Social Decision-Making in Bonobos and Chimpanzees

by

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Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
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ABSTRACT

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Abstract

Humans are natural politicians. We obsessively collect social information that is both observable (e.g., about third-party relationships) and unobservable (e.g., about others' psychological states), and we strategically employ that information to manage our cooperative and competitive relationships. To what extent are these abilities unique to our species, and how did they evolve? The present dissertation seeks to contribute to these two questions. To do so, I take a comparative perspective, investigating social decision-making in humans' closest living relatives, bonobos and chimpanzees. In Chapter 1, I review existing literature on theory of mind—or the ability to understand others' psychological states—in these species. I also present a theoretical framework to guide further investigation of social cognition in bonobos and chimpanzees based on hypotheses about the proximate and ultimate origins of their species differences. In Chapter 2, I experimentally investigate differences in the prosocial behavior of bonobos and chimpanzees, revealing species-specific prosocial motivations that appear to be less flexible than those exhibited by humans. In Chapter 3, I explore through decision-making experiments bonobos' ability to evaluate others based on their prosocial or antisocial behavior during third-party interactions. Bonobos do track the interactions of third-parties and evaluate actors based on these interactions. However, they do not exhibit the human preference for those who are prosocial towards others, instead

consistently favoring an antisocial individual. The motivation to prefer those who demonstrate a prosocial disposition among groupmates may be a unique feature of human psychology that contributes to our ultra-cooperative nature. In Chapter 4, I investigate the adaptive value of social cognition in wild primates. I show that the recruitment behavior of wild chimpanzees at Gombe National Park, Tanzania is consistent with the use of third-party knowledge, and that those who appear to use third-party knowledge receive immediate proximate benefits. They escape further aggression from their opponents. These findings directly support the social intelligence hypothesis that social cognition has evolved in response to the demands of competing with one's own group-mates. Thus, the studies presented here help to better characterize the features of social decision-making that are unique to humans, and how these abilities evolved.

Dedication

This dissertation is dedicated to my mother, Sandy Krupenye, who worked tirelessly to ensure that my siblings and I experienced an intellectually rich upbringing, despite very limited financial means.

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Acknowledgements

I often feel like the luckiest person in the world. I am able to spend my days with people and animals who challenge me, and to pursue work about which I can't imagine feeling more passionate. This dissertation is the embodiment of the last five years of that dream. There are so many people to whom I am forever indebted for their guidance and support along the way. A comprehensive list would be the length of this dissertation, but I hope to at least acknowledge a few with the greatest impact.

It all began with my parents, Sandy and Peter. They nurtured my nascent adoration of animals and my excitement for learning. Since I was four, they have allowed us to share our home with innumerable individuals of many species, beginning with cats and eventually a dog but also including a much more eccentric array. We raised rabbits, hatched ducks and chickens, cared for fish, hermit crabs, frogs, turtles, and lizards, and even shared our life with one of the most beautiful animals I've ever had the privilege of knowing—a flying squirrel named Nieve. My parents have worked hard to keep themselves afloat and, despite their very limited means, to provide their children with the best possible opportunities to learn and grow. My mom found programs that allowed us to

attend summer camp and identified every free day or event at the museums, zoos, and libraries in our area and in New York City, to ensure that we still had access to these richly stimulating resources. My time at the Bronx Zoo was especially formative. I still remember my excitement as I careened past other buildings on my way to the monkey house; I could watch those monkeys for hours. With my dad especially, I spent a lot of time outside. We often went out on the wooden row boats that he built. Whether we were boating through the great swamp in search of turtles, exploring the woods near our house in hopes of discovering salamanders beneath the moist, shaded rocks, or parking on the properties of local businesses to catch frogs in their ponds, my parents did everything they could to cultivate my curiosity about the natural world.

Along for the ride were my siblings, Ben, Ann, and Danny. We shared so many of those adventures together, and I'm excited for those to come. Although we sometimes fought while growing up, I am proud of who Ben and Ann have become and I cherish them far more than I think that they know. The youngest of us, Danny, is still just six. He is a curious and inspiring kid, who gives me hope. His enthusiasm for learning, especially about nature, is contagious, and reminds me how excited I am to share my passion with future generations as a teacher.

Academically, I have been fortunate to have been under the care of some remarkable mentors. I would be remiss to not acknowledge the wonderful faculty who guided me at Connecticut College. Connecticut College took a chance on me—a poor kid from upstate New York—and offered more resources and opportunities than I could have hoped for. It was there that I learned that regardless of financial means anything is possible.

However, I owe my passion for animal cognition to Laurie Santos. I chanced upon an advertisement to work as an intern in Laurie's lab, where I spent the summer of 2009. At the time I was interested in participating in non-invasive research with nonhuman primates, but knew little about psychology. In her lab, I realized that what excited me most about primates was their intelligence. Laurie turned me on to theory of mind and social cognition more broadly. Even though I was not an undergraduate at Yale, she noticed my excitement and invested in me. She provided countless opportunities and generously shared her time and energy to guide me, ultimately mentoring my undergraduate thesis and providing a strong and compassionate letter of recommendation that I am sure was instrumental in my admission to Duke.

The streak of engaged and transformative mentorship did not stop at Duke. My primary advisor, Brian Hare, has guided me every step of the way through my development into a scientist. He has allowed me the control to pursue the questions that most excite me, while providing both the necessary resources and the brilliant guidance to ensure my success in each of my past endeavors. An elegant experimentalist with unmatched experience, he is responsible for any skill that I have in designing and conducting cognitive experiments. Moreover, his eye has been not only on my immediate success during graduate school but also on my career in academia and my viability as a scientist at large. I will always be grateful to him.

As my secondary advisor, Anne Pusey is the perfect complement to Brian. With her expertise in behavioral ecology, she has provided invaluable feedback, further ensuring that my studies of animal behavior and cognition are grounded in evolutionary theory and an understanding of the natural ecology and behavior of my study species. She is a nurturing mentor who has challenged me to think about things from perspectives rarely held by psychologists. She also managed to both always support my enthusiasm for developing new projects while encouraging me to remain focused on those at hand.

I am also indebted to the other members of my committee—Makeba Wilbourn, Steve Churchill, and until her move to Penn Liz Brannon. Each of them has been hugely supportive, sharing their time and insights to guide me throughout the whole process. My time at Duke has also been deeply enriched by the graduate students, postdocs, and research scientists who have passed through Brian and Anne's labs during this time. I have learned so much from each of them. These include Ian Gilby, Alex Rosati, Evan MacLean, Jingzhi (Hippo) Tan, Aleah Bowie, Steffen Foerster, Kara Schroepfer-Walker, Emily Boehm, and Joseph Feldblum. Similarly, I am incredibly thankful for the mentorship I have received from several key people outside of Duke. Ikuma Adachi, Fumihiro Kano, Josep Call, and Mike Tomasello have all taken a chance on me, providing me with dedicated training and support.

I could not have asked for a more fun and stimulating grad school experience and that is in no small part thanks to the wonderful friends with whom I've shared this time. They have been there with me every step of the way, not only when things were good but also to support me during the most challenging times. This is by no means a comprehensive list, and I apologize that I cannot mention all of the people I love nor express the individual gratitude that

I have for each of these individuals, but I must at least acknowledge a handful of friends who have been with me during my time in Durham: India, Emily, Amelia, Joseph, Vlad, Aleah, Paul, Jackson, Sara, Anthony, Casey, Aria, Rachna, Lauren, Michael, Kara, Randi, Caroline, Billy, Marissa, Nadia, and Jeremy. You have made this an unforgettable experience. I will always cherish our friendship. Thanks are also owed to the other wonderful friends I've made in Durham, Inuyama, and Leipzig, and to my friends from college and high school who have been there all along.

Next, I would like to thank my partner, Simone. Through the highs and lows of the last couple years, he has been everything that one can hope for in a partner. He is endlessly supportive, grounding, and fun. He both celebrates my successes and challenges me to improve in areas where I flounder. I am a better person because of him.

I have also learned so much from each of the wonderful animals that I've had the privilege to get to know. I must acknowledge them—and especially the bonobo, Lukuru—for the boundless curiosity that they have inspired and the satisfying relationships that we have shared. I am thankful to the people at Lola ya Bonobo, Tchimpounga Chimpanzee Sanctuary, the Gombe Chimpanzee

Project, the North Carolina Zoo, the Duke Lemur Center, the Primate Research Institute, the Max Planck Institute for Evolutionary Anthropology, and Duke University's Evolutionary Anthropology department for facilitating my research. In particular, I am hugely thankful to the help and friendship of Lisa Jones, Lisa Squires, and LaMonda Sykes. For assistance in data collection, I thank Suzy Kwetuenda and Delphin Bilua, and for help with coding, Laura Lewis, Joe Sullivan, Danielle Su, Malia Budd, Nicole Kim, James Brooks, Elizabeth Barker, and Shannon Roivas. Finally, I must thank the National Science Foundation, USAID, the National Academy of Sciences, and Duke University for their generous financial support.

The work presented within this dissertation reflects collaborations with Brian Hare (Chapters 1-3), Evan MacLean (Chapter 1), Jingzhi Tan (Chapter 2), Anne Pusey (Chapter 4), Ian Gilby (Chapter 4), Joseph Feldblum (Chapter 4), and Ashley Mooney (Chapter 4).

1 Introduction: Does the bonobo have a (chimpanzee-like) theory of mind?

Humans are adept at making inferences about the psychological states of others, including their emotions, desires, and beliefs. These inferences then inform our attempts to cooperate, resolve conflicts, and communicate effectively. Such *theory of mind* abilities, as they are known, were long believed to be unique to humans, but there is now evidence that in some contexts chimpanzees are capable of attributing to others a range of psychological states (Tomasello and Call, 1997, Hare, 2011). Less work has been accomplished with bonobos, but even the limited comparisons that are now possible between the two species are helping to test hypotheses about how such skills might evolve across species—including our own (Hare, 2011).

In 1978, Premack and Woodruff first posed the question, "Does the chimpanzee have a theory of mind?" At the time, chimpanzees were a clear choice for the first comparative investigations of human social cognition. Humans have two closest relatives, but bonobos were discovered much later than chimpanzees, in large part because they inhabit a much more restricted range, south of the Congo river, as compared to chimpanzees' distribution throughout East, Central, and West Africa. Bonobos were still barely known to science in 1978 while chimpanzees were relatively common in captivity and were already the subject of a number of captive and field research programs. However, even after field sites were established to study bonobos in the wild, they remained little studied in captivity.

We currently find ourselves at an exciting moment in bonobo research since there has been more work on bonobo cognition in the past ten years than the previous hundred. For the first time quantitative and qualitative comparisons between bonobos and chimpanzees are possible. Here we summarize what has been learned about theory of mind in chimpanzees since Premack and Woodruff's seminal investigations. We then present two hypotheses relevant to the selective pressures that have shaped—and proximate mechanisms that underlie—ape social cognition. From these hypotheses, we generate predictions about possible differences in social cognition between chimpanzees and bonobos. Finally, we evaluate our hypotheses against existing data and discuss the most pressing directions for future research.

1.1 Theory of Mind in Chimpanzees

1.1.1 Historical Perspective

Premack and Woodruff (1978) showed videos to a human-raised chimpanzee, Sarah. These videos depicted humans facing a variety of problems (e.g., a banana was out of reach, or the actor shivered because the heater was broken). Sarah was then allowed to choose among photographs of various objects, only one of which would solve the problem presented in the video (e.g., a stick to retrieve the banana, or a lit wick for the heater). Sarah consistently chose the correct photograph, leading the authors to conclude that she understood the goals of the actors in the videos. Later, in 1990, Povinelli and colleagues reported a study in which chimpanzees discriminated between a knowledgeable and an ignorant informant and selectively followed pointing gestures from the knowledgeable informant in order to find hidden food. However, in 1993, Heyes offered compelling alternative interpretations for existing data on animal mindreading, and in the years that followed a number of studies reported that chimpanzees did not follow the communicative cues of a knowledgeable human or conspecific when searching for food (Povinelli et al., 1997, Call et al., 1998, Itakura and Tanaka, 1998). These data led Tomasello and Call (1997) to conclude, in their landmark book *Primate Cognition*, that "there is no solid evidence that nonhuman primates understand the intentionality or mental states of others" (p. 340). Theory of mind was therefore an aspect of human cognition in which the differences between humans and other animals were thought to be qualitative, rather than quantitative, in nature.

This view began to change when Hare (2001) noted that primate social life is highly competitive and suggested that since primate cognitive abilities have likely been adapted for such a setting, it may be in competitive situations that primates are most motivated to exhibit their cognitive skills. Lyons and Santos (2006) even argued that theory of mind skills expressed in competitive contexts may represent domain-specific traits. Accordant with both hypotheses, Hare and Tomasello (2004) showed that chimpanzees performed better on cognitive tasks when they were interacting with a competitor than with a cooperator. Additionally, Tomasello et al. (2003b) suggested that chimpanzees' failure to follow the communicative cues of a knowledgeable informant may not owe to a lack of theory of mind abilities in general but rather to a specific inability to understand the cooperative intentions underlying such communicative cues. If chimpanzees do not produce cooperative communicative cues themselves, why should they understand such cues when others produce them? Through more ecologically relevant paradigms—that used a combination of spontaneous behavioral measures, larger sample sizes, and competitive social contexts—substantial evidence for chimpanzees' understanding of others' psychological states has accumulated.

1.1.2 Understanding of Perception

Much work has explored what chimpanzees understand of others' perception. This research has largely focused on *seeing* and *hearing*. Like many species, chimpanzees are capable of following the gaze of conspecific or human social partners (Povinelli and Eddy, 1996, Tomasello et al., 1998, Brauer et al., 2005, Rosati and Hare, 2009). Gaze following could reflect an appreciation of the other's visual perspective or it could be a simple reflexive response that evolved for its clear adaptive benefits (Tomasello et al., 1998, Emery, 2000). Indeed, co-orienting to match the target of another's attention may alert the gaze follower to important resources, such as food or mates, as well as threats, such as predators or aggressive conspecifics. In chimpanzees at least, gaze following appears to be more than just a reflexive response. This species follows gaze geometrically, around barriers, and checks back with the actor when it cannot identify the target of her gaze (Call et al., 1998, Tomasello et al., 1999, Brauer et al., 2005, Okamoto-Barth et al., 2007). Chimpanzees are also sensitive to an agent's attentional state.

For example, when begging for food, they spontaneously use more gestures when their target's face or body is oriented toward them than when it is oriented away (Kaminski et al., 2004, Hostetter et al., 2007, Tempelmann et al., 2011). When attempting to communicate with an agent who is facing away from them, chimpanzees will walk around to the front of the agent before attempting to communicate (Liebal et al., 2004, Call and Tomasello, 2007). They also shift their use of gestural versus vocal communication depending on whether their target is facing toward or away from them (Hostetter et al., 2001, Leavens et al., 2004).

To test the idea that chimpanzees can assess what another individual can see, Hare et al. (2000) pitted two chimpanzees against one another to compete over food. The chimpanzees were situated in separate testing rooms on either side of a central room where food was hidden. Each could see her competitor on the other side of the central room. Since dominance is relatively strict in chimpanzees, dominant individuals were able to monopolize visible food. However, in each experiment, there was a critical condition in which both pieces of food were visible to the subordinate competitor but only one of the pieces was visible to the dominant in the pair. In these conditions, subordinates preferentially targeted the food that the dominant could not see. In these crucial tests subordinates were given a slight head-start, and could not see the dominant when they made their choice, to ensure that they were not simply responding to the behavior or gaze direction of their competitor. These studies provided the first compelling evidence that chimpanzees may be sensitive to others' visual perspectives (Whiten, 2013).

An important question is whether apes can use their knowledge of others' perspectives to manipulate what others perceive. To address this question, Hare et al. (2006) presented chimpanzees with a series of studies in which the subject was attempting to steal food from a human competitor and had to choose between paths that either concealed or exposed their approach. The chimpanzees consistently preferred a path behind the competitor's back rather than in front of him, behind an opaque barrier rather than a transparent one, and behind a complete barrier rather than a partial one. Moreover, they commonly used indirect approaches where they initially moved away from the food and appeared disinterested until they were out of view of their competitor. In a similar setup in which chimpanzees could remain concealed until the final step of their approach in which they needed to reach through an opaque or transparent tube to retrieve the food, they reliably chose the opaque tube (Melis et al., 2006a).

Recently, Karg et al. (2015a) also showed that chimpanzees strategically manipulate not only whether they themselves can be seen by another agent but also what other features of the environment the agent can see. Food was located in several small trays. The chimpanzees could move the individual trays behind or in front of an occluder, but could not retrieve the food themselves. Subjects left food concealed more often when interacting with a competitor who would steal the food than when interacting with a cooperator who would retrieve it for them. They exposed more food to the cooperator than the competitor; however, they did not actively hide visible food from the competitor.

Research has also explored whether chimpanzees are sensitive to what others can hear. Melis et al. (2006a) showed that, when visually concealed from their competitor, chimpanzees preferred to steal food using an approach that was silent over one that that was noisy. However, Brauer et al. (2008) found that when chimpanzees competed with conspecifics for hidden food in a manner similar to Hare et al. (2000), they did not appear to infer which piece of food their competitor was aware of based on what their competitor could hear. They were equally likely to approach a piece of food that their competitor could not see but could hear during baiting and one that their competitor could not see or hear.

The main alternative explanation offered for positive findings is a behavior-reading interpretation that could potentially explain chimpanzees' choices equally as well as a mindreading interpretation (Heyes, 1993, Heyes, 1998, Penn and Povinelli, 2007, but see Table 1 in Hare, 2011 for a summary of evidence against this and other alternative explanations). For example, chimpanzees might simply have learned during the course of their lives that agents pursue anything in their environment as long as a direct line can be drawn between the agent and the target and nothing obstructs this line. One recent test of this type of behavior-reading hypothesis involved giving subjects unique self-experience with unfamiliar equipment that alters one's perceptual access. Then these subjects were tested to evaluate whether their self-experience aided their ability to correctly predict the effect of this same equipment on the visual experience of others (Heyes, 1998, Povinelli and Vonk, 2003, Povinelli and Vonk, 2004). To do so, Karg et al. (2015b) used a competitive setup very similar to Melis et al. (2006a). Chimpanzees attempted to steal food from a human experimenter who could not see them until they reached their hand into the tubes where the food was located. From a distance, both tubes appeared to block the human's view but one was actually see-through. Before the test phase, subjects were shown peanuts behind each surface so that they could experience the occlusive properties of the tubes. In the test phase, they avoided the see-through tube, even though from afar both looked identical. These results suggest that chimpanzees were able to infer what their competitor could see based on their own self-experience with these novel objects.

1.1.3 Attributing Knowledge, Ignorance, and False Belief to Others

In addition to reasoning about what others can perceive in the present, experimental evidence suggests that chimpanzees are capable of understanding what others *have perceived* in the past. In a competitive paradigm, subordinate chimpanzees were more likely to approach hidden food when their competitor was uninformed or misinformed about its location than when he was knowledgeable (Hare et al., 2001). Similarly, chimpanzees were reluctant to approach food when their competitor had witnessed it being hidden but not if their competitor was switched out for a new dominant individual who had not seen the baiting process (Hare et al., 2001). In the "chimp chess" paradigm in which food was baited in several cups and two chimpanzees took turns searching for that food—each blind to the other's choices—subjects adjusted their behavior depending on whether their competitor was knowledgeable or ignorant of the food's location (Kaminski et al., 2008). When the subject chose second, she avoided food that her competitor knew about (inferring that the competitor would have already retrieved this item). MacLean and Hare (2012) presented chimpanzees with a series of experiments in which subjects witnessed an experimenter become aware of or remain ignorant to an object that was placed in her vicinity (by visually orienting to it or not). The experimenter later looked in the direction of the object and mimicked surprise. Subjects recognized when the experimenter already knew about the object, and in these cases were more likely to follow the experimenter's line of sight beyond the object in search of an alternate target of his attention. Together, these studies show that chimpanzees can discriminate between knowledgeable and ignorant individuals, they have different expectations of how these agents will behave, and they use this information both to outcompete ignorant groupmates, and potentially even to inform them of danger (Crockford et al., 2012).

To date, however, no experimental demonstration is consistent with chimpanzees explicitly attributing false beliefs to others (Call and Tomasello, 1999, Hare et al., 2001, Kaminski et al., 2008, Krachun et al., 2009, Krachun et al., 2010). A false belief exists when an individual believes something that is different from reality. Unlike knowledge or ignorance, understanding false beliefs requires representing not only whether or not the individual is aware of the true state of the world, but also specifically the way in which she construes the world to be different than it is. In humans, this ability appears to be tightly linked to language development (Lohmann and Tomasello, 2003, Milligan et al., 2007). In one study with chimpanzees, an experimenter baited food in one of two containers out of view of the subject but within view of a human competitor (Krachun et al., 2009). In the critical condition, the competitor then either turned around or left the room and the experimenter switched the locations of the cups. When the competitor returned she reached effortfully for the now incorrect location (a competitive gesture that chimpanzees have previously been shown to follow to find hidden food: e.g., Hare and Tomasello, 2004). While in one experiment chimpanzees tended to look at the baited container in false belief trials, they still followed the competitor's reaching gesture and selected the incorrect cup. Although their looking behavior may reflect some implicit understanding of belief, unlike human children, chimpanzees were unable to act on this understanding.

1.1.4 Recognizing Others' Goals and Intentions

A variety of experiments suggest that chimpanzees and other apes have some understanding of others' goals and intentions. Chimpanzees treat the actions of humans, but not mechanical claws, as goal-directed and anticipate the outcomes of these goal-directed actions (Myowa-Yamakoshi et al., 2012, Kano and Call, 2014b). They correctly identify an actor's goal based on the context of his actions (Buttelmann et al., 2012). Chimpanzees are also able to complete others' failed actions (Tomasello and Carpenter, 2005). They provide targeted help to conspecific and human partners based on a specific understanding of their partner's needs (Warneken and Tomasello, 2006, Warneken et al., 2007, Yamamoto et al., 2009, Melis et al., 2011, Yamamoto et al., 2012, Melis and Tomasello, 2013, Bullinger et al., 2014). Chimpanzees also discriminate intentional from accidental actions (Call and Tomasello, 1998, Tomasello and Carpenter, 2005) and respond differently to an experimenter when he is unwilling to help them versus unable to do so, even though the experimenter performs very similar actions in each case (Call et al., 2004). Taken together, these studies suggest that chimpanzees have a robust understanding of the goals and intentions that govern others' actions.

Given the cooperative nature of human society, humans are also known to exhibit shared intentionality (Tomasello et al., 2005). Shared intentionality describes our ability to hold, and attribute to others, shared goals and intentions that structure collaborative or joint activities. For example, when performing a collaborative activity, such as building a house, all collaborators are aware of their shared goal (i.e., to complete the house) as well as each other's complementary roles required to accomplish the task. Although chimpanzees engaged in triadic turn-taking activities with humans and even elicited further interaction after the activities were terminated, it remains unknown if these activities are supported by an understanding of shared intentions (Warneken et al., 2006, MacLean and Hare, 2013). Some evidence suggest that chimpanzees are aware of their partners' role in collaborative activities and even the means that are necessary for the partner to accomplish that role, suggesting that differences in motivation rather than cognition may underlie species differences in shared intentionality (Melis et al., 2006b, Melis and Tomasello, 2013, Bullinger et al., 2014).

1.1.5 Summary

Chimpanzees have at least a basic understanding of others' perspectives: they know *whether* or not an agent can see or hear an object. They also know whether or not an agent is knowledgeable or ignorant about that object. And they can reason about the goals and intentions that underlie agents' actions. If we were to consult these data alone to make inferences about the cognitive phenotype of the last common ancestor of humans and chimpanzees, we would conclude that it possessed some aspects of a human-like theory of mind but not others. It knew, for example, whether or not an agent could see an object, but not *how* the object looked from the agent's perspective. It knew whether or not an agent was aware of or ignorant about an object, but not how the agent misconstrued attributes of the object when she held a false belief about it. And it understood the goals that guide an agent's actions, but may not have possessed the right cooperative motivations to exhibit shared intentionality. But this evolutionary inference is heavily dependent on either assuming bonobo theory of mind is highly similar to chimpanzees or that the last common ancestor is more chimpanzee-like cognitively.

1.2 Bonobo Cognitive Evolution

The singular focus on chimpanzees as a model for human cognitive evolution is problematic because, like humans, chimpanzees too have experienced 5 to 7 million years of evolution since our lineages diverged and therefore are also different from our last common ancestor. Likewise, bonobos and chimpanzees have experienced several million years of independent evolution. Thus, although the general assumption has often been that bonobos will perform similarly to chimpanzees on most cognitive tasks, this is not always the case (Herrmann et al., 2010). Only through studying the three species can we confidently infer which aspects of our cognition are evolutionarily ancient, and shared with our closest relatives, and which are unique to each species. Perhaps even more importantly, there is much reason to believe that bonobos will offer some very different clues than chimpanzees about human evolutionary history (Hare, 2011). Below, we outline a framework that guides our analysis of existing comparative studies and our suggested directions for future work. We describe the self-domestication and empathizing-systemizing hypotheses, which together provide testable ultimate and proximate explanations for differences in chimpanzee and bonobo social cognition (Figure 1).

1.2.1 The Self-Domestication Hypothesis

The self-domestication hypothesis is based on the observation that domestication—which frequently involves artificial selection against aggression—consistently produces a suite of changes in morphology, physiology, behavior, and cognition relative to a species' wild counterpart (Hare et al., 2012). Importantly, in many cases of domestication, including that of dogs from wolves, a phase of self-domestication has been proposed to have preceded domestication by artificial selection. During self-domestication of dogs, natural selection likely favored individuals who were more socially tolerant and less fearful of humans, as these individuals could live in closer proximity to humans and exploit new resources such as human refuse. In this way, selection against aggression is thought to have exerted pressures on canine evolution through natural selection even before the intervention of artificial selection (Hare and Woods, 2013).

Relative to chimpanzees, bonobos exhibit many of the characteristic changes associated with the domestication syndrome, and are hypothesized to have been self-domesticated via natural selection for prosociality and against aggression (Hare et al., 2012). Bonobos exhibit higher levels of tolerance while co-feeding than chimpanzees and consequently are more flexible cooperators in instrumental tasks (Hare et al., 2007). Whereas chimpanzees are highly xenophobic, bonobos are known to be prosocial even with strangers (Hare and Kwetuenda, 2010, Tan and Hare, 2013, Wilson et al., 2014, Williams et al., 2004, Goodall, 1986). Researchers have also documented species differences in apes' neuroanatomy and hormonal profiles and a delayed pattern of social development in bonobos relative to chimpanzees, which likely constitute the proximate underpinnings of bonobos' greater social tolerance and prosocial flexibility (Wobber et al., 2010b, Wobber et al., 2010c, Rilling et al., 2012, Stimpson et al., 2015). Importantly, although both species live in similar large multi-male, multi-female, promiscuous, fission-fusion societies, bonobos are believed to experience more relaxed feeding competition than chimpanzees (Wrangham, 1993). Reduced competition may have allowed selection to favor increased social tolerance and ultimately produce the other correlated by-products of the self-domestication process.

From the self-domestication hypothesis, we can derive several predictions about the social cognitive abilities of chimpanzees and bonobos. First, the self-domestication hypothesis posits heterochonic shifts—changes in the timing or pattern of development—as a major proximate mechanism underlying species differences. Specifically, domesticates show juvenilization, or retention of paedomorphic traits into adulthood that in non-domesticates are only present in infants and juveniles. They also often exhibit delayed patterns of development. Since relaxed feeding competition is believed to have facilitated selection against aggression in bonobos, delays are expected to impact behaviors related to feeding competition. Such delays have been shown relative to chimpanzees in the ontogeny of social intolerance, social inhibition, and spatial memory (Wobber et al., 2010c, Rosati and Hare, 2012).

Therefore, the chief prediction that we can draw from the self-domestication hypothesis is that there will be a relationship between delayed patterns of development and theory of mind abilities in bonobos. However, there are several competing hypotheses about the specific influence that delayed development will have on adult theory of mind. Additionally, it is not clear whether all theory of mind skills will be impacted in the same way.

One possibility is that social cognitive traits themselves will be delayed. Nevertheless, despite the delay, bonobos may eventually demonstrate comparable performance to chimpanzees on theory of mind tasks. Indeed, despite bonobos' very slow maturation of social inhibition throughout the juvenile period, by adulthood bonobos and chimpanzees perform equivalently on some social inhibition tasks (Wobber et al., 2010c). Alternatively, developmental delay may result in bonobos failing to show comparable social cognitive flexibility to chimpanzees. A similar outcome has been documented in other domains of social and cognitive development: as juveniles both bonobos and chimpanzees exhibit high levels of social tolerance and low performance on spatial memory tasks; however, whereas chimpanzees become less socially tolerant and better at memory tasks with age, bonobos maintain juvenile levels of both traits into adulthood (Wobber et al., 2010c, Rosati and Hare, 2012).

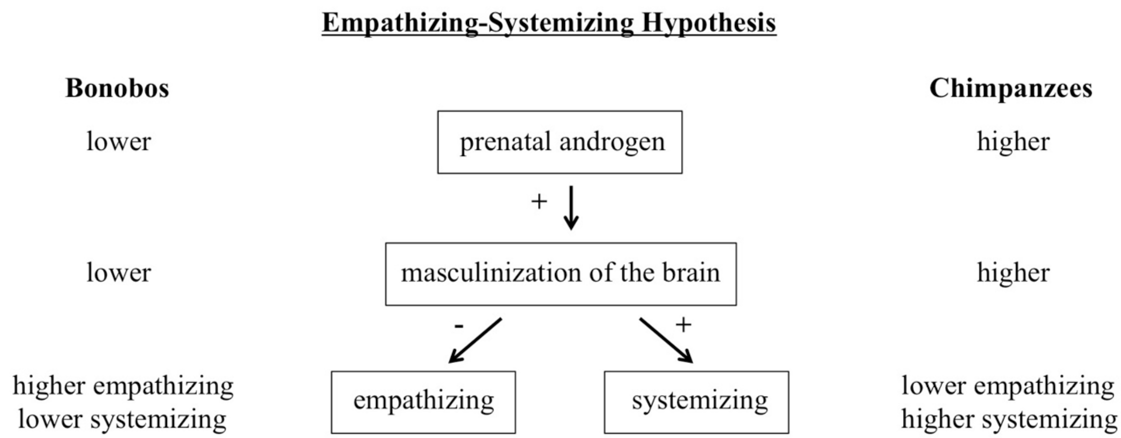
Moreover, since both inhibitory control and memory play key ancillary roles in theory of mind, it is conceivable that a delay in the emergence of these traits may constrain the development of theory of mind in bonobos.

It is also possible that delayed development may result in a longer period of developmental plasticity and permit bonobos to develop skills that chimpanzees do not. Indeed, humans have evolved an extended period of juvenility and adolescence that is associated with greater cognitive flexibility (Kaplan et al., 2000). Consistent with this hypothesis, there is evidence that bonobos reach certain developmental milestones much later than chimpanzees. For example, chimpanzees experience changes in TT3 thyroid hormone levels at the end of their somatic growth, and bonobos exhibit juvenile levels of these hormones ten years longer than chimpanzees do (Behringer et al., 2014).

A final alternative is that social cognition may not have been directly shaped by self-domestication; however, traits that were shaped by selection against aggression may still influence the ontogeny of social cognition. For example, retention of juvenile levels of social tolerance into adulthood (Wobber et al., 2010c) may provide more opportunities for bonobos to learn about the behavior and mental states of their conspecifics, ultimately resulting in more flexible theory of mind skills in bonobos. Research in human children has already linked temperament to theory of mind, showing in particular that children who are less aggressive, more shy, and more observant at age 3 perform better on false belief tasks at age 5 (Wellman et al., 2011). Wellman et al. (2011) hypothesize that more socially tolerant children experience more opportunities to interact with others and learn about their mental states. Further evidence that self-domestication may indirectly lead to greater theory of mind abilities has been provided in other taxa, where selection against aggression has resulted in greater sensitivity to social cues (Hare et al., 2005). Paedomorphic levels of social tolerance have previously been associated with more flexible prosocial behavior in bonobos (Hare et al., 2007). It is therefore possible that bonobos will exhibit more advanced theory of mind skills in general, or specifically in those abilities that are involved in cooperation—such as empathy, understanding of cooperative intentions, and shared intentionality. It is even possible that self-domestication's selection for prosociality has produced changes in cooperative theory of mind skills in the absence of developmental change.

1.2.2 The Empathizing-Systemizing Hypothesis

A potentially complementary hypothesis—this one relevant to the proximate origins of chimpanzee and bonobo species differences—comes from the literature on autism spectrum disorders. This hypothesis, the empathizing-systemizing hypothesis, links degree of masculinization of the brain during prenatal development to differences in adult theory of mind skills. Variation in masculinization has been documented between chimpanzees and bonobos, perhaps resulting from self-domestication. According to the empathizing-systemizing hypothesis, this variation may cause pronounced differences in the theory of mind abilities of the two species (Figure 1).



Bonobos	Predictions	Chimpanzees
higher	Social Tolerance	lower
higher	Theory of Mind Skills	lower
lower	Casual Reasoning and Tool Use	higher
lower	Signs of Masculinization	higher

Figure 1: Diagram and predictions of the Empathizing-Systemizing Hypothesis

The empathizing-systemizing hypothesis was originally developed to provide an explanation for why people with autism spectrum disorders are characterized by deficits in empathizing and average or above average abilities in systemizing (Baron-Cohen, 2009). Empathizing in this context refers to the ability to understand others' mental states and to respond appropriately to their emotions. Systemizing refers to a propensity for creating and analyzing predictable, rule-governed systems. Men tend to exhibit higher levels of systemizing and lower levels of empathizing than women, and the even more extreme pattern of high systemizing and low empathizing seen in autism spectrum disorder is thought to result from hyper-masculinization of the brain during prenatal development (Baron-Cohen, 2009).

Bonobos have more human-like 2D:4D ratios than chimpanzees, suggesting lower prenatal androgen exposure and less masculinization of the brain during development (McIntyre et al., 2009). If nonhuman apes adhere to the pattern of individual differences seen in humans, bonobos should exhibit greater skill in empathizing but less skill in systemizing than chimpanzees. Neurological evidence further supports this claim: relative to chimpanzees, bonobos have more gray matter in the right dorsal amygdala and the right anterior insula—areas that function to perceive distress (Rilling et al., 2012). They also have stronger connections between the amygdala and the ventral anterior cingulate cortex, a pathway that contributes to aversion to others' harm, as well as greater serotonergic innervation of the amygdala than chimpanzees (Rilling et al., 2012, Stimpson et al., 2015). Relative to other apes, humans and bonobos also have a larger and more diversified posterior orbitofrontal cortex, which has been implicated in emotional responsiveness to social stimuli (Semendeferi et al., 1998). Thus, both physiological and neurological evidence support the empathizing-systemizing hypothesis and suggest that bonobos may be more sensitive to others' mental states than chimpanzees.

