Effects of early care on joint attention and social behavior in Pan, Gorilla & Pongo

Caisie Anne Pitman
Iowa State University

Follow this and additional works at: http://lib.dr.iastate.edu/rtd
Part of the Anthropology Commons, and the Cognitive Psychology Commons

Recommended Citation
http://lib.dr.iastate.edu/rtd/14660

This Thesis is brought to you for free and open access by Iowa State University Digital Repository. It has been accepted for inclusion in Retrospective Theses and Dissertations by an authorized administrator of Iowa State University Digital Repository. For more information, please contact digirep@iastate.edu.
Effects of early care on joint attention and social behavior in *Pan, Gorilla & Pongo*

by

Caisie Anne Pitman

A thesis submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

MASTER OF ARTS

Major: Anthropology

Program of Study Committee:
Jill Pruetz, Major Professor
Nancy Coimman
Mack Shelley
Robert Shumaker

Iowa State University
Ames, Iowa
2007

Copyright © Caisie Anne Pitman, 2007. All rights reserved.
TABLE OF CONTENTS

LIST OF FIGURES iii

LIST OF TABLES iv

ABSTRACT v

CHAPTER 1. INTRODUCTION 1
 Research Question and Hypotheses 1
 Attachment Theory: An Overview 2
 Attachment & Responsive Care: Impact on Cognition and Social Behavior 11
 Social Cognition and Joint Attention: An Overview 21
 Joint Attention in Nonhuman Primates 24

CHAPTER 2. METHODS 33
 Participants 33
 Experimental Procedure 38
 Condition 1: Following the Gaze of a Human Social Partner 38
 Condition 2: Following the Gaze of a Conspecific Social Partner 39
 Condition 3: Joint Attention with a Human Social Partner 41
 Condition 4: Joint Attention with a Human Social Partner 42
 Observational Procedure 43

CHAPTER 3: RESULTS 46

CHAPTER 4: DISCUSSION 63
 Summary and Conclusions 76
 Directions for Future Research 78

BIBLIOGRAPHY 80

APPENDIX A: BIOGRAPHICAL PROFILE TEMPLATE 96

APPENDIX B: SOCIAL BEHAVIOR CATALOG 99

ACKNOWLEDGMENTS 101
LIST OF FIGURES

Figure 1. Mean proportion of responses in experimental and control trials 55
Figure 2. Mean proportion of care group responses within each gaze task 56
Figure 3. Mean proportion of care group responses in GFH vs. GFC tasks 56
Figure 4. Mean proportion of species responses within each gaze task 57
Figure 5. Mean proportion of species responses in gaze task with humans 57
Figure 6. Mean proportion of species responses in GFH vs. GFC 58
Figure 7. Mean proportion of care group responses within each joint attention task 59
Figure 8. Mean proportion of care group responses in JAH vs. JAC tasks 59
Figure 9. Mean proportion of species responses within each joint attention task 60
Figure 10. Mean proportion of species responses in JAH vs. JAC tasks 60
Figure 11. Count of agonistic behavior based on species 61
Figure 12. Mean frequency of affiliative behavior to conspecifics based on care group 61
Figure 13. Mean frequency of affiliative behavior to participants based on care group 62
Figure 14. Mean duration of time engaged in solitary behavior 62
LIST OF TABLES

Table 1. An overview of studies investigating joint attention behaviors in great apes 32
Table 2. Care style, caregiver, species, age, and sex of participants 37
ABSTRACT

The ability to share attention with another individual is the foundation upon which more cognitively complex capacities, such as perspective taking, attribution of intention, and deception, develop in humans (Carpenter, Nagell, & Tomasello, 1998; Charman et al., 2000; Tomasello, 1995a). Joint attention, the ability to coordinate attention with another individual around an object or event, emerges during early infancy (Carpenter et al., 1998). Studies with human infants suggest that the quality of care received during the first six months of life is related to increased production of joint attention behaviors during early infancy (Hobson, Patrick, Crandell, Perez, Lee, 2004; Morales, Mundy, Crowson, Neal, Delgado, 2005) and social skill proficiency during childhood and adolescence (Laible, 2007; Pastor, 1981; Sroufe, Bennett, Englund, Urban, & Shulman, 1993). These phenomena have not been thoroughly investigated in nonhuman great apes despite the close genetic relationship among members of the Hominidae family (Gagneux & Varki, 2001; Groves, 2001).

The purpose of the current study is to assess the effects of care style during the first six months of life provided by either a great ape mother or human(s) on joint attention skills and social behavior in great apes—chimpanzees, bonobos, gorillas, and orangutans. This study provides experimental evidence that great apes engage in joint attention behaviors with both conspecifics and humans, and they do so in ways that suggest they possess an understanding of others as intentional agents (Tomasello, 1995a). The ability of great apes to engage in joint attention behaviors with conspecifics and humans was not affected by differences in style of care provided by either great ape mothers or humans during apes’ first six months of life. This result suggests that joint attention is a durable cognitive process that is impervious to insufficiently distinct differences in care during the first six months of life.
Finally, the results of the social behavior observations indicate that care style during the first six months and the type of individual who provided care affected the frequency and duration of some, but not all, behaviors in great apes.
CHAPTER 1: INTRODUCTION

The study of social cognition in nonhuman primates is an important vehicle through which hominid\(^1\) evolution may be explored (Byrne & Bates, 2007; Russon, 2004). Extant primates, especially great apes, can serve as referential models that provide a means through which hypothesis testing regarding hominid cognitive evolution may be tested through direct behavioral observation (McGrew, 1992). The aim of this study is to investigate the effects of early care on the joint attention skills and social behavior of great apes: chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla gorilla*), and orangutans (*Pongo spp.*). This topic is significant because there is a relatively small body of knowledge on the impact of early care on great ape socio-cognition, the majority of which has focused on chimpanzees, humans' closest living relative along with bonobos. The presence or absence of specific socio-cognitive capacities in great apes, especially humans' most distant great ape relative the orangutan, can help determine the timing of the evolutionary emergence of those capacities.

Research Question and Hypotheses

The purpose of this study is to investigate the effects of care style received during the first six months of life on the joint attention skills and social behavior of great apes. Great ape joint attention skills will be assessed with both conspecific and human social partners. In addition, any effects of the type of caregiver, great ape mothers or humans, on joint attention and social behavior is considered because great apes sometimes require human care as a result of maternal neglect or illness. This study is justified because there have been no

\(^{\text{1}}\) The term hominid includes extant and extinct bipedal apes (Wolpoff, 1999).
investigations on the impact of both care style and caregiver type on joint attention skills and social behavior in all four types of great ape.

The first null hypothesis is that there will be no differences in the ability of great apes to produce joint attention behaviors in experimental conditions compared to control conditions. Second, there will be no differences in the production of joint attention behavior with conspecifics and humans based on the care style participants received from either great ape mothers or humans during the first six months of life. Finally, there will be no differences in the frequency of social behavior and the duration of time spent engaged in solitary behavior in great apes based on the care style participants received from either great ape mothers or humans during the first six months of life.

Attachment Theory: An Overview

One of the most prolific theoretical frameworks through which primate infant development has been examined in the last three decades is attachment theory (Bowlby, 1969; Cassidy & Shaver, 1999). Harlow and colleagues' experiments with rhesus macaques (Macaca mulatta) remains one of the most influential bodies of work on the effects of caregiver-infant relations on the behavior and cognition of nonhuman primates (Harlow, 1958, 1960; Harlow & Harlow, 1966; Harlow & Zimmerman, 1959; Novak & Sackett, 2006). Prior to this seminal body of work, the origin and development of the human caregiver-infant relationship were viewed in terms of basic or primary drives such as hunger, thirst, pain, and other feelings of discomfort. This theoretical approach posited that an infant learned to associate the physical comfort provided by its mother with a reduction of these primary drives. The mother served as the active agent, while the infant simply reacted to the
mother as a stimulus. In essence, this approach suggested that these early learned associations provided the motive for human social behavior (Ainsworth, 1969). Harlow (1958) tested this theoretical approach after he observed distressed behavior by maternally deprived infant rhesus macaques when cloth blankets in their cage were removed for cleaning. Harlow gave the infants the opportunity to nurse from a “wire mother” through a feeding tube or access to a “cloth mother” with no feeding tube. He found that the infants preferentially chose the cloth mother over the wire mother indicating that the need for contact comfort exceeded the basic or primary drive for food.

Harlow’s (1958) cloth mother experiment was followed by a series of studies focusing on the effects of total social and sensory deprivation on nonhuman primate infants. The subjects in these studies, predominantly rhesus macaques and chimpanzees, demonstrated a large array of abnormal behaviors, including deficits in sexual, reproductive, and maternal competence, substandard motor and cognitive skills, and stereotypical behaviors (Davenport & Menzel, 1963; Davenport & Rogers, 1968; Harlow, 1960; Menzel, 1963, 1964; Menzel, Davenport & Rogers, 1961, 1970; Rogers & Davenport 1969; Seay, Hansen, & Harlow, 1962; Novak & Sackett, 2006). In follow up studies with rhesus macaques, the types and levels of social interaction experienced by infants were manipulated to assess effects on social behaviors. For example, macaque infants who were raised with inanimate cloth surrogate mothers developed a wide array of abnormal social behaviors (Harlow & Harlow, 1966). Macaque infants raised with visual, auditory, and olfactory access to same-aged peers but no direct physical contact also developed abnormal social behaviors similar to isolated infants in earlier studies (Suomi, Harlow, & Kimball, 1971). Macaques raised only in the company of same-aged peers demonstrated some abnormal
behaviors, including delays in the development of certain social behaviors. In contrast, macaque infants raised by their biological mothers exhibited species-typical behaviors and few abnormal behaviors (Novak & Sackett, 2006).

The maternal deprivation work with rhesus macaques (Harlow, 1958, 1960; Harlow & Harlow, 1966; Harlow & Zimmerman, 1959) influenced Bowlby’s (1969) conclusion that the processes of attachment or bonding were not unique to humans. Rather, he outlined the similarities between human and nonhuman primate attachment processes, and paralleled the development of attachment among humans, chimpanzees, gorillas, baboons (Papio spp.), and rhesus macaques. Since the publication of Bowlby’s (1969) seminal work, several theoretical and empirical studies have been conducted with nonhuman primates using the attachment framework (e.g., Bard & Gardner, 1996; Bloomsmith et al., 2003; Dienske & Griffin, 1978; Kondo-Ikemura & Waters, 1995; McKenna, 1979; Nadler, 1994; Nadler & Codner, 1983; Rogers & Davenport, 1970; Suomi, 1995, 2005; Tarou, Bashaw, & Maple, 2000; Weaver & de Waal, 2002, 2003), although the majority of the attachment literature has focused on human children (see Cassidy & Shaver, 1999).

Bowlby (1969) used an evolutionary framework to examine the processes through which primate infants and caregivers became attached. He hypothesized that infants possess an innate ability to communicate with a caregiver who is biologically predisposed to respond to certain signals produced by the infant. These signals or “attachment behaviors” stimulate the caregiver to maintain close proximity to the relatively helpless infant (Bowlby, 1969). Attachment behaviors include crying, smiling, sucking, vocalizing, approaching, clinging, and following. Bowlby (1969) acknowledged that the primary caregiver is most typically the
infant's mother, but this role is not necessarily restricted to the biological mother or a female figure.

Bowlby (1969) suggested that the primary function of attachment behavior was increased protection from predators, and therefore an infant's proclivity to seek proximity to a caregiver is most pronounced during times of distress. The resulting survival advantage allowed the infant to benefit from other important proximity-related social learning opportunities, such as food identification and food processing. The preeminence of predator protection in attachment theory is problematic. For example, it does not sufficiently explain instances in which primate mothers carry their dead infants, sometimes for days (Goodall, 1986; Warren & Williamson, 2004). The infant is no longer in need of protection from predators, becomes an additional energy burden, and poses a potential disease risk for the caregiver. Critics of the primacy of predator protection in attachment theory have suggested that emotion, empathy and responsibility play a major role in motivating caregivers to care for their offspring (Bell & Richard, 2000).

Bowlby (1969) proposed that attachment behaviors were organized in an attachment behavioral system. This system allows individuals to respond flexibly to changes in the environment to achieve a goal. For example, a distressed infant may have to express more than one attachment behavior to achieve the goal of increased proximity with its caregiver, such as crying if following the caregiver did not produce a response. Bowlby's (1969) attachment behavioral system was composed of several other important biologically-based behavior systems, including the exploratory and fear behavioral systems. The adaptive benefits of the exploratory behavioral system included access to new knowledge about the environment, such as obtaining food through tool use and navigating physical obstacles. In
this system, the caregiver was used as a secure base from which the infant explored the surrounding physical and social environments (Bowlby, 1969). The infant’s attachment behavioral system responds flexibly to situations in which exploratory behavior may be either potentially advantageous or dangerous. The fear behavioral system, like the attachment system, serves a protective function and therefore has adaptive value. It is advantageous for infants to fear certain stimuli, such as darkness, loud noises, and being left alone, because it may increase their survival by avoiding potentially dangerous situations. The fear behavioral system works in conjunction with the attachment behavioral system because a fearful infant is more likely to seek protection from its caretaker and therefore avoid danger (Bowlby, 1969).

Bowlby (1969) outlined four phases of attachment that characterize normal primate infant development (Harlow & Harlow, 1966). During the indiscriminate social responsiveness phase, one to two month old infants develop a suite of communicative signals that are subsequently directed to any available caregiver or caregivers. The infant’s visual system is particularly important for establishing attachment behaviors, and most infants are capable of visual orientation and tracking at this stage (Corkum & Moore, 1995).

The infant develops a preference for a specific caregiver during the discriminating sociability phase of attachment at approximately two to seven months of age. The most significant factor that determines the assignment of the principal caregiver is the nature of the response to the infant’s attachment behaviors and cues (Ainsworth, 1973). The types of social interaction that promote attachment include a mixture of tactile, visual, auditory, and olfactory stimulation. For example, mother-infant relations in nonhuman great apes are characterized by almost constant direct physical contact from birth until between three and
six months of age when brief contact breaks are allowed by the mother (Bard, 1995). In addition, correlational and observational studies with human infants have indicated that direct physical contact is an antecedent to attachment (Ainsworth, Blehar, Waters, & Wall, 1978; Anisfeld, Casper, Nozyce, Cunningham, 1990).

Bowlby (1969) acknowledged that infants could also become attached to more than one individual, but he classified these individuals as subsidiary figures to the principle figure. Subsidiary attachment figures included socially responsive individuals who were consistent figures in the infant’s world, such as grandparents, older siblings, and other relatives. It is possible that the concept of subsidiary figures applies to both human and nonhuman great apes, particularly in the case of highly gregarious species such as chimpanzees and bonobos, which often live in large social groups (Goodall, 1986; Kano, 1986).

