

# ScholarWorks@GSU

## Tool Use in Pan: Two Modalities, Two Species

Authors	Mahovetz, Lindsay M.
Citation	Mahovetz, Lindsay M.. "Tool Use in Pan: Two Modalities, Two Species." 2018. Dissertation, Georgia State University. <a href="https://doi.org/10.57709/12567779">https://doi.org/10.57709/12567779</a>
DOI	<a href="https://doi.org/10.57709/12567779">https://doi.org/10.57709/12567779</a>
Download date	2026-05-08 12:29:39
Link to Item	<a href="https://hdl.handle.net/20.500.14694/12926">https://hdl.handle.net/20.500.14694/12926</a>

# TOOL USE IN *PAN*: TWO MODALITIES, TWO SPECIES

by

LINDSAY MAHOVETZ

Under the Direction of William D. Hopkins, PhD

## ABSTRACT

A notable difference between the two *Pan* species is their tool using ability. Though many studies on physical tool use exist, few investigate social tool use and, to my knowledge, none focus on their potential relationship or cognitive foundations. While captive and wild chimpanzees are recognized as proficient tool users, captive bonobos exhibit some tool using skills but evidence in wild bonobos is rare. An important similarity, however, is their flexible and intentional use of communicative signals. Captive bonobos and chimpanzees are known to use their communicative behaviors to manipulate humans to obtain an unreachable food, a form of social tool use. With growing interest in social tool use, an emerging central question is to what extent different species utilize these two tool strategies. Thus, 27 bonobos and 29 chimpanzees were given a physical tool task requiring retrieval of a reward at increasing

distances such that the physical tool no longer solved the problem while a human who could be solicited was present. Although both species successfully retrieved rewards with the physical tool and solicited the human, chimpanzees showed greater proficiency and flexibility by making fewer attempts to retrieve rewards, retrieving rewards faster, and making more solicitations. For both species, solicitation behavior was prevalent at further distances where the reward was unable to be retrieved, supporting previous research showing these species intentionally produce attention-getting/directing behaviors to indicate toward desired out-of-reach items. In this study, bonobos and chimpanzees exhibited cognitive flexibility by switching tool strategies from using a physical tool at closer distances to using a social tool (a human) at further distances. Regardless of species, physical and social tool performance was related to performance on previous physical and social cognition tasks, including the Primate Cognition Test Battery. The results of this study support the idea that physical and social cognition may not be two separate cognitive domains, as they are so often treated. Rather, cognition may be a single entity in which certain behaviors and processes are elicited by physical and/or social contexts, allowing the transition between physical and social tool modalities.

INDEX WORDS: Tool use, Bonobos, Chimpanzee, Physical cognition, Social cognition,  
Attention-getting

TOOL USE IN *PAN*: TWO MODALITIES, TWO SPECIES

by

LINDSAY M. MAHOVETZ

A Dissertation Submitted in Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

in the College of Arts and Sciences

Georgia State University

2018

Copyright by  
Lindsay Marie Mahovetz  
2018

TOOL USE IN *PAN*: TWO MODALITIES, TWO SPECIES

by

LINDSAY M. MAHOVETZ

Committee Chair: William Hopkins

Committee: Michael Beran

Sarah Brosnan

Jill Pruetz

David Washburn

Electronic Version Approved:

Office of Graduate Studies

College of Arts and Sciences

Georgia State University

August 2018

## **DEDICATION**

I dedicate this work to my family and friends who have been there by my side through the many ups and downs. It is without them that I would not have had the courage to follow my dreams. I also dedicate this work to all of my bonobo and chimpanzee subjects who taught me great patience and whom I already and will continue to greatly miss.

## ACKNOWLEDGEMENTS

I would like to thank my advisor and dissertation committee chair Dr. William Hopkins, and committee members Drs. Mike Beran, Sarah Brosnan, Jill Pruett, and David Washburn for their guidance and support throughout the entire dissertation process. I especially would like to extend my deepest gratitude to Dr. William Hopkins for providing me with the opportunity to join his research team and providing me with research, funding, academic, and moral support throughout my graduate career. Additionally, I would like to thank all of the bonobo caretakers at ACCI, Jacksonville Zoo and Gardens, and Milwaukee County Zoo, and the chimpanzee caretakers at Maryland Zoo and Yerkes National Primate Research Center for their flexibility and assistance with making my project possible. Lastly, I would like to thank all of my subjects for it is without their excitement to participate that this study would not be possible.

## TABLE OF CONTENTS

<b>ACKNOWLEDGEMENTS .....</b>	<b>V</b>
<b>LIST OF TABLES.....</b>	<b>IX</b>
<b>LIST OF FIGURES.....</b>	<b>X</b>
<b>LIST OF ABBREVIATIONS.....</b>	<b>XI</b>
<b>1 INTRODUCTION .....</b>	<b>1</b>
<b>1.1 <i>Pan</i> Tool Use.....</b>	<b>1</b>
<b><i>1.1.1 Explanations for Tool Using Differences .....</i></b>	<b>2</b>
<b><i>1.1.2 Object Manipulation and Motivations for Tool Use.....</i></b>	<b>8</b>
<b>1.2 Social Behavior &amp; Communication.....</b>	<b>10</b>
<b>1.3 Social Tool Use .....</b>	<b>12</b>
<b>2 AIMS, QUESTIONS, AND HYPOTHESES.....</b>	<b>15</b>
<b>2.1 Species Differences.....</b>	<b>18</b>
<b>2.2 Distance Differences .....</b>	<b>18</b>
<b>2.3 Individual Differences .....</b>	<b>18</b>
<b>3 METHODS.....</b>	<b>19</b>
<b>3.1 Subjects.....</b>	<b>19</b>
<b>3.2 Attention-Getting Assessment .....</b>	<b>20</b>
<b>3.3 Solicit for Tool.....</b>	<b>23</b>
<b>3.4 Physical versus Social Testing .....</b>	<b>23</b>

3.5	Data Analyses .....	25
4	RESULTS .....	25
4.1	Descriptive Statistics and Normality Tests .....	25
4.2	Condition Differences .....	26
4.3	Species Differences.....	28
4.3.1	<i>Retrieval Attempts</i> .....	28
4.3.2	<i>Retrieval Latency</i> .....	30
4.3.3	<i>Number of Solicitations</i> .....	32
4.3.4	<i>Solicitation Latency</i> .....	33
4.4	Distance Differences .....	34
4.4.1	<i>Retrieval Attempts</i> .....	34
4.4.2	<i>Retrieval Latency</i> .....	35
4.4.3	<i>Number of Solicitations</i> .....	36
4.4.4	<i>Solicitation Latency</i> .....	38
4.4.5	<i>Time at Table</i> .....	39
4.5	Individual Differences .....	40
4.5.1	<i>PCTB</i> .....	40
4.5.2	<i>Attention-Getting Assessment</i> .....	50
4.5.3	<i>Solicit for Tool</i> .....	50
4.5.4	<i>Return to Tool</i> .....	50

<b>5</b>	<b>DISCUSSION.....</b>	<b>51</b>
5.1	Evolution of Hominin Tool Use .....	52
5.2	Cognition Dichotomy .....	56
5.3	Behavioral/Cognitive Flexibility .....	58
5.4	Summary.....	60
	<b>REFERENCES .....</b>	<b>62</b>

**LIST OF TABLES**

Table 3.1 Subject demographic information .....	21
Table 3.2 Ethogram of attention-getting signals .....	22
Table 4.1 Descriptive statistics and normality test results .....	26
Table 4.2 PCTB partial correlation analyses summary .....	41

## LIST OF FIGURES

<b>Figure 1.1 African ape geographic distribution.....</b>	<b>3</b>
<b>Figure 3.1 Experimental set-up and retrieval example.....</b>	<b>24</b>
<b>Figure 4.1 Overall trials solicited on during EA and EP conditions.....</b>	<b>27</b>
<b>Figure 4.2 Number of trials solicited for each distance during EA and EP conditions .....</b>	<b>28</b>
<b>Figure 4.3 Mediation of Close retrieval attempts by time at table .....</b>	<b>29</b>
<b>Figure 4.4 Mediation of Close retrieval latency by time at table .....</b>	<b>31</b>
<b>Figure 4.5 Mediation of Far number of solicitations by time at table .....</b>	<b>33</b>
<b>Figure 4.6 Mean retrieval attempts by species .....</b>	<b>35</b>
<b>Figure 4.7 Mean retrieval latency by species .....</b>	<b>36</b>
<b>Figure 4.8 Mean number of solicitations by species.....</b>	<b>37</b>
<b>Figure 4.9 Mean number of retrieval attempts and solicitations .....</b>	<b>38</b>
<b>Figure 4.10 Mean solicitation latency by species .....</b>	<b>39</b>
<b>Figure 4.11 Mean time spent at table by species.....</b>	<b>40</b>
<b>Figure 4.12 PCTB performance and retrieval performance .....</b>	<b>43</b>
<b>Figure 4.13 PCTB performance and solicitation behaviors .....</b>	<b>44</b>
<b>Figure 4.14 Physical PCTB performance and retrieval performance .....</b>	<b>46</b>
<b>Figure 4.15 Tool PCTB performance and retrieval performance .....</b>	<b>47</b>
<b>Figure 4.16 Social PCTB performance and solicitation behaviors .....</b>	<b>49</b>
<b>Figure 4.17 Return to tool frequency.....</b>	<b>51</b>

**LIST OF ABBREVIATIONS**

ACCI	Ape Cognition and Conservation Initiative
AG	Attention-Getting
ASD	Autism Spectrum Disorder
AUD	Alcohol Use Disorder
JZG	Jacksonville Zoo and Gardens
MCZ	Milwaukee County Zoo
MDZ	The Maryland Zoo in Baltimore
MR	Medium Retrievable
MNR	Medium Not Retrievable
PCTB	Primate Cognition Test Battery
THV	Terrestrial Herbaceous Vegetation
UWA	Universal Weighted Average
UWA_g	General Intelligence Score “g”
YNPRC	Yerkes National Primate Research Center

## 1 INTRODUCTION

Diverging from each other just one to two million years ago, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) are very similar to one another behaviorally, physically, and genetically (Herrmann, Hare, Call, & Tomasello, 2010; Kano, 1992). However, these species also have notable differences pertaining to their social behavior and systems as well as their use of tools. Some of the highlighted differences between bonobos and chimpanzees have been attributed to the differing environments in which they live and the foods that are available. More specifically, many important food sources are available year round in bonobo habitats while many preferred or high protein foods are seasonally available in chimpanzee habitats. This has led some to suggest that seasonality of high valued foods may have led to increased selection for advanced extractive foraging techniques such as tool use (Gruber, Reynolds, & Zuberbühler, 2010; Hohmann & Fruth, 2003).

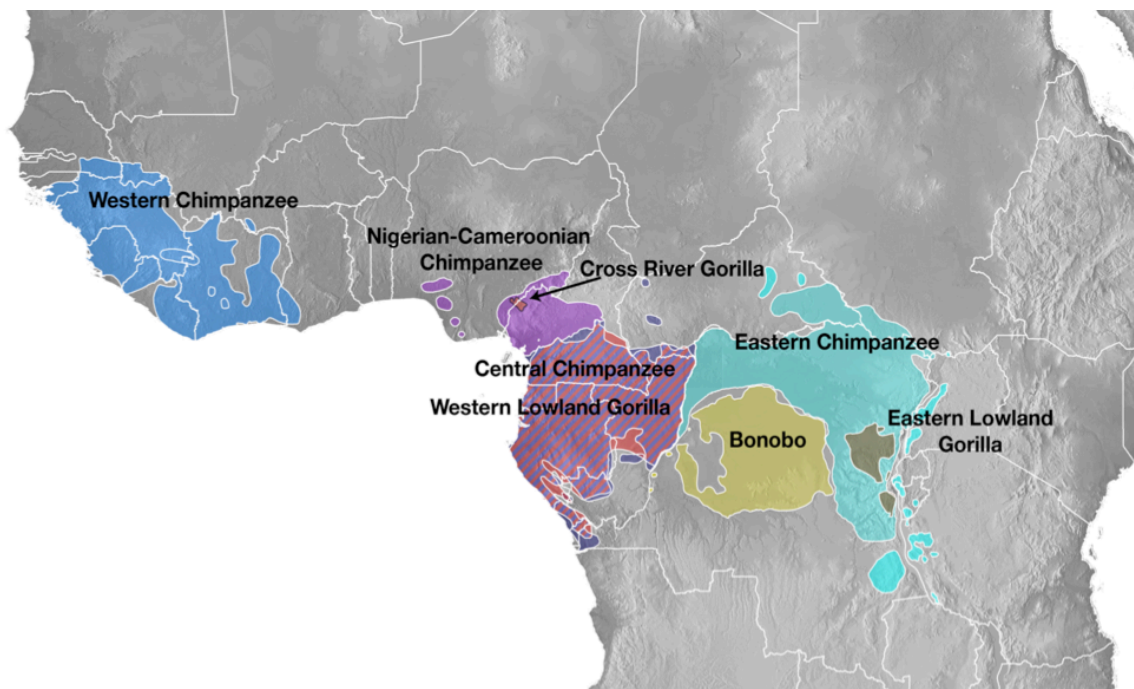
### 1.1 *Pan* Tool Use

Chimpanzees are recognized for their tool using ability in various contexts (mostly during foraging) both in the wild and in captivity. Wild chimpanzees have an extensive tool using repertoire including probing, digging, and hunting using sticks, cracking nuts open using rocks or other hammer-like objects, and sponging/wadging using leaves, just to name a few. Similarly, captive chimpanzees also show proficiency in many of these same activities, especially probing, nut cracking, and sponging/wadging, and have been shown to use properties of weight (Schrauf, Call, Fuwa, & Hirata, 2012), length (Mahovetz, 2015; Sabbatini, Truppa, Hribar, Gambetta, Call, & Visalberghi, 2012), shape and rigidity (Mahovetz, 2015) to select effective tools. (*For detailed catalogues/reviews of tool use see: Beck, 1980; Goodall, 1986; Shumaker, Walkup, & Beck, 2011*)

While some have reported tool use in captive bonobos (Gruber, Clay, & Zuberbühler, 2010; Jordan, 1982), evidence of material tool use in wild bonobos remains essentially non-existent, and, if manifest, occurs during social and not foraging contexts (Koops, Furuichi, & Hashimoto, 2015). This difference was originally proposed to result from food availability differences limiting (or heightening) the need for tools. This hypothesis, called the “necessity hypothesis,” proposes that tool use developed as a response to scarcity in resources by enabling practitioners to exploit novel food sources (Fox, Sitompul, & van Schaik, 1999; Furuichi, Sanz, Koops, Sakamaki, Ryu, Tokuyama, & Morgan, 2015; Sanz & Morgan, 2013).

### ***1.1.1 Explanations for Tool Using Differences***

A number of studies investigated differences in tool use across ape populations. One of the earliest by Fox and colleagues (1999) focused on the orangutan populations at Suaq Balimbing, in the Kluet Pleat swamps of Gunung Leuser National Park, Sumatra. It was suggested that the large population created increased food competition, leading orangutans to devise alternative foraging strategies to exploit novel resources. When it comes to differences in the use of tools between bonobos and chimpanzees, resource scarcity is suggested to have led to the innovation of tool strategies to supplement diets, within *Pan troglodytes* (Sanz & Morgan, 2013). For instance, chimpanzees inhabit 22 African countries, including areas north of the Congo River and as far northwest as Senegal, ranging from rain forest habitats to savannas (*see Figure 1.1 for African ape geographic distribution*). Bonobos, in contrast, live in a relatively concentrated area in the equatorial forests of the Democratic Republic of Congo south of the Congo River.



**Figure 1.1 African ape geographic distribution**

African ape distribution adapted by Peter Sudmant from Figure 1a from Prado-Martinez, Sudmant, Kidd, Li, Kelley, Lorente-Galdos, et al. (2013).

Though both species feed heavily on fruits and consume terrestrial herbaceous vegetation (THV; Heilbrunner, Rosati, Stevens, Hare, & Hauser, 2008; Wrangham & Peterson, 1996), chimpanzees are reported to typically rely more on foods that are more variable in availability (Gruber et al., 2010; Heilbrunner et al., 2008; Wrangham & Peterson, 1996), and on extractive foraging (Herrmann et al., 2010). Bonobos, living in a habitat characterized by high abundance of large, dense food patches with low seasonality and high densities of THV (Gruber & Clay, 2016), may rely more on the herbaceous vegetation, a more consistent food source that may buffer against seasonal shortages in fruit (Wrangham & Peterson, 1996). While at least 13 different types of tools have been found in Wamba, the longest running bonobo field site, there are no observed accounts of their actual use in foraging by bonobos (Gruber & Clay, 2016). However, it is plausible that tool use might have occurred in response to opportunity and

profitability rather than to resource scarcity (Sanz & Morgan, 2013). Scientists have sought to determine more specifically the factors corresponding with the emergence of complex tool use, particularly within the hominin lineage (Sanz & Morgan, 2013). With increasing investigation, ecological and social hypotheses have been used to account for variation in tool use among great apes (Fox et al., 1999; Koops, McGrew, & Matsuzawa, 2013; Roffman, Savage-Rumbaugh, Rubert-Pugh, Stadler, Ronen, & Nevo, 2015; Sanz & Morgan, 2013), though none alone seem sufficient to explain the lack of tool foraging in bonobos (Furuichi et al., 2015; Roffman et al., 2015).

#### *1.1.1.1 Ecological Hypotheses*

Three prominent ecological hypotheses offered to explain species differences in tool use include the necessity hypothesis, the opportunity hypothesis, and the terrestrial herbaceous vegetation (THV) hypothesis.

The necessity hypothesis posits that staple resource scarcity led to tool foraging strategies to exploit otherwise unavailable food sources (Fox et al., 1999), allowing one to then predict changes in frequency and/or variety of tool use based upon resource availability (Sanz & Morgan, 2013). Seasonality may increase diversity in the types of foods consumed or create a switch to other ‘keystone’ resources (Fox, van Schaik, Sitompul, & Wright, 2004; Terborgh, 1986; Yamakoshi, 1998) along with individual energetic needs. If insect-extraction developed as a response to food scarcity, the necessity hypothesis would predict that insects are a fall back food, a food only exploited when fruit is scarce and negatively correlated with availability of preferred foods (Koops et al., 2013). Thus, according to the necessity hypothesis, bonobos having a less variable food resource than chimpanzees would explain the differences in tool use because an abundance of food resources would alleviate the need for fallback strategies such as

tool use (Furuichi et al., 2015). Previous reports suggest that chimpanzee tool use correlates with fruit abundance at Bossou, Guinea (Furuichi et al., 2015; Sanz & Morgan, 2013; Yamakoshi, 1998). However, when directly comparing habitat characteristics and fluctuation of fruit production between the bonobo habitat in Wamba and the chimpanzee habitat in Goualougo, Furuichi and colleagues (2015) found comparable seasonal fluctuation patterns in ripe fruit availability between the two sites. Therefore, while links between seasonal scarcity and tool use have been suggested for some primate species, unequivocal evidence is lacking, warranting more investigation (Koops, Visalberghi, & van Schaik, 2014). Perhaps insects are less of a fallback food resultant of resource shortages, but rather provide the opportunities contributing to tool derived insect extraction (Fox et al., 2004).

The opportunity hypothesis supposes that the invention of tool use is a function of increased opportunities to use tools (Fox et al., 1999; Fox et al., 2004; Spagnoletti, Visalberghi, Verderane, Ottoni, Izar, & Frigaszy, 2012). Specifically, exposure to both foods requiring extraction (nuts, insects) and tools for extraction drive tool using behavior in populations; limited or lack of exposure would explain absence of tool use in a given population (Koops et al., 2013). At Taï, Koops et al. (2013) suggested that limited opportunities to find nuts, not of opportunities to find tools, explained absence of nut cracking. If the opportunity hypothesis holds, then it should also predict that differing populations would use tools to extract seeds of a particular tree if the trees are present in both locations. However, Koops and colleagues (2013) point out that for chimpanzees in Taï, it may not simply be the presence or absence of the nut trees or termite mounds but rather the distribution and density that seems to coincide with opportunity and thus invention of tool behaviors. Though the opportunity hypothesis has some support at various sites (Koops et al., 2014), it seems opportunity alone is not sufficient for tool use to emerge.

