

TABLE C.1 Results of the model of tool transfer probability (estimates, together with standard errors, confidence limits, results of tests, as well as minimum and maximum of estimates derived when excluding levels of random effects one at a time)

Term	Estimate	SE	lower Cl	upper Cl	χ^2	df	P	min	max
Intercept	0.026	0.643	-1.265	1.536			(1)	-0.415	0.676
Population(2)	0.811	0.944	-0.862	2.629			(1)	0.058	1.346
Request(3)	-2.055	0.585	-4.443	-0.888			(1)	-2.561	-0.871
Recipient sex(4)	-1.489	0.746	-3.629	-0.110	4.064	1	0.044	-2.057	-1.069
Recipient age, 5-10(5)	1.915	1.144	0.067	4.841	7.260	2	0.027	1.459	2.909
Recipient age, 10-15(5)	2.833	1.446	0.798	16.046				2.288	18.177
Population:Request	2.773	0.868	1.074	6.005	9.687	1	0.002	1.623	3.616

(1) not shown because of having a very limited interpretation
(2) dummy coded with Gombe being the reference level
(3) dummy coded with no request being the reference level
(4) dummy coded with female being the reference level
(5) dummy coded with age 0 to 5 being the reference level; the indicated test refers to the overall effect of age

TABLE C.2 Results of the model of reactive tool transfer probability (estimates, together with standard errors, confidence limits, results of tests, as well as minimum and maximum of estimates derived when excluding levels of random effects one at a time)

Term	Estimate	SE	lower Cl	upper Cl	χ^2	df	P	min	max
Intercept	-1.954	1.500	-12.747	1.231			(1)	-6.432	-1.163
Population(2)	4.579	2.248	1.522	28.332	7.400	1	0.007	3.505	14.742
Recipient sex(3)	-0.982	1.503	-17.704	2.151	0.381	1	0.537	-2.263	0.369
Recipient age, 5-10(4)	0.365	1.506	-3.160	11.231	0.984	2	0.611	-0.964	1.830
Recipient age, 10-15(4)	2.113	2.014	-1.815	18.355				0.605	18.144

(1) not shown because of having a very limited interpretation
(2) dummy coded with Gombe being the reference level
(3) dummy coded with female being the reference level
(4) dummy coded with age 0 to 5 being the reference level; the indicated test refers to the overall effect of age

TABLE C.3 Results of the model of resistance probability (estimates, together with standard errors, confidence limits, results of tests, as well as minimum and maximum of estimates derived when excluding levels of random effects one at a time)

Term	Estimate	SE	lower Cl	upper Cl	χ^2	df	P	min	max
Intercept	-1.782	0.435	-2.973	-1.007			(1)	-2.262	-1.286
Population(2)	0.354	0.642	-1.186	1.786			(1)	-0.211	0.786
Request(3)	1.743	0.582	0.777	3.076			(1)	0.943	2.606
Recipient sex(4)	-0.218	0.478	-1.153	0.715	0.221	1	0.639	-0.426	-0.043
Recipient age, 5-10(5)	-0.606	0.768	-13.069	0.739	1.889	2	0.389	-1.557	-0.335
Recipient age, 10-15(5)	-1.228	1.129	-13.664	0.616				-17.860	-0.884
Population:Request	-1.847	0.892	-3.834	-0.199	4.688	1	0.030	-2.698	-1.057

(1) not shown because of having a very limited interpretation

(2) dummy coded with Gombe being the reference level

(3) dummy coded with no request being the reference level

(4) dummy coded with female being the reference level

(5) dummy coded with age 0 to 5 being the reference level; the indicated test refers to the overall effect of age