Interactions between the infant and caregiver during the *discriminating sociability phase* are particularly important for subsequent adaptive social development (Ainsworth et al., 1978, Bowlby, 1969; Cassidy & Shaver, 1999). Specifically, Bowlby (1969) highlighted the concepts of trust, reciprocity and motivation as elements that form the basis of an infant’s “internal working model.” The internal working model involves mental representations of the caregiver, the environment, and the self. The internal working models enable an individual to make predictions about the behavior of others, which increased an individual’s ability to navigate novel situations.

In the third phase of attachment, the infant continues to seek out and maintain proximity to preferred caregivers. This behavior occurs from approximately seven months to two years of age and is characterized by the infant’s intentional attempt to remain near the preferred caregiver. Separation from the preferred caregiver at this stage often causes
distress to the infant (Bowlby, 1969). This phase typically begins between six and seven months of age, but it may be delayed until after one year for infants with little opportunity for contact with a primary caregiver.

The final phase of attachment occurs at approximately three years of age (Bowlby, 1969). During this goal corrected partnerships phase, the maturing infant begins to infer information about the caregiver’s goals by observing the caregiver’s behavior. At this stage, the infant is capable of understanding the perspective of the caregiver, including the caregiver’s motives and feelings. This shift marks an increase in the complexity of the caregiver-infant relationship, which includes a dramatic increase in joint attention or triadic communications (Bakerman & Adamson, 1984). The ability to attend to an object or an event jointly with another individual constitutes a significant form of social engagement in infancy and is considered to be important to the early development of social competence and social understanding (Call & Tomasello, 1996; Mundy & Acra, 2006; Whiten & Byrne, 1997). Infants also develop increasing levels of autonomy from the preferred caregiver during this phase. The caregiver still provides guidance regarding socially appropriate behavior, but the infant increasingly relies on the internal working model to navigate through complex social situations. Conflicts may arise during this transition to independence, but ideally this further strengthens the development of the individual’s internal working models. The combination of these attachment behavior phases provides the individual with a template for future social negotiations and problem solving skills.

Bowlby (1969) posited that infants who did not become attached to a primary caregiver by the age of six months would have a more difficult time becoming attached subsequently. The empirical evidence for both human and nonhuman primate infants
indicates that infants who lacked access to a primary caregiver during the first six months of life experienced delayed or disrupted attachment in subsequent social relationships. (Novak & Sackett, 2006; Rutter, 2006).

Although attachment theory is one of the most prevalent frameworks through which caregiver-infant relations have been examined in the last four decades (Cassidy & Shaver, 1999), criticisms of both the theoretical framework and some of the empirical work must be discussed (Hazan & Shaver, 1994). One of the early criticisms of the theory came predominantly from feminist researchers who argued against the implicit assumption that caregivers were female by default, and that there was an inherent caregiving quality associated with mothers (Hrdy, 1999). Although much of the early attachment work did focus on mother-infant dyads (Ainsworth, 1973; Ainsworth et al., 1978), Bowlby (1969) never specified that primary caregivers had to be female. More recent studies have focused on caregiver-infant relations outside of the mother-infant dyad, including attachment with non-parental caregivers of both genders (Cassidy & Shaver, 1999; Kostan & Snowdon, 2002). Empirical studies indicated that infants became securely attached to non-related, non-parental caregivers who were appropriately responsive to the infant’s needs (Goossens & van Ijzendoorn, 1990; Howes & Hamilton, 1992).

Another debate regarding attachment theory involves the existence of a critical period in which the pattern of attachment becomes fixed, or if there are circumstances under which patterns of attachment change (Hamilton, 2000; van Ijzendoorn, 1995; Waters, Hamilton, & Weinfeld, 2000; Waters, Merrick, Treboux, Crowell, & Albersheim, 2000; Waters, Weinfeld, & Hamilton, 2000; Thompson, 1999). Bowlby (1969) suggested that infants who did not become attached to a primary caregiver by the age of six months would have a more difficult
time becoming attached to another individual subsequently. However, he also described infants as environmentally labile during the first five years of life and therefore patterns of attachment were sensitive to environmental changes. In a recent longitudinal study conducted by Waters, Merrick, et al. (2000), 72% of infants who received responsive care, an inference made based on their classification as secure at 12 months of age, were also classified as secure at 20 years of age based on interview results. However, infants who were originally classified as secure at 12 months of age, but experienced a serious negative life event before the age of 18 years, were more likely to change attachment classifications than individuals who did not experience these events. Negative life events included the loss of a parent, parental divorce, life threatening illness of the parents or child, parental psychiatric disorders, and physical or sexual abuse by a family member. This study demonstrated the overall stability of attachment, but also revealed circumstances under which the pattern could change.

O'Connor, Rutter, Beckett, Keaveney, and Kreppner (2000) conducted a relatively long term study on the effects of institutional care on the cognition of Romanian children who were adopted into families at various ages up to 42 months of age. Cognitive assessments were conducted at four years of age using the Denver Pre-Screening and Developmental Questionnaire, a tool that measures developmental abilities such as fine motor skills, gross motor skills, and language skills. The Wechsler Intelligence Scale for Children, an intelligence test that assesses verbal comprehension, perceptual reasoning, processing speed, and working memory, was administered at six and 11 years of age. O'Connor et al. (2000) found a significant improvement on cognitive performance between ages four and 11 years for the majority of the subjects, with the biggest gains made in the
first two years of living in a family environment. The mean IQ score at 11 years was only slightly below the population mean score. O’Connor et al. (2000) concluded that resilience and a normalized caregiving environment played a role in mediating the effects of early institutional care. Subjects who did not experience a reversal of these behaviors post-adoption lived in the institutional environment from shortly after birth through six months of age or more (O’Connor et al., 2000; Rutter, 2006).

**Attachment & Responsive Care: Impact on Cognition and Social Behavior**

Ainsworth (1973) expanded Bowlby’s (1969) original theoretical framework to investigate the origins of individual differences in caregiver-infant relations and the effects on patterns of attachment and infant social development. She predicted that the quality of the caregiver-infant relationship would have an impact on the type of attachment relationship that developed (i.e., secure or insecure). In a study with human mother-infant dyads, Ainsworth (1973) assessed the following caregiver behaviors: responsiveness to crying, behavior relevant to separation and reunion, behavior relevant to close bodily contact, behavior relevant to face-to-face interaction, and behavior relevant to feeding. Ainsworth (1973) also rated general caregiver characteristics such as sensitivity-insensitivity to the infant’s signals, acceptance-rejection, cooperation-interference, and accessibility-ignoring. These behaviors were first assessed in the infants’ first three months of life. Additional assessments took place from nine months of age through 12 months of age (Ainsworth, 1973).

Responsive care to crying was assessed in two ways, including the mean number of crying episodes per infant’s waking hour to which the caregiver made no response.
whatsoever and the mean number of minutes per infant’s waking hour that he/she spent crying during which there was no response from caregiver. Behaviors relevant to separation and reunion included the caregiver’s acknowledgement of the infant upon entering a room. This behavior was rated based on the percentage of times the caregiver entered the infant’s room in which the caregiver smiled, talked to, approached or otherwise socially engaged the infant. Ainsworth (1973) examined several measures of behavior relevant to close bodily contact including the following: the mean duration of a pick-up episode, the percentage of pick-up episodes in which the caregiver behaved affectionately towards the infant, the percentage of pick-up episodes that constituted an active interference with the infant’s ongoing activities, the percentage of total holding time in which the caregiver was tender and careful in handling the infant, the percentage of total holding time in which caregiver was inept or abrupt in handling the infant, and the percentage of total holding time devoted to routine care such as feeding, changing, and transport.

Behaviors relevant to face-to-face interaction included the percentage of face-to-face episodes in which the caregiver paced interventions slowly and gently and modified them in keeping with the infant’s cues, the percentage of face-to-face interactions initiated by the caregiver in which she looked impassively at the infant, rather than smiling or talking to the infant, and the percentage of face-to-face episodes in which the caregiver behaved in a matter of fact way typical of routine behavior. Behavior relevant to feeding included the extent to which the caregiver synchronized feeding interactions in accordance with the infant’s signals the caregiver’s skills in perceiving the infant’s signal that it’s hunger was satisfied, whether the caregiver forced the infant to eat disliked food, and the degree to which the caregiver respected the infant’s autonomy during feeding.
Ainsworth (1973) also investigated general maternal characteristics on nine point scales. Using the sensitivity-insensitivity to infant's signals scale, the caregiver would be rated as sensitive if she saw things from the infant's view, was alert to the infant's signals, interpreted the signals correctly, and responded quickly and appropriately. The acceptance-rejection scale measured the balance between the caregiver's positive and negative feelings about the infant. The cooperation-interference scale assessed the caregiver's behavior regarding the infant's independence. The accessibility-ignoring scale measured whether the caregiver was both psychologically and physically accessible to infant.

Ainsworth (1973) found that infants who received prompt and appropriate responses to crying within the first three months of life cried less between nine and 12 months of age, and instead relied on gestures, vocalizations, and facial expressions to communicate with their mothers. Infants who received tender physical contact during the first three months sought physical contact less often between nine and 12 months of age, but when direct contact did occur it was rated as more affectionate. Ainsworth et al. (1978) suggested that infants who received responsive care from a primary caregiver early in life developed an expectation that similar types of care behaviors would continue in future social interactions. Therefore, these infants perceive their caregivers as secure bases from which to explore their physical and social environment (Ainsworth et al., 1978; Bowlby, 1969).

The presence or absence of responsive care appears to have at least short term effects on the development of human social skills and cognitive abilities related to social understanding. Empirical studies that compared the behavior of human infants raised by a primary caregiver using a responsive care style to infants raised with multiple caregivers in an environment with little opportunity for social interaction (i.e., basic care) found that the
former were more socially competent (Laible, 2007; Pastor, 1981; Sroufe, Bennett, Englund, Urban, & Shulman 1993). The former group was also more proficient on socio-cognitive tasks involving joint attention, the capacity to coordinate attention with a social partner in relation to an object or an event (Hobson, Patrick, Crandell, Perez, Lee, 2004; Morales, Mundy, Crowson, Neal, Delgado, 2005; Mundy & Acra, 2006). This skill is considered to be an important precursor to more sophisticated mental abilities related to social understanding (Charman et al., 2000).

Ainsworth’s (1973) conclusion that the presence or absence of responsive care was the most significant factor in determining patterns of infant attachment has been challenged (see Belsky, 1999 for a review). For example, Lamb, Thompson, Gardner, Charnov, Estes (1984) questioned the strength of the findings based on the small sample size (N=26). A meta-analysis of 15 studies from 1978 to 1987 determined that the association between responsive care and patterns of attachment was not as strong as previously believed (Goldsmith & Alansky, 1987). A more substantive meta-analysis of 66 studies covering over four thousand caregiver-infant dyads found at least a moderate association between responsive care and patterns of attachment (DeWolff & van IJzendoorn, 1997). The most recent meta-analysis on the relationship between responsive care and attachment in human children found that sensitivity or responsive care played a causal role in shaping attachment (Bakermans-Kranenburg, van IJzendoorn, & Juffer, 2003). In addition, a recent empirical study reported that human infants who experienced responsive care engaged in joint attention episodes more often than those who did not receive responsive care during that period (Hobson et al., 2004).
The majority of the literature examining the effects of care style on social behavior and cognition is focused on human infants (Cassidy & Shaver, 1999). There is a relatively small amount of literature on this phenomenon in nonhuman primates, with the majority of studies on chimpanzees (Bard & Gardner, 1996; Bloomsmith et al., 2003; Bloomsmith, Baker, Ross, Lambeth, 2006; Dienske & Griffin, 1978; Nadler, 1994; Rogers & Davenport, 1970). Bloomsmith et al. (2003) used responsive care criteria outlined by Rogers and Davenport (1970) to categorize successful versus unsuccessful chimpanzee maternal care. Responsive care behaviors included readjusting the infant so that he/she was better positioned to nurse, playing with the infant, grooming the infant, and carrying/holding the infant in appropriate ways. Bloomsmith et al. (2003) found that 16 of 23 chimpanzee mothers studied were categorized as successful caregivers because they provided responsive care for their infants. The remaining seven mothers had their infants removed because the life of the infant was in jeopardy due to neglect from the mother. Specifically, successful mothers were in direct physical contact with their infants 99% of the time during observations compared to 92.7% of the time in the case of the unsuccessful mothers.

Successful mothers nursed their infants 14.2% of the time during observations, while unsuccessful mothers nursed only 5.7% of the time. Successful mothers also carried and held their infants in appropriate ways more often than the unsuccessful mothers. Finally, infants of successful mothers cried less frequently over time, which comports with results from studies of human children (Ainsworth, 1973; Ainsworth et al., 1978).

Only a small number of the studies examining responsive care in chimpanzees addressed the effects of that care on the cognitive or social behaviors of the infants (Bard & Gardner, 1996; Bloomsmith, Baker, Ross, & Pazol, 2002, Bloomsmith et al., 2006; Dienske
& Griffin, 1978). Dieske & Griffin (1978) assessed the effects of nursery care on chimpanzee infants who were separated from their mothers shortly after birth due to inadequate maternal care. Younger infants were housed in incubators and older infants were housed with peers. Direct social interaction between caregivers took place only in the context of routine care, and care was provided during the day over a period of eight hours by multiple people. Infants who experienced this type of nursery care produced a number of abnormal behaviors, such as body rocking. Dienske & Griffin (1978) concluded that the lack of opportunity for expanded social interactions with the human caregivers likely was responsible for these behaviors.

Bard and Gardner (1996) assessed the effects of three different types of early care on the cognition, behavior, and personality traits of infant chimpanzees using the Bayley Scales of Infant Development, a test used to assess behavioral, cognitive, and manipulative ability, and temperament in human infants. The first group of infants received responsive care from human caregivers from birth through 12 months of age. Responsive care included continuous physical contact with two to five human caregivers for at least four hours per day, five days per week. Caregivers provided infants with bottles on demand and infants were fed with body contact appropriate for their age. In addition, infants in this group had visual, olfactory, and auditory exposure to infant, juvenile and adult chimpanzees. The second group of infants received standard nursery care from humans from birth through 12 months of age. Standard nursery care included care provided by a larger number of caregivers, mostly in the context of routine care. The infants spent the majority of their time housed with same-aged peers and had relatively little physical contact with humans. These infants did not have access to adult chimpanzees. The final group experienced a combination of
early care, during which they were raised by their mothers for days or weeks and subsequently had to be removed for standard nursery care because of maternal competency issues.

Bard and Gardner (1996) found no cognitive differences among chimpanzee infants who received responsive care from humans immediately after birth, infants who received standard nursery care from humans immediately after birth, and infants who received combination care. However, when month-by-month performance was considered, infants in the first group performed significantly better on the cognitive tasks than the last group during 3-5 month and 8-9 month testing periods (Bard & Gardner, 1996). The authors concluded that differential early care resulted in few differences in basic cognitive capacity, but several significant differences in personality traits. Specifically, the responsive care chimpanzees were more persistent in attaining goals, had longer attention spans, and exhibited higher levels of cooperation than the chimpanzees in the two standard care groups (Bard & Gardner, 1996).