Recent human evolution has been characterized by a reduction in androgen activity, as reflected in the feminization of craniofacial morphology (Cieri et al., 2014). This shift is believed to partially explain our unusual levels of within-group social tolerance (Cieri et al., 2014). It may therefore be that the same forces involved in bonobo evolution have shaped the cognitive and behavioral phenotype of our species. If the predictions of the self-domestication and empathizing-systemizing hypotheses are supported in bonobos and chimpanzees, there is reason to believe that humans' unique social cognitive abilities also evolved, at least in part, through a process of feminization in response to selection for prosociality and against aggression.

1.3 Theory of Mind in Bonobos

The self-domestication hypothesis predicts developmental delays that may impact the emergence of bonobos' theory of mind abilities. Consistent with this prediction MacLean and Hare (2012) found that chimpanzees succeeded in three related perspective-taking tasks whereas bonobos succeeded in only one. MacLean and Hare (2012) suggested that this differential performance might reflect a developmental delay in bonobos relative to chimpanzees (Wobber et al., 2010c). However, this potential species difference must be interpreted with extreme caution for several reasons. First, the bonobos tested in the task were, on average, three years younger than the chimpanzees and roughly half were non-adults. Second, bonobos did not respond to certain aspects of the stimuli in a control condition, making it unclear whether the differential performance reflects an actual species difference or simply methods that were more ecologically relevant for chimpanzees. Beyond this study, which was not directly aimed at exploring developmental differences in chimpanzee and bonobo social cognition, there is no published work that directly addresses this question. Wobber et al. (2014) did conduct a battery of cognitive tests to investigate differences in early cognitive development between humans and the other apes. Unfortunately, although the authors were able to show that social cognition emerges earlier and develops more rapidly in humans than in chimpanzees and bonobos, they did not report analyses of differences in developmental trends between the nonhuman apes.

The principal prediction of the empathizing-systemizing hypothesis is that bonobos will show more flexibility than chimpanzees on theory of mind tasks but not systemizing tasks. Herrmann et al. (2010) administered a cognitive test battery of 16 tasks to a large sample of bonobos and chimpanzees. As predicted by the empathizing-systemizing hypothesis, the results showed that chimpanzees are more skilled than bonobos' on tasks requiring understanding of physical causality and tool use (traits associated with systemizing) whereas bonobos performed more skillfully than chimpanzees on tasks involving social causality and theory of mind (traits related to empathizing). However, a wider range of tasks than presented in Herrmann et al. (2010) is needed to more fully characterize the differences in theory of mind abilities between chimpanzees and bonobos.

For example, bonobos consistently appear to be more sensitive than chimpanzees to certain types of social information. They gaze follow more reliably and more flexibly than chimpanzees (Herrmann et al., 2010), including in response to allospecific models (Kano and Call, 2014a). They also make more eye contact with conspecifics than chimpanzees (Kano et al., 2015), which in humans is often associated with greater sensitivity to others' mental states (e.g., Phillips et al., 1992) and in other species appears to be a product of domestication (Miklosi et al., 2003, Gácsi et al., 2009, Hernadi et al., 2012).

However, in most other theory of mind skills for which both species have been tested, their performance has been comparable (except MacLean and Hare, 2012, reviewed earlier). For example, in basic understanding of attention and agency, it appears that there are no differences between species. Both species, as well as the other great apes, interpret others' actions as goal-directed (Buttelmann et al., 2012, Kano and Call, 2014b). They also follow gaze geometrically and check back with the actor when they cannot identify the target of her gaze (Povinelli and Eddy, 1996, Call et al., 1998, Tomasello et al., 1999, Brauer et al., 2005, Okamoto-Barth et al., 2007). In addition, all great apes will walk to the front of an agent before attempting to communicate with her (Liebal et al., 2004), and use more gestural communication when the recipient of their gestures is oriented toward them than away (Kaminski et al., 2004, Hostetter et al., 2007, Tempelmann et al., 2011).

In object choice tasks where subjects must follow a human's gesture to locate hidden food, bonobos have always performed similarly to chimpanzees (Brauer et al., 2006, Herrmann and Tomasello, 2006, Herrmann et al., 2010, MacLean and Hare, 2015). The one study that tested bonobos on their understanding of others' beliefs also did not find positive evidence in either bonobos or chimpanzees (Krachun et al., 2009).

In addition to controlled cognitive experiments, several studies have investigated in each species behaviors that may be related to empathy. Though no studies have quantitatively compared the two species in these behaviors, bonobos and chimpanzees have both exhibited contagious yawning and consolation behavior (Fraser et al., 2008, Romero et al., 2010, Campbell and de Waal, 2011, Demuru and Palagi, 2012, Clay and de Waal, 2013, Palagi and Norscia, 2013, Palagi et al., 2014). Contagious yawning is believed to be a rudimentary form of emotional contagion that is linked to empathy because it is exhibited most frequently in response to bonded partners or close kin. Consolation occurs when, in the wake of an agonistic interaction, a bystander responds to the distress of the victim by providing affiliative contact. Both chimpanzees and bonobos direct this post-conflict affiliation toward their bond partners. These behavioral measures have been argued to represent evidence for a rudimentary form of empathy (Preston and de Waal, 2002).

Taken together, the existing qualitative and quantitative work that allows for comparisons between bonobo and chimpanzee theory of mind abilities suggests comparable skill in both species. The exceptions is that bonobos have shown greater sensitivity than chimpanzees to eye contact and gaze. Eye contact and gaze following are related to empathy in humans (e.g., Dadds et al., 2012), and are used for gathering social information that informs inferences about others' psychological states. Meanwhile, chimpanzees exhibit more skill in tasks relating to tool use and causal reasoning. These data provide preliminary support for the empathizing-systemizing hypothesis that chimpanzees are the systemizers and bonobos the empathizers of the *Pan*-clade. These findings are also consistent with the self-domestication hypothesis. However, developmental comparisons thus far suggest, for the most part, that if self-domestication has shaped bonobo social cognitive abilities any developmental delay that bonobos experience may be overcome by adulthood through the developmental plasticity that such a delay affords. Future work will be essential in further testing the predictions of these hypotheses.

1.4 Moving Forward

Theory of mind abilities are among the defining features of our species, yet there remain many unanswered questions about their evolutionary origins. Comparative research involving humans' two closest relatives, chimpanzees and bonobos, provides the most powerful tool for understanding the evolution of these skills in the lineage leading to humans. While work in chimpanzees has demonstrated that they possess many, but not all, of the theory of mind skills that are exhibited by humans, many more gaps exist in our knowledge of these abilities in bonobos (see Table 1). These gaps hinder inferences about the cognitive phenotype of the last common ancestor of chimpanzees, bonobos, and humans as well as the selective forces that shaped the cognitive abilities of each species.

Table 1: Theory of mind skills in chimpanzees and bonobos

Understanding of others'	Chimpanzees	Bonobos
Gaze direction[1]	✓	✓
Attention[2]	✓	✓
Seeing[3]	✓	?
Hearing[4]	✓ •?	?
Knowledge and Ignorance[5]	✓	✓ ?
False Beliefs (Implicitly)[6]	✓ ?	✓ ?
False Beliefs (Explicitly)[7]	✖	✖
Goals[8]	✓	✓
Intentions[9]	✓	✓ ?
Shared Goals[10]	?	?

1: (Brauer et al., 2005, Call et al., 1998, Okamoto-Barth et al., 2007, Povinelli and Eddy, 1996, Tomasello et al., 1999); **2:** (Hostetter et al., 2007, Kaminski et al., 2004, Leavens et al., 2004, Liebal et al., 2004, Tempelmann et al., 2011); **3:** (Hare et al., 2000, Hare et al., 2006, Karg et al., 2015a, Karg et al., 2015b, Melis et al., 2006a); **4:** (Brauer et al., 2008, Melis et al., 2006a); **5:** (Crockford et al., 2012, Hare et al., 2001, Kaminski et al., 2008, MacLean and Hare, 2012); **6:** (Krupenye et al., in preparation-a); **7:** (Call and Tomasello, 1999, Hare et al., 2001, Kaminski et al., 2008, Krachun et al., 2009, Krachun et al., 2010); **8:** (Bullinger et al., 2014, Buttelmann et al., 2012, Kano and Call, 2014b, Krachun et al., 2010, Melis and Tomasello, 2013, Melis et al., 2011, Myowa-Yamakoshi et al., 2012, Tomasello and Carpenter, 2005, Warneken and Tomasello, 2006, Warneken et al., 2007, Yamamoto et al., 2009, Yamamoto et al., 2012); **9:** (Call et al., 2004, Call and Tomasello, 1998, Krupenye and Hare, in preparation-b, Tomasello and Carpenter, 2005); **10:** (Bullinger et al., 2014, MacLean and Hare, 2013, Melis et al., 2006b, Melis and Tomasello, 2013, Warneken et al., 2006)

We have outlined two hypotheses—the self-domestication hypothesis and the empathizing-systemizing hypothesis—that together may explain the evolutionary origins of differential theory of mind abilities in bonobos, chimpanzees, and humans. The self-domestication hypothesis suggests that selection against aggression and for prosociality may have resulted in heterochronic changes that impact the emergence of theory of mind skills. These same selective pressures may also be responsible for less masculinization of the brain during prenatal development in bonobos than chimpanzees. The empathizing-systemizing hypothesis, in turn, suggests that these differences in masculinization may be responsible for greater flexibility in empathizing (i.e., theory of mind abilities) in bonobos and in systemizing (i.e., physical causal understanding) in chimpanzees.

There are several key areas that should be explored in order to powerfully test these hypotheses and provide the most direct insights into the evolutionary history of humans and their closest relatives. First, if the social cognitive abilities of these species have been shaped by a self-domestication process, delayed development relative to chimpanzees should in some way impact the theory of mind skills of bonobos. Therefore, a critical test of this hypothesis requires a comparative developmental investigation of chimpanzee and bonobo theory of mind. Second, the empathizing-systemizing hypothesis predicts that bonobos will exhibit greater competence than chimpanzees in employment of some, if not all, theory of mind abilities. Thus, future work must address the existing gaps in our understanding of theory of mind in both species.

To address these gaps, several concurrent strategies are necessary. On the one hand, it will be important to replicate with bonobos theory of mind studies that have been completed with chimpanzees. For example, almost no work has investigated their perspective-taking skills, including their understanding of what others perceive and what others know. In other areas, such as understanding of others' goals and intentions, bonobos have only been tested on a minority of paradigms. It will also be critical to develop new paradigms that maximize ecological relevance for bonobos. Indeed, the bonobo-chimpanzee comparison highlights some key challenges in comparative psychology. Despite being sister species, bonobos and chimpanzees exhibit significant differences in behavior, physiology, and neurobiology. Consequently, previous experiments that have been designed to study social cognition in chimpanzees may not hold the same ecological relevance for bonobos, and poor performance by bonobos in such tasks could reflect species differences in experimental motivation more than cognitive ability. Just as efforts to study animal cognition by directly adapting experimental paradigms from developmental psychology have not always been successful at accurately characterizing nonhuman cognition, relying solely on chimpanzee-specific paradigms may introduce a source of bias when testing bonobos since those paradigms have been tailored to chimpanzees for the past two decades. Thus, a combination of existing paradigms and new approaches adapted for the unique characteristics of bonobos will be essential to fully capture the nuanced cognitive and motivational differences between the two species.

Since motivation and temperament interact with theory of mind abilities, many of the most successful studies of chimpanzee theory of mind have capitalized on competitive settings that maximize chimpanzees' motivation to demonstrate their cognitive skill (Hare et al., 2000, Hare et al., 2001). However, competitive contexts may not motivate bonobos in the same way that they do chimpanzees. Research has shown that whereas chimpanzees experience a spike in testosterone preceding competition over food, bonobos experience a spike in cortisol (Wobber et al., 2010b). These differential responses indicate that while chimpanzees are emboldened in anticipation of conflict, bonobos become stressed and are probably motivated to avoid, rather than engage in, competition. In contrast, bonobos have been shown to perform a handful of cooperative behaviors more flexibly than chimpanzees, owing to their heightened social tolerance (Hare et al., 2007, Hare and Kwetuenda, 2010, Tan and Hare, 2013). Therefore, it may be in cooperative contexts that bonobos are most motivated to demonstrate their cognitive skill. Future work should take advantage of such contexts to investigate social cognition in bonobos. For example, studies of targeted helping and sharing could shed light on bonobos' understanding of other's goals and intentions. Krupenye et al. (in preparation-b) have found that bonobos actively transfer food, even doing so proactively (without request by the recipient)—prosocial behaviors not exhibited by chimpanzees—although, unlike chimpanzees, bonobos do not transfer tools or other objects. These findings suggest that while bonobos and chimpanzees have a similar understanding of others' needs, motivational differences impact their tendency to demonstrate that understanding.

Human infants discriminate agents based on their prosocial and antisocial actions and intentions (Hamlin et al., 2007, Hamlin et al., 2010b, Hamlin and Wynn, 2011, Hamlin, 2013), and these abilities may also be particularly pronounced in bonobos. Indeed, Krupenye and Hare (in preparation-a; in preparation-b) found that bonobos are able to discriminate between unfamiliar social partners based on both their actions and intentions. Bonobos either witnessed interactions in which one unfamiliar individual behaved prosocially and another antisocially toward a third party, or they were directly subjected to this prosocial and antisocial behavior. They were then allowed to choose between (or to beg for food from) the prosocial or antisocial individual. When bonobos were evaluating humans and animated agents based on those individuals' interactions with third parties, they preferred antisocial individuals over prosocial ones. A follow-up study suggested that this pattern might be related to bonobos' preference for dominant over subordinate individuals, since dominance is often clearly conveyed by antisocial behavior (Krupenye and Hare, in preparation-a). However, when evaluating others based on direct interactions between the bonobo and those individuals, they reliably preferred prosocial over antisocial individuals and, surprisingly, even privileged intentions over outcomes in their evaluations: in the most extreme study, they preferred an individual who attempted but failed to give them food over one who teased them but accidentally gave them food (Krupenye and Hare, in preparation-b). Future research should continue to examine social cognition in cooperative settings, including perspective-taking abilities, cognitive and affective empathy, and shared intentionality.

Finally, many areas of theory of mind are understudied in general. For example, to date no study has provided positive evidence of false belief understanding in nonhumans, but researchers have not attempted to assess an implicit understanding of false belief using the kinds of spontaneous anticipatory looking or violation of expectation measures that have proven fruitful in human infants (e.g., Onishi and Bailargeon, 2005, Southgate et al., 2007). Recently, using an anticipatory looking paradigm, Krupenye et al. (in preparation-a) discovered that—just like human infants—bonobos, chimpanzees, and orangutans predicted that agents would search for a hidden object where they last saw it, even if the object had been moved while the agent wasn't looking. While further work is necessary to confirm the mechanism underlying these results and identify its limits, Krupenye et al. (in preparation-a) data provide the first evidence that great apes may have at least an implicit understanding of others' false beliefs.

Future research on social cognition in bonobos and chimpanzees promises to yield exciting developments. Examining these traits will clarify whether social cognition is largely similar between the two species—that is, whether both species have a *Pan*-typical theory of mind. Alternatively, future work may demonstrate that the species' independent evolutionary histories have produced key differences in their social cognitive abilities. In many cases, this work will permit more accurate reconstructions of the cognitive phenotype of the last common ancestor by clarifying which social cognitive abilities are shared by bonobos, chimpanzees, and humans. Additionally, by identifying cognitive differences between the three species and elucidating the selective forces that shaped cognitive evolution in our closest relatives, we will gain critical insights into the evolution of social cognition in our own species.

2 Bonobos actively share food but not their toys or tools

Prosociality, or voluntary behavior that benefits others (Batson and Powell, 2003, Eisenberg et al., 2006), is extraordinary in humans for its ubiquity, intensity and flexibility. Human prosociality is among the key traits that make our species unique (Hill et al., 2009). However, other animals exhibit some human-like forms of prosocial behavior (Cronin, 2012). Careful comparisons are therefore required to specify exactly what distinguishes human from nonhuman prosociality (Hare and Tan, 2011, Silk and House, 2011).

Humans may have a higher intrinsic motivation to benefit others than nonhuman primates (e.g., Burkart et al., 2009). To test this *strong prosociality hypothesis* experimentally, researchers have focused their investigations primarily on food-related contexts, interpreting active sharing (i.e., transfer from the possession of the donor to the recipient) of food as evidence of strong prosocial motivations (Jaeggi et al., 2010a, Burkart et al., 2014). However, prosociality can manifest in numerous contexts that involve food as well as non-food currencies (Warneken and Tomasello, 2009). Accordingly, the *versatile prosociality hypothesis* argues that it is the extreme flexibility of human prosociality—made possible by both strong prosocial motivations and socio-cognitive capacities—that makes it unique (Warneken, 2015). This hypothesis predicts that only humans will exhibit active sharing across food and non-food contexts.

Current evidence from chimpanzees is consistent with both hypotheses. Chimpanzee (*Pan troglodytes*) prosociality is comparable to that of human children in some contexts, but constrained in others—especially in food-related contexts (Stevens, 2004, Warneken and Tomasello, 2009). Chimpanzees will remove a physical obstacle preventing a conspecific from retrieving out-of-reach items (Warneken et al., 2007, Melis et al., 2011). They also actively transfer *objects already in their possession* in response to requests from both humans and conspecifics (Warneken and Tomasello, 2006, Warneken et al., 2007, Yamamoto et al., 2009). This active transfer is motivated to meet the goal of the recipient (Yamamoto et al., 2012). However, the transfer of *food in chimpanzees' possession* primarily occurs passively or in response to harassment (Gilby, 2006, Jaeggi et al., 2010b, although see mixed results in token-trading tasks: Horner et al., 2011, Amici et al., 2014). In one experiment when chimpanzee food possessors were separated from conspecifics by a physical partition, active transfer of food did not occur (Stevens, 2004, Melis et al., 2006b). Xenophobia toward conspecifics in chimpanzees (e.g., Wilson et al., 2014, Williams et al., 2004, Goodall, 1986) also likely prevents any kind of prosociality toward strangers. Relative to humans, chimpanzees appear to help less in quantity and across contexts—particularly when sharing requires actively giving food already in their possession.

Bonobos (*Pan paniscus*) are more tolerant than chimpanzees (Hare et al., 2012, but see Jaeggi et al., 2010b). They prefer to eat with a conspecific rather than monopolize high quality food. When given the choice of eating alone or releasing a conspecific to eat together, bonobos share their food voluntarily (Hare and Kwetuenda, 2010). This sharing is even xenophilic. They prefer to share with a stranger over a groupmate when sharing also results in a potential physical interaction (Tan and Hare, 2013). Remarkably no aggression is observed in these sharing episodes. This level of dyadic tolerance allows bonobos to spontaneously outperform chimpanzees in a novel instrumental cooperative task that requires sharing monopolizable food (Hare et al., 2007). Similar to chimpanzees, bonobos will also help a conspecific obtain out-of-reach food that they themselves cannot obtain. They will even help an unfamiliar conspecific in this same context (Tan and Hare, 2013, Tan et al., submitted).

The limits of bonobo food sharing are also becoming apparent. Bonobos do not share high quality food (i.e. fruit) *in their possession* when experiments control for harassment. Bonobos also do not always share with groupmates (Hare and Kwetuenda, 2010, Bullinger et al., 2013, Tan and Hare, 2013) and in group contexts may show less sharing than chimpanzees (Jaeggi et al., 2010b). Anecdotally bonobos also seem unwilling to retrieve objects in their enclosure for a caretaker in the way chimpanzees do (Hare, personal observation; see also Liebal et al., 2014). Additionally, they are no more tolerant than chimpanzees during dyadic interactions involving object play (MacLean and Hare, 2013). These observations raise the possibility that bonobos and chimpanzees differ in their prosocial tendencies due to different motivations for food and non-food items. Alternatively, if tested in a similar context to chimpanzees, bonobos may share objects as readily or even more readily than chimpanzees.

Here we investigate food and object sharing in bonobos to examine the flexibility of bonobo prosociality. Based on Warneken et al. (2007) we first tested whether bonobos would help a human by retrieving an out-of-reach object. In a second experiment, using a tool-use context like Yamamoto et al. (2012), we compared their active transfer of food (nuts) and non-food items (tools to crack nuts). Bonobos could either show a higher degree of flexibility than chimpanzees, sharing both food and non-food items, or different sharing tendencies than chimpanzees and a level of context-specificity not observed in humans.

2.1 Experiment 1

2.1.1 Materials and Methods

2.1.1.1 Subjects

We tested 18 semi-free ranging bonobos (*Pan paniscus*) living at Lola ya Bonobo sanctuary in Kinshasa, Democratic Republic of Congo (6M:12F, ages 3-15). These noninvasive behavioral studies were approved by Duke University (IACUC #A078-08-03) and adhered to the legal requirements of the Ministry of Research and the Ministry of Environment in D.R. Congo (permit MIN.RS/SG/004/2009). Animal husbandry and care practices complied with the policies of Lola ya Bonobo, as well as the Pan-African Sanctuary Alliance Primate Veterinary Healthcare Manual. Bonobos were born in the wild, orphaned by the bushmeat trade, and rescued by the sanctuary at an early age (~2-3 years old). Previous work indicates that sanctuary apes are psychologically healthy relative to other captive populations (Wobber and Hare, 2011). All bonobos were socially housed and free-ranged in large tracts of tropical forest during the day (30 hectares across groups). In the evening, they spent the night in indoor dormitories (12 m^2-160 m^2). Subjects voluntarily participated in the studies in their dormitories. They could leave any time during testing by sitting near the exit. After testing, they re-joined their social groups in the forest. Subjects were fed a variety of fruits, vegetables, and other species-appropriate foods four times daily, and were never food or water deprived for testing. Experiment 1 involved a between-subjects design with two conditions: reaching versus no-reaching, with nine subjects (matched roughly for age and sex) participating in each condition. Each subject participated in a single session on one day of testing.

2.1.1.2 Procedure

To facilitate a direct comparison with chimpanzees and human infants, we adapted our procedures directly from those used by Warneken et al. (2007). With the exception of one dependent offspring tested while his mother was in the room and one mother tested with a young infant, bonobos participated alone in a testing room (the subject room). The first experimenter (E1) was positioned in a demonstration area, facing the subject room and a long hallway. This hallway was adjacent to the subject room and separated from the demonstration area by a mesh door (see Figure 2A). All walls were constructed of mesh, allowing subjects visual access to events in the demonstration area and the hallway.

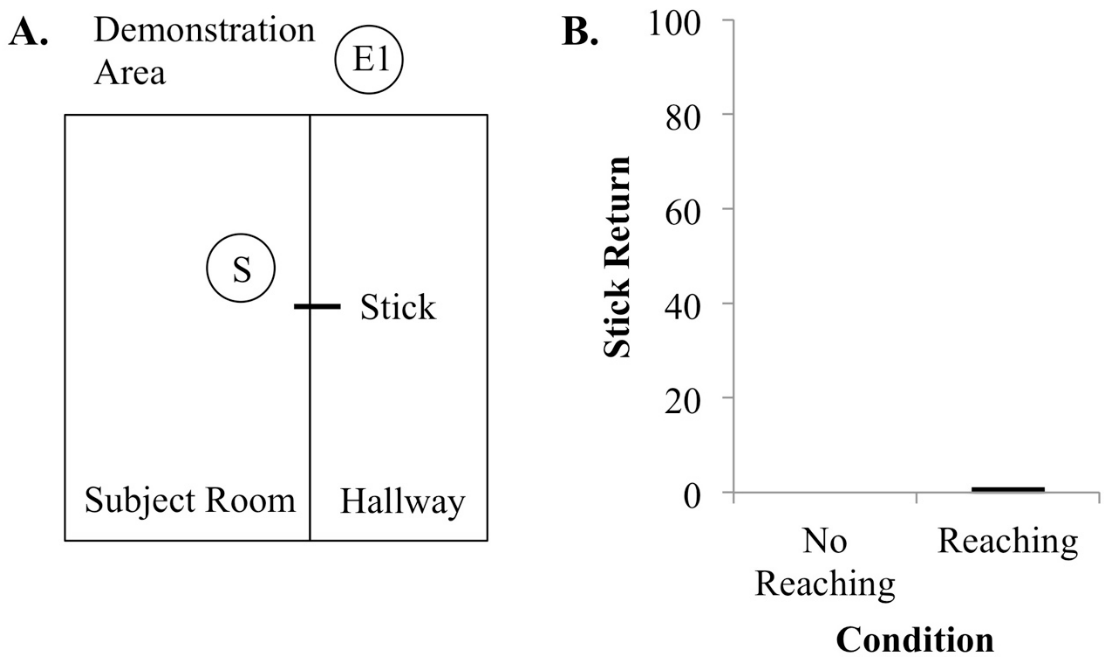


Figure 2: Testing setup (A) and results (B) of Chapter 2 Experiment 1.

Test trials began with E1 sitting on the floor playing with a stick. A second experimenter (E2) entered the demonstration area and approached E1. E2 grabbed a hold of the stick (with E1 still holding it as well) and the two struggled over it, pulling each other back and forth three times and making effortful vocalizations. On the third tug, E2 successfully stole the stick from E1. E2 entered the hallway and closed the door behind him. E1 followed E2, whimpering and grabbed onto the closed door. Inside the hallway, E2 placed a small piece of banana under the mesh between the subject room and the hallway to position the subject at the starting location. E2 kept walking through the hallway and placed the stick partially through the mesh about one meter from the banana. E2 then left the testing area by walking down the hallway.

We started timing when the subject took the banana. In the first 30 seconds, E1 leaned against the door, looked, and vocalized toward the stick. If, after 30 seconds the subject had not transferred the stick to E1, E1 became more communicative by calling the subject's name, banging the door and alternating his gaze between the subject and the stick. In the reaching condition, E1 provided an additional ostensive cue of desire: he reached effortfully toward the stick throughout the duration of the trial. In the no-reaching condition, this additional cue was absent: E1 kept his arms at his side or on the door. Each trial ended when the subject transferred the stick, or after one minute. Each subject participated in a 12-trial session with ten test trials as just described and two baseline trials—one at the beginning and one at the end. Baseline trials were identical to test trials except that E1 was never present. As in test trials, they began when the subject took the banana. These baseline trials served to assess subjects' baseline motivation to manipulate and transfer the stick. Whenever possible, E2 or the bonobo keepers retrieved any untransferred sticks from the subject before the next trial began.

2.1.1.3 Coding and analysis

Two cameras, one in the demonstration area and one in the hallway, recorded the subject's behavior. One coder blind to condition and hypotheses reviewed all trials and coded the following behaviors. The subject was marked as having *retrieved* the stick if she picked it up from its starting location. A *transfer* was coded if the subject handed the stick to E1, pushed it through the mesh into the demonstration area, or pushed it into the hallway within E1's reach. Finally, a *teasing* event was coded if the subject was in the corner near E1, facing him, and gesturing toward him with the stick in hand. A second coder blind to condition coded all trials for 28% of (randomly selected) subjects (N=5 of 18) with near-perfect reliability (retrieval: Cohen's kappa = 0.966; transfer: Cohen's kappa = 1; teasing: Cohen's kappa = 0.889) (Landis and Koch, 1977). All statistics were non-parametric and two-tailed. We used Mann-Whitney U tests to compare between conditions the proportion of trials in which each subject performed each type of behavior. We used related samples Wilcoxon signed rank tests to compare between baseline and test trials the proportion of trials in which subjects performed each type of behavior.

2.1.2 Results and discussion

In the reaching condition, only one bonobo transferred the stick on a single test trial (Figure 2B). In the no reaching condition, no bonobos ever transferred the stick on any test trials. One subject transferred the stick once on a baseline trial. Although bonobos almost never transferred the stick, they interacted with the stick in 33.33% of trials in the reaching condition and 43.33% of trials in the no reaching condition. There was no difference in the frequency of stick retrieval between conditions (baseline: $U = 37.5$, $N_1 = N_2 = 9$, p = NS; test: $U = 33.0$, $N_1 = N_2 = 9$, p=NS, Mann-Whitney U tests), or between the baseline and test trials (reaching condition: $z = -1.590$, $N = 9$, $T+ = 5$, ties = 3, p =NS; no reaching: $z = -0.849$, $N = 9$, $T+ = 3$, ties = 1, p=NS, related samples Wilcoxon signed rank tests). Six subjects (33% of the sample) retrieved the stick in the majority of test trials, but still did not transfer it. This suggests that subjects attended to and were interested in the stick, but were not motivated to return it. Anecdotally, subjects sometimes responded instead by teasing E1. Four subjects teased the experimenter on a total of 11 trials in the reaching condition and two subjects teased the experimenter on a total of two trials in the no reaching condition.

Bonobos' behavior in Experiment 1 contrasts the behavior of chimpanzees and human infants in the same paradigm (Warneken et al., 2007). Whereas chimpanzees and human infants retrieved the objects for the experimenter in about half of reaching trials, bonobos did so in only 1.1% of these trials. This finding suggests that bonobos do not exhibit the same motivation to share objects as chimpanzees. Alternatively, it's possible that the paradigm was in some way less ecologically relevant for bonobos. One possibility is that bonobos are less motivated than chimpanzees to share with humans. Although there is some evidence that bonobos are more cautious than chimpanzees around unfamiliar humans (Herrmann et al., 2011), most subjects had interacted with E1 during this and a previous field trip. Moreover, both bonobos and chimpanzees readily engage with humans in triadic interactions involving objects (MacLean and Hare, 2013). In one study, only male bonobos responded to affiliative interactions with humans (Schroepfer-Walker et al., 2015). However, chimpanzees exhibited the same sex difference in that study, and in the present study lack of helping was not restricted to one sex.

Another possibility is that subjects did not help because they failed to understand E1's goal. However, other studies have shown that bonobos, like chimpanzees, interpret reaching behavior as goal-directed and, in a battery of cognitive tasks, bonobos performed better than chimpanzees on those related to theory of mind (Herrmann et al., 2010, Kano and Call, 2014b). Moreover, bonobos sometimes responded to E1 by teasing and did so more in the reaching condition than the no-reaching condition, further suggesting that they were aware of E1's desire for the object.

Warneken et al. (2007) included in the original study conditions in which subjects were rewarded for retrieving the stick. Although the presence of a reward did not increase helping by chimpanzees or human infants, it is possible that bonobos would have been more motivated to help in order to receive a reward. Critically, even such a finding would suggest a motivational difference for object sharing between chimpanzees and bonobos, since chimpanzees did not need to be rewarded in order to demonstrate high rates of helping. A final possibility is that bonobos were more motivated to engage in solo or joint object play than they were to help. Bonobos retrieved the stick on at least a third of trials and sometimes teased the experimenter, perhaps to engage in play. However, MacLean and Hare (2013) found in a series of studies that bonobos and chimpanzees generally engaged equally in object play with humans, although if anything chimpanzees were more playful than bonobos.

2.2 Experiment 2

To confirm our finding that bonobos are less motivated to share objects than chimpanzees and control for alternative explanations, we performed a second experiment. In Experiment 2, subjects were partnered in adjacent rooms with conspecifics rather than humans. We tested bonobos in a tool-use context since this is another context in which chimpanzees reliably share objects (Yamamoto et al., 2009, Yamamoto et al., 2012, Melis and Tomasello, 2013). One subject was equipped with several rocks that could be used to crack nuts, while her partner was provisioned with several nuts. The possession of multiple items of each currency meant that subjects could keep at least one for themselves for use as a tool or toy while still having more to share. Critically, this task also allowed us to compare bonobos' proclivity for sharing food and non-food items.

2.2.1 Materials and Methods

2.2.1.1 Subjects

Twelve bonobos (2M:10F; aged 5-15 years) participated in Experiment 2, none of whom were subjects in Experiment 1. We selected subjects who were frequently seen cracking nuts in their enclosure to ensure that they were capable of cracking nuts and that they valued the nuts and were motivated to consume them. Subjects had to pass two pretests (see Procedure) and were then tested in pairs (N = 10). Within a pair each bonobo was assigned to be either a 'nut-owner' or a 'rock-owner'. Most subjects (N = 8) played both roles in two different pairings (i.e., each of these subjects was a nut-owner in one pairing and a rock-owner in another pairing). In this way we maximized the possible number of pairs and controlled for direct reciprocity within the experiment. The pairs were not created based on any other attributes of our subjects (e.g. sex, age, dominance, etc.). The other four subjects were only tested in one pairing due to loss of motivation or insufficient time during our field trip. An additional six subjects were excluded because they failed to pass both pre-tests.

2.2.1.2 Setup

During the test phase, subjects were situated in adjacent rooms and could only view one another or interact through a mesh window (roughly 1m x 1m) between the rooms (see Figure 3A and B). In the center of the mesh window was a hole large enough to permit passage of rocks, nuts, and subjects' arms but not subjects' heads or bodies. One experimenter was stationed outside of each room to provide experimental materials to the subjects, and to videotape all trials. Experimental materials included palm nuts and a pair of flat, portable rocks.

Palm nuts are a component of our subjects' daily diet that is acquired through foraging in their forested enclosures. The bonobos consume palm nuts by cracking them with rocks or, occasionally, by crushing them forcefully with their teeth. The rocks used in this experiment were collected within the sanctuary. A hole was drilled in each rock so that a rope could be threaded through the hole and the rock could be tethered to a wall. One rock (the transferable rock) was tethered with a long rope, allowing it to be transferred to the adjacent room through an opening in the window. The second rock (the nontransferable rock) was tethered with a shorter rope, so that it could be used to crack nuts but could not be transferred. The tethers also ensured that rocks could be returned to the correct starting location between trials.