The third ecological hypothesis is the terrestrial herb vegetation (THV) hypothesis, which suggests that differences in bonobo and chimpanzee behavior are derived from the presence of sufficient THV as fallback foods (Yamakoshi, 2004). While both species depend on highly nutritious ripe fruits, they also feed on THV (Yamakoshi, 2004). This hypothesis assumes that THV is a good alternative nutrient source sufficient to support higher group cohesion when ripe fruit is scarce. It also assumes that bonobos may have greater access to and thus consume more THV than chimpanzees who live sympatrically with gorillas (Yamakoshi, 2004) because THV comprises the bulk of the gorilla diet (Wrangham, 1986; Wrangham, Chapman, Clark-Arcadi, & Isabirye-Basuta, 1996). Evidence supporting the THV hypothesis stems from observations in the Lomako Forest where bonobos eat more THV than chimpanzees in Kibale National Park (Malenky & Wrangham, 1994; Wrangham et al., 1996) and that THV can be a fallback food when competition for it is less (Wrangham et al., 1996).

Important to note is that chimpanzee populations differ too. While the THV hypothesis may hold for East African chimpanzees, it may not for other populations that overlap in habitat with other species that also consume THV. Further, the Kanyawara chimpanzees in Kibale National Park in East Africa are not necessarily representative of other chimpanzee populations. Additionally, some data shows that even when THV was abundant the Kanyawara chimpanzees forage on figs instead of THV (Wrangham, 1986; Wrangham et al., 1996), contradicting the THV hypothesis. Furthermore, most reported differences in behavior, particularly regarding tool use and social behavior, are between bonobos and East African chimpanzees (Yamakoshi, 2004). West African chimpanzees, on the other hand, show behavioral similarities to bonobos and differences to East African chimpanzees (Yamakoshi, 2004). West African chimpanzees do not live sympatrically with gorillas, suggesting that segregation from gorillas may result in the

similarities we see, particularly because East African chimpanzees may face competition with gorillas (Yamakoshi, 2004). There are also contrasting effects of seasonal abundance/scarcity on chimpanzees seen between Kibale (eastern) and Bossou (western) chimpanzees. Chimpanzees at Kibale do not have access to good fallback foods other than THV while Bossou chimps have palm pith and nuts (which require tools; Yamakoshi, 2004). However, for Taï (western) chimpanzees, nuts are present when fruit abundance is high. Thus, nuts are not considered a fallback food and may impede exploration of nut cracking in the Taï population (Koops et al., 2013).

Taken as a whole it seems as though ecological conditions are not alone sufficient to explain the differences in tool use between bonobos and chimpanzees as well as geographically separated chimpanzees.

#### *1.1.1.2 Social Hypothesis: Limited Invention Hypothesis*

Strictly ecologically based ideas explaining the evolution of, and differences in, tool using behaviors, such as those mentioned above, neglect to consider the cognitive and social components of invention and maintenance of such behavior (Fox et al., 1999). The limited invention hypothesis, however, suggests that the presence of tool use should be geographically limited (Fox et al., 1999); not only must the invention of tool use occur, but the behavior must be reliably transmitted and maintained across a population (Van Schaik & Knott, 2001). The invention of tool using behaviors is infrequent, and so opportunities for social learning facilitate the spread and maintenance of these behaviors such that they may become frequent within a population. Thus, it has also been suggested that differences in tool using behaviors between populations may be better explained by social transmission and the reliability of copying such behaviors once they have been invented (Van Schaik & Knott, 2001).

Rather than just one specific factor contributing to the emergence of tool use in some species, ecology, sociality, and cognition might all be working together (Koops et al., 2014). The environment provides opportunities through food abundance and density, which increase encounter rates, which facilitate innovation of novel tool using behaviors. Living in social groups, being tolerant of social partners, and leaving behind tool artifacts aid the transmission of tool using behaviors via social learning once innovated.

### ***1.1.2 Object Manipulation and Motivations for Tool Use***

Predisposition for tool use is also an important factor to consider when investigating differences both across and within species. These predispositions may be measured through object manipulation and object play, which have been suggested as precursors of tool use (Hayashi, Takeshita, & Matsuzawa, 2006) as observable proxies of tool use tendencies. Numerous animals interact with and manipulate objects in their environment. These manipulations help provide the foundation for developing both functional and conceptual knowledge about the physical environment (Bennett, 1996; Piaget, 1974). As such, object manipulation likely provides a pathway toward understanding related behaviors, particularly tool using behaviors (Bennett, 1996). By manipulating objects, individuals are provided with experiences that may promote tool use through object combination and other actions which may increase the chances of a successful tool-dependent strategy (Bennett, 1996; Westergaard & Fragaszy, 1987) or aid in ones understanding of causal relationships (Bennett, 1996).

Early evidence suggest that bonobos, not chimpanzees, exhibit greater object manipulation tendencies (Bard & Vauclair, 1984; Vauclair & Bard, 1983). However, testing a sample of seven captive bonobos and 42 captive chimpanzees, Bennett (1996) found no differences in the overall number of manipulation bouts despite chimpanzees exhibiting more

bouts with social interaction as compared to bonobos. While individual differences were apparent, so were group differences, such that age and species were more predictive of the type of manipulation than sex (Bennett, 1996). Bennett's study suggests that object manipulation is useful "as a measure reflective of differences in behaviors linked to tool use" (p. 91, 1996).

More recently, Koops and colleagues (2015) investigated differences in tool use between wild bonobos and chimpanzees, separating the motivations underlying tool use into extrinsic and intrinsic motivations. Extrinsic motivations are described as the ecological and social opportunities, measured by availability of resources requiring tools and opportunities for social learning (as discussed above in section 1.1.3). Intrinsic motivations are described as the predispositions for tool use that are not in response external stimuli, including object manipulation and object play.

Koops and colleagues (2015) found that intrinsic predispositions explained the differences in tool use between wild bonobos and chimpanzees. Specifically, chimpanzees exhibited higher rates of object manipulation and object play than bonobos, leading to the question of why bonobos seem less interested in objects. One possibility is that bonobos may pay more attention to social cues while chimpanzees pay more attention to 'action target objects', such as foods or toys, as shown by Kano, Hirata, and Call's (2015) eye-tracking study. Bonobos and chimpanzees were shown three sets of stimuli: 1) full faces of apes with eyes and mouth, 2) full bodies of apes with action target objects (i.e., food, toys), and 3) full bodies of apes with the ano-genital area visible. Though overall viewing time was comparable between species, bonobos looked at the eyes in full-face stimuli and the face in full body stimuli containing an action target object and ano-genital areas longer than chimpanzees. In contrast, chimpanzees looked longer at the mouth in full-face stimuli and the action target objects and

ano-genital areas in full body stimuli containing those features. In terms of fixation, bonobos fixated on the eyes while chimpanzees fixated on the mouth. This greater attention toward eyes and faces compared to action target items, which included tools, exhibited by bonobos suggests that there may be a trade-off between motivation for using tools and that for social attention (Koops et al., 2015).

## **1.2 Social Behavior & Communication**

While these species differ in the dominance structure of their societies (bonobos are matriarchal, chimpanzees are patriarchal), they both exhibit fission-fusion, females emigrate from their natal group, and both flexibly use communicative signals (vocalizations and gestures alone and in combination) with other group members as a major part of their daily lives. Both species produce vocalizations that are context-specific in a variety of ecological, social and behavioral situations (Crockford & Boesch, 2003; Hopkins, Taglialatela, & Leavens, 2007; Notman & Rendall, 2005; Slocombe & Zuberbühler, 2005; Taglialatela, Savage-Rumbaugh, & Baker, 2003). These communicative signals are not only context-specific but are also intentional.

Captive chimpanzees are known to intentionally produce manual gestures (Call & Tomasello, 1994; Hostetter, Cantero, & Hopkins, 2001; Krause & Fouts, 1997; Leavens, Hostetter, Wesley, & Hopkins, 2004; Tomasello, Call, Nagell, Olguin, & Carpenter, 1994) that include attention-directing gestures such as pointing (Leavens, Russell, & Hopkins, 2005), attention-getting gestures such as clapping (Hostetter et al., 2001; Leavens et al., 2004), and facial expressions that are considered iconic gestures and include the ‘juice me’ face (Leavens & Hopkins, 1998). Like chimpanzees, captive bonobos have also been reported to intentionally produce attention-directing and attention-getting behaviors (Savage-Rumbaugh, 1984;

Zimmermann, Zemke, Call, & Gómez, 2009). These types of behaviors are typically produced when food is located out of reach or when indicating hidden items to people (Zimmermann et al., 2009). An important factor, though, is that these gestures are exhibited only when a human is present and oriented toward the subject (Call & Tomasello, 1994; Hostetter et al., 2001; Kaminski, Call, & Tomasello, 2004; Krause & Fouts, 1997; Leavens, Hopkins, & Bard, 1996; Leavens et al., 2004; Poss, Kuhar, Stoinski, & Hopkins, 2006; Tomasello, Call, Nagell, Olguin, & Carpenter, 1994), allowing for engagement in joint attention by alternating their gaze between the food and the human while gesturing (Leavens & Hopkins, 1998). Chimpanzees also intentionally produce sounds/vocalizations, including raspberries and extended grunts (Hopkins et al., 2007). These sounds are also made more often when a human and food are present than when either is presented alone, highlighting the context-specificity and intentionality of their communication.

Both species have shown flexibility in their communication by altering or combining the modalities of communication depending on the context and communicative demands of the situation. For example, individuals produce more visual AG gestures to a human facing them than one turned away (Hostetter et al., 2001; Hostetter, Russell, Freeman, & Hopkins, 2007; Kaminski et al., 2004). Most importantly, they are able to repair their communication when it has failed by persisting and elaborating their communicative behaviors (Leavens et al., 2005; Savage-Rumbaugh, 1984; wild bonobos: Pika, Liebal, & Tomasello, 2005). Recently, Lurz and colleagues (2018) found that chimpanzees produced more visual AG behaviors both when an experimenter was facing them and when looking at them in a mirror with his/her back to the chimpanzee, than when the experimenter had his/her back to the chimpanzee and was looking at the non-reflective side of the mirror. In these examples, apes are using their communicative

behaviors to engage in joint attention and manipulate a human to obtain food they are unable to otherwise obtain. This is what some have defined as “social tool use.”

### **1.3 Social Tool Use**

Social tool use can be defined as “the physical and psychological manipulations of animate beings towards some goal” (p. 127, Völter, Rossano, & Call, 2015). Some of the earliest accounts of social tool use are reported in studies by Crawford in the late 1930s and early 1940s. Crawford investigated cooperative problem solving tactics in five juvenile chimpanzees on a box-pulling task (1937, 1941). Crawford found that two of the juveniles employed solicitation behaviors toward their partner. These behaviors typically occurred when the partner did not attempt to pull, resulting in either bringing their partner to the grill or to motivate them to pull. Such behaviors included begging gestures, whimpers, retrieving the partner, and touching the partner. The solicitations varied in intensity, duration, and frequency depending on factors such as how responsive the partner was, closeness of friendship, and motivation toward reward. Crawford suggests that the “solicitation of another animal’s help can be regarded as the selection of a tool or instrument...[implying] familiarity on the part of the solicitor with the use of other animals as means or instruments” (p. 69, 1937).

In the late 1980s Gómez investigated the problem solving strategies of a gorilla, the manipulation of objects (physical environment) and of humans (social environment) via communication. Gómez describes the development of a communicative strategy as starting from manipulating humans as object tools to “intentional communicative behaviors requesting the assistance of the human in the attainment of the goal” (p.178, 1986) and become concurrently available strategies (Gómez, 1988). Thus, it appears that the manipulative (acting on the physical environment) strategies come before communicative strategies, similar to previous

suggestions that in human children tool use may be a prerequisite for intentional communication (i.e., Bates, Benigni, Bretherton, Camaioni, & Volterra, 2014).

In Piaget's stages of communication, infants show intention when they do something in order to bring about something else, or in other words use a means to achieve a goal (Frye, 1981). It has been suggested by some that the first communicative gestures of an infant emerge as a new means to achieve a goal, to direct an adult's attention to a toy, for example. These communicative gestures resemble the tool use in Piaget's 5th stage of communication, where the infant's gestures are the tools (Bard, 1990; Frye, 1981). Communicative gestures indicate the ability to recognize another as a causal agent that has the role of providing a means to an end (Bard, 1990).

Tool use is typically described as using an object as an intermediate means to achieve a goal. Communicative gestures can be used as an alternative for direct manipulation of an object and can be considered a 'social tool' where social agents obtain the goal (Bard, 1990). Bard (1990) has reported that young orangutans use communicative gestures to get their mothers to give them food and to help them locomote and argues that Piaget's idea of instrumentalization (discovery and use of detached objects as a means) lends credence to the ideal of social tool use.

However, 'social tool use' can be problematic because what exactly is the tool? Is the mother the tool because she is the causal agent that brings the goal to the infant? Is the gesture the tool because it is used to influence the mother's behavior to achieve the goal? Many would suggest that the mother is the tool because it is her behavior that is being manipulated, however, this provides a lack of distinction between the infant physically acting upon the mother and indirectly acting upon the mother via communication. Here, the mother's behavior is not under the infant's control in the same way that an object used as a tool is, thus Bard (1990) prefers that

the gesture is the tool because it is an intentional ‘act’ by the infant. Social tool use requires understanding of the functional relations between objects and social agents.

Völter and colleagues (2015) break down social tool use, as defined above, into two, non-mutually exclusive parts: motivational and instrumental. The motivational component involves the motives underlying the manipulations of others toward a goal. These motives may be either self- or other-regarding; for example, the ‘user’, or manipulator, must have motivation for exploiting another to obtain a goal, whereas the ‘tool’, or the manipulated, must have motivation for helping the ‘user’ (Völter et al., 2015). The instrumental component involves the actual manipulations of others, ranging from direct physical manipulation/control of others as though they are inanimate objects to indirect manipulation through the use of communication. An example of the former would be a mother grabbing her infant’s arm and putting it through a space too small for her own in order to retrieve a desired object on the other side, much like one would use a stick (Völter et al., 2015). An example of the latter would be an individual producing gestures to solicit cooperation/help from another (Crawford, 1937, 1941; Völter, Rossano, & Call, 2016). Clearer-cut cases of social tool use involve direct physical manipulations of others as though they are a tool. Some go on to argue that although communicative behaviors may manipulate another’s behavior, it remains uncertain whether such behavior is used intentionally to influence the other’s behaviors (Povinelli & O’Neill, 2000). However, for direct manipulations to occur, there usually has to be a power difference between partners; such power differences are often associated with low social tolerance (Völter et al., 2015), making these types of social tool use experiments difficult to conduct and often limited to mother-offspring and other adult-juvenile pairings.

It appears that the cognitive processes underlying physical tool use, especially those related to executive functions such as attention control, response inhibition, causal understanding, and planning, likely create the basis of social tool use, particularly in the cases where users physically manipulate their social tool as they would inanimate tool-objects such as sticks. Furthermore, there are several important features characterizing physical tool use that are found in social tool use, including: sequential tool use, goal-directedness, and dissociation between a tool and its functions (Völter et al., 2015). However, social tool use goes beyond physical tool use in the sense that the users treat the social tool as self-propelled beings. Inherent is the expectation for the social tool to execute the actions needed for bringing the goal to the user. Thus, the biggest difference between physical and social tool use is that the tool user takes into account, and even predicts, the actions of the social tool that they do not directly control (Völter et al., 2015). Völter and colleagues (2016) suggest that “shared variance between physical and social tool use might not only be found on the species level but also within species at the individual level” (p. 16) and the possibility of whether skilled tool users exhibit more sophisticated forms of social manipulations.

## **2 AIMS, QUESTIONS, AND HYPOTHESES**

While many studies have investigated physical tool use and a small but increasing number on social tool use, none thus far have explicitly compared physical and social tool use. Perhaps this is a result of cognition traditionally being dichotomized into two separate components, physical and social, as manifest by the Primate Cognition Test Battery (PCTB). Developed by Herrmann, Call, Hernández-Lloreda, Hare, and Tomasello (2007) based on the “theoretical analysis of primate cognition by Tomasello and Call (1997)” (p. 1361), the PCTB includes a series of physical and social cognition tasks. While Herrmann and colleagues (2007) acknowledge that

primates use physical and social cognition together in the wild, they argue that these cognitive domains are distinct because “physical cognition deals with inanimate objects and their spatial-temporal-causal relations, whereas social cognition deals with other animate beings and their intentional actions, perceptions, and knowledge” (p. 1361). Furthermore, they reason that primate physical cognition abilities evolved mostly in foraging contexts: the ability to deal with space to find food and the ability to understand causal relations for extracting foods (i.e., tool use). On the other hand, social cognition evolved in relation to group living, particularly in relation to cooperation and competition among members: the ability to communicate to manipulate others’ behavior and the ability to understand others’ states (Theory of Mind) to predict behavior (Herrmann et al., 2007).

Investigating the factor structure underlying PCTB performance, Herrmann and colleagues (2010) found that a two-factor model explained chimpanzee performance, one factor accounting for spatial task performance and the other accounting for physical and social task performance. Though human children also exhibited a factor model with one factor accounting for spatial task performance, they showed a three-factor model including two separate factors accounting for physical and social task performance. While the PCTB is comprised of tasks assessing both cognitive domains (physical and social), it treats them as separate despite being used together in the natural world and despite chimpanzees exhibiting a factor model combining physical (except for spatial tasks) and social task performance into a single factor.

Another explanation for the lack of comparison between physical and social tool use is that tool use has generally been defined within the domain of physical cognition, though there is now a growing interest in what is defined as social tool use. Like physical tool use, social tool use has been hypothesized to involve means-end reasoning but with the user manipulating a

social (rather than physical) agent to obtain a desired object that cannot be obtained without assistance. Though the user is often no longer the agent in social tool use, the goal is the same in both circumstances (*see Leavens et al., 2005 for discussion*). Unfortunately, to what extent similar cognitive processes may underlie physical and social tool use remains largely uninvestigated from both a developmental and evolutionary perspective.

It seems reasonable that there would be a continuum where a transition between physical and social modalities happens as one ceases use of the physical tool and solicits help from an able other. Perhaps, then, cognition is one entity expressed in two ways, one in the physical domain and one in the social; a consideration initially prompted by anecdotal evidence from previous research conducted in our laboratory with captive chimpanzees where individuals will engage in, or initiate, joint attention (pointing/gesturing toward an object and alternating gaze between the object and whom the communication is directed; e.g., Carpenter, Nagell, Tomasello, Butterworth, & Moore, 1998; Mundy, 1995; Mundy & Crowson, 1997) when a task is or becomes too difficult for them.

Given the cognitive abilities of chimpanzees and bonobos, the two overarching aims of this study were to determine whether there are species differences in tool use (both physical and social) and whether a threshold exists between physical and social tool use. This study investigated these aims by presenting subjects with a physical tool use task that increased in difficulty such that it became a social tool use task. Individual differences were also compared to previous scores on other tool and socio-communicative tasks, since performance would likely depend on and change according to task difficulty, motivation, and individual abilities, among other factors.

## **2.1 Species Differences**

Based upon what is known regarding the tool using, social, and communicative behaviors of bonobos and chimpanzees, some hypotheses can be proposed about species differences in both physical and social tool use performance. Because chimpanzees are known for their tool using abilities in the physical realm and bonobos are not, I hypothesized that chimpanzees would make fewer retrieval attempts and retrieve rewards faster using a physical tool than bonobos at closer or reachable distances. However, at further or out of reach distances, chimpanzees would make more attempts before soliciting help from an experimenter than bonobos. Conversely, I hypothesized that bonobos would make more solicitations and solicit sooner than chimpanzees.

## **2.2 Distance Differences**

As a consequence of the reward being position at further distances, reward retrieval becomes more difficult. Thus, I hypothesized there would be distance differences in reward retrieval and solicitation behaviors. With the increase in distance, the task transfers from being a physical task to a social task requiring subjects to switch strategies from a physical strategy (using the tool) to a social one (solicit for help). Therefore, I hypothesized that there would be a decrease in physical tool retrieval attempts and an increase in solicitation when rewards were out of reach. More specifically, I hypothesized individuals would make fewer retrieval attempts, make more solicitations, and solicit sooner at these distances. Data supporting these hypotheses would suggest that there is a transfer between physical and social cognition modalities and that they lie on a single cognitive continuum.

## **2.3 Individual Differences**

As with any study, there are likely to be individual differences, regardless of species, which may relate to communicative and cognitive abilities, or intrinsic motivations. I

hypothesized that physical tool use performance measured by retrieval attempts and latency would correlate with PCTB physical task performance, while social tool performance, measured by number of solicitations and solicitation latency, would correlate with PCTB social task performance and social performance measures on an AG assessment and solicit for tool task (see methods for description of the two latter mentioned tasks). As mentioned earlier, the PCTB is used to assess the social and physical cognition skills of nonhuman primates (Herrmann et al., 2007). Regarding social cognition, the PCTB quantifies gaze following, initiating joint attention, comprehension of declarative social cues (i.e., gaze and pointing), and elaboration and persistence in initiating joint attention. Regarding physical cognition, the PCTB tests number discrimination, tool use, problem solving, understanding causality, spatial discrimination, and object permanence. Given my hypothesis, I predicted that those with higher scores on the physical portions of the PCTB, especially those related to tool use, would make fewer attempts before successfully retrieving the reward and retrieve the reward faster than those with lower scores, particularly at retrievable distances. I also predicted that those with higher scores on the social portions of the PCTB, especially those related to communication, would make more solicitations and solicit sooner. I also expected there to be similar relationships between solicitation behaviors in this study with AG assessment and solicit for tool performance.

