GAZE-FOLLOWING, SOCIAL MONITORING, AND JOINT ATTENTION IN THE GREAT APES: A COMPARATIVE ANALYSIS OF VISUAL COMMUNICATION AND POTENTIAL IMPLICATIONS FOR COGNITION

by

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ABSTRACT

DANAY CYNTHIA DOWNING. Gaze-following, social monitoring, and joint attention in the great apes: A comparative analysis of visual communication and potential implications for cognition. (Under the direction of DR. DIANE K. BROCKMAN)

Previous experimental studies indicate that gaze-following is a reliable indicator of advanced cognitive capacity in social primates. Group-living primates, in particular, must navigate complex social relationships among group members and other conspecifics, and individuals thus require higher-level social-cognitive skills. The purpose of this research was to evaluate species-specific variation in the cognitive abilities of a unique population of semi-free-ranging apes composed of 15 orangutans and 30 chimpanzees housed at the Center for Great Apes in Wauchula, Florida, assess the degree to which individuals in these populations visually communicate with conspecifics via gaze-following, as well as investigate their capacity for joint visual attention. This research involved three separate observational studies, the goals of which were: to determine the capacity of subjects to follow the gaze of a human social partner; to assess individual frequencies of social monitoring as a function of age, sex, and species; and to investigate the ability of subjects to engage in joint attention with a human social partner toward functional objects (i.e. manipulative toys/possible tools) versus non-functional objects. Results of ANOVA and *t*-tests provided strong evidence for all three abilities and demonstrated that variation in frequencies of these behaviors between and within species was a consequence of the effects of sex and age. The significance of this research resides in the new insights that may be gained into the phylogenetic cognitive substrates underpinning the evolution of cognition and visual communication in the human lineage via our closest relatives, the great apes.

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My sweet Mama, I share my heart with you. You have made me who I am, and I could never tell you how much I love you for the support you have continuously given me to accomplish my academic goals. You give me strength, you bring me up when I am down, you have been with me through all of my adventures, you light up my life, and you love my furry friends. You are an equal partner in my success. Thank you so much for sharing my passion with others. Granny Darling and Mandy ~ you spread so much love for the remarkable animals of the world; you feel the emotion I do for them; you understand the concern and duty of conservation, and especially the plight of great apes and the many other hallmark species that are valuable to our earth. From the bottom of my heart, thank you!!! Daddy, it has been eight years since you passed. Thank you from your Top Gun Girl ~ you wouldn’t believe some of things I have been able to do, but I know you’d be proud. Lexi Sophia, my constant companion, always by my side, and forever my biggest fan, what I would do without you?

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LIST OF ABBREVIATIONS

≤18	18 years of age or younger
19+	19 years of age or older
Funct.	functional (object)
Non-Funct.	non-functional (object)
NP	non-pointing (condition)
Obj.	object
pg.	page
Pt.	pointing (condition)
SD	standard deviation
Sp.	species
vs.	versus

INTRODUCTION

The goal of this research was to gain a better understanding of the cognitive capacities of a population of captive orangutans (*Pongo* spp.) and chimpanzees (*Pan troglodytes*) housed at the Center for Great Apes in Wauchula, Florida. Previous experimental studies indicate that gaze-following is a reliable indicator of advanced cognitive capacity in social primates, to include monkeys and apes (reviewed in Rosati and Hare, 2009). However, no study to date has examined gaze-following, social monitoring, and joint attention in a large population of socially-housed apes nor the potential effects of age and sex on social monitoring and gaze-following behavior. The uniqueness of this research resides in its observational rather than experimental context, the responses of subjects having been elicited when socially-housed with conspecifics (i.e. other members of the individual's social group). The purpose of this research was to evaluate species-, sex-, and age-specific variation in the cognitive abilities of a unique population of semi-free-ranging apes, assess the degree to which individuals in these populations visually communicate with conspecifics via gaze-following, as well as investigate their capacity for joint visual attention. The importance of this research consequently resides in the new insights that may be gained into the phylogenetic cognitive substrates underpinning the evolution of cognition in the human lineage via our closest relatives, the great apes (Downing, 2009; Lyons, Santos, and Keil, 2006).

The theoretical foundations underpinning studies of cognition in primates have focused on hypotheses concerning the role of ecology and social living in the evolution of large neocortices (Isler and van Schaik, 2009). Special emphasis has been centered on the idea that the particular socio-ecological challenges faced by primates are mediated through individual action or individuals acting collectively in complex ways to meet these challenges, thus requiring higher-level social-cognitive skills (Page, 1999; Rogers and Kaplan, 2004). The social brain hypothesis, or social intelligence hypothesis, posits that the cognitive demands (i.e. challenges associated with social complexity) of living in large, stable social groups of familiar conspecifics selected for increases in executive brain function (i.e. neocortex) (Dunbar, 2003; Holekamp, 2006). Executive function, or the conscious control of behavior, is dependent upon the prefrontal cortex which processes both recent sensory information and information from long-term memory, thereby facilitating the actor's ability to assess the effects of decision-making processes on behavior (Acuña, Pardo-Vásquez, and Leborán, 2010; Smaers, Steele, Case, Cowper, Amunts, and Zilles, 2011). Enhanced executive brain function is thought to be crucially important for the role it plays in learning (i.e. relatively permanent changes in one's behavioral repertoire that occur as a result of experience), providing important cognitive-behavioral feedback mechanisms that allow individuals to adjust their behavior to new situations, thereby fostering the development of novel adaptive responses to ever-changing socio-ecological environments, the latter being essential to survival (Acuña *et al*., 2010; Terry, 2006).

The vast majority of primates live in social groups, which require them to navigate complex social relationships among kin and non-kin, as well as with conspecifics in neighboring groups (Strier, 2011). Within-group relationships depend upon gathering and exploiting information concerning food resources, mating opportunities, predators, and the social imperatives of conspecifics that others have acquired to which the individual might not otherwise have access. The challenges of surviving in such complex social environments may have, in fact, driven the evolution of primate cognitive abilities, with the evolution of group living being at the root of a progressive increase in visually-based communication (Anderson and Vick, 2008).

This research involved three separate studies of unconditioned (i.e. experimentally naïve) orangutans and chimpanzees, the goals of which were: to determine the capacity of subjects to follow the gaze of a human social partner (Study 1); to assess frequencies of gaze direction and duration (i.e. social monitoring) as a function of species, sex, and age (Study 2); and to investigate the ability of subjects to engage in joint attention (i.e. coordinated attention with a human around an object) (Study 3).

❖ Gaze-Following

Gaze perception is one of the most critical social/cognitive abilities that a primate can possess (Itakura, 1996; Tomonaga and Imura, 2010). For instance, joint visual attention is an important part of social interaction and referential communication in humans, and reviews of recent literature show a similar capacity in non-human primates (Tomonaga and Imura, 2010). Eye contact and mutual gaze play an important role in regulating social interactions by providing information about intentions and current states of being (Argyle and Cook, 1976). Gaze-following — or looking in the direction that others are looking — provides important proximate clues regarding what conspecifics observe and thus consider salient in their social/ecological environment. Using information about social attention has been argued to be crucially important for primates to be competent members of their society, even though the cognitive basis of the behavior among primates is known to vary widely across species (Rosati and Hare, 2009). A growing body of literature suggests that numerous primate species appear to be behaviorally responsive to the direction of a conspecific's gaze as shown by the orientation of the eyes, head and/or body and to spontaneously follow the gaze of human experimenters or conspecifics. Gaze-following behavior is fairly widespread among primates, having been observed in lemurs (*Eulemur, Lemur*), common marmosets (*Callithrix jacchus*), capuchins (*Cebus*), sooty mangabeys (*Cercocebus atys torquatus*), cotton-top tamarins (*Saguinus oedipus*), gibbons (*Hylobates agilis*), several macaque species (*M. mulatta, M. arctoides, M. nemestrina*), and the great apes (*Pan, Pongo, Gorilla*), suggesting that the ability to gain information about one's environment from the gaze direction of conspecifics is common in the Order Primates (reviewed in Rosati and Hare, 2009; Bräuer, Call, and Tomasello, 2005; Shepherd, 2010; Tomonaga and Imura, 2010). Investigators have defined multiple functions of gaze, and examples are given accordingly:

- Direct stare – as a mild threat (e.g. lemurs, macaques, baboons, chimpanzees, gorillas); in appeasement or in soliciting sexual favors; during non-aggressive social interactions; in postconflict approaches (e.g. wild gorillas) (Goodenough, McGuire, and Wallace, 1993; Yamagiwa, 1992)
- Prolonged gazing – as a sexual overture inviting homosexual interactions (e.g. subadults gazing at dominant male gorillas) (Goodenough *et al*., 1993; Yamagiwa, 1992)
- Eye contact – as a prerequisite for reconciliation (e.g. chimpanzees) (de Waal, 1983)

Members of many primate species have been found to follow the gaze direction of other individuals (i.e. conspecifics and human experimenters), but few empirical studies of gaze perception and gaze-following in non-human primates have been conducted in the laboratory (Okamoto-Barth, Call, and Tomasello, 2007; Tomonaga and Imura, 2010). As a consequence, our understanding of interspecific variation in this ability and its relationship to phylogenetic distance from humans remains elusive. Even though researchers have long recognized the importance of gaze in studies of social cognition and theory of mind, it has nevertheless been difficult for observers to precisely identify the target of an animal's gaze in the context of natural or semi-natural habitats (Tomonaga and Imura, 2010). Although the results of experimental research show that non-human primates can, and do, discriminate gaze direction, the visual sensitivity of monkeys, apes, and lemurs is quite variable, and the cues used by each species for making judgments about being watched by others is ambiguous (Tomonaga and Imura, 2010). For example, great apes have been found to frequently exhibit social staring behavior; Tomonaga and Imura (2010) define this behavior as prolonged gazing by one individual at another when both are in close proximity to each other. However, in many simian species, mutual gaze and eye contact can often trigger aggressive interactions between individuals, and as a consequence, these species exhibit 'gaze aversion' to mitigate potential agonism (Tomonaga and Imura, 2010).

Gaze-following research with humans, for example, has been part of a general investigative effort into the developmental origin of theory of mind, aiming to increase understanding of how these abilities develop in the course of evolution. Theory of mind is an ability "…that exists in part because exercising it brings benefits obtaining which depends on exploiting or influencing facts about others' mental states" (Butterfill and Apperly, 2013, pg. 607). Comparative studies of the early precursors of theory of mind have focused largely on the understanding of other individuals' visual behavior, and so primatologists have begun to test non-human primates' knowledge of the mental significance of attention (Emery, Lorincz, Perrett, Oram, and Baker, 1997). From a comparative perspective, primatologists were among the first to address the issue as an offshoot of a broader evolutionary interest in whether mental-state attribution is unique to humans (Povinelli, 1993). Yet, it may be more productive for researchers to abandon the simple dichotomy between either having *or* not having a theory of mind (i.e. moving toward the *degree* to which versus either an absence or presence) (Hare, Call, Agnetta, and Tomasello, 2000; Hare, Call, and Tomasello, 2001; Suddendorf and Whiten, 2001; Suddendorf and Whiten, 2003). Among non-human primates, gaze-following ability permits individuals to get salient information about the location of objects and engage in complex forms of social cognition, such as visual perspective-taking, deception, empathy, and theory of mind (Baron-Cohen, 1994; de Waal, 2011; Emery, 2000; Tomasello, 1995). While Emery (2000) proposed that social gaze leads to a theory of mind, Povinelli and Eddy (1996), on the other hand, have suggested that the ability to understand the mental significance of another's gaze is a dissociable ability from simple gaze-following, although one may be a precursor to the other (Emery *et al*., 1997; Povinelli, 1993). Whiten (1996) speculated that behavior reading, or inferring goal-directed behavior, emotion, and intention from external perceptual signals and a representation of an individual's behavioral patterns, may have developed through evolution into a mind-reading ability or a theory-of-mind mechanism (Butterworth, 1991; Emery *et al*., 1997; Whiten, 1996).

Okamoto-Barth *et al*. (2007) caution, however, that interpreting gaze-following behavior is not always straightforward. It is possible that gaze-following denotes a cognitively complex process of knowing that an individual is 'seeing,' or fixating on something, and thus indicative of perspective-taking skills, though this idea is difficult to test empirically. On the other hand, gaze-following might be a co-orientation mechanism or represent a simple, reflexive tendency (Okamoto-Barth *et al*., 2007). Bräuer *et al*. (2005) argue that great apes do not simply orient to another individual's target, but that they actually attempt to take the visual perspective of the other individual (i.e. individuals are able to understand how they look from another's perspective). Results of laboratory tests of great ape subjects (i.e. bonobos, chimpanzees, gorillas, and an orangutan) using humans as visual targets support the perspective-taking model over the orienting-response model because 1) individuals from all four species were able to adjust their position in order to visually locate the place where the human was looking, and did not merely stare at the object that the human was fixated upon and 2) the apes produced 'double looks' (Call, Hare, and Tomasello, 1998 in Bräuer *et al*., 2005), wherein a chimpanzees would trace the gaze of a human to a specific location and when he or she found nothing of interest, they very often looked back to the human's face and re-tracked their gaze direction a second time, presumably because they expected to see what the human experimenter was looking at (Bräuer *et al*., 2005). Therefore, Bräuer *et al.* (2005) argue that this perspective-taking and gaze-following behavior are clear indicators of a developmental cognitive trajectory, because the double look behavior was absent in the infants, appeared occasionally in the juveniles, and was most frequently observed in adults.

Tomasello, Call, and Hare (1998) report that in the few primate studies to date, gaze-following experiments have used human experimenters as the visual target whose gaze was being followed. Tomonaga and Imura (2010) further caution that most of these studies have used human or schematic faces with high-contrast eyes and that this must be taken into consideration when designing these kinds of studies. Yet, great apes follow human gaze quite reliably in a wide variety of paradigms, and in some studies, the overall level of gaze-following of apes was actually higher than that of human infants (Emery *et al*., 1997; Tomasello, Hare, and Agnetta, 1999). Tomasello *et al.* (1998) tested the ability of individuals from five primate species to follow the visual gaze of ‘conspecifics’ by inducing individual ‘A’ in each species to look at a food item being displayed and then recording the reaction of individual ‘B’ who was observing conspecific individual ‘A’ (Tomasello *et al*., 1998). They found that in general, these particular primates were much more interested in where conspecifics were looking than where human experimenters were looking. Accordingly, they assert that the ability to follow the direction of a conspecific’s gaze is an important social skill, allowing individuals to acquire information about the environment, both ecological and social, that does not have to be gained individually, but draws upon the cumulative knowledge of conspecifics that can be communicated via gaze (Tomasello *et al*., 1998). Kaplan and Rogers (2002) expand upon this idea and focus on the value of eyes and facial expressions in communication and stress the importance of gaze as a ‘social signal’, that may reveal information about social milieu, the emotional states/intentions of others, and perhaps an awareness of self and others (Kaplan and Rogers, 2002; Meltzoff and Brooks, 2007).

From an evolutionary perspective, it is incredibly important for individuals to show some kind of sensitivity to social context and to be able to adjust gestural and/or visual signals to the attentional state of the recipient (Pika, Liebal, and Tomasello, 2003). Visual communication is inherently important for great apes, and for social animals in general; however, one could argue that visual communication is equally important in less gregarious primate species as well. Visual communication has been shown to be fundamental in the development of social relationships, the acquisition of observational learning, and the comprehension of multi-faceted responses involved in social interaction; mastering these skills can aid in the development and maintenance of social connections, ultimately impacting the survival and successful reproduction of generations to come. Gaze-following, for instance, attains signal function only if the message delivered by gazing alone can be seen and interpreted by the receiver (Kaplan and Rogers, 2002). Kobayashi and Koshima (2001) report that humans have the largest scleral exposure among primates (see Figure 1) and argue that the sclera (i.e. the white of the eye) is a special feature of humans, because it communicates direction of gaze (reviewed in Kaplan and Rogers, 2002). Kobayashi and Koshima (2001) further link this trait to higher consciousness, or an awareness of the mental states of others, asserting that the large scleral area is a uniquely human adaptation used to extend the visual field thus enhancing detection of the direction of gaze by others (Kaplan and Rogers, 2002), though consensus is lacking in this regard.

Enhanced visual acuity is one of the distinguishing characteristics of primates compared to many other mammals, associated in part with the forward-facing eyes that create overlapping fields of vision for depth perception, as well as the differentiation of rods and cones with variable abilities to perceive colors (Strier, 2007). The eye region is particularly salient in primate species, yet it is well-known that the morphology of the eyes of chimpanzees and other non-human primates is quite different from that of humans, greatly varies by species, and even changes with age (Emery, 2000; Emery *et al*., 1997; Kaplan and Rogers, 2002; Kobayashi and Hashiya, 2011; Kobayashi and Kohshima, 2001). For example, the color of the exposed area of sclera in a human is much lighter than that of a chimpanzee, as chimpanzees typically have scleras that are darker than the iris, which contrasts with the former in being a lighter color (Figure 1; Tomonaga and Imura, 2010). With such lower-contrast eyes, the form of visual communication frequently observed in humans, may not be analogous to the visual communicative cues in apes. The eyes of orangutans, for example, possess several unique features that change with age: infants have pink to white eyelids and light-colored circumocular skin that later darkens; adult Sumatran orangutans also have light pink eyelids, which are quite conspicuous when the eyes are closed (Figure 2). Moreover, their eyelashes are a different color from that of the eyelids and surrounding area (Figure 3). They also have silver-colored eyelashes in the center of the top eyelid; so that when the individual looks down, exposing the silver eyelashes, this may give the impression that the individual is alert and watching when, in fact, he or she could be focusing on an object in the lower field of vision (Figure 4; Kaplan and Rogers, 2002). Bornean orangutans, in particular, commonly use a sideways gazing technique that exposes a larger area of sclera – sideways looking and avoidance of direct gazing for prolonged periods being characteristic of social communication in Bornean orangutans (Kaplan and Rogers, 2002). This raises questions about what cues primates are actually using during gaze discrimination (Tomonaga and Imura, 2010). However, whether these features are actively used to communicate remains unknown.