A small number of studies have examined the effects of a certain style of nursery care on the social behaviors of chimpanzees (Bloomsmith et al., 2002; Bloomsmith et al., 2006). Bloomsmith et al. (2006) examined the impact of nursery care on the frequency of abnormal behaviors in 41 juvenile chimpanzees. Nursery care included 24 hour direct physical access to same-aged peers, two hours of social interaction with human caregivers per day, feeding and object enrichment, and access to a dog companion for a large portion of the day and night (Bloomsmith et al., 2006). Twenty-two of the chimpanzees were mother-raised, seven were mother-raised until two years of age after which time they were housed with peers in a nursery environment, and 12 were raised in a nursery environment from birth. Although the
chimps raised from birth in the nursery demonstrated the highest level of abnormal behaviors, the mother-raised infants also displayed some abnormal behaviors (Bloomsmith et al., 2006). Infants who were raised by their mothers for two years and were then placed in a nursery environment with peers demonstrated lower rates of abnormal behaviors than continually mother-reared infants. Stereotyped rocking was only observed in chimpanzees who received nursery care from birth, and coprophagy, a behavior that Bloomsmith et al. (2006) considered abnormal, occurred most frequently in mother-reared infants. An earlier study with the same chimpanzees found that subjects raised from birth in the nursery environment engaged in sexual behavior less often than the those who were mother-raised from birth or for at least the first two years of their lives (Bloomsmith et al., 2002). However, this difference became minimized as those subjects matured, with rates of sexual behaviors approaching those of continually mother-reared chimpanzees by four to six years of age.

In a case study examining a mother-infant gorilla dyad, Crosby and Lukas (2004) found that the mother’s care was adequate, but not as robust as care demonstrated by other gorilla mothers. For example, direct physical contact occurred infrequently and the mother rarely approached the infant, despite repeated attempts by the infant to initiate contact. These general patterns continued after the dyad was introduced to a new social group of eight gorillas. The authors concluded that despite this minimal level of care, the infant was not detrimentally affected. Specifically, Crosby and Lukas (2004) found that the infant did not show high frequencies of self-directed behaviors and showed appropriate social interactions with group members. Long-term effects of care style were not assessed in this study.
Studies with orangutans were limited to broader areas of attachment, such as infant response to separation and reunion (Nadler & Codner, 1983; Tarou et al., 2000) and general discussions of maternal competence (Nadler, 1994). Finally, there is a recent study comparing maternal styles of chimpanzees and bonobos (de Lathouwers & van Elsacker, 2004), but there is no specific focus on the effects of responsive care per se.

It is important to note that there are many additional studies focusing on the social, reproductive and, to a lesser degree, cognitive effects of mother-reared versus human-reared primates (Baker, Seres, Aureli, & de Waal, 2000; Beck & Power, 1988; Bloomsmith & Haberstroh, 1995; Brent, Bloomsmith & Fisher, 1995; Brent, Williams-Blangero & Stone, 1996; Call & Tomasello, 1996; Gold, 1992; Meder, 1989; Nash, Fritz, Alford & Brent, 1999; Ryan, Thompson, Roth & Gold, 2002; Stoinski, Kuhar, Lukas, Maple, 2004; Videan & McGrew, 2003). According to these studies, human-raised chimpanzees were wounded more often than mother-reared individuals (Baker et al., 2000), had higher rates of abnormal behaviors, such as rocking and self-sucking (Bloomsmith & Haberstroh, 1995; Nash et al., 1999), made and used nests less frequently (Videan & McGrew, 2003), were less proficient using tools (Brent, et al., 1995), and displayed less competent maternal behavior (Brent et al., 1996). Research with gorillas who had early exposure to human caregiving elucidated similar trends. Gorillas developed stereotyped behaviors, showed more aggression, showed more solitary play, and demonstrated less social play (Meder, 1989; Stoinski et al., 2004). Gorillas also demonstrated less competent sexual and reproductive behavior (Beck & Power, 1988; Ryan et al., 2002) and higher levels of self-directed behavior (Gold, 1992).

In contrast, some studies demonstrated a positive effect of human-rearing on primate cognitive capacities (Call & Tomasello, 1996). Call and Tomasello (1996) posited that apes
could be placed in one of the following five categories based on their familiarity with humans and human artifacts: 1) apes who spent the entire length of their lives in natural habitats; 2) captive apes who had minimal interactions with humans and human artifacts, including some zoo and laboratory born apes; 3) apes raised from a young age with routine access to humans, peer conspecifics, and human artifacts, but with no training aimed at certain outcomes; 4) apes raised in human captivity who have been trained in certain tasks; and 5) apes raised in a human cultural environment with daily interactions with people and artifacts in meaningful interactions. Call and Tomasello (1996) concluded that increased exposure to humans and human artifacts, especially early in life, can affect apes’ cognitive skills, especially regarding imitation and gestural communication. More recently, Tomasello and Call (2004) concluded that apes raised in a variety of normal environments are capable of a range of cognitive behaviors that they previously believed required increased levels of access to humans and human cultural environments. However, Furlong, Boose, & Boysen (2007) found that chimpanzees who had long-term stable relationships with both people and conspecifics, access to enriched environments, and experience participating in a variety of cognitive tests, outperformed semi-enculturated chimpanzees on one of two tool tasks.

Despite the important contributions of these studies, the impact of early care on great ape cognition and social behavior was typically assessed using only one variable, the species of the caregiver. There was no examination of the impact of care style, from either the great ape mother or human caregivers, on the cognitive abilities or social behavior of great apes. In other words, there was an implicit assumption in these investigations that the quality of care provided by humans for great ape infants was equivalent. The same assumption was made about the care of great ape mothers. The failure to take an integrative approach and
consider more than one variable, the species of the caregiver, is problematic because a large body of literature suggests that the quality of care that both human and nonhuman primate infants receive impacts cognition and social behavior (Ainsworth, 1973; Bard & Gardner, 1996; Bowlby, 1969; Davenport & Menzel, 1963; Davenport & Rogers, 1968; Harlow, 1960; Menzel, 1963, 1964; Menzel, Davenport & Rogers, 1961, 1970; Rogers & Davenport 1969; Seay, Hansen, & Harlow, 1962; Novak & Sackett, 2006; O’Connor et al., 2002).

Social Cognition and Joint Attention: An Overview

Social cognition is a set of processes or abilities that explain how individuals navigate their social environment. Social cognition is not a prerequisite for social competence; however, the possession of certain socio-cognitive skills, such as the ability to take the mental perspectives of other individuals, allows individuals to engage their social environment in more cognitively sophisticated ways compared to those who do not possess these skills. Premack and Woodruff's (1978) query into the possibility that chimpanzees possessed sophisticated socio-cognitive abilities, a so-called “theory of mind”, stimulated a substantial body of research with both human children and nonhuman primates (Astinton, Harris, & Olson, 1988; Brune & Brune-Cohrs, 2006; Byrne & Whiten, 1988; Call & Tomasello, 1996; Carpendale & Lewis, 2004; Flavell, 1999, 2004; Fry & Moore, 1991; Gopnik & Meltzoff, 1994; Heyes, 1998; Parker & McKinney, 1999; Parker, Mitchell, & Boccia, 1994; Parker, Mitchell, & Miles, 1999; Russon, Bard, & Parker, 1996; Suddendorf & Whiten, 2001; Tomasello & Call, 1996; Wellman, 1993; Whiten, 1991; Whiten & Byrne, 1997). Premack and Woodruff (1978) defined Theory of Mind (ToM) as the ability to impute mental states to one’s self and others, such as intentions, beliefs, thinking, liking,
guessing, doubting, and pretending. Since the publication of Premack and Woodruff's (1978) seminal work, a range of ToM-related capacities have been investigated including joint attention, visual perspective taking, knowledge state attribution, mirror self-recognition, attribution of intention, and deception. Some of these skills emerge in human infants as early as three months of age, while others are not fully expressed until six years of age (Flavell, 1999, 2004). There is debate regarding the precise time during which some of these skills emerge, as well as to what degree, if any, some of these abilities reflect a representational understanding of mind (Astington et al., 1988; Baron-Cohen, Tager-Flusberg, & Cohen, 1993; Flavell, 1999, 2004; Frye & Moore, 1991). A variety of ToM capacities have been explored in nonhuman primates since Premack & Woodruff's (1978) study with chimpanzees (Suddendorf & Whiten, 2001). Suddendorf and Whiten (2001) suggest that the body of research on the mental abilities of great apes strongly supports the conclusion that they possess ToM capacities. Other researchers have concluded that apes do not possess ToM skills at all (Heyes, 1998; Povinelli & Vonk, 2003) or that they are capable of some ToM behaviors but not to the same extent as humans (Brauer, Call, & Tomasello, 2005; Tomasello, Call, & Hare, 2003). Despite the valuable research that has been conducted thus far on ToM skills in nonhuman primates, only a relatively small number of species have been studied and there is a small body of research on the ontogeny of these skills compared to studies with human infants (Matsuzawa, Tomonaga, & Tanaka, 2006; Tomasello, Hare, & Fogleman, 2001).

Joint attention is a set of cognitive processes upon which more complex ToM skills are built (Charman et al., 2000). Most simply, joint attention is the ability to coordinate attention with another individual on an object or event simultaneously. Despite this
relatively simple description, there are several distinct phenomena that form the suite of skills known as joint attention behaviors. Joint attention behaviors include following the gaze direction of another individual, alternating gaze between an object and another individual, and the use of communicative gestures to attract or redirect the attention of another individual, such as pointing, and referential language (Carpenter, Nagell, & Tomasello, 1998; Tomasello, 1995a). Joint attention is a significant area of exploration because it is the foundation upon which more complex forms of ToM skills are built (Carpenter et al., 1998; Charman et al., 2000; Tomasello, 1995a).

Gaze following, the ability to follow the line of sight of another individual, is considered a behavioral response to joint attention (Mundy & Acra, 2006). The ability to follow gaze emerges in human infants as early as three months of age (Butterworth & Jarrett, 1991; D'Entremont, Hains, & Muir, 1997; D'Entremont, Yazbek, Morgan, MacAulay, 2007; Scaife & Bruner, 1975). However, several researchers have argued that gaze following abilities prior to nine months of age are the result of conditioning rather than spontaneous gaze following which emerges reliably after 10-11 months (Corkum & Moore, 1995; Meltzoff & Brooks, 2007; Tomasello, 1995a). Between 12 and 18 months of age, human infants are capable of more complex forms of gaze following, such as checking back on the attentional state of an adult and following gaze direction outside of their visual field (Butterworth & Jarrett, 1991; Tomasello, 1995). There is disagreement as to whether the skills that emerge between 9 and 15 months of age indicate a mentalistic understanding of others as intentional agents (Carpenter et al., 1998; Tomasello, 1995a) or a leaner interpretation that does not imply such a cognitively complex understanding of gaze (Corkum & Moore, 1995; Leekham, Hunnisett & Moore, 1998; Moore & Corkum, 1994). In the
nonmentalistic explanation, human infants in this age range simply use gaze cues to direct their attention to interesting objects.

The ability to spontaneously initiate joint attention with another individual around an object or event represents a more sophisticated socio-cognitive skill than just responding to attention (Mundy & Acra, 2006; Tomasello, 1995a). According to Tomasello (1995a) true joint attention must emerge spontaneously during an ongoing social interaction between an infant and an adult around an object or an event. This skill reliably emerges in human infants after 12 months of age. This behavior may be contrasted with passive joint engagement, in which an infant looks at an object that an adult is examining, is prompted to look at an adult due to a noise made by the adult and then looks back at the object again (Carpenter et al., 1998; Tomasello, 1995a). Gaze alternation, the ability to share visual attention by looking back and forth at an object and an adult, is one established way of measuring the initiation of joint attention (Seibert, Hogan, & Mundy, 1982; Mundy et al., 2003). It should be noted that human infants develop increasingly sophisticated skills of attention after the first two years of life, including visual perspective taking and the transition from "seeing" limited to a purely perceptual attention state to "seeing" as a state of understanding the mental perspective of others (Flavell, 1999).

**Joint Attention in Nonhuman Primates**

There has been great interest in the ability of nonhuman primates to respond to attention through gaze following (Emery 2000; Gomez, 2005; Itakura, 2004; Itakura, Das, & Farshid, 2007; Okamoto-Barth, Call, & Tomasello, 2007; Shepherd & Platt, 2007; Tomasello, Call, & Hare, 1998; Tomasello, Hare, Lehmann, & Call, 2007). Field studies have reported
that several primate species follow the gaze of conspecifics (Byrne & Whiten, 1992; Kummer, 1967; Whiten & Byrne, 1988). Experimental studies have also documented the ability of primates to follow the gaze of conspecifics. For example, Shepherd & Platt (2007) found that captive ringtailed lemurs (*Lemur catta*) spontaneously followed the gaze of conspecifics. Tomasello et al. (1998) reported that chimpanzees, sooty mangabeys (*Cercopithecus atys torquatus*), rhesus macaques, stump-tail macaques (*M. arctoides*), and pigtails macaques (*M. nemestrina*) reliably followed the gaze of conspecifics in 80% of experimental trials compared to 20% of control trials. However, Kaplan & Rogers (2002) found only two instances of orangutans following the gaze of conspecifics out of over 200 observations of both semi-wild rehabilitants and captive individuals. There are a limited number of studies that have investigated the ability of nonhuman primates to initiate attention with a conspecific (Okamoto-Barth & Tomonaga, 2006). It should be noted that there have been several recent studies examining some of the more sophisticated “seeing-knowing” skills among conspecific great apes (Hare, Call, Agnetta, & Tomasello, 2000; Hare, Call, & Tomasello, 2001).