### **3 METHODS**

#### **3.1 Subjects**

Subjects consisted of 29 chimpanzees including 18 from the Yerkes National Primate Research Center, Atlanta and Lawrenceville, Georgia (YNPRC) and 11 from the Maryland Zoo in Baltimore, Baltimore, Maryland (MDZ). There were also 27 bonobo subjects that were housed at the Ape Cognition and Conservation Initiative, Des Moines, Iowa (ACCI, N = 5), the

Milwaukee County Zoo, Milwaukee, Wisconsin (MCZ,  $N = 14$ ), and Jacksonville Zoo and Gardens, Jacksonville, Florida (JZG,  $N = 8$ ). Within both samples, 22 apes were male (13 bonobos, 9 chimpanzees) and 34 were female (14 bonobos, 20 chimpanzees), and they ranged in age from 7 to 50 years ( $M = 24.43$ ,  $SD = 11.19$ ; see *Table 3.1 for more detailed demographic information*). Subjects had *ad libitum* access to water and were not food deprived, as all food rewards were supplemental to their normal daily diet. Testing spanned from November 2016 to March 2018. This study was conducted in accordance with the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates, the Committee on the Care and Use of Laboratory Animal Resources (NRC, 2011), and was approved by the local institutional animal care and use committee at each institution, including the Chimpanzee Species Survival Plan for MDZ.

### **3.2 Attention-Getting Assessment**

All subjects underwent an attention-getting assessment prior to testing on the tool use task. The aim of this was to assess individual tendencies to get or direct attention, which may be associated with performance on the tool task. During this assessment, the experimenter sat in front of the subject with a container of food and engaged the subject in husbandry behaviors (i.e., body exam commands such as “hand”, “foot”, “belly”) for which they were rewarded with a piece of food. Once the subject was engaged, the experimenter ceased interaction keeping the container of food positioned in front of the subject. When an attention-getting or attention-directing vocalization or gesture, hereafter “AG” (*see Table 3.2 for ethogram*), was made toward the experimenter or two minutes elapsed, the experimenter resumed husbandry behavior interaction to begin the next trial. Subjects were not rewarded immediately following their production of AG signals in order to avoid associations being formed between those

communicative signals and receiving food. Subjects received a total of 10 assessment trials. The number of trials in which subjects made AG signals and the latency of each signal were recorded.

*Table 3.1 Subject demographic information*

<b>Bonobos</b>	<b>Age</b>	<b>Sex</b>	<b>Chimpanzees</b>	<b>Age</b>	<b>Sex</b>
<b>MCZ (N=14)</b>			<b>YNPRC (N=18)</b>		
<b>Brian</b>	28	Male	<b>Azalea</b>	20	Female
<b>Claudine</b>	15	Female	<b>Barbi</b>	41	Female
<b>Deidre</b>	14	Female	<b>Carl</b>	31	Male
<b>Faith</b>	12	Female	<b>Cathy</b>	28	Female
<b>Hanna</b>	10	Female	<b>Drew</b>	24	Male
<b>Katu</b>	7	Male	<b>Evelyne</b>	26	Female
<b>Laura</b>	50	Female	<b>Jacqueline</b>	41	Female
<b>Lola</b>	13	Female	<b>Jaimie</b>	22	Female
<b>Makanza</b>	23	Male	<b>Julie</b>	23	Female
<b>Murphy</b>	19	Male	<b>Liza</b>	23	Female
<b>Ricky</b>	22	Male	<b>Patrick</b>	24	Male
<b>Tamia</b>	21	Female	<b>Rita</b>	30	Female
<b>Zomi</b>	18	Female	<b>Sabrina</b>	39	Female
<b>Zuri</b>	19	Male	<b>Steward</b>	24	Male
<b>ACCI (N=5)</b>			<b>Tai</b>	50	Female
<b>Elikya</b>	20	Female	<b>Travis</b>	28	Male
<b>Kanzi</b>	37	Male	<b>Vivienne</b>	43	Female
<b>Maisha</b>	17	Male	<b>Winston</b>	30	Male
<b>Nyota</b>	19	Male	<b>MDZ (N=11)</b>		
<b>Teco</b>	7	Male	<b>Asali</b>	12	Female
<b>JZG (N=8)</b>			<b>Baby Jane</b>	33	Female
<b>Jenga</b>	7	Male	<b>Bunny</b>	27	Female
<b>Jo-T</b>	16	Female	<b>Carole</b>	29	Female
<b>Jumanji</b>	22	Male	<b>Jack</b>	18	Male
<b>Kuni</b>	33	Female	<b>Jambo</b>	11	Female
<b>Laney (Baker)</b>	7	Female	<b>Joice</b>	45	Female
<b>LoREL</b>	49	Female	<b>Kasoje</b>	19	Male
<b>Mabruki</b>	35	Male	<b>Louie</b>	22	Male
<b>Marilyn-Lori</b>	31	Female	<b>Raven</b>	22	Female
			<b>Rozi</b>	12	Female

*Note. MCZ = Milwaukee County Zoo, ACCI = Ape Cognition and Conservation Initiative, JZG = Jacksonville Zoo and Gardens, YNPRC = Yerkes National Primate Research Center, MDZ = Maryland Zoo in Baltimore*

Table 3.2 Ethogram of attention-getting signals

---

<b>Attention-getting Auditory Signals</b>	
Cage Bang	Subject hits mesh or other resonant surface in cage with hand, foot or object with the intention of creating audible noise
Vocalizations	Sounds directed at experimenter and appears under voluntary control
<i>Raspberries</i>	Sounds made by protruding the lips and blowing air out to produce a splutter type sound
<i>Kisses</i>	Sounds made by pursing the lips and sucking air in
<i>Extended Grunts</i>	Low frequency sounds made with an open mouth while expelling air from the lungs
<i>Other</i>	Other vocal sounds not listed but have intention of creating audible noise (i.e., directed panting)
Clap	Subject hits hands together or hits hand on another body part with the intention of creating audible noise
Stomp	Subject hits foot on ground with the intention of creating audible noise
<b>Attention-getting Visual Signals</b>	
Whole Hand Point	Pointing with the whole hand with arm extended toward food reward and fingers spread apart slightly and the palm either held vertically or facing down
Single Finger Pointing	Only a single finger is extended while the other fingers curled in toward the palm
Food Beg	Subject extends arms towards experimenter with palm facing up and hand maintaining a cupping posture
Body Present	Subject presents body part(s) towards experimenter
Trade/Barter	Subject trades/barters items from cage by 'offering' item to experimenter
Other	Other visual not listed but are directed toward experimenter (i.e., head bob, shake body part, etcetera)
<b>Gaze Alternation</b>	Subject alternates gaze between food reward and experimenter

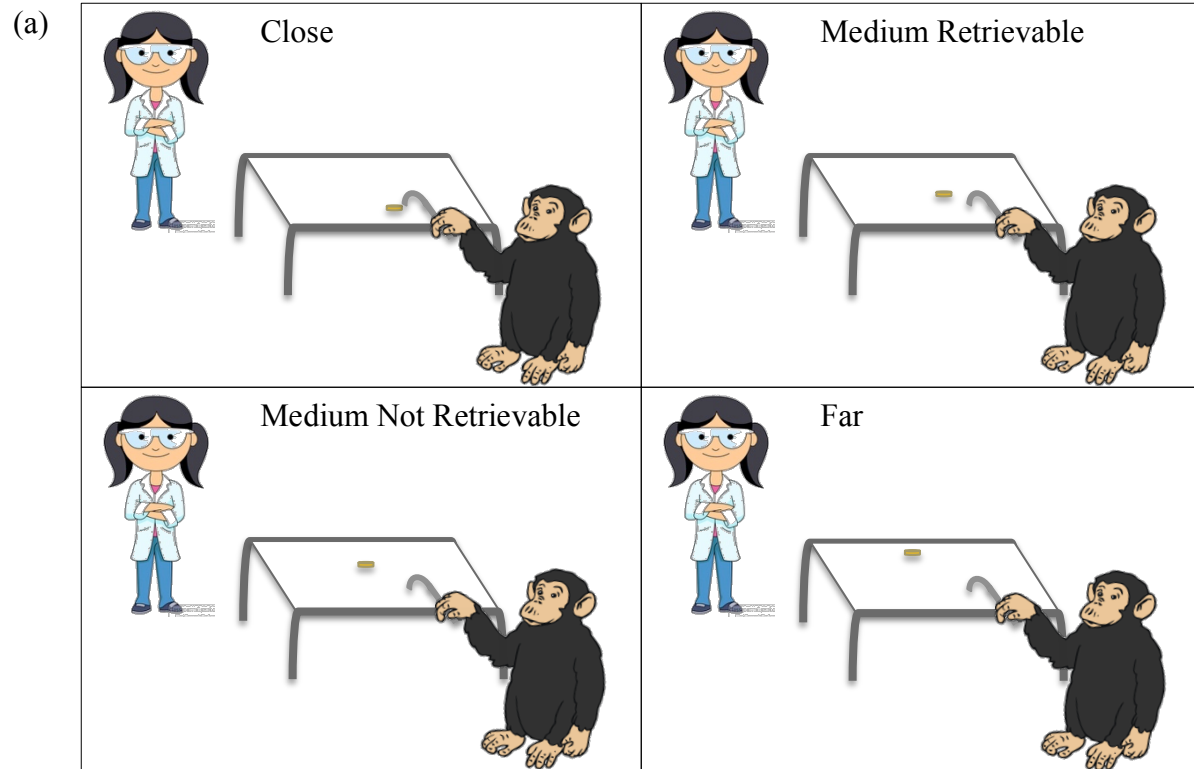
---

### 3.3 Solicit for Tool

After completing the AG assessment, subjects underwent a task in which they were unable to retrieve a reward unless they requested a tool from the experimenter. Criterion for the task was 90% successful solicits for tool on two consecutive sessions of 10 trials. Latencies to solicit for the tool and the number of sessions to reach criterion were recorded.

### 3.4 Physical versus Social Testing

After completing the solicit for tool trials, subjects underwent a tool task aimed to investigate whether a threshold between physical and social tool use exists and whether species and individual account for differences in this threshold (*see Figure 3.1a for depiction of experimental set-up*). Subjects were presented with a tool task on which they had previously been trained. Briefly, subjects had been trained to use a hook/J-shaped tool (paper lollipop stick approximately 30.48 cm in total length) to retrieve a food item placed on a table in front of them (Figure 3.1b). All subjects included in this study had reached a criterion of 90% successful retrievals on two consecutive test sessions of at least 10 trials each. For testing, subjects underwent two testing conditions, one in which an experimenter was absent (EA) and another which an experimenter was present (EP). Within each condition there were four trials where a food item was presented at increasing distances from the subject: 1) Close, 2) medium retrievable with a tool (MR), 3) medium not retrievable with a tool (MNR), and 4) Far. Each subject underwent two complete sessions of each condition-distance combination for a total of 16, 4-minute long trials in a counterbalanced fashion spread across four days. Subjects were matched based on age, sex, species and rearing when possible, and sessions were counterbalanced across subjects/matches such that approximately half received EA-EP-EP-EA while the others received EP-EA-EA-EP.



**Figure 3.1 Experimental set-up and retrieval example**

Depiction of (a) experimental set-up and (b) retrieval by a chimpanzee on the tool task using a hook/J-shaped tool. Experimenter and chimpanzee images from images.google.com.

At the start of each trial, the experimenter placed a food item in the center of the table at a predetermined distance (Close, MR, MNR, or Far). The hooked/J-shaped tool was handed to the subject either on left or right side of the table, such that side was equally randomized across trials. The experimenter then placed additional tools in an accessible location near the table for the subject and left for the entire four-minute trial during EA trials or remained present during EP trials. The number of retrieval attempts, latency of retrieval, number of solicitation behaviors, and the duration of time before a solicitation behavior occurred were recorded. All trials were recorded via video camera and coded for the measures mentioned above.

### **3.5 Data Analyses**

As previously mentioned, subjects were matched based on age, sex, and rearing when possible. Independent variables for analyses included species, distance, sex, and age (the latter treated as a covariate whenever possible). Dependent variables included retrieval attempts, retrieval latency, number of solicitations, solicitation latency, time at table, and return to tool. Specifically for individual difference analyses both sex and age were controlled for. Significance level was set at  $\alpha = 0.05$  for all analyses unless otherwise noted. When data violated assumptions of parametric tests, non-parametric equivalents were used for analyses with appropriate non-parametric post-hoc comparisons when needed.

## **4 RESULTS**

### **4.1 Descriptive Statistics and Normality Tests**

All dependent variables violated normality for each distance except time at table for MNR and overall distances (Table 4.1). Thus, non-parametric tests were used for analyses, including Wilcoxon-Signed Ranks, Mann-Whitney U, Kruskal-Wallis, and Friedman tests, with appropriate non-parametric post-hoc comparisons.

Table 4.1 Descriptive statistics and normality test results

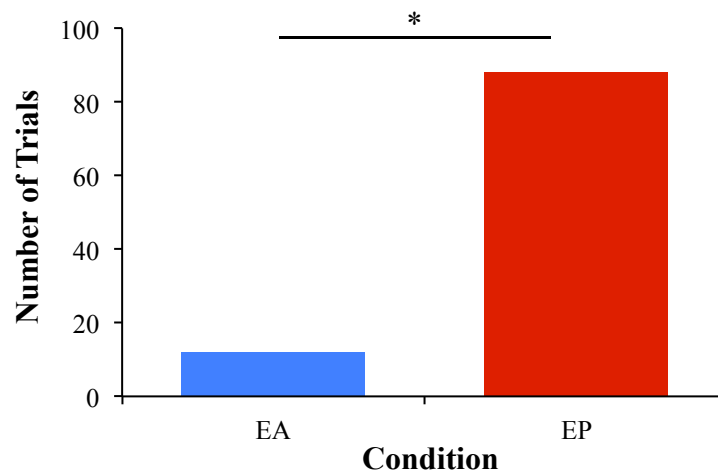
	N	Mean	SE	Shapiro-Wilk
<b>Retrieval Attempts</b>				
Close	56	4.946	0.392	<b>0.928*</b>
MR	56	8.330	0.984	<b>0.794**</b>
MNR	56	7.545	0.813	<b>0.867**</b>
Far	56	2.152	0.335	<b>0.773**</b>
Overall	56	5.743	0.362	<b>0.956*</b>
<b>Retrieval Latency</b>				
Close	56	28.857	3.724	<b>0.749**</b>
MR	49	38.225	5.175	<b>0.761**</b>
Overall	56	31.521	2.866	<b>0.862**</b>
<b>Number of Solicitations</b>				
Close	56	-	-	n/a
MR	56	0.018	0.013	<b>0.184**</b>
MNR	56	4.500	0.683	<b>0.815**</b>
Far	56	4.714	0.628	<b>0.884**</b>
Overall	56	2.598	0.344	<b>0.880**</b>
<b>Solicitation Latency</b>				
Close	0	-	-	n/a
MR	2	-	-	n/a
MNR	43	76.547	8.302	<b>0.904*</b>
Far	43	55.477	8.514	<b>0.820**</b>
Overall	49	74.722	6.884	<b>0.901**</b>
<b>Time at Table</b>				
Close	56	40.071	5.320	<b>0.784**</b>
MR	56	62.875	7.587	<b>0.838**</b>
MNR	56	154.518	8.633	0.972
Far	56	112.929	9.873	<b>0.915**</b>
Overall	56	92.598	4.829	0.991

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

## 4.2 Condition Differences

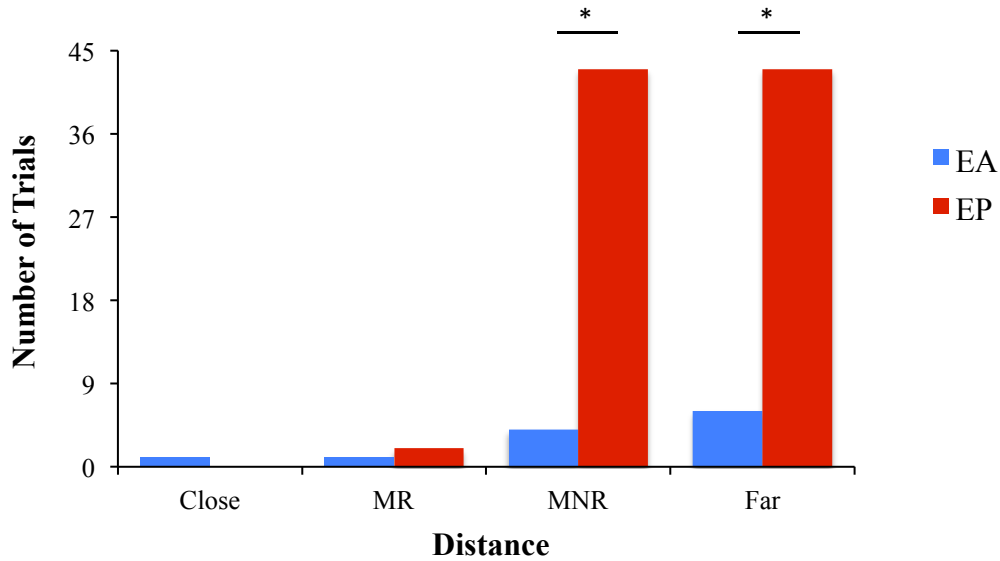
The purpose of including an EA condition was to determine if there was an audience effect on performance, specifically solicitation behavior. Thus, the variable of interest for this analysis was solicitation during EA and EP trials. Individuals were scored a 0 if they did not solicit on any trials and a 1 if they solicited on one or more trials. Solicitation was rare during

the EA condition, occurring on only 12 of 224 trials (~5%), compared to 88 (~39.3%) during the EP condition (Figure 4.1). Chi-Square analyses showed this to be a significant difference ( $\chi^2(1) = 72.41, p < 0.001$ ). Within the EA condition, solicitation was rare for all distances (1 Close, 1 MR, 4 MNR, 6 Far, out of 56 total trials per distance). Solicitation was equally rare during the EP condition on Close and MR trials (0 and 2 of 56 trials; Fisher's Exact Test,  $p = 1.00$ ). This was expected since the reward was retrievable and solicitation was not necessary. Solicitation had a significantly higher occurrence during the MNR and Far distances in the EP condition (43 trials or 76.3% each) than the EA condition (MNR: 4 or 7.2%,  $\chi^2(1) = 52.393, p < 0.001$ ; Far: 6 or 10.8%,  $\chi^2(1) = 47.020, p < 0.001$ ; Figure 4.2). Because the presence of a person significantly altered solicitation behaviors, only data from the EP condition were used in all subsequent analyses.



**Figure 4.1 Overall trials solicited on during EA and EP conditions**

Overall number of trials in which individuals solicited across experimenter absent (EA) and experimenter present (EP) conditions. \*  $p < 0.05$



**Figure 4.2 Number of trials solicited for each distance during EA and EP conditions**  
 Number of trials in which individuals solicited across experimenter absent (EA) and experimenter present (EP) conditions according to distance. \*  $p < 0.05$

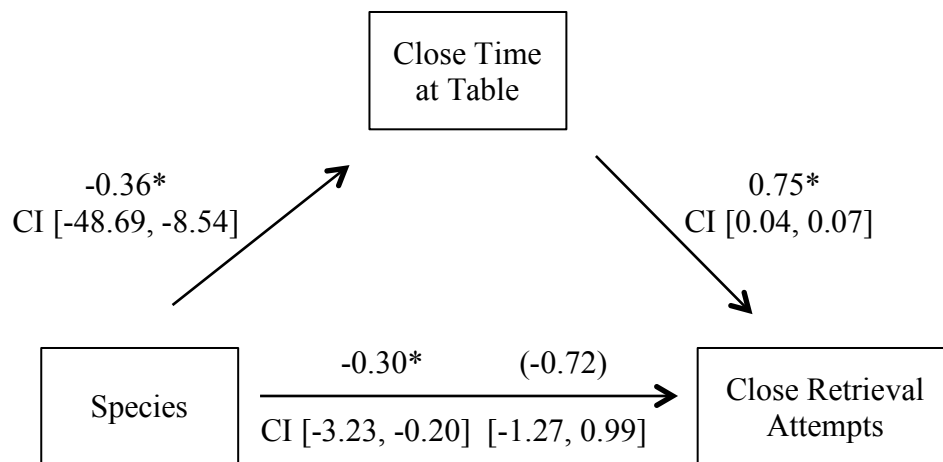
### 4.3 Species Differences

#### 4.3.1 Retrieval Attempts

For this and all other species comparisons  $N = 56$  (bonobo = 27, chimpanzee = 29) unless otherwise noted. Kruskal-Wallis tests with species as the independent variable and retrieval attempts as the dependent variable were used to determine whether species differences exist in retrieval attempts for each distance. The tests revealed bonobos made more retrieval attempts than chimpanzees at Close (mean rank bonobo = 33, chimpanzee = 24;  $\chi^2(1) = 4.53, p = 0.033$ ) and Far (mean rank bonobo = 35, chimpanzee = 22;  $\chi^2(1) = 8.83, p = 0.003$ ) distances. There were no species differences at the two intermediate distances (MR:  $\chi^2(1) = 0.190, p = 0.663$ ; MNR:  $\chi^2(1) = 0.097, p = 0.755$ ).