In Study 1, I determined the occurrence of gaze-following in unconditioned orangutans and chimpanzees and investigated the ability of great apes to engage in gaze-following of a human social partner. I sought to elucidate species, sex, age, and individual differences in this ability, by testing the capability of captive apes to follow the gaze of a human social partner (by either head/eye direction alone or via pointing gestures). I predicted that both species of great apes would engage in gaze-following behavior and that higher occurrences of gaze-following would be observed when the human social partner included a pointing/hand gesture with her gaze/looking direction. I also predicted there would be species, age, and sex differences in this ability.

❖ Social Monitoring

Social monitoring — within-group visual scanning of conspecifics — is thought to be widespread among social primates. Putative adaptive benefits of visual scanning/monitoring of conspecifics include a more efficient means of locating food or predators, rather than having to directly scan the entire environment by oneself (McNelis and Boatwright-Horowitz, 1998). Although the distinct cues that elicit social monitoring have yet to be determined, it is suspected that an animal's attention is systematically related to other types of interactions with group members, including those involving hierarchical relationships within groups (McNelis and Boatwright-Horowitz, 1998).

Generally speaking, however, it seems that using head and/or face direction as a major visual cue could be advantageous for all animals, as head direction can readily be seen from a much larger distance than can eye direction alone. For example, if eye direction is difficult to determine because of low eye visibility, individuals could benefit from head direction, because it offers a far more accessible indicator of another individual's attention (Kaminski, Call, and Tomasello, 2004 reviewed in Tomasello, Hare, Lehmann, and Call, 2007b). This can be exceptionally important in competitive situations in which misjudging where a dominant animal is looking may have dire consequences for a subordinate animal. As Tomasello *et al*. (2007b) point out:

> "From the point of view of the looker, the fact that another individual exploits the information provided by its gaze direction may, in some cases, be detrimental (e.g., the other sees and gets the food first), and so, encouraging this behavior in others would seem to be risky. At the very least, individuals in constant competition with onlookers should not evolve morphological characteristics to help these others follow their gaze direction" (Tomasello *et al*., 2007b, pg. 318).

Tomasello *et al*. (2007b) further postulate that the evolution of highly visible, human-like eyes would thus seem to imply that cooperative group-mates would not exploit the gaze direction of a conspecific, especially if it would disadvantage that particular individual. They then go on to apply this logic across species, by reiterating the context-dependence of these varied behaviors, and by suggesting that the great apes may even pay more attention to eyes and be less concerned about others following their eyes in highly cooperative and/or mutualistic situations, such as grooming (Tomasello *et al*., 2007b).

Gazing and social monitoring can certainly reinforce group structure, dominance hierarchies, and the quality of group relationships, though the degree to which individuals conform their visual attention based on previous encounters and experience is currently unknown (Kaplan and Rogers, 2002). The underlying cognitive processes of social monitoring are also unclear, but previous research suggests that inferences concerning relationships among members of the social group can be made through displacements of subordinates by dominants and by using visual scanning as a direct measure of social interest (McNelis and Boatwright-Horowitz, 1998). Chance (1967) hypothesized that the most dominant individual in a primate group should receive the most visual attention from group members compared to that directed towards other conspecifics (reviewed in McNelis and Boatwright-Horowitz, 1998). Empirical support for this idea is weak, in large measure due to the paucity of studies testing the effect of rank on social monitoring in primates. If a chain of attention exists, in which each animal is linked to the conspecific higher in status, as proposed by Chance (1967), the highest-ranking animal would be the final focus of attention (McNelis and Boatwright-Horowitz, 1998).

Although numerous social species (corvids, cetaceans, and elephants) have been found capable of using cues analogous to ‘attentional structure’ of conspecifics to gather information about external events, Caine and Marra (1988) caution that this capability could be detrimental to the individual (Emery and Clayton, 2004; Greco, Brown, Andrews, Swaisgood, and Caine, 2013; Marino, 2007; Plotnik, Lair, Suphachoksahakun, and de Waal, 2011; Tomasello *et al*., 1998). They suggest that individual rates of detection of predators may be reduced in those social systems in which individuals must pay more social attention in order to avoid aggression, monitor threats, or maintain a certain distance from the dominant individual, because vigilance for predators is likely to diminish the more an individual directs its attention toward conspecifics, rather than the environment (Caine and Marra, 1988; McNelis and Boatwright-Horowitz, 1998).

While a number of factors (e.g. habitat quality, dominance/rank, group spatial relationships) have been found to affect the relationship between group living and individual rates of social monitoring, sociality and vigilance have not been studied specifically in terms of the demands they impose upon an individual's visual time (Caine and Marra, 1988). In addition, little is known about how relative rank, age, and kinship affect social monitoring in group-living populations. Thus, detailed studies are imperative to assess the prevalence of vigilance and the costs and benefits of engaging in social monitoring (Gaynor and Cords, 2012; Hirsch, 2002; McNelis and Boatwright-Horowitz, 1998).

However, the assessment of gaze direction/glancing in free-ranging primates can be difficult because of the necessity of determining the direction the individual is looking and thus precisely identifying the target of gaze. Nevertheless, McNelis and Boatright-Horowitz (1998) have successfully utilized a combination of focal animal and on-the-dot sampling (Altmann, 1974) techniques to quantify visual scanning among captive adult female, socially-housed patas monkeys (*Erythrocebus patas*). Results showed that the highest ranking individual received significantly higher gaze frequency than did the subordinates. The authors argue that visual scanning behavior, or social monitoring, may allow an animal to observe the focus of another animal's attention, monitor the movement and behaviors of other members in its social group, and quite possibly modify its own behavior according to changing contextual cues (McNelis and Boatwright-Horowitz, 1998). It can also allow individuals to regulate spacing within groups, possibly reducing the likelihood of aggressive encounters (McNelis and Boatwright-Horowitz, 1998). Social monitoring, therefore, likely plays an important role in primate group dynamics, and as such, it has been hypothesized to be a vital component of primate social behavior.

In Study 2, I assessed ape-to-ape social monitoring in various groups of socially-housed orangutans and chimpanzees by quantifying the frequency of looking behavior, including gazing, glancing, and staring (Table 1). I predicted that differences in looking behavior would be observed, and that species, sex, and age may influence the frequency and direction of the various modes of looking.

❖ Joint Visual Attention

As noted previously, it has been argued that the evolution of primate cognitive abilities has been driven principally by the challenges of surviving in large, complex social environments (Anderson and Vick, 2008). The evolution of group living in primates has been accompanied by a progressive increase in visually-based communication, likely because valuable information about the social and ecological environments can be obtained by visually monitoring group-mates (Anderson and Vick, 2008; Emery, 2000). Therefore, gaze-following and joint attention are extremely important for social animals, because they reveal an adaptive social-cognitive skill for developing social interactions among group-mates and for vicariously detecting food, predators, and mating opportunities (Itakura, 2004). Furthermore, it has been argued that determining the precise direction of another’s attention is vital to social group living:

> “…attending to faces is central to social information gathering [and] for extracting categorical information such as identity or sex, more transient information such as hormonal status, and dynamic information in communicative facial displays. The eyes are of particular interest as gaze is uniquely both a signal and channel; while an individual is gathering visual information about the environment, it is also signaling this attention to others by virtue of its visual orientation” (Argyle, 1988 reviewed in Anderson and Vick, 2008, p. 39).

How primates might interpret this language of the eyes, as well as which specific properties are determined and used, is currently unknown, since few studies have examined the ability of non-human primates to employ joint visual attention nor considered the sophistication of such gaze-reading abilities in animals (Anderson and Vick, 2008). Although an extensive body of literature exists on the cognitive underpinnings of gaze movements in humans, few studies have investigated this topic from a broader evolutionary perspective (Kano, Hirata, Call, and Tomonaga, 2011).

Joint attention typically refers to a set of socio-cognitive skills that involve sharing attention with others and having the ability to intentionally co-orient towards a common focus (Leavens and Racine, 2009; Pitman and Shumaker, 2009). Appreciation of the seeing-knowing relationship is one of the most central propositions in theory of mind (Itakura, 2004). In fact, the ability to share attention with another is thought to be the foundation upon which other theory of mind skills are formed (Pitman and Shumaker, 2009; Shepherd, 2010; Wellman and Brandone, 2009). Being able to assess another’s attentional state during social maneuverings is fundamental to successful social living, particularly in communicative interactions involving visual signals, because only if the other individual is attending, will the visual signal be successful

(Perrett and Emery, 1994; Tempelmann, Kaminski, and Liebal, 2011). In a review of recent evidence, Leavens and Racine (2009) determined that great apes do display every phenomenon described as joint attention in humans, although there is considerable variation among apes of different rearing histories.

In Study 3, I assessed joint attention between apes and humans. Pitman and Shumaker (2009) indicate that joint attention is unambiguously present in great apes, although this conclusion derives from studies of 24 great apes (i.e. seven orangutans, chimpanzees, and gorillas and three bonobos). Additional studies such as those conducted here, using a larger sample size of orangutan and chimpanzee subjects, are crucial for validating these results. Therefore, I expanded this research to include joint visual attention tasks with 15 orangutan and 21 chimpanzee subjects, as a means of exploring possible interspecific variation in joint attention capacity. I elucidated species, sex, and individual differences in the ability of apes to engage in joint attention with humans, by testing the capability of captive apes to share attention and focus on a common object with a human social partner. I predicted that individuals in both species would show varying degrees of joint visual attention, and given this capacity, I predicted there would be species and sex differences in this ability. Previous investigators have asserted that the capacity for joint visual attention in apes is a result of enculturation, or having had extensive interactions with humans since a very young age (Inoue, Inoue, and Itakura, 2004; Itakura and Tanaka, 1998; Carpenter, Tomasello, and Savage-Rumbaugh, 1995). As a consequence, I also considered the effects of rearing history and social group size on the degree of joint attention capacity.

The novelty of Study 3, however, is the assessment of object functionality within the joint attention task. While it is understood that most objects can be utilized as tools or formed into an item that can serve a purpose, the stimulus-objects used in the joint attention task of Study 3 were specifically discriminated as being either functional/manipulative toys/possible tools – or – non-functional objects. Discrimination between surrounding objects is an essential ability in life (Hanazuka, Kurotori, Shimizu, and Midorikawa, 2012), and great apes have likely evolved extraordinary capacities to live within dynamic challenging communities that require recognizing individual members, remembering those that may have left the group for a considerable period of time, understanding the complexities of the social hierarchy and rule structure of the community, and having the necessary attentional and observational skills to learn the many types of tool use that have now been documented for wild ape populations (Boysen, 2009). The idea, however, of joint attention performance being influenced by object functionality or a shared attentional preference being exhibited for functional objects, remains a considerable challenge. Nevertheless, the observationally-driven experiment of Study 3, in particular, is unprecedented and has the potential to make important contributions to the primate cognition literature.

BACKGROUND: TERMS AND TAXA

❖ Cognition

Cognition is defined as "…the mechanisms by which animals acquire, process, store, and act on information from the environment" (Shettleworth, 1998, p. 5). Specifically, "…[a]nimal cognition is concerned with explaining animal behavior on the basis of cognitive states and processes, as well as on the basis of observable variables such as stimuli and responses" (Griffin, 1992, p. 21). These mechanisms include learning, memory, perception, problem solving, planning, rule and concept formation, communication, decision making, cultural transmission, recognition, and even imitative actions within the correct functional contexts (Boysen, 2009; Rogers and Kaplan, 2004; Shettleworth, 1998).

The history of the development of cognitive studies in primates shows that most of what is known about the mental abilities of primates has been discovered in the last half of the twentieth century, the vast majority of primate cognitive research being focused on chimpanzees and bonobos due to their close kinship with humans (Marks, 2003; Shumaker and Beck, 2003). Controlled observations and laboratory studies on the cognitive capacities of gorillas and orangutans are few, but research is expanding and progressing to other species with great vigor (Downing, 2009).

❖ *Hominoidea*

The great apes are large-bodied, sexually dimorphic primates that comprise the families *Pongidae* (great apes) and *Hominidae* (humans) (Rowe, 1996). They are morphologically characterized by having relatively large brains, a semi-upright stance which enables facultative bipedalism, the absence of foreheads, chins, and tails, and the

Pongidae are the primates most closely related to humans (Marks, 2003; Rowe, 1996). The great apes are also very long-lived, have high behavioral plasticity, and have extensive life histories, with average life spans ranging from 35 to 60 years (Spelman, 2012). Infants have very slow rates of development, and maternal investment is high, lasting several years. In fact, orangutans have the longest period of infant development of all the non-human great apes, being mother-dependent for 9 to 10 years and having the longest interbirth interval of all primates, including humans (Shumaker, 2007; Spelman, 2012).

Sharing more than 98 percent of their DNA with humans, the great apes are thought to be most similar in size, biology, life history, and behavior to ancestral hominids and provide an evolutionary context for better understanding our own morphological/behavioral evolution (Spelman, 2012; Strier, 2007). Additionally, the brains of great apes differ from those of other mammals, specifically with respect to how information is processed (Rilling, 2006; Sherwood, Subiaul, and Zawidzki, 2008). “More nerve cells, for example, are devoted to processing sight compared to smell” (Spelman, 2012, p. 92). Additionally, the cerebral cortex, or the frontal region of the brain, is considerably larger in highly social primate species, the cerebrum having functional significance for intelligence, thinking, communicating, and planning (Spelman, 2012). The primate brain may have even evolved biological specializations for implementing social functions, deciphering immediate social contexts, and translating social and nonsocial perceptual signals into motivational signals which command behavior (Chang, Brent, Adams, Klein, Pearson, Watson, and Platt, 2013).

However, the social structure and behavioral ecology of each genus is very different (Rowe, 1996).

❖ The Orangutan

Orangutans are composed of two species — *Pongo abelii* and *Pongo pygmaeus* — and are indigenous to the Indonesian islands of Sumatra and Borneo, respectively. They are the most arboreal and the least gregarious of the great apes, though males do tend to travel on the ground more so than females. Among orangutans, fully-adult flanged males have priority of access to ovulatory females and defend their territories against intruders, particularly during the mast fruiting season of food abundance (Redmond, 2011; Rowe, 1996). Orangutans are an individual-based fission-fusion species, deriving social benefits from inter-individual encounters, such as mating (van Schaik, 1999). Social organization is characterized by nayau – permanent groupings composed of females and their dependent offspring who normally stay with their mothers until they are 9 or 10 ten years old (Spelman, 2012). Females typically have their first infant between the ages of 15 and 16 and give birth only every 6 to 9 years after that (Rowe, 1996). Subadult male orangutans, though sexually mature, often do not develop the facial flanges that characterize a fully adult male (i.e. fatty cheek pads) until they are between 15 and 19 years old (Rowe, 1996). Lifespan of the orangutan is up to 60 years, with sexual maturity being reached at ~10-11 years for females and ~9.5 years for males (Redmond, 2011; Shumaker, Wich, and Perkins, 2008).

An orangutan's average home-range size, day-range length, and population density are all dependent upon the abundance and distribution of fruit availability and vary between locations, seasons, and ecosystems, although males do tend to have larger home ranges (Caldecott and Kapos, 2005). Rapidly expanding palm oil plantations, habitat fragmentation, poaching, and the illegal pet trade continue to threaten orangutan populations and their rainforest habitats, and as a consequence, they are considered highly endangered (Boysen, 2009). Life history attributes, including low reproductive rates, make it very difficult for orangutan populations to recover from rapid habitat destruction and other forms of exploitation, and as a result, wild populations of Sumatran orangutans have steeply declined to ~6,600 individuals and are listed among the top 25 most endangered primates (Mittermeier, Wallis, Rylands, Ganzhorn, Oates, Williamson, Palacios, Heymann, Kierulff, Yongcheng, Supriatna, Roos, Walker, Cortés-Ortiz, and Schwitzer, 2009).

- The Chimpanzee

The chimpanzee (*Pan troglodytes* with four subspecies) has by far the most widespread distribution and broad-based ecology of any great ape; they show high levels of diversity, adaptability, and opportunism (Caldecott and Miles, 2005; Downing, 2009). Chimpanzees, found across 21 countries in west, central, and east Africa, live in a wide variety of ecosystems from dry savanna habitats and mosaic woodlands, through tropical moist and rain forests, to deciduous and humid evergreen forests (Caldecott and Kapos, 2005; Downing, 2011; Report of the World Summit on Sustainable Development, 2002). Chimpanzees are opportunistic omnivores, and Caldecott and Miles (2005) note that dietary flexibility, coupled with ecological variation over a huge geographical range, within which seasonality is important, can only result in highly variable foraging and ranging behavior. Therefore, community size for a population of chimpanzees varies greatly. Social organization is fission-fusion wherein the community splits into smaller foraging groups during the day, feed in shifting parties, and then reconvene at the end of the day (Redmond, 2011; Strier, 2007). Large territorial communities, dominated by males in chimpanzees and females in bonobos, live in a variety of habitats to include primary and secondary forest, dry woodland, and wooded savanna, from lowlands to 10,000 feet (Redmond, 2011). Males, who make complete border patrols around the community's territory, on average every four days, form coalitions with socially-bonded, and often related, males. Females, on the other hand, leave their natal community once sexually mature and emigrate to another community, where female alliances become strong social ties (Boysen, 2009).

Female chimpanzees usually give birth to their first infant between the ages of 14 and 15, with interbirth intervals of approximately 5 years (Rowe, 1996). The lifespan of the chimpanzee is approximately 53 years, with sexual maturity being reached at ~11 years for females and ~13 years for males (Redmond, 2011).

Conservation status is also critical for chimpanzees, as local populations are threatened by extinction (Chapman and Peres, 2001 reviewed in Downing, 2011). Populations across Africa are in steep decline due to several primary threats, such as habitation destruction, the poaching and illegal bushmeat trades, illegal logging and coal concessions, lack of resources from human expansion and over-consumption, and even epidemic disease. Other forms of exploitation include the pet trade on the black market and the use of chimpanzees in the biomedical industry, the United States still being the world's largest user of chimpanzees for invasive research, with approximately 1,300 individuals currently confined to nine U.S. labs (Downing, 2011; Lonsdorf, 2010).