There is evidence that all great apes are capable of following the gaze of a human experimenter (Barth, Reaux & Povinelli, 2005; Brauer, Call & Tomasello, 2005; Itakura, 1996; Kaplan & Rogers, 2002; Povinelli & Eddy, 1996a, 1996b; Tomasello, Hare & Agnetta, 1999). Significantly, all great ape subjects looked back at the human experimenter a second time if they followed his/her initial gaze to an area of little interest, similar to the reaction of human children (Brauer et al., 2005). All great apes in this study also followed the gaze of human experimenters around barriers and to distant locations (Brauer et al., 2005; Povinelli & Eddy, 1996a; Tomasello et al., 1999).
A more recent study, however, found species differences in a gaze following task in which the line of sight of the human experimenter was manipulated so that sometimes the human had a clear line of sight to a target through a transparent window and sometimes the line of sight to a target was occluded with a barrier (Okamoto-Barth et al., 2007). Okamoto-Barth et al. (2007) predicted that the great apes would look towards the target more often when the human’s line of sight was clear in the transparent window condition than when his/her line of sight was occluded, that they would look at the inside of the barrier more often in the opaque barrier condition, that they would produce more double looks in the opaque barrier condition than in the transparent window condition, and that bonobos and chimpanzees would be more attentive to the line of sight of the experimenter than would gorillas or orangutans. Okamoto-Barth et al. (2007) concluded that bonobos and chimpanzees had a better understanding of the referential nature of seeing because they followed gaze significantly more often in the transparent window condition and they looked at the human’s side of the barrier when that barrier was opaque more often than other species. Additionally, bonobos produced more double looks in the opaque barrier condition. Gorillas performed as well as chimpanzees and bonobos on the first condition only. Orangutans followed gaze at levels comparable to the other species, but there was no significant difference between gaze following in the transparent window versus opaque barrier condition, they produced few looks inside of the human’s barrier during the opaque condition, and they produced few double looks. The authors suggested that sensitivity to visual perspective taking skills increased in the lineage of bonobos, chimpanzees, and humans (Okamoto-Barth et al., 2007). However, there is experimental evidence that orangutans are capable of complex visual perspective taking skills (Shillito et al., 2005).
Kaplan and Rogers (2002) reported that the orangutans in their study visually attended to both conspecifics and humans using sideways glances, except for juveniles who engaged in more instances of social staring than either adults or infants. Specifically, the Kaplan and Rogers (2002) posited that gaze avoidance may compensate for instances in which orangutans aggregate in larger numbers in close proximity during a mast fruiting event.

The evidence for gaze following capabilities in monkeys is somewhat less clear than in great apes. Several studies demonstrated the ability of some monkey species to follow the gaze of human experimenters (Itakura; 2004; Sato & Nakamura, 2001; Tomasello et al., 2001). However, a number of studies contradicted these findings or were inconclusive (Anderson, Sallaberry and Barbier, 1995; Itakura, 1996). It should be noted that although some monkeys have demonstrated the ability to follow another individual's visual gaze, there is no evidence that they do so in more complex scenarios, such as checking back and following an experimenter's gaze past barriers.

There are fewer studies investigating the ontogeny of gaze following behaviors in nonhuman primates compared to studies with human infants (Ferrari, Kohler, Fogassi, & Gallese, 2000; Myowa-Yamakoshi & Tomonaga, 2001; Okamoto-Barth & Tomonaga, 2006; Okamoto, Tomonaga, Ishii, Kawai, Tanaka & Matsuzawa, 2002; Tomasello et al., 2001). These studies have been limited to a small number of species. For example, Tomasello et al. (2001) found that chimpanzee infants did not reliably follow human gaze until three to four years of age, while Okamoto et al. (2002) and Okamoto-Barth & Tomonaga (2006) found that chimpanzee infants followed human gaze at the age of 13 months. It is possible that this discrepancy is related to different methodologies used in the studies. Myowa-Yamakoshi & Tomonaga (2001) found that a gibbon (*Hylobates agilis*) infant preferred to look at a human
face with direct rather than averted gaze. Tomasello et al. (2001) reported that rhesus macaques followed the gaze of a human experimenter by 5.5 months of age. Ferrari et al. (2000) found that gaze following behaviors improved with age in rhesus macaques, and that juveniles relied more heavily on a combination of head direction and eye gaze cues than adults.

There are several experimental studies using an object-choice paradigm to investigate the ability of great apes to attend to a variety of visual cues provided by human experimenters (Barth et al., 2005; Byrnt, 2004; Call, Agnetta, & Tomasello, 2000; Call, Hare, & Tomasello, 1998; Peignot & Anderson, 1999). Specifically, the object-choice paradigm involves human-provided cues such as gazing, glancing, and pointing to one of two opaque, food-baited containers. Despite the robust performance of all great apes on a series of recent gaze following studies (Barth et al., 2005; Brauer et al., 2005), results are mixed for great apes in the object-choice paradigm. For example, there is positive evidence that chimpanzees and orangutans can use a combination of head and eye cues or eye cues alone to locate food hidden under a container to which the human is directing their cue (Povinelli & Eddy, 1996b; Itakura & Tanaka, 1998), but negative evidence for chimpanzees from other studies (Tomasello et al., 2003). Itakura, Agnetta, Hare, & Tomasello (1999) found that chimpanzees had difficulty using gazing and pointing cues to locate hidden objects, but were able to do so more successfully when humans combined gaze and auditory cues. Hare & Tomasello (2004) suggested that chimpanzees performed poorly on these tasks because they were forced to cooperate, rather than compete, with a human experimenter over food.

Gorillas tested in an object-choice paradigm tended to avoid direct eye contact with a human experimenter and failed to use the human’s gaze cue alone to select the baited container
It is possible that the poor performance on this task is related to the relationship of prolonged eye contact and threat in gorillas (Goodall, 1986, but see Yamigawa, 1992). Byrnit (2004) reported that three “nonenculturated” orangutans used human pointing cues in an object-choice task to locate food hidden under a container, but that performance was poor when the human experimenter gazed or glanced at the container.

There are only a small number of studies examining the ability of great apes to initiate attention with a human experimenter (Bard, 1990; Carpenter, Tomasello, & Savage-Rumbaugh, 1995; Gomez, 1990, 1991, 1996; Leavens & Hopkins, 1998; Miles, Mitchell, & Harper, 1996; Russell, Adamson, & Bard, 1997). Russell et al. (1997) reported that chimpanzee infants successfully alternated gaze between objects and a human experimenter. In contrast, Okamoto-Barth & Tomonaga (2006) stated that the single chimpanzee infant in the study followed the gaze of a human experimenter but did not check back by alternating gaze with him/her. Carpenter et al. (1995) investigated the joint attention skills of enculturated bonobos, mother-raised bonobos, and human children in a study on imitation. The authors found that enculturated bonobos performed similarly to human children in social interactions involving objects, in contrast to mother-raised bonobos. However, the duration of enculturated and mother-raised bonobos’ looks to the human experimenters’ faces was less than human children. Gomez (1990, 1991, 1996) reported on the emergence of gaze-related behaviors in an infant gorilla. He stated that the gorilla alternated gaze between an object and a person when she was 20 months old, but not prior to this age. Miles et al. (1996) provided a review of the imitation capacities of an orangutan, including manually directing his caregiver’s direction of gaze before signing. Finally, Bard (1990) reported instances of
gaze alternation between an orangutan infant and mother at two years of age in food begging scenarios.

In summary, great apes have demonstrated a range of joint attention behaviors (see Table 1). Gaze following emerges in chimpanzee infants between one and three years of age (Myowa-Yamakoshi & Tomonaga, 2001; Tomasello et al., 2001). All great apes are capable of following the gaze of humans around barriers and to distant locations and would check back with the human partner if gaze led to an area of little interest (Brauer et al., 2005). Chimpanzees are also capable of following the gaze of conspecifics (Tomasello et al., 1998). All great apes have demonstrated the ability to initiate joint attention with a human around an object, although adequate controls were not administered in all studies (Bard, 1990, Carpenter et al., 1995; Gomez, 1990, 1991, 1996; Leavens & Hopkins, 1998; Miles et al., 1996; Russell et al., 1997). The ability of great apes to follow the gaze of humans using the object choice paradigm is mixed (Barth et al., 2005; Byrnit, 2004; Call et al., 1998; Call et al., 2000; Itakura & Tanaka, 1998; Peignot & Anderson, 1999; Povinelli & Eddy, 1996b). Finally, Okamoto-Barth et al., (2007) suggested that chimpanzees and bonobos understand the referential nature of gaze more than gorillas or orangutans based on a series of complex gaze following tasks.

A summary of the existing literature on attachment and joint attention in great apes reveals several areas that have not been explored. There are no studies on the relationship between care style and joint attention in great apes. In addition, the effects of care style and the species of the caregiver on great ape behavior are rarely considered simultaneously. Any impact of early care, typically human care, has either focused on cognition or social behavior in great apes rather than assessing both. There are no studies on the continuity of attachment
in great apes. All four types of great apes are generally not well represented in attachment and joint attention studies. Finally, great ape joint attention abilities are most often tested with human partners.

The purpose of this study is to investigate the effects of care style and the type of caregiver during the first six months of life on the joint attention skills and social behavior of great apes. Great ape joint attention skills will be assessed with both conspecific and human social partners. This study is justified because there have been no investigations of the impact of both care style and caregiver type on joint attention skills and social behavior in all four types of great ape.

The first null hypothesis tested here is that there will be no differences in the ability of great apes to produce joint attention behaviors in experimental conditions compared to control conditions. Second, there will be no differences in the production of joint attention behavior with conspecifics and humans based on the care style participants received from either great ape mothers or humans during the first six months of life. Finally, there will be no differences in the frequency of social behavior and the duration of time spent engaged in solitary behavior in great apes based on the care style participants received from either great ape mothers or humans during the first six months of life.
<table>
<thead>
<tr>
<th>Phenomenon</th>
<th>Chimpanzees</th>
<th>Bonobos</th>
<th>Gorillas</th>
<th>Orangutans</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ontogeny of gaze following</td>
<td>Tomasello et al., 2001 (✓) H, C</td>
<td>Myowa-Yamakoshi &amp; Tomonaga, 2006 (✓) H, C</td>
<td></td>
<td>Kaplan &amp; Rogers, 2002 (✓) CO, W</td>
</tr>
<tr>
<td>General gaze following behaviors</td>
<td>Byrne &amp; Whiten, 1992 (✓) CO, W</td>
<td>Goodall, 1986 (✓) CO, W</td>
<td>Tomasello et al., 1998 (✓) CO, C</td>
<td>Tomasello et al., 1999 (✓) H, C</td>
</tr>
<tr>
<td>Follow gaze to distant locations and around barriers</td>
<td>Brauer et al., 2005 (✓) H, C</td>
<td></td>
<td></td>
<td>Brauer et al., 2005 (✓) H, C</td>
</tr>
<tr>
<td>Follow gaze and “check back” if gaze direction led to area of little interest</td>
<td>Brauer et al., 2005 (✓) H, C</td>
<td></td>
<td></td>
<td>Brauer et al., 2005 (✓) H, C</td>
</tr>
<tr>
<td>Reliance on eye cues only (no head)</td>
<td>Tomasello et al., 2007 (X) H, C</td>
<td>Tomasello et al., 2007 (X) H, C</td>
<td>Tomasello et al., 2007 (X) H, C</td>
<td>Tomasello et al., 2007 (X) H, C</td>
</tr>
<tr>
<td>Understanding gaze</td>
<td>Okamoto-Barth et al., 2007 (✓) H, C</td>
<td>Okamoto-Barth et al., 2007 (✓) H, C</td>
<td>Okamoto-Barth et al., 2007 (X) H, C</td>
<td>Okamoto-Barth et al., 2007 (✓) H, C</td>
</tr>
<tr>
<td>Understanding gaze</td>
<td>Harc et al., 2000 (✓) CO, C</td>
<td></td>
<td></td>
<td>Shillito et al., 2005 (✓) H, C</td>
</tr>
<tr>
<td></td>
<td>Leavens &amp; Hopkins, 1998 (✓) H, C</td>
<td></td>
<td></td>
<td>Miles et al., 1996 (✓) H, C</td>
</tr>
</tbody>
</table>

C = captive; CO = conspecific partner; H = human partner; W = wild; (✓) = demonstrated behavior; (✓) = mixed performance; (X) = did not demonstrate behavior reliably
CHAPTER 2: METHODS

Participants

Twenty-four great apes participated in the study including seven chimpanzees, seven gorillas, seven orangutans, and three bonobos. Participants included 12 females and 12 males ranging in age from 3 years to 49 years (Table 2). All participants were socially housed at five separate institutions. The International Species Information System, an international database of species holdings in zoos and other institutions, was the first phase in the process used to identify potential participants. A series of questions was then used to determine the style of care experienced by potential participants during their first six months of life based on institutional records and interviews with informants (Appendix A).

The questions used to determine the style of early care participants experienced during the first six months of life were based on the attachment literature focusing on both great apes and humans (Ainsworth, 1973; Bard, 1995; Bard & Gardner, 1996; Bloomsmith et al., 2003; Bowlby, 1969; de Lathouwers & van Elsacker, 2004; Dienske & Griffin, 1978; Maple, 1980; Nadler, 1990, 1994). Participants were assigned to one of four groups based on data collected from informants and institutional records on the style of care they received during the first six months of life and the type of caregiver, great ape mother or human, who provided the care. The period from birth through six months was chosen because research suggests that there is a critical period for the normal development of attachment (Bowlby, 1969; O’Connor et al., 2002; Rutter, 2006). Although many potential participants were considered for the current study, only great apes whose early histories were sufficiently complete were included (N=24).
Responsive Care Mother (RCM) Group

The RCM group included eight participants raised by the biological mother or ape surrogate from birth through at least six months of age. Informants, using a combination of personal recollections and institutional records, agreed that participants in this category were raised by great ape mothers who generally engaged in frequent direct physical contact with them during the first six months of life, including almost constant physical contact during the first three months. In addition, mothers were frequently observed accepting infant-initiated bids for contact. Mothers were also regularly observed cradling and transporting participants in an appropriate manner and allowing nursing on demand. Informants also indicated that mothers inspected participants’ bodies and encouraged the development of motor skills through direct physical contact. Mothers also generally allowed participants to explore the environment at appropriate age levels but physically comforted them if they became distressed. Finally, informants confirmed that they observed responsive great ape mothers frequently accepting and initiating play behavior with participants during the first six months of life.

Basic Care Mother (BCM) Group

The BCM group included four participants raised by the biological mother or ape surrogate from birth or shortly after birth through at least six months of age. Informants agreed that participants in this category were raised by great ape mothers who engaged in moderate to relatively little direct physical contact with the infant, including frequent rejection of infant-initiated bids for contact. Mothers were observed cradling and transporting participants relatively infrequently, and they sometimes did so in inappropriate
ways, such as picking up participants by their foot. In addition, mothers rejected participants’ bids to nurse on demand relatively frequently. Mothers infrequently inspected participants’ bodies or encouraged motor skills through direct physical contact. Mothers were observed providing moderate to little physical comfort to distressed participants. Finally, great ape mothers in this category were observed engaging in moderate to little play behavior with participants, or if this behavior was observed more frequently, it occurred to the exclusion of other caregiving behaviors.

**Responsive Care Human (RCH) Group**

The RCH group included six participants cared for by humans from birth or shortly after birth through at least six months of age. Records indicated that the number of caregivers ranged from one through six individuals. Informants reported that participants in this category were raised by human caregivers who engaged in frequent direct physical contact with them, including 24-hour contact for a large portion of the first six months. Human caregivers had frequent opportunities for social engagement with participants that took place outside of the context of routine care. Social engagement included cradling and transporting the infant, allowing participants to explore the environment, but physically comforting them during times of distress and playing with the participant.