However, because the total time spent at the table during trials varied, it was suspected that this might influence effects related to reward retrieval. Thus, regression analyses were used

to investigate whether the relationship between species and retrieval attempts at Close and Far distances was mediated by time at table. Results indicated that species was a significant predictor of Close time at table ( $B = -28.613$ ,  $SE = 10.014$ ,  $p = 0.006$ ) and Close time at table was a significant predictor of Close retrieval attempts ( $B = 0.055$ ,  $SE = 0.007$ ,  $p < 0.001$ ), suggesting mediation. When controlling for Close time at table species was no longer a significant predictor of Close retrieval attempts ( $B = -0.142$ ,  $SE = 0.562$ ,  $p = 0.802$ ); thus, the effect was completely mediated by time at table, which accounted for over 90% of the effect. A Sobel test revealed this to be a significant mediation effect (Sobel Test = 5.469,  $p < 0.001$ ). Standardized regression coefficients and confidence intervals related to the mediation analysis are found in Figure 4.3.



**Figure 4.3 Mediation of Close retrieval attempts by time at table**

Standardized regression coefficients for the relationship between species and Close retrieval attempts as mediated by time at table. The standardized regression coefficient for the indirect effect between species and Close retrieval attempts is in parentheses. \*  $p < 0.05$

When comparing species on time at table, Mann-Whitney U tests showed that bonobos stay longer at the table at Close distances than chimpanzees (mean rank bonobo = 35.39, chimpanzee = 22.09;  $U = 205.5$ ,  $p = 0.002$ ). With regard to Far retrieval attempts, time at table

was not related to retrieval attempts ( $r(54) = 0.130, p = 0.339$ ) and thus did not have a significant mediating effect. However, Mann-Whitney U tests indicated that chimpanzees stayed longer at the table at Far distances than bonobos (mean rank bonobo = 23.76, chimpanzee = 32.91;  $U = 519.5, p = 0.036$ ). No species differences on MR and MNR retrieval attempts were evident, and tests indicated no species differences on time at table for either MR (Mann-Whitney U: 337.5,  $p = 0.294$ ) or MNR (ANOVA:  $F_{(1,54)} = 3.758, p = 0.058$ ) distance.

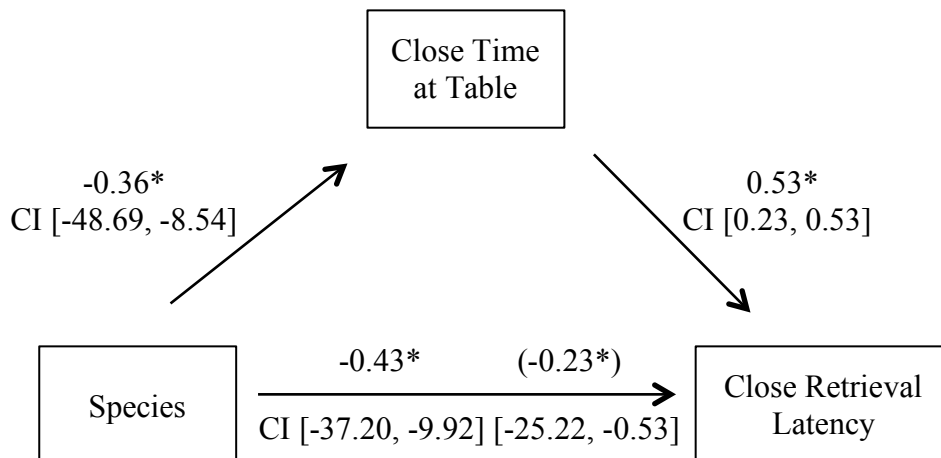
Although no species differences on MR and MNR retrieval attempts were evident, regression analyses were used to account for time at table, with species and sex included in the model. The regression analyses revealed that the independent variables (IVs) explained 64% of the variance in attempt differences at MR distances ( $F_{(3,52)} = 30.682, p < 0.001; R^2 = 0.639, R^2_{\text{adjusted}} = 0.618$ ) and 21% of the variance in attempt differences at MNR distances ( $F_{(3,52)} = 4.491, p = 0.007; R^2 = 0.206, R^2_{\text{adjusted}} = 0.160$ ). Only time at table significantly added to the model for MR ( $t = 9.462, p < 0.001$ ) and MNR distance (time:  $t = 3.503, p = 0.001$ ). Additionally, there were no species differences on time at table for either MR (Mann-Whitney U: 337.5,  $p = 0.294$ ) or MNR (ANOVA:  $F_{(1,54)} = 3.758, p = 0.058$ ) distance.

#### **4.3.2 Retrieval Latency**

Univariate ANOVAs with species and sex as independent variables, age as a covariate, and retrieval latency as the dependent variable were used to determine whether there were differences in retrieval latency between species at Close ( $N = 56$ ) and MR ( $N = 49$ ) distances. However, the data violated the equality of error variance assumption (Levene's Test  $F_{(3,52)} = 8.866, p = .001$ ) for Close distances, so a Mann-Whitney U test was run. The test revealed that bonobos (mean rank 35.78) were slower at retrieving reward at Close distances than chimpanzees (mean rank 21.72;  $U = 195.00, Z = -3.22, p = 0.001$ ). There were no species

differences in retrieval latency at MR distances ( $F_{(1,44)} = 1.124, p = 0.295$ ), but older individuals were slower ( $F_{(1,44)} = 6.850, p = 0.012, y = 11.6 + 1.06x$ ).

As mentioned previously, it was suspected that total time spent at the table during trials, which varied, might influence effects on reward retrieval. Thus, regression analyses were used to investigate whether the relationship between species and retrieval latency at Close and MR distances was mediated by time at table. With respect to Close distance, results indicated that species was a significant predictor of time at table ( $B = -28.613, SE = 10.014, p = 0.006$ ) and time at table was a significant predictor of retrieval latency ( $B = 0.432, SE = 0.075, p < 0.001$ ), suggesting mediation. When controlling for time at table, species had a dampened effect on retrieval latency ( $B = -12.876, SE = 6.156, p = 0.041$ ), thus the effect was partially mediated by time at table, accounting for approximately 45% of the effect. A Sobel test revealed this to be a significant mediation (Sobel Test = 4.05,  $p < 0.001$ ). Standardized regression coefficients and confidence intervals related to the mediation analysis can be found in Figure 4.4. As reported earlier, bonobos stayed longer at the table at Close distances than chimpanzees.



**Figure 4.4 Mediation of Close retrieval latency by time at table**

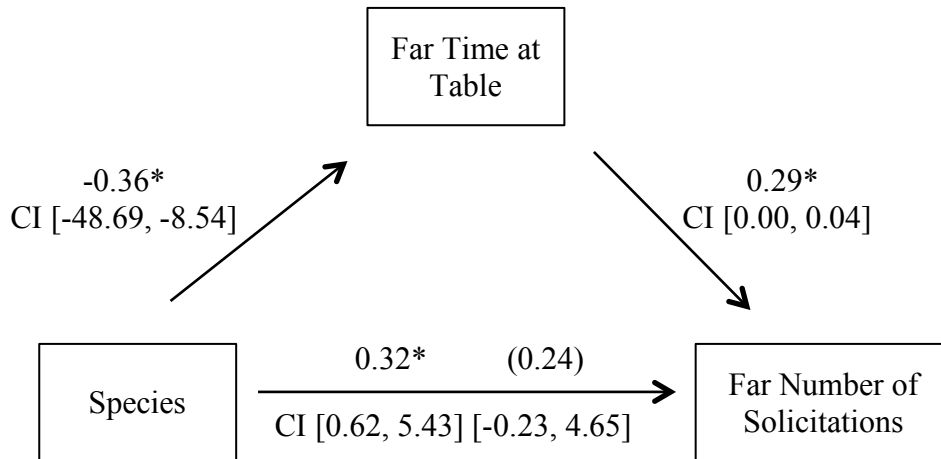
Standardized regression coefficients for the relationship between species and Close retrieval latency as mediated by time at table. The standardized regression coefficient for the indirect effect between species and Close retrieval latency is in parentheses. \*  $p < 0.05$

Although no species differences on MR retrieval latency were evident, an additional Univariate ANOVA was run with time at table included as a covariate. Age was no longer significant ( $F_{(1,43)} = 0.255, p = 0.616$ ), while time at table was with those spending more time at table were slower at retrieving ( $F_{(1,43)} = 26.074, p < 0.001, y = 10.2 + 0.6x$ ).

### ***4.3.3 Number of Solicitations***

Kruskal-Wallis tests with species and sex as independent variables and number of solicitations as the dependent variable were used to determine whether there were differences in number of solicitations between species at each distance. With regard to the number of solicitations, chimpanzees solicited a greater number of times than bonobos for MNR (mean rank bonobos = 28.6, chimpanzees = 38.1;  $\chi^2(1) = 4.70, p = 0.029$ ) and Far (mean rank bonobos = 22.8, chimpanzees = 33.8;  $\chi^2(1) = 6.34, p = 0.012$ ) distances but not at the two closest distances (Close:  $\chi^2(1) = 0.00, p = 1.00$ ; MR:  $\chi^2(1) = 0.003, p = 0.959$ ). This result is in opposition to what was hypothesized. Since the total time spent at the table during trials might influence effects on number of solicitations, regression analyses were run to investigate whether the relationship between species and number of solicitations at MNR and Far distances was mediated by time at table. With regard to MNR distance, time at table did not correlate with number of solicitations ( $r(54) = 0.235, p = 0.081$ ), suggesting no significant mediation. With respect to Far distance, species was a significant predictor of time at table, as reported previously, and time at table was a significant predictor of number of solicitations ( $B = 0.023, SE = 0.007, p = 0.006$ ), suggesting mediation. When controlling for time at table, species no longer had a significant effect on retrieval attempts ( $B = 2.209, SE = 1.216, p = 0.075$ ). Because the effect of species disappeared when accounting for time at table, the effect completely mediated by time at table, which accounted for approximately 27% of the effect. A Sobel test revealed this to be a significant

mediation (Sobel Test = 2.129,  $p = 0.033$ ). Standardized regression coefficients and confidence intervals related to the mediation analysis can be found in Figure 4.5.



**Figure 4.5 Mediation of Far number of solicitations by time at table**

Standardized regression coefficients for the relationship between species and Far number of solicitations as mediated by time at table. The standardized regression coefficient for the indirect effect between species and Far number of solicitations is in parentheses. \*  $p < 0.05$

#### 4.3.4 Solicitation Latency

Univariate ANOVAs with species and sex as independent variables, age as a covariate, and solicitation latency as the dependent variable were used to determine whether there were differences in solicitation latency between species at each distance. However, because no individuals solicited at Close distances and only two at MR distances, comparisons at these distances could not be made. In comparison, 43 individuals solicited at the MNR and Far distances. Results showed there was no significant difference in solicitation latency at MNR distance between species ( $F_{(1,38)} = 0.398$ ,  $p = 0.532$ ), and a trend toward significance for Far with chimpanzees soliciting sooner than bonobos ( $F_{(1,38)} = 4.039$ ,  $p = 0.052$ ). Time at table was neither related to MNR ( $r(43) = -0.102$ ,  $p = 0.517$ ) or Far ( $r(43) = -0.090$ ,  $p = 0.568$ ) solicitation latency, indicating no mediating effect.

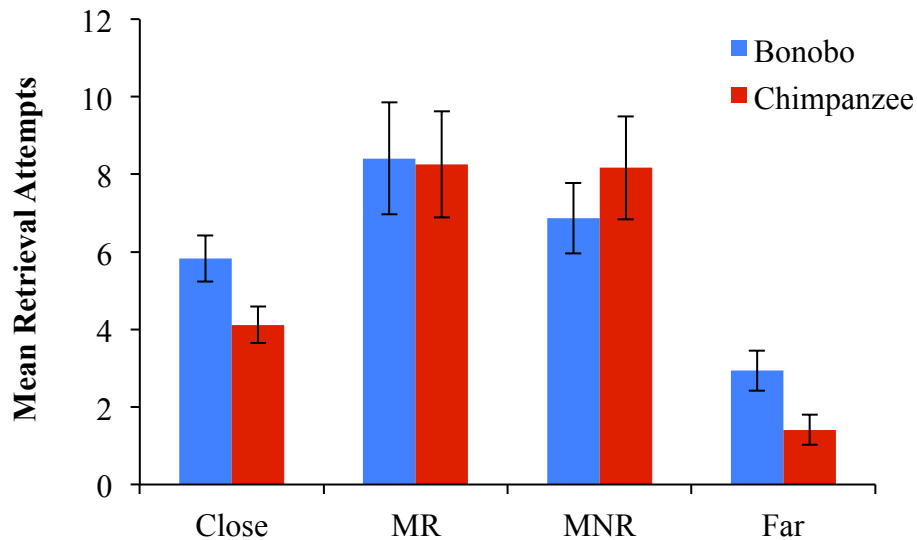
## 4.4 Distance Differences

### 4.4.1 Retrieval Attempts

A Friedman test with distance as the independent variable and retrieval attempts as the dependent variable was run to determine whether distance had an effect on retrieval attempts. There were significant differences in the number of attempts according to distance ( $\chi^2(3) = 59.189, p < .001$ ). To see where these differences were, a Wilcoxon Signed-Rank test was run using a Bonferroni adjusted significance value,  $\alpha = 0.008$ . These comparisons showed that individuals made fewer attempts before retrieval at Close distances than MR ( $p = 0.004$ ) and more attempts at Close ( $p < 0.001$ ), MR ( $p < 0.001$ ), and MNR ( $p < 0.001$ ) distances than Far. Close ( $p = 0.017$ ) and MR ( $p = 0.669$ ) did not differ from MNR. To account for time at table, results indicated that distance was a significant predictor of time at table ( $B = 31.021, SE = 3.943, p < 0.001$ ) and time at table was a significant predictor of retrieval attempts ( $B = 0.027, SE = 0.005, p < 0.001$ ), suggesting mediation. When controlling for time at table, distance had a strengthened effect on retrieval attempts ( $B = -2.260, SE = 0.325, p < 0.001$ ), suggesting inconsistent mediation. A Sobel test revealed this to be a significant mediation (Sobel Test =  $4.736, p < 0.001$ ).

When looking at each species individually, Friedman tests showed significant differences within each species according to distance (bonobos:  $\chi^2(3) = 22.98, p < 0.001$ ; chimpanzees:  $\chi^2(3) = 39.03, p < 0.001$ ). Wilcoxon Signed-Rank tests with Bonferroni adjusted significance level ( $\alpha = 0.008$ ) revealed that bonobos attempted significantly more at Close ( $Z = 2.692, p = 0.007$ ), MR ( $Z = -4.017, p < 0.001$ ), and MNR ( $Z = -3.380, p = 0.001$ ) distances than Far. Chimpanzees attempted at Close distances significantly less than MR ( $Z = -3.220$ ) and more than Far ( $Z =$

3.583,  $p < 0.001$ ), and significantly more at MR ( $Z = -4.001$ ,  $p < 0.001$ ) and MNR ( $Z = -4.706$ ,  $p < 0.001$ ) than Far (Figure 4.6).



**Figure 4.6 Mean retrieval attempts by species**

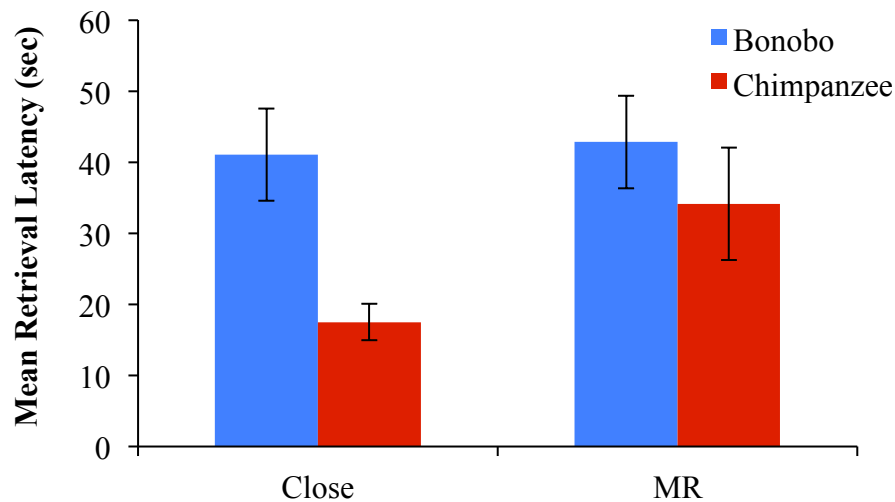
Mean number of retrieval attempts as a function of distance for bonobos and chimpanzees.

#### 4.4.2 Retrieval Latency

Wilcoxon Signed-Rank tests with distance as the independent variable and retrieval latency as the dependent variable were run to determine whether distance had an effect on retrieval latency. Since the reward could only be retrieved on Close and MR distances, comparisons were run on 49 overlapping cases between these two distances. The test showed that individuals were faster at retrieving rewards at Close distances than MR distances ( $Z = -2.248$ ,  $p = 0.025$ ; mean Close = 29.23 versus MR = 38.22). When taking into account time spent at table, a regression model with time and distance shows 42% of the variance in retrieval latency differences is explained by the independent variables ( $F_{(2,102)} = 36.237$ ,  $p < 0.001$ ;  $R^2 = 0.415$ ,  $R^2_{\text{adjusted}} = 0.404$ ), but only time at table added significantly to the model ( $t = 8.293$ ,  $p < 0.001$ ).

When separating species, Wilcoxon Signed-Ranks tests showed there was no significant difference in retrieval latency between distances for bonobos ( $Z = -0.456, p = 0.648$ ).

Chimpanzees, however, retrieved rewards significantly quicker at Close distance than MR ( $Z = -2.858, p = 0.004$ ; Figure 4.7).



**Figure 4.7 Mean retrieval latency by species**

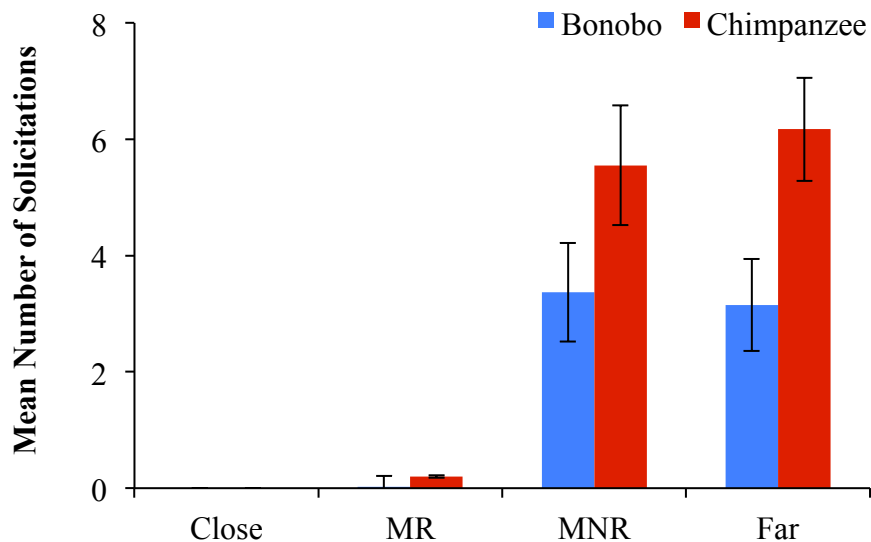
Mean retrieval latency for Close and MR distances for bonobos and chimpanzees.