STUDY SITE AND SUBJECTS

❖ Study Site

This research was conducted at the Center for Great Apes (CGA), a 100-acre, non-profit sanctuary in Wauchula, Florida (27.582087, -81.676976) (Figure 5) (Center for Great Apes, n.d.; Google Maps, 2013). Situated approximately 123 km southeast of Tampa, the CGA is located in a heavily wooded region of Florida interspersed with grapefruit and orange groves. The sanctuary, established in 1997, was developed to replicate a tropical forest setting, consisting of oak, pine, magnolia, sweet gum, willow, bamboo, palm, guava, mango, ginger, banana, and other exotic fruit trees similar to great apes' native habitats (Center for Great Apes, n.d.). Facilities include on-site food preparation and storage (Figure 6), as well as a medical facility staffed by on-site veterinarians in the Arcus Great Ape Health Center (Figure 7) (Center for Great Apes, n.d.), and are maintained by full-time maintenance personnel and a high-quality team of animal care staff and administrators.

Housing for the great apes is comprised of 12 three-story, high-domed, wire enclosures ranging from 50-80 feet long and 34 feet tall (Figure 8); 3 special-needs enclosures for quarantining new arrivals and for handicapped and geriatric apes (Figure 9); attached night houses which are heated and capable of withstanding hurricanes (Figure 10); and an elevated 5,400 foot tunnel/chute system that connects all the enclosures, allowing residents the ability to utilize their respective network of enclosures to socialize with conspecifics (Figure 11). Besides plenty of running room, climbing space, and height for swinging throughout the environment, all outdoor habitats feature a variety of climbing structures, swinging ropes and vines, as well as numerous play materials including barrels, culverts, tires, fire hose swings, barge-rope vines, and giant rubber tubs for pools. More naturalistic toys such as tree branches, banana leaves, bamboo poles, palm fronds, sand piles, and coconuts are regularly provided, in addition to other daily enrichment devices. The night houses have high nesting areas, hammocks, and bed-shelves, and not only do they provide a place to sleep at night but also a place to rest during the day if individuals wish to retreat from summer rainstorms or the hot Florida sun. All indoor and outdoor habitats have security cameras and audio monitors for monitoring residents and ensuring the security of the facility. (Center for Great Apes, n.d.)

Diets are individually designed by a nutritionist according to age, weight, and health of individual residents and consist of commercially produced primate biscuits, 3-4 fresh fruits per day, 9-10 different vegetables per day, various leafy greens, fresh browse, as well as nutrient supplements for special-needs individuals (Center for Great Apes, n.d.).

The mission of the CGA is to provide a permanent sanctuary for orangutans and chimpanzees who have been rescued or retired from the entertainment industry, from research, or who are no longer wanted as pets, by providing lifetime care with dignity in a safe, healthy, and enriching environment (Center for Great Apes, n.d.). A major goal of the sanctuary is to promote the coexistence of individuals with his or her own species, while also encouraging natural behavior.

❖ Subjects

From a population of 30 chimpanzees (*Pan troglodytes*) and 15 orangutans (*Pongo spp.*) (Table 2), a minimum of 3 male and 3 female subjects from each species were selected for focal animal sampling (Study 2) based upon the availability of groups, the degree of social interaction among individuals within those groups, and a relatively high-contrast sclera/iris color differential (Figure 1; Table 7). Studies 1 and 3 were conducted with as many individuals as would voluntarily participate (Tables 6 and 8). These semi-free-ranging individuals were socially-housed (species composition was not socially-integrated), and each come from extremely diverse backgrounds with varying levels of former quality of life. The social groups in which subjects reside vary from day-to-day, depending upon animal management protocols. This population consists of former entertainment, circus, road-side zoo, biomedical research, and pet apes, including some neutered males and Sumatran-Bornean hybrids, as well as those with various disabilities.

The developmental and social history of the individuals in these populations is unique and atypical, in that many of these individuals were not exposed to an appropriate species-specific social milieu. Nevertheless, the staff of the CGA have successfully acclimated the vast majority of residents to conspecifics, thereby creating functioning social groupings facilitated by a network of tunnels which allow movement of individuals among various social groups (Figure 11). As a consequence, the apes have a choice regarding with whom they spend their time and for how long.

DATA COLLECTION AND RECORDING

This eight-week observational and behavioral study was conducted from May 20, 2013 to July 15, 2013. Behavioral observations occurred at a minimum distance of three-to-four feet from the enclosures. Behavioral ethograms were designed and used to identify the occurrence of gaze-following of a human (Study 1) (Table 5), quantify social monitoring via visual communicative behavior (Study 2) (Tables 1, 3, and 4), and assess joint visual attention with a human social partner (Study 3), by using focal animal and on-the-dot sampling techniques (Altmann, 1974; Paterson, 2001). Data were recorded using data sheets, and a video camera was utilized for Study 3. At least three males and females from each species were used as focal subjects in Study 2; 12 subjects sampled across the 57-day study period yielded approximately 4.75 days of data collection per subject. However, subjects for Studies 1 and 3 were chosen based upon availability and willingness of subjects to participate in the study.

METHODS

❖ Study 1

The objective of this study was to identify the occurrence of gaze-following and investigate the ability of great apes to engage in gaze-following of a human (i.e. follow the gaze of a human social partner) (McNelis and Boatright-Horowitz, 1998; Pitman and Shumaker, 2009). To test the robustness of this ability, participants were given the opportunity to voluntarily participate in this task as part of an enrichment activity (Table 6). The distance between the ape and human was approximately three feet.

Modeled after a study conducted by Pitman and Shumaker (2009), great ape participants either approached the testing area unsolicited, were approached by the human partner, or were asked to approach by the human experimenter/social partner. Trials began once the human partner gained the attention of the participant (i.e. participant was facing the human and was within 1 m of the wire mesh and human). One trial was given to each subject and included 14 different looking behaviors: 8 pointing and 6 non-pointing behaviors (Table 5). While maintaining body position oriented towards the subject, the experimenter used her eyes and head to look in various directions for ~ 30 seconds (e.g. left, right, up, behind subject) for the non-pointing condition (Figure 12). The same procedure was employed for the pointing condition, but the experimenter also used behavioral cues (i.e. common pointing gesture) that were consistent with gaze direction (Figure 13). A behavior was scored as gaze-following if the subject looked in the direction of the experimenter’s gaze/pointing with both head and eyes simultaneously or with eyes alone within 15 seconds. Scoring derived from live observations of the subject's visual response (i.e. whether or not the subject looked in the same direction as the experimenter).

- Study 2

The objective of this study was to identify the occurrence of social monitoring behavior among group-living chimpanzees and orangutans and to assess frequencies and direction of looking behavior as a function of species, sex, and age (McNelis and Boatright-Horowitz, 1998; Table 14). Selection of subjects was randomized to enable the collection of an equal number of focal samples in the A.M. and P.M (Table 7). 15-minute focal animal samples, with ten minutes between samples to ensure independence, were used to quantify the occurrence and frequency of gaze-related behavior, as well as whether or not the actor's gaze, glance, or stare elicited a response from the receiver (Tables 1, 3, and 4). Data were collected using the following procedure: the experimenter visually located the focal animal subject and positioned herself 6-to-12 feet from the subject; with binoculars, the experimenter obtained visual access to the subject's face and eyes and initiated the 15-minute focal animal sample, recording the occurrence and frequency of gaze-following between the subject and the conspecific target, including subsequent behavioral responses (Tables 3 and 4).

- Study 3

The objective of this study was to investigate the ability of great apes to engage in joint attention: coordinated attention with a human around an object (Pitman and Shumaker, 2009). To test the robustness of this ability, participants were again given the opportunity to voluntarily participate in these tasks as part of an enrichment activity. The distance between the ape and human was approximately three feet.

Utilizing the methods employed by Pitman and Shumaker (2009), a modified version of a common protocol used to assess joint attention and other socio-cognitive behaviors in human infants was used for this procedure. Two trials were presented to each subject, with approximately 17 days between each trial to eliminate habituation (Mundy, Delgado, Block, Venezia, Hogan, and Seibert, 2003 reviewed in Pitman and Shumaker, 2009). Again, the trial commenced when the individual voluntarily sat in front of the human social partner.

- Visual Stimuli

Multi-dimensional objects, each mounted on a wooden block (~ 20 cm x 6 cm x 5 cm) were presented in two different trials. Each stimulus-object consisted of brightly colored stationary items (e.g. sandbox play shapes and shovels, plastic toy boats, etc.) (Figures 14 and 15). A total of 7 stimuli were presented in random order to each subject for each trial (3 stimuli being considered functional, or manipulative toys/possible tools, versus 4 stimuli being non-functional objects). Different stimuli were used for trials 1 and 2 (Figures 14 and 15).

- Methods

The experimenter held each stimulus-object by grasping the wooden block, thereby displaying each object clearly. With arm extended and while looking directly at the subject’s eyes, the experimenter presented each stimulus (randomly and only once) to the subject at eye level (Figures 16 and 17). A behavior was scored as coordinated attention if the participant initiated attention with the human by alternating gaze between the stimulus, the human partner’s face, and then back to the stimulus within a 15-second period. To be accepted as an indication of awareness of the human partner’s attention on the object in relation to his or her own, the ape must have completed the full gaze alternation cycle: beginning with an examination of the object, looking at the partner, and then returning his or her attention to the object again (Carpenter, Nagell, and Tomasello, 1998 reviewed in Pitman and Shumaker, 2009). I predicted that apes would alternate gaze with the human partner more often when an interesting object, one around which individuals could socially engage, was presented (specifically a manipulative toy/possible tool (i.e. functional) (e.g. Trial 1 items: 3 (shovel), 6 (rake), and 7 (pail/bucket); Trial 2 items: 4 (sifter scoop), 5 (bowl), and 6 (spade)) as depicted in Figures 14 and 15) than when a less-interesting (i.e. nonfunctional) object was presented.

DATA ANALYSES

Statistical analyses were performed using SIGMAPLOT 10 (Systat Software Inc., Point Richmond, CA). Multi- and univariate statistical analyses were used to identify which variable(s) best predicted variation in mean rates of gaze-following, social monitoring, and joint attention capacity. The effects of species, sex, and age on each form of visual communication were tested using multivariate (multiple linear and linear regression) and univariate (t-test, ANOVA, Wilcoxon signed-rank test, Mann-Whitney U-test) analyses (Brockman, Harrison, and Nadler, 2009). Variables were tested for normality and equal variance. Results were then reported as means and standard deviations, with significance set at $p \leq 0.05$.

RESULTS

❖ Study 1: Gaze-Following of a Human Social Partner – Non-Pointing vs. Pointing Conditions

▪ Non-Pointing Condition

In the gaze-following non-pointing condition, there was no effect of species or sex (Table 9, A and B). Both within and between species, there was no effect of sex on gaze-following behavior (Table 9, C, D, E, and F). However, there were marked differences in mean gaze-following frequencies between sex and species, male orangutans and female chimpanzees exhibiting higher mean gaze-following frequencies than their opposite-sex conspecifics, although none of the differences approached significance (male orangutans: mean=2.75 +/- 1.17 and female chimpanzees: mean=2.64 +/- 1.29 versus female orangutans: mean=2.00 +/- 1.29 and male chimpanzees: mean=2.00 +/- 1.25 (Table 9, E and F; Figure 18).

There was a strong effect of age in gaze-following behavior within species: a significant effect of age was observed in *Pongo*, frequencies of gaze-following being 2-fold higher in older (i.e. 19+ years of age) orangutans than younger (i.e. ≤18 years of age) orangutans (means=3.00 +/- 1.00 versus 1.50 +/- 1.05, respectively, *p*=0.015) (Table 10, B; Figure 19). In contrast, younger chimpanzees exhibited a higher mean frequency of gaze-following than older chimpanzees, but not significantly so (means=2.73 +/- 1.19 and 1.90 +/- 1.29, respectively) (Table 10, C; Figure 20).

A significant effect of species was found in gaze-following behavior in the younger age-class of females, chimpanzee females having a 3-fold higher mean frequency of gaze-following than orangutan females (means=3.00 +/- 1.29 versus 1.00

+/- 1.00, respectively, *p*=0.045) (Table 10, F; Figure 21). Among orangutan females, older individuals showed a 2.5-fold higher level of gaze-following than younger females, but not significantly so (means=2.75 +/- 0.96 and 1.00 +/- 1.00, respectively, *p*=0.065) (Table 10, D).

- Pointing Condition

Concordant with predictions of a higher frequency of gaze-following occurring when accompanied by a pointing gesture, there was a significant 2.7-fold greater mean frequency of gaze-following when the human social partner pointed in the direction of her gaze (all individuals non-pointing mean=2.36 +/- 1.25 versus pointing mean=6.39 +/- 1.54, *p*<0.001) (Table 11; Figure 22). Within the gaze-following pointing condition, there was no effect of species or sex (Table 12, A and B); within and between species, there was no effect of sex on gaze-following behavior (Table 12, C, D, E, and F). Additionally, there was no effect of age on the pointing condition (Table 13, A, B, and C). However, older orangutans and younger chimpanzees tended to follow the pointing gesture more often than their counterpart conspecifics, but not significantly so (*p*=0.147 and *p*=0.056, respectively) (Table 13, B and C; Figure 23).

- Study 2: Social Monitoring Among Conspecifics

Pongo subjects tended to exhibit higher mean frequencies of social monitoring behavior than *Pan* subjects (*p*=0.064) (Table 15, A). A significant effect of species on social monitoring behavior was found for females, orangutan females engaging in higher rates of social monitoring than chimpanzee females (*p*=0.001) (Table 15, C). A significant effect of sex was found within species for *Pongo,* females exhibiting higher rates of social monitoring than males (*p*=0.009) (Table 15, B). Within *Pongo*, a significant effect of sex was also observed in older individuals (within species/same age class/between sex), older females engaging in higher rates of social monitoring than older males (older female orangutans: mean=1.70 +/- 0.81 versus older male orangutans: mean=1.00 +/- 0.00, $p<0.001$) (Table 15, H).

Age also exerted a significant effect on social monitoring behavior within species of the same sex (younger male orangutans: mean=2.16 +/- 0.69 versus older male orangutans: mean=1.00 +/- 0.00, $p<0.001$; younger male chimpanzees: mean=1.07 +/- 0.26 versus older male chimpanzees: mean=1.57 +/- 0.85, $p=0.007$; and younger female chimpanzees: mean=1.08 +/- 0.27 versus older female chimpanzees: mean=1.80 +/- 0.92, $p<0.001$) (Table 15, G; Figure 24). The older chimpanzees of each sex exhibited higher mean frequencies of social monitoring behavior than their younger conspecifics, whereas among orangutans, the younger individuals of both sexes exhibited higher mean frequencies of social monitoring than their older conspecifics, although the female orangutans not significantly so (Table 15, G).

Significant effects of species were observed among younger individuals: younger orangutans exhibited higher mean rates of social monitoring behavior than younger chimpanzees, within the same sex and same age class counterparts ($p<0.001$ and $p<0.001$, respectively) (Table 15, I; Figure 25). The younger orangutan males exhibited a significant two-fold higher mean rate of social monitoring above that observed in young male chimpanzees (means=2.16 +/- 0.69 versus 1.07 +/- 0.26, respectively, $p<0.001$) (Table 15, I; Figure 25). However, older male chimpanzees exhibited significantly higher mean rates of social monitoring than older male orangutans ($p=0.009$) (Table 15, I; Figure 25).

Results of an ANOVA examining variation in mean frequencies of the three types of social monitoring/looking behavior (glancing, gazing, and staring) revealed that *glancing* at conspecifics was the predominant mode of looking in this population of apes (Table 16; Figure 26). Mean glance rates were significantly elevated above those of the two other modes of looking; mean rates of glancing were 2-to-3-fold higher than the mean rates of gazing or staring (Glance: mean=8.36 +/- 5.05 SD; Gaze: mean=3.86 +/- 3.72 SD; Stare: mean=2.86 +/- 3.51 SD; *p*=0.003). Combining both species and sexes indicated that glances were employed more often by younger individuals, while gazes and stares were practiced more frequently by older individuals (Table 17). However, there was no effect of species, sex, or age class on any individual mode of looking, including glancing (Table 18).

- Study 3: Joint Attention with a Human Social Partner – Functional vs. Non-Functional Objects

Results of *t*-tests examining the effect of trial (e.g. Trial One or Trial Two) on joint attention performance showed there was no significant difference in performance between trials for either species (Total Objects for T1 versus T2 when pooled with *Pan* and *Pongo* = NS) (Table 19, A). Thus, no effect of trial on the joint attention study was observed. No effect of species was observed for either trial nor for the overall study with trials combined (Table 19, A and B).

However, there was a significant effect of object type (i.e. functional/manipulative toys/possible tools vs. non-functional objects) observed when pooling both trials and both species overall (*p*<0.001) (Table 19, I; Figure 27). A significant effect of object functionality (i.e. functional versus non-functional objects) occurred within trials of *Pongo* (Trials 1 and 2) (*p*=0.042 and *p*=0.015, respectively)

(Table 19, G), and this effect was even more pronounced when the trials were pooled (*p*=0.001) (Table 19, H). When trials were combined, orangutans engaged in significantly higher mean rates of joint attention toward functional objects than non-functional objects (*p*=0.001), whereas chimpanzees showed no significant difference in mean levels of joint attention based upon object functionality (*p*=0.094) (Table 19, H; Figure 28).

Females of both species engaged in significantly higher levels of joint attention toward functional objects than did their male counterparts (females: mean=0.75 +/- 0.21 vs. males: mean=0.56 +/- 0.32, *p*=0.018) (Table 19, D).

DISCUSSION

❖ Study 1: Gaze-Following of a Human Social Partner – Non-Pointing vs. Pointing Conditions

The results of Study 1 accord with previous studies of gaze-following in primates (Rosati and Hare, 2009; Bräuer *et al*., 2005; Shepherd, 2010; Tomonaga and Imura, 2010) and confirmed that the apes in this population exhibited gaze-following behavior with a human social partner. However, this study was the first to examine the effect of age, sex, and species on this behavior. A strong effect of age was found within species; frequencies of gaze-following behavior were 2-fold higher in older than in younger orangutans, while younger chimpanzees exhibited higher mean frequencies of gaze-following than older individuals. In addition, a significant effect of species was found in the younger age-class of females, chimpanzee females having a 3-fold higher mean frequency of gaze-following than orangutan females, for reasons that are unclear, but may be related to the complex social environment young chimpanzees occupy in this colony. For example, the chimpanzee females in this population must navigate relationships with larger groups of conspecifics, whereas orangutan females are pair-living here. Two of the seven orangutan females were either housed solitarily or had no interaction/proximity with a conspecific companion, while only two of the eleven chimpanzee female subjects were solitary. Thus, those individuals housed in large social groups, with a possibly reduced burden of social monitoring (e.g female chimpanzee alliances), may be able to show greater interest in a human social partner than those individuals pair-living with an opposite-sex conspecific (e.g. as demonstrated in Study 2, female orangutans socially monitored significantly more often than did the female chimpanzees).