**Basic Care Human (RCH) Group**

The BCH group included six participants cared for by humans from birth or shortly after birth through at least six months of age. Records indicate that the number of caregivers throughout the six month period ranged from six to 14 individuals. Informants reported that
participants in this category were raised by human caregivers who spent a moderate amount of time in direct physical contact with them, including care that typically occurred during an eight hour day. Social engagement was generally limited to interactions that occurred in the context of routine care such as feeding.

Overview of Procedures

An experimental procedure and an observational procedure were conducted in this study. The experimental procedure consisted of the following four conditions under which each participant was tested: 1) following the gaze of a human social partner (GFH); 2) following the gaze of a conspecific social partner (GFC); 3) joint attention with a human social partner (JAH); and 4) joint attention with a conspecific social partner (JAC). The order in which each condition was presented to participants was counterbalanced. All subjects participated in the four conditions except for one individual. An orangutan (BCH group) did not participate in the GFC experiment because the conditions that were necessary for trials to begin, such as having the participant face away from the experimenters, did not occur. The experimental procedure will be described first, followed by the observational procedure.
### Table 1. Care Style, Caregiver, Species, Age, and Sex of Participants

<table>
<thead>
<tr>
<th>Care Style</th>
<th>Caregiver</th>
<th>Species</th>
<th>Institution</th>
<th>Age</th>
<th>Sex</th>
</tr>
</thead>
<tbody>
<tr>
<td>Responsive</td>
<td>Mother</td>
<td><em>Pongo abelii</em></td>
<td>1</td>
<td>12</td>
<td>Female</td>
</tr>
<tr>
<td>Responsive</td>
<td>Mother</td>
<td><em>Gorilla gorilla</em></td>
<td>2</td>
<td>10</td>
<td>Male</td>
</tr>
<tr>
<td>Responsive</td>
<td>Mother</td>
<td><em>Pan troglodytes</em></td>
<td>4</td>
<td>7</td>
<td>Female</td>
</tr>
<tr>
<td>Responsive</td>
<td>Mother</td>
<td><em>Gorilla gorilla</em></td>
<td>3</td>
<td>7</td>
<td>Male</td>
</tr>
<tr>
<td>Responsive</td>
<td>Mother</td>
<td><em>Pongo pygmaeus</em></td>
<td>3</td>
<td>10</td>
<td>Male</td>
</tr>
<tr>
<td>Responsive</td>
<td>Mother</td>
<td><em>Pan paniscus</em></td>
<td>1</td>
<td>10</td>
<td>Female</td>
</tr>
<tr>
<td>Responsive</td>
<td>Mother</td>
<td><em>Pan paniscus</em></td>
<td>1</td>
<td>7</td>
<td>Male</td>
</tr>
<tr>
<td>Basic</td>
<td>Mother</td>
<td><em>Pan troglodytes</em></td>
<td>4</td>
<td>13</td>
<td>Female</td>
</tr>
<tr>
<td>Basic</td>
<td>Mother</td>
<td><em>Pan troglodytes</em></td>
<td>4</td>
<td>16</td>
<td>Male</td>
</tr>
<tr>
<td>Basic</td>
<td>Mother</td>
<td><em>Gorilla gorilla</em></td>
<td>2</td>
<td>14</td>
<td>Male</td>
</tr>
<tr>
<td>Basic</td>
<td>Mother</td>
<td><em>Pongo pygmaeus</em></td>
<td>5</td>
<td>3</td>
<td>Male</td>
</tr>
<tr>
<td>Responsive</td>
<td>Human</td>
<td><em>Pongo spp.</em></td>
<td>1</td>
<td>29</td>
<td>Male</td>
</tr>
<tr>
<td>Responsive</td>
<td>Human</td>
<td><em>Pan troglodytes</em></td>
<td>4</td>
<td>43</td>
<td>Female</td>
</tr>
<tr>
<td>Responsive</td>
<td>Human</td>
<td><em>Gorilla gorilla</em></td>
<td>2</td>
<td>25</td>
<td>Female</td>
</tr>
<tr>
<td>Responsive</td>
<td>Human</td>
<td><em>Pongo spp.</em></td>
<td>3</td>
<td>30</td>
<td>Female</td>
</tr>
<tr>
<td>Responsive</td>
<td>Human</td>
<td><em>Pan paniscus</em></td>
<td>1</td>
<td>21</td>
<td>Female</td>
</tr>
<tr>
<td>Responsive</td>
<td>Human</td>
<td><em>Gorilla gorilla</em></td>
<td>2</td>
<td>24</td>
<td>Male</td>
</tr>
<tr>
<td>Basic</td>
<td>Human</td>
<td><em>Pongo spp.</em></td>
<td>1</td>
<td>27</td>
<td>Female</td>
</tr>
<tr>
<td>Basic</td>
<td>Human</td>
<td><em>Pongo pygmaeus</em></td>
<td>2</td>
<td>4</td>
<td>Female</td>
</tr>
<tr>
<td>Basic</td>
<td>Human</td>
<td><em>Pan troglodytes</em></td>
<td>4</td>
<td>49</td>
<td>Male</td>
</tr>
<tr>
<td>Basic</td>
<td>Human</td>
<td><em>Gorilla gorilla</em></td>
<td>2</td>
<td>22</td>
<td>Male</td>
</tr>
<tr>
<td>Basic</td>
<td>Human</td>
<td><em>Pan troglodytes</em></td>
<td>4</td>
<td>42</td>
<td>Female</td>
</tr>
<tr>
<td>Basic</td>
<td>Human</td>
<td><em>Gorilla gorilla</em></td>
<td>2</td>
<td>12</td>
<td>Female</td>
</tr>
</tbody>
</table>

### Stimuli

Wooden blocks measuring 7 cm in length, 7 cm in width, and 1.5 cm in height were presented to the participants during experimental trials in the GFC, JAC, and JAH conditions. Each stimulus had a unique and colorful stationary item mounted on its platform, such as brightly painted buttons, blocks, and plastic pieces of varying shapes and sizes (Harlow, 1959). The stimuli used in the experimental trials were randomly chosen from a larger set of 18 items. Participants were presented with a novel stimulus during each experimental trial. Stimuli were not used during the observational procedure.
Experimental Procedure

Condition 1: Following the Gaze of a Human Social Partner

A well-established tool for measuring a human infant's ability to respond to and initiate attention with an adult is the Early Social Communications Scales (Seibert et al., 1982; Mundy et al., 2003). A modified version of this protocol was used in each of the experimental conditions. Participants were tested alone, or while they were at least 3m away from conspecifics, by a human experimenter (E1) with whom they were familiar. Familiarity was defined as daily or near daily interaction with the apes in the context of animal care and/or behavioral research work. Relationships of this nature between participants and human experimenters ranged from at least one year to over 20 years. E1 was positioned approximately 1m away from the wire mesh of the enclosure for testing. Participants either approached the testing area unsolicited, or were asked to approach by E1. In a few instances, E1 used a food incentive to entice the participant to the testing area. Trials began once the participant was within 1m of the wire mesh and facing E1. During experimental trials, E1 looked straight above for 10 seconds (using eyes and head, body facing towards the participant). E1 looked directly at the participant for 10 seconds in control trials. If the participant moved away from the testing area, E1 would ask the ape to return before proceeding to the next trial. A second experimenter (E2), the PI, filmed the trials while standing behind or next to E1.

A participant's behavior was scored as gaze following if he or she looked up in the direction of E1's gaze, with both head and eyes simultaneously, or eyes alone. Due to the sometimes subtle nature of visual gaze variability in lighting conditions, and the darkly pigmented sclera in great apes, E2's observations were recorded as auditory comments.
during trials or noted in writing immediately after trials were completed to complement video recorded data (Bethell, Vick, & Bard, 2007).

Participants were offered multiple opportunities to complete 12 trials in this condition, two blocks of six trials each, with the order of trial type randomized and an equal number of experimental and control trials administered. Inter-block intervals ranged from at least a half hour to more than 24 hours. The two blocks were administered by different experimenters on some occasions due to staff availability. Trials in which the task had to be aborted because the ape left the testing area or otherwise became distracted or disengaged for extended periods were not used in the quantitative analyses. Likewise, trials in which a behavior and a potential confound occurred simultaneously were not scored, such as looking up during a control trial when a loud noise suddenly occurred in that area. Based on a statistical consultation, ten percent of scoreable trials in this condition were randomly selected and scored by an independent observer. Interobserver reliability was calculated using Cohen’s kappa at 0.90 (Bakeman & Gottmann, 1986).

**Condition 2: Following the Gaze of a Conspecific Social Partner**

This condition is a slightly modified version of a gaze following experiment conducted by Tomasello et al. (1998). E1 tested participants in this condition when the ape was in his/her social group and within 3m of at least one conspecific. Social group size ranged from two to seven members and was composed of individuals from a range of age/sex classes. E1’s position was determined by the most advantageous place to conduct the trials in this condition. For example, E1 stood on an elevated area with a clear view of the social group below when possible to stimulate a demonstrative gaze following behavior (Tomasello
et al., 1998). This was not possible in all institutions due to variability in facility design and access to elevated areas. In instances when elevated areas were not available or optimal, E1 stood within 1-3m of mesh wire on the same plane as the participants to conduct trials. In both of these scenarios, participants and conspecifics ranged between 1-6 m away from E1. Tomasello et al. (1998) reported observation distances of between 8-30m.

Trials began when the participant was facing away from E1 and one or more conspecifics were at least partially facing the subject and E1 simultaneously. During experimental trials, E1 presented a predetermined stimulus to one or more of the conspecifics who were in the position described above. In control trials, E1’s hand was held in the same position as in experimental trials, but with no object present. The maximum trial length was 60 seconds, although some trials concluded earlier if the conditions were broken. E2 filmed the trials while standing behind, next to, or sometimes more than 3m away from E1 depending on the best filming angle.

A participant’s behavior was scored as gaze following if he or she looked in the direction of the conspecific’s line of sight within the first 10 seconds of the trial period using either head and eyes simultaneously, or eyes alone. Participants were offered multiple opportunities to complete 12 trials in this condition, two blocks of six trials each, with the order of trial type randomized and an equal number of experimental and control trials administered. Inter-block intervals ranged from at least a half hour to more than 24 hours. The two blocks were administered by different experimenters on some occasions due to staff availability. Trials in which the task had to be aborted because the ape left the testing area or otherwise became distracted or disengaged for extended periods were not used in the quantitative analyses. Likewise, trials in which a behavior and a potential confound occurred
simultaneously were not scored. Based on a statistical consultation, ten percent of scoreable
trials in this condition were randomly selected and scored by an independent observer.
Interobserver reliability was calculated using Cohen’s kappa at 1.0 (Bakeman & Gottmann,
1986).

Condition 3: Joint Attention with a Human Social Partner

E1 tested participants alone, or while they were at least 3m away from conspecifics.
E1 was positioned approximately 1m away from wire mesh for testing. Trials began once the
participant was within 1m of the wire mesh and facing E1. During experimental trials, E1
presented the object in his or her hand approximately 25-30 cm below the ape’s eye level.
The object was held far enough away from the wire mesh, generally 1m, so that participants
could not touch the object during trials. E1 looked directly at the ape’s face, but remained
silent. E1 only spoke if the participant alternated gaze between the object, E1’s face, then
back to the object within a 10 second period. In control trials, E1’s hand was held in the
same position as in experimental trials, but with no object. The maximum trial length was 60
seconds, although some trials concluded earlier if the conditions were arrested. E2 filmed the
trials while standing behind or next to E1.

A participant’s behavior was scored as joint attention if he or she looked at the object,
E1’s face, then back to the object within 10 seconds. Participants were offered multiple
opportunities to complete 12 trials in this condition, two blocks of six trials each, with the
order of trial type randomized and an equal number of experimental and control trials
administered. Inter-block intervals ranged from at least a half hour to more than 24 hours.
The two blocks were administered by different experimenters on some occasions due to staff
availability. Trials in which the task had to be aborted because the ape left the testing area or otherwise became distracted or disengaged for extended periods were not used in the quantitative analyses. Likewise, trials in which a behavior and a potential confound occurred simultaneously were not scored. Based on a statistical consultation, ten percent of storable trials in this condition were randomly selected and scored by an independent observer. Interobserver reliability was calculated using Cohen’s kappa at 0.89 (Bakeman & Gottmann, 1986).

**Condition 4: Joint Attention with a Conspecific Social Partner**

Trials began once the participant and the conspecific were within 1-3m of each other and 1m away from the wire mesh and facing E1. Participants were paired with a compatible conspecific in this condition based on E1’s recommendation. During experimental trials, E1 presented a stimulus to the dyad with the entire body turned away from the pair. E1 held the object in the hand either above the shoulder or below the shoulder depending on the best angle for presentation at both apes’ eye levels. Consistent positioning was used by E1 in all experimental and control trials. The object was held far enough away from the wire mesh, generally 1m, so that participants could not touch the object during trials. In control trials, E1’s hand was held in the same position as in experimental trials, but with no object. The maximum trial length was 60 seconds if conditions were maintained. E2 filmed the trials while standing behind or next to E1.

A participant’s behavior was scored as joint attention if he or she looked at the object, the conspecific’s face, then back to the object within 10 seconds. Participants were offered multiple opportunities to complete 12 trials in this condition, two blocks of six trials each,
with the order of trial type randomized and an equal number of experimental and control trials administered. Inter-block intervals ranged from at least a half hour to more than 24 hours. The two blocks were administered by different experimenters on some occasions due to staff availability. Trials in which the task had to be aborted because the ape left the testing area or otherwise became distracted or disengaged for extended periods were not used in the quantitative analyses. Trials in which a behavior and a potential confound occurred simultaneously were not scored. Based on a statistical consultation, ten percent of scoreable trials in this condition were randomly selected and scored by an independent observer. Interobserver reliability was calculated using Cohen’s kappa at 0.77 (Bakeman & Gottmann, 1986).

**Observational Procedure**

Data were collected over a nine month period with observations completed within a time range of several days to or over two weeks depending on how many individuals participated from each institution. Participants were observed for a total of four hours each while in their normal social group. Social groups ranged from 2-7 members and the age/sex class composition of individuals varied. Data were collected using a tablet PC in one-hour blocks balanced across the morning and afternoon.

Continuous focal animal sampling was used to capture behaviors outlined in the behavioral catalog (Appendix B) (Altmann, 1974). Great ape social behavior ethograms from previous studies were consulted for the development of the behavioral catalog used the current study (Enomoto, 1990; Ross & Lukas, 2001). The behavioral catalog in the current study was designed to record social behavior data across the four types of great ape, so the
behavior categories were simplified and condensed compared to the referenced ethograms (Enomoto, 1990; Ross & Lukas, 2001).