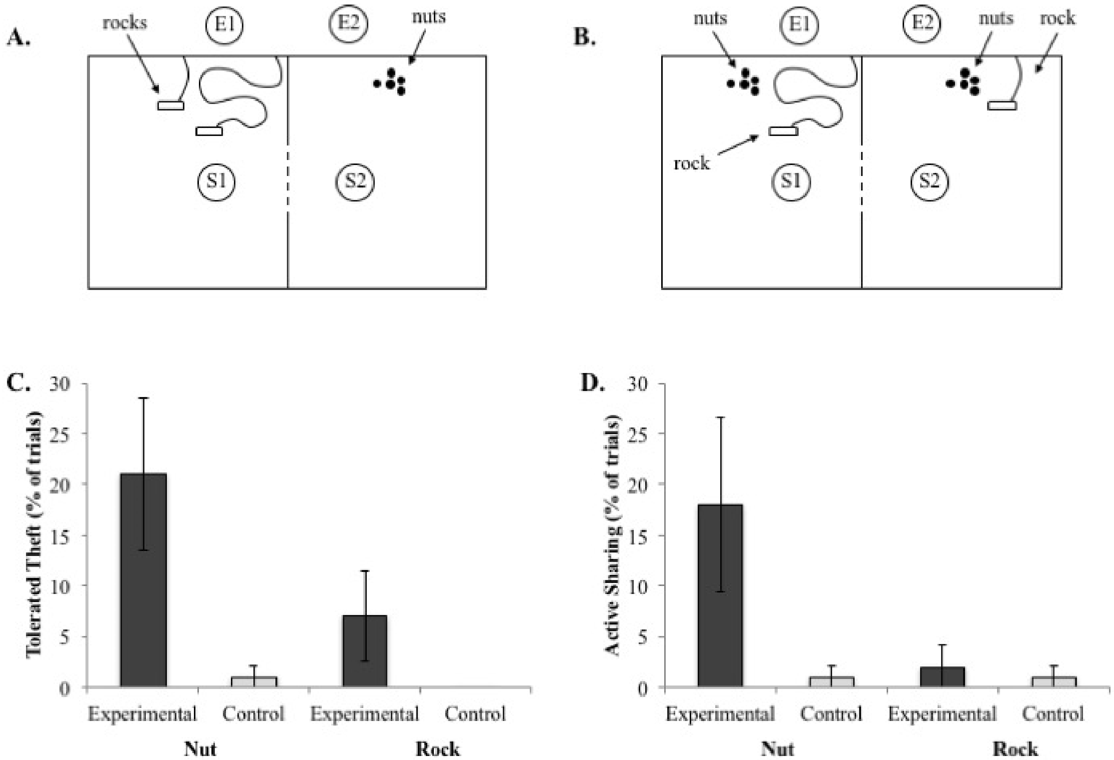


Figure 3: Testing setup and results of Chapter 2 Experiment 2. A. Experimental condition. B. Control condition. S1 and S2 are the subjects, located in adjacent rooms, who can interact through a single window (dashed line). Round circles represent nuts provided to subjects in each trial while rectangles attached to rounded lines depict rocks and their tethers. E1 and E2 are the experimenters and camera-people. C. Percent of trials in which subjects exhibited tolerated theft of rocks and nuts in the experimental and control conditions. D. Percent of trials in which subjects exhibited active sharing of rocks and nuts in the experimental and control conditions. Error bars denote standard error.

2.2.1.3 Procedure

Before qualifying for the test phase, bonobos had to pass two pretests. The *self regard pretest* was designed to ensure that subjects were skilled and motivated nut-crackers. Alone in a testing room, a subject was provided with one rock and three nuts. Subjects were required to crack one nut within five minutes in order to succeed on a trial and needed to succeed on two consecutive trials to advance to the next pretest. If after two trials, subjects had succeeded on neither, they were excluded.

The *tool mastery pretest* was designed to ensure that subjects understood the importance of the rock to successful nut cracking. Each subject was given three nuts in the testing room, and a rock was placed on the opposite side of the room. Subjects had to transport the nuts to the rock and crack at least one nut within five minutes to succeed on a trial and only needed to succeed on a single trial to advance to the test phase. If after two trials, subjects had failed to meet this criterion, they were excluded.

In the *test* phase, subjects participated in pairs in adjacent rooms, one as the nut-owner and the other as the rock-owner (Figure 3). The test phase began with a single *motivation* trial in which the rock-owner, who always possessed at least one rock regardless of conditions (see below), was given a single nut. This motivation trial ended after one minute or as soon as the nut had been cracked. It served to attract the attention of the nut-owner and to generate motivation for nut cracking. After the motivation trial, five test trials were administered in one block. Each test trial lasted five minutes. In the experimental condition (Figure 3A), the rock-owner began each trial with both the transferable and nontransferable rock, while the nut-owner was provisioned with five nuts. Thus, each subject possessed an excess of one resource but required both their resource and that of their partner to solve the task. In the control condition (Figure 3B), the rock-owner began each trial with only the transferable rock; the nut-owner was now in possession of the nontransferable rock. In addition, both subjects were provided with five nuts, i.e. both subjects were equipped from the start with both of the resources that they needed to solve the task. In this way transfer of either resource was unnecessary in the control condition. Pairs completed one session per day on four separate days, for a total of two experimental and two control sessions, counterbalanced in ABBA or BAAB order. Each pair thus participated in 10 experimental and 10 control trials.

To test for any impact of dominance relationship on performance in the task, each pair participated in seven dominance trials during a single session, using a standard food competition test (e.g., Wobber et al., 2010b). Most pairs were tested after they had completed all test and control sessions. Dominance trials were performed in a testing room that experimenters could access from three sides, and both subjects were in the same room. During dominance trials, a pair of experimenters centered the bonobos on opposite sides of the testing room with small pieces of food while a third experimenter positioned a larger—though monopolizable—piece of banana just outside the mesh, centrally between, and roughly two meters from, each of the two bonobos. This third experimenter then said, “ok,” at which time the other two experimenters stepped back and the bonobos were allowed to pursue the food. The subject who retrieved the piece of food was scored as the winner. After this subject had finished consuming the food, both were re-positioned and the next trial began. In all trials, both subjects immediately pursued the food and there was always a clear winner. In each pair, one individual won six or seven of seven dominance contests, indicating clear dominance relationships. All trials were filmed.

2.2.1.4 Coding and Analysis

Two experimenters recorded all trials on handheld cameras, focusing primarily on any interactions around the window between the testing rooms. One coder blind to hypotheses reviewed all trials and coded the following transfer behaviors. For reliability, a second blind coder coded all videos from a randomly selected 30% of pairs. Our definitions largely followed de Waal (1997). A transfer was coded as *active sharing* if the possessor transferred the item through the window into the adjacent room. It was coded as *tolerated theft* if the recipient acquired the item from the possessor's side of the window (including on the floor and in the hands of the possessor) without resistance from the possessor. Finally, a transfer was coded as a *forced claim* if the recipient acquired an item from the possessor's side of the window while the possessor resisted by pulling back the recipient's hand, pulling back the item, or racing to grab the item off the floor. In addition, we coded several communicative behaviors. Gestures were recorded whenever an individual reached through the window empty handed, as long as her hand remained empty when she retracted it. We coded grooming as manually manipulating the fur or skin of the other subject. Teasing was recorded if an actor held an object through the window without releasing it or released the object on the partner's side but quickly retrieved it.

Data were converted into binary measures (i.e., "1" if a given behavior occurred within a trial, and "0" if it did not). All measures had near-perfect inter-rater reliability (nut sharing, rock theft, teasing by the rock owner: Cohen's kappa = 1; grooming by the rock owner: Cohen's kappa = 0.937; gesture by the rock owner: Cohen's kappa = 0.921; nut theft: Cohen's kappa = 0.869; agreement for rock sharing was also perfect, but Cohen's kappa could not be calculated because there were no positive cases among the trials reviewed by both coders) (Landis and Koch, 1977).

We used related-samples Wilcoxon signed rank tests to compare the frequency of trials involving nut and rock transfer between test and control conditions, and to compare, within each condition, the frequency of nut transfer trials with the frequency of rock transfer trials. In addition, we used Generalized Linear Mixed Models (GLMMs) to explore the factors that contributed to transfers. GLMMs assess the relative influence of predictor variables on the dependent measure (in this case, nut or rock transfer), while controlling for repeated measures, confounding variables, and covariation between predictor variables. We used the glmer function in the LME4 package in R to fit binomial models with a logit link function.

2.2.2 Results and discussion

Bonobo sharing occurred by tolerated theft and active sharing but not by forced claims (Figure 3C and D). Importantly, bonobos transferred nuts on significantly more trials in the experimental condition than in the control both by tolerated theft and by active sharing (tolerated theft: $M = 2.1 \pm$ s.e. $= 0.745$ in experiment, 0.1 ± 0.105 in control, $z = -2.207$, $N = 10$, $T+ = 6$, ties $= 4$, $p = 0.027$;

active sharing: 1.8 ± 0.858 trials in experiment, 0.1 ± 0.105 in control, z = -1.980, N = 10, T+ = 6, ties = 3, *p* = 0.048, related samples Wilcoxon signed rank tests). However, frequency of rock transfer by tolerated theft or by active sharing did not differ between conditions (tolerated theft: 0.7 ± 0.446 in experiment, 0 ± 0 in control, z = -1.604, N = 10, T+ = 3, ties = 7, *p* = 0.109; active sharing: 0.2 ± 0.211 in experiment, 0.1 ± 0.105 in control, z = -1, N = 10, T+ = 1, ties = 9, *p* = 0.317, related samples Wilcoxon signed rank tests).

There was no difference in the number of trials involving transfer of nuts versus rocks in the control condition (tolerated theft: z = -1.000, N = 10, T+ = 1, ties = 9, *p* = 0.317; active sharing: z = 0, N = 10, T+ = 1, ties = 8, *p* = NS, related samples Wilcoxon signed rank tests). However, in the experimental condition subjects transferred nuts on significantly more trials than rocks both by tolerated theft and by active sharing (tolerated theft: z = -2.401, N = 10, T+ = 7, ties = 3, *p* = 0.016; active sharing: z = -2.226, N = 10, T+ = 6, ties = 4, *p* = 0.026, related samples Wilcoxon signed rank tests). Together, these results reveal that bonobos both passively and actively shared nuts but not rocks.

To further explore bonobos' food sharing behavior, we investigated the predictors of tolerated theft and active sharing of nuts in separate GLMMs on a trial-by-trial basis. Both models included the same random effects and predictor variables, but differed in the dependent measure: tolerated theft or active sharing of nuts. To account for multiple observations, we included the subject pair as a random effect. Our models also included several predictors: condition (to account for differences in transfer between the experimental and control conditions), gesture by the rock owner (to determine whether help was provided proactively, or in response to request; Yamamoto et al., 2009, Melis et al., 2011), rock transfer (combined tolerated theft and active transfer; to assess the influence of within-trial interchange), dominance (to determine whether transfers are directed up or down the hierarchy), and trial (to account for changes over time). Theoretically it is plausible that bonobos might exchange nuts for grooming or that they might tease their partner to reduce proximity; however, both behaviors occurred infrequently (grooming: 6.5% of trials; teasing: 3.0% of trials) and neither co-occurred with tolerated theft or active sharing on more than a single trial. Therefore, we did not include either factor.

Consistent with our previous analyses, both models showed that bonobos transferred nuts significantly more in the experimental condition than in the control ($p < 0.005$ for both models; see Table 2). However, there was no effect of trial in either model, indicating that learning or changes in motivation did not influence transfers of either type. There was also no impact of gesturing by the rock owner on tolerated theft or active sharing, suggesting that transfers were likely unsolicited. This finding is in line with evidence that bonobos perform prosocial behaviors proactively (Tan and Hare, 2013, Tan et al., submitted), which contrasts with the reactive nature of chimpanzee helping (Warneken et al., 2007, Yamamoto et al., 2009, Melis et al., 2011, Yamamoto et al., 2012, but see Horner et al., 2011).

Table 2: Factors influencing likelihood of tolerated theft and active sharing of nuts in Experiment 2. Condition (with control as a baseline), trial (1-10), gesturing by the rock owner, rock transfer (tolerated theft and active sharing of rocks combined), and dominance (with the rock owner being dominant as baseline) were included as covariates in the model. Significant p-values are bolded.

	Tolerated Theft of Nuts			*Active Sharing of Nuts*		
Factor	*Estimate*	*S.E.*	*p-value*	*Estimate*	*S.E.*	*p-value*
Intercept	-5.025	1.261	**<0.001**	-6.900	1.579	**< 0.001**
Condition	3.235	1.068	**0.002**	3.484	1.085	**0.001**
Trial	-0.040	0.091	0.662	0.030	0.102	0.766
Gesture	-0.004	0.581	0.994	-0.006	0.673	0.993
Rock Transfer	1.775	0.876	**0.043**	0.262	1.005	0.794
Dominance	0.559	0.733	0.446	2.181	1.039	**0.036**

We found that tolerated theft of nuts was predicted by transfer of rocks ($p = 0.043$). This apparent reciprocal pattern might result from intentional interchange of resources or, more parsimoniously, from the physical proximity shared by tolerant partners. The majority of rock transfers (7 of 10) were also tolerated thefts (i.e., symmetry-based reciprocity; Brosnan and de Waal, 2002, Schino and Aureli, 2010). Active sharing of nuts, on the other hand, was not predicted by transfer of rocks, but by dominance. Subordinates actively shared nuts with dominant partners more than dominants shared nuts with subordinates ($p = 0.036$). Active food-sharing in this context may therefore be politically motivated, with individuals transferring food in attempt to win favor from higher-ranking social partners (Seyfarth, 1977, Noë and Hammerstein, 1995, Schino, 2001). This finding aligns with other work showing that bonobos tend to transfer certain currencies up or down the hierarchy, such as food and solicitations for sex (Clay and Zuberbuhler, 2012, Yamamoto, 2015). Both reciprocity and sharing up the hierarchy are consistent with the possibility that bonobos are operating within a biological market system in which individuals monitor their relationships with others and trade goods and services in one currency for favors in another (e.g., Stevens et al., 2005, Jaeggi et al., 2013).

Bonobos shared food but not tools even though they had passed a self-regard pretest and a tool fetching pretest, ensuring that they were motivated to crack nuts and understood the need for both the tool and the nut to solve the task. Interestingly, although there was no cost to transferring the rock in the experimental condition since subjects always had a second (nontransferable) rock, just as in Experiment 1 subjects did not exhibit transfers of this kind. Instead, subjects chose to actively share their food, directly incurring a cost in the amount of food that they could ultimately ingest.

Why might bonobos exhibit strong enough motivations to actively share food? It is unlikely that subjects were sharing under pressure since they had complete control over the items in their rooms and were physically separated from their partner, preventing harassment. Although chimpanzees sometimes share food in response to harassment, unlike bonobos, they do not share when physically separated from their partner (Gilby, 2006, Stevens, 2004). Bonobos are more socially tolerant in dyadic food contexts than chimpanzees, maintaining juvenile levels of social tolerance into adulthood (Hare et al., 2007, Wobber et al., 2010c). They also exhibit lower levels of social inhibition than chimpanzees, suggesting more relaxed dominance relations and a low-pressure environment for sharing.

One possibility is that sharing may have resulted from an unselfish motivation. Indeed in the past bonobos have unselfishly helped others to access food that was never accessible to the helper (Tan and Hare, 2013), but not when the food was of high value and already in their possession (Bullinger et al., 2013). It could be that the nuts were of low enough immediate value—since they required great effort to crack with one's teeth or a rock to crack with ease—that bonobos unselfishly shared them. Alternatively, it's possible that sharing was strategic and selfishly motivated. Bonobos will allow another individual to enter their room and share their food if the two bonobos can interact socially (Hare and Kwetuenda, 2010, Tan and Hare, 2013). This and other previous work (e.g., Yamamoto, 2015, Wittig et al., 2014a), coupled with our finding that bonobos shared food up the hierarchy, raise the possibility that food is an important currency in building and maintaining social relationships. Finally, it's possible that bonobos were attempting to initiate a reciprocal exchange. Consistent with this hypothesis, bonobos' failed investments (i.e., unreciprocated transfers) were more often initiated by the nut-owner who had a greater quantity of resources and would not lose all bargaining power with a single transfer, unlike the rock-owner who had a single transferable resource. Future work will be necessary to disentangle these hypotheses. Whether bonobos' motivations were selfish or unselfish, it may be that relaxed feeding competition and resultant high social tolerance in feeding contexts has alleviated constraints on food sharing that persist in non-food contexts (Wrangham, 1993, Hare et al., 2007, Yamamoto, 2015).

2.3 General Discussion

A range of experimental paradigms have documented chimpanzees' propensity to actively share tools and other objects in their possession—but not food (Stevens, 2004, Warneken et al., 2007, Warneken and Tomasello, 2006, Yamamoto et al., 2009, Yamamoto et al., 2012). In contrast to these findings, we present evidence from two studies that bonobos actively share food in their possession, but not non-food items. In Experiment 1, bonobos did not help a human experimenter by picking up an out-of-reach object and transferring it to the experimenter—a context in which both chimpanzees and 18-month-old human infants readily help (Warneken and Tomasello, 2006, Warneken et al., 2007). In Experiment 2, bonobos again did not transfer a surplus tool that was needed by a conspecific partner—again in a context very similar to one in which chimpanzees help (Yamamoto et al., 2009, Yamamoto et al., 2012). They did, however, frequently transfer food to their partner—both passively through tolerated theft and actively, directly transferring the food by hand to the recipient or into her room. Together, these findings suggest that bonobos and chimpanzees differ in their prosocial motivations. Whereas chimpanzees are active donors of non-food, but not food, items, bonobos exhibit the opposite pattern of active sharing (Table 3).

Table 3: Distribution of active sharing behavior involving food and non-food items across bonobos, chimpanzees, and humans

	Humans	Bonobos	Chimpanzees
Food	YES	YES	NO
Non-Food	YES	NO	YES

Human food: (Gurven and Jaeggi, 2015); Human non-food: (Warneken and Tomasello, 2006, Warneken et al., 2007); Bonobo food: Experiment 1; Bonobo non-food: Experiments 1 and 2; Chimpanzee food: (Stevens, 2004, Melis et al., 2006b); Chimpanzee non-food: (Warneken and Tomasello, 2006, Warneken et al., 2007, Yamamoto et al., 2009, Yamamoto et al., 2012, Melis and Tomasello, 2013)

Our findings largely align with, and expand on, previous experiments with chimpanzees and bonobos in food contexts. Chimpanzees have consistently been shown to be reluctant food donors, actively sharing infrequently and almost exclusively in response to solicitation or harassment (Stevens, 2004, Gilby, 2006, Jaeggi et al., 2010b, Silk et al., 2013, Byrnit et al., 2015). Bonobos, on the other hand, have often shown high social tolerance for co-feeding (e.g., Hare et al., 2007, Wobber et al., 2010b, Wobber et al., 2010c, but see Cronin et al., 2015). Moreover, they cooperated effectively to acquire food (Hare et al., 2007), and even preferred to let a stranger bonobo enter their room and share their food (Hare and Kwetuenda, 2010, Tan and Hare, 2013). However, outside of dyadic interactions, bonobos, like chimpanzees, may be reluctant to actively share highly monopolizable food (Byrnit et al., 2015, Jaeggi et al., 2010b). Differences in food sharing may have evolved in response to more relaxed feeding competition during bonobo evolution. Reduced competition permitted the evolution of greater social tolerance and elevated prosocial motivations in feeding contexts (Wrangham, 1993, Hare et al., 2007, Hare et al., 2012).

The current experiments also provide the first test of sharing of objects in possession by bonobos. Both experiments suggest that bonobos do not actively share non-food items, even in contexts in which chimpanzees do (Melis and Tomasello, 2013, Warneken et al., 2007, Warneken and Tomasello, 2006, Yamamoto et al., 2009, Yamamoto et al., 2012). This species difference in object sharing may be related to the lack of extractive foraging in wild bonobos. Although bonobos readily use tools in captivity and in the wild (e.g., Hohmann and Fruth, 2003, Mulcahy and Call, 2006), they have not been observed to use tools to obtain or process food in the wild (Hohmann and Fruth, 2003, Furuichi et al., 2015). Wild chimpanzees also manipulate objects more than bonobos, and may have evolved a higher level of motivation for object manipulation to promote the acquisition of extractive foraging not seen in bonobos (Furuichi et al., 2015, Koops et al., 2015a, Koops et al., 2015b). The lack of instrumental helping by the bonobos in the current study may be a by-product of their reduced interest in objects overall (Herrmann et al., 2011).

Bonobos' active food-sharing did not occur in response to partners' gestures. Sharing was thus *proactive* (i.e., unsolicited), as opposed to *reactive* (i.e., in response to request) (Burkart et al., 2014, Jaeggi et al., 2010b, Warneken et al., 2007). Proactivity, by definition, does not depend on overt signals from a recipient, and is therefore likely a characteristic of more flexible prosociality (Warneken, 2013). Although proactive prosociality emerges early in human development (Warneken, 2013), chimpanzee prosociality appears to be almost completely reactive (Warneken et al., 2007, Yamamoto et al., 2009, Melis et al., 2011, Yamamoto et al., 2012, but see Horner et al., 2011). Consequently, Warneken (2013) has suggested that proactive prosociality may be unique to humans. Bonobos may falsify this claim. Regardless of whether bonobos were facilitating a recipient's access to out-of-reach food (Hare and Kwetuenda, 2010, Tan and Hare, 2013, Tan et al., submitted) or transferring food in their possession (the current study), their prosocial behaviors were reliably proactive. The existence of both active and proactive food sharing in bonobos also directly challenges the strong prosocial hypothesis since bonobos exhibit such strong prosocial motivations for food sharing. Future work should probe the limits of this prosocial motivation by manipulating both the value of the currency and the subtlety of the cues that communicate the recipient's needs (Warneken, 2013).

Bonobos exhibit a different context-specific prosociality profile than chimpanzees. However, between the two species, our closest relatives exhibit much of the breadth of sharing behavior that is seen in humans. This includes both passive and active transfer of food and non-food items, as well as both reactive and proactive sharing. Both species of apes clearly understand others' goals (e.g., Yamamoto et al., 2012, Kano and Call, 2014b) and bonobos may exhibit strong prosocial motivations in food sharing contexts. Taken together, these data lend support to the versatile prosociality hypothesis: only humans appear to exhibit this entire suite of prosocial traits, and it may be the extreme flexibility with which we employ this diversity of prosocial behaviors across contexts that sets humans apart from our closest relatives.

3 Bonobos prefer individuals that hinder third-parties over those that help

3.1 Main Text

Humans' moral and cooperative tendencies are among the traits that most clearly define our species (Tomasello and Vaish, 2013). Humans closely monitor the cooperative relationships between individuals within their group (Wedekind and Milinski, 2000). Both adults and children willingly incur costs to reward those who are helpful or punish those who are not—even when they are only bystanders (Burnham and Johnson, 2005, McAuliffe et al., 2015, Tasimi and Wynn, 2016). This prosocial preference in third-party interactions has been suggested to be a derived feature of human psychology that explains the unique scope and strength of human cooperation (Bowles and Gintis, 2004, Fehr and Fischbacher, 2003). Research with infants has shown that they are intrinsically motivated to see others' helped and that by three months of age already exhibit a preference for individuals that demonstrate prosocial dispositions during third-party interactions (Hamlin et al., 2007, Hamlin and Wynn, 2011, Hamlin et al., 2010a, Hepach et al., 2012). For instance, when infants were shown displays in which one agent (the Climber) attempted but failed to climb a hill and was either pushed up the hill by one agent (the Helper) or down the hill by another (the

Hinderer), infants consistently reached for, or looked longer at, the Helper (Hamlin et al., 2007, Hamlin et al., 2010a). Such an early bias for cooperators could be one of the core motivational differences explaining why humans exhibit more sophisticated cooperation among groupmates than other apes.

Some evidence challenges this idea since humans' closest living relatives, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*), share some of our prosocial preferences. Both species exhibit active, and often reciprocal, preferences for grooming and coalition partners (Watts, 2002, Surbeck et al., 2011, Wrangham, 1993). In captive experiments, chimpanzees can recruit help, prefer the most effective partner, and understand different roles in novel cooperative tasks (Melis et al., 2006b, Melis and Tomasello, 2013). Finally, chimpanzees and orangutans spontaneously requested food from a human they had observed sharing food with a third-party over one who had refused to share (Herrmann et al., 2013, Russell et al., 2008, Subiaul et al., 2008).

Critically, existing findings are consistent with both the prosocial preference hypothesis and the social tool hypothesis. This latter hypothesis suggests that nonhuman apes are not sensitive to the unobservable prosocial or antisocial dispositions of each actor but instead are evaluating individuals' usefulness based on observable context-specific actions (Melis et al., 2006b, Herrmann et al., 2013, Russell et al., 2008, Subiaul et al., 2008). For example, they may recognize that a human who has shared food previously is more likely to share food again than another human who never shared food. However, they may not attribute a prosocial disposition to the food-sharer and therefore may not favor the food-sharer, or expect her to exhibit different types of prosociality, in other contexts. Such a finding would support the social tool hypothesis and suggest that true prosocial preference based on evaluation of actors' dispositions is unique to humans.

To test the prosocial preference and social tool hypotheses, we showed bonobos displays in which one actor behaved prosocially and another antisocially toward a third-party in one context. Then we allowed bonobos to choose between the actors in a completed unrelated context. Although bonobos and chimpanzees are equally closely related to humans genetically, they exhibit pronounced behavioral and cognitive differences (Hare et al., 2012). For instance, bonobos are more gregarious and socially tolerant than chimpanzees, and as a result can more flexibly obtain food through cooperation (Hare et al., 2007, Wobber et al., 2010a). Bonobos voluntarily share food with strangers even when they do not directly benefit (Tan and Hare, 2013). Relative to chimpanzees, their neural architecture even exhibits a suite of characteristics that are associated with greater sensitivity to others (Rilling et al., 2012, Stimpson et al., 2015). Bonobo sociality is hypothesized to have evolved due to selection against male aggression (Hare et al., 2012). For example, to thwart males' attempts at coercion, female bonobos form alliances (Wrangham, 1993). Meanwhile, males obtain status and mating opportunities by behaving prosocially toward females—especially their mothers (Surbeck et al., 2011). Bonobos may exhibit this distinct pattern of sociality because they share though common descent with humans a preference for those who are prosocial toward others, rather than a more egocentric or utilitarian preference for the best social tools. We therefore investigated bonobos' preference for helpers versus hinderers in four experiments using methods highly similar to those employed with human infants (Hamlin et al., 2007, Hamlin et al., 2010a).

3.1.1 Experiment 1

Twenty-four bonobos participated in Experiment 1 (12 females, M_{age}=10.42 years, range=4-19 years), completing both a test and control condition on separate days with condition order counterbalanced across subjects. In each condition, the experimenter sat at a table just outside the subject's enclosure and showed the subject two different animated videos on an iPad. The videos, modeled closely after the stimuli used by Hamlin et al. (2007), depicted a pair of 2-dimensional shapes interacting. As cues to their agency, each shape had two eyes with white sclera and dark pupils, and exhibited goal-directed movements. In the test condition, each video began with a circle, the Climber, entering the scene and attempting but failing three times to climb a steep hill. On the third attempt, the Climber encountered another agent. In the *helper animation* (Figure 4A), a second shape (e.g., a blue triangle) entered from below and pushed the climber up to the top of the hill before returning down the hill and exiting the screen. In the *hinderer animation* (Figure 4B), a different shape (e.g., a red square) entered from above and pushed the climber back down the hill before returning to the top of the hill and exiting the screen. Videos were of equal length and the Helper and Hinderer each spent approximately the same amount of time and screen and in contact with the Climber.

The Control condition controlled for the influence of the nonsocial features of our animations. In the animations for this condition, agents pushed an eye-less, inanimate circle up or down the hill (see Figure 5). Unlike the Climber, the inanimate circle never exhibited independent movement or goal-directed action.

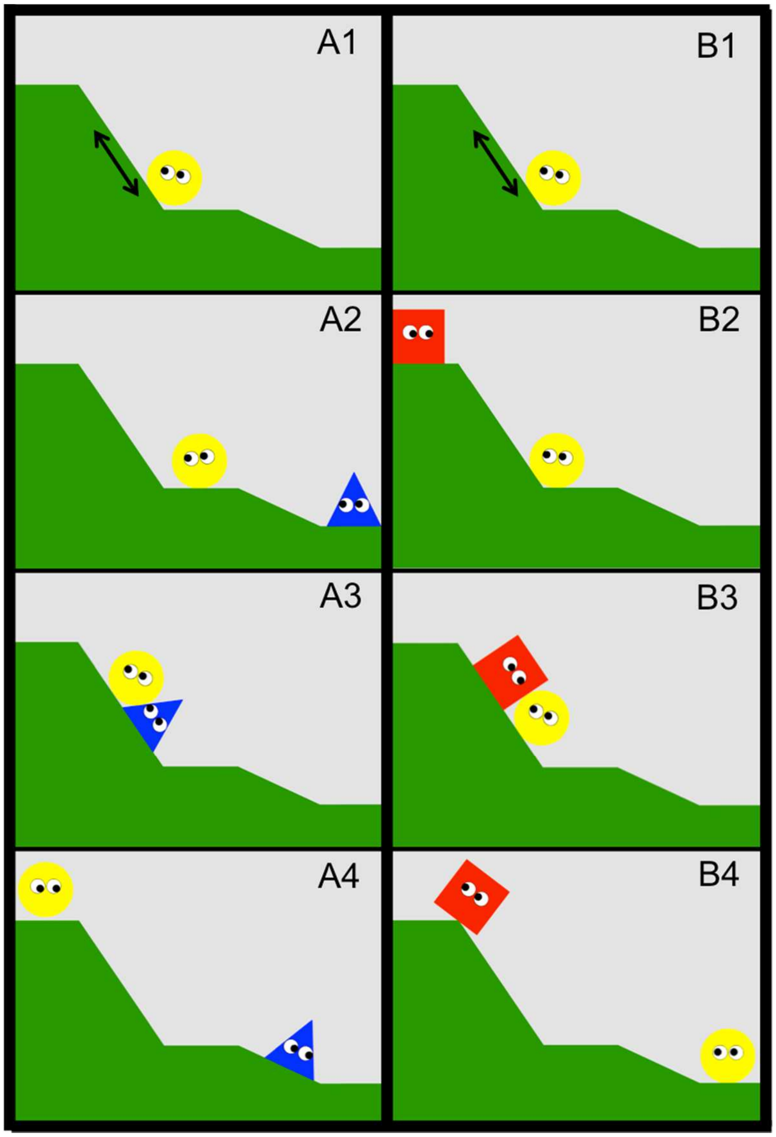


Figure 4: Animations used in the test condition of Chapter 3 Experiment 1: in both the Helper (A) and Hinderer (B) animations, the climber (yellow circle) tries but fails to scale the hill (A1 and B1) three times before encountering another agent. In the *helper animation*, the Helper (blue triangle) enters from below (A2), pushes the climber up the hill (A3), and exits the screen (A4). In the *hinderer animation*, the Hinderer (red square) enters from above (B2), pushes the climber down the hill (B3), and exits the screen (B4).

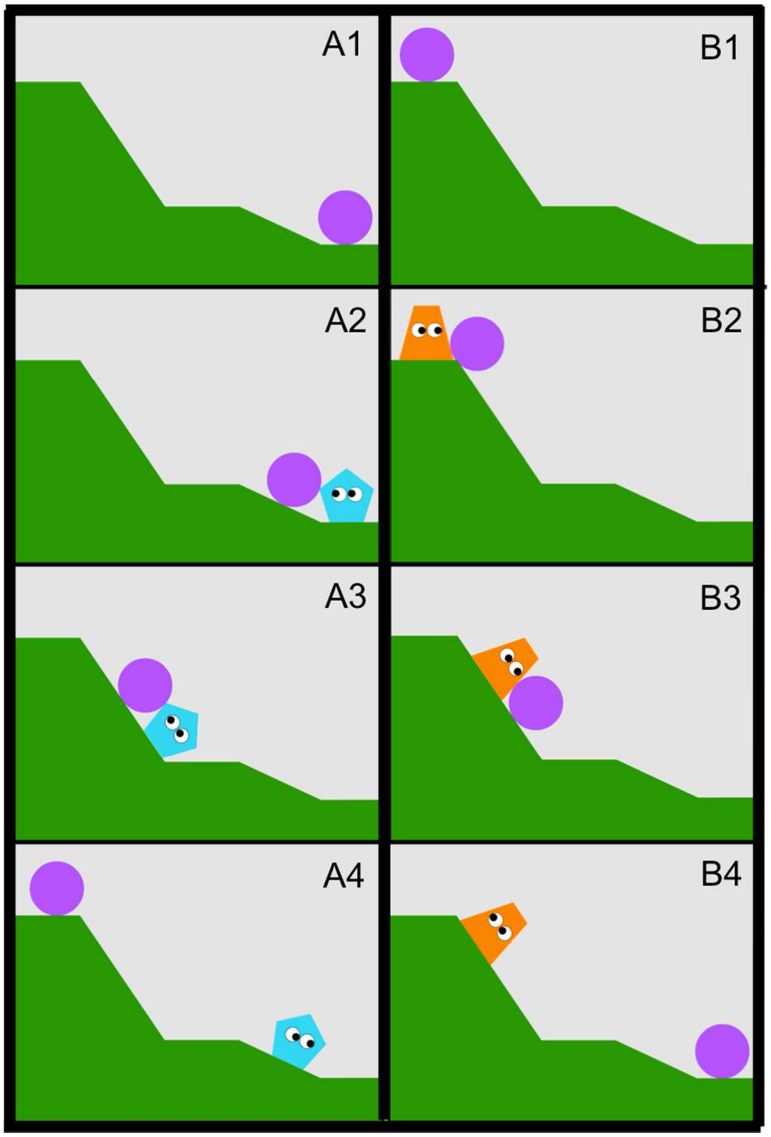


Figure 5. Animations used in the control condition of Chapter 3 Experiment 1. The *Upward animation* begins with a static ball at the base of the hill (A1). The Upward agent enters from below (A2), pushes the ball up the hill (A3), and exits the screen (A4). Conversely, the *Downward animation* begins with a static ball at the top of the hill (B1). The Downward agent enters from above (B2), pushes the ball down the hill (B3), and exits the screen (B4).

Subjects were first familiarized to the animations as they alternated in a loop for a total of four presentations of each animation, with order counterbalanced across subjects. Four test trials were conducted immediately following familiarization. In each test trial, subjects again watched each video once—again in counterbalanced order within and between subjects. The experimenter (E) then put down the iPad, and simultaneously set two identical pieces of apple on the left and right sides of the testing table just out of the subject's reach. E then held paper replicas (5cm x 5cm) of the Helper (e.g., blue triangle) and Hinderer (e.g., red square) upright in front of the pieces of apple for 2 seconds before placing each on top of one of the apple pieces, with locations counterbalanced. E then slid the table top within reach, allowing the subject to touch one of the two paper replicas. The subject received whichever paper replica and apple piece she gestured toward first (i.e., by extending a finger through the mesh). To avoid biasing the subject's choice, all actions involved in presenting the choices occurred simultaneously, the locations of the Helper and Hinderer replicas (and Upward and Downward controls) were counterbalanced across trials, and the experimenter looked directly at the ape while pushing the table forward and waiting for the ape to make a choice (Krupenye et al., 2015). In this and all other experiments, subjects' choices were live-scored by the experimenter, and video was coded for reliability by a coder blind to condition and hypotheses. Reliability in all experiments was excellent (see 3.2 Supplemental Methods and Results for details),

Based on previous work with infants and nonhuman apes, we interpret reaching behavior as a measure of preferences (e.g., Hamlin et al., 2007, Krupenye et al., 2015). Subjects received the same quality and quantity of food reward regardless of their choice. The agents in the video never interact with food. Therefore, any preference observed here cannot be based on subject's evaluating the agents' as a social tool. Unless otherwise noted all analyses for all experiments represent one sample Wilcoxon signed rank tests of the proportion of trials in which subjects chose the Hinderer (or its control).