Concordant with predictions of a higher gaze-following frequency when accompanied by a pointing gesture, there was a 2.7-fold greater mean frequency of gaze-following behavior when the human social partner pointed in the direction of her gaze. In the pointing condition, older orangutans and younger chimpanzees again exhibited a higher frequency of gaze-following behavior, as they tended to follow the pointing gesture more often than did their counterpart conspecifics.

Developmental studies of gaze-following in non-human primates have shown that both rhesus macaques and chimpanzees start to follow gaze quite reliably during infancy (Tomasello *et al*., 1999; Tomasello, Hare, and Fogleman, 2001). Tomasello *et al.* (2001) concluded that during the period between infancy and adulthood, individuals of these two species come to integrate their gaze-following skills with their more general social-cognitive knowledge about other animate beings and their behavior. Thus, there are developmental stages in gaze-following behavior of non-human primates just as in human infants. For example, human infants understand pointing and head orientation first, and then understand glancing, and data on non-human primates indicate that they seem to show the same order of development, a pattern very similar to human infants (Itakura, 2004). Revealed through cross-sectional studies, pig-tailed macaques were shown to follow the gaze of human experimenters, and Ferrari, Kohler, Fogassi, and Gallese (2000) demonstrated that there were developmental stages to such an ability. Results showed that gaze-following in pig-tailed macaques improves dramatically with age. Compared with adults, juvenile monkeys exhibited a marked difference in head gaze-following compared with adults, presumably because they were unable to understand the direction of another’s gaze by employing eye cues alone (Ferrari *et al*., 2000). Although their results indicated that macaques can follow the gaze of the experimenter by using head/eye and eye cues alone, their findings suggest that juveniles, in particular, were not able to orient their attention on the basis of eye cues alone. Ferrari *et al*. (2000) propose that the orientation of the head and eyes together is the first feature that triggers a shift in visual attention, thus suggesting that in young macaques, head and eyes orientation provide more salient signals to the direction of another’s gaze than eyes alone (Tomasello *et al*., 2007b). Additionally, gaze-following in general was more frequently observed in adults than in the juvenile monkeys. Because gaze-following abilities in macaques significantly improves with age, as in humans, Ferrari *et al.* (2000) state that the transition to adulthood is a crucial period in the development of gaze-following behavior.

After testing 11 species of non-human primates to examine whether they would look in the direction the experimenter looked or pointed, Itakura (1996) found that only chimpanzees and an orangutan reliably followed the experimenter’s pointing and head + eye cue. In a similar gaze monitoring task, Povinelli and Eddy (1996) found that chimpanzees followed the experimenter’s eye movements alone (Itakura, 1996). Anderson, Sallaberry, and Barbier (1995) pioneered the assessment of the ability of animals to use human-given facial and gestural cues in an object-choice task. Using an experimenter-given cue paradigm, where the human’s behavioral cues were pointing, gaze, and pointing + gaze, they found that capuchin monkeys (*Cebus apella*) could utilize the human’s pointing or pointing + gaze cues (Itakura, 2004). Anderson, Montant, and Schmit (1996) tested rhesus monkeys using the same paradigm and reported that rhesus monkeys could use pointing or pointing + gaze much like capuchin monkeys (Itakura, 2004). However, research designed to train monkeys to use the significance of gaze cues have so far been relatively unsuccessful. Pettigrew, Forsyth, and Perrett (1993) were only able to train 2 out of 6 rhesus monkeys to follow human attention direction (defined by eye or head direction) for food reward (Emery *et al*., 1997).

Itakura and Tanaka (1998) found that chimpanzees, an orangutan, and human infants could all use gaze cues, pointing, and a glance cue to locate a hidden toy or food item. Results showed that all subjects were quite skillful responding to the local enhancement cue, regardless of whether a human or chimpanzee provided it; however, few subjects were as skilled with the gaze + point cue, whether it came from a human or chimpanzee (most of these having been raised in infancy by humans). Povinelli, Bierschwale, and Cech (1999) tested chimpanzees and found that the chimpanzees were not able to use the experimenter's gestural cues to locate hidden food when using eye movements alone. Likewise, Peignot and Anderson (1999) found that captive gorillas used pointing and/or head + gaze cues to find hidden food, but they also did not use eyes alone as a cue.

Alternatively, Inoue *et al*. (2004) reported that a white-handed gibbon (*Hylobates lar*) could use an experimenter's pointing, gaze, and glance to locate hidden food. They argued that the gibbon's use of a human's glance as a cue resulted from enculturation, because the subject had had extensive interactions with humans since a very young age. The orangutans and chimpanzees in the current study have also had numerous experiences and face-to-face interactions with humans from a very young age (e.g. having been trained to perform in movies and commercials, as well as in the circus and live entertainment shows), lending support to the idea that having sole contact with a human during development results in enculturation (i.e. primary socialization via a human) and modification of social attentional and interactional skills (Freeman and Ross, 2014; Tomasello and Call, 2004). The effects of enculturation are presumed to be emphasized in species with a greater degree of behavioral plasticity, but as Tomasello and Call (2004) point out — rigorous experimental evidence since 1996 has reinforced the case for the existence of systematic differences between apes with different rearing histories but also for the existence of some unsuspected cognitive skills in all apes. These recent data have given us a different perspective on the question of what kinds of influence humans may have on the cognitive development of apes. Because even non-enculturated apes can understand some aspects of intentional actions, it is likely that human experience only serves to modify existing social interactional and attentional skills — rather than creating new ones (Tomasello and Call, 2004). In that regard, there is some evidence that great apes raised by humans are more attuned to human eyes than are their mother-reared conspecifics (Call and Tomasello, 1994; Gómez, 1996; Itakura and Tanaka, 1998).

On the other hand, gaze-following behavior is widespread in the animal kingdom with recent evidence coming from widely diverse species. It has been shown to occur in domestic animals such as dogs, horses, and goats, ravens and other corvids, in addition to many primate species (Bräuer, Kaminski, Riedel, Call, and Tomasello, 2006; Hare, Rosati, Kaminski, Bräuer, Call, and Tomasello, 2010; Inoue *et al*., 2004;

Itakura, 2004; Kaminski, Riedel, Call, and Tomasello, 2005; Proops, Walton, and McComb, 2010; Shepherd, 2010). In fact, elephants have recently demonstrated what appears to be an instinctive understanding of human gesture (Smet and Byrne, 2013). The elephants in this study had previously been trained to respond to vocal cues from a human handler walking behind the elephant. However, they did not have experience using gestures. Researchers were surprised that the elephants in the experiment did not seem to have to learn anything – because the elephants were able to grasp the meaning of pointing from the outset, it seemed the ability to understand pointing was naturally possessed by the elephants, these findings further positing that elephants may be cognitively much more like us than previously realized. Although unrelated to us, studies of elephants have helped to build a map of a part of the evolutionary tree that is quite distant from humans. Professor Byrne thus speculates "…if we find human-like abilities in an animal like an elephant, that hasn't shared a common ancestor with people for more than 100 million years, we can be pretty sure that it's evolved completely separately, by what's called convergent evolution" (Gill, 2013, para. 15). Chimpanzees, in particular, seem to understand the seeing-knowing relationship and other's knowledge, but emerging evidence has increasingly shown the possibility that other non-human animals recognize the seeing-knowing relationship to a certain extent as well (Emery, 2000; Hare *et al*., 2001; Itakura, 2004).

In the present study, several attention cues were oriented in the same direction, suggesting that the great ape subjects may have used eye gaze, head orientation/posture, torso/body posture, and pointing gestures (in the pointing condition only) to follow the human social partner's direction of attention. These results indicate that the subjects exhibited unambiguous gaze-following behavior in response to the experimenter's gestural/behavioral cues, suggesting that the apes' gaze-following was controlled by the 'social' properties of the experimenter-given cues (Itakura, 2004; Okamoto, Tomonaga, Ishii, Kawai, Tanaka, and Matsuzawa, 2002). In fact, results show that the frequency of gaze-following behavior increased when the experimenter employed gazing + pointing. That is, the subjects adjusted their gaze and looked significantly more often in the socially-cued direction under the pointing condition of Study 1. Pointing, a common way of establishing reference, was used here as a directive action. Subjects were able to utilize the pointing + gaze cues, using the experimenter-given pointing gesture as a social cue. Pointing itself, is a special gesture which functions to direct an individual's attention to something which does not convey a specific meaning in the manner of most conventionalized, symbolic gestures. Rather, pointing can convey an almost infinite variety of meanings by saying, in effect, 'If you look over there, you'll know what I mean' (Tomasello, Carpenter, and Liszkowski, 2007a). Interpreting the intended meaning of a pointing gesture, therefore, requires considerable 'mindreading' (Baron-Cohen, 1994; Gómez, 1996). In most cases, the pointing act is predication, or focus, informing the recipient of something new and worthy of attention; in other cases, however, pointing serves to establish a new topic, about which further things may then be communicated (Tomasello, 2007). Although variations in form exist, such as lip- or chin-pointing, the basic inter-individual function of pointing seems to be universal. Moreover, evidence exists for the deep social context of this behavior in which pointing is best understood on many levels and in many ways and may even be dependent on unique skills and motivations for cooperation and shared intentionality (e.g. joint intentions and attention with others) (Tomasello *et al*., 2007a).

In terms of eye direction specifically, the only systematic evidence for the capacity to use solely eye cues to follow one's gaze is for rhesus and pigtail macaques (Ferrari *et al*., 2000; Deaner and Platt, 2003). Deaner and Platt (2003) found that importantly, rhesus monkeys showed sensitivity to eye direction alone in the absence of head direction, which is generally consistent with that observed in humans. This raises the possibility, therefore, that relative sensitivity to the eyes and the head may differ across primate species (Tomasello *et al*., 2007b).

Tomasello *et al.* (2007b) argue that humans, and only humans among primates, have developed a morphological feature – the highly visible eye – that affords their gaze direction easier for others to follow across all contexts. However, within the current study population, a wide range of individual differences in eye morphology was observed. In addition, the investigator identified a novel characteristic of the eyes in this population of great apes, namely a distinct white ring surrounding the iris in Subject Kiki (Figures 1 and 29). An examination of the eyes of the other apes showed that this feature occurred in 80% of the orangutan population while it occurred in only 37% of the chimpanzee population, albeit less distinctly so (Figure 1). It appears, therefore, that this 'white ring' is an individual-specific feature. Although no reference to this trait has been found in the mammalian literature, it is nevertheless intriguing, because the larger, more visible 'white of the eye' that humans possess, is argued to be a unique feature in humans (Kobayashi and Hashiya, 2011; Tomasello *et al*., 2007b). The readily-seen sclera is a common human trait, and the cooperative eye hypothesis posits that the eye's distinctive visible characteristics evolved to make it easier for humans to follow another's gaze while communicating or working together on tasks (Kobayashi and Hashiya, 2011; Tomasello *et al*., 2007b). The variation in color, specifically the degree of whiteness, in the scleras of non-human apes, as well as the addition of this unique white ring, calls into question the so-called distinctness of human eyes (Figures 1 and 29).

❖ Study 2: Social Monitoring Among Conspecifics

Ape-to-ape social monitoring was found to occur among the socially-housed orangutans and chimpanzees within the populations of the current study. A significant effect of species on social monitoring was found in females, and a significant effect of sex was found within species for *Pongo*. Female orangutans monitored conspecific males more often than the males monitored conspecific females, a likely consequence of extreme sexual dimorphism in this species, wherein males are able to routinely displace females from favored feeding areas. Female orangutans also monitored their conspecific male partners significantly more often than female chimpanzees monitored their group members, a result that may be related to pair-living versus group-living housing conditions.

A significant effect of sex was also observed in older individuals within *Pongo*, with older females engaging in higher mean rates of social monitoring than older males. Highly significant effects of age were observed within species of the same sex. Older chimpanzees exhibited higher mean frequencies of social monitoring behavior than their younger conspecifics, whereas among orangutans, younger individuals exhibited higher mean frequencies of social monitoring than their older conspecifics, although not significantly so among female orangutans. Explanations for this interspecific age difference are few, but increased visual monitoring among adult male chimpanzees may be related to the increased probability of aggression occurring among socially-housed adult males. In contrast, younger male orangutans exhibited significantly higher frequencies of social monitoring than the older male orangutans for reasons that remain unclear.

Significant effects of species on rates of social monitoring were observed among younger individuals: younger orangutans exhibited higher mean rates of social monitoring behavior than younger chimpanzees, and this finding suggests that orangutans in this sanctuary socially monitor conspecifics more often than the chimpanzees in general. In fact, younger orangutan males exhibited a two-fold higher mean rate of social monitoring above that observed in the young male chimpanzees. However, among the older age class individuals, older male chimpanzees exhibited significantly higher mean rates of social monitoring than older male orangutans. The reasons for this difference are indeterminate, but it is likely associated with the larger social groupings of chimpanzees which include multiple adult males.

Among the three forms of social monitoring — glancing, gazing, staring — examined in this study, *glancing* at conspecifics was found to be the predominant mode of looking behavior within these populations and is the form of looking that is the shortest in duration (i.e. instantaneous; Table 1).

There was no significant effect of species, sex, or age on glance rates in this great ape population (Table 17). This finding is not surprising, since social monitoring also functions as an anti-predator strategy. The various roles of vigilance behavior include: within-group or extra-group conspecific monitoring; avoiding competition of food, mates, and territory; sharing information and communicating; expressing dominance relationships; identifying social partners; planning travel routes; food search and even detecting opportunities for food stealing (Campos and Fedigan, 2014; Gaynor and Cords, 2012).

- Study 3: Joint Attention with a Human Social Partner – Functional vs. Non-Functional Objects

Results of Study 3 clearly show that joint attention does indeed appear to be a robust ability in the great apes of these populations. Having the ability to engage in some form of coordinated attention could potentially benefit long-lived individuals who must navigate dynamic and complex social environments. Equally important, the findings from this study showed that object functionality was crucially important in explaining variation in rates of joint attention in these populations. A significant effect of object type (i.e. functional/manipulative toys/possible tools versus non-functional objects) was observed when pooling both trials and both species overall. A significant effect of object functionality also occurred within trials for *Pongo*, and this effect was even more pronounced when the trials were pooled. When trials were combined within species, orangutans engaged in significantly higher mean rates of joint attention toward functional objects than toward non-functional objects, whereas chimpanzees showed no significant difference in mean frequencies of joint attention based upon object functionality. Furthermore, females of both species engaged in higher levels of joint attention directed at the functional objects, the sex difference favoring females being statistically significant when the mean rates for both species were pooled. The reasons for this sex differences in rates of joint attention directed at functional objects are unclear, but studies of wild ape populations suggest that females — and juveniles — may be technologically more innovative than males, particularly in the areas of tool-making and -using behavior (Breuer, Ndoundou-Hockemba, and Fishlock, 2005; Pruetz and Bertolani, 2007).

In this study, I defined/assigned objects as functional and non-functional according to our conventional understanding of what constitutes a functional versus a nonfunctional tool in human terms. The functional objects/tools I used in this study were identical representations of common, everyday tools that humans use frequently to accomplish a task (e.g. various types of shovels and rakes; the bowl and pail/bucket, which serve similar overall purposes as containers) (Figures 14 and 15). Previous studies of captive chimpanzees show that individuals are more likely to be attracted to complex objects introduced into their environment, particularly those that can be manipulated with higher levels of controllability, as well as those that require high levels of dexterity and motor coordination (Videan, Fritz, Schwandt, Smith, and Howell, 2005).

It is important to note that some investigators have used the terms *joint attention* and *gaze-following* interchangeably. Scaife and Bruner (1975), for example, defined the ability to gaze follow as the ‘visual attention of the mother-infant pair . . . directed jointly to objects and events in the visual surround,’ although no object was used as a specific focus of attention in their study (Emery *et al*., 1997). On the other hand, other researchers have not included ‘the object of attention’ in their definition, even though they used an object in directing the attention of a subject (e.g. ‘the ability to follow another's direction of gaze,’ Corkum and Moore, 1994; ‘looking where someone else is looking,’ Butterworth, 1991). Gaze-following has been defined as “looking where someone else is looking” by Corkum and Moore (1994), while this same definition has been used by Butterworth to define joint visual attention (Emery *et al.*, 1997). Emery *et al*. (1997) have persuasively concluded that gaze-following and joint attention are indeed different, yet intimately related abilities: they define gaze-following as the ability of one individual (X) to follow the direction of gaze of a second individual (Y) to a position in space (not an object) (Figure 30B), while joint attention has the additional requirement that X follows the direction of Y's gaze to the object (Z) that is the focus of Y's attention (Figure 30C). Joint attention thus requires extra cognitive computation to process the object of attention, and not just the direction of gaze.

More recently, Emery (2000) proposed a classification system for clearly differentiating among the various types of social gaze (Itakura, 2004, pg. 217):

> “Mutual Gaze [Figure 30A] occurs when attention of individuals A and B is directed to each other. Averted gaze occurs when individual A is looking at B, but the latter’s focus of attention is elsewhere [see also Figure 30A]. Gaze following occurs when individual A detect[s] that [individual] B’s gaze is not directed towards him, and follows the line of sight of B to a point in space [Figure 30B]. Joint visual attention is the same as gaze following except that there is a focus of attention, such as an object [Figure 30C]. Shared attention is a combination of mutual attention and joint visual attention, where the focus of individual A and B’s attention is on the object of joint focus and each other (i.e. “I know you are looking at X, and you know I am looking at X”) [Figure 30D]” … “[Figure 30E] shows mental state attribution or theory of mind. This uses a combination of the previous A-D attentional processes and higher-order cognitive strategies to determine that an individual is attending to a particular stimulus[,] because they intend to do something with the object, or believe something about the object.”

According to these classifications, shared attention differs in fundamental ways from joint visual attention, and the results of Study 3 demonstrate that the subjects in this study clearly engaged in shared attention with the human social partner. This is a novel and important finding, because as Emery (2000) points out, shared attention is a more complex form of communication, because it requires that individuals A and B each have knowledge of the direction of the social partner's attention, such that individuals can focus on each other and the object of joint focus. (Emery, 2000 reviewed in Itakura, 2004).