#### 4.4.3 Number of Solicitations

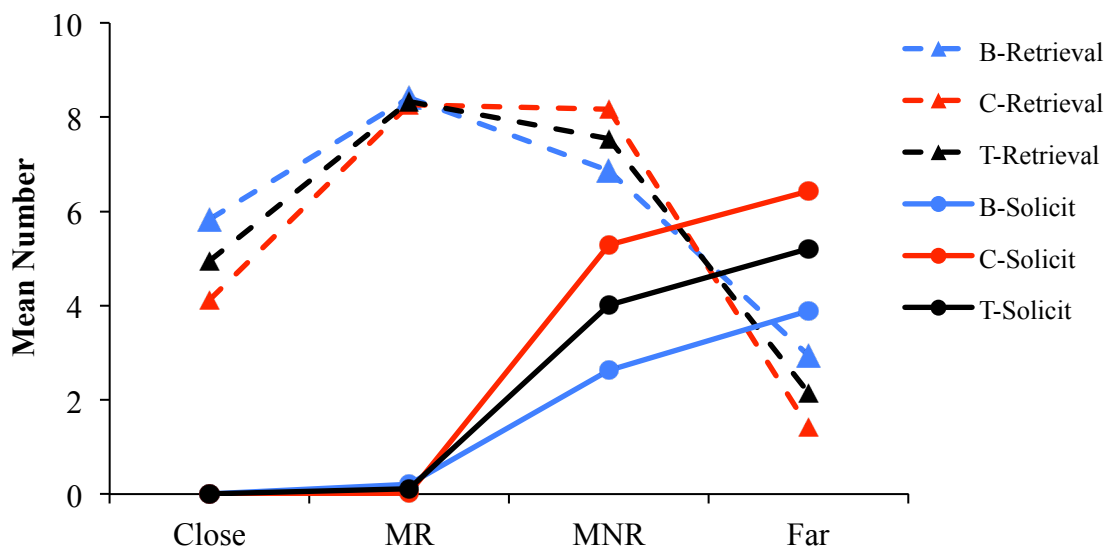
A Friedman test with distance as the independent variable and number of solicitations as the dependent variable was run to determine whether there was an effect of distance on number of solicitations. There were significant differences in the number of solicitations according to distance ( $\chi^2(3) = 107.37, p < 0.001$ ). To determine where these differences occurred, a Wilcoxon Signed-Rank test was run using a Bonferroni adjusted significance value,  $\alpha = 0.008$ . These comparisons showed that individuals made fewer solicitations at Close and MR distances than MNR and Far ( $p < 0.001$  for all). Close and MR ( $p = 0.157$ ) did not differ from each other, nor did MNR and Far ( $p = 0.515$ ). When taking into account time spent at table, regression analyses indicated that distance was a significant predictor of time at table ( $B = 31.021, SE = 3.943, p <$

0.001) and time at table was a significant predictor of number of solicitations ( $B = 0.029$ ,  $SE = 0.003$ ,  $p < 0.001$ ), suggesting mediation. When controlling for time at table, distance had a dampened effect on retrieval attempts ( $B = 1.050$ ,  $SE = 0.235$ ,  $p < 0.001$ ). Thus the effect of distance was partially mediated by time at table, which accounted for approximately 39% of the effect. A Sobel test revealed this to be a significant mediation (Sobel Test = 4.02,  $p < 0.001$ ).

Evaluating each species individually, Friedman tests showed significant differences within each species according to distance (bonobos:  $\chi^2(3) = 44.10$ ,  $p < 0.001$ ; chimpanzees:  $\chi^2(3) = 63.28$ ,  $p < 0.001$ ). Wilcoxon Signed-Rank tests with Bonferroni adjusted significance level ( $\alpha = 0.008$ ) revealed that bonobos solicited significantly less at Close and MR distances than MNR (both  $Z = -3.623$ ,  $p < 0.001$ ) and Far (both  $Z = -3.733$ ,  $p < 0.001$ ). Chimpanzees solicited at Close and MR distances significantly less than MNR (Close:  $Z = -4.460$ ,  $p < 0.001$ ; MR:  $Z = -4.375$ ,  $p < 0.001$ ) and Far (Close:  $Z = -4.374$ ,  $p < 0.001$ ; MR:  $Z = -4.433$ ,  $p < 0.001$ ; Figure 4.8). Figure 4.9 depicts these results in comparison to the retrieval attempt results as described in section 4.2.1.



**Figure 4.8 Mean number of solicitations by species**  
Mean number of solicitations as a function of distance for bonobos and chimpanzees.



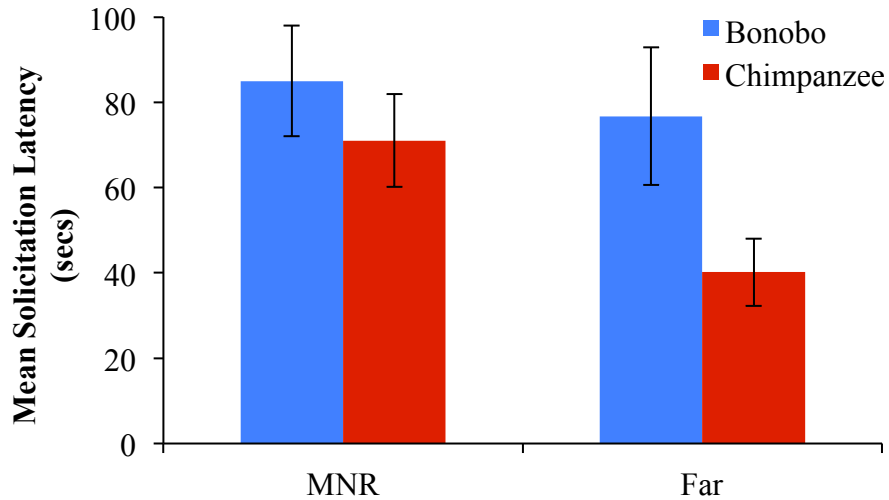
**Figure 4.9 Mean number of retrieval attempts and solicitations**

Mean number of retrieval attempts (Retrieval) and solicitations (Solicit) as a function of distance for bonobos (B), chimpanzees (C), and the two species combined (T).

#### 4.4.4 Solicitation Latency

Since no individuals solicited at Close distances and only two at MR distances, comparisons at these distances could not be made. Thus, a Wilcoxon Signed-Rank test with distance as the independent variable and solicitation latency as the dependent variable was run to determine whether there were differences between MNR and Far distances. Comparisons were performed on 37 overlapping cases between these two distances. The tests showed that individuals solicit sooner at Far (mean solicitation latency:  $55.5 \pm 55.8$ ) distances than MNR (mean solicitation latency:  $76.5 \pm 54.4$ ;  $Z = -2.489$ ,  $p = 0.013$ ). When incorporating time spent at the table, correlation analysis showed no relation with solicitation latency ( $r = -0.030$ ,  $p = 0.789$ ).

When separating species, Wilcoxon Signed-Ranks tests showed there was no significant difference in solicitation latency between distances for bonobos ( $Z = -1.036$ ,  $p = 0.300$ ). Chimpanzees, however, solicited significantly sooner at Far distance than MNR ( $Z = -2.464$ ,  $p = 0.014$ ; Figure 4.10).



**Figure 4.10 Mean solicitation latency by species**

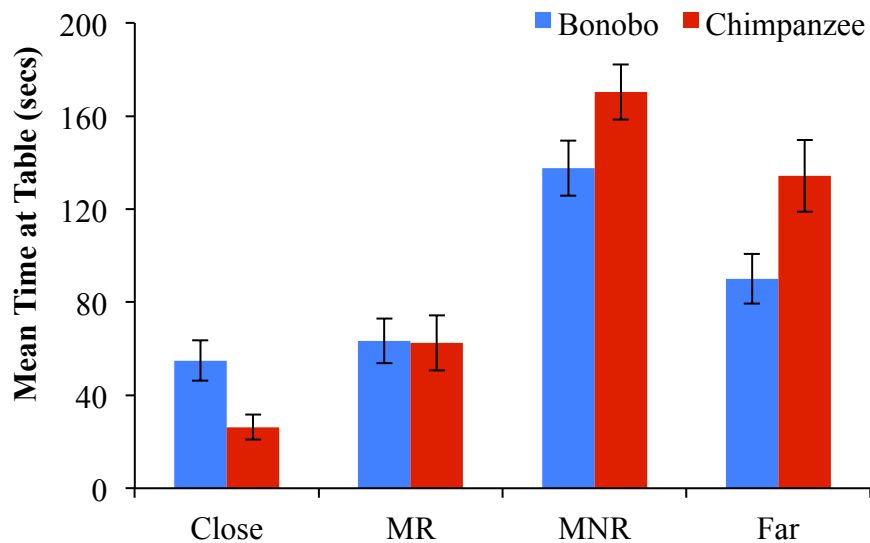
Mean solicitation latency for MNR and Far distances for bonobos and chimpanzees.

#### 4.4.5 Time at Table

A Friedman test with distance as the independent variable and time at table as the dependent variable was used to determine whether there was an effect of distance on time spent at the table. There were significant differences in the time spent at the table according to distance ( $\chi^2(3) = 70.64, p < 0.001$ ). To see where these differences were a Wilcoxon Signed-Rank test was run using a Bonferroni adjusted significance value,  $\alpha = .0083$ . These comparisons showed that individuals stayed at the table longer at MNR distance than all other distances ( $p < 0.001$  for all). Additionally, individuals stayed longer at Far than MR ( $p = 0.001$ ) and Close ( $p < 0.001$ ) distances, and MR longer than close ( $p = 0.001$ ).

When looking at each species individually, Friedman tests showed significant differences within each species according to distance (bonobos:  $\chi^2(3) = 25.489, p < 0.001$ ; chimpanzees:  $\chi^2(3) = 48.813, p < 0.001$ ). Wilcoxon Signed-Rank tests with Bonferroni adjusted significance level ( $\alpha = 0.008$ ) revealed that bonobos spent significantly less time at the table at Close ( $Z = -4.000, p < 0.001$ ) and MR ( $Z = -3.568, p < 0.001$ ) distances than MNR, and more time at the

table at MNR than Far ( $Z = -3.808, p < 0.001$ ). Chimpanzees spent significantly less time at the table at Close distance than MR ( $Z = -4.023, p < 0.001$ ), MNR ( $Z = -4.682, p < 0.001$ ), and Far ( $Z = -4.119, p < 0.001$ ), less time at the table at MR than MNR ( $Z = -4.487, p < 0.001$ ) and Far ( $Z = -2.915, p = 0.004$ ), and more time at the table at MNR than Far ( $Z = -3.272, p = 0.001$ ; Figure 4.11).



**Figure 4.11 Mean time spent at table by species**

Mean time spent at the table as a function of distance for bonobos and chimpanzees.

## 4.5 Individual Differences

### 4.5.1 PCTB

For all PCTB comparisons  $N = 45$  (bonobo = 27, chimpanzee = 18) unless otherwise noted. A summary of analyses can be found in Table 4.2.

To see whether PCTB performance was related to behavioral outcomes of this study, PCTB scores were broken down into the following categories:  $g$  = total performance on all tasks (general intelligence measure), physical = total performance on all physical domain tasks, tool = total performance on all tool use tasks within the physical domain, social = total performance on all social domain tasks, and communication = total performance on communication tasks within

the social domain. Each task was converted to a z-score then averaged together to create a universal weighted average (UWA).

*Table 4.2 PCTB partial correlation analyses summary*

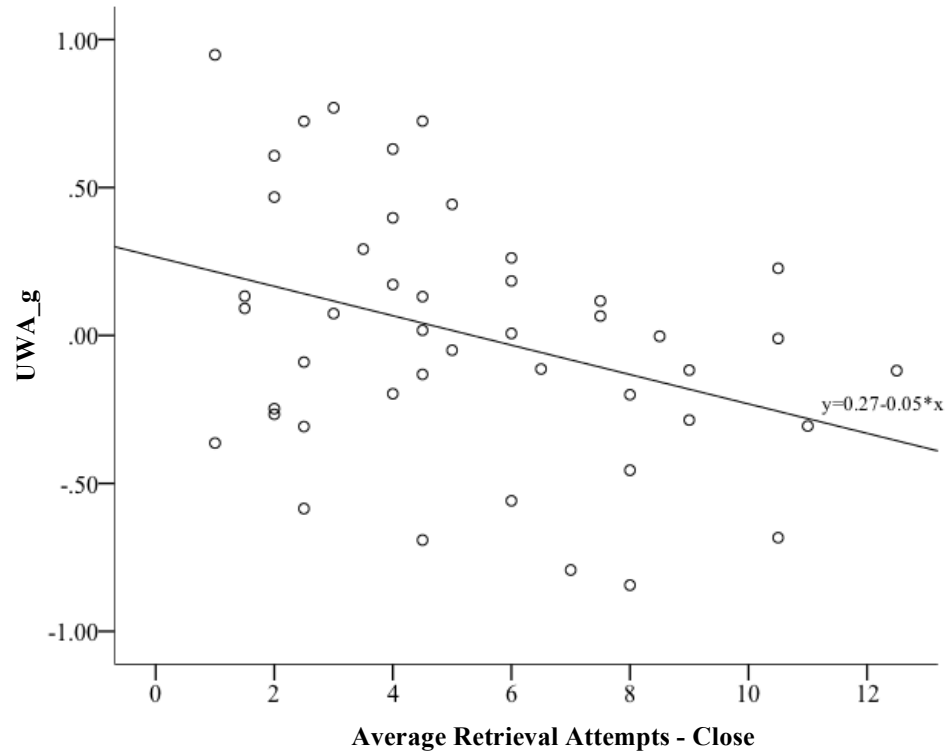
	Close		MR		MNR		Far		Overall	
	df	r	df	r	df	r	df	r	df	r
<b>UWA_g</b>										
Retrieval Attempts	41	<b>-0.325*</b>	41	0.169	41	0.114	41	0.106	41	0.102
Retrieval Latency	41	<b>-0.325*</b>	41	-0.208	-	-	-	-	41	<b>-0.382*</b>
Number of Solicitations	-	-	41	-0.185	41	0.28	41	0.135	41	0.260
Solicitation Latency	-	-	-	-	28	<b>-0.370*</b>	28	-0.268	34	<b>-0.339*</b>
<b>UWA_physical</b>										
Retrieval Attempts	41	<b>-0.388*</b>	41	0.218	41	0.146	41	0.037	41	0.128
Retrieval Latency	41	<b>-0.320*</b>	41	-0.183	-	-	-	-	41	<b>-0.356*</b>
<b>UWA_tool</b>										
Retrieval Attempts	41	<b>-0.347*</b>	41	0.032	41	-0.078	41	-0.158	41	-0.157
Retrieval Latency	41	0.017	41	-0.250	-	-	-	-	41	-0.148
<b>UWA_social</b>										
Number of Solicitations	-	-	41	-0.157	41	0.109	41	0.067	41	0.094
Solicitation Latency	-	-	-	-	28	<b>-0.393*</b>	28	-0.175	34	-0.312
<b>UWA_communication</b>										
Number of Solicitations	-	-	41	-0.202	41	0.192	41	0.099	41	0.189
Solicitation Latency	-	-	-	-	28	<b>-0.466*</b>	28	-0.153	34	-0.327

Note. \* $p < 0.05$

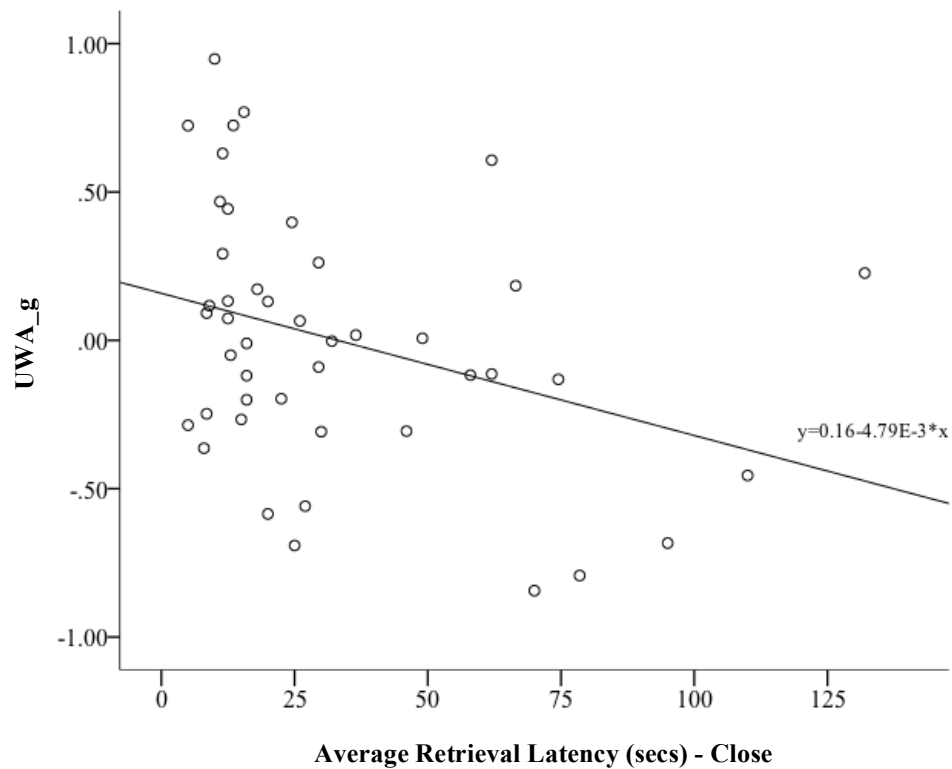
Partial correlations regarding UWA\_g were run with retrieval attempts, retrieval latency, number of solicitations, and solicitation latency. The analyses revealed a significant negative relationship between UWA\_g and Close retrieval attempts (Figure 4.12a), Close and Overall retrieval latency (Figures 4.12b, c), and MNR and Overall solicitation latency (Figures 4.13a, b).

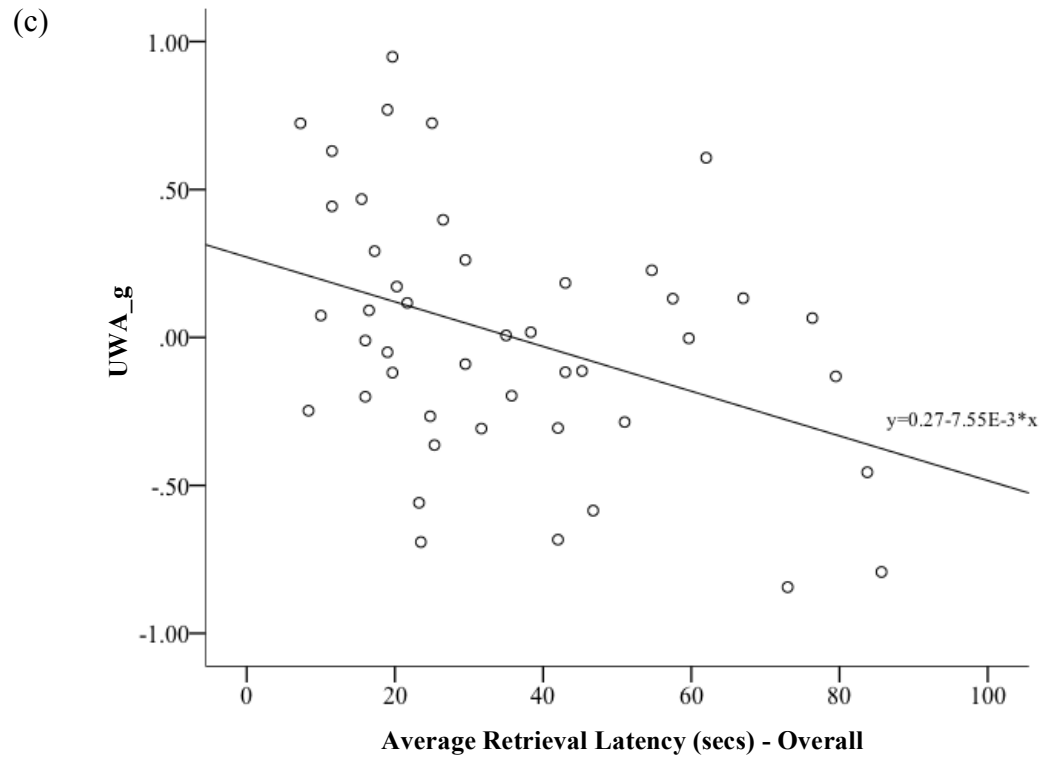
Specifically, those with higher intelligence scores made fewer attempts to retrieve the reward, retrieved the reward faster, and solicited sooner at those respective distances.