Bonobos exhibited a significant preference for selecting the Hinderer [N=24, M=0.625±SE=0.044, p=0.011; see Figure 5A]. Only two individuals chose the Helper on a majority of trials while 11 favored the Hinderer. These results indicate that bonobos can discriminate between prosocial and antisocial agents but do not show the human preference for prosocial agents. Separate analysis of adult and subadult subjects revealed that only adults showed a significant preference (Figure 5A; see 3.2.2.2.2 Developmental Analyses for details). Thus, whereas humans discriminate helpers from hinderers very early in infancy, bonobos may not do so, or at least may not exhibit strong social preferences based on third-party interactions, until adulthood.

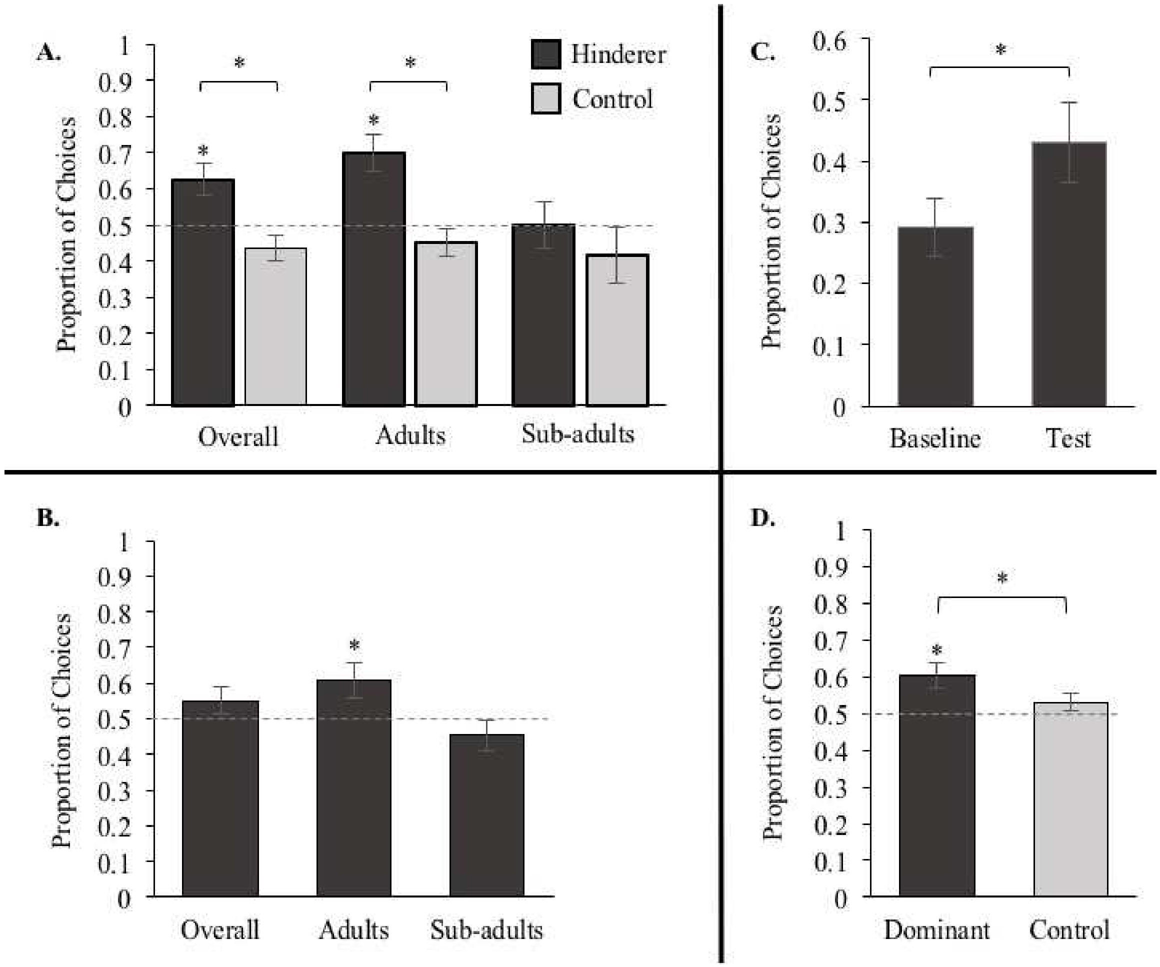


Figure 6: A. Mean proportion of choices for the Hinderer and Control in Chapter 3 Experiment 1, overall and for adults and sub-adults. B. Mean proportion of choices for the Hinderer in Chapter 3 Experiment 2, overall and for adults and subadults. C. Shift in proportion of choices for the Hinderer between baseline and test in Chapter 3 Experiment 3. D. Mean proportion of choices for the Dominant and Control in Chapter 3 Experiment 4. Asterisks indicated significant effects ($p < 0.05$). Error bars depict standard error.

If bonobos were responding to perceptual rather than social features of the animations, they should prefer the Downward agent whose movements mirrored those of the Hinderer. However, subjects showed no preference for either agent in the control condition [N=24, M=0.438±0.035 choice of Downward agent, p=0.084; see Figure 6A]. A direct comparison of the two conditions also revealed a significant difference in choice patterns [related samples Wilcoxon signed rank test, z=-2.884, N=24, T+=13, ties=9, p=0.004], with subjects selecting the Hinderer significantly more than the Downward control. Thus, perceptual features alone do not appear to explain our subjects' preference for the Hinderer.

3.1.2 Experiment 2

In Experiment 2, we tested whether the preference observed in Experiment 1 would generalize to a different social context. Twenty-two bonobos (ages 4-17, 11 females) witnessed a pair of experimenters sitting on either side of a third neutral actor (E1) just outside the subject's enclosure. E1 was playing with a plush toy, tossing it in the air, when he dropped the toy out of grasp and reached effortfully for it—vocalizing and gazing at it with arm outstretched. The Helper calmly picked up the toy, made eye contact with E1, and attempted to return the toy to E1. Before E1 could take the toy, the Hinderer snatched the toy from the Helper, aggressively grunted, and turned his back to the other two, surreptitiously depositing the toy in a bucket between himself and E1. E1 then said, “ok,” and the three stood up with their backs to the subject. E1 gave the Helper and Hinderer a piece of apple, positioned the bonobo centrally with a piece of food, and then directed the experimenters to simultaneously approach the bonobo with the food in their outstretched hands. Subjects had one minute to beg for food from either experimenter with their hand or mouth, and were given the first food they approached. They participated in eight trials, each involving the same social demonstration and choice phase, with the experimenters’ locations counterbalanced across trials. The roles of the experimenters remained constant for a given bonobo, but were counterbalanced across subjects.

Overall, subjects tended to select the Hinderer more frequently than the Helper (M=0.551±0.037 of trials), but not significantly above chance [N=22, p=0.158; Figure 6B]. Since in Experiment 1 only adults (i.e., 9 and above) exhibited a Hinderer preference, we again separated our sample into adults and subadults, replicating the age-dependent pattern. Adults, but not subadults, exhibited a significant preference for the Hinderer [adults: $N_{aged9\text{-}17}$=14, M=0.607±0.049, p=0.047; subadults: $N_{aged4\text{-}8}$=8, M=0.453±0.043, p=0.257; Figure 6B].

3.1.3 Experiment 3

To further confirm our results, Experiment 3 employed identical methods to Experiment 2 except that subjects participated in four baseline trials followed by four test trials (*N*=18, ages 10-18, 9 females) (see Schroepfer-Walker et al., 2015 for similar design). Baseline trials only involved the choice phase of the procedure, whereas test trials involved the social demonstration and the choice phase. Additionally, after making their choice, subjects did not receive food from the experimenter. If subjects approached one experimenter during the majority of baseline trials, this experimenter was assigned the role of Helper. If subjects approached the experimenters equally during baseline trials, roles were assigned semi-randomly, with the aim of counterbalancing the role played by each experimenter across subjects (Schroepfer-Walker et al., 2015). Experiment 3 therefore tests whether bonobos will shift their preference from an initially preferred experimenter toward the Hinderer once he begins to behave antisocially.

Bonobos exhibited a significant shift between the baseline and test phases in response to the social demonstrations [*N*=18, *p*=0.032; Figure 6C]. Specifically, 10 of 18 individuals shifted from their baseline preference toward the Hinderer, and only 3 exhibited the opposite shift. Taken together, Experiments 1-3 provide evidence that bonobos have a robust preference for individuals that are antisocial over those that are prosocial in third-party interactions.

3.1.4 Experiment 4

In Experiment 4, we tested whether subjects' preferences might be explained by an attraction to individuals perceived as dominant. This experiment was identical to Experiment 1, except for the animations (N=24, ages 4-17, 10 females). In the test condition subjects watched videos in which two animated agents competed for access to a central location in the scene, with the Dominant agent repeatedly displacing the Subordinate one. Subjects exhibited a significant preference for the Dominant agent [N=24, M=0.604±0.034 p=0.008; Figure 6D]. No subjects chose the Subordinate on a majority of trials while eight favored the Dominant. To ensure that this preference did not relate to perceptual features, in the control condition of Experiment 4 subjects witnessed the same videos (with new agents) except that the agents' actions were separated in time such that they were no longer contingent. Here, bonobos showed no preference for either agent [N=24, M=0.531±0.023, p=0.180; Figure 6D]. One favored the Subordinate control and four the Dominant control. Within-subject comparisons revealed that subjects selected the Dominant agent significantly more than its control counterpart [related samples Wilcoxon signed rank test, N=24, p=0.035; Figure 6D].

3.1.5 Discussion

These results support the social tool hypothesis and suggest that the motivation to prefer prosocial individuals based on evaluation of their unobservable dispositions evolved uniquely in the human lineage. In three experiments, adult bonobos spontaneously chose a human or animated agent that hindered over one that helped. In contrast, by three months human infants already show the *opposite* preference in related paradigms (Hamlin and Wynn, 2011, Hamlin et al., 2007, Hamlin et al., 2010a). Most strikingly, bonobos failed to show the human preference despite their human-like levels of tolerance and prosociality in dyadic interactions (Tan and Hare, 2013, Hare et al., 2007). Crucially, bonobos were sensitive to the actors' goal-directed actions towards others, clearly discriminating between the Helpers and Hinderers. Bonobos do therefore track interactions between third-parties and evaluate potential social partners based on these interactions; however, they appear to based their judgments on actors' actions rather than their dispositions.

Our main effect is reproducible having replicated in three different experiments, involving multiple paradigms with both humans and animated agents as actors. Even in experiments utilizing animated agents, it is unlikely that bonobos' preferences were driven by an attraction to different colors, shapes, or motion patterns. Agent color and shape were counterbalanced between subjects and, when key social features were removed, bonobos showed no preference for control agents that exhibited similar motor patterns. By using non-differential or zero rewarding and few trials subjects did not have an opportunity to form preferences based on food acquisition. Moreover, our use of both novel animated agents and unfamiliar human experimenters allowed us to eliminate biases in social preference based on social information that is unrelated to the goals of our study (such as sex, age, reproductive status, and size of the agents). Critically, bonobos' preferences were tested in a context that differed from the one in which the actors' dispositions were demonstrated, ensuring that subjects would not simply prefer the prosocial individual based on their context-specific utility as a social tool. Bonobos' choices within this design support the interpretation that they do not evaluate others based on unobservable dispositions. Presumably, bonobos did not expect the Hinderer to behave antisocially toward themselves, although they may have expected that the

Hinderer would continue to exhibit the observed types of antisocial behavior toward third-parties.

Bonobos may prefer Hinderers because they appear to be more dominant than Helpers. When intervening in third-party conflicts, primates often support the higher-ranking contestant or the one who is already winning (i.e., "winner-support"), and they may gain reproductive benefits from doing so (Chapais, 1995, Vervaecke et al., 2000). For example, high-ranking male primates, who often prevent others from mating, have been shown to be more tolerant of mating by their supporters (Duffy et al., 2007). In support of this interpretation, in Experiment 4, bonobos exhibited a preference for a dominant agent over a subordinate one. Regardless of what future research reveals about the motivations underlying social preference in human infants and bonobos, the current study demonstrates that in nearly identical settings the two species exhibit *very* different preferences. Thus, while nonhuman apes possess the cognitive architecture to track third-party interactions and flexibly evaluate conspecifics as social tools (Herrmann et al., 2013, Melis et al., 2006b, Russell et al., 2008, Subiaul et al., 2008), there currently remains no evidence that they positively evaluate partners based on their prosocial dispositions toward others. Therefore, an early emerging preference for those that are prosocial toward others may be among the species-specific traits at the foundation of humans' uniquely cooperative nature.

3.2 Supplemental Methods and Results

3.2.1 General Methods

3.2.1.1 Subjects

Forty-three semi-free-ranging bonobos (aged 4-19; 21 females) were tested at Lola Ya Bonobo sanctuary in Kinshasa, Democratic Republic of Congo (www.friendofbonobos.org) during two field seasons (October-December, 2012: Study 1; May-June, 2015: Studies 2-4; see Table 4). Animal husbandry and care practices complied with the Pan-African Sanctuary Alliance (PASA) Primate Veterinary Healthcare Manual, as well as the policies of Lola ya Bonobo Sanctuary. These non-invasive behavioral studies were approved by Duke University IACUC and adhered to host country's laws. Apes in African sanctuaries are typically born in the wild, and enter the sanctuary after being confiscated at an early age (~2-3 years old) as a result of the trade in wildlife for pets and bushmeat. Previous work indicates that sanctuary apes are psychologically healthy relative to other captive populations (Wobber and Hare, 2011). All subjects were socially housed, and free-ranged in large tracts of tropical forest during the day (5-40 hectares across groups). In the evening, all apes spent the night in indoor dormitories (12 m^2-160 m^2). Apes were tested individually in these familiar dormitory buildings. Following testing, all subjects were released back with their larger social groups outside. Subjects had ad libitum access to water and were not food-restricted during testing. In addition to the food the apes could eat in their forest enclosures, they were fed a variety of fruits, vegetables, and other species-appropriate foods two to four times daily. Apes were tested on only one session per day and all tests were voluntary. In Experiments 1 and 4, if a subject did not make a choice within five minutes, the session was aborted and the subject excluded from analyses. In Experiments 2 and 3, if a subject did not make a choice within one minute, the trial was repeated. If the subject did not make a choice for more than three trials, the session was aborted and the subject was excluded from any analyses.

Table 4: **Subject characteristics and participation in Chapter 3 Experiments 1-4. For sex, 'M' refers to males and 'F' to females. Age refers to age estimate in years. Asterisks denote subjects tested by Herrmann et al. (2013).**

Subject	Sex	Age		Exp. Participation
		Exp. 1	Exp. 2-4	
Api*	M	12	15	1 & 3
Bandundu*	F	15		1
Bili*	M	11	14	1 & 3
Bisengo	M	7		1
Boma	F		4	2 & 4
Chibombo	M		10	2-4
Dilolo*	M	11	14	1-4
Eleke	M		12	3 & 4
Elikiya	F		10	3
Fizi*	M	12		1
Ilebo*	M		14	2 & 4
Kalina*	F	14	17	1, 2, & 4
Kananga	F	5	8	1, 2, & 4
Kasongo*	M	10	13	1, 2, & 4
Katako	F	8	11	1-4
Kikwit*	M	15	17	1, 2, & 4
Kinshasa	F		10	2-4
Kinzia	F		4	2
Kisantu	F	14		1
Kodoro	M		8	2
Kole	M		9	4
Likasi*	F		14	2
Lisala*	F	11		1
Lomako	M		8	2 & 4
Lomami*	M	13	16	1-3
Lukuru	F		10	2-4
Mabali*	M		14	3 & 4
Malaika	F	5	8	1 & 2
Masisi	F	7	10	1, 3, & 4
Matadi*	M	11	14	1, 3, & 4
Maya	F	19		1
Mbandaka*	M		14	2
Moyi	M		8	2 & 4
Muanda	F		12	3 & 4
Opala*	F	7		1
Oshwe	M	4	7	1 & 4
Pole	M	6		1
Sake	F	7		1
Salonga*	F		18	3
Sandoa	F		10	2-4
Singi	M		6	2 & 4
Waka	F	7	10	1-4
Yolo*	M	9	12	1, 3, & 4

3.2.2 Experiment 1

3.2.2.1 Materials and Methods

3.2.2.1.1 Subjects

Twenty-four bonobos (aged 4-19; 12 females) participated in Experiment 1 (Table 5). All subjects completed each condition within one session on a single day. One additional subject, Chibombo (age 7, male), who was small enough to reach his entire arm through the bars, was excluded for repeatedly disrupting the experimenter's attempts to present the choices and ultimately making it impossible for the experimenter to test him.

Table 5: Subject characteristics and average choices in the test and control conditions of Chapter 3 Experiment 1. Test and Control refer to proportion of choices for the Hinderer and the Downward agent respectively.

Subject	Sex	Age	Test	Control
Api	M	12	0.75	0
Bandundu	F	15	0.5	0.5
Bili	M	11	0.75	0.5
Bisengo	M	7	0.5	0.5
Dilolo	M	11	0.5	0.5
Fizi	M	12	0.75	0.5
Kalina	F	14	1.0	0.5
Kananga	F	5	0.75	0.25
Kasongo	M	10	0.5	0.5
Katako	F	8	0.5	0.5
Kikwit	M	15	0.75	0.5
Kisantu	F	14	0.5	0.5
Lisala	F	11	0.75	0.5
Lomami	M	13	0.5	0.5
Malaika	F	5	0.5	0.25
Masisi	F	7	0.25	0.5
Matadi	M	11	0.75	0.5
Maya	F	19	1.0	0.25
Opala	F	17	1.0	0.5
Oshwe	M	4	0.5	0.75
Pole	M	6	0.5	0.5
Sake	F	7	0.75	0.5
Waka	F	7	0.25	0
Yolo	M	9	0.5	0.5

3.2.2.1.2 Procedure

Subjects were tested alone in a testing room. The experimenter positioned himself at a small table just outside of the testing room, across the mesh from the subject. The experimenter presented video stimuli to the subjects via an iPad and then allowed subjects to make choices by protruding their fingers through the mesh toward options presented on the table. The options were paper cutouts of animated agents from the videos. Importantly, previous work has demonstrated that apes equate 2-D depictions in video with real life objects (Leighty et al., 2008).

To begin presentation of the animations, the experimenter attracted the subject's attention by calling her name and began the video sequence, shifting the direction of the iPad to maximize viewing even if the subject moved or shifted her gaze. Additionally, subjects who moved to the back of the room (i.e., away from the iPad) or looked away from the iPad for more than several seconds were offered small pieces of food to regain their attention.

After the experimenter finished showing the animations, he either moved the table so that the subject was sitting at the midline of the table or used a piece of food to attract the subject to that location. This process ensured that during the choice phase, subjects had equal access to both options. The experimenter then simultaneously placed two pieces of apple on the middle of the table, held up $5cm^2$ cutouts of the two agents, laid them on top of the pieces of apples, moved the agents (and now occluded apples) to opposite sides of the table, and pushed the table forward to allow the subject to make a choice. To make a choice, subjects gestured toward one of the agents (i.e., protruding her finger through the mesh to touch the agent). Once the subject had made a choice, she was provided the paper cutout and associated apple. The other agent and apple piece were removed from the table. If a subject double-pointed (i.e., used both hands to select both options at the same time) or did not make a choice within a minute, the experimenter pulled the table back, and waited a few seconds before presenting the choice again. If the subject did not make a choice within five minutes, the session was aborted. However, this criterion was never met (i.e., all subjects made choices within the permitted time frame). The order of event presentation and locations of agents during choice was counterbalanced within subjects.

3.2.2.1.3 Design

All bonobos participated in both the test and control conditions, but at least two days elapsed between sessions. We counterbalanced condition order between subjects such that half began with the test condition and half the control.

Animated events were made on Adobe Flash Professional CS6. To control for the effect of any potential individual preferences for shape or color, four pairs of agents were created: red square and blue triangle, blue square and red triangle, orange pentagon and aqua trapezoid, and aqua pentagon and orange trapezoid. Each subject witnessed different agent pairs in test and control conditions that did not share any physical characteristics with each other (e.g. if the test agents were red square and blue triangle, the control agents could be orange pentagon and aqua trapezoid or aqua pentagon and orange trapezoid, but not blue square and red triangle). Agent pairs were assigned to subjects at equal frequency and the role of each agent as the Helper, Hinderer, Upward agent, and Downward agent was counterbalanced across subjects. The pair of agents assigned to a subject remained constant throughout the session.

To control for the fact that the Helper and Upward agent enter from the opposite side of the scene as the Hinderer and Downward agent, we created mirrored versions of all videos. For each subject, half of the presentations of each video were the original version and half were the mirrored version. We counterbalanced the order of original versus mirrored presentations within and between subjects.

Since during the familiarization phase, the video type (e.g., Helper video or Hinderer video) alternated four times (eg., Helper, Hinderer, Helper, Hinderer, Helper, Hinderer, Helper, Hinderer), we counterbalanced between subjects which video was shown first. We also counterbalanced within and between subjects which video played first during test trials.

3.2.2.1.4 Scoring and Analysis

Choices were scored live by the experimenter. All tests were videotaped, and a second coder blind to conditions and hypotheses scored 100% of sessions with excellent reliability [99.0% agreement, Cohen's kappa = 0.979]. Specifically, to ensure that the coder was blind, we renamed all videos with a number and told the coder to review the videos with the sound turned off. Since the vantage point of the video did not allow the coder to see the media displayed to the bonobo on the iPad, there was no way that he could have inferred the condition or the roles of the agents.

Although our sample size is large for animal cognition studies, it is not large enough to warrant parametric statistics. Therefore, we used non-parametric statistics. We analyzed subjects' choices in each condition using one-sample Wilcoxon signed rank tests and compared their choices between conditions using related samples Wilcoxon signed rank tests. Since our hypotheses offered opposite directional predictions, all analyses were two-tailed. We analyzed first-trial choices using Binomial tests, and used related samples Wilcoxon signed rank tests to compare subjects' performance on the first half versus the second half of a session.

3.2.2.2 Results

3.2.2.2.1 Coding and Analyses of Unintentional Cueing

To ensure that subjects' choices were not influenced by unintentional cuing in the experimenter's presentation of the choices in the test phase, two additional coders blind to condition and the role of each agent (see process for ensuring blindness in *Scoring and Analysis* section) reviewed the videos to determine if during the presentation of choices in either experiment the experimenter had placed either choice closer to the edge of the table, or stopped moving one choice earlier than the other. VirtualDub was used to allow coders to view the experimental videos frame by frame (30 frames/second). For each trial, coders skipped to a time when both options had been presented but before the subject had made a choice. To test whether E subconsciously placed the agents in a manner that might encourage the choice of one agent over the other simply because it was slightly closer to the subject, coders recorded whether one agent was placed closer to the edge of the table than the other. Visibility in videos permitted this "moved closer" coding in 190 of 192 trials. To test whether E subconsciously placed the agents in a manner that might encourage the choice of one agent over the other simply because the movements of the two agents ended at slightly different times, coders watched frame by frame in reverse, recording the frame for the moment when each hand first moved the agent. Watched forward this is the hand's final movement of the agent to its final choice location. One agent was considered to have stopped moving perceptibly earlier than the other if the difference between the left and right hands' final movement times was greater than 6 frames (200 ms) since this is the minimum time differential nonhuman apes need to perceive events (Inoue and Matsuzawa, 2007). Visibility in videos permitted this "moved later" coding in 182 of 192 trials.

Reliability on these measures was substantial (Landis and Koch, 1977) [moved closer: 91.1% agreement, Cohen's kappa = 0.767; moved later: 95.6%

agreement, Cohen's kappa = 0.754]. To determine if these measures contributed to our results, we reanalyzed the data from Experiment 1, excluding the trials on which both coders agreed that one agent was moved closer (35 trials) or moved later (14 trials). In both cases, we replicated our findings in the test condition: subjects exhibited a significant preference for the Hinderer [one sample Wilcoxon signed rank tests: moved closer trials excluded: $N = 23$, $p = 0.013$; moved later trials excluded: $N = 24$, $p = 0.015$]. Reanalysis of the control condition revealed that with moved closer trials excluded subjects had a preference for the Upward bound agent [$N = 24$, $p = 0.043$], the agent whose motor patterns mirrored the Helper not the Hinderer, and with moved later trials excluded subjects had no preference for either agent [$N = 24$, $p = 0.114$]. We also replicated our finding that subjects' choices in the test condition were significantly different from their patterns of choice in the control [related samples Wilcoxon signed rank tests: moved closer trials excluded: $z = -2.833$, $N = 23$, $T+ = 3$, ties = 4, $p = 0.005$; moved later trials excluded: $z = -2.913$, $N = 24$, $T+ = 3$, ties = 8, $p = 0.004$]. These results suggest that subjects' selection of the Hinderer in the test condition cannot be accounted for by a preference for the agent's motor pattern, and that presentation of one agent closer or later than the other is unlikely to have influenced our findings.

3.2.2.2.2 Developmental Analyses

To test whether humans are precocious relative to our closest relatives in the development of third-party social evaluation, we examined the relationship between age and social preference in bonobos. We split our subjects into adults and subadults, using a relatively conservative measure of maturity. Although in the wild bonobo females disperse from their natal group by ten years of age, individuals at Lola ya Bonobo sanctuary begin to reach sexual maturity at the very earliest at age 8 (Tan and Hare, 2013, Furuichi, 2011). Therefore, we grouped individuals 9 and above into our adult cohort (N = 15; aged 9-19; 6 females) and those 8 and below into our subadult cohort (N = 9; aged 4-8; 6 females). Like the population overall, adults exhibited a robust preference for the Hinderer [one-sample Wilcoxon signed rank test, $N = 15$, $p = 0.006$] but no preference in the control condition [$N = 15$, $p = 0.180$], and chose the Hinderer significantly more frequently than the Downward agent [related samples Wilcoxon signed rank test, $z = -2.719$, $N = 15$, $T+ = 9$, ties = 6, $p = 0.007$]. Subadults, however, showed no preference in the test [$N = 9$, $p = 1.000$] or control [$N = 9$, $p = 0.257$], and no difference in choice patterns between conditions [$z = -1.000$, $N = 9$, $T+ = 4$, ties = 3, $p = 0.317$]. Further, there was a significant difference in choice patterns between the older and younger cohorts in the test [Mann-Whitney U test: U = 33.000, z = -2.211, $N_{age\ 4\text{-}8} = 9$, $N_{age\ 9\text{-}19} = 15$, $p = 0.027$] but not in the control [Mann-Whitney U test: U = 61.000, z = -0.510, $N_{age\ 4\text{-}8} = 9$, $N_{age\ 9\text{-}19} = 15$, $p = 0.610$]. These results suggest that social preference may not emerge in bonobos until maturity, and that there may have been a shift in the ontogeny of this trait since humans and bonobos diverged. Studies with chimpanzees are necessary to more confidently infer whether bonobos are developmentally delayed, or humans precocious, relative to the ancestral condition.

3.2.2.2.3 Within-Session Analyses

To assess how quickly bonobos formed their preferences we examined their choices on the first trial. Subjects did not show a first trial preference for either agent in the test [Binomial test, $N = 24$, $p = 1.000$] or control [Binomial Test, $N = 24$, $p = 0.064$], and showed no difference between conditions [Wilcoxon signed rank test, z = -1.508, $N = 24$, T+ = 8, ties = 13, $p = 0.132$). For each condition, we then compared subjects' preferences in the first half of the session with that of the second half. There were no differences in choice patterns between the first and second half of the test [Wilcoxon signed rank test, z = -0.443, $N = 24$, T+ = 6, ties = 11, $p = 0.658$] or control conditions [Wilcoxon signed rank test, z = -0.707, N

= 24, T+ = 2, ties = 19, $p = 0.480$], indicating that subjects' choices (i.e., preference for the Hinderer and no preference among Upward/Downward agents) were consistent throughout each session.

3.2.3 Experiment 2

3.2.3.1 Materials and Methods

3.2.3.1.1 Subjects

Twenty-two bonobos participated in this experiment (ages 4-17, 11 females; see Table 6). An additional subject (Mabali) was tested but excluded due to experimenter error. We also attempted to test two other subjects (Api and Tshilomba) who were dropped for refusing to participate (see exclusion criteria in General Methods: Subjects).

Table 6: Subject characteristics and proportion of trials in which each subject selected the Hinderer in Chapter 3 Experiment 2.

Subject	Sex	Age	Hinderer Choice
Boma	F	4	0.625
Chibombo	M	10	0.875
Dilolo	M	14	0.25
Ilebo	M	14	0.5
Kalina	F	17	0.75
Kananga	F	8	0.375
Kasongo	M	13	0.5
Katako	F	11	0.5
Kikwit	M	17	0.625
Kinshasa	F	10	0.75
Kinzia	F	4	0.375
Kodoro	M	8	0.5
Likasi	F	14	0.5
Lomako	M	8	0.5
Lomami	M	16	0.75
Lukuru	F	10	0.75
Malaika	F	8	0.25
Mbandaka	M	14	0.625
Moyi	M	8	0.5
Sandoa	F	10	0.75
Singhi	M	6	0.5
Waka	F	10	0.375

3.2.3.1.2 Procedure

Subjects participated in a series of eight trials in a single session. Each trial consisted of a social demonstration followed by a choice between two experimenters. Social demonstrations involved three human experimenters: E1, the Helper, and the Hinderer. E1 was always played by CK. The Helper and

Hinderer were played by two Congolese men of similar age who were familiar with the sanctuary but had never interacted with the bonobos. Their roles were counterbalanced across subjects. Before the first trial, subjects watched the social demonstration two times (i.e., three times before the first choice) to ensure that by their first choice they were familiarized to the behavior of each experimenter. If before the start of a social demonstration the subject was distracted or in the back of the testing room E1 gave the subject a piece of food to attract her over to witness the social demonstration. The social demonstration began promptly after her approach.

During each social demonstration, E1 sat on the floor between the Helper and the Hinderer (unfamiliar human actors). All three faced the subject just outside of the subject's testing room. E1 held a stuffed cookie-monster toy, which he threw in the air and caught several times while mimicking bonobo laughter. On the third throw, E1 dropped the toy and it landed in front of him, out of reach. He said, "oh!" and reached effortfully for it. At this time, the Helper calmly picked up the toy, made eye contact with E1, and attempted to hand the toy to E1. Just before E1 was able to take the toy, the Hinderer quickly snatched it from E1, made an aggressive vocalization, turned his back to the other actors, and surreptitiously deposited the toy in a bucket between himself and E1.

In test trials, the choice phase immediately followed the social demonstration. All three experimenters stood up and turned their backs to the bonobo. At the same time, E1 handed the Helper and the Hinderer a piece of apple. E1 then turned around, made sure that the Helper and Hinderer were roughly 1m apart, and used a piece of apple to attract the bonobo a position in between them. When the bonobo was centered, E1 said, "ok." At this time, the Helper and Hinderer turned around to face the subject, and approach the bonobo's enclosure at the same time, with apple in hand. When the experimenters arrived, E1 started a stopwatch and the bonobo had one minute to choose between the experimenters. A choice was made if the subject approached one experimenter and gestured toward the food with her hand or mouth (i.e., put her hand or mouth up to the mesh where the experimenter held the food). She was then given the piece of apple by the experimenter she chose. All experimenters then turned around and the unchosen experimenter's food was placed in the bucket. The experimenters sat in the appropriate location for the next trial's social demonstration, which began immediately.

3.2.3.1.3 Design

We counterbalanced the locations of the Helper and Hinderer across trials (i.e., which experimenter was positioned to the left and which to the right of E1). Half of the subjects experienced ABBABAAB order while the other half experienced BAABABBA order. Experimenters remained in the same location for the social demonstration and choice phase of a given trial. During the two familiarization social demonstrations that preceded the first trial, experimenters occupied the positions assigned to them for the first trial.

3.2.3.1.4 Scoring and Analysis

E1 live-scored the subject's choices. A second coder, blind to hypotheses and experimenters' roles, reviewed video footage of 23% of trials and coded subjects' choices for reliability, achieving perfect agreement (100% agreement, Cohen's kappa = 1.0). Coders recorded which experimenter (Left or Right) the subject selected first. As with live-scoring, a choice was made if the subject approached one experimenter and gestured toward the food with her hand or mouth (i.e., put her hand or mouth up to the mesh where the experimenter held the food).

We calculated the proportion of choices of the Hinderer for each subject and performed a one-sample Wilcoxon signed-rank test to determine whether subjects exhibited a significant bias for choosing the hinderer. To remain conservative, analyses were again two-tailed.

3.2.4 Experiment 3

3.2.4.1. Materials and Methods

3.2.4.1.1 Subjects

Eighteen subjects participated in this experiment (ages 10-18, 9 females; Table 7). Because of our finding in Experiment 2 that only adults exhibited the Hinderer preference, we restricted our sample to individuals 9 and older. We attempted to test an additional eight subjects who were dropped for refusing to participate (Bandundu, Boende, Isiro, Kalina, Lisala, Maya, Mbandaka, and Tshilomba; see exclusion criteria in General Methods: Subjects).

Table 7: Subject characteristics and choices in Chapter 3 Experiment 3. Baseline and Test reflect proportion of choices for the experimenter who played the Hinderer in the test. Shift is the difference score between these values—the shift in favor of the Hinderer.

Subject	Sex	Age	Baseline	Test	Shift
Api	M	15	0	0.5	0.5
Bili	M	14	0.25	0.25	0
Chibombo	M	10	0.25	0.25	0
Dilolo	M	14	0.5	0.5	0
Eleke	M	12	0	0.25	0.25
Elikiya	F	10	0.25	0	-0.25
Katako	F	11	0.5	0.25	-0.25
Kinshasa	F	10	0.5	1.0	0.5
Lomami	M	16	0.25	0.25	0
Lukuru	F	10	0.5	0.25	-0.25
Mabali	M	14	0.5	0.75	0.25
Masisi	F	10	0.5	0.75	0.25
Matadi	M	14	0	0.25	0.25
Muanda	F	12	0	0.25	0.25
Salonga	F	18	0.5	0.75	0.25
Sandoa	F	10	0.25	0.75	0.5
Waka	F	10	0.25	0.25	0
Yolo	M	12	0.25	0.5	0.25

3.2.4.1.2 Procedure and Design

The procedure and design of this study were similar to that of Study 2, except for three key differences. First, we altered the choice phase of the task. Although the Helper and Hinderer still held out a piece of apple to the bonobo, this food was not given to the subject after she made her choice. That is, the Helper and Hinderer never provisioned the subject; the subject only received food from E1, the neutral actor. Second, test trials were preceded by four baseline trials to measure any pre-existing preferences for the experimenters. Baseline trials involved only the choice phase from Experiment 2. If the subject demonstrated a preference for one experimenter during baseline trials (i.e., choosing him three or four times), that experimenter was assigned to the role of the Helper. If the subject chose each experimenter twice, the experimenters were assigned to their roles pseudo-randomly, based on the criteria of counterbalancing each individual's roles across subjects. Finally, subjects only participated in four instead of eight test trials. As in Experiment 2, subjects witnessed the social demonstration three times before the choice phase of the first test trial, but only once before the choice phase of each of the other test trials. The social demonstration was identical to that in Experiment 2. Locations of the experimenters were counterbalanced across trials, with the same order repeated in both baseline and test trials. Half of subjects experienced ABBA order and the other half BAAB order.