Furthermore, recent investigations of joint attention in humans suggest that joint attention can be accomplished without the actual process of gaze-following (Yu and Smith, 2013), although more research will be required to validate these findings.

> "Previous research has focused on one pathway to the coordination of looking behavior by social partners, gaze following. The extant evidence shows that even very young infants follow the direction of another's gaze but they do so only in highly constrained spatial contexts because gaze direction is not a spatially precise cue as to the visual target and not easily used in spatially complex social interactions. Our findings, derived from the moment-to-moment tracking of eye gaze of one-year-olds and their parents as they actively played with toys, provide evidence for an alternative pathway, through the coordination of hands and eyes in goal-directed action. In goal-directed actions, the hands and eyes of the actor are tightly coordinated both temporally and spatially, and thus, in contexts including manual engagement with objects, hand movements and eye movements provide redundant information about where the eyes are looking. Our findings show that one-year-olds rarely look to the parent's face and eyes in these contexts but rather infants and parents coordinate looking behavior without gaze following by attending to objects held by the self or the social partner. This pathway, through eye-hand coupling, leads to coordinated joint switches in visual attention and to an overall high rate of looking at the same object at the same time, and may be the dominant pathway through which physically active toddlers align their looking behavior with a social partner" (Yu and Smith, 2013, pg. 1).

Researchers have often compared great ape gestural communication to prelinguistic gestures of human infants, especially pointing, and the cognitive and social-cognitive skills underlying these gestures, such as joint attention, communicative intention (intentions about intentional states), and the motivation to share experience with others (Caron, Kiel, Dayton, and Butler, 2002; Tomasello, 2007; Tomasello *et al*., 2007a). Pointing gestures may rely on a common social-cognitive, social-motivational infrastructure of shared intentionality, suggesting that the symbolic and functional dimensions of communication may represent animal precursors to language (Call and Tomasello, 1994; Tomasello, 2007). Communicative gestures can be highly sophisticated and serve just as much purpose as words that are vocalized. Tomasello *et al*. (2007a) explain that humans communicate with one another linguistically (via socially learned, intersubjectively shared symbols) or gesturally, and they assert that the ways in which humans communicate are unique. The results of Study 3 suggest that the cognitive underpinnings of communication once thought unique to humans (i.e. shared joint attention with a human social partner) may certainly be shared by our closest non-human primate relatives, the great apes.

CONCLUSION

The present studies provide strong evidence for the existence of gaze-following, social monitoring, and joint attention abilities in the population of captive orangutans (*Pongo* spp.) and chimpanzees (*Pan troglodytes*) housed at the Center for Great Apes in Wauchula, Florida. The current findings, along with those from previous experimental studies, indicate that gaze-following and visually communicative behavior are indeed reliable indicators of advanced cognitive capacity in social primates.

The uniqueness of this research, however, resides in its observational context and its assessment of the potential effects of species, sex, and age on gaze-following, social monitoring, and joint visual attention. The responses of subjects were elicited while socially-housed with conspecifics, and the subject pool is considerably larger than that of any previous study. By evaluating species-specific variation in cognitive capacities as a function of sex and age, the study of this unique population of semi-free-ranging great apes provides new insights into the degree to which individuals visually communicate with conspecifics and human social partners.

It is well-known that gaze-following and joint attention are important skills for social animals and can provide invaluable advantages while living in close association of others throughout a long life duration. Primate species have been a primary focus in the comparative study of cognition, and because of their recently-shared evolutionary descent with humans, we assume that primates share many cognitive abilities with humans (McKinley and Sambrook, 2000). However, future comparative research regarding gaze-following, social monitoring, and joint attention needs to examine vertebrates other than primates including dolphins, elephants, and other social animals and should also involve domestic animals (e.g. dogs, goats, horses), as their gaze-following abilities may provide important clues regarding selection pressures during the process of domestication, for special skills related to social cognition and communication with humans (keeping in mind that the distinctive properties of animals' communication systems are simply the result of different evolutionary pressures) (Hare *et al*., 2010; Kaminski *et al*., 2005, Pepperburg, 1999). To enhance our understanding of how social complexity and other variables may affect the evolution of intelligence, our theoretical frameworks must also take into account both interspecific differences and similarities in cognition and should consider how selection pressures associated with sociality interact with those imposed by non-social forms of environmental complexity (e.g. how functional demands interact with phylogenetic and developmental constraints) (Holekamp, 2006).

The ability to follow the attention direction of others is one of the primary cognitive mechanisms enabling social interaction and communication, and this is a great asset in maintaining complex relationships and surviving in large groups. Great apes possess a repertoire of vocalizations and also communicate using facial expressions, body postures, gestures, and gait; they can send very subtle, nuanced signals by varying any one of those components (Arbib, Liebal, and Pika, 2008; Mark Bekoff reviewed in Kramer, 2014). The present findings certainly confirm that this population of orangutans and chimpanzees can readily orient their gaze direction, as an observer, towards a particular place of interest in the environment, as indicated by an actor/director. The results obtained in this research may suggest that the ability to assess other individuals' attentional states via the direction of the eyes and/or orientation of the face may very well represent a skill already present in the last common ancestor of the great apes. Although this hypothesis remains to be empirically tested, this research contributes substantially to a better understanding of the cognitive dimensions underlying the evolution of social cognition via visual and gestural communication in the human lineage.

Study 1 (non-pointing condition) strengthened previous findings showing that great apes exhibit gaze-following behavior with a human social partner. However, the first to examine the effect of species, sex, and age on this behavior, the current research shows a strong effect of age within species (e.g. gaze-following frequencies being higher in older orangutans and younger chimpanzees) and between species for the younger age-class of females (e.g. chimpanzees following gaze 3 times more often than orangutans). A striking contrast in mean gaze-following frequencies was also observed between species and within sexes (e.g. male orangutans and female chimpanzees exhibiting higher mean gaze-following frequencies than their opposite-sex conspecifics), and finally, in contrast to the non-pointing condition, gaze-following frequencies rose steeply in the pointing condition of Study 1 (e.g. a 2.7-fold greater mean frequency of gaze-following). Future studies should extend beyond those focused on age and examine the effects of rank on gaze-following behavior, and the phenomenon of pointing by *Hominoidea* should be further explored.

Results from Study 2 showed a significant effect of sex on social monitoring within species for *Pongo* (e.g. females monitored males significantly more often) and a significant effect of species for females (e.g. pair-living female orangutans monitored their conspecific males significantly more often than the group-living female chimpanzees did their group-mates). Consequently, future studies should investigate whether pair versus group composition has an effect on the frequency of social monitoring and also examine the effect of sex related to the dominance hierarchy. Significant effects of age were observed within species of the same sex, and significant effects of species were observed among younger individuals. Finally, results from Study 2 revealed that *glancing* was the predominant mode of looking behavior between conspecifics within these populations. While *glancing* is an instantaneous method to attend to one's environment, much more research is needed to determine any differences in relative glance rates.

The findings from Study 3, in particular, are unprecedented and can offer important contributions to the primate cognition literature. Results showed a notably significant effect of object type on shared, joint attention, when pooling trials and species of these populations. Significant effects of object functionality also occurred within *Pongo* (e.g. individuals engaged in significantly higher mean rates of joint attention toward functional, rather than non-functional, objects). Furthermore, females of both species engaged in higher rates of joint attention directed at the functional objects. While studies of wild ape populations indicate that females and juveniles are the forerunners in manufacturing tools and modifying them for countless purposes (Breuer *et al*., 2005; Pruetz and Bertolani, 2007), further research is required to determine how sex differences affect joint attention for functional objects/tools.

Although vertebrate species are inherently distinct in multiple ways, studying the cognitive abilities of nonhuman animals has the potential to provide important insights into human cognitive abilities. Prospective studies addressing the question of the extent to which a variety of animal species share with humans the phenomena of gaze-following and joint attention has the potential to expand our understanding of how these abilities have developed in the course of primate evolution. Future cognitive research will need to be multidisciplinary in order to successfully bridge our gaps in understanding patterns of variation in this capacity across vertebrates more broadly, but the findings of this research offer a valuable platform for future investigations. The importance of this research consequently resides in the new insights that may be gained into the phylogenetic substrates underpinning the evolution of cognition and visual communication in the human lineage via our closest relatives, the great apes.

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APPENDIX A: FIGURES

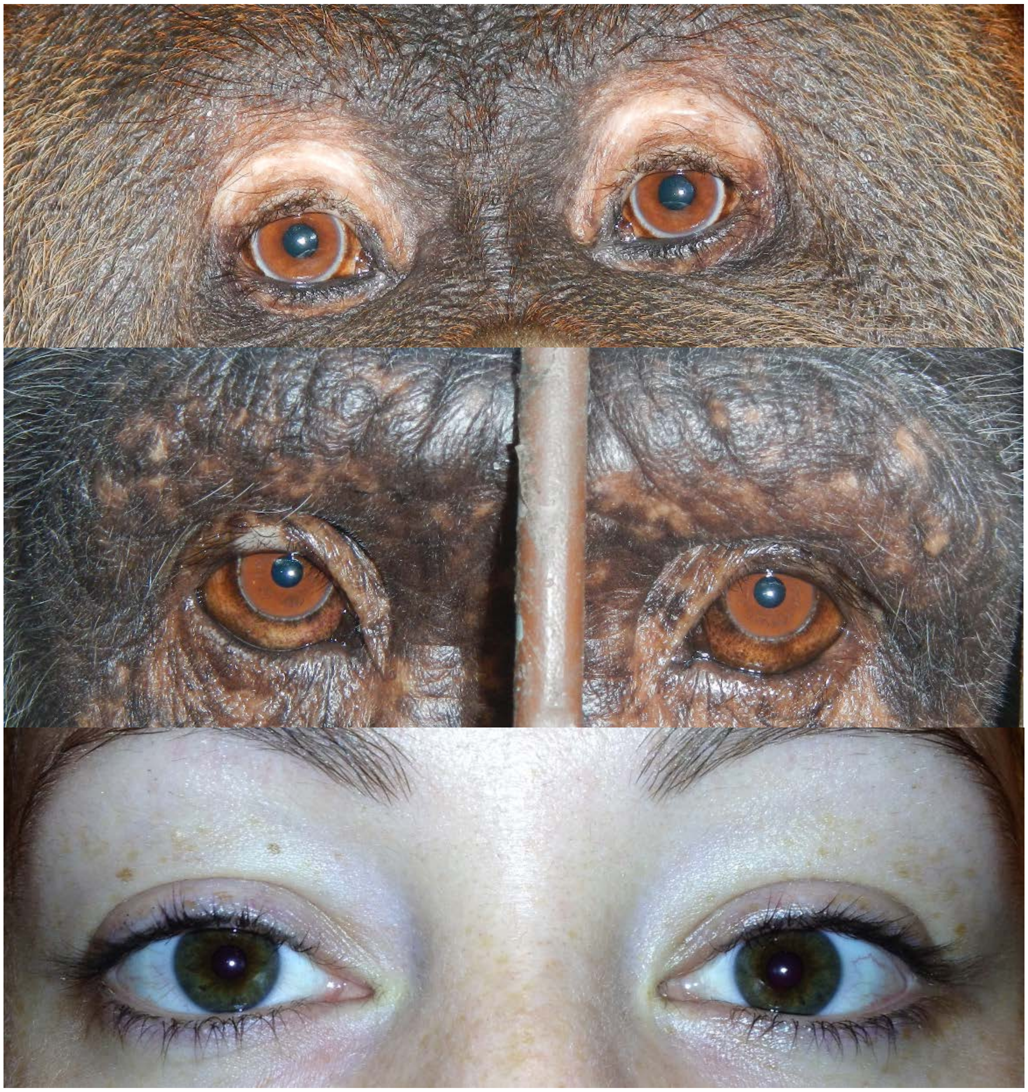

Figure 1. Orangutan, chimpanzee, and human eyes. (Scientists speculate that human eyes stand out more than other apes, because there is an advantage for humans in being able to see the subtle cues communicated by eye movement.) (Photographs by Danay C. Downing)

Figure 2. The pink eyelids of a male juvenile orangutan. (Photograph by Danay C. Downing)

Figure 3. The eyelashes of an adult male orangutan. (Photograph by Danay C. Downing)

Figure 4. Silver-colored eyelashes in the center of the eyelid are exposed when this adult male orangutan looks down. This may give the impression that an individual is alert and watching, when in fact, he or she could be focusing on an object in the lower field of vision. (Center for Great Apes ©)

Figure 5. Location of the Center for Great Apes, Wauchula, Florida, USA. (Center for Great Apes ©)

Figure 6. Food Prep Center. (Center for Great Apes ©)

Figure 7. Arcus Great Ape Health Center. (Center for Great Apes ©)

Figure 8. Great Ape Habitats. (Center for Great Apes ©)

Figure 9. Special Needs Habitat. (Center for Great Apes ©)

Figure 10. Night Houses. (Center for Great Apes ©)

Figure 11. The network of elevated tunnels/chute system (5,400-foot long; arches up to 25 feet tall) facilitates voluntary (chosen/intentional) movement over one mile throughout the property. (Center for Great Apes ©)

Figure 12. The experimenter’s procedural methods. (Study One, Non-Pointing Condition) (Photograph by Danay C. Downing)

Figure 13. The experimenter’s procedural methods. (Study One, Pointing Condition) (Photograph by Chris Godfrey)

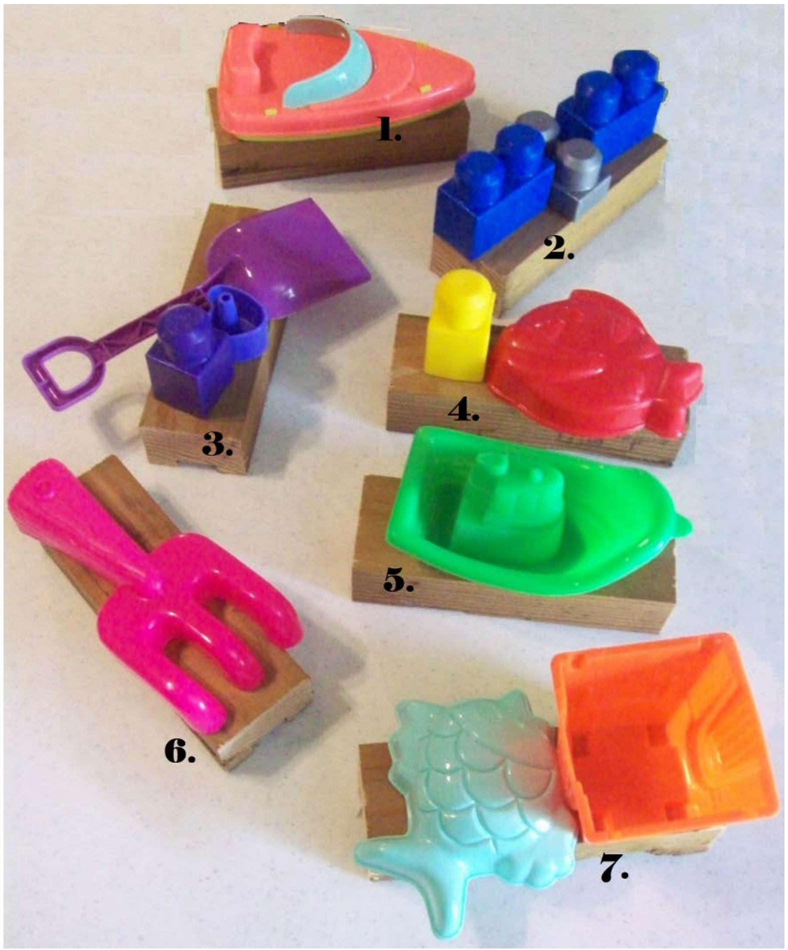

Figure 14. The visual stimuli used in the joint attention task. (Study 3, Trial 1) (Photograph by Danay C. Downing)

Figure 15. The visual stimuli used in the joint attention task.
(Study 3, Trial 2) (Photograph by Danay C. Downing)

Figure 16. The experimenter’s procedural methods. (Study Three, Example One) (Photograph by Danay C. Downing)

Figure 17. The experimenter's procedural methods. (Study Three, Example Two) (Photograph by Danay C. Downing)

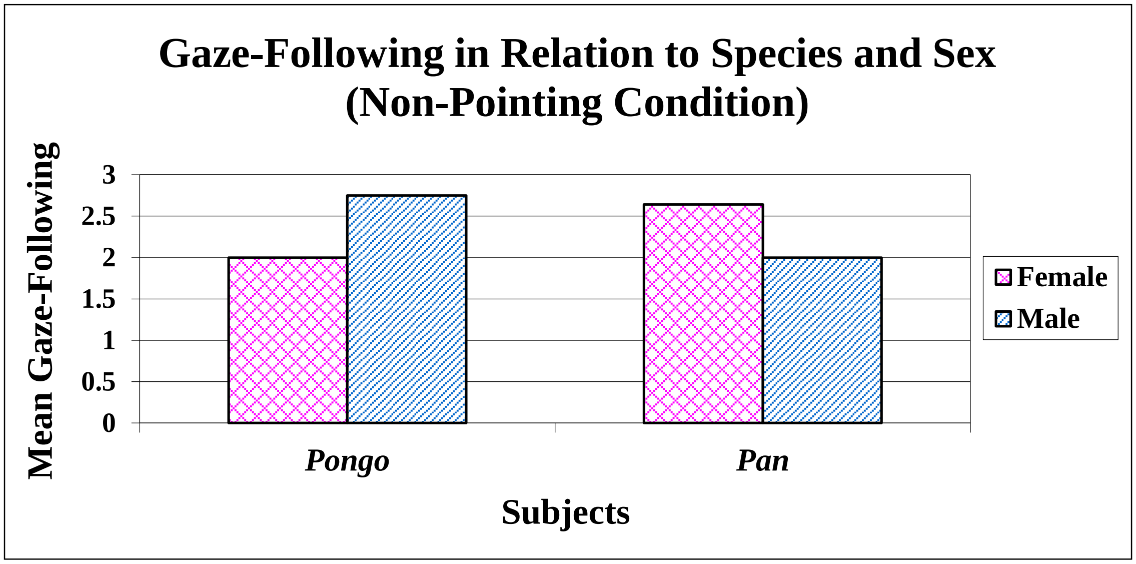

Figure 18. Gaze-following in relation to species and sex. (Study One – Gaze-Following, Non-Pointing Condition)