(a)



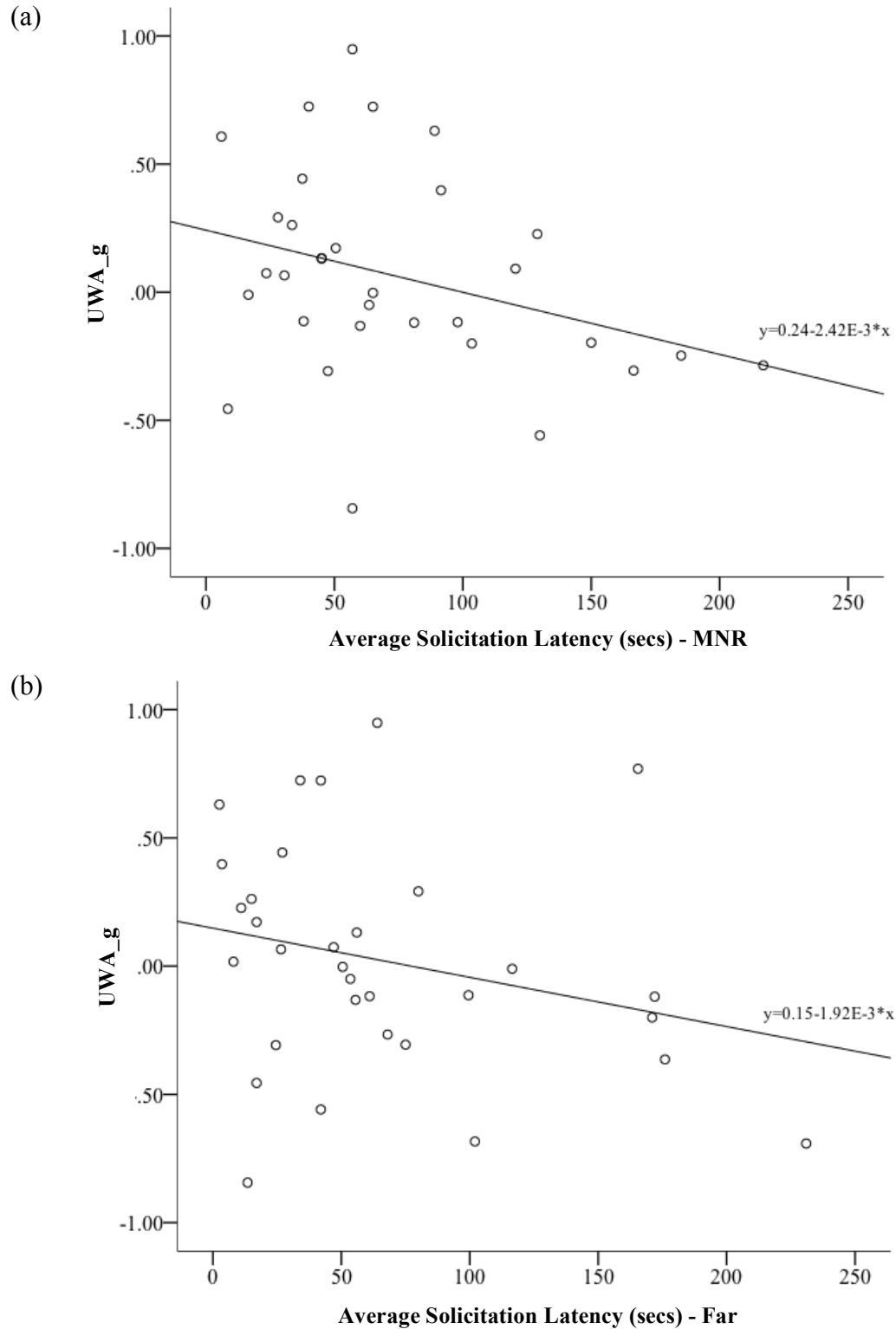
(b)





**Figure 4.12 PCTB performance and retrieval performance**

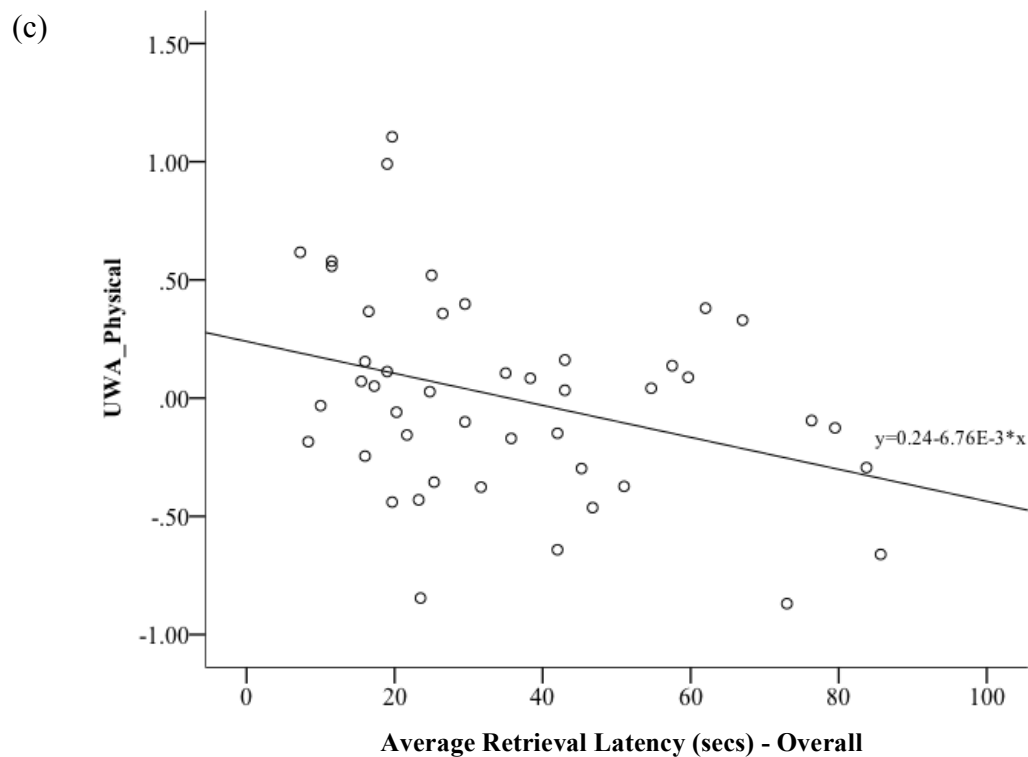
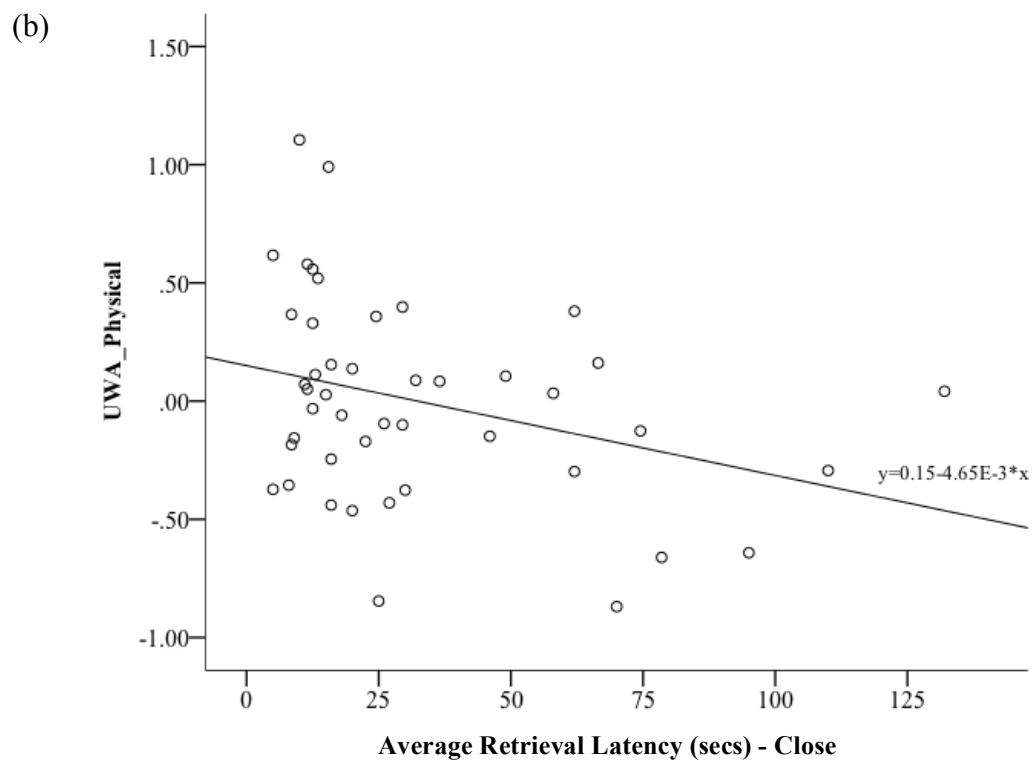
General intelligence scores (UWA\_g) as a function of (a) average retrieval attempts at Close distances, (b) average retrieval latency at Close distances, and (c) average retrieval latency overall, or regardless of distance.



**Figure 4.13 PCTB performance and solicitation behaviors**

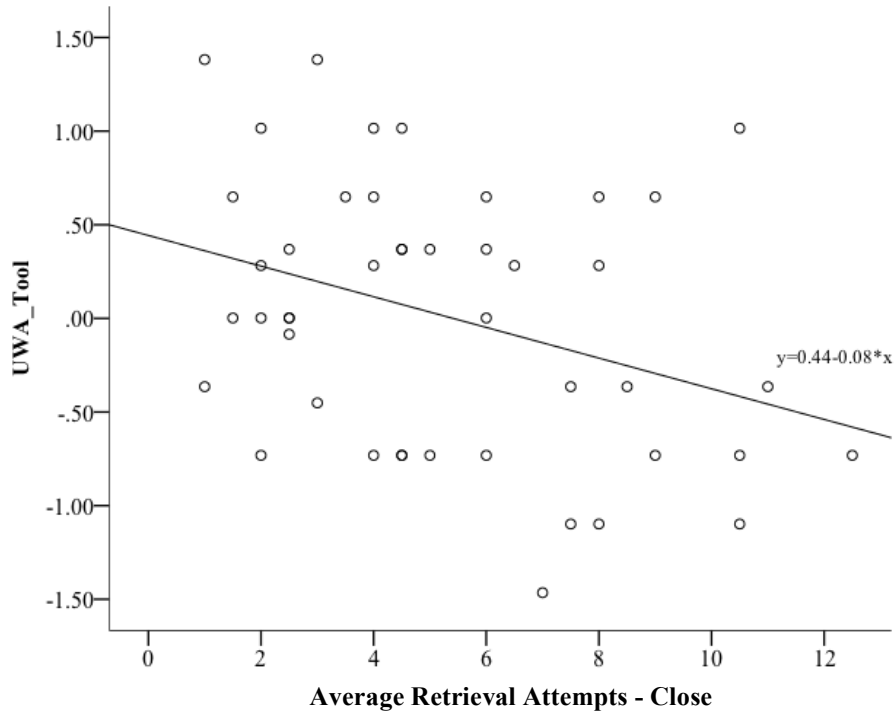
General intelligence scores (UWA\_g) as a function of (a) average solicitation latency at MNR distances and (b) average solicitation latency at Far distances.





**Figure 4.14 Physical PCTB performance and retrieval performance**

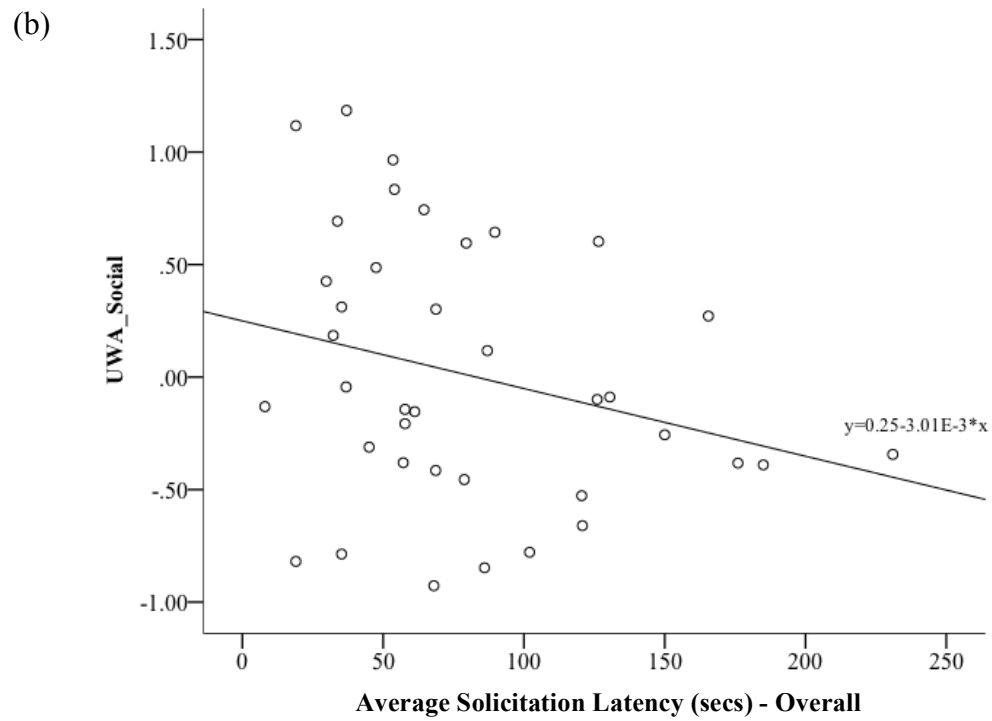
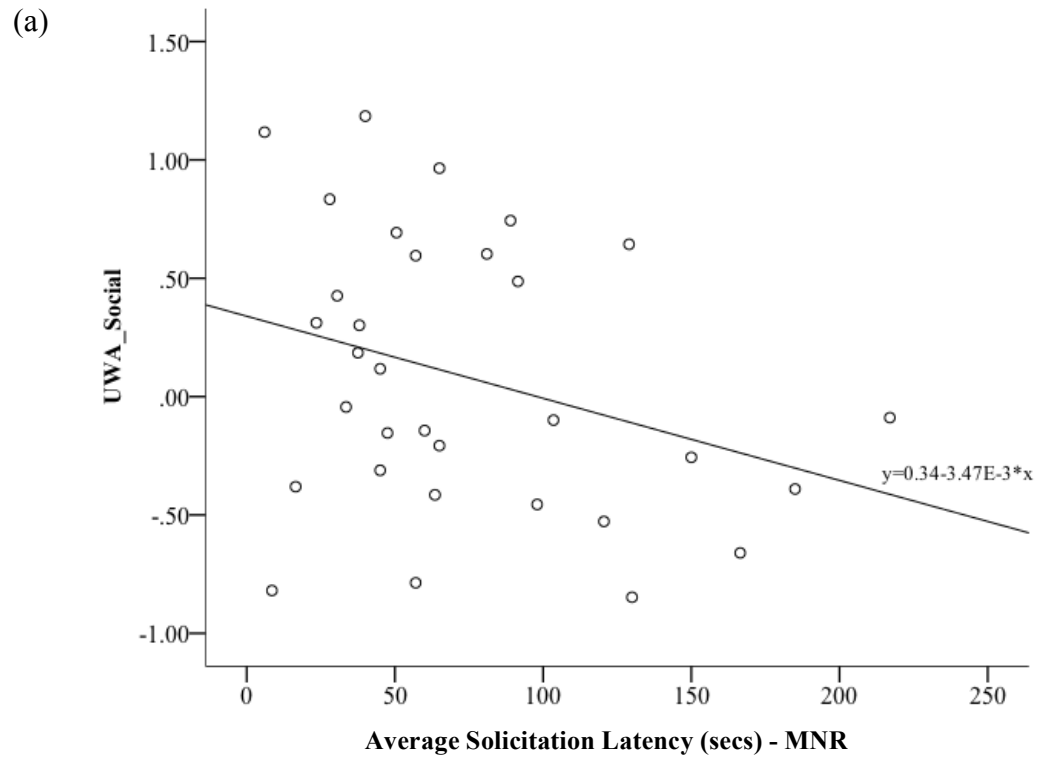
Physical PCTB scores (UWA\_Physical) as a function of (a) average retrieval attempts at Close distances, and average retrieval latency at (b) Close distances and (c) overall.

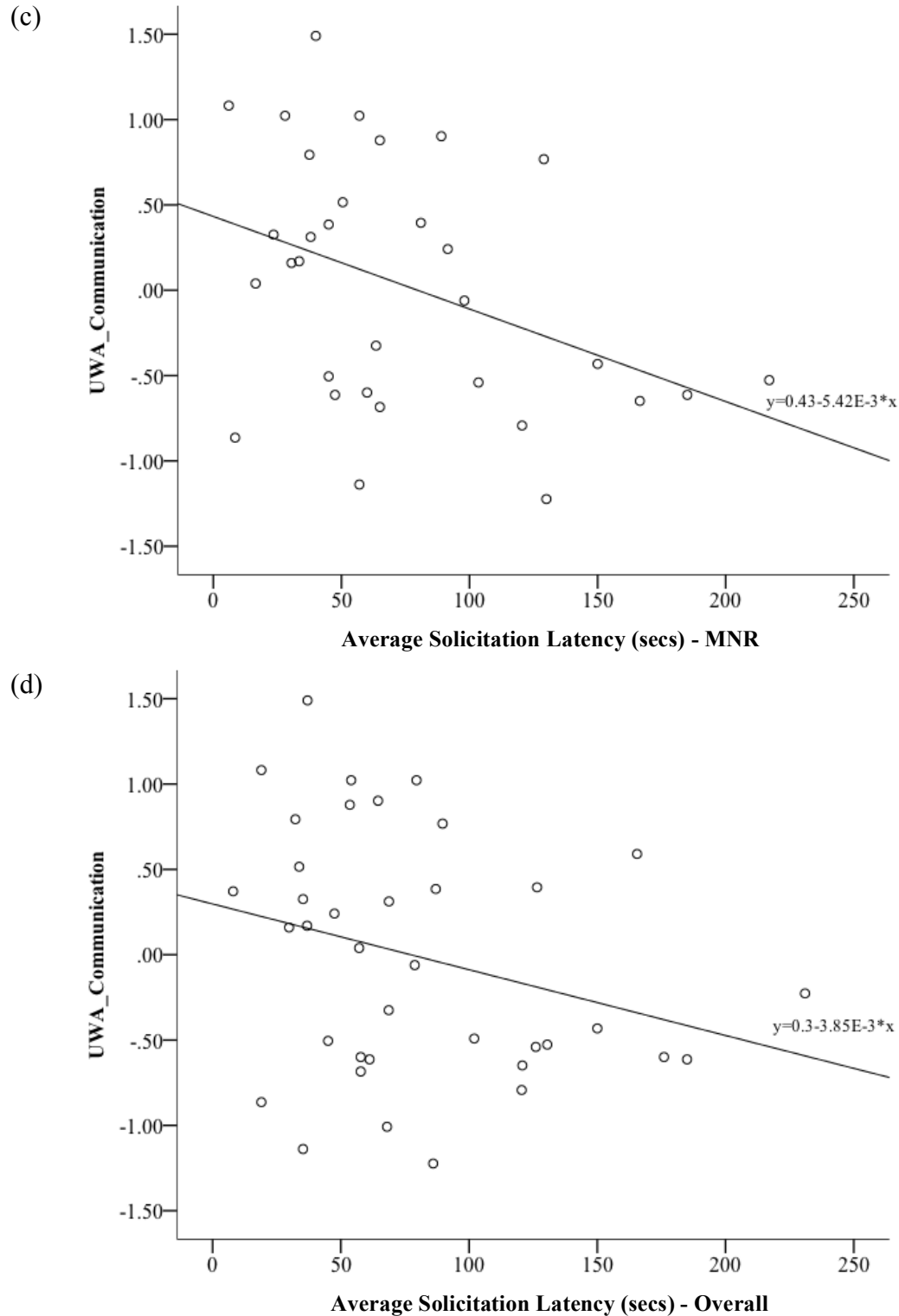


**Figure 4.15 Tool PCTB performance and retrieval performance**

Tool PCTB scores (UWA\_Tool) as a function of average retrieval attempts at Close distances.

Analyses regarding UWA\_social and UWA\_communication were run with number of solicitations and solicitation latency. Both of these were significantly negatively correlated with MNR and Overall solicitation latency (Figure 4.16a-d). Specifically, those with higher scores on the social and communication portions of the PCTB solicited sooner.





**Figure 4.16 Social PCTB performance and solicitation behaviors**

Social PCTB scores (UWA\_Social) as a function of average solicitation latency at (a) MNR distances and (b) overall, and communication PCTB scores (UWA\_Communication) as a function of average solicitation latency at (c) MNR distances and (d) overall.

#### **4.5.2 Attention-Getting Assessment**

To see whether AG assessment performance was related to solicitation behavior in this study, partial correlations were run using average latency of AG signals during the AG assessment. Sex and age were controlled. Latency to AG was significantly positively related to the number of solicitations in this study only at MR distances ( $r(49) = 0.297, p = 0.033$ ). However, this result should be interpreted cautiously as the total number of solicitations was only equal to two.