3.2.4.1.3 Scoring and Analysis

Again, E1 live coded subjects' choices and a second blind coder reliability coded 22% of trials, using the same choice criteria as Experiment 2. Agreement was perfect (100% agreement, Cohen's kappa = 1.0). We then calculated a difference score by subtracting the proportion of choices of the hinderer in test trials from that in baseline trials. We performed a one-sample Wilcoxon signed-rank test to determine whether this value differed significantly from zero, which would indicate a significant preference shift toward the Hinderer.

3.2.5 Experiment 4

3.2.5.1 Materials and Methods

3.2.5.1.1 Subjects

Twenty-four subjects participated in this experiment (ages 4-17, 10 females; Table 8). We attempted to test one additional subject (Kalina) who was dropped for refusing to participate (see exclusion criteria in General Methods: Subjects).

Table 8: Subject characteristics and choices in Study 4. Test and Control refer to proportion of choices for the Dominant agent and for the Dominant Control agent respectively. Choices that differ from 0.5 are bolded.

Subject	Sex	Age	Test	Control
Boma	F	4	**0.75**	0.5
Chibombo	M	10	0.5	0.5
Dilolo	M	14	**1.0**	**0.75**
Eleke	M	12	0.5	0.5
Ilebo	M	14	0.5	**0.75**
Kalina	F	17	0.5	0.5
Kananga	F	8	**0.75**	0.5
Kasongo	M	13	0.5	0.5
Katako	F	11	0.5	0.5
Kikwit	M	17	**0.75**	**0.25**
Kinshasa	F	10	0.5	0.5
Kole	M	9	0.5	0.5
Lomako	M	8	0.5	0.5
Lukuru	F	10	**0.75**	0.5
Mabali	M	14	**0.75**	0.5
Masisi	F	10	**1.0**	**0.75**
Matadi	M	14	0.5	0.5
Moyi	M	8	0.5	0.5
Muanda	F	12	**0.75**	**0.75**
Oshwe	M	7	0.5	0.5
Sandoa	F	10	0.5	0.5
Singi	M	6	0.5	0.5
Waka	F	10	0.5	0.5
Yolo	M	12	0.5	0.5

3.2.5.1.2 Procedure and Design

The procedure and design of Experiment 4 were identical to that of Experiment 1, save for the use of different animations. In addition, in these studies both animated shapes were included within a single animation. The test animation featured one Subordinate agent moving to a coveted location and being displaced several times by a second more Dominant agent. That is, each time that the Subordinate moved to the coveted location, the Dominant rushed in, pushed the Subordinate off of the spot, and returned to occupy the location briefly. Eventually the Dominant moved from the coveted location. Once the Dominant arrived at its rest location, the Subordinate then slowly inched back to the coveted location before being displaced again by the Dominant.

To ensure that subjects' choices did not reflect preferences for a motion pattern rather than for the social content of the video, the control animation involved identical movements as those in the test but the contingency between the agents' actions was removed. That is, the first agent moved to and then away from the coveted location before the second agent moved to and away from that location. As in Experiment 1, the shapes and colors of the agents were counterbalanced such that for a given subject each role (i.e., Dominant, Subordinate, Control Dominant, Control Subordinate) was occupied by a different agent, but across subjects each agent was used equally for each role.

3.2.5.1.3 Scoring and Analysis

E1 live scored subjects' choices and a second coder, blind to condition, role of the agents, and hypotheses, coded 100% of trials, using the same criteria for marking a choice as Experiment 1. Agreement was perfect (100% agreement, Cohen's kappa = 1.0). We calculated for each subject the proportion of choices of the Dominant agent in the test and the Dominant control in the control condition. We performed one-sample Wilcoxon signed-rank tests to determine whether subjects exhibited a significant bias for choosing that Dominant or Dominant control. We also compared subjects' tendency to choose the Dominant in the test condition with their tendency to choose the Dominant control in the control condition using a related samples Wilcoxon signed rank test. All analyses were two-tailed.

4 Proximate benefits of third-party knowledge in wild chimpanzees

Humans are defined, in no small part, by their social intelligence. An acute awareness of their social environment—and of the minds and relationships that comprise it—enables humans to advance their own interests in the face of the conflicting interests of others. Understanding others' perspectives facilitates the management of both cooperative and competitive relationships and one's own reputation within the group. According to the dominant evolutionary explanation, the demands posed by this complex social environment are the very pressures that selected for the evolution of social intelligence. Specifically, the *social intelligence hypothesis* (Jolly, 1966, Humphrey, 1976, Byrne and Whiten, 1988) proposes that, since social animals must compete with their own groupmates for access to reproductive opportunities, those individuals who can outwit their competitors will experience higher fitness, and selection will favor more advanced social cognition.

In support of the social intelligence hypothesis, phylogenetic comparisons across primates have identified a robust positive relationship between coarse proxies for social complexity (e.g., group size) and various measures of brain size (Dunbar and Shultz, 2007). Further, some studies have shown that more "socially complex" species exhibit greater social cognitive skill than closely-related but less social species (where social complexity is defined by group size or fission fusion social systems: e.g., Bond et al., 2003, Maclean et al., 2008, Sandel et al., 2011, Maclean et al., 2013, Amici et al., 2008). However, very few studies have investigated either the proximate or ultimate benefits of social cognition in wild populations (Seyfarth and Cheney, 2015).

Evidence that social cognition may be under selection in wild primate populations is limited to a few studies that have linked potentially cognitively complex social behavior, such as deception and coalitionary support, to mating or paternity success (Duffy et al., 2007, Schulke et al., 2010, Gilby et al., 2013a, le Roux et al., 2013). For example, individuals of many species—including chimpanzees (*Pan troglodytes*)—team up with one another in an attempt to overpower their rivals and improve their own social status—and many have argued that these strategic coalitionary alliances likely rely on a sophisticated knowledge of third-party relationships (de Waal, 1982, Muller and Mitani, 2005, Watts, 2009, Silk, 1999). According to this *third-party relationships hypothesis*, animals solicit coalition partners based on awareness of the available partners' relationships with the solicitor's opponent, e.g., recruiting individuals who outrank their opponent or avoiding the kin, bond, or coalition partners of their opponent. The alternative (though not mutually exclusive) *direct relationships hypothesis* suggests that animals base their choices on their own relationships with the available recruits, preferring their own kin, bond, and coalition partners, and individuals who outrank themselves. Gilby et al. (2013a) demonstrated that, for male chimpanzees, coalitionary aggression is positively associated with attainment of high rank and reproductive success. This finding raises the possibility that third-party knowledge evolved in part due to its benefits during coalitionary aggression—if it is indeed involved in coalitionary decision-making. However, existing studies that have explored links to fitness have used only social behavior (e.g. the occurrence of coalitionary aggression) as a proxy for social cognition; none have used controlled measures of social cognition themselves.

Moreover, although the studies that have directly demonstrated social cognition in the wild have often speculated about the proximate benefits of these cognitive abilities (e.g., Cheney and Seyfarth, 1990, Bergman et al., 2003, Perry et al., 2004, Cheney and Seyfarth, 2007, Crockford et al., 2007, Slocombe and Zuberbuhler, 2007, Wittig and Boesch, 2010, Crockford et al., 2012, Wittig et al., 2014b), there exists little, if any, evidence of empirical links between cognitive traits and any proximate benefits in wild primates. For example, Slocombe and

Zuberbuhler (2007) examined recruitment calls of chimpanzees who were victims of aggression. Although chimpanzees modified their recruitment calls to exaggerate the severity of aggression when in the presence of a bystander who outranked their attacker (as compared to one who just outranked themselves), the authors did not find evidence that this apparent application of third-party knowledge had any impact on bystander intervention. Therefore, there exists little direct evidence for proximate mechanisms that may mediate a relationship between social intelligence and fitness in wild primates.

Chimpanzees experience a particularly dynamic social environment. They live in large communities of familiar individuals, sometimes numbering almost 200 (Wilson et al., 2014). These communities are characterized by a fission-fusion grouping structure wherein individuals range in smaller foraging parties that may change in social composition many times per day (Goodall, 1986), and consequently—even more than in species that live in fixed groups—chimpanzees possess the agency to intentionally select their social partners (Foerster et al., 2015). These characteristics may also make tracking third-party relationships particularly cognitively demanding for chimpanzees, since the number of dyadic relationships in the largest groups can exceed tens of thousands and at best they only have incomplete social information (given that they spend varying amounts of time in ranging parties with each dyad).

According to the social intelligence hypothesis, social cognition evolved in response to exactly the types of complex within-group competition (e.g., involving coalitions) that chimpanzees experience. Indeed, observational and experimental studies have demonstrated that chimpanzees possess cognitive abilities that could provide fitness benefits in this environment: they track third-party relationships and understand others' perspectives (e.g., Hare et al., 2000, Hare et al., 2001, Slocombe and Zuberbuhler, 2007, Call and Tomasello, 2008, Wittig and Boesch, 2010, Hare, 2011, Yamamoto et al., 2012, Herrmann et al., 2013, Wittig et al., 2014b). For example, in several studies after viewing human actors sharing or refusing to share food with a third-party, chimpanzees preferred to beg for food from the individual who previously shared (Herrmann et al., 2013, Russell et al., 2008, Subiaul et al., 2008). In a field experiment, two hours after an aggressive interaction, chimpanzees heard playbacks of aggressive barks by a bystander who was or was not a close affiliate of their recent opponent. Chimpanzees looked longer and moved away more often in response to barks by the close affiliate. Regardless of the specific mechanism underlying social knowledge (Cheney and Seyfarth, 2007, Fagot and Cook, 2006, Flemming et al., 2013), these studies show that chimpanzees inform their social decisions based on observations of third-party interactions and relationships.

Critically, however, no studies have demonstrated that chimpanzees use third-party knowledge to strategically recruit coalition partners (although experimental work has shown that they use direct relationship information for recruitment: Melis et al., 2006b). Therefore, to investigate the selective advantage of social intelligence in wild chimpanzees, we sought first to provide evidence that they exploit awareness of third-party relationships in partner choice, and second to determine whether they accrue any proximate benefits from doing so.

4.1 Results

4.1.1 Chimpanzees exploit third-party knowledge in partner choice

From 18 years of data on wild chimpanzees (*P. t. schweinfurthii*) at Gombe National Park, Tanzania, we identified clear instances of dyadic male aggression in which one contestant (the "solicitor") attempted to recruit support from a bystander (the "recruit") against his "opponent". We recorded all adult male bystanders present at each event (i.e., all potential recruits, since only adult males were targets of recruitment attempts) and quantified their relationships with both the solicitor and the opponent. To fully characterize each pair's relationship, we calculated separate measures for kinship, social-bond strength (based on grooming), coalition frequency, and rank.

The direct relationships hypothesis, which holds that recruitment decisions are based on one's own relationship with potential coalition partners, predicts that solicitors preferentially recruit their own kin, individuals with whom they have stronger social bonds or frequently form coalitions, and individuals who are most dominant to them. The third-party relationships hypothesis, which asserts that chimpanzees rely on third-party knowledge to make recruitment decisions, predicts that they preferentially recruit bystanders who are most dominant to their opponent and avoid their opponent's kin and individuals with whom their opponent has strong bonds or a history of frequent coalitions.

We used a Generalized Linear Mixed Model (model 1) to identify which relationship measures predicted whether the solicitor attempted to recruit a given bystander. We included three rank-based predictors in our model: (1) rank difference between the bystander and the opponent (as a measure of third-party knowledge), (2) rank difference between the bystander and the solicitor (to control for the possibility that chimpanzees simply solicit individuals who are most dominant to themselves, without regard for third-party relationships; the direct relationship alternative), and (3) whether the bystander was the highest ranking individual present (to control for the possibility that chimpanzees can discern, and choose, the most dominant individual through subtle behavioral cues; the dominance heuristic alternative). We also included in the model binary measures of kinship between the bystander and the solicitor and opponent and continuous measures of bond strength and coalition frequency between the bystander and both the solicitor and opponent.

As predicted by the direct relationships hypothesis, chimpanzees' own relationships with bystanders significantly influenced which bystanders were solicited (Table 9). Chimpanzees were more likely to solicit help from their own kin ($p = 0.036$), from individuals with whom they had stronger social bonds ($p = 0.054$), from individuals with whom they frequently formed coalitions ($p = 0.003$), and from individuals who were most dominant to them ($p = 0.018$). Critically, we also found support for the third-party relationships hypothesis: the rank difference between the bystander and the opponent significantly predicted whether the bystander was solicited ($p = 0.031$). This variable was significant while controlling for the two alternative cognitively simpler strategies (i.e., the direct relationship and dominance heuristic alternatives). However, there was no evidence that chimpanzees avoided the kin, bond partners, or frequent coalition partners of their opponents. Taken together, these results suggest that chimpanzees employ a mixed strategy in partner choice, soliciting their own kin, bond partners, and coalitionary allies, but also using third-party rank knowledge in order to specifically recruit bystanders who can overpower their opponent.

Table 9: Results of model 1 examining the impact of direct and third-party relationship measures on solicitors' choice of recruits. Significant main effects ($p < 0.05$) are shown in bold and italics and trends ($p < 0.10$) only in bold.

	Estimate	Std. Error	z-value	p-value
Intercept	-2.708	0.242	-11.169	<0.001
Bystander-Opponent Rank Difference	1.662	0.769	2.162	***0.031***
Bystander-Solicitor Rank Difference	2.000	0.846	2.363	***0.018***
Highest-ranking bystander?	-0.014	0.404	-0.036	0.971
Bystander-Opponent Kinship	0.484	0.451	1.072	0.284
Bystander-Solicitor Kinship	0.866	0.412	2.100	***0.036***
Bystander-Opponent Bond Strength	19.806	23.194	0.854	0.393
Bystander-Solicitor Bond Strength	47.364	24.59	1.926	**0.054**
Bystander-Opponent Coalition Frequency	-1.393	0.963	-1.447	0.148
Bystander-Solicitor Coalition Frequency	2.638	0.900	2.945	***0.003***

4.1.2 Third-party knowledge conveys proximate benefits

Having provided evidence that wild chimpanzees exploit third-party knowledge of relative dominance rank in partner choice, we sought to determine whether doing so provided any proximate benefits. To test this hypothesis, we ran two additional multiple regression models, each investigating whether any direct or third-party relationship measures predicted a particular outcome. In the first of these models (model 2; Table 10), we examined which relationship measures influenced recruit intervention. Interestingly, although interventions occurred following 51.6% of recruitment attempts, none of the direct or third-party metrics predicted whether the recruit intervened in support of the solicitor (Table 10).

Table 10: Results of model 2 examining the impact of direct and third-party relationship measures on recruit intervention. Significant main effects (*p* < 0.05) are shown in bold and italics and trends (*p* <0.10) only in bold.

	Estimate	Std. Error	z-value	p-value
Intercept	-0.207	0.42	-0.492	0.623
Recruit-Opponent Rank Difference	0.303	1.202	0.252	0.801
Recruit-Solicitor Rank Difference	0.849	1.184	0.717	0.473
Highest-ranking bystander?	0.181	0.592	0.305	0.76
Recruit-Opponent Kinship	0.108	0.618	0.174	0.862
Recruit-Solicitor Kinship	-0.405	0.726	-0.558	0.577
Recruit-Opponent Bond Strength	1.911	33.820	0.056	0.955
Recruit-Solicitor Bond Strength	12.180	42.326	0.288	0.774
Recruit-Opponent Coalition Frequency	-0.989	1.593	-0.621	0.535
Recruit-Solicitor Coalition Frequency	0.706	1.132	0.624	0.533

It may be that the threat of intervention by a powerful bystander is sufficient to subdue the opponent following a well-targeted recruitment attempt. Therefore, in the final model (model 3; Table 11), we investigated the link between the direct and third-party relationship measures and whether or not, following the recruitment attempt, the opponent ceased aggression toward the solicitor. Critically, only the rank difference between the recruit and the opponent predicted whether the opponent terminated aggression (Table 11; p = 0.01). That is, when solicitors selected a powerful recruit who was most dominant to their opponent, they were significantly more likely to avoid further aggression. This finding therefore suggests that chimpanzees are able to reap an immediate proximate benefit—escaping aggression—through tactical employment of third-party knowledge.

Table 11: Results of model 3 examining the impact of direct and third-party relationship measures on whether or not the opponent ceased aggression toward the solicitor. Significant main effects ($p < 0.05$) are shown in bold and italics and trends ($p < 0.10$) only in bold.

	Estimate	Std. Error	z-value	p-value
Intercept	0.567	0.567	0.999	0.318
Recruit-Opponent Rank Difference	4.089	1.596	2.562	***0.010***
Recruit-Solicitor Rank Difference	-0.783	1.581	-0.495	0.62
Highest-ranking bystander?	-0.950	0.864	-1.099	0.272
Recruit-Opponent Kinship	1.124	1.007	1.117	0.264
Recruit-Solicitor Kinship	0.209	0.920	0.227	0.820
Recruit-Opponent Bond Strength	11.278	44.281	0.255	0.799
Recruit-Solicitor Bond Strength	-11.871	55.889	-0.212	0.832
Recruit-Opponent Coalition Frequency	5.038	3.098	1.626	0.104
Recruit-Solicitor Coalition Frequency	-0.332	1.536	-0.216	0.829

4.2 Discussion

We have shown here that wild chimpanzees appear to employ a mixed strategy to solve competitive social problems. Our findings provide support for both the direct relationships and third-party relationships hypotheses, and are consistent with the hypothesis that male chimpanzees in dyadic conflicts attempt to recruit coalition partners based both on their own relationships with the available bystanders, and also on those bystanders' relationships with the solicitor's opponent. Specifically, chimpanzees attempted to recruit their own kin, individuals with whom they had stronger social bonds and more frequent histories of coalitions, and individuals who were most dominant to them. Most interestingly, controlling for solicitors' use of their own dominance relationship with the available bystanders, chimpanzees also directed their recruitment attempts at bystanders who were most dominant to their opponent. Our models included co-variates to control for two alternative explanations—that chimpanzees solicited individuals who were most dominant to themselves, and that they solicited the most dominant individual available—suggesting that our findings reflect use of third-party knowledge.

The strongest alternative account is that behavioral cues by bystanders, for example of their interest in intervening, influenced chimpanzees' solicitations. However, when controlling for the other factors in our model, we did not find evidence that chimpanzees tended to solicit help from the highest-ranking available bystander—who may be most likely to exhibit such cues. Moreover, bystanders who were targeted for recruitment did not intervene in roughly half of our events, suggesting that chimpanzees were not simply cuing into reliable indicators of a bystander's interest in joining the conflict. Similarly, we did not find evidence that the relationship measures that predicted solicitors' choices actually influenced whether the recruit intervened. This finding further suggests that chimpanzees were not simply responding to behavioral cues of a bystander's desire to intervene. Finally, captive experiments have provided evidence that chimpanzees do use third-party information in partner choice, while controlling for the behavior of third-parties (e.g., Russell et al., 2008, Subiaul et al., 2008, Herrmann et al., 2013). While we can't completely rule out this alternative account, these findings support the interpretation that wild chimpanzees relied on awareness of third-party relationships when attempting to recruit coalition partners. Our results contribute to a growing literature on chimpanzees' and other primates' complex understanding of their social environment, which includes both observational studies and well-controlled experiments (e.g., Dasser, 1988, Cheney and Seyfarth, 1990, Silk, 1999, Hare et al., 2000, Hare et al., 2001, Bergman et al., 2003, Perry et al., 2004, Schino et al., 2006, Cheney and Seyfarth, 2007, Slocombe and Zuberbuhler, 2007, Wittig and Boesch, 2010, Hare, 2011, Yamamoto et al., 2012, Herrmann et al., 2013, Wittig et al., 2014b).

Although recruits often intervened in support of the solicitor, there was no evidence that reliance on any specific direct or third-party relationship information when selecting a recruit affected whether a recruit came to the solicitor's aid. However, we did find that evidence that exploitation of third-party knowledge successfully functioned to subdue the opponent, allowing the solicitor to escape further aggression. Specifically, the more the recruit outranked the opponent, the greater the probability that the opponent ceased aggression toward the solicitor. Presumably, the threat of intervention by a more powerful bystander was sufficient to intimidate the opponent. Thus, our findings suggest that strategic decision-making based on third-party knowledge yields immediate proximate benefits in wild chimpanzees. That a chimpanzee's attainment of rank and reproductive success is directly impacted by his position within the coalitionary network—and specifically his connection to males that are not themselves well connected (Gilby et al., 2013a)—further suggests that there may be a direct link, though current untested, between third-party knowledge and fitness in this species.

Our findings provide support for the social intelligence hypothesis that the demands of within-group competition have shaped the minds of social animals, favoring individuals with the greatest social intelligence (Byrne and Whiten, 1988, Humphrey, 1976, Jolly, 1966). Chimpanzees who appeared to use social intelligence to solve social conflicts were more successful at escaping further aggression than those who didn't. Future work in primates and nonprimates alike should continue to test this hypothesis by investigating links between controlled measures of social cognition and proximate and ultimate benefits in wild populations. Our sample size was unfortunately too small to investigate a relationship between individual differences in choice patterns and differential attainment of proximate benefits or reproductive success, and doing so should be a priority of future research. Controlled experiments should also aim to further pin down the cognitive underpinnings of third-party knowledge in primates and other animals. Still, the findings presented here are consistent with the hypothesis that social intelligence is directly linked to the attainment of proximate benefits in wild primates. They therefore help to elucidate the proximate mechanisms that have likely shaped the social cognitive abilities of primates, including humans, throughout evolutionary history.

4.3 Materials and Methods

4.3.1 Study site and data collection

The Kasekela chimpanzee community in Gombe National Park, Tanzania has been studied since 1960. Since 1973, field assistants have conducted full-day focal follows of adult chimpanzees (Goodall, 1986), recording party composition, grooming involving the focal individual, pant grunts (submissive vocalizations), and detailed accounts of all observed aggressive interactions, among other behaviors, in the focal chimpanzee's party. Field data are digitized, translated, and extracted into a relational database that is maintained by the Jane Goodall Institute Research Center at Duke University and Arizona State University.

We adapted methods used by Silk (1999). Using 18 years of data from 1994-2011 (which have been fully translated and digitized), we performed keyword searches of the narrative notes to identify all explicit instances of dyadic male aggression in which one contestant (the solicitor) solicited help from a bystander male (the recruit) against their opponent. We restricted our sample to those events in which (1) all actors (solicitor, opponent, and recruit) were adults (at least age 12—the youngest age of successful male reproduction at Gombe: (Wroblewski et al., 2009)), (2) the description of the help solicitation was clear (e.g., using language such as "solicit help," "seek help," or "seek support.") and targeted at a specific bystander, and (3) there were at least two adult male bystanders who could have been solicited. We favored these conservative inclusion criteria as our aim was not to capture every single help solicitation event (e.g., to characterize their frequency), but rather to identify and analyze cases with the highest degree of certainty.

In total, we identified 102 events that met these criteria, involving 15 solicitors and13 opponents. Since males exclusively solicited help from other adult males (i.e. never from females or juvenile males), we documented all adult males who were present in the party at the time of the event (*N* = 19 different males across events), and treated these bystanders as potential recruits. We then quantified the relationship between the solicitor and the opponent with each of these bystanders, in terms of kinship, bond strength (based on patterns of grooming), coalition frequency, and rank.

4.3.2 Relationship measures

4.3.2.1 Kinship

For the purposes of this study, we counted as kin only maternal brothers because this relationship can be discerned from joint association with a mother and evidence for paternal kin recognition remains limited (Lehmann et al., 2006). Moreover, partner preference should be most pronounced in kin who are most closely related and who have the highest degree of certainty of relatedness—if kin selection actually impacts cooperative behavior in this species (Langergraber et al., 2007, Packer et al., 1991). In total our sample includes 5 pairs of maternal brothers (AL/AO, GB/GL, FD/FR, FD/FO, and FR/FO).

4.3.2.2 Bond Strength (Grooming Index)

To quantify social bonds between individuals, we divided the data into two-year periods and calculated *grooming indices (GI)* between all males who were adults at the start of a period and still alive at the end of it. Use of two year periods for assessing grooming relationships is established in the literature, since this window allows researchers to maximize sample size (i.e., to avoid losing subjects in cases of sparse grooming data) while still capturing changes in relationships over time (e.g., Foerster et al., 2015, Machanda et al., 2013). This formula, based on Machanda et al. (2013), produces a grooming rate that controls for the time a dyad spent together. Since grooming is only recorded for focal chimpanzees, we quantified the duration of time that chimpanzees A and B were observed grooming and divided that value by duration in which chimpanzee A or B was focal and the other was present in the group:

$$Groom_{AB} = \frac{A_f B_{groom} + B_f A_{groom}}{A_f B_p + B_f A_p}$$

where A_fB_{groom} is the duration of time that A groomed B, B_fA_{groom} is the duration of time that B groomed A, A_fB_p is the duration of time in which A was focal and B was present in the party, and B_fA_p is the duration of time in which B was focal and A was present in the party (Machanda et al., 2013). The principal drawback of using a grooming rate that controls for time observed together is that it treats as equal dyads that spend vastly different amounts of time together but groom at the same rate when they are together. However, this method is preferable to an absolute measure of time spent grooming, since such a measure is influenced by biases in time spent observing each chimpanzee.

4.3.2.3 Coalition Frequency

Coalitions are defined as events in which two or three adult males jointly direct aggression toward a single target male (Harcourt and de Waal, 1992). We used the list of coalitions identified by Gilby et al. (2013a) (N=365) and expanded it using the same extraction methods. We ensured that no help solicitation events were included in this sample to avoid circularity. We used the same two-year periods and a similar procedure to that used to produce the GI, to calculate our *coalition frequencies (CF)*. The CF is the number of coalitions a dyad performed within a period divided by the amount of time (per 100 hrs) the dyad spent in the same party while at least one other adult male was present (who could be targeted for a coalition).

4.3.2.4 Rank

We used the ELO score method (Neumann et al., 2011) to calculate rank, since this method allows for the calculation of each male's rank on the day of each solicitation event. As is customary with chimpanzee field studies (Bygott, 1979, Hayaki et al., 1989), rank calculations were based on pant grunts, since these vocalizations communicate submission. K, which determines how drastically ranks change following each dominance interaction, was set at 200. All males entered the hierarchy with a value of 1000 at age 10, so that they would have an accurate rank (based on a minimum of nine dominance interactions (Neumann et al., 2011)) by age 12. After each pant grunt interaction, the ranks of both participants are updated, with the winner gaining points and the loser losing points. Unexpected outcomes (i.e., those incongruent with existing rank relationships) yield greater changes in rank than unexpected outcomes. To ensure model stability, we scaled Elo scores (to the same range as our other variables, i.e., 0-1) by dividing each by the maximum rank within the dataset. We performed this scaling based on our sample maximum rather than each event maximum, since absolute ranks may meaningfully reflect an individual's power and the degree of despotism within the hierarchy at a given time.

4.3.3 Event Outcomes

To generate a reliable measure of whether or not the opponent ceased aggression toward the solicitor following the recruitment attempt, one author and a second individual blind to the hypotheses of the study independently coded the descriptions of all events in which the outcome could be determined (79 cases). Reliability was excellent (93.7% agreement, Cohen's Kappa = 0.825).

4.3.4 Statistical Analyses

Using the LME4 package in R, we ran three binomial GLMMs fit by maximum likelihood (laplace approximate) with a logit link function (R-Development-Core-Team, 2014, Bates et al., 2015). In model 1 we included one row of data per bystander present at each event at which one or more solicitations occurred. We restricted our analyses to events in which at least one bystander outranked the opponent and the solicitor, to ensure that there was variation in rank information to warrant use of third-party knowledge. This included 84 events and 610 event-bystander data points. We did not face the problem of pseudo-replication, since more than one individual could be sequentially solicited within the same event (which happened on one occasion). The dependent measure in this model was whether or not the bystander was solicited (i.e, 1 or 0). We included as main effects kinship (binary), GI, and CF between the bystander and the solicitor and between the bystander and the opponent. We also included three rank-based measures: rank difference between the bystander and the opponent, rank difference between the bystander and the solicitor, and whether the bystander was the highest-ranking individual present. Our model included random effects to control for repeated measures. To determine the appropriate set of random effects to include in our models, we ran models with each potential combination of random effects (i.e., solicitor ID, opponent ID, recruit ID, and event ID) and then used AIC as the model selection criterion. We considered models with deltaAIC <2 to have equivalent support. Models with a single random effect had significantly more support than those with two or more, although results were consistent across models with different random effects. Thus, we included in the final model only the ID of the solicitor as a random effect. We also attempted models that included only the variables associated with one type of relationship measure (e.g., kinship) and the results of these simpler models were largely identical to the findings reported here.

The datasets for models 2 and 3 included one row per solicitation attempt. In these models we used the same variables as those in the first model but only for the bystander who was solicited (i.e., we no longer included data for bystanders who were not solicited). These models thus investigated whether any direct or third-party relationship measures predict a given outcome given the solicitor's choice of recruit. Model 2 assessed whether any relationship measures predicted recruit intervention in response to the solicitation. Model 3 assessed whether any relationship measures predicted the opponent ceasing aggression toward the solicitor. Model 2 involved the 93 cases in which sufficient information was available to determine whether or not the recruit intervened, and the model 3 involved the 79 cases in which sufficient information was available to determine whether or not the opponent terminated solicitor-directed aggression. In each of these models, the ID of the recruit was the only random effect included in the reported model. However, as in model 1, we ran versions of both models with all possible random effects, and found effects to be consistent across models. Again, using fewer random effects significantly improved model fit. We also ran models involving subsets of the predictor variables and, as in model 1, the results were consistent.

5 Conclusion

The present dissertation seeks to advance our understanding of the evolution of human social cognition through several targeted investigations of social decision-making in humans' closest living relatives, bonobos and chimpanzees. To this end, I have generated data to address three key questions (sections 5.1-5.3).

5.1 What differences exist in prosocial behavior between bonobos and chimpanzees?

Prosocial behavior is among the key traits that appear to define our species (Hill et al., 2009). However, the features that distinguish human from nonhuman prosociality remain heavily debated (Cronin, 2012, Hare and Tan, 2011, Silk and House, 2011). Many argue that human prosociality is driven by unusually strong prosocial motivations, demonstrated most clearly by active food sharing (the strong prosociality hypothesis) (Burkart et al., 2014, Burkart et al., 2009, Jaeggi et al., 2010a). Others have suggested that it is the flexibility with which we exhibit prosocial behavior across food and non-food contexts that uniquely defines human prosociality (the versatile prosociality hypothesis) (Warneken, 2015). In the wild, chimpanzees are known to participate in a number of cooperative behaviors, which may reflect the strong prosocial motivations and prosocial flexibility that are seen in humans. For example, chimpanzees hunt monkeys socially (Gilby et al., 2006, Gilby et al., 2015, Gilby and Wrangham, 2007, Mitani, 2009, Goodall, 1986). Following hunts, the possessors of the carcass frequently share portions of the meat with others—one of several types of food sharing that have been documented in wild chimpanzees (Mitani, 2009, Gilby, 2006, Gilby et al., 2006, Goodall, 1986). Chimpanzees also participate in coalitionary aggression in which multiple individuals jointly direct aggression toward their rivals—a behavior which helps them to attain rank and reproductive success (Muller and Mitani, 2005, Mitani, 2009, Gilby et al., 2013a, Goodall, 1986). Finally, chimpanzees patrol the borders of their territory, and even attack and kill lone individuals from neighboring communities that they encounter on these patrols (Wrangham, 1999, Watts and Mitani, 2001, Mitani, 2009, Mitani et al., 2010, Gilby et al., 2013b, Wilson et al., 2014, Williams et al., 2004, Goodall, 1986).

Over the past couple decades, research on social cognition in chimpanzees has proliferated (Chapter 1), including experimental investigations of the social cognitive underpinnings of cooperative behavior in this species (Warneken and Tomasello, 2009). Although chimpanzees are able to both cooperate and provide help in instrumental tasks (Melis et al., 2006b, Melis et al., 2006c, Warneken and Tomasello, 2006, Warneken et al., 2007, Yamamoto et al., 2009, Melis et al., 2011, Melis and Tomasello, 2013), their skills seem to be limited by motivational rather than cognitive abilities (Hare, 2001, Hare et al., 2002, Hare and Tomasello, 2004, Hare and Tomasello, 2005, Melis et al., 2006c, Hare, 2007, Hare, 2009, Hare, 2011, Warneken et al., 2012, MacLean and Hare, 2015, Hare, Submitted). Chimpanzees know when they need assistance, they recruit individuals with whom they've most effectively cooperated before, they can negotiate to maximize participation from their partners, and they can provide help based on an understanding of their partners' goals and roles (Melis et al., 2006b, Melis et al., 2006c, Melis et al., 2009, Melis and Tomasello, 2013, Yamamoto et al., 2012). However, chimpanzees are constrained by their level of tolerance with potential partners, and by their obsession with food (Melis et al., 2006c, Stevens, 2004). Consequently, captive experiments have largely failed to show prosocial food sharing in chimpanzees (Stevens, 2004, Melis et al., 2006b), suggesting that they neither possess the strong prosocial motivations or prosocial flexibility that characterize human cooperation.

Wild bonobos are also known to engage in a number of cooperative behaviors, including food sharing and coalitionary aggression (Furuichi, 2011, Yamamoto, 2015, Surbeck et al., 2011). However, our knowledge of the cognitive and motivational underpinnings of these behaviors remains impoverished. Previous work has shown that bonobos' heightened social tolerance in feeding contexts facilitates greater success on cooperative tasks, relative to chimpanzees (Hare et al., 2007). Bonobos also voluntarily share limited food resources, even with strangers (Hare and Kwetuenda, 2010, Tan and Hare, 2013). It could therefore be that, unlike chimpanzees, bonobos exhibit the strong prosocial motivations and prosocial flexibility exhibited by humans, actively sharing both food and non-food items. However, no previous work had experimentally investigated object or tool sharing in bonobos.

To test the strong prosociality and versatile prosociality hypotheses, we performed two studies (Chapter 2). In the first, we tested bonobos on an established instrumental helping task involving object retrieval (Warneken et al., 2007). Unlike chimpanzees and human infants, bonobos did not share objects in this context. Next, we paired subjects with conspecific partners, providing one partner with a surplus of nuts and the other with a surplus of rocks needed to crack the nuts. Again bonobos refused to share non-food items, although they frequently actively transferred food to their partners. Thus, we have shown that whereas chimpanzees actively share non-food items, but not food, bonobos exhibit the opposite pattern of sharing. These divergent context-specific sharing profiles suggest that bonobos may possess strong prosocial motivations for food sharing, but that neither chimpanzees nor bonobos exhibit the prosocial flexibility that characterizes human sharing—lending support to the versatile prosociality hypothesis. Species differences in motivation likely contribute substantially to observed differences in cooperative behavior, and a flexible expression of prosocial motivations was likely foundational in the evolution of humans' uniquely cooperative nature.