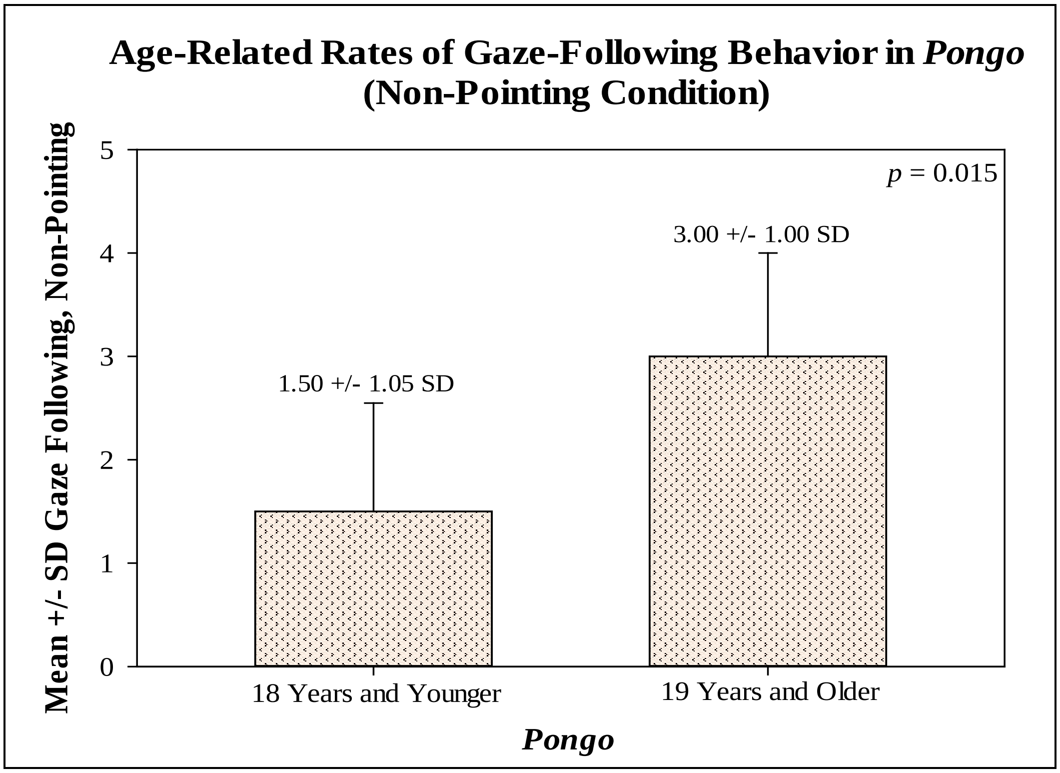

Figure 19. Gaze-following in relation to species and age. (Study One – Gaze-Following, Non-Pointing Condition)

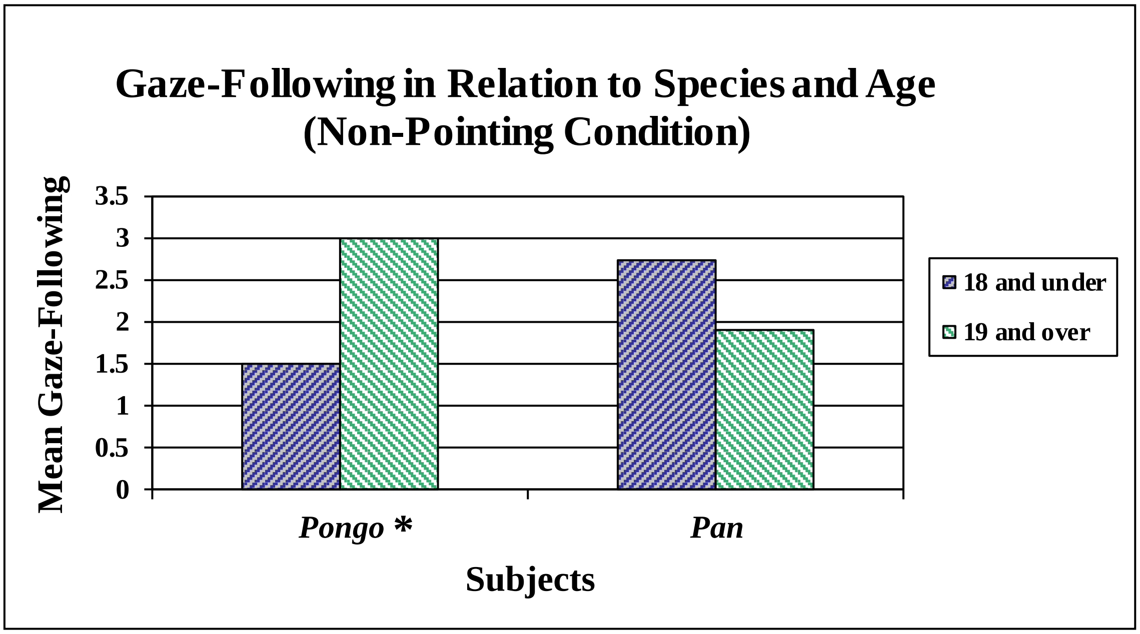

Figure 20. Age-related rates of gaze-following behavior in *Pongo*. (Study One – Gaze-Following, Non-Pointing Condition) (* $p = 0.015$)

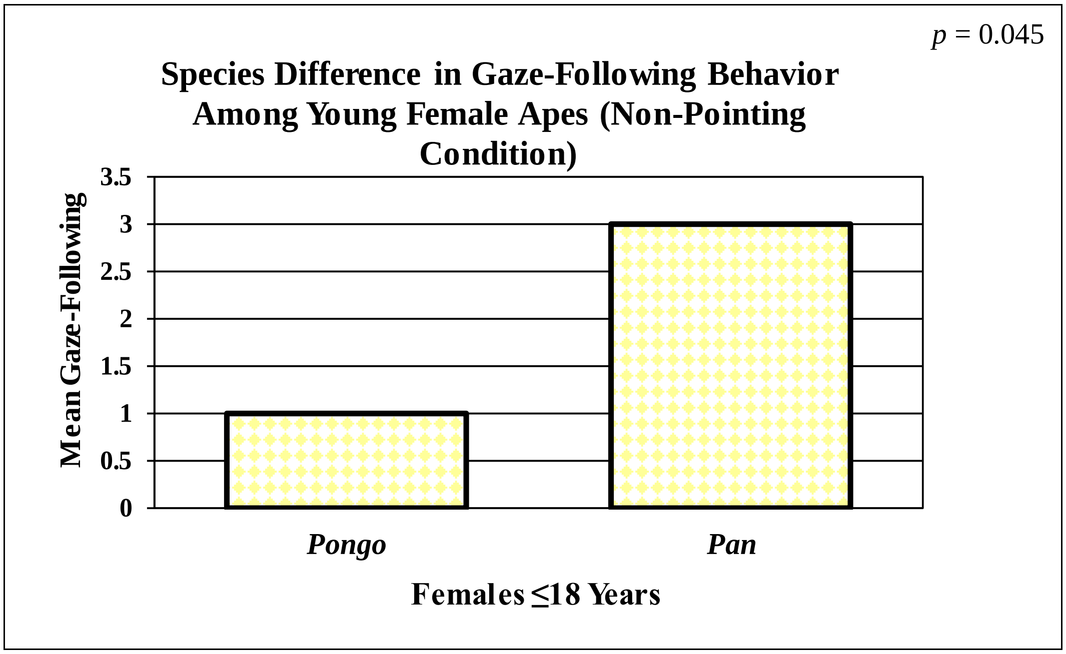

Figure 21. Species-related rates of gaze-following behavior among females under the age of 18. (Study One – Gaze-Following, Non-Pointing Condition)

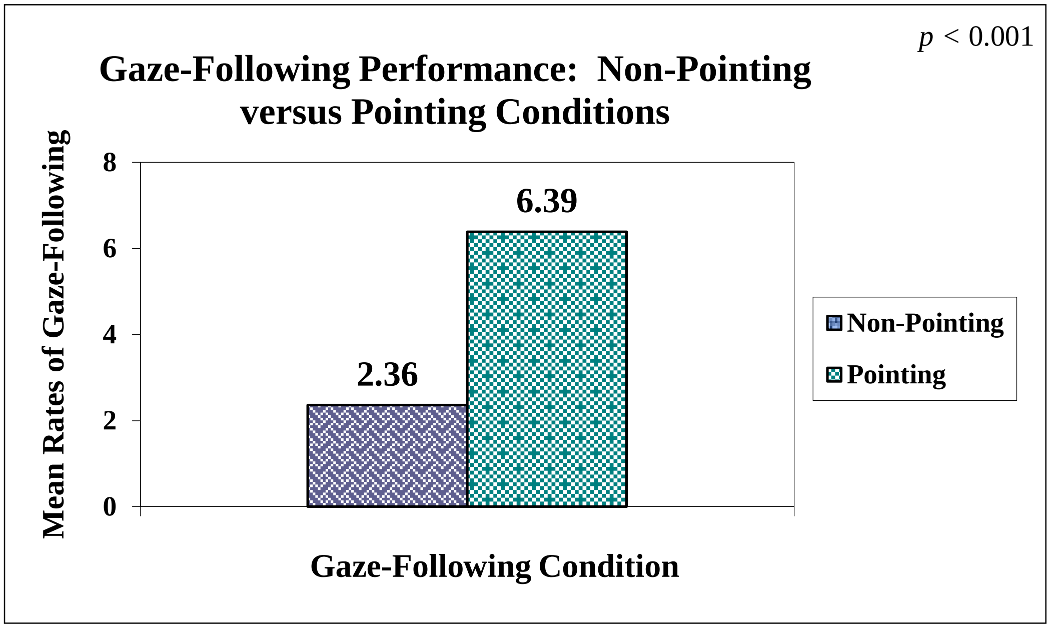

Figure 22. Gaze-Following: Non-Pointing vs. Pointing Condition (Study One)

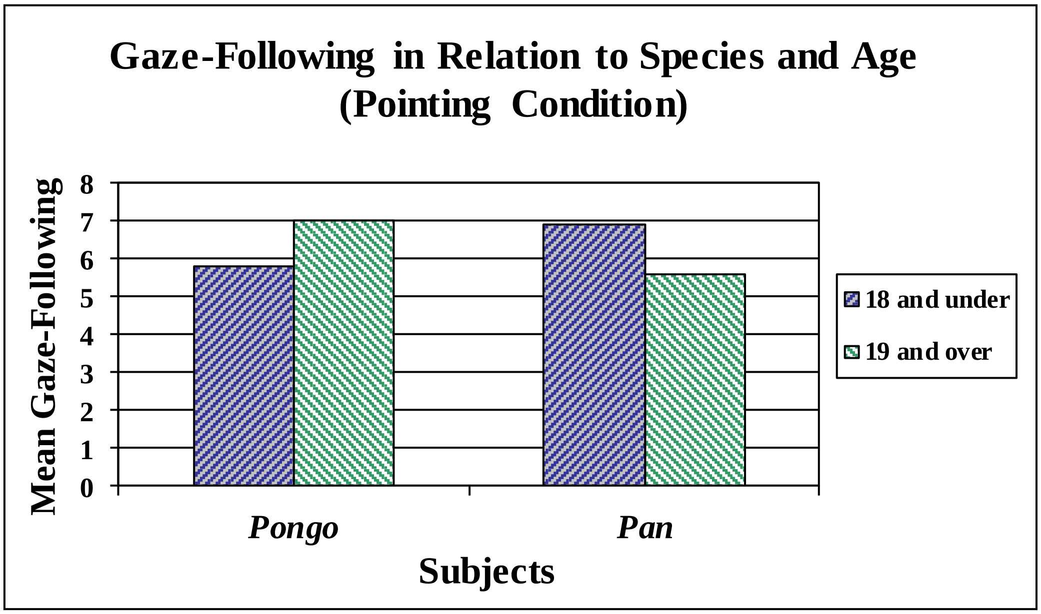

Figure 23. Gaze-following in relation to species and age. (Study One – Gaze-Following, Pointing Condition)

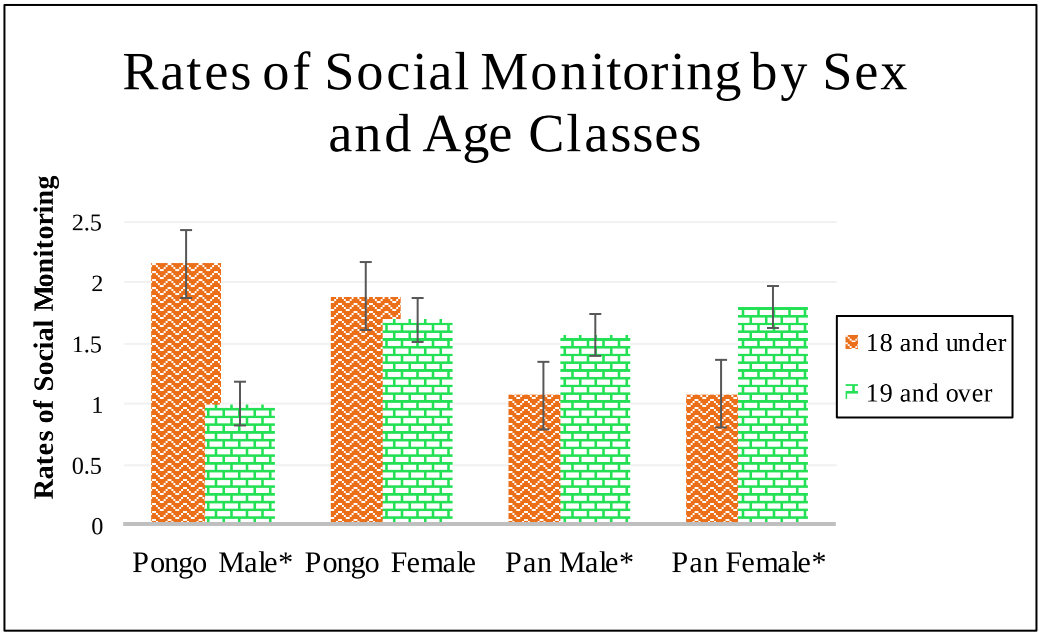

Figure 24. Rates of Social Monitoring by Species, Sex, and Age Class. (Study Two – Rates of Social Monitoring/Looking Behaviors: Glance, Gaze, and Stare) (* $p < 0.001$, $p = 0.007$, $p < 0.001$, respectively)

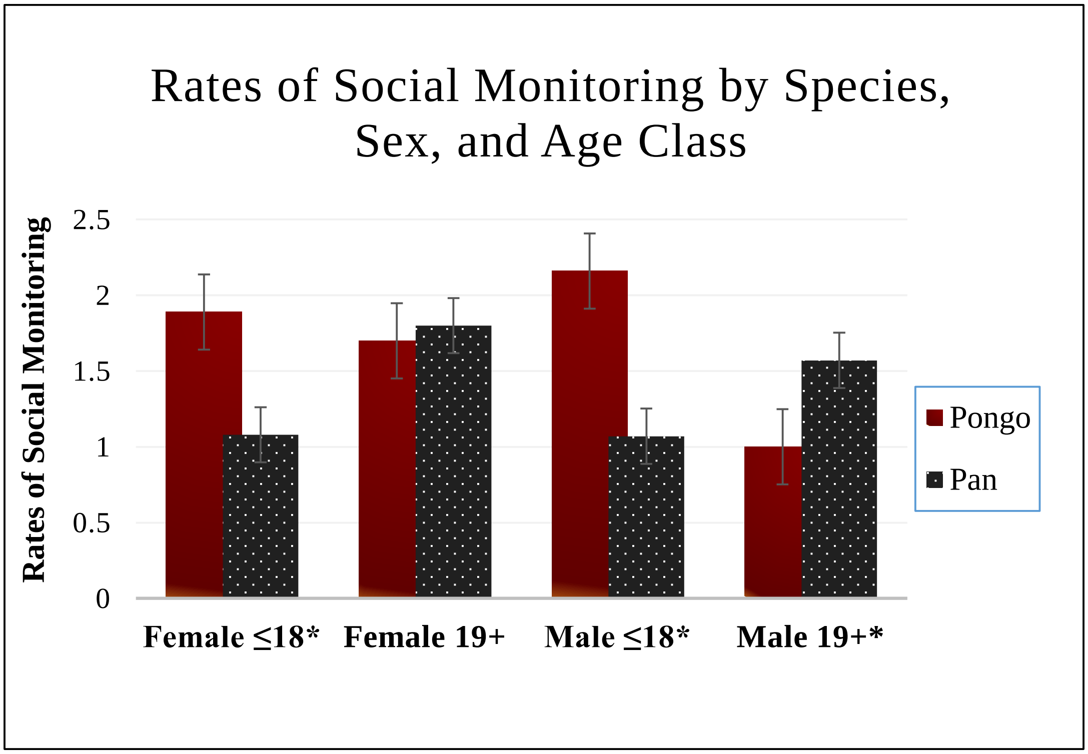

Figure 25. Rates of Social Monitoring by Species, Sex, and Age Class. (Study Two – Rates of Social Monitoring/Looking Behaviors: Glance, Gaze, and Stare) (* $p < 0.001$, $p < 0.001$, and $p = 0.009$, respectively)

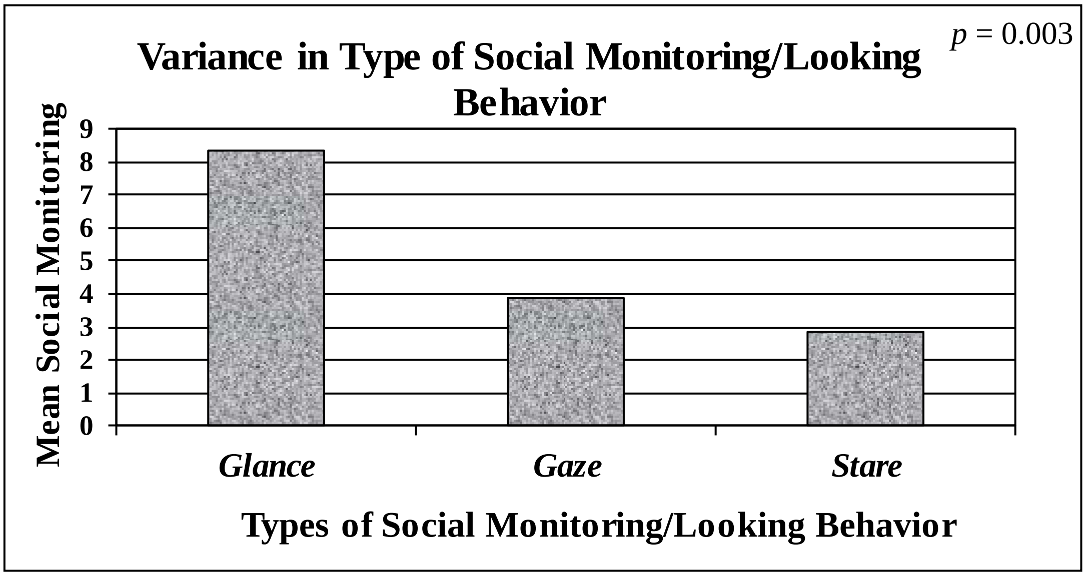

Figure 26. Social monitoring in relation to type of looking behavior. (Study Two)