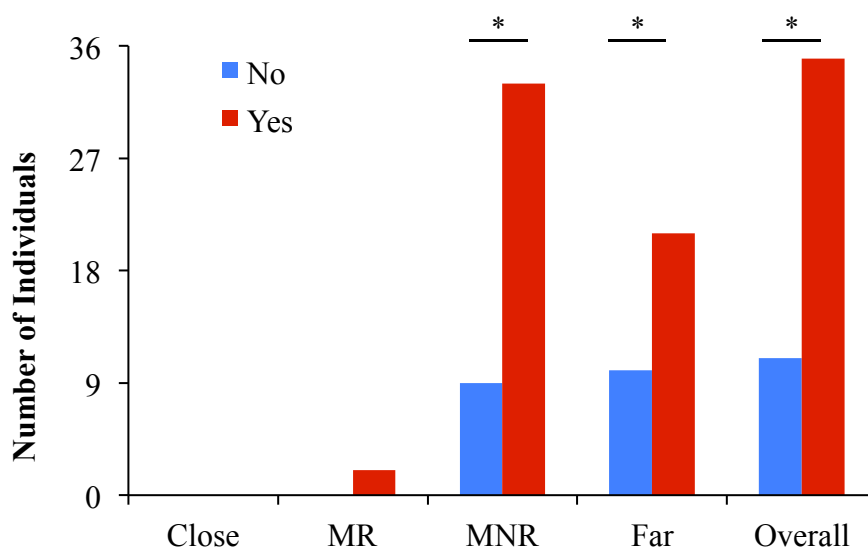
#### **4.5.3 Solicit for Tool**

To evaluate whether solicitation behavior during the solicit for tool task was related to solicitation behaviors of this study, partial correlations controlling for sex and age were run with average latency to solicit for tool and number of sessions to pass the task. Latency to solicit for the tool significantly negatively correlated with the number of solicitations at MNR ( $r(52) = -0.346, p = 0.010$ ) and regardless of distance ( $r(52) = -0.360, p = 0.008$ ). Thus, those who took longer to solicit for the tool during that task made fewer solicitations during this study. The number of solicit for tool sessions was significantly positively related to solicitation latency at Far distances ( $r(39) = 0.336, p = 0.032$ ), such that those requiring more solicit for tool sessions also took longer to solicit during this study.

#### **4.5.4 Return to Tool**

Whether or not an individual returned to using the tool after making a solicitation was recorded. Individuals were scored NA if they never made a solicitation, a 0 if they did not return to using the tool after making a solicitation, and a 1 if they did return to using the tool after making a solicitation. No individuals solicited on Close trials and only two on MR trials. Of the two that solicited on MR trials, both returned to using the tool. In contrast, 42 individuals

solicited at MNR and 31 at Far distances. Of those who solicited, chi-square analyses showed that significantly more individuals returned to using the tool than did not (MNR:  $\chi^2(1) = 13.71$ ,  $p < 0.001$ ; Far:  $\chi^2(1) = 3.90$ ,  $p = 0.048$ ). Regardless of distance, significantly more individuals returned to using the tool after soliciting than did not ( $\chi^2(1) = 12.52$ ,  $p < 0.001$ ; Figure 4.17).



**Figure 4.17 Return to tool frequency**

The number of individuals that did (red) or did not (blue) return to tool after soliciting the experimenter. \*  $p < 0.05$

## 5 DISCUSSION

In this study, bonobos and chimpanzees exhibited proficiency in both physical and social tool use by successfully retrieving rewards at within reach distances and soliciting an experimenter when rewards were out of reach. In addition, both species were able to effectively switch tool strategies according to task constraints. However, species differences were evident across both physical and social tool performance at some distances, such that chimpanzees made fewer attempts to retrieve rewards, retrieved rewards faster, and solicited sooner. This suggests that chimpanzees were more skilled at retrieving rewards than bonobos as well as recognizing the need to solicit for help sooner. Individual differences at some distances in the present study were

associated with performance on other tool and social tasks, providing validity across measures. Distance differences were also prevalent; specifically, individuals made fewer attempts and retrieved rewards faster at Close than MR distances, made fewest attempts at Far distances, and solicited when rewards were at out-of-reach distances. The ability of the apes to switch tool modalities as shown by decreases in tool attempts and increases in solicitation highlights their cognitive flexibility and provides evidence that cognition may be a single continuous module on which physical and social domains lie.

### **5.1 Evolution of Hominin Tool Use**

By studying primate species and factors educing tool use in those that are naturally living, we can gain insights into the types of conditions that led to and drove human technology (Koops et al., 2015; Sanz & Morgan, 2013) and what types of intrinsic motivations were selected for in hominins that led to proficient tool use (Koops et al., 2015). It is important to investigate why tool use is not common among all primates, why some use tools more readily in captive settings, and why tool use varies even within the species that use tools (Van Schaik, Deaner, & Merrill, 1999). Evidence suggests both ecological pressures and social factors play a role in the origination of and preservation of complex tool behaviors (Sanz & Morgan, 2013). Since ecology alone cannot explain tool use in the wild, social and cognitive factors must also be considered, particularly in relation to the invention and transmission of tool use within populations (Van Schaik et al., 1999). The presence of tool use in wild populations relies on opportunities for extractive foraging, manipulability of foods by the foragers, cognitive abilities allowing for the invention and learning of tool use, and social tolerance to facilitate transmission (Van Schaik et al., 1999).

Investigating tool using abilities in captive populations can inform us of ‘hidden’ abilities of a given species that are not elicited by their natural environment. The present study investigated tool use in two of our closest living relatives, bonobos and chimpanzees. Though these apes split from a common ancestor as recently as one to two million years ago, the tool using abilities are vastly different in these two *Pan* species, particularly when comparing wild populations. This study shows that while captive bonobos are capable of using tools effectively, they are less proficient than their skilled counterparts, the chimpanzee. Species differences found on the task used in this study related to physical tool use were in line with the outlined hypotheses regarding reward retrieval. While both bonobos and chimpanzees were able to correctly and effectively use the physical tool on trials where the reward was at a retrievable distance, bonobos were less adept. Specifically, bonobos made more retrieval attempts and were slower at retrieving the reward at Close distances than chimpanzees. Bonobos also made more attempts at Far distances than chimpanzees. It should be noted, however, that the effect of species on retrieval attempts at Close distances was mediated by time spent at table and the effect of species on retrieval latency at Close distances was partially mediated by time spent at table: bonobos spent more time at the table at Close distances than chimpanzees. The mediation effects could be an artifact of the bonobos being less skilled, where spending more time at the table is a consequence of taking longer to retrieve the reward.

In line with previous reports suggesting that captive bonobos are rather skillful at using tools (Gold, 2002; Herrmann, Wobber, & Call, 2008; Jordan, 1982; Mulcahy & Call, 2006; Toth, Schick, Savage-Rumbaugh, Sevcik, & Rumbaugh, 2013) and have a tool repertoire comparable to chimpanzees (Gruber et al., 2010), bonobos in this study were able to use tools successfully to retrieve rewards. As mentioned, though captive bonobos exhibit commensurate tool using

abilities, tool use remains remarkably limited in wild populations (Furuichi et al., 2015; Gruber & Clay, 2016).

With regard to social tool use, both bonobos and chimpanzees exhibited solicitation behaviors in attempt to receive help from an experimenter. While solicitation behavior was rare, if nonexistent, at distances where the reward was easily retrieved, solicitation behavior was prevalent at further distances where the reward was unable to be retrieved. These results are in line with previous studies showing that bonobos and chimpanzees intentionally produce attention-getting/directing behaviors to indicate to desired out of reach items (Savage-Rumbaugh, 1984; Zimmermann et al., 2009). By doing so, the apes are exhibiting social tool use by producing communicative signals to manipulating a social agent (the experimenter) to help obtain the reward for them. Crawford (1937) found that young chimpanzees exhibited solicitation behaviors when their partner did not attempt to pull on a box-pulling task and that solicitations varied depending on certain factors including how responsive the partner was and motivation toward reward. Solicitation behaviors in this study were extremely rare when an experimenter was absent and frequent when the reward was out of reach and an experimenter was present, suggesting that the presence and frequency of solicitation behavior depends on certain factors, particularly presence of another and motivation toward reward.

Species differences were evident in solicitation behaviors at further distances, but opposite to what was originally hypothesized. Specifically, bonobos made fewer solicitations than chimpanzees at MNR and Far distances, suggesting that chimpanzees were better at recognizing when the physical tool was no longer effective for retrieving the reward and increased solicitation efforts to get help from the experimenter. With regard to solicitation latency, when bonobos did solicit, they did so as quickly as the chimpanzees. These results

contradict previous social cognition research by Herrmann and colleagues (2010) utilizing the PCTB. The researchers found that bonobos outperformed chimpanzees on social cognition tasks of the PCTB, suggesting that bonobos are more socially adept. During the present study, chimpanzees appeared to outperform bonobos by making more solicitations and soliciting sooner at out-of-reach distances where the physical tool would fail and a social tool (human) presented an alternative strategy.

Differences in tool using ability do not end at the species level, but exist even within species. For example, chimpanzees in Bossou exhibit nut cracking behavior while the behavior is completely absent from chimpanzees at nearby at Seringbara in the Nimba Mountains (Koops et al., 2013) as well as the population at Kibale (Koops et al., 2013; Yamakoshi, 2004). Additionally, despite army ants living all across Africa, not all chimpanzee populations use tools to harvest these ants (Boesch, 1996; Koops et al., 2013). The present study investigated individual differences by comparing retrieval performance and solicitation behaviors on other tool using and socio-communicative tasks. Individual differences in reward retrieval were related to general intelligence scores (UWA\_g) and physical cognition tasks of the PCTB, such that those with higher intelligence scores and physical scores were more adept at retrieving rewards. More specifically, those individuals with higher intelligence, physical, and tool use scores made fewer attempts to retrieve the reward and retrieved rewards more quickly at Close distances than those with lower scores. Additionally, differences in solicitation latency were related to general intelligence scores and social cognition tasks of the PCTB. Those with higher intelligence, social, and communication scores solicited sooner at MNR distances. Additionally, those with higher intelligence scores solicited sooner overall than those with lower scores. On a separate task assessing AG behavior, those who had faster AG latencies during the assessment

made fewer solicitations on this task at MR distances. This relationship, however, should be interpreted with caution as only two individuals solicited during MR trials. On a solicit for tool task, those requiring more solicit for tool sessions before reaching criterion took longer to solicit at Far distances. Additionally, those who took longer to solicit for the tool made fewer solicitations overall during this study. Thus, this study provides additional evidence that tool using abilities not only vary between species, but also among individuals.

The species and individual differences, as well as the successful tool performance by bonobos, in this study highlight the importance of investigating tool using and other cognitive abilities in captive populations, in addition to wild populations. By studying different species and populations of species we may gain a better understanding of what types of predispositions or motivations were selected for leading to proficient tool use and of the potential limitations or environmental factors at play.

## **5.2 Cognition Dichotomy**

Possibly an artifact of the dichotomization of cognition into separate components (physical and social), many researchers have investigated physical tool use whereas few have investigated social tool use and none, prior to this study, investigated the relation between the two. Further contributing to this dichotomy, tool use is traditionally defined within the domain of physical cognition. With growing interest in what is defined as social tool use, we may begin to evaluate the nature and, indeed, necessity of this dichotomy. Though it has been proposed that similar cognitive processes may underlie physical and social tool use, to what extent these processes underlie both tool modalities remains largely uninvestigated from both a developmental and evolutionary perspective. Thus, with this study I hoped to elucidate whether cognition may be considered a single entity in which certain behaviors and processes are elicited

by different but not mutually exclusive contexts, physical and social, allowing the transition between physical and social tool modalities.

Though associations between individual performance in this study and other physical and social tasks, including the PCTB, reinforce the construct validity of the notion that tool behaviors are related to physical cognition and solicitation behaviors are related to social cognition, the effects of distance suggest a more continuous relationship. To investigate the ‘threshold’, or transition, between physical and social tool use, the task used in this study was one that created a situation in which, at first, a physical tool is sufficient to solve the task, but then becomes ineffective such that individuals must solicit for help. Distance differences on the task used in this study provide evidence that physical and social cognition lie along a continuum of a single module of cognition, at least with regard to tool use. Individuals attempted less at Close than MR distances and more at Close, MR, and MNR distances than Far. They were also faster at retrieving rewards at Close distances than MR. The fact that individuals made fewer attempts at Far distances suggests that they recognized more readily that the reward was too far to be retrieved with the physical tool, thus putting in less effort in trying to retrieve the reward. With respect to the MNR distance, the reward was visually ambiguously within/outside of reach which may have contributed to the erroneous perception that the reward was possibly close enough to reach, eliciting a greater number of attempts. Furthermore, individuals made fewer solicitations at Close and MR distances than MNR and Far, and made solicitations sooner at Far distances than MNR. The fact that individuals made more solicitations at further distances suggests that they recognized the need to shift strategies and increase attempts to get help from an experimenter. Moreover, that individuals make solicitations sooner at Far distances suggests they may recognize prior to any physical tool attempts that the reward is too far to be retrieved.

The fact that individuals attempt to solicit the experimenter supports Leavens et al. (1996) notion “that intentionally communicating individuals (here, chimpanzees) are aware of the need to establish mutual attention with another social agent (here, human observers) to achieve some goal, where successful completion of that goal requires manipulation of the behavior of that social agent” (p. 353).

### **5.3 Behavioral/Cognitive Flexibility**

As defined by Ragozzino (2007), “[b]ehavioral flexibility refers to the ability to shift strategies or response patterns with a change in environmental contingencies” (p. 355). The ability to switch between tool modalities (physical to social, or vice versa) requires some level of behavioral/cognitive flexibility. Being able to adapt one’s behavior in an environment constantly in flux is vital for life, both on a day-to-day scale and overall survival (Kehagia, Murray, & Robbins, 2010) and some also argue that it underlies what is considered to be voluntary action (Kehagia et al., 2010). In this study, bonobos and chimpanzees were able to effectively shift strategies by abandoning the physical tool and soliciting for help when rewards were out-of-reach.

Behavioral flexibility has traditionally been tested using reversal learning and attentional set-shifting tasks. Where reversal learning tasks involve lower order modalities (i.e., color, shape), attention set-shifting tasks require subjects to switch between higher order modalities (i.e., from shapes to lines; Kehagia et al., 2010). The later (also called extradimensional shift) is characteristic of higher-order processing because it demands a completely new approach to solve the task at hand (Ragozzino, 2007). Deficits in behavioral flexibility are evident in many clinical disorders including alcohol use disorder (AUD), schizophrenia, and autism spectrum disorder (ASD) among others.

Research has shown that, compared to control subjects, patients with AUD show deficits in their ability to switch behavior according to rule changes in intra-extradimensional set shift and reversal tasks compared to control subjects (Trick, Kempton, Williams, & Duka, 2014). Some of the most common impairments associated with schizophrenia include set-shifting and reversal learning, measures of behavioral flexibility as mentioned prior (Floresco, Zhang, & Enomoto, 2009). Patients with schizophrenia exhibit difficulty shifting between different strategies, which has been suggested to result from the inability to shift between stimulus dimensions (Floresco et al., 2009). Impairments in cognitive flexibility have also been suggested to underlie the repetitive and stereotypic behaviors exhibited by individuals with ASD (Geurts, Corbett, & Solomon, 2009; Ridley, 1994; Turner, 1999; Yeung, Han, Sze, & Chan, 2015). Cognitive flexibility is not just the ability to produce new behaviors (Gazzaniga, Ivry, & Mangun, 2002) but also the ability to modify preexisting ones to meet changing environmental demands (Monsell, 2003). On tasks testing cognitive flexibility, such as the Wisconsin Card Sorting Test, individuals with ASD performed worse than typically developing individuals, which may be attributed to ASD patients being more preservative in their responding (Yeung et al., 2015). Other studies utilizing set shift paradigms (i.e., CANTAB intradimensional/extradimensional shift task) have found that individuals with ASD show impairments in shifting conceptual sets but not perceptual sets (Brady, Schwean, Saklofske, McCrimmon, Montgomery & Thorne, 2013; Hughes, Russell, & Robbins, 1994; Ozonoff, Cook, Coon, Dawson, Joseph, Klin, et al., 2004).

Results from the present study suggest that both bonobos and chimpanzees exhibit behavioral/cognitive flexibility as shown by a decrease in using a physical tool when it is no longer effective that is matched with an increase in solicitation behavior (*refer to Figure 4.9*

*under section 4.4.3*). Individuals recognized when their physical tool use strategy was no longer fruitful and switched to a social strategy that involved solicitation behaviors.

This study is not without its own set of methodological limitations. For purposes outside of my control, one or more facilities disallowed rewarding solicitation behaviors. Thus, although individuals made a solicitation toward a human experimenter, they were not rewarded immediately. Nevertheless, solicitation behavior remained present and frequent. Because individuals were not rewarded immediately upon their first solicitation, whether or not they returned to using the tool became an additional outcome of interest, particularly with regard to cognitive flexibility.

When looking at whether individuals returned to using the tool after making a solicitation, additional evidence supporting the behavioral/cognitive flexibility of these species is provided. After making their first solicitation, more individuals returned to using the physical tool than did not at MNR and Far distances, and overall. This suggests that not only are bonobos and chimpanzees capable of switching from one strategy to another but also capable of shifting between the two tool strategies when one continues to fail. This is consistent with previous work by Leavens and colleagues (2005) showing that chimpanzees not only persist in the face of failure, but also elaborate their communicative strategies. Here, evidence points not only toward the ability of both bonobos and chimpanzees to persist and in the face of failure, but toward modification and repair of behavioral strategies through use of both physical and social means in order to achieve success.

#### **5.4 Summary**

This study is the first to directly compare physical and social tool use and explore differences between bonobos and chimpanzees. By studying these two closely related ape

species we may gain a better understanding of the factors that may have led chimpanzees to become proficient tool using *Pan* species in comparison to their non-tool using relatives, the bonobo. While both species successfully retrieved rewards with the physical tool and solicited an experimenter, chimpanzees showed greater tool use proficiency and flexibility by making fewer attempts to retrieve rewards, retrieving rewards faster, and making more solicitations. Regardless of species, physical and social tool performance was related to performance on previous physical and social cognition tasks. By introducing a task that switches tool modalities (physical to social), we are able to close the gap between physical and social cognition and gain a greater understanding of behavioral/cognitive flexibility with regard to tool use in these species. The results of this study support the idea that physical and social cognition may not be two separate cognitive domains, but rather make up single cognitive entity in which certain behaviors and processes are elicited by different, but not mutually exclusive contexts. Additionally, bonobos and chimpanzees exhibited cognitive flexibility by switching tool strategies from using a physical tool at closer distances to soliciting a social tool (the experimenter) at further distances. Thus, this study has the potential to have important implications with regard to the evolution of tool use, the relation between physical and social cognition, and behavioral/cognitive flexibility as studied through our closest living relatives.