5.2 What cognition and motivation underlie apes' social preferences? Do these traits differ between humans and the other apes?

By three months of age, humans are able to discriminate unfamiliar individuals based on their behavior during third-party interactions, and they exhibit a robust preference for individuals that help others over those that do not (Hamlin et al., 2007, Hamlin and Wynn, 2011, Hamlin et al., 2010a, Hamlin et al., 2011). Soon after, they begin to respond to others' expressions of need by providing targeted instrumental help, even selectively helping those with positive intentions (Warneken and Tomasello, 2006, Warneken et al., 2007, Warneken, 2013, Dunfield and Kuhlmeier, 2010, Vaish et al., 2010). Research suggests that this behavior is underlain by an intrinsic motivation to see others helped, as well as the cognitive abilities for discerning friends from foes based on both agents' actions and their underlying intentions (Hamlin et al., 2007, Hamlin and Wynn, 2011, Hamlin et al., 2010a, Hepach et al., 2012, Hamlin, 2013).

Human children do not, however, exhibit this prosocial preference invariably. In fact, as children develop, their social evaluations become more selective. For example, although 5-month olds reliably prefer those who help over those who hinder third-parties, by eight months, infants no longer exhibit this indiscriminant preference (Hamlin et al., 2011). Eight-month olds instead favor those who help prosocial third-parties over those who hinder them, but prefer those who hinder antisocial third-parties over those who help them. Before age two, toddlers begin to direct more prosocial acts toward prosocial individuals than antisocial individuals and more antisocial acts toward antisocial individuals than prosocial ones (Hamlin et al., 2011). Thus, while very young infants are equipped with the cognitive and motivational skills to discern prosocial from antisocial individuals and prefer prosocial ones indiscriminately, increasingly children become more sensitive to the contexts of prosocial and antisocial interactions. Ultimately, they favor punishment of antisocial individuals and rewarding of prosocial ones—behaviors that mirror adult enforcement of cooperative norms (Hamlin et al., 2011, Burnham and Johnson, 2005, McAuliffe et al., 2015).

In addition, their social preferences are influenced by evolutionarily ancient biases for ingroup individuals. For example, by 5-6 months, infants prefer to look at someone who had previously spoken their native language over someone who had spoken a different language (Kinzler et al., 2007). By ten months, they prefer to receive a toy from a speaker of their native language than a speaker of a foreign language, and, by five years, they choose native-language speakers over foreign-language speakers as friends (Kinzler et al., 2007). Nine- and 14-month old infants prefer those who help individuals similar to themselves and those who harm dissimilar others (Hamlin et al., 2013). By age six, children punish unfair behavior of outgroup members more harshly than they do ingroup ones (Jordan et al., 2014).

The early emergence of the cognitive and motivational skills for prosocial preference likely plays a key role in the development of the sophisticated forms of social decision-making and within-group cooperation that are seen in adult humans. Children's early motivations for behaving prosocially and for preferentially associating with those who do as well may provide the foundation for the existence of human societies that are largely cooperative in nature (at least internally), while also preparing children to learn the specific cooperative and moral norms of their culture as they develop (House et al., 2013, Blake et al., 2015). These skills become increasingly nuanced as they adapt to typical norms of prosocial norm enforcement and in-group favoritism.

To determine whether early emergent prosocial preference is unique to humans, we tested bonobos to see if they possess either the cognitive or motivational aspects of this trait. Bonobos provide a powerful test of whether this preference is derived in humans, since relative to chimpanzees bonobos are highly gregarious, socially tolerant, and even prosocial toward strangers (Hare and Kwetuenda, 2010, Hare et al., 2007, Tan and Hare, 2013, Wobber et al., 2010c, but see Jaeggi et al., 2010b). These traits may be driven by a shared preference with humans for individuals that are most prosocial to others. However, in four studies, we found evidence that bonobos do not exhibit a human-like prosocial preference (Chapter 3). In Study 1, bonobos preferred an animated agent that hindered a third-party's attainment of a goal over one that facilitated goal attainment. Importantly, we controlled for the key alternative accounts based on perceptual or logistical features of our design. Interestingly, we also found that our results were driven by the adults in the sample; sub-adults did not exhibit any consistent preference. In Study 2, adult but not sub-adult bonobos preferred an unfamiliar human actor who hindered a third-party over one who helped. Study 3 replicated this finding, controlling for arbitrary baseline preferences for the unfamiliar actors. Finally, in Study 4, we showed that bonobos preferred a dominant animated agent over a subordinate one.

These data suggest that bonobos possess the cognitive underpinnings of prosocial preference. Specifically, they are able to discriminate both novel animated agents and unfamiliar human actors based on their prosocial and antisocial behavior during third-party interactions. Despite this, bonobos did not show the human preference for helpers in several choice tasks, instead favoring the hinderer that obstructed another agent's goal. Thus, the motivation to favor helpers may be unique to humans and likely played a central role in the evolution of human development and cooperation. These findings align with a growing body of work that suggests that cooperative motivations may be at the heart of the differences observed between humans and the other apes (Tomasello et al., 2003a, Tomasello et al., 2005, Tomasello and Herrmann, 2010, Tomasello et al., 2012).

However, as described above, cooperative motivations are not context-independent. Human children and adults exhibit ingroup favoritism (Jordan et al., 2014, Kinzler et al., 2007). While it is true that their social evaluations are biased by information other than an actors' prosocial or antisocial disposition—such as group membership—this behavior was likely favorable throughout human evolution to protect against the dangers of outgroup individuals. In fact, ingroup preferences are widespread among nonhuman primates, with chimpanzee intergroup killings representing an extreme example (Wilson et al., 2014, Wrangham, 1999, Williams et al., 2004, Goodall, 1986). Bonobos, on the other hand, are less xenophobic in the wild and in captive experiments even preferentially direct prosocial behavior toward strangers (Furuichi, 2011, Tan and Hare, 2013, Tan et al., submitted). Thus, while humans still share with most other primates the ancestral state of xenophobia which influences their social evaluations and social preferences, they appear to have developed unique motivations for cooperating with groupmates (Herrmann and Tomasello, 2006, Hare, 2007, Hare, 2009, Hare, 2011, Hare, Submitted).

Bonobos' less xenophobic behavior makes them the critical species to test the hypothesis that human cooperation is supported by uniquely strong cooperative motivations. Yet, despite their pronounced social tolerance, even bonobos exhibited a preference for an individual who hinders a (familiar) third-party over one who helps across several contexts. To confirm that antisocial preference is robust in bonobos, future studies should vary the identity of the neutral individual that is the target of prosocial and antisocial behavior during the third-party interactions. Would bonobos still prefer an individual who was antisocial toward their groupmate over one who was prosocial? In the present experiments involving human actors, the neutral agent was a familiar experimenter and, in other studies, bonobos have shown xenophilic tendencies (Tan et al., submitted, Tan and Hare, 2013). These findings suggest that bonobos may exhibit this antisocial preference even when the target of the prosocial or antisocial behavior is a familiar groupmate; however, additional studies are necessary to test this possibility.

Perhaps importantly, in one follow-up study, bonobos also preferred a dominant individual over a subordinate one. It may be that bonobos interpret antisocial behavior as indicative of social dominance, and that their preference for antisocial individuals actually reflects a preference for dominant ones. Although at first humans' preference for helpers appears adaptive and bonobos' preference for hinderers bewildering, that bonobos' evaluations may be motivated by preference for dominant individuals suggests that social preference is also adaptive in this species. As in many primates, a bonobo's place in the dominance hierarchy can influence access to key resources like food, social support, and mating opportunities (Chapais, 1995, Vervaecke et al., 2000).

Consequently, associating with dominant individuals may convey benefits if dominant allies are more tolerant of their close social partners and permit access to these resources (e.g., Duffy et al., 2007). The evolution of prosocial preference in humans may thus have required a shift in the adaptive landscape such that the value of powerful allies declined while the importance of more generally cooperative ones rose. Presumably, selection began to favor prosocial preference following the emergence of increasingly interdependent and egalitarian societies, like those seen among hunter-gatherer populations (Tomasello et al., 2012).

5.3 What selective advantage does social cognition provide wild apes?

The social intelligence hypothesis argues that the demands of within-group competition were a principal driver of cognitive evolution among social species, including humans and other primates (Jolly, 1966, Humphrey, 1976, Byrne and Whiten, 1988). This hypothesis has received wide attention among evolutionary biologists and psychologists (though not to the exclusion of hypotheses that suggest the influence of other potentially important ecological selective pressures). Some studies have shown that more "socially complex" species exhibit better performance on cognitive tasks than their less "socially complex" close relatives (where social complexity is defined by group size or fission fusion social systems: e.g., Bond et al., 2003, Maclean et al., 2008, Sandel et al., 2011, Maclean et al., 2013, Amici et al., 2008). However, very few studies have tested whether social intelligence actually provides a selective advantage in wild populations (White et al., 2010, Seyfarth and Cheney, 2015). To do so, one must show that there is variation between individuals in a social cognitive trait, that this variation is heritable, and that it is linked to differential reproductive success (Endler, 1986). Additionally, demonstrating empirical links between variation in possession or expression of social cognitive skills and differential acquisition of proximate benefits would provide evidence for the proximate mechanisms through which complex traits like social cognitive abilities can provide a selective advantage and influence reproductive success.

Coalitionary aggression is an exemplar of complex within-group competition (de Waal, 1982, Muller and Mitani, 2005, Watts, 2009, Silk, 1999, Gilby et al., 2013a, Goodall, 1986). Although many social species pursue rank and reproductive success by cooperating with coalition partners to dominate their rivals, the cognitive underpinnings of this behavior remain unclear (Silk, 1999, Perry et al., 2004, Schino et al., 2006, Range and Noë, 2005, Watts, 2009). We tested the hypotheses that wild chimpanzees at Gombe National Park, Tanzania recruit coalition partners based on awareness of the third-party relationships between their opponent and the available coalition partners, or that they simply base their choices on their own direct relationships with the available partners. We found evidence consistent with the interpretation that chimpanzees relied on information about both their own kinship, grooming, and coalitionary relationships with the available partners, and also about third-party rank relationships between their opponent and each potential recruit. These findings add to a growing body of work, showing that the propensity for tracking third-party relationships may be widespread—although not universal (le Roux and Bergman, 2012)—among monkeys and apes (Chapter 3, Cheney and Seyfarth, 1990, Cheney and Seyfarth, 2007, Slocombe and Zuberbuhler, 2007, Russell et al., 2008, Subiaul et al., 2008, Wittig and Boesch, 2010, Herrmann et al., 2013, Wittig et al., 2014b, Seyfarth and Cheney, 2015). Moreover, they further highlight the breadth of sophisticated social cognitive abilities that are shared between humans and the other apes (Hare et al., 2000, Hare et al., 2001, Slocombe and Zuberbuhler, 2007, Call and Tomasello, 2008, Wittig and Boesch, 2010, Crockford et al., 2012, Wittig et al., 2014b).

We were able to rule out the alternative explanations that chimpanzees simply solicited bystanders who most outranked themselves and that they simply solicited the highest-ranking individual present (perhaps based on behavioral cues by the individual). However, another alternative is that solicitors made their decisions based on other aspects of the behavior of bystanders. For example, bystanders may have provided cues that communicated, for example, their interest in getting involved in the conflict, or their calmness may have made them appealing choices. Some of our findings suggest that this was not the case. For example, given the tendency of dominant males to police others' conflicts and since dominant individuals may be less likely targets of redirected aggression, these individuals may be among the most likely to exhibit such cues (e.g., de Waal, 1982). However, when controlling for the other factors in our model, we did not find evidence that chimpanzees tended to solicit help from the highest-ranking available bystander. Moreover, recruits did not intervene in roughly half of our events, suggesting that chimpanzees were not cuing into bystander behavior that indicated a bystander's interest in joining the conflict. Similarly, we did not find evidence that the relationship measures that predicted solicitors' choices actually influenced whether the recruit intervened. These things being true, we still cannot rule out the influence of bystander behavior on solicitor's choices.

To do so, controlled experiments are necessary. While experiments intended to investigate partner choice in aggressive conflicts would be unethical, some experimental work has shown that apes choose partners based on their behavior during third-party interactions (Chapter 3, Russell et al., 2008, Subiaul et al., 2008, Herrmann et al., 2013). Experiments have also shown that chimpanzees recruit partners for a cooperative task based on their past success with the various partners (Melis et al., 2006b). In these studies, one chimpanzee was alone in a testing room and had access to a food-acquisition task that required cooperation. In separate adjacent rooms were two other chimpanzees. The subject could open the door of either room to allow one of the chimpanzees in to help. This design ensured that the subject alone was responsible for recruitment. Importantly, it also allowed the authors to code the behavior of the potential recruits to ensure that a change in their behavior between baseline and test trials was not responsible for subjects' choices in test trials. While our findings in Chapter 4 are consistent with the hypothesis that chimpanzees exploit third-party knowledge to recruit cooperative partners, the kinds of controlled experiments used by Melis et al. (2006b) are necessary to completely rule out the influence of bystander behavior on recruitment decisions.

Importantly, there is good experimental evidence in other (non-recruitment) contexts that primates are aware of third-party relationships. In chimpanzees, such evidence is limited to one study in which, two hours after an aggressive interaction, chimpanzees heard playbacks of an aggressive bark by a bystander. Chimpanzees looked longer and moved away more often in response to barks by a bond partner of their former opponent than to either barks by a non-bond partner or benign calls by the bond partner (Wittig et al., 2014b). These results suggest that, based on their knowledge of their former opponent's social relationships, chimpanzees interpreted the same aggressive bark as directed at them (and indicating renewed aggression) or not. In a touchscreen task, two orangutans and one gorilla also demonstrated the ability to discriminate mother-offspring pairs from other types of social relationships (e.g., siblings, unrelated groupmates, mated pairs) and to match specific kinds of relationships with one another (Vonk, 2002). Moreover, a number of controlled experiments with old world monkeys suggest that they are aware of the rank, kinship, and even transient consortship relations between third-parties (Cheney and Seyfarth, 1980, Dasser, 1988, Cheney and Seyfarth, 1990, Cheney et al., 1995, Cheney and Seyfarth, 1999, Bergman et al., 2003, Kitchen et al., 2005, Cheney and Seyfarth, 2007, Crockford et al., 2007, Wittig et al., 2007a, Wittig et al., 2007b, Paxton et al., 2010).

Touchscreen tasks, like those utilized by Dasser (1988), Vonk (2002), and Paxton et al. (2010), are another particularly promising route for future work because they allow for complete control of stimuli, and can therefore easily rule out the influence of other animals' behavior on subjects' choices. Moreover, they permit researchers to investigate the cognitive mechanisms that allow animals to learn and remember social information. Future work must, for example, determine the extent to which animals simply rely on associative learning and classical conditioning versus a series of rules that allow them to classify and organize relationships conceptually and hierarchically (Fagot and Cook, 2006, Flemming et al., 2013, Cheney and Seyfarth, 2007, Dasser, 1988, Vonk, 2002). Studies like ours suggest that chimpanzees may be able to instantaneously consult their social knowledge to make well informed recruitment decisions (see also Silk, 1999, Perry et al., 2004, Schino et al., 2006). The ability to use social information rapidly may suggest that this knowledge is structured by concepts and rules that facilitate rapid retrieval of accurate information, but controlled studies are necessary to test this hypothesis.

To investigate the proximate benefits of third-party knowledge, we then explored whether our proxy for third-party knowledge was related to any desired outcomes. Interestingly, the strategies that chimpanzees appeared to use to choose whom to recruit did not impact whether the recruit actually intervened in support of the solicitor. However, it did impact whether the opponent ceased aggression toward the solicitor. Critically, when chimpanzees solicited recruits that more greatly outranked their opponent they were significantly more likely to escape further aggression. That is, those behavior was consistent with exploitation of third-party knowledge experienced immediate benefits. Our findings therefore provide direct support for the social intelligence hypothesis, and help to elucidate the proximate mechanisms that have likely shaped the social cognitive abilities of primates, including humans, throughout evolutionary history (Jolly, 1966, Humphrey, 1976, Byrne and Whiten, 1988).

Our study adds to a growing body of work that suggests that primates exhibit third-party knowledge in a number of social contexts in which they may experience benefits, and it provides support for at least one of the speculated benefits. For example, sensitivity to the rank relationships between third-parties may help primates to infer their own dominance relationship with unfamiliar individuals and avoid unnecessary aggression (Paz-y-Miño et al., 2004, Maclean et al., 2008). Knowledge of relationships between third-parties may also allow primates to decide when to involve themselves in aggressive conflicts and to predict the behavior of other bystanders to these conflicts (Wittig and Boesch, 2010, Wittig et al., 2014b, Wittig et al., 2007a, Wittig et al., 2007b). Further, primates may eavesdrop, for example on others' consortships, to identify mating opportunities (Crockford et al., 2007).

Our work also builds on studies that have identified relationships between complex social behavior and measures of reproductive success (Duffy et al., 2007, Schulke et al., 2010, Gilby et al., 2013a, le Roux et al., 2013). Gilby et al. (2013a) has shown that, in coalitionary networks, male chimpanzees with the highest *betweenness* experience greater increases in rank and higher paternity success than other chimpanzees. Betweenness describes the extent to which an individual has connections with others who themselves are not well connected. Gilby et al. (2013a) hypothesized that the importance of *betweenness* may reflect chimpanzees' use of third-party knowledge to foster strategic coalitionary relationships. Our finding that chimpanzees appear to rely on third-party knowledge when recruiting coalition partners provides some support for this hypothesis. It also suggests that a direct link, though currently untested, may exist between variation in social cognitive skill and differential reproductive success.

However, to confirm the hypothesis that third-party knowledge provides a selective advantage in wild chimpanzees, several steps are necessary. First, captive experiments should be completed that are designed to demonstrate third-party knowledge, controlling for all alternative accounts. The most powerful studies would be those that could be replicated, perhaps with fewer controls, in the wild. Because of their non-invasive nature and frequent use in the wild, playback studies are a clear candidate. For example, previous work in baboons has shown that they pay more attention to a series of vocalizations that simulate a rank reversal than a series that simulates normal dominance interactions (and pay more attention to a more significant between-matriline rank reversal than a within-matriline rank reversal), suggesting knowledge of existing rank and kin relations (Bergman et al., 2003). These types of studies could be replicated in captivity with even more controls and a greater number of trials per individual. Doing so would further verify that primates do exhibit third-party knowledge, while also testing whether there is variation in this cognitive skill. Then, a series of trials of these kinds could be completed with wild primates in the field, in order to measure variation in the trait. Heritability studies could be used to identify whether performance on these trials is heritable, while other studies could examine correlations between performance and reproductive success. Showing that there is variation in a cognitive skill, that it is heritable, and that it is linked to differential reproductive success would provide the strong evidence that the cognitive skill provides a selective advantage (Endler, 1986). Future work should also attempt to link individual differences in controlled measures of social cognition to variation in attainment of proximate benefits, in order to identify the proximate mechanisms through which social cognition confers a selective advantage.

5.4 What is unique about human social cognition?

For centuries, philosophers and biologists have mused about what makes humans unique (e.g., Huxley, 1863, Darwin, 1871, Aristotle, 1991). What are humans' key traits that distinguish them from the rest of the animal kingdom? Indeed, humans are different from other species in a variety of ways, including our possession of specialized social cognitive skills.

The process of identifying species differences necessarily requires determining what is the same. A significant body of work has shown that other apes, especially chimpanzees, exhibit many of the social cognitive skills that were once believed the unique domain of human psychology (e.g., Call and Tomasello, 2008). For example, apes can predict others' behavior not simply based on surface cues but rather an understanding of the goals and intentions that motivate others' actions (Call and Tomasello, 1998, Call et al., 2004, Tomasello and Carpenter, 2005, Warneken and Tomasello, 2006, Warneken et al., 2007, Call and Tomasello, 2008, Buttelmann et al., 2009, Melis et al., 2011, Yamamoto et al., 2012, Myowa-Yamakoshi et al., 2012, Buttelmann et al., 2012, Melis and Tomasello, 2013, Kano and Call, 2014b). Apes recognize what others perceive and what they know about (Tomasello et al., 1998, Tomasello et al., 1999, Hare et al., 2000, Hare et al., 2001, Brauer et al., 2005, Hare et al., 2006, Melis et al., 2006a, Okamoto-Barth et al., 2007, Kaminski et al., 2008, Crockford et al., 2012, MacLean and Hare, 2012, Karg et al., 2015a, Karg et al., 2015b). As we and others have shown, apes track the relationships between third parties and use this information to guide their social decisions (Chapters 3 and 4, Slocombe and Zuberbuhler, 2007, Wittig and Boesch, 2010, Wittig et al., 2014b, Herrmann et al., 2013, Russell et al., 2008, Subiaul et al., 2008, Wroblewski et al., 2009). Apes also exhibit a variety of prosocial behaviors, at least some of which rely on an understanding of others' goals and each partner's roles (e.g., Yamamoto et al., 2012, Melis and Tomasello, 2013). To some extent, these behaviors also involve similar prosocial motivations to those exhibited by humans.

5.4.1 Prosocial motivations

However, there remain a number of differences between human and non-human psychology. Motivation is one major candidate. Despite converging evidence from numerous paradigms that makes clear that apes understand others' goals and intentions, there is as yet no evidence that they possess shared intentionality—the tendency to structure cooperative activities around shared goals and an understanding of each partner's role in the cooperative activity (Warneken et al., 2006, Warneken et al., 2012, MacLean and Hare, 2013). Since apes can understand others' goals and intentions generally, it is likely that their lack of shared intentionality is a result of limited cooperative motivations rather than simply an absence of cognitive skill. Indeed, a large body of work suggests that chimpanzees reliably fail perspective-taking tasks that rely on understanding of cooperative communicative cues despite success on tasks that probe the same cognitive abilities in competitive contexts (Povinelli et al., 1997, Call et al., 1998, Itakura et al., 1999, Hare et al., 2000, Hare, 2001, Hare et al., 2001, Hare et al., 2002, Tomasello et al., 2003a, Hare and Tomasello, 2004, Hare and

Tomasello, 2005, Call and Tomasello, 2005, Hare et al., 2006, Hare, 2007, Call and Tomasello, 2008, Hare, 2009, Hare, 2011, Hare, Submitted). These results have led researchers to conclude that apes' failure does not reflect a lack of cognitive skill. Instead, apes do not appear to understand cooperative communicative cues because they do not possess the motivation to produce such cues themselves (Tomasello et al., 2003a, Herrmann and Tomasello, 2006, Hare, 2011, Hare, Submitted).

In the present dissertation, we have shown that chimpanzees and bonobos do possess some basic prosocial motivations (Chapter 2). For example, chimpanzees are motivated to provide low-cost help by actively sharing non-food items and bonobos are motivated to do the same with food items (Warneken et al., 2007, Warneken and Tomasello, 2006, Yamamoto et al., 2009, Hare and Kwetuenda, 2010, Yamamoto et al., 2012, Tan and Hare, 2013). However, each species' prosocial motivations appears to be constrained to specific contexts or currencies (Chapter 2, Stevens, 2004). As with any species, human behavior also has its constraints. However, while there are certainly limitations to prosocial motivations in human adults and children (e.g., when dealing with outrgroup individuals), these motivations appear to be much more flexibly expressed across context and currencies in humans than they are in the other apes, particularly when dealing with ingroup members (Chapter 2, Chapter 3).

Moreover, unlike humans, bonobos do not appear motivated to prefer unfamiliar individuals based on their prosocial behavior in third-party interactions (Chapter 3). However, bonobos do exhibit preferences for individuals who behave prosocially toward them (Krupenye and Hare, in preparation-b). Thus, although bonobos are capable of distinguishing individuals based on their prosocial and antisocial behavior in both direct and third-party interactions, their motivation to favor prosocial individuals does not appear to extend beyond direct interactions (Chapter 3, Krupenye and Hare, in preparation-b). Differences in strength and scope of prosocial motivations may thus explain much of the difference in degree and kind of cooperative behavior exhibited by humans relative to the other apes.

That being said, as noted in Chapter 1, motivations may differ wildly between species. Indeed, there is evidence to suggest that bonobos and chimpanzees respond very differently to the types of competitive environments that have motivated chimpanzees to demonstrate their most sophisticated cognitive skills (Wobber et al., 2010b). Whereas chimpanzees are primed for competition by a boost in testosterone, bonobos experience heightened levels of cortisol—which may deter them from competing (Wobber et al., 2010b). There's evidence instead that bonobos' heightened social tolerance in feeding contexts relative to chimpanzees may allow them to exhibit more cognitive skill in cooperative tasks involving food (e.g., Hare et al., 2007, Hare and Kwetuenda, 2010, Tan and Hare, 2013). Moreover, bonobos are highly sensitive to others' emotions, especially positive emotions, further suggesting that prosocial contexts may prove fruitful for future investigations of their cognition (Kret et al., 2016). By designing studies that maximize ecological relevance for bonobos, we will be able to better understand their cognitive skills and how they evolved. Importantly, since bonobos are thought to have evolved in response to selection for prosociality (Hare et al., 2012), studies of bonobo cognition and motivation in prosocial contexts will also provide the strongest test of the hypothesis that the strongest cooperative motivations are a derived feature of human psychology. Such an eye toward ecological relevance will prove essential as comparative psychologists continue to explore the minds of an increasing diversity of species whose morphology and psychology have been adapted to face very different challenges than those experienced during human and non-human primate evolution.

5.4.2 Representational theory of mind

Motivations alone are unlikely to be responsible for the remarkable differences that exist between the social behavior of humans and the other apes. Another trait that may be unique to humans is the ability to mentally represent others' perspectives. Although myriad studies have shown that other apes possess some theory of mind skills (Call and Tomasello, 2008, Hare, 2011), none of these confirmed skills necessarily requires the ability to represent others' perspectives. For example, in competitive paradigms, chimpanzees preferentially target food that a dominant competitor cannot see and attempt to steal food using a path that minimizes their competitor's ability to see their approach (Hare et al., 2000, Hare et al., 2001, Hare et al., 2006). Critically, studies like these confirm that chimpanzees understand *what* others can see—or have seen in the past—but not necessarily *how* the scene looks from another individual's perspective. This latter skill—to represent how things look (or sound) from someone else's point-of-view—is called level 2 perspective-taking (Flavel et al., 1978, Flavel et al., 1981). It is a pre-requisite for a "fully-blown," or representational, theory of mind, and is central to the richest theory of mind skills, like the ability to represent others' false beliefs.

In fact, explicit false belief understanding is often considered to be the "litmus test" of a full-blown theory of mind because a fully developed false belief understanding requires the ability to represent others' perspectives. To represent someone's false belief, one must recognize the true state of the world (i.e., reality) while simultaneously representing the specific way in which this other individual constures the world to be different than it is. A variety of attempts have been made to demonstrate false belief understanding in non-human apes (Call and Tomasello, 1999, Hare et al., 2001, Kaminski et al., 2008, Krachun et al., 2009, Krachun et al., 2010). Reliably, however, these explicit tasks have failed to provide positive evidence for false belief understanding in nonhuman apes, despite variation in the methodologies employed.

A single study has investigated level 2 perspective-taking in chimpanzees. Karg et al. (2016) tested pairs of chimpanzees and children in a competitive task in which they took turns selecting food options (that were hidden at the time of choice). The food options were two breadsticks attached to a barrier. From the subject's perspective, the entire breadsticks were visible and they were of equal length. However, the barrier occluded parts of the breadsticks from the competitor's perspective, making it seem to the competitor as though one breadstick was larger. The competitor was allowed to choose first (and the subject could not witness the competitor's choice). On the subjects' turn, they were significantly less likely to choose the breadstick that appeared larger to the competitor in the social condition than in a nonsocial control (presumably because they inferred in the social condition that the competitor would have already chosen this one). However, in the nonsocial control condition, while children chose randomly (since they knew that both options were equal in size), chimpanzees instead showed a preference for the less obscured option. These results suggest that while children likely relied on a representation of their competitor's perspective, chimpanzees may have instead attributed to their competitor their own preference. That is, when choosing second, they simply avoided the option that they would have chosen first. Taken together, the existing literature suggests that non-human apes may not be able to represent others' perspectives, including their false beliefs.

In developmental studies, the clear consensus is that children pass traditional explicit false belief tests involving verbal reporting, such as the Sally-Anne task, only after the age of four (Wellman et al., 2001). However, recent evidence has shown that infants younger than four can also pass modified false belief tests using simplified task procedures and spontaneous-gaze responses as measures (e.g., violation-of-expectation (Onishi and Baillargeon, 2005, Surian et al., 2007); anticipatory-looking (Clements and Perner, 1994, Southgate et al., 2007, Senju et al., 2011a)). For example, anticipatory looking paradigms, measured using noninvasive eye-tracking procedures, exploit individuals' tendency to look to a location in anticipation of an impending event, and thus measure participants' predictions, e.g., about what an agent is about to do—even when that agent holds a false belief. Although it is unclear whether or not such spontaneous measures of false belief understanding reflect representation of others' perspectives (Leslie et al., 2004, Baillargeon et al., 2010, Apperly and Butterfill, 2009, Perner and Roessler, 2012), existing research suggests that young infants have at least an implicit form of false belief understanding well before they demonstrate explicit comprehension in traditional tasks (e.g., Clements and Perner, 1994, Onishi and Bailargeon, 2005, Southgate et al., 2007, Surian et al., 2007, Scott et al., 2010, Southgate et al., 2010, Senju et al., 2011b, Luo, 2011, Low and Perner, 2012, Thoermer et al., 2012, Low and Watts, 2013, Buttelmann et al., 2014, Southgate and Vernetti, 2014, Buttelmann et al., 2015, Scott et al., 2015).

Such methods could prove fruitful in better characterizing the limits of theory of mind skills in primates. To date, only two published studies have used spontaneous-gaze false belief tasks with nonhuman primates. Both failed to replicate with monkeys the results with infants, despite monkeys' success in true belief conditions (Marticorena et al., 2011, Martin and Santos, 2014). However, a growing body of work has begun to use eye-tracking paradigms with nonhuman apes, demonstrating the promise of these methods (e.g., Kano and Tomonaga, 2010, Hattori et al., 2010, Kano and Tomonaga, 2011, Myowa-Yamakoshi et al., 2012, Kano and Call, 2014a, Kano and Call, 2014b, Kano and Hirata, 2015, Kano et al., 2015). In most of these studies, apes view through a transparent Plexiglas panel video or picture stimuli presented on a monitor just outside of their enclosure. An eye-tracker, attached to the monitor, records the subject's gaze as he views the stimuli. Subjects remain relatively still during viewing because they are allowed to drink juice through a nozzle. This procedure allows apes' gaze to be noninvasively recorded with high accuracy. As long as stimuli are relatively short (i.e., ideally under 45 seconds) and the content is interesting to the apes, most subjects will pay attention throughout the duration of the video.

Critically, several studies have already shown that great apes make anticipatory looks, predicting agents' actions based on an understanding of their goals or based on memory of past events (Kano and Call, 2014b, Kano and Hirata, 2015, Myowa-Yamakoshi et al., 2012). Recently, Krupenye et al. (in preparation-a) performed the first spontaneous-gaze false belief task based on anticipatory looking with a large sample of chimpanzees, bonobos, and orangutans. In two novel scenarios, apes predicted that an agent would search for a hidden object where he falsely believed it to be, even though participants knew that the object was no longer there. These data provide initial evidence that at least an implicit understanding of others' false beliefs may not be unique to humans. Although future research must confirm whether apes' ability to correctly predict the actions of an agent holding a false belief is based on level 2 perspective-taking, it is clear that anticipatory looking paradigms represent a powerful new tool for investigating the social cognitive skills of nonverbal populations. Future work should continue to adapt these methods to examine not only false belief understanding but also other theory of mind skills that have been difficult to assess using traditional, more cognitively demanding methods.

5.5 How did human social cognition evolve?

Once a species' cognitive phenotype has been characterized, the challenge becomes figuring out how it got that way. Tinbergen (1963) offered two approaches for understanding the ultimate origins of a behavior or cognitive ability: phylogeny and function. The first involves determining the phylogenetic distribution of a cognitive trait, with the aim of reconstructing the ancestral states of the trait through parsimony. For example, if all great apes, humans included, share a cognitive skill that is not found in monkeys, that skill most likely evolved once, 13 to 18 million years ago, in the common ancestor of all great apes. It is much less likely that the skill evolved independently in each great ape species. Many social cognitive skills, such as implicit false belief understanding, appear to be restricted to the great apes and likely evolved in their common ancestor (Krupenye et al., in preparation-a). Other traits, such as third-party knowledge and basic visual perspective-taking skills, are distributed much more broadly across primates (Cheney and Seyfarth, 1990, Flombaum and Santos, 2005, Cheney and Seyfarth, 2007, Drayton and Santos, 2014). These skills likely evolved much earlier, perhaps even multiple times in different taxa.

Recently, some studies have begun to link phylogeny with function (MacLean et al., 2012). These studies investigate across species, relationships between potential selective pressures (such as dietary or socio-ecology) and the presence or absence of (or variation in) a trait in question. The two most prominent hypotheses that have been developed to explain cognitive evolution are the ecological intelligence hypothesis and the social intelligence hypothesis. The ecological intelligence hypothesis postulates that cognitive complexity in primates evolved as a result of demands from the ecological environment (Clutton-Brock and Harvey, 1977, Milton, 1988). Such demands may include diet

(Clutton-Brock and Harvey, 1977, Milton, 1988), predation (Hill and Lee, 1998, Byrne and Bates, 2007), foraging efficiency (Pollard and Blumstein, 2008), technical foraging challenges (King, 1986), seasonality (Deaner et al., 2003), or how males and females are distributed (Wrangham, 1980). As described previously, the social intelligence hypothesis instead implicates the challenges of social living as the principal driver of cognitive evolution.

Studies that integrate phylogenetic and functional approaches have begun to explore variation in performance on cognitive tasks between species, on a range of scales. The first attempts at phylogenetic comparative psychology investigated two or three closely related species to determine, for example, whether species that live in larger social groups exhibit greater social cognitive skill (e.g., Bond et al., 2003, Maclean et al., 2008, Sandel et al., 2011, Maclean et al., 2013). Recently, however, phylogenetic cognitive comparisons have been undertaken at unprecedented scales (Burkart et al., 2014, MacLean et al., 2014). For example, MacLean et al. (2014) tested 36 different species on two tasks designed to measure their inhibitory control skills. They found that absolute brain size and, within primates, dietary breadth positively predicted performance on inhibitory control tasks. By identifying the ecological pressures that co-vary across species with cognitive skill, one can infer the function of the trait. For example, that dietary breadth was positively associated with inhibitory control suggests that inhibitory control may have evolved, at least in part, in order to solve foraging challenges. Phylogenetic comparative psychology is just in its infancy. Future broad phylogenetic comparisons will surely make significant contributions by harnessing this unprecedented mechanism for testing hypotheses about both the evolutionary history of cognition and the selective pressures that shaped cognitive abilities across taxa (MacLean et al., 2012).