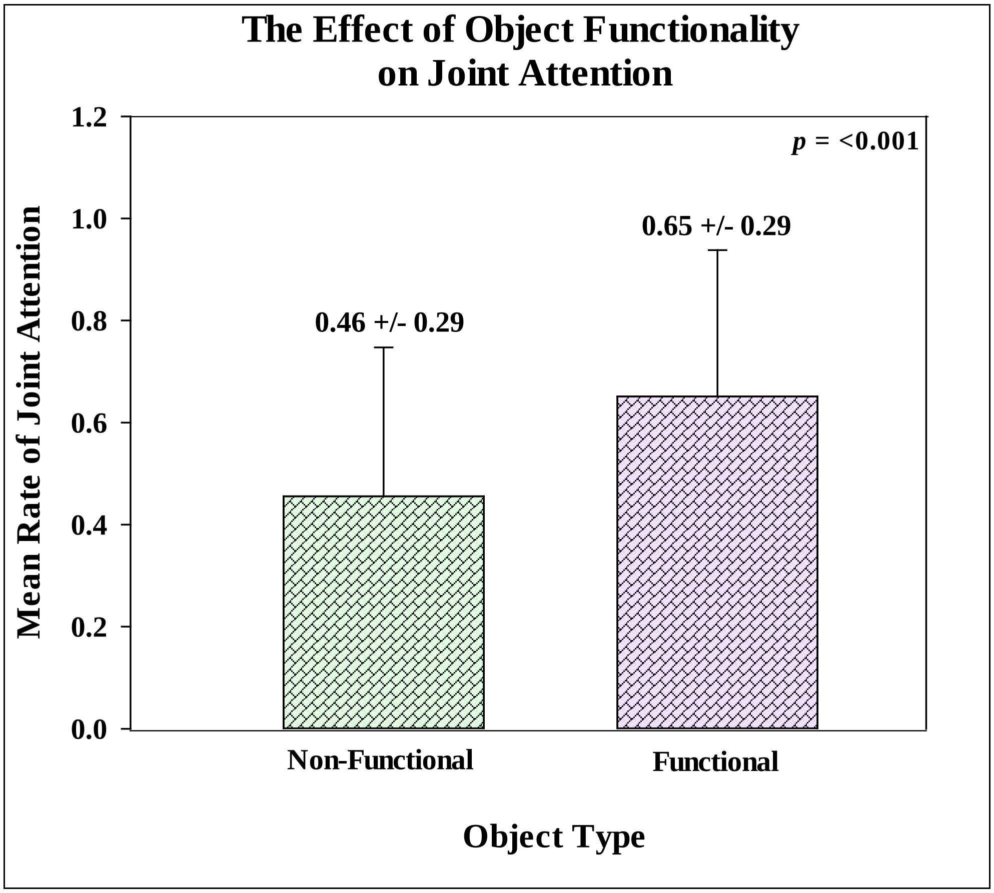

Figure 27. Joint Attention: Functional vs. Non-Functional Objects (Study Three – Both Species and Both Trials Combined)

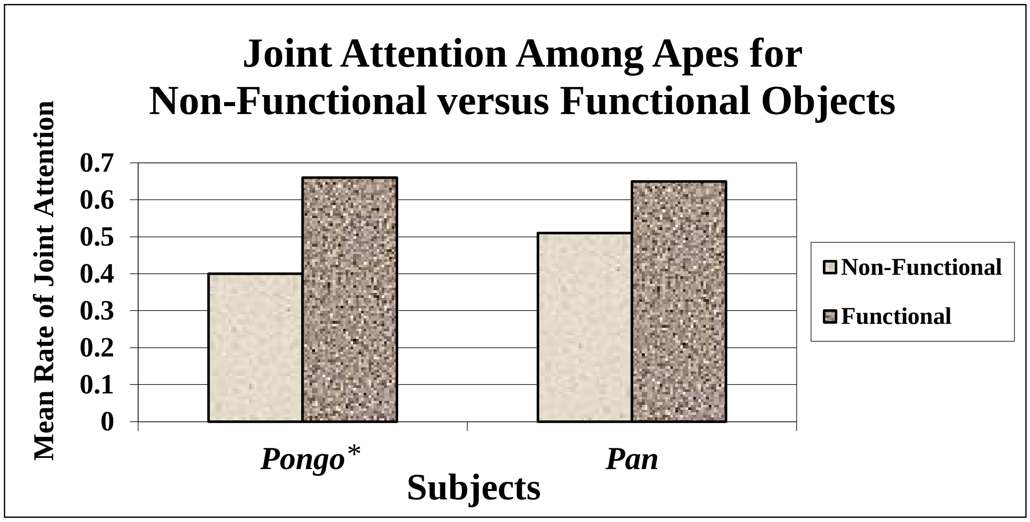

Figure 28. Joint attention in relation to object type. (Study Three – Joint Attention, Functional vs. Non-Functional Objects) (* $p = 0.001$)

Figure 29. Orangutan eye with a distinct white ring. (Photograph by Danay C. Downing)

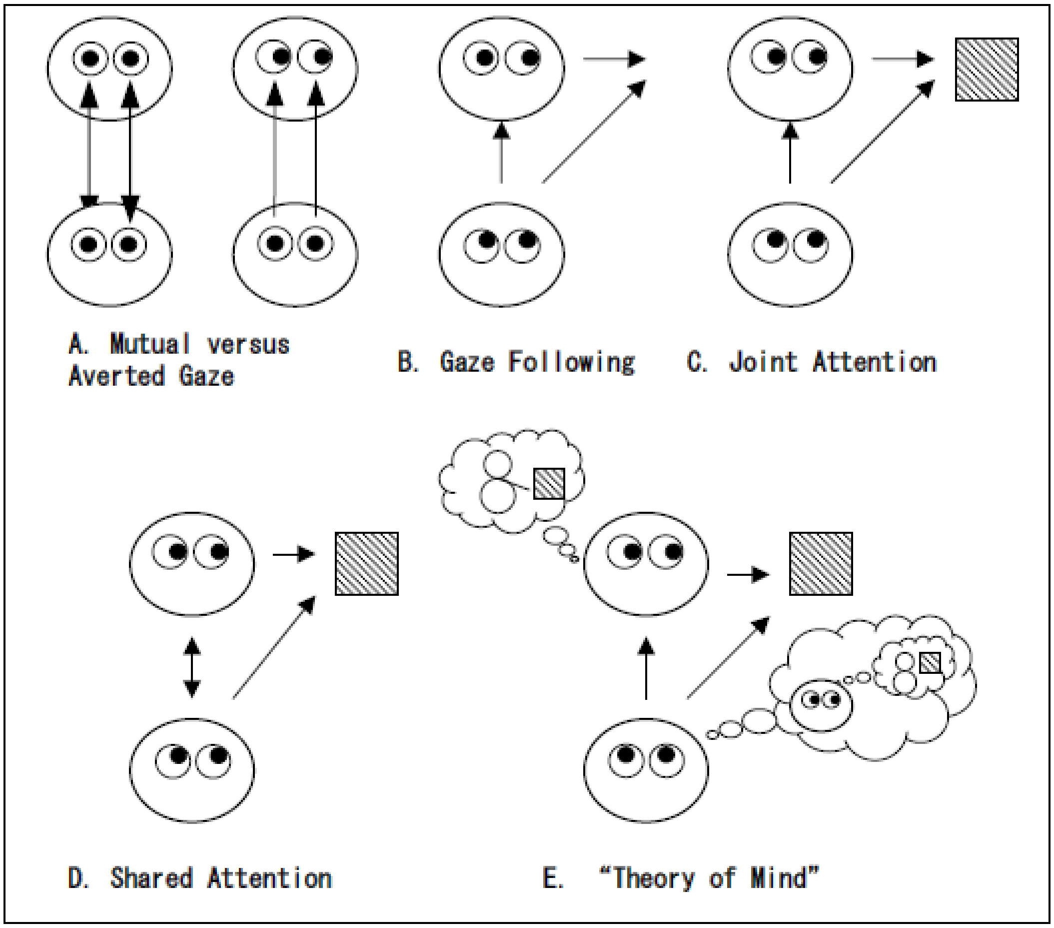

Figure 30. Schematic representation of each type of social gaze (From Emery, 2000 reviewed in Itakura, 2004).

APPENDIX B: TABLES

Table 1. Ethogram with designated descriptions of looking behavior.

Looking Behavior	**Defined Description (seconds)**
Gaze	3-10
Glance	Instantaneous
Stare	10 +

Table 2. Individuals of the population by species, name, age, and sex classes.

Species	**Subject**	**Age**	**Sex**
Pongo spp.	Allie	18	Female
Pongo spp.	BamBam	14	Male
Pongo spp.	Christopher	20	Male
*Pongo spp.**	Chuckie	28	Male
Pongo spp.	Geri	23	Female
Pongo spp.	Jam	12	Male
Pongo spp.	Kiki	27	Female
Pongo spp.	Linus	22	Male
Pongo spp.	Louie	17	Male
Pongo spp.	Mari	31	Female
Pongo spp.	Pebbles	12	Female
Pongo spp.	Pongo	22	Male
Pongo spp.	Popi	42	Female
*Pongo spp.**	Radcliffe	34	Male
Pongo spp.	Tango	18	Female
Pan troglodytes	Angel	16	Female
Pan troglodytes	Bella	15	Female
Pan troglodytes	Boma	27	Female
Pan troglodytes	Brooks	18	Male
Pan troglodytes	Bubbles	30	Male
Pan troglodytes	Butch	42	Male
Pan troglodytes	Casey	24	Female
Pan troglodytes	Chipper	39	Male
Pan troglodytes	Clyde	46	Male

Table 2 (continued)

Pan troglodytes	Daisy	32	Female
Pan troglodytes	Denyse	44	Female
Pan troglodytes	Ellie	16	Female
Pan troglodytes	Jacob	17	Male
Pan troglodytes	Jessie	25	Female
Pan troglodytes	Jonah	17	Male
Pan troglodytes	Katie	18	Female
Pan troglodytes	Kenya	20	Female
Pan troglodytes	Knuckles	13	Male
Pan troglodytes	Kodua	10	Female
Pan troglodytes	Maggie	19	Female
Pan troglodytes	Marco	53	Male
Pan troglodytes	Mickey	27	Male
Pan troglodytes	Mowgli	14	Male
Pan troglodytes	Murray	20	Male
Pan troglodytes	Natsu	14	Female
Pan troglodytes	Noelle	18	Female
Pan troglodytes	Oopsie	39	Female
Pan troglodytes	Ripley	23	Male
Pan troglodytes	Stryker	8	Male
Pan troglodytes	Toddy	39	Female

* Denotes hybrid (Bornean/Sumatran)

Table 3. Descriptions of behaviors observed during focal animal sampling.

Behavior	**Description of Behavioral Response**
Approach	individual approaches a conspecific within 1 meter
Avert Gaze	individual overtly looks away/avoids the gaze of a conspecific
Displace	individual moves out of the way of a more dominant individual
Display	individual hits, pushes, or throws an object in such a way as to make noise
Embrace	individuals hug each other
Fear Grimace	individual's face is frightened (erect hair, open mouth)
Groom	individual performs manual check of conspecific's hair, face, body, etc.
Play	playful interaction; rough and tumble
Turn Away	individual changes head/body orientation away from a conspecific
Vocal Response	individual vocalizes
Withdrawal	individual moves away

Table 4. Ethogram (behavioral checksheet used during focal animal sampling).

Focal/Actor				**Date**																	
Time	**Receiver**	**Visual Action (Gz, Gl, St)**		**No Response**	**Reciprocates Looking Behavior (Gz, Gl, St)**	**Averts Gaze**	**Gaze is Averted (by focal)**	**Turns Away**	**Approaches**	**Is Approached (by focal)**	**Withdraws**	**Displaces**	**Is Displaced (by focal)**	**Fear Grimace**	**Displays**	**Vocal Gesture**	**Embraces**	**Kisses / Is Kissed**	**Grooms Focal**	**Is Groomed (by focal)**	**Play**

Table 5. Ethogram (behavioral checksheet used during observations).

Type of Pointing Behavior*		**Subject**	**Subject**	**Subject**	**Subject**	**Subject**	**Subject**	**Subject**
Pt. Random								
Pt. Behind								
Up								
Left								
Right								
Pt. Up								
Pt. Left								
Pt. Right								
Up 2								
Left 2								
Right 2								
Pt. Up 2								
Pt. Left 2								
Pt. Right 2								

* Note: Non-Pointing unless otherwise indicated as Pointing condition by ‘Pt.’

Table 6. The subjects tested in Study One.

Orangutan Females	**Orangutan Males**	**Chimpanzee Females**	**Chimpanzee Males**
Allie	BamBam	Angel	Brooks
Geri	Christopher	Bella	Bubbles
Kiki	Chuckie	Boma	Chipper
Mari	Jam	Denyse	Clyde
Pebbles	Linus	Ellie	Jacob
Popi	Louie	Katie	Marco
Tango	Pongo	Kenya	Mowgli
	Radcliffe	Kodua	Murray
		Maggie	Ripley
		Natsu	Stryker
		Noelle	

Table 7. The subjects tested in Study Two.

Orangutan Females	**Orangutan Males**	**Chimpanzee Females**	**Chimpanzee Males**
Mari	BamBam	Ellie	Chipper
Pebbles	Jam	Kodua	Mowgli
Tango	Pongo	Natsu	Stryker
		Noelle	
		Oopsie	

Table 8. The subjects tested in Study Three.

Orangutan Females	**Orangutan Males**	**Chimpanzee Females**	**Chimpanzee Males**
Allie	BamBam	Angel	Brooks
Geri	Christopher	Bella	Bubbles
Kiki	Chuckie	Boma	Chipper
Mari	Jam	Denyse	Clyde
Pebbles	Linus	Ellie	Jacob
Popi	Louie	Katie	Marco
Tango	Pongo	Kenya	Mowgli
	Radcliffe	Kodua	Murray
		Maggie	Ripley
		Natsu	Stryker
		Noelle	

Table 9. Summary of descriptive statistics and analysis (*t*-test).
(Study One – Gaze-Following, Non-Pointing Condition)

	Variable	**Sample Size**	**Mean +/- SD**	***p*-value**
A.	**Species**			
	Pongo	15	2.40 +/- 1.24	
	Pan	21	2.33 +/- 1.28	0.934
B.	**Sex (Both Species)**			
	Females	18	2.39 +/- 1.29	
	Males	18	2.33 +/- 1.24	0.909
C.	***Pongo* (Within Species)**			
	Females	7	2.00 +/- 1.29	
	Males	8	2.75 +/- 1.17	0.258
D.	***Pan* (Within Species)**			
	Females	11	2.64 +/- 1.29	
	Males	10	2.00 +/- 1.25	0.265
E.	**Interspecific (Females)**			
	Pongo	7	2.00 +/- 1.29	
	Pan	11	2.64 +/- 1.29	0.322
F.	**Interspecific (Males)**			
	Pongo	8	2.75 +/- 1.17	
	Pan	10	2.00 +/- 1.25	0.210

Table 10. Summary of descriptive statistics and age analysis (*t*-test).
(Study One – Gaze-Following, Non-Pointing Condition)

	Variable	**Sample Size**	**Mean +/- SD**	***p*-value**
A.	**Age (All Subjects)**			
	All Apes ≤18	17	2.24 +/- 1.30	
	All Apes 19+	19	2.47 +/- 1.22	0.574
B.	**Age (*Pongo*)**			
	All *Pongo* ≤18	6	1.50 +/- 1.05	
	All *Pongo* 19+	9	3.00 +/- 1.00	***0.015***
C.	**Age (*Pan*)**			
	All *Pan* ≤18	11	2.73 +/- 1.19	
	All *Pan* 19+	10	1.90 +/- 1.29	0.142
D.	**Age Within Species/Same Sex**			
	Pongo Female ≤18	3	1.00 +/- 1.00	
	Pongo Female 19+	4	2.75 +/- 0.96	0.065*
	Pongo Male ≤18	3	2.00 +/- 1.00	
	Pongo Male 19+	5	3.20 +/- 1.10	0.174
	Pan Female ≤18	7	3.00 +/- 1.29	
	Pan Female 19+	4	2.00 +/- 1.16	0.233
	Pan Male ≤18	4	2.25 +/- 0.96	
	Pan Male 19+	6	1.83 +/- 1.47	0.634
E.	**Age Within Species/Between Sex**			
	Pongo Female ≤18	3	1.00 +/- 1.00	
	Pongo Male ≤18	3	2.00 +/- 1.00	0.288
	Pongo Female 19+	4	2.75 +/- 0.96	
	Pongo Male 19+	5	3.20 +/- 1.10	0.539

Table 10 (continued)

	Pan Female ≤18	7	3.00 +/- 1.29	
	Pan Male ≤18	4	2.25 +/- 0.96	0.341
	Pan Female 19+	4	2.00 +/- 1.16	
	Pan Male 19+	6	1.83 +/- 1.47	0.854
F.	**Age Between Species/Same Sex**			
	Pongo Female ≤18	3	1.00 +/- 1.00	
	Pan Female ≤18	7	3.00 +/- 1.29	***0.045***
	Pongo Female 19+	4	2.75 +/- 0.96	
	Pan Female 19+	4	2.00 +/- 1.16	0.356
	Pongo Male ≤18	3	2.00 +/- 1.00	
	Pan Male ≤18	4	2.25 +/- 0.96	0.751
	Pongo Male 19+	5	3.20 +/- 1.10	
	Pan Male 19+	6	1.83 +/- 1.47	0.121