## REFERENCES

- Bard, K. A. (1990). "Social tool use" by free-ranging orangutans: A Piagetian and developmental perspective on the manipulation of an animate object. In S. T. Parker & K. R. Gibson (Eds.), "Language" and intelligence in monkeys and apes: Comparative developmental perspectives (pp. 356-378). Cambridge, England: Cambridge University.
- Bard, K. A., & Vauclair, J. (1984). The communicative context of object manipulation in ape and human adult-infant pairs. *Journal of Human Evolution*, 13(2), 181-190.  
doi:10.1016/S0047-2484(84)80062-7
- Bates, E., Benigni, L., Bretherton, I., Camaioni, L., & Volterra, V. (2014). *The emergence of symbols: cognition and communication in infancy*. New York, NY: Academic Press.
- Beck, B. B. (1980). *Animal tool behavior: the use and manufacture of tools but animals*. Michigan: Garland STPM Press.
- Bennett, A. J. (1996). *Object manipulation in two species of chimpanzees (Pan troglodytes and Pan paniscus): Effect of age, sex and species on relational behavior*. (Doctor of Philosophy Dissertation), The University of Memphis.
- Boesch, C. (1996). The emergence of cultures among wild chimpanzees. *Proceedings of the British Academy*, 88, 251-268.
- Brady, D. I., Schwan, V. L., Saklofske, D. H., McCrimmon, A. W., Montgomery, J. M., & Thorne, K. J. (2013). Conceptual and perceptual set-shifting executive abilities in young adults with Asperger's syndrome. *Research in Autism Spectrum Disorders*, 7(12), 1631-1637. doi:10.1016/j.rasd.2013.09.009

- Call, J., & Tomasello, M. (1994). Production and comprehension of referential pointing by orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology*, 108, 307-317.  
doi:10.1037/0735-7036.108.4.307
- Carpenter, M., Nagell, K., Tomasello, M., Butterworth, G., & Moore, C. (1998). Social cognition, joint attention, and communicative competence from 9 to 15 months of age. *Monographs of the society for research in child development*, 63(4), 1-174.  
doi:10.2307/1166214
- Crawford, M. P. (1937). The cooperative solving of problems by young chimpanzees. *Comparative psychology monographs*, 14(2), 1-88.
- Crawford, M. P. (1941). The cooperative solving by chimpanzees of problem solving requiring serial responses to color cues. *The journal of Social Psychology*, 13(2), 259-280.
- Crockford, C., & Boesch, C. (2003). Context-specific calls in wild chimpanzees, *Pan troglodytes* verus: analysis of barks. *Animal Behaviour*, 66, 115-125. doi:10.1006/anbe.2003.2166
- Floresco, S. B., Zhang, Y., & Enomoto, T. (2009). Neural circuits subserving behavioral flexibility and their relevance to schizophrenia. *Behavioural Brain Research*, 204, 396-409. doi:10.1016/j.bbr.2008.12.001
- Fox, E. A., Sitompul, A. F., & van Schaik, C. P. (1999). Intelligent tool use in wild 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.
- Fox, E. A., van Schaik, C. P., Sitompul, A., & Wright, D. N. (2004). Intra-and interpopulational differences in orangutan (*Pongo pygmaeus*) activity and diet: implications for the invention of tool use. *American Journal of Physical Anthropology*, 125(2), 162-174.  
doi:10.1002/ajpa.10386

- Frye, D. (1981). Developmental changes in strategies of social interaction. In M. E. Lamb & L. R. Sherrod (Eds.), *Infant social cognition: Empirical and theoretical considerations* (pp. 315-331). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.
- Furuichi, T., Sanz, C., Koops, K., Sakamaki, T., Ryu, H., Tokuyama, N., & Morgan, D. (2015). Why do wild bonobos not use tools like chimpanzees do? *Behaviour*, 152(3-4), 425-460. doi:10.1163/1568539X-00003226
- Gazzaniga, M., Ivry, R. B., & Mangun, G. R. (2002). *Cognitive Neuroscience: The biology of the mind* (2nd ed.). New York: W.W. Norton & Company.
- Geurts, H. M., Corbett, B., & Solomon, M. (2009). The paradox of cognitive flexibility in autism. *Trends in Cognitive Sciences*, 13, 74-82. doi: 10.1016/j.tics.2008.11.006
- Gold, K. C. (2002). Ladder use and clubbing by a bonobo (*Pan paniscus*) in Apenheul Primate Park. *Zoo Biology*, 21(6), 607-611.
- Gómez, J. C. (1986). The development of intentional communication as a problem-solving strategy in the gorilla. *Primate Report*, 14, 178.
- Gómez, J. C. (1988). Tool-use and communication as alternative strategies of problem-solving in the gorilla. *Primate Report*, 19(25-28).
- Goodall, J. (1986). *The chimpanzees of Gombe: patterns of behavior*. Cambridge, MA: Cambridge University Press.
- Gruber, T., & Clay, Z. (2016). A comparison between bonobos and chimpanzees: A review and update. *Evolutionary Anthropology: Issues, News, and Reviews*, 25(5), 239-252. doi:10.1002/evan.21501

- 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, 1023-1033. doi:10.1016/j.anbehav.2010.09.005
- Gruber, T., Reynolds, V., & Zuberbühler, K. (2010). The knowns and unknowns of chimpanzee culture. *Communicative & integrative biology*, 3(3), 221-223. doi:10.4161/cib.3.3.10658
- Hayashi, M., Takeshita, H., & Matsuzawa, T. (2006). Cognitive development in apes and humans assessed by object manipulation. In T. Matsuzawa, M. Tomonaga, & M. Tanaka (Eds.), *Cognitive development in chimpanzees* (pp. 395-410). Tokyo: Springer.
- Heilbronner, S. R., Rosati, A. G., Stevens, J. R., Hare, B., & Hauser, M. D. (2008). A fruit in the hand or two in the bush? Divergent risk preferences in chimpanzees and bonobos. *Biology Letters*, 4(3), 246-249. doi:10.1098/rsbl.2008.0081
- Herrmann, E., Call, J., Hernández-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. doi:10.1126/science.1146282
- Herrmann, E., Hare, B., Call, J., & Tomasello, M. (2010). Differences in the cognitive skills of bonobos and chimpanzees. *PloS one*, 5(8), e12438. doi:10.1371/journal.pone.0012438
- Herrmann, E., Hernández-Lloreda, M. V., Call, J., Hare, B., & Tomasello, M. (2010). The structure of individual differences in the cognitive abilities of children and chimpanzees. *Psychological Science*, 21(1), 102-110. doi:10.1177/0956797609356511
- 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.

- Hohmann, G., & Fruth, B. (2003). Culture in Bonobos? Between - Species and Within - Species Variation in Behavior. *Current Anthropology*, 44(4), 563-571., 44(4), 563-571.  
doi:10.1086/377649
- Hopkins, W. D., Tagliatela, J. P., & Leavens, D. A. (2007). Chimpanzees differentially produce novel vocalizations to capture the attention of a human. *Animal Behaviour*, 73, 281-286. doi:10.1016/j.anbehav.2006.08.004
- Hostetter, A. B., Cantero, M., & Hopkins, W. D. (2001). Differential use of vocal and gestural communication by chimpanzees (*Pan troglodytes*) in response to the attentional status of a human (*Homo sapiens*). *Journal of Comparative Psychology*, 115(4), 337-343.  
doi:10.1037//0735-7036.115.4.337
- Hostetter, A. B., Russell, J. L., Freeman, H., & Hopkins, W. D. (2007). Now you see me, now you don't: evidence that chimpanzees understand the role of the eyes in attention. *Animal Cognition*, 10, 55-62. doi:10.1007/s10071-006-0031-x
- Hughes, C., Russell, J. L., & Robbins, T. W. (1994). Evidence for executive dysfunction in autism. *Neuropsychologia*, 32, 477-492. doi:10.1016/0028-3932(94)90092-2
- Jordan, C. (1982). Object manipulation and tool-use in captive pygmy chimpanzees (*Pan paniscus*). *Journal of Human Evolution*, 11(1), 35-39. doi:10.1016/S0047-2484(82)80029-8
- Kaminski, J., Call, J., & Tomasello, M. (2004). Body orientation and face orientation: two factors controlling apes' begging behavior from humans. *Animal Cognition*, 7(4), 216-223. doi:10.1007/s10071-004-0214-2

- Kano, F., Hirata, S., & Call, J. (2015). Social attention in the two species of pan: Bonobos make more eye contact than chimpanzees. *PloS one*, 10(6), e0129684.  
doi:10.1371/journal.pone.0129684
- Kano, T. (1992). *The last ape*. Stanford, CA: Stanford University Press.
- Kehagia, A. A., Murray, G. K., & Robbins, T. W. (2010). Learning and cognitive flexibility: frontostriatal function and monoaminergic modulation. *Current opinion in neurobiology*, 20(2), 199-204. doi:10.1016/j.conb.2010.01.007
- Koops, K., Furuichi, T., & Hashimoto, C. (2015). Chimpanzees and bonobos differ in intrinsic motivation for tool use. *Scientific reports*, 5. doi:10.1038/srep11356
- Koops, K., McGrew, W. C., & Matsuzawa, T. (2013). Ecology of culture: do environmental factors influence foraging tool use in wild chimpanzees, *Pan troglodytes* versus? *Animal Behaviour*, 85(1), 175-185. doi:10.1016/j.anbehav.2012.10.022
- Koops, K., Visalberghi, E., & van Schaik, C. P. (2014). The ecology of primate material culture. *Biology Letters*, 10(11), 20140508. doi:10.1098/rsbl.2014.0508
- Krause, M. A., & Fouts, R. S. (1997). Chimpanzee (*Pan troglodytes*) pointing: hand shapes, accuracy, and the role of eye gaze. *Journal of Comparative Psychology*, 111, 330-336.  
doi:10.1037/0735-7036.111.4.330
- Leavens, D. A., & Hopkins, W. D. (1998). Intentional communication by chimpanzee (*Pan troglodytes*): A cross-sectional study of the use of referential gestures. *Developmental Psychology*, 34, 813-822. doi:10.1037/0012-1649.34.5.813
- Leavens, D. A., Hopkins, W. D., & Bard, K. A. (1996). Indexical and referential pointing in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 110(4), 346-353.  
doi:10.1037/0735-7036.110.4.346

- Leavens, D. A., Hostetter, A. B., Wesley, M. J., & Hopkins, W. D. (2004). Tactical use of unimodal and bimodal communication by chimpanzees, *Pan troglodytes*. *Animal Behaviour*, 67, 467-476. doi:10.1016/j.anbehav.2003.04.007
- Leavens, D. A., Russell, J. L., & Hopkins, W. D. (2005). Intentionality as measured in the persistence and elaboration of communication by chimpanzees (*Pan troglodytes*). *Child Development*, 76(1), 291-306. doi:10.1111/j.1467-8624.2005.00845.x
- Lurz, R., Krachun, C., Mahovetz, L., Wilson, M. J., & Hopkins, W. (2018). Chimpanzees gesture to humans in mirrors: using reflection to dissociate seeing from line of gaze. *Animal Behaviour*, 135(239-249). doi:10.1016/j.anbehav.2017.11.014
- Mahovetz, L. M. (2015). Effective tool choice by chimpanzees (*Pan troglodytes*): Learning and flexibility. (Master of Arts), Georgia State University.
- Malenky, R. K., & Wrangham, R. W. (1994). A quantitative comparison of terrestrial herbaceous food consumption by *Pan paniscus* in the Lomako Forest, Zaire, and *Pan troglodytes* in the Kibale Forest, Uganda. *American Journal of Primatology*, 32(1), 1-12.  
doi:10.1002/ajp.1350320102
- Monsell, S. (2003). Task switching. *TRENDS in Cognitive Sciences*, 7(3), 134-140.  
doi:10.1016/S1364-6613(03)00028-7
- Mulcahy, N. J., & Call, J. (2006). How great apes perform on a modified trap-tube task. *Animal Cognition*, 9(3), 193-199.
- Mundy, P. (1995). Joint attention and social-emotional approach behavior in children with autism. *Development and Psychopathology*, 7(1), 63-82.  
doi:10.1017/S0954579400006349

- Mundy, P., & Crowson, M. (1997). Joint attention and early social communication: Implications for research on intervention with autism. *Journal of autism and developmental disorders*, 27(6), 653-676. doi:10.1023/A:1025802832021
- Notman, H., & Rendall, D. (2005). Contextual variation in chimpanzee pant hoots and its implications for referential communication. *Animal Behaviour*, 70, 177-190. doi:10.1016/j.anbehav.2004.08.024
- Ozonoff, S., Cook, I., Coon, H., Dawson, G., Joseph, R. M., Klin, A., McMahon, W. M., Minshew, N., Munson, J. A., Pennington, B. F., Rogers, S. J., Spence, M. A., Tager-Flusberg, H., Volkmar, F. R., Wrathall, D. (2004). Performance on Cambridge Neuropsychological Test Automated Battery subtests sensitive to frontal lobe function in people with autistic disorder: evidence from the Collaborative Programs of Excellence in Autism network. *Journal of autism and developmental disorders*, 34(2), 139-150. doi:10.1023/B:JADD.0000022605.81989.cc
- Piaget, J. (1974). *The origins of intelligence in children* (M. Cook, Trans.). New York: International University Press.
- Pika, S., Liebal, K., & Tomasello, M. (2005). Gestural communication in subadult bonobos (*Pan paniscus*): repertoire and use. *American Journal of Primatology*, 65(1), 39-61. doi:10.1002/ajp.20096
- Poss, S. R., Kuhar, C., Stoinski, T. S., & Hopkins, W. D. (2006). Differential use of attentional and visual communicative signaling by orangutans (*Pongo pygmaeus*) and gorillas (*Gorilla gorilla*) in response to the attentional status of a human. *American Journal of Primatology*, 68, 978-992. doi:10.1002/ajp.20304

- Povinelli, D. J., & O'Neill, D. K. (2000). Do chimpanzees use their gestures to instruct each other. In S. Baron-Cohen, H. Tager-Flusberg, & M. Lombardo (Eds.), *Understanding other minds: perspectives from developmental and cognitive neuroscience*. Oxford, U.K.: Oxford University Press.
- Prado-Martinez, J., Sudmant, P. H., Kidd, J. M., Li, H., Kelley, J. L., Lorente-Galdos, B., Veeramah, K. R., Woerner, A. E., O'Connor, T. D., Santpere, G., Cagan, A., Theunert, C., Casals, F., Laayouni, H., Munch, K., Hobolth, A., Halager, A. E., Malig, M., Hernandez-Rodriguez, J., Hernando-Herraez, I., Prüfer, K., Pybus, M., Johnstone, L., Lachmann, M., Alkan, C., Twigg, D., Petit, N., Baker, C., Hormozdiari, F., Fernandez-Callejo, M., Dabad, Michael L. Wilson, Laurie Stevison, Cristina Camprubí, Tiago Carvalho, Aurora Ruiz-Herrera, M., Vives, L., Mele, M., Abello, T., Kondova, I., Bontrop, R. E., Pusey, A., Lankester, F., Kiyang, J. A., Bergl, R. A., Lonsdorf, E., Myers, S., Ventura, M., Gagneux, P., Comas, D., Siegmund, H., Blanc, J., Agueda-Calpena, L., Gut, M., Fulton, L., Tishkoff, S. A., Mullikin, J. C., Wilson, R. K., Gut, I. G., Gonder, M. K., Ryder, O. A., Hahn, B. H., Navarro, A., Akey, J. M., Bertranpetit, J., Reich, D., Mailund, T., Schierup, M. H., Hvilsom, C., Andrés, A. M., Wall, J. D., Bustamante, C. D., Hammer, M.F., Eichler, E. E., & Marques-Bonet, T. (2013). Great ape genetic diversity and population history. *Nature*, 499(7459), 471. doi:10.1038/nature12228
- Ragozzino, M. E. (2007). The Contribution of the Medial Prefrontal Cortex, Orbitofrontal Cortex, and Dorsomedial Striatum to Behavioral Flexibility. *Annals of the New York Academy of Science*, 1121, 355-375. doi:10.1196/annals.1401.013
- Ridley, R. M. (1994). The psychology of perseverative and stereotyped behaviour. *Progress in neurobiology*, 44(2), 221-231. doi:10.1016/0301-0082(94)90039-6

- Roffman, I., Savage-Rumbaugh, S., Rubert-Pugh, E., Stadler, A., Ronen, A., & Nevo, E. (2015). Preparation and use of varied natural tools for extractive foraging by bonobos (*Pan paniscus*). *American Journal of Physical Anthropology*, 158(1), 78-91. doi:10.1002/ajpa.22778
- Sabbatini, G., Truppa, V., Hribar, A., Gambetta, B., Call, J., & Visalberghi, E. (2012). Understanding the functional properties of tools: Chimpanzees (*Pan troglodytes*) and capuchin monkeys (*Cebus apella*) attend to tool features differently. *Animal Cognition*, 15(577-590). doi:10.1007/s10071-012-0486-x
- Sanz, C. M., & Morgan, D. B. (2013). Ecological and social correlates of chimpanzee tool use. *The Royal Society B*, 368. doi:10.1098/rstb.2012.0416
- Savage-Rumbaugh, S. (1984). *Pan paniscus* and *Pan troglodytes*: Contrast in preverbal communicative competence. In R. L. Susman (Ed.), *The Pygmy Chimpanzee: Evolutionary Biology and Behavior* (pp. 395-413). New York: Plenum Press.
- Schrauf, C., Call, J., Fuwa, K., & Hirata, S. (2012). Do chimpanzees use weight to select hammer tools? *PloS one*, 7(7), e41044. doi:10.1371/journal.pone.0041044
- Shumaker, R. W., Walkup, K. R., & Beck, B. B. (2011). *Animal tool behavior: the use and manufacture of tools by animals*. Baltimore, Maryland: Johns Hopkins University Press.
- Slocombe, K. E., & Zuberbuhler, K. (2005). Agonistic screams in wild chimpanzees (*Pan troglodytes schweinfurthii*) vary as a function of social role. *Journal of Comparative Psychology*, 119, 67-77. doi:10.1037/0735-7036.119.1.67
- Spagnoletti, N., Visalberghi, E., Verderane, M. P., Ottoni, E., Izar, P., & Fragaszy, D. (2012). Stone tool use in wild bearded capuchin monkeys, *Cebus libidinosus*. Is it a strategy to

- overcome food scarcity? *Animal Behaviour*, 83(5), 1285-1294.  
doi:10.1016/j.anbehav.2012.03.002
- Tagliatalata, J. P., Savage-Rumbaugh, S., & Baker, L. A. (2003). Vocal production by a language-competent *Pan paniscus*. *International Journal of Primatology*, 24(1), 1-17.  
doi:10.1023/A:1021487710547
- Terborgh, J. (1986). Keystone plant resources in the tropical forest. In M. Soule' (Ed.), *Conservation biology: the science of scarcity and diversity* (pp. 333–344). Sunderland, MA: Sinauer.
- Tomasello, M., & Call, J. (1997). *Primate cognition*. New York: Oxford University Press.
- Tomasello, M., Call, J., Nagell, K., Olguin, R., & Carpenter, M. (1994). The learning and use of gestural signals by young chimpanzees: a trans-generational study. *Primates*, 35, 137-154. doi:10.1007/BF02382050
- Toth, N., Schick, K. D., Savage-Rumbaugh, E. S., Sevcik, R. A., & Rumbaugh, D. M. (2013). Pan the tool-maker: investigations into the stone tool-making and tool-using capabilities of a bonobo (*Pan paniscus*). *Journal of Archaeological Science*, 20(1), 81-91.
- Trick, L., Kempton, M. J., Williams, S. C. R., & Duka, T. (2014). Impaired fear recognition and attentional set-shifting is associated with brain structural changes in alcoholic patients. *Addiction Biology*, 19, 1041-1054. doi:10.1111/adb.12175
- Turner, M. (1999). Annotation: Repetitive behaviour in autism: A review of psychological research. *Journal of child psychology and psychiatry*, 40(6), 839-849.
- Van Schaik, C. P., Deaner, R. O., & Merrill, M. Y. (1999). The conditions for tool use in primates: implications for the evolution of material culture. *Journal of Human Evolution*, 36, 719-741. doi:10.1006/jhev.1999.0304

- Van Schaik, C. P., & Knott, C. D. (2001). Geographic variation in tool on *Neesia* fruits in orangutans. *American Journal of Physical Anthropology*, 114, 331-342.  
doi:10.1002/ajpa.1045
- Vauclair, J., & Bard, K. A. (1983). Development of manipulations with objects in ape and human infants. *Journal of Human Evolution*, 12(7), 631-645. doi:10.1016/S0047-2484(83)80003-7
- Völter, C. J., Rossano, F., & Call, J. (2015). From exploitation to cooperation: social tool use in orang-utan mother offspring dyads. *Animal Behaviour*, 100, 126-134.  
doi:10.1016/j.anbehav.2014.11.025
- Völter, C. J., Rossano, F., & Call, J. (2016). Social manipulation in nonhuman primates: Cognitive and motivational determinants. *Neuroscience & Biobehavioral Reviews*.  
doi:10.1016/j.neubiorev.2016.09.008
- Westergaard, G. C., & Fragaszy, D. M. (1987). The manufacture and use of tools by capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 101(2), 159-168.  
doi:10.1037/0735-7036.101.2.159
- Wrangham, R. W. (1986). Ecology and social evolution in two species of chimpanzees. In D. I. Rubenstein & R. W. Wrangham (Eds.), *Ecology and social evolution: Birds and mammals* (pp. 352-378). Princeton, NJ: Princeton University Press.
- Wrangham, R. W., Chapman, C. A., Clark-Arcadi, A. P., & Isabirye-Basuta, G. (1996). Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 45-57). Cambridge: Cambridge University Press.

- Wrangham, R. W., & Peterson, D. (1996). *Demonic males: apes and the origins of human violence*. Cambridge, MA: Harvard University Press.
- 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. doi:10.1002/(SICI)1096-8644(199807)106:3<283::AID-AJPA2>3.0.CO;2-O
- Yamakoshi, G. (2004). Food seasonality and socioecology in Pan: are West African chimpanzees another bonobo? *African Study Monographs*, 25(1), 45-60. doi:10.14989/68227
- Yeung, M. K., Han, Y. M. Y., Sze, S. L., & Chan, A. S. (2015). Abnormal Frontal Theta Oscillations Underlie the Cognitive Flexibility Deficits in Children With High-Functioning Autism Spectrum Disorders. *Neuropsychology*. doi:10.1037/neu0000231
- Zimmermann, F., Zemke, F., Call, J., & Gómez, J. C. (2009). Orangutans (*Pongo pygmaeus*) and bonobos (*Pan paniscus*) point to inform a human about the location of a tool. *Animal Cognition*, 12(2), 347-358.