The other approach to test hypotheses about function is to investigate the proximate and ultimate benefits of a trait among individuals in wild populations (Clutton-Brock, 1988, Seyfarth and Cheney, 2015). Finding, for example, that variation in a trait is heritable and is associated with higher reproductive success provides strong evidence that selection is acting on that trait (Endler, 1986), and linking cognition to proximate benefits can reveal the trait's function and the proximate mechanisms through which the trait provides a selective advantage. This approach is common in biology. However, it has only rarely been applied to the study of cognition, and almost exclusively in fish and birds (e.g., White et al., 2010, Boogert et al., 2011).

Indeed, those studies that have measured cognition in wild primates have generally only speculated about function (e.g., Cheney and Seyfarth, 1990, Bergman et al., 2003, Crockford et al., 2007, Cheney and Seyfarth, 2007). Meanwhile, the few studies that have found empirical links to measures of reproductive success have almost universally used potentially cognitively sophisticated behavior as a proxy for cognition (Duffy et al., 2007, Schulke et al., 2010, Gilby et al., 2013a, le Roux et al., 2013). For example, a few studies have linked centrality in coalitionary networks to reproductive success (Schulke et al., 2010, Gilby et al., 2013a), and one study linked deceptive behavior to mating success (le Roux et al., 2013). Before one can make strong claims that these studies provide evidence for the selective advantage of social cognition, one must, at a minimum, demonstrate that the purported social cognitive skills are utilized in these contexts. More importantly, the strongest claims can only be made by demonstrating empirical links between controlled measures of cognitive skill and differential reproductive success or the attainment of proximate benefits.

In Chapter 4, we provided some of the first evidence consistent with an empirical link between cognitive ability and attainment of proximate benefits. We showed, first, that wild chimpanzees appear to rely on third-party knowledge to determine which coalition partners to solicit, and, second, that chimpanzees who do so are more likely than others to escape aggression. That is, chimpanzees may experience immediate proximate benefits following the application of third-party knowledge, providing evidence for the influence of proximate mechanisms consistent with the social intelligence hypothesis. Studies like these provide the strongest tests of hypotheses about the adaptive value of intelligence, and, along with phylogenetic comparisons, should be prioritized among future research directions.

Existing evidence for how intelligence evolved in humans is much more meager than work aimed at characterizing what is unique about human cognition. This limited work has identified social competition, prosocial relationships, and feeding ecology as potentially key drivers in primate evolution (e.g., Chapter 4, Silk, 2007, MacLean et al., 2014, Pusey, 1997, Wroblewski et al., 2009). However, future efforts will be necessary to further test the influence of these and other potential selective pressures on the distribution of cognitive abilities across species, and on differential reproductive success within wild populations.

5.6 Integrating Experimental and Observational Approaches

The present dissertation showcases the value of integrating experimental and observational data to investigate the evolution of cognition in humans and other animals. Observational work is necessary to identify behavior that may reflect rich cognitive phenomena, to characterize the natural ecology of this behavior, and to inspire ecologically relevant experimental paradigms that may be used to isolate the phenomena. Controlled experiments in turn are necessary to rule out alternative explanations and determine whether the observed behavior does indeed reflect the hypothesized cognitive mechanism. Returning to the wild then permits exploration of the adaptive value of the cognitive trait.

Following observations of partner choice behavior in wild apes that may reflect third-party knowledge (e.g., Gilby et al., 2013a, Slocombe and Zuberbuhler, 2007, Wittig and Boesch, 2010), we have developed controlled experiments to investigate apes' propensity for tracking third-party interactions and using that information in partner choice (Chapter 3). We then used data from the field to develop proxies for social cognitive ability that control for as many alternative explanations as are permitted by the nature of the data (Chapter 4). While we cannot completely rule out some alternative explanations because these data are observational, the variety of findings indicating that apes exploit third-party knowledge in controlled experiments (e.g., Chapter 3, Herrmann et al., 2013, Russell et al., 2008, Subiaul et al., 2008, Wittig et al., 2014b) and the controls that we were able to implement suggest that our data may reflect the same underlying cognitive phenomenon. Using our proxy for social cognitive ability, we were then able to test for an empirical link between this proxy and the attainment of proximate benefits (Chapter 4). As they have often proven fruitful in the past, the use of observational data to inform experimental approaches and the use of experimental data to guide field studies will continue to provide the most powerful contributions to our understanding of animal minds and how they evolved (Hare, 2001, MacLean et al., 2012, Seyfarth and Cheney, 2015).

References

AMICI, F., AURELI, F. & CALL, J. 2008. Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Current Biology,* 18**,** 1415-1419.

AMICI, F., VISALBERGHI, E. & CALL, J. 2014. Lack of prosociality in great apes, capuchin monkeys and spider monkeys: convergent evidence from two different food distribution tasks. *Proc Biol Sci,* 281.

APPERLY, I. A. & BUTTERFILL, S. A. 2009. Do humans have two systems to track beliefs and belief-like states? *Psychological review,* 116**,** 953.

ARISTOTLE 1991. On the Soul. *In:* BARNES, J. (ed.) *The Complete Works of Aristotle.* Princeton: Princeton University Press.

BAILLARGEON, R., SCOTT, R. M. & HE, Z. 2010. False-belief understanding in infants. *Trends in cognitive sciences,* 14**,** 110-118.

BARON-COHEN, S. 2009. Autism: the empathizing-systemizing (E-S) theory. *Ann N Y Acad Sci,* 1156**,** 68-80.

BATES, D., MAECHLER, M., BOLKER, B. & WALKER, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software,* 67**,** 1-48.

BATSON, C. D. & POWELL, A. 2003. Altruism and prosocial behavior. *In:* MILTON, T. & LERNER, M. J. (eds.) *Handbook of Psychology, Volume 5: Personality and Social Psychology.* Hoboken, New Jersey: John Wiley & Sons.

BEHRINGER, V., DESCHNER, T., MURTAGH, R., STEVENS, J. M. & HOHMANN, G. 2014. Age-related changes in thyroid hormone levels of bonobos and chimpanzees indicate heterochrony in development. *J Hum Evol,* 66**,** 83-8.

BERGMAN, T. J., BEEHNER, J. C., CHENEY, D. L. & SEYFARTH, R. M. 2003. Hierarchical classification by rank and kinship in baboons. *Science,* 302**,** 1234-1236.

BLAKE, P. R., MCAULIFFE, K., CORBIT, J., CALLAGHAN, T. C., BARRY, O., BOWIE, A., KLEUTSCH, L., KRAMER, K. L., ROSS, E., VONGSACHANG, H., WRANGHAM, R. & WARNEKEN, F. 2015. The ontogeny of fairness in seven societies. *Nature*.

BOND, A. B., KAMIL, A. C. & BALDA, R. P. 2003. Social complexity and transitive inference in corvids. *Animal Behaviour,* 65**,** 479-487.

BOOGERT, N. J., FAWCETT, T. W. & LEFEBVRE, L. 2011. Mate choice for cognitive traits: a review of the evidence in nonhuman vertebrates. *Behavioral Ecology,* 22**,** 447-459.

BOWLES, S. & GINTIS, H. 2004. The evolution of strong reciprocity: cooperation in heterogeneous populations. *Theoretical Population Biology,* 65**,** 17-28.

BRAUER, J., CALL, J. & TOMASELLO, M. 2005. All great ape species follow gaze to distant locations and around barriers. *Journal of Comparative Psychology,* 119**,** 145-154.

BRAUER, J., CALL, J. & TOMASELLO, M. 2008. Chimpanzees do not take into account what others can hear in a competitive situation. *Animal Cognition,* 11**,** 175-178.

BRAUER, J., KAMINSKI, J., RIEDEL, J., CALL, J. & TOMASELLO, M. 2006. Making inferences about the location of hidden food: Social dog, causal ape. *Journal of Comparative Psychology,* 120**,** 38-47.

BROSNAN, S. F. & DE WAAL, F. B. M. 2002. A proximate perspective on reciprocal altruism. *Human Nature,* 13**,** 129-152.

BULLINGER, A. F., BURKART, J. M., MELIS, A. P. & TOMASELLO, M. 2013. Bonobos, Pan paniscus, chimpanzees, Pan troglodytes, and marmosets, Callithrix jacchus, prefer to feed alone. *Animal Behaviour,* 85**,** 51-60.

BULLINGER, A. F., MELIS, A. P. & TOMASELLO, M. 2014. Chimpanzees (Pan troglodytes) instrumentally help but do not communicate in a mutualistic cooperative task. *J Comp Psychol,* 128**,** 251-60.

BURKART, J. M., ALLON, O., AMICI, F., FICHTEL, C., FINKENWIRTH, C., HESCHL, A., HUBER, J., ISLER, K., KOSONEN, Z. K., MARTINS, E., MEULMAN, E. J., RICHIGER, R., RUETH, K., SPILLMANN, B., WIESENDANGER, S. & VAN SCHAIK, C. P. 2014. The evolutionary origin of human hyper-cooperation. *Nat Commun,* 5**,** 4747.

BURKART, J. M., HRDY, S. B. & VAN SCHAIK, C. P. 2009. Cooperative Breeding and Human Cognitive Evolution. *Evolutionary Anthropology,* 18**,** 175-186.

BURNHAM, T. C. & JOHNSON, D. D. P. 2005. The biological and evolutionary logic of human cooperation. *Analyse & Kritik,* 27**,** 113-135.

BUTTELMANN, D., CALL, J. & TOMASELLO, M. 2009. Do great apes use emotional expressions to infer desires? *Developmental Science,* 12**,** 688-698.

BUTTELMANN, D., OVER, H., CARPENTER, M. & TOMASELLO, M. 2014. Eighteen-month-olds understand false beliefs in an unexpected-contents task. *J Exp Child Psychol,* 119**,** 120-6.

BUTTELMANN, D., SCHÜTTE, S., CARPENTER, M., CALL, J. & TOMASELLO, M. 2012. Great apes infer others' goals based on context. *Animal cognition,* 15**,** 1037-53.

BUTTELMANN, F., SUHRKE, J. & BUTTELMANN, D. 2015. What you get is what you believe: eighteen-month-olds demonstrate belief understanding in an unexpected-identity task. *J Exp Child Psychol,* 131**,** 94-103.

BYGOTT, J. D. 1979. Agonistic behavior, dominance, and social structure in wild chimpanzees of the Gombe National Park. *In:* HAMBURG, D. & MCCOWN, E. (eds.) *The Great Apes.* Menlo Park, CA: Benjamin Cummings.

BYRNE, R. W. & BATES, L. A. 2007. Sociality, evolution and cognition. *Current Biology,* 17**,** R714-23.

BYRNE, R. W. & WHITEN, A. W. 1988. *Machiavellian intelligence : social expertise and the evolution of intellect in monkeys, apes, and humans,* Oxford, Clarendon Press.

BYRNIT, J. T., HOGH-OLESEN, H. & MAKRANSKY, G. 2015. Share your sweets: Chimpanzee (Pan troglodytes) and bonobo (Pan paniscus) willingness to share highly attractive, monopolizable food sources. *J Comp Psychol,* 129**,** 218-28.

CALL, J., HARE, B., CARPENTER, M. & TOMASELLO, M. 2004. 'Unwilling' versus 'unable': chimpanzees' understanding of human intentional action. *Developmental Science,* 7**,** 488-498.

CALL, J., HARE, B. & TOMASELLO, M. 1998. Chimpanzee gaze following in an object-choice task. *Animal Cognition,* 1**,** 89-99.

CALL, J. & TOMASELLO, M. 1998. Distinguishing intentional from accidental actions in orangutans (Pongo pygmaeus), chimpanzees (Pan troglodytes), and human children (Homo sapiens). *Journal of Comparative Psychology,* 112**,** 192-206.

CALL, J. & TOMASELLO, M. 1999. A nonverbal false belief task: The performance of children and great apes. *Child Development,* 70**,** 381-395.

CALL, J. & TOMASELLO, M. 2005. What chimpanzees know about seeing, revisited: An explanation of the third kind. *In:* EILAN, N., HOERLH, C., MCCORMACK, T. & ROESSLER, J. (eds.) *Joint Attention: Communication and Other Minds -- Issues in Philosophy and Psychology.* Oxford University Press.

CALL, J. & TOMASELLO, M. 2007. *The gestural communication of apes and monkeys,* Mahwah, N.J., Lawrence Erlbaum Associates, Publishers.

CALL, J. & TOMASELLO, M. 2008. Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Sciences,* 12**,** 187-192.

CAMPBELL, M. W. & DE WAAL, F. B. 2011. Ingroup-outgroup bias in contagious yawning by chimpanzees supports link to empathy. *PLoS One,* 6**,** e18283.

CHAPAIS, B. 1995. Alliances as a means of competition in primates: evolutionary, developmental, and cognitive aspects. *Yearbook of Physical Anthropology,* 38**,** 115-136.

CHENEY, D. L. & SEYFARTH, R. M. 1980. Vocal recognition in free-ranging vervet monkeys. *Anim Behav,* 28**,** 362-367.

CHENEY, D. L. & SEYFARTH, R. M. 1990. *How monkeys see the world: inside the mind of another species,* Chicago, University of Chicago Press.

CHENEY, D. L. & SEYFARTH, R. M. 1999. Recognition of other individuals social relationships by female baboons. *Anim Behav,* 58**,** 67-75.

CHENEY, D. L. & SEYFARTH, R. M. 2007. *Baboon metaphysics : the evolution of a social mind,* Chicago, University of Chicago Press.

CHENEY, D. L., SEYFARTH, R. M. & SILK, J. B. 1995. The responses of female baboons (Papio cynocephalus ursinus) to anomalous social interactions-evidence for causal reasoning? *J Comp Psychol,* 109**,** 134-141.

CIERI, R. L., CHURCHILL, S. E., FRANCISCUS, R. G., TAN, J. & HARE, B. 2014. Craniofacial Feminization, Social Tolerance, and the Origins of Behavioral Modernity. *Current Anthropology,* 55**,** 419-443.

CLAY, Z. & DE WAAL, F. B. 2013. Development of socio-emotional competence in bonobos. *Proc Natl Acad Sci U S A,* 110**,** 18121-6.

CLAY, Z. & ZUBERBUHLER, K. 2012. Communication during sex among female bonobos: effects of dominance, solicitation and audience. *Sci Rep,* 2**,** 291.

CLEMENTS, W. A. & PERNER, J. 1994. Implicit understanding of belief. *Cognitive development,* 9**,** 377-395.

CLUTTON-BROCK, T. H. (ed.) 1988. *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems,* Chicago: University of Chicago Press.

CLUTTON-BROCK, T. H. & HARVEY, P. H. 1977. Primate ecology and social organization. *J Zoology,* 183**,** 1-39.

CROCKFORD, C., WITTIG, R. M., MUNDRY, R. & ZUBERBUHLER, K. 2012. Wild chimpanzees inform ignorant group members of danger. *Curr Biol,* 22**,** 142-6.

CROCKFORD, C., WITTIG, R. M., SEYFARTH, R. M. & CHENEY, D. L. 2007. Baboons eavesdrop to deduce mating opportunities. *Animal Behaviour,* 73**,** 885-890.

CRONIN, K. A. 2012. Prosocial behaviour in animals: the influence of social relationships, communication and rewards. *Animal Behaviour,* 84**,** 1085-1093.

CRONIN, K. A., DE GROOT, E. & STEVENS, J. M. 2015. Bonobos show limited social tolerance in a group setting: a comparison with chimpanzees and a test of the relational model. *Folia Primatol (Basel),* 86**,** 164-77.

DADDS, M. R., ALLEN, J. L., OLIVER, B. R., FAULKNER, N., LEGGE, K., MOUL, C., WOOLGAR, M. & SCOTT, S. 2012. Love, eye contact and the developmental origins of empathy v. psychopathy. *Br J Psychiatry,* 200**,** 191-6.

DARWIN, C. 1871. *The descent of man, and selection in relation to sex,* New York, D. Appleton and company.

DASSER, V. 1988. A social concept in Java monkeys. *Anim Behav,* 36**,** 225-230.

DE WAAL, F. B. 1982. *Chimpanzee Politics: Power and Sex among Apes,* New York, Harper and Row.

DE WAAL, F. B. M. 1997. Food transfers through mesh in brown capuchins. *J Comp Psychol,* 111**,** 370-378.

DEANER, R. O., BARTON, R. A. & VAN SCHAIK, C. 2003. Primate brains and life histories: renewing the connection. *In:* KAPPELER, P. M. & PEREIRA, M. E. (eds.) *Primate Life Histories and Socioecology.* Chicago: University of Chicago Press.

DEMURU, E. & PALAGI, E. 2012. In bonobos yawn contagion is higher among kin and friends. *PLoS One,* 7**,** e49613.

DRAYTON, L. A. & SANTOS, L. R. 2014. A decade of theory of mind research on cayo santiago: Insights into rhesus macaque social cognition. *Am J Primatol*.

DUFFY, K. G., WRANGHAM, R. W. & SILK, J. B. 2007. Male chimpanzees exchange political support for mating opportunities. *Curr Biol,* 17**,** R586-7.

DUNBAR, R. I. & SHULTZ, S. 2007. Evolution in the social brain. *Science,* 317**,** 1344-7.

DUNFIELD, K. A. & KUHLMEIER, V. A. 2010. Intention-mediated selective helping in infancy. *Psychol Sci,* 21**,** 523-7.

EISENBERG, N., FABES, R. & SPINRAD, T. 2006. Prosocial Development. *In:* EISENBERG, N. (ed.) *Handbook of Child Psychology.* John Wiley & Sons.

EMERY, N. J. 2000. The eyes have it: the neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews,* 24**,** 581-604.

ENDLER, J. A. 1986. *Natural Selection in the Wild,* Princeton, Princeton University Press.

FAGOT, J. & COOK, R. G. 2006. Evidence for large long-term memory capacities in baboons and pigeons and its implications for learning and the evolution of cognition. *Proceedings of the National Academy of Sciences of the United States of America,* 103**,** 17564-17567.

FEHR, E. & FISCHBACHER, U. 2003. The nature of human altruism. *Nature,* 425**,** 785-791.

FLAVEL, J. H., EVERETT, B. A., CROFT, K. & FLAVEL, E. R. 1981. Young children's knowledge about visual perception: Further evidence for the Level 1–Level 2 distinction. *Dev Psychol,* 17**,** 99-103.

FLAVEL, J. H., SHIPSTEAD, S. G. & CROFT, K. 1978. Young children's knowledge about visual perception: hiding objects from others. *Child Dev,* 49**,** 1208-1211.

FLEMMING, T. M., THOMPSON, R. K. & FAGOT, J. 2013. Baboons, like humans, solve analogy by categorical abstraction of relations. *Anim Cogn,* 16**,** 519-24.

FLOMBAUM, J. I. & SANTOS, L. R. 2005. Rhesus monkeys attribute perceptions to others. *Current Biology,* 15**,** 447-452.

FOERSTER, S., MCLELLAN, K., SCHROEPFER-WALKER, K., MURRAY, C. M., KRUPENYE, C., GILBY, I. C. & PUSEY, A. E. 2015. Social bonds in the dispersing sex: partner preferences among adult female chimpanzees. *Anim Behav,* 105**,** 139-152.

FRASER, O. N., STAHL, D. & AURELI, F. 2008. Stress reduction through consolation in chimpanzees. *Proc Natl Acad Sci U S A,* 105**,** 8557-62.

FURUICHI, T. 2011. Female contributions to the peaceful nature of bonobo society. *Evol Anthropol,* 20**,** 131-42.

FURUICHI, T., KOOPS, K., RYU, H., SANZ, C., SAKAMAKI, T., MORGAN, D. & TOKUYAMA, N. 2015. Why do wild bonobos not use tools like chimpanzees do? *Behaviour,* 152**,** 425-460.

GÁCSI, M., GYÖRI, B., GYOÖRI, B., VIRÁNYI, Z., KUBINYI, E., RANGE, F., BELÉNYI, B. & MIKLÓSI, A. 2009. Explaining dog wolf differences in utilizing human pointing gestures: selection for synergistic shifts in the development of some social skills. *PloS one,* 4**,** e6584.

GILBY, I. C. 2006. Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Animal Behaviour,* 71**,** 953-963.

GILBY, I. C., BRENT, L. J., WROBLEWSKI, E. E., RUDICELL, R. S., HAHN, B. H., GOODALL, J. & PUSEY, A. E. 2013a. Fitness Benefits of Coalitionary Aggression in Male Chimpanzees. *Behav Ecol Sociobiol,* 67**,** 373-381.

GILBY, I. C., EBERLY, L. E., PINTEA, L. & PUSEY, A. E. 2006. Ecological and social influences on the hunting behaviour of wild chimpanzees, Pan troglodytes schweinfurthii. *Animal Behaviour,* 72**,** 169-180.

GILBY, I. C., MACHANDA, Z. P., MJUNGU, D. C., ROSEN, J., MULLER, M. N., PUSEY, A. E. & WRANGHAM, R. W. 2015. 'Impact hunters' catalyse cooperative hunting in two wild chimpanzee communities. *Philos Trans R Soc Lond B Biol Sci,* 370.

GILBY, I. C., WILSON, M. L. & PUSEY, A. E. 2013b. Ecology rather than psychology explains co-occurrence of predation and border patrols in male chimpanzees. *Anim Behav,* 86**,** 61-74.

GILBY, I. C. & WRANGHAM, R. W. 2007. Risk-prone hunting by chimpanzees (Pan troglodytes schweinfurthii) increases during periods of high diet quality. *Behavioral Ecology and Sociobiology,* 61**,** 1771-1779.

GOODALL, J. 1986. *The chimpanzees of Gombe: patterns of behavior,* Cambridge, Mass., Belknap Press of Harvard University Press.

GURVEN, M. & JAEGGI, A. V. 2015. Food Sharing. *In:* SCOTT, R. A. & KOSSLYN, S. M. (eds.) *Emerging Trends in the Social and Behavioral Sciences.* John Wiley & Sons, Inc.

HAMLIN, J. K. 2013. Failed attempts to help and harm: intention versus outcome in preverbal infants' social evaluations. *Cognition,* 128**,** 451-74.

HAMLIN, J. K., MAHAJAN, N., LIBERMAN, Z. & WYNN, K. 2013. Not like me = bad: infants prefer those who harm dissimilar others. *Psychol Sci,* 24**,** 589-94.

HAMLIN, J. K. & WYNN, K. 2011. Young infants prefer prosocial to antisocial others. *Cogn Dev,* 26**,** 30-39.

HAMLIN, J. K., WYNN, K. & BLOOM, P. 2007. Social evaluation by preverbal infants. *Nature,* 450**,** 557-9.

HAMLIN, J. K., WYNN, K. & BLOOM, P. 2010a. Three-month-olds show a negativity bias in their social
evaluations. *Developmental Science,* 13**,** 923-929.

HAMLIN, J. K., WYNN, K. & BLOOM, P. 2010b. Three-month-olds show a negativity bias in their social
evaluations. *Dev Sci,* 13**,** 923-929.

HAMLIN, J. K., WYNN, K., BLOOM, P. & MAHAJAN, N. 2011. How infants and toddlers react to antisocial others. *Proc Natl Acad Sci U S A,* 108**,** 19931-19936.

HARCOURT, A. H. & DE WAAL, F. B. M. 1992. *Coalitions and alliances in humans and other animals,* Oxford [England] ; New York, Oxford University Press.

HARE, B. 2001. Can competitive paradigms increase the validity of experiments on primate social cognition? *Animal Cognition,* 4**,** 269-280.

HARE, B. 2007. From nonhuman to human mind - What changed and why? *Current Directions in Psychological Science,* 16**,** 60-64.

HARE, B. 2009. What is the effect of affect on bonobo and chimpanzee problem solving? *In:* BERTHOZ, A. & CHRISTEN, Y. (eds.) *Neurobiology of the "Umwelt".* Springer Berlin Heidelberg.

HARE, B. 2011. From hominoid to hominid mind: what changed and why? *Annual Review of Anthropology,* 40**,** 293-309.

HARE, B. Submitted. Survival of the friendliest: Homo sapiens evolved via selection for prosociality.

HARE, B., BROWN, M., WILLIAMSON, C. & TOMASELLO, M. 2002. The domestication of social cognition in dogs. *Science,* 298**,** 1634-1636.

HARE, B., CALL, J., AGNETTA, B. & TOMASELLO, M. 2000. Chimpanzees know what conspecifics do and do not see. *Animal Behaviour,* 59**,** 771-785.

HARE, B., CALL, J. & TOMASELLO, M. 2001. Do chimpanzees know what conspecifics know? *Animal Behaviour,* 61**,** 139-151.

HARE, B., CALL, J. & TOMASELLO, M. 2006. Chimpanzees deceive a human competitor by hiding. *Cognition,* 101**,** 495-514.

HARE, B. & KWETUENDA, S. 2010. Bonobos voluntarily share their own food with others. *Current Biology,* 20**,** R230-R231.

HARE, B., MELIS, A. P., WOODS, V., HASTINGS, S. & WRANGHAM, R. 2007. Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology,* 17**,** 619-623.

HARE, B., PLYUSNINA, I., IGNACIO, N., SCHEPINA, O., STEPIKA, A., WRANGHAM, R. & TRUT, L. 2005. Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. *Current Biology,* 15**,** 226-30.

HARE, B. & TAN, J. 2011. How much of our cooperative behavior Is human? *In:* DE WAAL, F. B. M. & FERRARI, P. F. (eds.) *The Primate Mind: Built to Connect with Other Minds.* Cambridge, Massachussetts: Harvard University Press.

HARE, B. & TOMASELLO, M. 2004. Chimpanzees are more skilful in competitive than in cooperative cognitive tasks. *Animal Behaviour,* 68**,** 571-581.

HARE, B. & TOMASELLO, M. 2005. The emotional reactivity hypothesis and cognitive evolution. *Trends in Cognitive Sciences,* 9**,** 464-465.

HARE, B., WOBBER, V. & WRANGHAM, R. 2012. The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour,* 83**,** 573-585.

HARE, B. & WOODS, V. 2013. *The Genius of Dogs: How Dogs Are Smarter than You Think*, Dutton Adult.

HATTORI, Y., KANO, F. & TOMONAGA, M. 2010. Differential sensitivity to conspecific and allospecific cues in chimpanzees and humans: a comparative eye-tracking study. *Biology Letters*.

HAYAKI, H., HUFFMAN, M. A. & NISHIDA, T. 1989. Dominance among male chimpanzees in the Mahale Mountains National Park, Tanzania: a preliminary study. *Primates,* 30**,** 187-197.

HEPACH, R., VAISH, A. & TOMASELLO, M. 2012. Young children are intrinsically motivated to see others helped. *Psychol Sci,* 23**,** 967-72.

HERNADI, A., KIS, A., TURCSAN, B. & TOPAL, J. 2012. Man's underground best friend: domestic ferrets, unlike the wild forms, show evidence of dog-like social-cognitive skills. *PLoS One,* 7**,** e43267.

HERRMANN, E., HARE, B., CALL, J. & TOMASELLO, M. 2010. Differences in the cognitive skills of bonobos and chimpanzees. *Plos One,* 5.

HERRMANN, E., HARE, B., CISSEWSKI, J. & TOMASELLO, M. 2011. A comparison of temperament in nonhuman apes and human infants. *Developmental Science*.

HERRMANN, E., KEUPP, S., HARE, B., VAISH, A. & TOMASELLO, M. 2013. Direct and indirect reputation formation in nonhuman great apes (Pan paniscus, Pan troglodytes, Gorilla gorilla, Pongo pygmaeus) and human children (Homo sapiens). *J Comp Psychol,* 127**,** 63-75.

HERRMANN, E. & TOMASELLO, M. 2006. Apes' and children's understanding of cooperative and competitive motives in a communicative situation. *Developmental Science,* 9**,** 518-529.

HEYES, C. M. 1993. Anecdotes, training, trapping and triangulating: do animals attribute mental states? *Animal Behaviour,* 46**,** 177-188.

HEYES, C. M. 1998. Theory of mind in nonhuman primates. *Behavioral and Brain Sciences,* 21**,** 101-14; discussion 115-48.

HILL, K., BARTON, M. & HURTADO, A. M. 2009. The Emergence of Human Uniqueness: Characters Underlying Behavioral Modernity. *Evolutionary Anthropology,* 18**,** 187-200.

HILL, R. A. & LEE, P. C. 1998. Predation risk as an influence on group size in cercopithecoid
primates: implications for social structure. *J Zoology,* 245**,** 447-456.

HOHMANN, G. & FRUTH, B. 2003. Culture in Bonobos? Between - Species and Within - Species Variation in Behavior. *Current Anthropology,* 44**,** 563-571.

HORNER, V., CARTER, J. D., SUCHAK, M. & DE WAAL, F. B. 2011. Spontaneous prosocial choice by chimpanzees. *Proc Natl Acad Sci U S A,* 108**,** 13847-51.

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**,** 337-343.

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.

HOUSE, B. R., SILK, J. B., HENRICH, J., BARRETT, H. C., SCELZA, B. A., BOYETTE, A. H., HEWLETT, B. S., MCELREATH, R. & LAURENCE, S. 2013. Ontogeny of prosocial behavior across diverse societies. *Proc Natl Acad Sci U S A,* 110**,** 14586-14591.

HUMPHREY, N. K. 1976. The social function of intellect. *In:* BATESON, P. & HINDE, R. (eds.) *Growing points in ethology.* Cambridge: Cambridge University Press.

HUXLEY, T. H. 1863. *Man's Place in Nature,* London, Williams & Norgate.

INOUE, S. & MATSUZAWA, T. 2007. Working memory of numerals in chimpanzees. *Curr Biol,* 17**,** R1004-5.

ITAKURA, S., AGNETTA, B., HARE, B. & TOMASELLO, M. 1999. Chimpanzee use of human and conspecific social cues to locate hidden food. *Developmental Science,* 2**,** 448.

ITAKURA, S. & TANAKA, M. 1998. Use of experimenter-given cues during object-choice tasks by chimpanzees (*Pan troglodytes*), an orangutan (*Pongo pygmaeus*), and human infants (*Homo sapiens*). *Journal of Comparative Psychology,* 112**,** 119-126.

JAEGGI, A. V., BURKART, J. M. & VAN SCHAIK, C. P. 2010a. On the psychology of cooperation in humans and other primates: combining the natural history and experimental evidence of prosociality. *Philos Trans R Soc Lond B Biol Sci,* 365**,** 2723-35.

JAEGGI, A. V., DE GROOT, E., STEVENS, J. M. G. & VAN SCHAIK, C. P. 2013. Mechanisms of reciprocity in primates: testing for short-term contingency of grooming and food sharing in bonobos and chimpanzees. *Evolution and Human Behavior,* 34**,** 69-77.

JAEGGI, A. V., STEVENS, J. M. & VAN SCHAIK, C. P. 2010b. Tolerant food sharing and reciprocity is precluded by despotism among bonobos but not chimpanzees. *Am J Phys Anthropol,* 143**,** 41-51.

JOLLY, A. 1966. Lemur Social Behavior and Primate Intelligence. *Science,* 153**,** 501-506.

JORDAN, J. J., MCAULIFFE, K. & WARNEKEN, F. 2014. Development of in-group favoritism in children's third-party punishment of selfishness. *Proc Natl Acad Sci U S A,* 111**,** 12710-5.

KAMINSKI, J., CALL, J. & TOMASELLO, M. 2004. Body orientation and face orientation: two factors controlling apes' begging behavior from humans. *Animal Cognition,* 7**,** 216-223.

KAMINSKI, J., CALL, J. & TOMASELLO, M. 2008. Chimpanzees know what others know, but not what they believe. *Cognition,* 109**,** 224-234.

KANO, F. & CALL, J. 2014a. Cross-species variation in gaze following and conspecific preference among great apes, human infants and adults. *Animal Behaviour,* 91**,** 137-150.

KANO, F. & CALL, J. 2014b. Great apes generate goal-based action predictions: an eye-tracking study. *Psychol Sci,* 25**,** 1691-8.

KANO, F. & HIRATA, S. 2015. Great Apes Make Anticipatory Looks Based on Long-Term Memory of Single Events. *Curr Biol,* 25**,** 2513-7.

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**,** e0129684.

KANO, F. & TOMONAGA, M. 2010. Face scanning in chimpanzees and humans: continuity and discontinuity. *Animal Behaviour,* 79**,** 227-235.

KANO, F. & TOMONAGA, M. 2011. Perceptual mechanism underlying gaze guidance in chimpanzees and humans. *Animal Cognition,* 14**,** 377-386.

KAPLAN, H., HILL, K., LANCASTER, J. & HURTADO, A. M. 2000. A theory of human life history evolution: diet, intelligence, and longevity. *Evol Anthropol,* 9**,** 156-185.

KARG, K., SCHMELZ, M., CALL, J. & TOMASELLO, M. 2015a. Chimpanzees strategically manipulate what others can see. *Anim Cogn,* 18**,** 1069-76.

KARG, K., SCHMELZ, M., CALL, J. & TOMASELLO, M. 2015b. The goggles experiment: can chimpanzees use self-experience to infer what a competitor can see? *Animal Behaviour,* 105**,** 211-221.

KARG, K., SCHMELZ, M., CALL, J. & TOMASELLO, M. 2016. Differing views: Can chimpanzees do Level 2 perspective-taking? *Anim Cogn*.

KING, B. J. 1986. Extractive foraging and the evolution of primate intelligence. *J Hum Evol,* 1**,** 361-372.

KINZLER, K. D., DUPOUX, E. & SPELKE, E. S. 2007. The native language of social cognition. *Proc Natl Acad Sci U S A,* 104**,** 12577-12580.

KITCHEN, D. M., CHENEY, D. L. & SEYFARTH, R. M. 2005. Male chacma baboons (Papio hamadryas ursinus) discriminate loud call contests between rivals of different relative ranks. *Anim Cogn,* 8**,** 1-6.

KOOPS, K., FURUICHI, T. & HASHIMOTO, C. 2015a. Chimpanzees and bonobos differ in intrinsic motivation for tool use. *Sci Rep,* 5**,** 11356.

KOOPS, K., FURUICHI, T., HASHIMOTO, C. & VAN SCHAIK, C. P. 2015b. Sex Differences in Object Manipulation in Wild Immature Chimpanzees (Pan troglodytes schweinfurthii) and Bonobos (Pan paniscus): Preparation for Tool Use? *PLoS One,* 10**,** e0139909.

KRACHUN, C., CARPENTER, M., CALL, J. & TOMASELLO, M. 2009. A competitive nonverbal false belief task for children and apes. *Developmental Science,* 12**,** 521-535.

KRACHUN, C., CARPENTER, M., CALL, J. & TOMASELLO, M. 2010. A New Change-of-Contents False Belief Test- Children and Chimpanzees Compared. *Int J Comp Psychol,* 23**,** 145-165.

KRET, M. E., JAASMA, L., BIONDA, T. & WIJNEN, J. G. 2016. Bonobos (Pan paniscus) show an attentional bias toward conspecifics' emotions. *Proc Natl Acad Sci U S A*.