Two global categories of social interaction, affiliative and agonistic behaviors, were included in the behavioral catalog. Social play, sexual behavior, and contact behavior were included within the affiliative behavior category. Specific agonistic behaviors included display, displace, and agonistic contact. The frequency of affiliative and agonistic behaviors was collected. Specific solitary behaviors included play and rest. Duration data were collected for time engaged in solitary behavior. Finally, there was a “not visible” category for instances in which the observer’s view of the focal animal was briefly obscured. Interobserver reliability was calculated using Cohen’s kappa at 0.90 (Bakeman & Gottmann, 1986).

The results of the experimental procedure will be reported in three sections. The first section will report participants’ production of joint attention behaviors in experimental trials compared control trials. The second section will report the effects of care style and the type of caregiver on gaze following behaviors. Species effects on gaze following behaviors will also be reported in this section. The final section will relay the effects of care style and the type of caregiver on joint attention behaviors. Any species effects on joint attention behaviors will also be reported.

The results of the social behavior observations will be reported in three sections. The first section will report the effects of care style and the type of caregiver on the occurrence of agonistic behavior in great apes. Species effects on the occurrence of agonistic behavior will also be reported. The second section will report the effects of care style and the type of caregiver on the frequency of affiliative behavior. The final section will report the effects of
care style and the type of caregiver on the duration of time spent engaged in solitary behavior. Any species effects on time spent in solitary behavior will also be reported.
CHAPTER 3: RESULTS

Performance on Experimental Trials Compared to Control Trials

A Wilcoxon signed-rank test was conducted to assess if participants produced behaviors in experimental trials more often than in control trials in each of the four experimental conditions: gaze following with a human [GFH], gaze following with a conspecific [GFC], joint attention with a human [JAH], and joint attention with a conspecific [JAC]. Behaviors relevant to each condition were: 1) look up or no look up (GFH), 2) follow gaze of conspecific or no following the gaze of conspecific (GFC), 3) alternate gaze between object, human’s face and object or no alternate gaze; and 4) alternate gaze between object, conspecific’s face and object or no alternate gaze (JAC). The mean proportion response in experimental trials vs. control trials was significantly different in each condition, $p < 0.0001$. Figure 1 presents the mean proportion of behaviors in experimental and control trials within each condition.

Experimental Conditions: Data Analysis Overview

The difference in the mean proportion between experimental and control trials was used as the dependent measure in analyses of each of the four experimental conditions due to the low production of behaviors in control trials. In some instances, participants completed an unequal number of experimental and control trials due to a disruption in the conditions necessary to continue a task, such as remaining within proximity to a conspecific or human partner. Therefore, mean proportions were weighted in all four experimental conditions. Specifically, observations based on a higher number of trials were assigned more weight than observations based on fewer trials because the statistical assumption is that the variability of
observed values is inversely proportional to the number of experimental trials. An alpha level of 0.05 was used for all statistical tests unless otherwise indicated.

Gaze Following: Effect of Care Group and Species

A 2 (care style: responsive, basic) x 2 (caregiver: mother, human) x 2 (gaze following with a human social partner, gaze following with a conspecific social partner) repeated measure analysis of variance (ANOVA) revealed no main effects of care style, \( F_{1, 19.4} = 2.97, p = 0.10 \) or caregiver, \( F_{1, 19.4} = 0.0, p = 0.99 \); no significant interaction between care style and caregiver, \( F_{1, 19.4} = .01, p = 0.91 \); no main effect of condition type, \( F_{1, 21} = 0.37, p = 0.55 \); no significant interaction between care style and condition type, \( F_{1, 21} = 0.0, p = 0.96 \); no significant interaction between caregiver and condition type, \( F_{1, 21} = 0.0, p = 0.98 \); and no significant interaction among care style, caregiver, and condition type, \( F_{1, 21} = 0.21, p = 0.65 \). The mean proportions for the four care groups on the gaze following tasks are presented in Figure 2. A t-test was used to assess differences in the means for care group performance on task comparisons (gaze following human vs. gaze following conspecific). There were no significant differences in the RCM group performance, \( t_{9.6} = -0.14, p = 0.89 \), BCM group performance, \( t_{21.7} = -0.41, p = 0.69 \), RCH group performance, \( t_{19.6} = -0.60, p = 0.55 \) and BCH group performance, \( t_{22.3} = -0.03, p = 0.97 \). The mean proportions for care group performance on gaze following with humans compared to gaze following with conspecifics are presented in Figure 3.

\(^2\) The non-integer number of the degrees of freedom is an effect of using weighted means in the analyses.
A 4 (species: bonobo, chimpanzee, gorilla, orangutan) x 2 (task: gaze following with a human social partner, gaze following with a conspecific social partner) repeated measures ANOVA revealed a significant interaction between species and condition type within tasks, F(3, 20.8) = 4.83, p = 0.01. Mean proportions according to species for each gaze task are presented in Figure 4. Pairwise comparison tests were conducted on each of the six possible species combinations (bonobo-gorilla, bonobo-orangutan, chimpanzee-gorilla, chimpanzee-orangutan, gorilla-orangutan, and bonobo-chimpanzee). Bonferroni’s correction procedure was used to control the type I error error (α = .05) across the set of multiple pairwise species comparisons. This correction was appropriate because it adjusted for multiple tests of statistical significance on the same data set to protect against the possibility that the repeated multiple comparison may have falsely indicated significance purely due to chance. The adjusted cut-off for the p-value was obtained by dividing the alpha level by the number of comparisons (0.05/6, p < 0.0083). The pairwise comparisons revealed that bonobos (M = 83.33, SE = 12.46) responded to human social partners significantly more often than chimpanzees (M = 20.22, SE 9.03), p = 0.0003 and gorillas (M = 37.11, SE = 8.32), p = 0.0043, while orangutans (M = 54.76, SE = 8.16) responded to human social partners significantly more often than did chimpanzees (M = 20.22, SE 9.03), p = 0.0077. Mean proportions regarding the gaze following task with humans according to species are presented in Figure 5. There were no significant pairwise comparisons when the social partner was a conspecific. Between task comparisons (gaze following human vs. gaze following conspecific) yielded a significant difference for bonobos (M = -54.61, SE = 18.22), t(20.2) = -3.00, p = 0.0071. Species mean proportions between gaze tasks are presented in Figure 6.
Joint Attention: Effect of Care Group and Species

A 2 (care style: responsive, basic) x 2 (caregiver: mother, human) x 2 (joint attention with a human, joint attention with a conspecific) repeated measures ANOVA revealed no significant main effects of care style, $F(1, 21.1) = 0.23$, $p = 0.64$ or caregiver, $F(1, 21.1) = 0.06$, $p = 0.81$ and no significant interaction between care style and caregiver, $F(1, 21.1) = 0.03$, $p = 0.86$. There was no main effect of condition type, $F(1, 22.6) = 2.25$, $p = 0.15$; no significant interaction between care style and condition type, $F(1, 22.6) = 0.20$, $p = 0.66$; no significant interaction between caregiver and condition type $F(1, 22.6) = 2.79$, $p = 0.11$; no significant interactions across care style, caregiver, and condition type $F(1, 22.6) = 0.43$, $p = 0.52$. Mean proportions within each joint attention task according to care group are presented in Figure 7. A t-test was used to assess differences in the means for care group performance on task comparisons (joint attention with human vs. joint attention with conspecific). There were no significant differences on the RCM group performance, $t(22) = -0.58$, $p = 0.56$, BCM group performance, $t(40) = -0.41$, $p = 0.58$, RCH performance, $t(24.1) = -1.45$, $p = 0.16$ or BCH performance, $t(23) = -1.65$, $p = 0.11$. Mean proportions between joint attention tasks according to care group are presented in Figure 8.

A 4 (species: bonobo, chimpanzee, gorilla, orangutan) x 2 (task: joint attention with a human, joint attention with a conspecific) repeated measure ANOVA revealed no main effect of species, $F(3, 22.5) = 0.71$, $p = 0.55$, or condition type within joint attention tasks, $F(1, 22.1) = 1.93$, $p = 0.18$. There was no significant interaction between species and condition type within joint attention tasks, $F(3, 22.3) = 1.04$, $p = 0.39$. Mean proportions within each joint attention task according to species are presented in Figure 9. Between task comparisons (joint attention with human vs. joint attention with conspecifics) yielded no significant
differences for species. Species mean proportions between joint attention tasks are presented in Figure 10.

**Agonistic Behavior: Effect of Care Group and Species**

Multiple tests of independence with the 2-sided Fisher's exact test were required to address the agonistic behavioral data due to the low occurrence of these behaviors for each individual participant. A chi-square test was not appropriate because the assumption of expected counts equaling five or more for each cell was not satisfied. Agonistic behavior was categorized as either present (score of 1) or absent (score of 0) for each individual participant across the four hours of observation.

Various tests of independence using the 2-sided Fisher's exact test revealed no evidence of association between the occurrence of agonistic behavior directed towards conspecifics based on the following care group factors: care style only (responsive, basic) ($p > 0.99$), caregiver only (mother, human) ($p > 0.99$), a combination of care style and caregiver ($p = 0.94$), caregiver (human) and care style (responsive, basic) ($p > 0.99$), caregiver (mother) and care style (responsive, basic) ($p > 0.99$), care style (basic) and caregiver (mother, human) ($p > 0.99$), and care style (responsive) and caregiver (mother, human) ($p = 0.63$). Likewise, various tests of independence using the 2-sided Fisher’s exact test revealed no evidence of association between the occurrence of agonistic behavior directed towards participants by conspecifics and the following factors: care style only (responsive, basic) ($p = 0.68$), caregiver only (mother, human) ($p = 0.40$), a combination of care style and caregiver ($p = 0.40$), caregiver (human) and care style (responsive, basic) ($p > 0.99$), caregiver (mother) and care style (responsive, basic) ($p = 0.55$), care style (basic) and
caregiver (mother, human) \( (p > 0.99) \), and care style (responsive) and caregiver (mother, human) \( (p = 0.14) \).

Multiple tests of independence using the 2-sided Fisher’s exact test revealed a significant association between the occurrence of agonistic behavior directed towards conspecifics and the species of the participants \( (p = 0.0040) \). Pairwise comparison tests were conducted on each of the six possible species combinations (bonobo-gorilla, bonobo-orangutan, chimpanzee-gorilla, chimpanzee-orangutan, gorilla-orangutan, and bonobo-chimpanzee). Bonferroni’s correction procedure was used to control the type I error \( (\alpha=0.05) \) across the set of multiple pairwise species comparisons. This correction was appropriate because it adjusted for multiple tests of statistical significance on the same data set to protect against the possibility that the repeated multiple comparison may have falsely indicated significance purely due to chance. The adjusted cut-off for the \( p \)-value was obtained by dividing the alpha level by the number of comparisons \( (0.05/6, p < 0.0083) \). The pairwise comparisons revealed that overall gorillas initiated agonistic behaviors significantly more often than orangutans, \( p = 0.0047 \). Each gorilla in the study initiated agonistic behavior (at least once) across the four observation hours, so there was never an absence of agonistic behavior in gorillas. In contrast, agonistic behavior was present for only one orangutan across the four hours of observation. It should be emphasized that this result does not indicate that gorillas never affiliated with each other. Affiliative behavior based on care group is presented in Figure 12. The species pairwise comparisons are presented in Figure 11. A test of independence using the 2-sided Fisher’s exact test revealed no significant species association in the frequency of agonistic behavior directed towards participants \( (p = 0.58) \).
In the current study, gorillas were the only species participants who lived in social groups that included all males or a mixed-sex group. A Wilcoxon rank-sum test was used to assess any difference in the average frequency of male gorillas directing agonistic behavior towards conspecifics based on living in a mixed-sex group or an all male group. There was no significant difference between groups, $p = 0.20$.

**Affiliative Behavior: Effect of Care Group and Species**

Due to variability in the mean ages of early care groups [RCM ($M = 8.75$), BCM ($M = 11.5$), RCH ($M = 25.33$), BCH ($M = 26$)] and species groups [chimpanzees ($M = 25.29$), bonobos ($M = 12.67$), gorillas ($M = 16.29$), and orangutans ($M = 16.43$)], a Pearson’s correlation coefficient was used to examine the strength and direction of the relationship between age and the frequency of affiliative behavior directed towards conspecifics and the frequency of affiliative behavior directed towards participants. The Pearson’s product-moment correlation coefficient revealed a moderate association between age and the frequency of affiliative behavior directed towards conspecifics ($r = -0.52$, $p = 0.009$). The correlation was negative, indicating that higher age was linearly related to a lower frequency of affiliative behavior directed towards conspecifics. Based on this information, an analysis of covariance (ANCOVA) procedure was used to compare the averages of the dependent variables after removing the potentially confounding variable of age by treating all participants as though they have the same mean age.

A 2-way ANCOVA (2 factors: care style and caregiver, 2 levels for each factor: responsive, basic and mother, human) revealed a significant interaction between care style and caregiver, $F = 4.58$, $p = 0.0455$ on the average log frequency of affiliative behavior
directed towards conspecifics. Mean frequencies of affiliative behavior towards conspecifics including care style and caregiver are presented in Figure 12. The interaction indicates that the RCM group initiated affiliative behavior with conspecifics significantly more often than the RCH group. The covariate of age was not significant, $F = 1.30, p = 0.27$, and therefore did not effect the frequency of affiliative behavior directed towards conspecifics. There was a main effect of caregiver on the frequency of affiliative behavior directed towards participants, $F = 4.42, p = 0.0491$. The mean frequencies of affiliative behavior directed toward participants are presented in Figure 13. The effect indicates that conspecifics directed affiliative behavior towards mother-raised participants significantly more often than towards human-raised participants. The covariate of age was not significant, $F = 0.28, p = 0.61$, and therefore did not effect the frequency of affiliative behavior directed towards participants.

A 1-way ANCOVA (1 factor: species, 4 levels: bonobos, chimpanzees, gorillas, orangutans) revealed no significant effect of species type on the frequency of affiliative behavior directed towards conspecifics, $F = 0.34, p = 0.79$ or on the frequency of affiliative behavior directed towards participants, $F = 1.76, p = 0.19$. The covariate of age was not significant for the frequency of affiliative behavior directed towards participants, $F = 2.45, p = 0.13$. However, the covariate of age was significant for the frequency of affiliative behavior directed towards conspecifics, $F = 5.14, p = 0.04$, but the ANCOVA procedure removed the potentially confounding variable of age by treating all participants as though they have the same mean age.
Solitary Behavior: Effect of Care Group and Species

A 2-way ANCOVA (2 factors: care style and caregiver, 2 levels: responsive, basic and mother, human) revealed a main effect of caregiver on the average duration of time spent engaged in solitary behavior, $F(1) = 6.23, p = 0.02$. Post-hoc pairwise comparisons of the six combinations of care style and caregiver using Tukey's method showed that the RCH group spent a significantly higher percentage of time engaged in solitary behavior than the RCM group ($p = 0.004$). The mean percentage of time spent in solitary behavior based on care group is presented in Figure 14. No significant interactions between care style and caregiver were revealed, $F = 2.17, p = 0.16$. The covariate of age was not significant, $F = 1.33, p = 0.26$, and therefore did not affect the duration of time spent engaged in solitary behaviors.