Table 11. Summary of descriptive statistics and analysis (*t*-test).
(Study One – Gaze-Following, Non-Pointing vs. Pointing Conditions)

Variable	**Sample Size**	**Mean +/- SD**	***p*-value**
All Apes NP	36	2.36 +/- 1.25	
All Apes Pt.	36	6.39 +/- 1.54	***<0.001***
Pongo NP	15	2.40 +/- 1.24	
Pongo Pt.	15	6.53 +/- 1.51	***<0.001***
Pan NP	21	2.33 +/- 1.28	
Pan Pt.	21	6.29 +/- 1.59	***<0.001***
Pongo Female NP	7	2.00 +/- 1.29	
Pongo Female Pt.	7	6.00 +/- 1.73	***<0.001***
Pongo Male NP	8	2.75 +/- 1.17	
Pongo Male Pt.	8	7.00 +/- 1.20	***<0.001***
Pan Female NP	10	2.73 +/- 1.19	
Pan Female Pt.	10	6.55 +/- 1.29	***<0.001***
Pan Male NP	11	1.90 +/- 1.29	
Pan Male Pt.	11	6.00 +/- 1.89	***<0.001***
All Female NP	18	2.39 +/- 1.29	
All Female Pt.	18	6.33 +/- 1.46	***<0.001***
All Male NP	18	2.33 +/- 1.24	
All Male Pt.	18	6.44 +/- 1.65	***<0.001***
All Apes ≤18 NP	17	2.24 +/- 1.30	
All Apes ≤18 Pt.	17	6.53 +/- 1.28	***<0.001***
All Apes 18+ NP	19	2.47 +/- 1.22	

Table 11 (continued)

All Apes 19+ Pt.	19	6.26 +/- 1.76	***<0.001***
Pan Male ≤18 NP	4	2.25 +/- 0.96	
Pan Male ≤18 Pt.	4	7.25 +/- 5.00	***<0.001***
Pan Male 19+ NP	6	1.83 +/- 1.47	
Pan Male 19+ Pt.	6	5.17 +/- 2.04	***0.009***

Table 12. Summary of descriptive statistics and analysis (*t*-test).
(Study One – Gaze-Following, Pointing Condition performance)

	Variable	**Sample Size**	**Mean +/- SD**	***p*-value**
A.	**Species**			
	Pongo	15	6.53 +/- 1.51	
	Pan	21	6.29 +/- 1.59	0.656
B.	**Sex (Both Species)**			
	Females	18	6.33 +/- 1.46	
	Males	18	6.44 +/- 1.65	0.732
C.	***Pongo* (Within Species)**			
	Females	7	6.00 +/- 1.73	
	Males	8	7.00 +/- 1.20	0.211
D.	***Pan* (Within Species)**			
	Females	11	6.55 +/- 1.29	
	Males	10	6.00 +/- 1.89	0.588
E.	**Interspecific (Females)**			
	Pongo	7	6.00 +/- 1.73	
	Pan	11	6.55 +/- 1.29	0.455
F.	**Interspecific (Males)**			
	Pongo	8	7.00 +/- 1.20	
	Pan	10	6.00 +/- 1.89	0.251

Table 13. Summary of descriptive statistics and age analysis (*t*-test).
(Study One – Gaze-Following, Pointing Condition performance with regards to age)

	Variable	**Sample Size**	**Mean +/- SD**	***p*-value**
A.	**Age (All Subjects)**			
	All Apes ≤18	17	6.53 +/- 1.28	
	All Apes 19+	19	6.26 +/- 1.76	0.819
B.	**Age (*Pongo*)**			
	All *Pongo* ≤18	6	5.83 +/- 1.33	
	All *Pongo* 19+	9	7.00 +/- 1.50	0.147
C.	**Age (*Pan*)**			
	All *Pan* ≤18	11	6.91 +/- 1.14	
	All *Pan* 19+	10	5.60 +/- 1.78	0.056*
D.	**Age Within Species/Same Sex**			
	Pongo Female ≤18	3	5.00 +/- 1.00	
	Pongo Female 19+	4	6.75 +/- 1.89	0.211
	Pongo Male ≤18	3	6.67 +/- 1.16	
	Pongo Male 19+	5	7.20 +/- 1.30	0.582
	Pan Female ≤18	7	6.71 +/- 1.38	
	Pan Female 19+	4	6.25 +/- 1.26	0.594
	Pan Male ≤18	4	7.25 +/- 5.00	
	Pan Male 19+	6	5.17 +/- 2.04	0.085
E.	**Age Within Species/Between Sex**			
	Pongo Female ≤18	3	5.00 +/- 1.00	
	Pongo Male ≤18	3	6.67 +/- 1.16	0.132
	Pongo Female 19+	4	6.75 +/- 1.89	
	Pongo Male 19+	5	7.20 +/- 1.30	0.730

Table 13 (continued)

	Pan Female ≤18	7	6.71 +/- 1.38	
	Pan Male ≤18	4	7.25 +/- 5.00	0.788
	Pan Female 19+	4	6.25 +/- 1.26	
	Pan Male 19+	6	5.17 +/- 2.04	0.375
F.	**Age Between Species/Same Sex**			
	Pongo Female ≤18	3	5.00 +/- 1.00	
	Pan Female ≤18	7	6.71 +/- 1.38	0.091
	Pongo Female 19+	4	6.75 +/- 1.89	
	Pan Female 19+	4	6.25 +/- 1.26	0.675
	Pongo Male ≤18	3	6.67 +/- 1.16	
	Pan Male ≤18	4	7.25 +/- 0.50	0.398
	Pongo Male 19+	5	7.20 +/- 1.30	
	Pan Male 19+	6	5.17 +/- 2.04	0.088

Table 14. Raw data-count of social monitoring/looking behavior samples: glance (GL), gaze (GZ), and stare (ST). (Study Two)

Orangutans	**Chimpanzees**
GL – 58	GL – 70
GZ – 30	GZ – 24
ST – 18	ST – 11
Males – 42	Males – 55
Females – 64	Females – 50
18 & Under – 52	18 & Under – 81
19 + – 54	19 + – 24

Table 15. Summary of descriptive statistics and analysis (*t*-test).
(Study Two – Rates of Social Monitoring/Looking Behaviors: Glance, Gaze, and Stare)

	Variable	**Sample Size**	**Mean +/- SD**	***p*-value**
A.	**Species**			
	All *Pongo*	106	1.62 +/- 0.76	
	All *Pan*	105	1.44 +/- 0.68	0.064*
B.	**Sex (Within Species)**			
	Pongo Female	64	1.78 +/- 0.81	
	Pongo Male	42	1.38 +/- 0.62	***0.009***
	Pan Female	50	1.34 +/- 0.66	
	Pan Male	55	1.53 +/- 0.69	0.085
C.	**Sex (Between Species)**			
	Pongo Female	64	1.78 +/- 0.81	
	Pan Female	50	1.34 +/- 0.66	***0.001***
	Pongo Male	42	1.38 +/- 0.62	
	Pan Male	55	1.53 +/- 0.69	0.269
D.	**Age (All Subjects)**			
	All Apes ≤18	133	1.48 +/- 0.70	
	All Apes 19+	78	1.62 +/- 0.76	0.191
E.	**Age (Within Species)**			
	Pongo ≤18	52	1.56 +/- 0.75	
	Pongo 19+	54	1.69 +/- 0.77	0.355
	Pan ≤18	81	1.43 +/- 0.67	
	Pan 19+	24	1.46 +/- 0.72	0.941
F.	**Age (Between Species)**			
	Pongo ≤18	52	1.56 +/- 0.75	
	Pan ≤18	81	1.43 +/- 0.67	0.351

Table 15 (continued)

	Pongo 19+	54	1.69 +/- 0.77	
	Pan 19+	24	1.46 +/- 0.72	0.197
G.	**Age Within Species/Same Sex**			
	Pongo Female ≤18	27	1.89 +/- 0.80	
	Pongo Female 19+	37	1.70 +/- 0.81	0.334
	Pongo Male ≤18	25	2.16 +/- 0.69	
	Pongo Male 19+	17	1.00 +/- 0.00	***<0.001***
	Pan Female ≤18	40	1.08 +/- 0.27	
	Pan Female 19+	10	1.80 +/- 0.92	***<0.001***
	Pan Male ≤18	41	1.07 +/- 0.26	
	Pan Male 19+	14	1.57 +/- 0.85	***0.007***
H.	**Age Within Species/Between Sex**			
	Pongo Female ≤18	27	1.89 +/- 0.80	
	Pongo Male ≤18	25	2.16 +/- 0.69	0.202
	Pongo Female 19+	37	1.70 +/- 0.81	
	Pongo Male 19+	17	1.00 +/- 0.00	***<0.001***
	Pan Female ≤18	40	1.08 +/- 0.27	
	Pan Male ≤18	41	1.07 +/- 0.26	0.983
	Pan Female 19+	10	1.80 +/- 0.92	
	Pan Male 19+	14	1.57 +/- 0.85	0.529
I.	**Age Between Species/Same Sex**			
	Pongo Female ≤18	27	1.89 +/- 0.80	
	Pan Female ≤18	40	1.08 +/- 0.27	***<0.001***

Table 15 (continued)

	Pongo Female 19+	37	1.70 +/- 0.81	
	Pan Female 19+	10	1.80 +/- 0.92	0.798
	Pongo Male ≤18	25	2.16 +/- 0.69	
	Pan Male ≤18	41	1.07 +/- 0.26	***<0.001***
	Pongo Male 19+	17	1.00 +/- 0.00	
	Pan Male 19+	14	1.57 +/- 0.85	***0.009***

Table 16. Analysis of variation in gaze-following behaviors (One-Way ANOVA). (Study Two – Rates of Social Monitoring/Looking Behaviors: Glance, Gaze, and Stare)

Social Monitoring/Looking Behavior	**Mean +/- SD**	**Sample Size**	***p*-value**
Glance	8.36 +/- 5.05	14	
Gaze	3.86 +/- 3.72	14	
Stare	2.86 +/- 3.51	14	***0.003***

Table 17. Mean totals of looking behaviors (number of combined occurrences per individual, by age class) (Study Two – Social Monitoring/Looking Behaviors: Glance, Gaze, and Stare)

Social Monitoring/Looking Behavior	**≤18 years**	**19+ years**
Glance	9.1	6.5
Gaze	3.6	4.5
Stare	2.3	4.25

Table 18. Summary of descriptive statistics and analysis (*t*-test).
(Study Two – Glance Rates in relation to species, sex, and age)

Glance Rates	**Sample Size**	**Mean +/- SD**	***p*-value**
Orangutans	21	2.76 +/- 1.73	
Chimpanzees	26	2.69 +/- 2.49	0.458
Females (Both Species)	24	2.79 +/- 2.36	
Males (Both Species)	23	2.65 +/- 1.99	0.974
Orangutan Females	10	2.90 +/- 2.03	
Orangutan Males	11	2.64 +/- 1.50	0.737
Chimpanzee Females	14	2.00 +/- 1.00	
Chimpanzee Males	12	1.50 +/- 1.00	1.000
≤18 years old (Both Species)	31	2.94 +/- 2.25	
19+ years old (Both Species)	16	2.31 +/- 1.99	0.325

Table 19. Summary of descriptive statistics and analysis (*t*-test).
(Study Three – Joint Attention performance with a human social partner, Functional vs. Non-Functional Objects)

	Variable	**Sample Size**	**Mean +/- SD**	***p*-value**
A.	**Total Objects (By Trial)**			
	Total Objects Orangutan T1	15	0.53 +/- 0.25	
	Total Objects Orangutan T2	15	0.49 +/- 0.26	0.652
	Total Objects Chimpanzee T1	16	0.54 +/- 0.19	
	Total Objects Chimpanzee T2	16	0.59 +/- 0.27	0.588
	Total Objects All Species T1	31	0.54 +/- 0.22	
	Total Objects All Species T2	31	0.54 +/- 0.27	0.931
B.	**Total Objects (By Species)**			

Table 19 (continued)

	Total Objects Orangutan T1	15	0.53 +/- 0.25	
	Total Objects Chimpanzee T1	16	0.54 +/- 0.19	0.901
	Total Objects Orangutan T2	15	0.46 +/- 0.26	
	Total Objects Chimpanzee T2	16	0.59 +/- 0.27	0.178
	Total Objects Orangutan Both Trials	15	0.51 +/- 0.25	
	Total Objects Chimpanzee Both Trials	16	0.57 +/- 0.23	0.335
C.	**Functional Objects (By Trial)**			
	Functional Obj. Orangutan T1	15	0.67 +/- 0.31	
	Functional Obj. Orangutan T2	15	0.65 +/- 0.27	0.742
	Functional Obj. Chimpanzee T1	16	0.58 +/- 0.26	
	Functional Obj. Chimpanzee T2	16	0.71 +/- 0.32	0.179
	Functional Obj. All Species T1	31	0.63 +/- 0.28	
	Functional Obj. All Species T2	31	0.68 +/- 0.29	0.473
D.	**Functional Objects (By Sex)**			
	Functional Objects Orangutan Female	14	0.76 +/- 0.20	
	Functional Objects Orangutan Male	16	0.56 +/- 0.32	0.064*
	Functional Objects Chimpanzee Female	16	0.73 +/- 0.22	
	Functional Objects Chimpanzee Male	16	0.56 +/- 0.34	0.106
	Functional Orangutan Female	14	0.76 +/- 0.20	
	Functional Chimpanzee Female	16	0.73 +/- 0.22	0.707
	Functional Orangutan Male	16	0.56 +/- 0.32	
	Functional Chimpanzee Male	16	0.56 +/- 0.34	0.968
	Functional All Female	30	0.75 +/- 0.21	
	Functional All Male	32	0.56 +/- 0.32	***0.018***

Table 19 (continued)

E.	**Functional Obj. Between Species (By Trial)**			
	Orangutan T1 Functional	15	0.67 +/- 0.31	
	Chimpanzee T1 Functional	16	0.58 +/- 0.26	0.372
	Orangutan T2 Functional	15	0.65 +/- 0.27	
	Chimpanzee T2 Functional	16	0.71 +/- 0.32	0.452
F.	**Non-Funct. Obj. Between Species (By Trial)**			
	Orangutan T1 Non-Functional	15	0.43 +/- 0.29	
	Chimpanzee T1 Non-Functional	16	0.52 +/- 0.27	0.417
	Orangutan T2 Non-Functional	15	0.37 +/- 0.30	
	Chimpanzees T2 Non-Functional	16	0.50 +/- 0.32	0.206
G.	**Funct. vs. Non-Funct. By Trial (Within Sp.)**			
	Orangutan T1 Non-Functional	15	0.43 +/- 0.29	
	Orangutan T1 Functional	15	0.67 +/- 0.31	***0.042***
	Orangutan T2 Non-Functional	15	0.37 +/- 0.30	
	Orangutan T2 Functional	15	0.65 +/- 0.27	***0.015***
	Chimpanzee T1 Non-Functional	16	0.52 +/- 0.27	
	Chimpanzee T1 Functional	16	0.58 +/- 0.26	0.465
	Chimpanzee T2 Non-Functional	16	0.50 +/- 0.32	
	Chimpanzee T2 Functional	16	0.71 +/- 0.32	0.084*
H.	**Funct. vs. Non-Funct. All Trials (Within Sp.)**			
	All Orangutan Non-Functional	30	0.40 +/- 0.29	
	All Orangutan Functional	30	0.66 +/- 0.29	***0.001***
	All Chimpanzee Non-Functional	32	0.51 +/- 0.29	
	All Chimpanzee Functional	32	0.65 +/- 0.29	0.094

Table 19 (continued)

I.	**Funct. vs. Non-Funct. All Trials (Between Sp.)**			
	All Orangutan Non-Functional	30	0.40 +/- 0.29	
	All Chimpanzee Non-Functional	32	0.51 +/- 0.29	0.147
	All Orangutan Functional	30	0.66 +/- 0.29	
	All Chimpanzee Functional	32	0.65 +/- 0.29	0.952
	Both Species All Trials Non-Funct. Objects	62	0.46 +/- 0.29	
	Both Species All Trials Functional Objects	62	0.65 +/- 0.29	***<0.001***

VITA

Danay C. Downing was born and raised in Hickory, NC. She joined the military at age 17 and served as a linguist and intelligence analyst for the U.S. Army for five years. After being honorably discharged, and as a first-generation university student, she moved to Charlotte, NC to pursue a higher education. A graduate of the University of North Carolina at Charlotte, she holds a Bachelor of Arts Degree in Biology and a Bachelor of Science Degree in Psychology, both with a special emphasis on animal behavior and physiology.

In 2011, Danay joined the first cohort of graduate-level students in the Department of Anthropology at the University of North Carolina at Charlotte where she completed a Master of Arts Degree in Anthropology and a Graduate Certificate in Cognitive Science from the Department of Psychology. A multi-disciplinary scientist, her research interests are in comparative cognition, with special interests in language, intelligence, learning, culture, social behavior, and enrichment, with a particular focus on primates and marine mammals.

Danay's first academic publication was as an undergraduate in 2009. "The Great Ape Cognitive Mind: A Fundamental Evaluation of the Evidence" was published in the Undergraduate Journal of Psychology (22: 27-34) at the University of North Carolina at Charlotte.

Her subsequent publications include:

- The Effect of the Bushmeat Trade on African Ape Populations: Critical Evaluation of the Evidence and Potential Solutions (2011). *CJA AnthroJournal – The Collegiate Journal of Anthropology Vol. 1 Premier:* Viewpoints.
- Species and Habitat Variation in Activity Profiles among White-Faced Capuchin (*Cebus capucinus*) and Black-Mantled Howler (*Alouatta palliata*) Monkeys in Costa Rica and Nicaragua (2013). *CJA AnthroJournal – The Collegiate Journal of Anthropology Vol. 1 Premier:* Cover Stories, General Anthropology.

Danay's university-level teaching experience includes two years as the instructor for the Biological Anthropology undergraduate laboratories. Professional affiliations include: Animal Behavior Society, Center for Great Apes, Dolphin Research Center, Omicron Delta Kappa National Leadership Honor Society, Psi Chi – The National Honor Society in Psychology, and The Honor Society of Phi Kappa Phi.