KRUPENYE, C. & HARE, B. in preparation-a. Bonobos prefer individuals that hinder third parties over those that help.

KRUPENYE, C. & HARE, B. in preparation-b. Intentions outweigh outcomes in bonobos' social evaluations.

KRUPENYE, C., KANO, F., HIRATA, S., CALL, J. & TOMASELLO, M. in preparation-a. Great apes anticipate actions based on agents' false beliefs.

KRUPENYE, C., ROSATI, A. G. & HARE, B. 2015. Bonobos and chimpanzees exhibit human-like framing effects. *Biol Lett,* 11**,** 20140527.

KRUPENYE, C., TAN, J. & HARE, B. in preparation-b. Bonobos actively share food but not their toys or tools.

LANDIS, J. R. & KOCH, G. G. 1977. The measurement of observer agreement for categorical data. *Biometrics,* 33**,** 159-174.

LANGERGRABER, K. E., MITANI, J. C. & VIGILANT, L. 2007. The limited impact of kinship on cooperation in wild chimpanzees. *Proc Natl Acad Sci U S A,* 104**,** 7786-90.

LE ROUX, A. & BERGMAN, T. J. 2012. Indirect rival assessment in a social primate, Theropithecus gelada. *Animal Behaviour,* 83**,** 249-255.

LE ROUX, A., SNYDER-MACKLER, N., ROBERTS, E. K., BEEHNER, J. C. & BERGMAN, T. J. 2013. Evidence for tactical concealment in a wild primate. *Nat Commun,* 4**,** 1462.

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.

LEHMANN, J., FICKENSCHER, G. & BOESCH, C. 2006. Kin biased investment in wild chimpanzees. *Behaviour,* 143**,** 931-955.

LEIGHTY, K. A., MENZEL, C. R. & FRAGASZY, D. M. 2008. How young children and chimpanzees (Pan troglodytes) perceive objects in a 2D display: putting an assumption to the test. *Dev Sci,* 11**,** 778-92.

LESLIE, A. M., FRIEDMAN, O. & GERMAN, T. P. 2004. Core mechanisms in 'theory of mind'. *Trends in cognitive sciences,* 8**,** 528-533.

LIEBAL, K., CALL, J., TOMASELLO, M. & PIKA, S. 2004. To move or not to move: How apes adjust to the attentional state of others. *Interaction Studies,* 5**,** 199-219.

LIEBAL, K., VAISH, A., HAUN, D. & TOMASELLO, M. 2014. Does sympathy motivate prosocial behaviour in great apes? *PLoS One,* 9**,** e84299.

LOHMANN, H. & TOMASELLO, M. 2003. The role of language in false belief understanding development: a training study. *Child Dev,* 74**,** 1130-1144.

LOW, J. & PERNER, J. 2012. Implicit and explicit theory of mind: state of the art. *Br J Dev Psychol,* 30**,** 1-13.

LOW, J. & WATTS, J. 2013. Attributing false beliefs about object identity reveals a signature blind spot in humans' efficient mind-reading system. *Psychol Sci,* 24**,** 305-11.

LUO, Y. 2011. Do 10-month-old infants understand others' false beliefs? *Cognition,* 121**,** 289-98.

LYONS, D. E. & SANTOS, L. R. 2006. Ecology, Domain Specificity, and the Origins of Theory of Mind: Is Competition the Catalyst? *Philosophy Compass,* 1**,** 481-492.

MACHANDA, Z. P., GILBY, I. C. & WRANGHAM, R. W. 2013. Male–Female Association Patterns Among Free-ranging Chimpanzees (Pan troglodytes schweinfurthii). *International Journal of Primatology,* 34**,** 917-938.

MACLEAN, E. & HARE, B. 2013. Spontaneous triadic engagement in bonobos (Pan paniscus) and chimpanzees (Pan troglodytes). *J Comp Psychol,* 127**,** 245-55.

MACLEAN, E. L. & HARE, B. 2012. Bonobos and chimpanzees infer the target of another's attention. *Animal Behaviour,* 83**,** 345-353.

MACLEAN, E. L. & HARE, B. 2015. Bonobos and chimpanzees exploit helpful but not prohibitive gestures. *Behaviour,* 152**,** 493-520.

MACLEAN, E. L., HARE, B., NUNN, C. L., ADDESSI, E., AMICI, F., ANDERSON, R. C., AURELI, F., BAKER, J. M., BANIA, A. E., BARNARD, A. M., BOOGERTL, N. J., BRANNON, E. M., BRAY, E. E., BRAY, J., BRENT, L. J. N., BURKART, J. M., CALL, J., CANTLON, J. F., CHEKE, L. G., CLAYTON, N. S., DELGADO, M. M., DIVINCENTIS, L. J., FUJITA, K., HERRMANN, E., HIRAMATSU, C., JACOBS, L. F., JORDAN, K. E., LAUDEW, J. R., LEIMGRUBER, K. L., MESSER, E. J. E., MOURAY, A. C., OSTOJIC, L., PICARD, A., PLATT, M. L., PLOTNIK, J. M., RANGE, F., READER, S. M., REDDY, R. B., SANDEL, A. A., SANTOS, L. R., SCHUMANND, K., SEED, A. M., SEWALL, K. B., SHAW, R. C., SLOCOMBE, K. E., SU, Y., TAKIMOTO, A., TAN, J., TAO, R., VAN SCHAIK, C. P., VIRÁNYI, Z., VISALBERGHI, E., WADE, J. C., WATANABE, A., WIDNESS, J., YOUNG, J. K., ZENTALL, T. R. & ZHAO, Y. 2014. The evolution of self-control. *Proceedings of the National Academy of Sciences,* 111**,** E2140-E2148.

MACLEAN, E. L., MATTHEWS, L., HARE, B., NUNN, C., ANDERSON, R., AURELI, F., BRANNON, E., CALL, J., DREA, C., EMERY, N., HAUN, D., HERRMANN, E., JACOBS, L., PLATT, M., ROSATI, A., SANDEL, A., SCHROEPFER, K., SEED, A., TAN, J., VAN SCHAIK, C. & WOBBER, V. 2012. How does cognition evolve? Phylogenetic comparative psychology. *Animal Cognition***,** 1-16.

MACLEAN, E. L., MERRITT, D. J. & BRANNON, E. M. 2008. Social complexity predicts transitive reasoning in prosimian primates. *Anim Behav,* 76**,** 479-486.

MACLEAN, E. L., SANDEL, A. A., BRAY, J., OLDENKAMP, R. E., REDDY, R. B. & HARE, B. A. 2013. Group size predicts social but not nonsocial cognition in lemurs. *PLoS One,* 8**,** e66359.

MARTICORENA, D. C., RUIZ, A. M., MUKERJI, C., GODDU, A. & SANTOS, L. R. 2011. Monkeys represent others' knowledge but not their beliefs. *Developmental science,* 14**,** 1406-1416.

MARTIN, A. & SANTOS, L. R. 2014. The origins of belief representation: monkeys fail to automatically represent others' beliefs. *Cognition,* 130**,** 300-8.

MCAULIFFE, K., JORDAN, J. J. & WARNEKEN, F. 2015. Costly third-party punishment in young children. *Cognition,* 134**,** 1-10.

MCINTYRE, M. H., HERRMANN, E., WOBBER, V., HALBWAX, M., MOHAMBA, C., DE SOUSA, N., ATENCIA, R., COX, D. & HARE, B. 2009. Bonobos have a more human-like second-to-fourth finger length ratio (2D:4D) than chimpanzees: a hypothesized indication of lower prenatal androgens. *Journal of Human Evolution,* 56**,** 361-365.

MELIS, A. P., CALL, J. & TOMASELLO, M. 2006a. Chimpanzees (Pan troglodytes) conceal visual and auditory information from others. *Journal of Comparative Psychology,* 120**,** 154-162.

MELIS, A. P., HARE, B. & TOMASELLO, M. 2006b. Chimpanzees recruit the best collaborators. *Science,* 311**,** 1297-300.

MELIS, A. P., HARE, B. & TOMASELLO, M. 2006c. Engineering cooperation in chimpanzees: tolerance constraints on cooperation. *Animal Behaviour,* 72**,** 275-286.

MELIS, A. P., HARE, B. & TOMASELLO, M. 2009. Chimpanzees coordinate in a negotiation game. *Evolution and Human Behavior,* 30**,** 381-392.

MELIS, A. P. & TOMASELLO, M. 2013. Chimpanzees' (Pan troglodytes) strategic helping in a collaborative task. *Biol Lett,* 9**,** 20130009.

MELIS, A. P., WARNEKEN, F., JENSEN, K., SCHNEIDER, A. C., CALL, J. & TOMASELLO, M. 2011. Chimpanzees help conspecifics obtain food and non-food items. *Proc Biol Sci,* 278**,** 1405-13.

MIKLOSI, A., KUBINYI, E., TOPAL, J., GACSI, M., VIRANYI, Z. & CSANYI, V. 2003. A simple reason for a big difference: Wolves do not look back at humans, but dogs do. *Current Biology,* 13**,** 763-766.

MILLIGAN, K., ASTINGTON, J. W. & DACK, L. A. 2007. Language and theory of mind: Meta-analysis of the relation between language ability and false-belief understanding. *Child Dev,* 78**,** 622-646.

MILTON, K. 1988. Foraging behavior and the evolution of primate cognition. *In:* WHITEN, A. & BYRNE, R. (eds.) *Machiavellian Intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans.* Oxford: Oxford University Press.

MITANI, J. C. 2009. Cooperation and competition in chimpanzees: Current understanding and future challenges. *Evolutionary Anthropology: Issues, News, and Reviews,* 18**,** 215-227.

MITANI, J. C., WATTS, D. P. & AMSLER, S. J. 2010. Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Curr Biol,* 20**,** R507-8.

MULCAHY, N. J. & CALL, J. 2006. Apes save tools for future use. *Science,* 312**,** 1038-40.

MULLER, M. N. & MITANI, J. C. 2005. Conflict and cooperation in wild chimpanzees. *In:* SLATER, P. J. B., ROSENBLATT, J., SNOWDON, C., ROPER, T. & NAGUIB, M. (eds.) *Advances in the study of behavior.* New York: Elsevier.

MYOWA-YAMAKOSHI, M., SCOLA, C. & HIRATA, S. 2012. Humans and chimpanzees attend differently to goal-directed actions. *Nature Communications,* 3**,** 693.

NEUMANN, C., DUBOSCQ, J., DUBUC, C., GINTING, A., IRWAN, A. M., AGIL, M., WIDDIG, A. & ENGELHARDT, A. 2011. Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour,* 82**,** 911-921.

NOË, R. & HAMMERSTEIN, P. 1995. Biological markets. *Trends Ecol Evol,* 10**,** 336-339.

OKAMOTO-BARTH, S., CALL, J. & TOMASELLO, M. 2007. Great apes' understanding of other individuals' line of sight. *Psychological Science,* 18**,** 462-468.

ONISHI, K. H. & BAILARGEON, R. 2005. Do 15-month-old infants understand false beliefs? *Science,* 308**,** 255-258.

ONISHI, K. H. & BAILLARGEON, R. 2005. Do 15-month-old infants understand false beliefs? *Science,* 308**,** 255-258.

PACKER, C., GILBERT, D. A., PUSEY, A. E. & O'BRIEN, S. J. 1991. A molecular genetic analysis of kinship and cooperation in African lions. *Nature,* 351**,** 562-565.

PALAGI, E. & NORSCIA, I. 2013. Bonobos protect and console friends and kin. *PLoS One,* 8**,** e79290.

PALAGI, E., NORSCIA, I. & DEMURU, E. 2014. Yawn contagion in humans and bonobos: emotional affinity matters more than species. *PeerJ,* 2**,** e519.

PAXTON, R., BASILE, B. M., ADACHI, I., SUZUKI, W. A., WILSON, M. E. & HAMPTON, R. R. 2010. Rhesus monkeys (Macaca mulatta) rapidly learn to select dominant individuals in videos of artificial social interactions between unfamiliar conspecifics. *J Comp Psychol,* 124**,** 395-401.

PAZ-Y-MIÑO, C. G., BOND, A. B., KAMIL, A. C. & BALDA, R. P. 2004. Pinyon jays use transitive inference to predict social dominance. *Nature,* 430**,** 778-81.

PENN, D. & POVINELLI, D. 2007. On the lack of evidence that non-human animals possess anything remotely resembling a 'theory of mind'. *Philos Trans R Soc Lond B Biol Sci,* 362**,** 731-44.

PERNER, J. & ROESSLER, J. 2012. From infants’ to children's appreciation of belief. *Trends in cognitive sciences,* 16**,** 519-525.

PERRY, S., BARRETT, H. C. & MANSON, J. H. 2004. White-faced capuchin monkeys show triadic awareness in their choice of allies. *Animal Behaviour,* 67**,** 165-170.

PHILLIPS, W., BARON-COHEN, S. & RUTTER, M. 1992. The role of eye-contact in the detection of goals: Evidence from normal toddlers, and children with autism or mental handicap. *Development and Psychopathology,* 4**,** 375-383.

POLLARD, K. A. & BLUMSTEIN, D. T. 2008. Time allocation and the evolution of group size. *Animal Behaviour,* 76**,** 1683-1699.

POVINELLI, D. J. & EDDY, T. J. 1996. Chimpanzees: Join visual attention. *Psychological Science,* 7**,** 129-135.

POVINELLI, D. J., NELSON, K. E. & BOYSEN, S. T. 1990. Inferences about guessing and knowing by chimpanzees (Pan troglodytes). *J Comp Psychol,* 104**,** 203-10.

POVINELLI, D. J., REAUX, J. E., BIERSCHWALE, D. T., ALLAIN, A. D. & SIMON, B. B. 1997. Exploitation of pointing as a referential gesture in young children, but not adolescent chimpanzees. *Cognitive Development,* 12**,** 327-365.

POVINELLI, D. J. & VONK, J. 2003. Chimpanzee minds: suspiciously human? *Trends Cogn Sci,* 7**,** 157-160.

POVINELLI, D. J. & VONK, J. 2004. We don't need a microscope to explore the chimpanzee's mind. *Mind and Language,* 19**,** 1-28.

PREMACK, D. & WOODRUFF, G. 1978. Does the chimpanzee have a theory of mind. *Behavioral and Brain Sciences,* 1**,** 515-526.

PRESTON, W. D. & DE WAAL, F. B. M. 2002. Empathy: Its ultimate and proximate bases. *Behav Brain Sci,* 25**,** 1-72.

PUSEY, A. 1997. The Influence of Dominance Rank on the Reproductive Success of Female Chimpanzees. *Science,* 277**,** 828-831.

R-DEVELOPMENT-CORE-TEAM. 2014. *R: A language and environment for statistical computing* [Online]. http://www.r-project.org/. Available: http://www.r-project.org/ [Accessed].

RANGE, F. & NOË, R. 2005. Can simple rules account for the pattern of triadic interactions in juvenile and adult female sooty mangabeys? *Animal Behaviour,* 69**,** 445-452.

RILLING, J. K., SCHOLZ, J., PREUSS, T. M., GLASSER, M. F., ERRANGI, B. K. & BEHRENS, T. E. 2012. Differences between chimpanzees and bonobos in neural systems supporting social cognition. *Social Cognitive and Affective Neuroscience,* 7**,** 369-379.

ROMERO, T., CASTELLANOS, M. A. & DE WAAL, F. B. M. 2010. Consolation as possible expression of sympathetic concern among chimpanzees. *Proc Natl Acad Sci U S A,* 107**,** 12110-12115.

ROSATI, A. G. & HARE, B. 2009. Looking past the model species: diversity in gaze-following skills across primates. *Current Opinion in Neurobiology,* 19**,** 45-51.

ROSATI, A. G. & HARE, B. 2012. Chimpanzees and bonobos exhibit divergent spatial memory development. *Dev Sci,* 15**,** 840-53.

RUSSELL, Y. I., CALL, J. & DUNBAR, R. I. 2008. Image scoring in great apes. *Behav Processes,* 78**,** 108-11.

SANDEL, A. A., MACLEAN, E. & HARE, B. 2011. Evidence from four lemur species that ringtailed lemur social cognition converges with that of haplorhine primates. *Animal Behaviour,* 81**,** 925-931.

SCHINO, G. 2001. Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour,* 62**,** 265-271.

SCHINO, G. & AURELI, F. 2010. Primate reciprocity and its cognitive requirements. *Evolutionary Anthropology: Issues, News, and Reviews,* 19**,** 130-135.

SCHINO, G., TIDDI, B. & DI SORRENTINO, E. P. 2006. Simultaneous classification by rank and kinship in Japanese macaques. *Animal Behaviour,* 71**,** 1069-1074.

SCHROEPFER-WALKER, K., HARE, B. & WOBBER, V. 2015. Experimental evidence that grooming and play are social currency in bonobos and chimpanzees. *Behaviour,* 152**,** 545-562.

SCHULKE, O., BHAGAVATULA, J., VIGILANT, L. & OSTNER, J. 2010. Social bonds enhance reproductive success in male macaques. *Curr Biol,* 20**,** 2207-10.

SCOTT, R. M., BAILLARGEON, R., SONG, H. J. & LESLIE, A. M. 2010. Attributing false beliefs about non-obvious properties at 18 months. *Cogn Psychol,* 61**,** 366-95.

SCOTT, R. M., RICHMAN, J. C. & BAILLARGEON, R. 2015. Infants understand deceptive intentions to implant false beliefs about identity: New evidence for early mentalistic reasoning. *Cogn Psychol,* 82**,** 32-56.

SEMENDEFERI, K., ARMSTRONG, E., SCHLEICHER, A., ZILLES, K. & VAN HOESEN, G. W. 1998. Limbic frontal cortex in hominoids: A comparative study of area 13. *American Journal of Physical Anthropology,* 106**,** 129-155.

SENJU, A., SOUTHGATE, V., SNAPE, C., LEONARD, M. & CSIBRA, G. 2011a. Do 18-month-olds really attribute mental states to others? A critical test. *Psychological science,* 22**,** 878-880.

SENJU, A., SOUTHGATE, V., SNAPE, C., LEONARD, M. & CSIBRA, G. 2011b. Do 18-month-olds really attribute mental states to others? A critical test. *Psychol Sci,* 22**,** 878-80.

SEYFARTH, R. M. 1977. A model of social grooming among adult female vervet monkeys. *J Theor Biol,* 65**,** 671-698.

SEYFARTH, R. M. & CHENEY, D. L. 2015. Social cognition. *Animal Behaviour,* 103**,** 191-202.

SILK, J. B. 1999. Male bonnet macaques use information about third party rank relationships to recruit allies. *Anim Behav,* 58**,** 45-51.

SILK, J. B. 2007. Social components of fitness in primate groups. *Science,* 317**,** 1347.

SILK, J. B., BROSNAN, S. F., HENRICH, J., LAMBETH, S. P. & SHAPIRO, S. J. 2013. Chimpanzees share food for many reasons: the role of kinship, reciprocity, social bonds and harassment on food transfers. *Anim Behav,* 85**,** 941-947.

SILK, J. B. & HOUSE, B. R. 2011. Evolutionary foundations of human prosocial sentiments. *Proc Natl Acad Sci U S A,* 108**,** 10910-10917.

SLOCOMBE, K. E. & ZUBERBUHLER, K. 2007. Chimpanzees modify recruitment screams as a function of audience composition. *Proc Natl Acad Sci U S A,* 104**,** 17228-33.

SOUTHGATE, V., CHEVALLIER, C. & CSIBRA, G. 2010. Seventeen-month-olds appeal to false beliefs to interpret others' referential communication. *Developmental science,* 13**,** 907-12.

SOUTHGATE, V., SENJU, A. & CSIBRA, G. 2007. Action anticipation through attribution of false belief by 2-year-olds. *Psychol Sci,* 18**,** 587-92.

SOUTHGATE, V. & VERNETTI, A. 2014. Belief-based action prediction in preverbal infants. *Cognition,* 130**,** 1-10.

STEVENS, J. M. G., VERVAEKE, H., DE VRIES, H. & VAN ELSAKER, L. 2005. The influence of the steepness of dominance hierarchies on reciprocity and interchange in captive groups of bonobos (Pan paniscus). *Behaviour,* 142**,** 941-960.

STEVENS, J. R. 2004. The selfish nature of generosity: harassment and food sharing in primates. *Proc Biol Sci,* 271**,** 451-6.

STIMPSON, C. D., BARGER, N., TAGLIALATELLA, J. P., GENDRON-FITZPATRICK, A., HOF, P. R., HOPKINS, W. D. & SHERWOOD, C. C. 2015. Differential serotonergic innervation of the amygdala in bonobos and chimpanzees. *Social Cognitive and Affective Neuroscience*.

SUBIAUL, F., VONK, J., OKAMOTO-BARTH, S. & BARTH, J. 2008. Do chimpanzees learn reputation by observation? Evidence from direct and indirect experience with generous and selfish strangers. *Anim Cogn,* 11**,** 611-23.

SURBECK, M., MUNDRY, R. & HOHMANN, G. 2011. Mothers matter! Maternal support, dominance status and mating success in male bonobos (Pan paniscus). *Proc Biol Sci,* 278**,** 590-8.

SURIAN, L., CALDI, S. & SPERBER, D. 2007. Attribution of beliefs by 13-month-old infants. *Psychological Science,* 18**,** 580-586.

TAN, J., ARIELY, D. & HARE, B. submitted. Bonobo xenophilia supports the first impression hypothesis.

TAN, J. & HARE, B. 2013. Bonobos share with strangers. *PLoS One,* 8**,** e51922.

TASIMI, A. & WYNN, K. 2016. Costly rejection of wrongdoers by infants and children. *Cognition,* 151**,** 76-79.

TEMPELMANN, S., KAMINSKI, J. & LIEBAL, K. 2011. Focus on the essential: all great apes know when others are being attentive. *Anim Cogn,* 14**,** 433-9.

THOERMER, C., SODIAN, B., VUORI, M., PERST, H. & KRISTEN, S. 2012. Continuity from an implicit to an explicit understanding of false belief from infancy to preschool age. *Br J Dev Psychol,* 30**,** 172-87.

TINBERGEN, N. 1963. On aims and methods of ethology. *Zeitschrift für Tierpsychologie,* 20**,** 410-433.

TOMASELLO, M. & CALL, J. 1997. *Primate cognition,* New York, Oxford University Press.

TOMASELLO, M., CALL, J. & HARE, B. 1998. Five primate species follow the visual gaze of conspecifics. *Animal Behaviour,* 55**,** 1063-1069.

TOMASELLO, M., CALL, J. & HARE, B. 2003a. Chimpanzees understand psychological states – the question is which ones and to what extent. *Trends in Cognitive Sciences,* 7**,** 153-156.

TOMASELLO, M., CALL, J. & HARE, B. 2003b. Chimpanzees understand psychological states: the question is which ones and to what extent. *Trends in Cognitive Sciences,* 7**,** 153-156.

TOMASELLO, M. & CARPENTER, M. 2005. The emergence of social cognition in three young chimpanzees. *Monographs of the Society for Research in Child Development,* 70.

TOMASELLO, M., CARPENTER, M., CALL, J., BEHNE, T. & MOLL, H. 2005. Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences,* 28**,** 675-+.

TOMASELLO, M., HARE, B. & AGNETTA, B. 1999. Chimpanzees, *Pan troglodytes,* follow gaze direction geometrically. *Animal Behaviour,* 58**,** 769-777.

TOMASELLO, M. & HERRMANN, E. 2010. Ape and Human Cognition: What's the Difference? *Current Directions in Psychological Science,* 19**,** 3-8.

TOMASELLO, M., MELIS, A. P., TENNIE, C., WYMAN, E. & HERRMANN, E. 2012. Two Key Steps in the Evolution of Human Cooperation. *Current Anthropology,* 53**,** 673-692.

TOMASELLO, M. & VAISH, A. 2013. Origins of human cooperation and morality. *Annu Rev Psychol,* 64**,** 231-55.

VAISH, A., CARPENTER, M. & TOMASELLO, M. 2010. Young children selectively avoid helping people with harmful intentions. *Child Dev,* 81**,** 1661-1669.

VERVAECKE, H., DE VRIES, H. & VAN ELSACKER, L. 2000. Function and distribution of coalitions in captive bonobos (Pan paniscus). *Primates,* 41**,** 249-265.

VONK, J. 2002. Can orangutans and gorillas acquire concepts for social relationships? *Int J Comp Psychol,* 15**,** 257-277.

WARNEKEN, F. 2013. Young children proactively remedy unnoticed accidents. *Cognition,* 126**,** 101-8.

WARNEKEN, F. 2015. Precocious Prosociality: Why Do Young Children Help? *Child Development Perspectives,* 9**,** 1-6.

WARNEKEN, F., CHEN, F. & TOMASELLO, M. 2006. Cooperative activities in young children and chimpanzees. *Child Development,* 77**,** 640-63.

WARNEKEN, F., GRÄFENHAIN, M. & TOMASELLO, M. 2012. Collaborative partner or social tool? New evidence for young children's understanding of joint intentions in collaborative activities. *Developmental Science,* 15**,** 54-61.

WARNEKEN, F., HARE, B., MELIS, A. P., HANUS, D. & TOMASELLO, M. 2007. Spontaneous Altruism by Chimpanzees and Young Children. *PLoS Biology,* 5**,** e184.

WARNEKEN, F. & TOMASELLO, M. 2006. Altruistic helping in human infants and young chimpanzees. *Science,* 311**,** 1301-1303.

WARNEKEN, F. & TOMASELLO, M. 2009. The roots of human altruism. *Br J Psychol,* 100**,** 455-71.

WATTS, D. P. 2002. Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour,* 139**,** 343-370.

WATTS, D. P. 2009. Dominance, power, and politics in nonhuman and human primates. *In:* KAPPELER, P. & SILK, J. (eds.) *Mind the Gap: Tracing the Origins of Human Universals.* Heidelberg: Springer Verlag.

WATTS, D. P. & MITANI, J. C. 2001. Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour,* 138**,** 299-327.

WEDEKIND, C. & MILINSKI, M. 2000. Cooperation through image scoring in humans. *Science,* 288**,** 850-852.

WELLMAN, H. M., CROSS, D. & WATSON, J. 2001. Meta-analysis of theory-of-mind development: The truth about false belief. *Child development***,** 655-684.

WELLMAN, H. M., LANE, J. D., LABOUNTY, J. & OLSON, S. L. 2011. Observant, nonaggressive temperament predicts theory of mind development. *Dev Sci,* 14**,** 319-26.

WHITE, D. J., GERSICK, A. S., FREED-BROWN, G. & SNYDER-MACKLER, N. 2010. The ontogeny of social skills: experimental increases in social complexity
enhance reproductive success in adult cowbirds. *Animal Behaviour,* 79**,** 385-390.

WHITEN, A. 2013. Humans are not alone in computing how others see the world. *Animal Behaviour,* 86**,** 213-221.

WILLIAMS, J. M., OEHLERT, G. W., CARLIS, J. V. & PUSEY, A. E. 2004. Why do male chimpanzees defend a group range? *Animal Behaviour,* 68**,** 523-532.

WILSON, M. L., BOESCH, C., FRUTH, B., FURUICHI, T., GILBY, I. C., HASHIMOTO, C., HOBAITER, C. L., HOHMANN, G., ITOH, N., KOOPS, K., LLOYD, J. N., MATSUZAWA, T., MITANI, J. C., MJUNGU, D. C., MORGAN, D., MULLER, M. N., MUNDRY, R., NAKAMURA, M., PRUETZ, J., PUSEY, A. E., RIEDEL, J., SANZ, C., SCHEL, A. M., SIMMONS, N., WALLER, M., WATTS, D. P., WHITE, F., WITTIG, R. M., ZUBERBUHLER, K. & WRANGHAM, R. W. 2014. Lethal aggression in Pan is better explained by adaptive strategies than human impacts. *Nature,* 513**,** 414-7.

WITTIG, R. M. & BOESCH, C. 2010. Receiving post-conflict affiliation from the enemy's friend reconciles former opponents. *PLoS One,* 5**,** e13995.

WITTIG, R. M., CROCKFORD, C., DESCHNER, T., LANGERGRABER, K. E., ZIEGLER, T. E. & ZUBERBUHLER, K. 2014a. Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. *Proc Biol Sci,* 281**,** 20133096.

WITTIG, R. M., CROCKFORD, C., LANGERGRABER, K. E. & ZUBERBUHLER, K. 2014b. Triadic social interactions operate across time: a field experiment with wild chimpanzees. *Proc Biol Sci,* 281**,** 20133155.

WITTIG, R. M., CROCKFORD, C., SEYFARTH, R. M. & CHENEY, D. L. 2007a. Vocal alliances in Chacma baboons (Papio hamadryas ursinus). *Behavioral Ecology and Sociobiology,* 61**,** 899-909.

WITTIG, R. M., CROCKFORD, C., WIKBERG, E., SEYFARTH, R. M. & CHENEY, D. L. 2007b. Kin-mediated reconciliation substitutes for direct reconciliation in female baboons. *Proc Biol Sci,* 274**,** 1109-15.

WOBBER, V., HARE, B., MABOTO, J., LIPSON, S., WRANGHAM, R. & ELLISON, P. T. 2010a. Differential changes in steroid hormones before competition in bonobos and chimpanzees. *Proceedings of the National Academy of Sciences,* 107**,** 12457–12462.

WOBBER, V., HARE, B., MABOTO, J., LIPSON, S., WRANGHAM, R. & ELLISON, P. T. 2010b. Differential changes in steroid hormones before competition in bonobos and chimpanzees. *Proc Natl Acad Sci U S A,* 107**,** 12457-12462.

WOBBER, V., HERRMANN, E., HARE, B., WRANGHAM, R. & TOMASELLO, M. 2014. Differences in the early cognitive development of children and great apes. *Dev Psychobiol,* 56**,** 547-73.

WOBBER, V., WRANGHAM, R. & HARE, B. 2010c. Bonobos exhibit delayed development of social behavior and cognition relative to chimpanzees. *Current Biology,* 20**,** 226-230.

WOBBER, V. T. & HARE, B. 2011. Psychological health of orphan bonobos and chimpanzees in African sanctuaries. *Plos One,* 6**,** e17147.

WRANGHAM, R. W. 1980. An ecological model of female-bonded primate groups. *Behaviour,* 75**,** 262-300.

WRANGHAM, R. W. 1993. The evolution of sexuality in chimpanzees and bonobos. *Human Nature,* 4**,** 47-49.

WRANGHAM, R. W. 1999. Evolution of Coalitionary Killing. *Yearbook of Physical Anthropology,* 42**,** 1-30.

WROBLEWSKI, E. E., MURRAY, C. M., KEELE, B. F., SCHUMACHER-STANKEY, J. C., HAHN, B. H. & PUSEY, A. E. 2009. Male dominance rank and reproductive success in chimpanzees, Pan troglodytes schweinfurthii. *Anim Behav,* 77**,** 873-885.

YAMAMOTO, S. 2015. Non-reciprocal but peaceful fruit sharing in wild bonobos in Wamba. *Behaviour,* 152**,** 335-357.

YAMAMOTO, S., HUMLE, T. & TANAKA, M. 2009. Chimpanzees help each other upon request. *Plos One,* 4**,** e7416.

YAMAMOTO, S., HUMLE, T. & TANAKA, M. 2012. Chimpanzees' flexible targeted helping based on an understanding of conspecifics' goals. *Proc Natl Acad Sci U S A,* 109**,** 3588-3592.

Biography

Christopher Krupenye was born on November 10, 1989 in New Rochelle, New York. He grew up in Patterson, New York with his parents, Sandy and Peter, and siblings, Ben, Ann, and Danny. Christopher is the oldest. He attended Connecticut College, receiving a Bachelor's degree in Biological Sciences with a minor in French in May of 2011. In the fall of the same year, he entered the Ph.D. program in Evolutionary Anthropology at Duke University.

Publications

Krupenye, C., Rosati, A. G., and Hare, B. (2016). What's in a frame? Response to Kanngiesser & Woike (2016). *Biology Letters*, 12(1): 20150959. doi: 10.1098/rsbl.2015.0959.

Foerster, S., McLellan, K., Schroepfer-Walker, K., Murray, C., **Krupenye, C.**, Gilby, I.C., and Pusey, A. (2015). Social bonds in the dispersing sex: partner preferences among adult female chimpanzees. *Animal Behaviour*, 105: 139-152. doi: 10.1016/j.anbehav.2015.04.012.

Krupenye, C., Rosati, A.G., and Hare, B. (2015). Bonobos and chimpanzees exhibit human-like Framing effects. *Biology Letters*, 11(2). doi: 10.1098/rsbl.2014.0527.

MacLean, E., **Krupenye, C.**, and Hare, B. (2014). Dogs account for body orientation but not visual barriers when responding to pointing gestures. *Journal of Comparative Psychology*, 128(3): 285-297. doi: 10.1037/a0035742.

Bray, J., **Krupenye, C.**, and Hare, B. (2014). Ring-tailed lemurs (Lemur catta) exploit information about what others can see but not what they can hear. *Animal Cognition*, 17(3): 735-744. doi: 10.1007/s10071-013-0705-0.

Rosati, A.G., Herrmann, E., Kaminski, J., **Krupenye, C.**, Melis, A.P., Schroepfer, K., Tan, J., Warneken, F., Wobber, V. & Hare, B. (2012). Assessing the psychological health of captive and wild apes: A response to Ferdowsian et al. (2011). *Journal of Comparative Psychology*, 127(3): 329-336. doi: 10.1037/a0029144.

Gruber, T., Potts, K.B., **Krupenye, C**., Byrne, M., Mackworth-Young, C., McGrew, W.C., Reynolds, V., & Zuberbuhler, K. (2012). The influence of ecology on chimpanzee cultural behavior: A case study of five Ugandan chimpanzee communities. *Journal of Comparative Psychology*, 126(4): 446-57. doi: 10.1037/a0028702

Awards, Fellowships, and Grants

2011-2016 National Science Foundation Graduate Research Fellowship, $135,000

2011-2016 Duke University Institutional Fellowship

2015-2016 Undergraduate Mentorship Award, Duke University, $1,000

2015 International Dissertation Research Travel Award, Duke University, $1,500

2014-2015 USAID & National Academy of Sciences Research and Innovation Fellowship, $8,968

2014-2015 Undergraduate Mentorship Award, Duke University, $1,000

2014 Psychology & Neuroscience Vertical Integration Program, Duke University, $1,800

2014 Summer Undergraduate Mentorship Award, Duke University, $1,000

2014 Evolutionary Anthropology Graduate Research Fund, Duke University, $700

2013-2014 Undergraduate Mentorship Award, Duke University, $900

2013 Evolutionary Anthropology Graduate Research Fund, Duke University, $700

2012-2013 Undergraduate Mentorship Award, Duke University, $1,000

2012 Visiting Graduate Student Fund, CICASP, Primate Research Institute, Kyoto University

2011-2012 Undergraduate Mentorship Award, Duke University, $1,000