A 1-way ANCOVA (1 factor: species, 4 levels: bonobos, chimpanzees, gorillas, orangutans) revealed no significant effect of species type on the average duration of time spent engaged in solitary behavior, $F = 2.55, p = 0.08$. The covariate of age was not significant, $F = 2.36, p = 0.14$, and therefore did not effect the average duration of time spent engaged in solitary behaviors.
Figure 1. Mean proportion of behavioral responses in experimental vs. control trials in the four conditions. The response measured in the joint attention tasks was gaze alternation and the response measured in the gaze following task was look up. Participants engaged in joint attention behaviors significantly more often in experimental trials compared to control trials. Error bars represent standard error of the mean. (***) indicates a significant difference, $p<0.001$. 
Figure 2. Mean proportion of behavioral responses (look up) in the gaze following tasks with both conspecific and human social partners based on care group. There are no statistically significant differences among care groups. Error bars represent standard error of the mean.

Figure 3. Mean proportion of care group behavioral responses (look up) in the gaze following tasks. Group performance on gaze following with a human is directly compared to gaze following with a conspecific. There are no statistically significant differences among care groups. Error bars represent standard error of the mean.
Figure 4. Mean proportion of behavioral responses (look up) in gaze following tasks with both conspecific and human social partners according to species. There was a significant interaction between species and gaze following with a human. The species interaction is presented in Figure 5. Error bars represent standard error of the mean. (*) indicates a significant difference, $p < 0.05$.

Figure 5. Mean proportion of behavioral responses (look up) in gaze following tasks with a human social partner based on species. Bonobos followed human gaze more often than chimpanzees and gorillas. Orangutans followed human gaze more often than chimpanzees. Error bars represent standard error of the mean. (***) indicates a significant difference, $p < 0.001$; (**) indicates a significant difference, $p < 0.01$. 
Figure 6. Mean proportion of behavioral responses (look up) in the gaze following tasks based on species. Species performance on gaze following with a human is directly compared to gaze following with a conspecific. Error bars represent standard error of the mean. (***) indicates a significant difference, $p < 0.01$. 
Figure 7. Mean proportion of care group behavioral responses (*gaze alternation*) in the joint attention tasks with both conspecific and human social partners. There are no statistically significant differences among care groups. Error bars represent standard error of the mean.

Figure 8. Mean proportion of care group behavioral responses (*gaze alternation*) in the joint attention tasks. Group performance on joint attention with a human is directly compared to joint attention with a conspecific. There are no statistically significant differences among care groups. Error bars represent standard error of the mean.
Figure 9. Mean proportion of species behavioral responses \((\text{gaze alternation})\) in joint attention tasks with both conspecific and human social partners. There are no statistically significant differences among species. Error bars represent standard error of the mean.

Figure 10. Mean proportion of species behavioral responses \((\text{gaze alternation})\) in the joint attention tasks. Species performance on joint attention with a human is directly compared to joint attention with a conspecific. There are no statistically significant differences among species groups. Error bars represent standard error of the mean.
Figure 11. Agonistic behavior directed towards conspecifics based on individual participants (N=24). Agonistic behavior was counted as present (1) or absent (0) for each individual across four hours of observation. All the gorillas in the study (N=7) initiated agonistic behavior at least once across four observation sessions (i.e., there was never an absence of agonistic behavior for each gorilla). (**) indicates a significant association, $p < 0.01$.

Figure 12. Mean frequency of affiliative behavior directed towards conspecifics based on care group. Great apes raised with responsive care by the mother initiated affiliative behavior with conspecifics more often than apes raised by responsive humans. (*) indicates a significant difference, $p < 0.05$. 
Figure 13. Mean frequency of affiliative behavior directed towards participants by conspecifics based on care group. Mother-raised great apes were the recipients of affiliative behavior more often than human-raised great apes. (*) indicates a significant difference, $p < 0.05$.

Figure 14. Mean percent of time engaged in solitary behavior based on care group. Great apes raised by responsive humans spent more time engaged in solitary behaviors than great apes raised by mothers. (**) indicates a significant association, $p < 0.01$. 
CHAPTER 4: DISCUSSION

The primary result of the current study provides evidence that all great apes are capable of joint attention behaviors with other individuals. Specifically, great apes responded to gaze cues and initiated joint attention around an object with both conspecifics and humans significantly more often in experimental trials compared to control trials. Although all four types of great ape have demonstrated the ability to follow the gaze of humans around barriers and to distant locations (Brauer et al., 2005) the current study is the first to experimentally demonstrate the ability of bonobos, gorillas, and orangutans to follow the gaze of conspecifics. Chimpanzee participants also followed the gaze of conspecifics more often in experimental trials compared to control trials. This finding supports the results of an earlier experimental study which reported that chimpanzees reliably followed the gaze of conspecifics (Tomasello et al., 1998). The finding that great apes are capable of initiating joint attention with humans around an object concurs with results from several studies (Bard, 1990; Carpenter et al., 1995; Gomez, 1990, 1991, 1996; Leavens & Hopkins, 1998; Miles et al., 1996; Russell et al., 1997). However, the current study is unique because great apes’ ability to initiate joint attention around an object was tested with both conspecific and human social partners in an experimental setting. Great apes demonstrated proficiency in initiating joint attention with both types of social partners and did so significantly more often in experimental conditions compared to control conditions.

Great apes’ joint attention abilities have been interpreted in several different ways. Some researchers have concluded that great apes lack any mentalistic understanding of visual gaze (Heyes, 1998; Karin-D’Arcy, 2005; Povinelli & Vonk, 2003), while others have proposed that the attention abilities of great apes, particularly chimpanzees, suggest at least
some understanding of the psychological state of others but not to the same extent as humans (Brauer et al., 2005; Call, 2001; Tomasello et al., 2003). Specifically, Tomasello et al. (2003) posited that chimpanzees know what others’ have seen by monitoring their gaze and they know that barriers block visual access. Additionally, chimpanzees know whether others have seen something in the immediate past and they know something about the goals of others. However, Tomasello et al. (2003) concluded that chimpanzees, unlike human children, may not understand attention, defined as a comprehension that others can attend to different aspects of items or things within the same gaze direction. In addition, Tomasello et al. (2003) suggested that chimpanzees may not understand that others can view the same object from different perspectives, and they may not fully comprehend the intentions or beliefs of others. Finally, some researchers have concluded that great apes understand attention and intention, but that evidence is still lacking for an understanding of false beliefs (Parker & McKinney, 1999; Suddendorf & Whiten, 2001).

The current study proposes that the ability of great apes to initiate joint attention with other individuals indicates that they possess an understanding of others as intentional agents. Tomasello (1995a) defined joint attention as a social phenomenon in which two individuals, in his example a human adult and human infant, know that they are attending to a common object or event. He suggested that mutual knowledge is present if both individuals simultaneously attend to a particular item and that the infant alternates gaze between the object and the adult’s face. This exchange is most convincingly described as joint attention if the infant spontaneously initiates attention with an adult, as opposed to the adult soliciting the infant to attend to the object (Tomasello, 1995a). Tomasello (1995a) interpreted these behaviors as evidence that human infants understand something about the intentional state of
others, and that this understanding is critical to the development of a sophisticated appreciation of the mental states of others. The great apes in the current study satisfied the criteria for joint attention behavior outlined by Tomasello (1995a). Specifically, great apes initiated joint attention with both humans and conspecifics through gaze alternation between an object and partners’ faces. In the case of joint attention with humans, the experimenter remained silent and only verbally engaged with the participant after he or she solicited the human’s attention with alternating gaze behaviors. Data from this study do not address if whether great apes who demonstrate gaze following and joint attention behaviors around objects possess a different level of understanding others as intentional agents compared to great apes who have demonstrated the full range of joint attention behaviors, including declarative pointing, imitation, social referencing, and referential language. An additional study testing these behaviors with the current study’s participants would be necessary to address this question. However, reports from other studies suggest that great apes are capable of a range of joint attention behaviors, including social referencing and use of declaratives such as pointing (Carpenter et al., 1995; Gomez, 1990, 1991, 1996; Leavens & Hopkins, 1999; Russell et al., 1997).

The second result of the current study demonstrates that there are no effects of care style received by participants during the first six months of life or the species of the caregiver on joint attention behaviors with conspecifics and humans in great apes. Several possible explanations for these results are considered. The most plausible explanation is that the qualitative differences between basic care and responsive care examined in this study were not sufficiently distinct enough to impact great apes’ ability to produce joint attention behaviors with conspecifics or humans. It is a strong possibility that joint attention is a
durable cognitive process that is impervious to insufficiently distinct differences in early care in great apes. Basic forms of attention, such as gaze cues, appear to have adaptive benefits for a range of species because they provide information about salient features in the environment, such as the location of food or predators (Emery, 2000; Tomasello et al., 1998; Whiten, 1991). Gaze cues may be particularly significant for nonhuman primates, many species of whom must keep track of the social behaviors and interactions of conspecifics (Emery, 2000).

However, the processes through which primates share attention and observe information vary according to species (Parker & Russon, 1996). For example, evidence suggests that great apes, in contrast to monkeys, are capable of social learning through true imitation (Russon & Galdikas, 1993; Tomasello, Kruger & Ratner, 1993). There are also reports of great apes actively teaching infants (Boesch, 1991; Fouts, 1994) or infants observing the skillful behavior of the mother through a master-apprentice style of education (Matsuzawa et al., 2001). The capacity of great apes to take the mental perspective of another individual would not be possible if the basic cognitive processes upon which these skills are built, including joint attention, were overly sensitive to subtle changes in the environment (Brune & Brune-Cohrs, 2006; Parker & Russon, 1996). From an evolutionary perspective, possession of the cognitive capacities that allow for the development of these skills increases individuals' inclusive fitness (Brune & Brune-Cohrs, 2006).

An alternative explanation for the lack of an effect of care style on great ape joint attention behavior is that environmental changes mediated any effects of care style on joint attention that may have originally been evident in early infancy. For example, studies with humans suggest that exposure to serious negative life events, such as the death of a family
member, parental divorce, or serious illness, can result in a reversal of a secure attachment classification during infancy to an insecure classification during adulthood (Hamilton, 2000; Lewis, Feiring, & Rosenthal, 2000; Waters et al., 2000). In addition, research with Romanian orphans who were living in seriously deprived institutional environments since shortly after birth significantly showed that they improved cognitive performance once they were placed in a stable family environment (O’Connor et al., 2000; Rutter, 2006). O’Connor et al. (2000) concluded that resilience and a normalized caregiving environment played a role in mediating the effects of early institutional care. Although it has been demonstrated that environmental factors can mediate the effects of early care in humans (Hamilton, 2000; Lewis, Feiring, & Rosenthal, 2000; O’Connor et al., 2000; Rutter, 2006; Waters et al., 2000), the current study cannot directly address this issue for several reasons. First, since the care style under which participants were raised during their first six months of life was determined retrospectively through records and interviews, it was not possible to make assessments of joint attention skills during that period of early infancy. Therefore, it is impossible to determine if participants were either proficient or deficient in joint attention behaviors and whether this determination was affected by the style of care they received during early infancy. Likewise, there are no data from the current study regarding environmental variables that may have mitigated the effects of early care on joint attention for these participants if in fact a difference was detected during and after the infancy period.

Another possible explanation regarding the lack of an effect of early care on joint attention is that the emergence of joint attention behaviors is not dependent on any variables of early care, including responsive care, in great apes. For example, Tomasello (1995b) has suggested that although there are certain similarities between human and chimpanzee
mother-infant interactions, such as eating, sleeping, and traveling together, human mothers
provide a significantly more active role in shaping their infant's development. Tomasello
(1995b) stressed that scaffolding, the ways in which human adults assist and instruct children
to work through certain activities, is a unique human characteristic that is critical to the
cultural transmission of knowledge. Tomasello (1995b) suggested that the ability to view
others as intentional agents is necessary to engage in social learning and imitation, which he
posits are the first steps involved in cultural learning. Cultural learning is embodied by the
transmission of culture over time, including continual modifications of artifacts, technology
and concepts. This modification throughout multiple generations is also referred to as the
ratchet effect (Tomasello, 1995b). Tomasello and Call (1996) proposed that the ratchet
effect only occurs in humans and cited the virtual lack of evidence of teaching in nonhuman
primates to support the position that human culture, and the cognitive processes that support
it, are uniquely human. More recently, Tomasello et al. (2003) has argued that great apes,
particularly chimpanzees, are capable of understanding some of the psychological states of
others, but that they may not have a mentalistic understanding of attention. The current study
has demonstrated that all great apes are capable of joint attention around an object with both
conspecifics and humans, and they do so in ways that indicate an understanding of attention
as outlined by Tomasello (1995a).

There is a body of evidence that suggests that social engagement during early infancy
plays at least some role in fostering the development of cognitive skills in great apes.
Chimpanzee mothers encourage infant development through a variety of tactile behaviors,
and mother and infants also engage in frequent mutual gaze during early infancy (Bard,
1995; Bard et al., 2005; Goodall, 1986; Okamoto-Barth et al., 2007). Bard et al. (2005)
investigated how chimpanzee mothers participated in the socialization of attention with their infants and found that they did so in ways similar to human mother-infant dyads.

Specifically, Bard et al. (2005) reported that human mother-infant dyads engaged in mutual gaze at comparable rates to chimpanzee mother-infant dyads during the first three months of life. One major difference was that the duration of mutual gaze was longer in human mother-infant pairs than in chimpanzees (Bard et al., 2005). Although there are relatively few examples of active teaching in great apes (e.g., Boesch, 1991; Fouts, 1994), Matsuzawa, Biro, Humle, Inoue-Nakamura, Tonooka, & Yamakoshi (2001) described a unique form of social learning in chimpanzees through the master-apprentice method. The master-apprentice method of education is characterized by a lack of active teaching or formal instruction, an offspring's prolonged exposure to the activities of the mother based on the long period of maturation and the strength of the mother-infant attachment, and the motivation of the offspring to copy the mother's behavior (Matsuzawa et al., 2001; Matsuzawa, 2007). Matsuzawa (2007) makes the point that chimpanzee mother-infant dyads in the wild typically do not interact around an object and each other in a triadic manner, but rather the infant's close observation of the mother's behavior may assist with the infant's problem solving skills. However, the capacity for engaging in triadic relations or joint attention around an object in great apes has been demonstrated in the current study, as well as in previous studies (Carpenter et al., 1995; Gomez, 1990, 1991, 1996; Leavens & Hopkins, 1999; Russell et al., 1997). Although speculation remains about the role of great ape mothers in the development of joint attention, data were not available from the current study on the ways in which ape mothers or human caregivers may have facilitated the development of participants' attention abilities during the first six months of life.
Although care style during the first six months of life did not affect joint attention behaviors of great apes in this study, there were species differences related to certain aspects of following the gaze cues of human partners. Bonobos responded to the gaze of humans significantly more often than gorillas and chimpanzees, and orangutans responded to the gaze of humans significantly more often than chimpanzees. It is possible that there are true species differences in great apes' attention to human visual cues. Okamoto-Barth et al. (2007) recently suggested that bonobos and chimpanzees possess a better understanding of the referential nature of seeing because they followed gaze of a human experimenter significantly more often than gorillas and orangutans in a series of tasks that included visual barriers and targets. However, the results of the current study suggest that orangutans and bonobos are more sensitive to human gaze than chimpanzees or gorillas. Finally, Brauer et al. (2005) found no statistically significant differences across the four types of great ape in their ability to follow the gaze of a human experimenter to both distant locations and around barriers. It is possible that the variation in great ape species performance in these studies is related to methodological differences. For example, Brauer et al. (2005) tested apes' ability to follow the gaze direction of a human to a location behind a barrier. Okamoto-Barth et al. (2007) also incorporated barriers into the experimental design, but they used barriers to block experimenters' line of sight to a target rather than obscuring the apes' visual access to a target. Okamoto-Barth et al. (2007) suggest that this design is more complex because great apes must choose among different locations as possible targets of the experimenter's gaze. The current study did not employ any barriers in the gaze following tasks, but all great ape participants produced joint attention behaviors with both conspecifics and humans around an object and did so in ways that indicate an understanding of others as intentional agents.
(Tomasello, 1995a). It would be useful to replicate the Okamoto-Barth et al. (2007) study with different great ape subjects to determine if similar species results were elucidated.

An alternative explanation is that some participants were more attuned to the visual cues of humans because they experienced increased opportunities for routine interaction with people and human cultural artifacts than the other great apes in the study. For example, the bonobo participants were all raised in an environment in which there was frequent interaction with humans and human cultural artifacts in the context of cognitive testing (Carpenter et al., 1995). Despite being raised in a similar cultural environment, however, the bonobo participants did experience different early histories. For example, two of the bonobos were raised by responsive mothers from birth and the remaining bonobo was raised by a primary human caregiver in a responsive style. All of the bonobos have had long-term, stable relationships with conspecifics in addition to similar relationships with human caregivers. The remaining great ape participants in the study were raised in environments in which interactions with humans and human cultural artifacts varied considerably on the spectrum of enculturation. For example, the backgrounds of the orangutans and chimpanzees in the study ranged from extensive experience with cognitive testing for some individuals, moderate levels of interaction with humans outside the context of routine care for others, and a complete absence of cognitive testing and little opportunity to interact with humans outside the context of routine care for the remaining great ape participants.

Although the enculturation effect is the most likely explanation for the propensity of the bonobos to follow the gaze of human experimenters (Carpenter et al., 1995), it is less likely enculturation explains the disparate performance of orangutans and chimpanzees because these participants experienced more variability in their exposure to humans,
cognitive testing, and human cultural artifacts. Several researchers have posited that chimpanzees and bonobos are more sensitive to gaze due to the gregarious nature of their social systems compared to orangutans, whose social system is often described as solitary (Brauer et al., 2005; Liebal et al., 2004). However, it is inaccurate to classify orangutans as solitary. Rather, they have an extended social system and varying levels of sociality in particular populations (Utami, Wich, Sterck, & van Hoof, 1997; van Schaik, 1999; Wich et al., 2004). It is possible that orangutans are more sensitive to the gaze of humans compared to chimpanzees because the lack of a social hierarchy allows orangutans the flexibility to attend human caregivers. However, the mixed results regarding species performances on visual attention tasks with humans (Okamoto-Barth et al., 2007; Brauer et al., 2005), including the current study, requires that additional studies be conducted before this issue may be fully addressed.

The observations of social behavior in the current study demonstrated that great apes who received responsive care during the first six months of life initiated affiliative behavior with conspecifics significantly more often than great apes who received responsive care from humans. In addition, conspecifics directed affiliative behavior towards mother-raised great apes significantly more often than towards human-raised great apes. Two possible explanations for these results are considered. Responsive great ape mothers may transmit information about social behavior to infants during the first six months of life that is especially salient for infants’ propensity to exhibit prosocial behavior with conspecifics. Similarly, early exposure to great ape mothers whose infants received either responsive or basic care during the first six months equipped great apes with social skills that stimulated others to direct affiliative behavior towards them more often than great apes who received
care from humans. There are several studies that support the importance of great ape infants' exposure to their mothers in early infancy for the development of appropriate social behaviors (Bloomsmith et al., 2002; Meder, 1989; Novak & Sackett, 2006). An alternative explanation is that the difference in frequency of affiliative behavior based on care style and the species of the caregiver is an artifact related to the relatively small number of observation hours in this study. In order for a definitive explanation to be chosen, additional behavioral observations are needed.

There was no effect of care style or the species of the caregiver on the frequency with which great ape participants initiated, or were the recipients of, agonistic behavior. The low rates of agonistic behavior across all participants, regardless of the style of care received during the first six months, fall within the typical range based on Sussman, Garber, and Cheverud's (2005) review of primate sociality which found that agonistic behavior typically makes up less than 1% of great apes' activity budget. Based on these results, Sussman, Garber and Cheverud (2005) suggested that the dominant paradigm in which primate sociality has traditionally been examined, namely through a focus on competition and aggression, has overlooked the importance of cooperation and affiliation. If affiliation and cooperation are the most important behaviors governing primate sociality, as suggested by Sussman, Garber and Cheverud (2005), it is possible that any minor differences in care style received during the first six months of life do not impact rates of agonistic behavior in great apes. Conversely, the importance of affiliative and cooperative behavior proposed by Sussman and colleagues (2005) may help to explain participants' sensitivity to information from responsive mothers regarding the initiation of affiliative behaviors with conspecifics. It is also possible that this result, like the result regarding affiliative behavior, is an artifact
related to the relatively small number of observation hours in this study. For example, several studies reported higher rates of agonism in human-reared apes than in mother-reared apes (Baker et al., 2000; Gold, 1992; Meder, 1985, 1989). In order for a definitive explanation to be provided, additional hours of behavioral observations are needed.

The only species effect elucidated in the social behavior observations involved the production of agonistic behaviors. Gorillas initiated agonistic behavior with conspecifics significantly more often than orangutans. Reports in the literature of gorillas initiating agonistic behavior with conspecifics more often in all male bachelor groups than in mixed-sex groups (Pullen, 2005; Robbins, 1996) prompted an additional analysis to assess if the gorillas in the current study produced differential rates of agonistic behavior based on the type of social group in which they lived. No significant differences were found in the occurrence of gorillas initiating agonistic behavior in the all male group compared to the mixed-sex group. It is possible that the relatively high occurrence with which gorillas initiated agonistic behavior with conspecifics is due to the impact of other factors. For example, a preliminary report by Wells (2005) found that a high density of visitors in a zoo environment correlated with an increase of agonistic behavior among gorillas. However, the current study was limited to behavioral observations among gorillas only, and did not capture information about factors outside of these interactions that may have affected behavior. Two explanations are offered regarding these results. The first is that the occurrence of agonistic behavior in gorillas is not affected by the type of social group in which they live, namely all male or mixed-sex groups. An alternative explanation is that the relatively high occurrence of agonistic behavior among gorillas is an artifact of the small number of hours of behavioral observation conducted.
The final result from the social behavior observations is that great apes who received responsive care from humans during the first six months of life spent a significantly higher percentage of time engaged in solitary behavior than great apes raised by responsive mothers. The first possible explanation for this result is that great apes who received responsive care from humans during the first six months of life were less prosocial than great apes who received responsive care from their mothers. However, the percentage of time engaged in solitary behavior by all participants, regardless of the style of care they received during infancy and the species of the caregiver, fall within the normal range according to Sussman, Garber and Cheverud (2005), whose analysis of primate sociality found that diurnal primates spend approximately 80-90% of their activity budgets engaged in solitary behaviors, such as foraging and traveling. Therefore, it is unlikely that the higher percentage of time spent engaged in solitary behavior indicates a social deficiency in great apes raised by responsive humans. An alternative explanation is that human care is characterized by distinctive cultural features that may impact the behavior of great apes. Matsuzawa (2007) observed that extended bouts of physical separation between mother and infants are unique to humans, which may have ultimately facilitated vocal exchange. It is possible that this cultural characteristic of care promotes a higher level of independence in great apes raised by responsive humans compared to great apes raised by responsive mothers, who remain in almost constant direct physical contact with infants during the first three to six months of life (Bard, 1995). Bowlby’s (1969) concept that secure infants use responsive caregivers as a base from which they can confidently explore their environment may be particularly salient for infants raised by humans. However, it is possible that the results on solitary behavior, as is the case for all of the social behavior observations, may be an artifact of the small number
of observation hours collected. A larger sample of behaviors is necessary to make firm conclusions about any relationship between early care and solitary behavior in great apes.

Summary and Conclusions

Great apes engage in joint attention behaviors with both conspecifics and humans, and they do so in ways that suggest they possess some understanding of others as intentional agents (Tomasello, 1995a). The ability of great apes to engage in joint attention behaviors with conspecifics and humans was not affected by differences in care style during the first six months of life. The qualitative differences between basic care and responsive care were not sufficiently distinct enough to impact great apes' ability to produce joint attention behaviors with other individuals. Therefore, there is an implication that joint attention is a durable cognitive process in great apes and humans which increases individuals' fitness by providing a foundation upon which more sophisticated cognitive processes, such as perspective taking and deception, are built (Brune & Brune-Cohrs, 2006; Parker & Russon, 1996). Disruptions to this basic cognitive process could greatly reduce great apes' ability to survive and reproduce.

In the current study, bonobos attended to the visual gaze of humans significantly more often than chimpanzees or gorillas. Despite the fact that two of the bonobo participants experienced responsive care from great ape mothers, while the other bonobo was cared for by responsive humans, it is likely that the shared cultural environment in which the bonobos were all raised explains their sensitivity to human gaze. Specifically, the cultural environment was characterized by daily opportunities to interact with both humans and human cultural artifacts in the context of cognitive testing, as well as with conspecifics. It is
less likely that orangutans’ propensity to attend to human gaze compared to chimpanzees can be explained by enculturation because the backgrounds of these participants ranged from exposure to cognitive testing for some individuals, a moderate amount of interactions with humans for others, and a complete absence of cognitive testing and little opportunity for interaction with humans outside of the context of routine care for the remaining participants. It is possible that there are real species differences between orangutans’ and chimpanzees’ sensitivity to human gaze, but more studies using a standard methodology are needed to address this question in detail.

The care that great apes received during the first six months of life appears to affect some social behaviors, but not others. Great apes who received responsive care initiated affiliative behavior with conspecifics significantly more often than great apes who received responsive care from humans. In addition, conspecifics directed affiliative behavior towards mother-raised great apes significantly more often than towards human-raised great apes. Finally, great apes who received responsive care from humans during the first six months of life spent a significantly higher percentage of time engaged in solitary behavior than great apes raised by responsive mothers. Early care did not appear to have an impact on the occurrence of agonistic behavior, but gorillas initiated agonistic behavior more often than orangutans. A series of possible explanations for these results were considered, however, the relatively small number of observation hours prohibits any definitive conclusions based on the current study regarding the relationship between early care, social behavior, and solitary behavior.

It is challenging to generate hypotheses about the evolution of cognition in hominid ancestors based on the fossil record alone. The study of cognition in extant great apes may
provide some insight into this question (Russon & Begun, 2004). The results of the current study demonstrate that two joint attention behaviors, responding to gaze cues and initiating joint attention around an object, are present in all four types of living great apes. The presence of joint attention behaviors in *Pongo*, the lineage of which diverged from a common ancestor 14-18 mya (Hobolth Christensen, Mailund & Schierup, 2007; Patterson, Richter, Gnerre, Lander, & Reich, 2006), is illuminating and suggests that the character trait of joint attention was present in the last common ancestor. Joint attention appears to be a basic cognitive process that has adaptive benefits such as the ability to understand the intention of others, as well as the ability to detect predators and food through following gaze cues of conspecifics.

**Directions for Future Research**

One major finding of the current study is that joint attention appears to be a durable cognitive process in great apes that is impervious to insufficiently distinct differences in care style during the first six months of life. There are three questions, however, that the current study could not address: 1) are the effects of early care on joint attention in great apes continuous across time, from infancy through adulthood?; 2) if not, what changes in the environment may mediate the effects of early care on joint attention over time in great apes?; and 3) are more sophisticated theory of mind skills, such as perspective taking, attribution of knowledge and beliefs, and an understanding of false beliefs, also durable cognitive processes like joint attention or are they more sensitive to subtle differences in early care?

First, there are no studies on the continuity of joint attention skills across time based on the early care experienced by great apes. Second, there are no studies examining possible
mediating effects of environmental change on great ape social cognition, although this concept has been explored in the human literature (Hamilton, 2000; Lewis, Feiring, & Rosenthal, 2000; O'Connor et al., 2000; Rutter, 2006; Waters et al., 2000). Finally, there are a relatively few number of studies on the ontogeny of ToM skills in great apes, mostly focusing on chimpanzees (Okamoto-Barth & Tomonaga, 2006; Okamoto et al., 2002; Tomasello et al., 2001) and the conditions under which a range of ToM skills may develop normally or be impeded have not been investigated.

Great apes, like humans, have long periods of development and maturation, large brains relative to their body size, and complex emotional, social, and intellectual lives. It is clear that an array of developmental, social, and environmental factors should be considered when investigating great ape cognitive abilities and social behaviors. Therefore, an integrative approach to the study of great ape cognition is valuable. Specifically, longitudinal studies are needed to examine the continuity of psychological and cognitive processes in great apes; environmental factors that may mediate negative effects of early social experiences must be investigated, including the role of personality, gene-environment interactions and the concept of resilience (Fuertes, Santos, Beeghly, & Tronick, 2006; Rutter, 2000, 2006; Suomi, 2006) and other important factors in the social environment; all four types of great ape should be represented in these studies; and great ape cognitive abilities should be assessed with not only human partners but also conspecifics (Hare & Tomasello, 2004).
BIBLIOGRAPHY


gaze following of great apes and human infants: the cooperative eye hypothesis.

Brain Sciences, 16, 495-552.

competition between wild orangutans in large fig trees. International Journal of
Primatology, 18, 909-927.

Primates, 40, 69-86.

troglodytes) [Abstract]. American Journal of Primatology, 60, 79.

mothers and unrelated females. Zoo Biology, 23, 375-378.

from infancy to adolescence and early adulthood: general introduction. Child
Development, 71, 678-683.

security in infancy and early adulthood: a twenty year longitudinal study. Child

from infancy to adolescence and early adulthood: general discussion. Child
Development, 71, 703-706.

Weaver, A., & de Waal, F.B.M. (2002). An index of relationship quality based on
attachment theory. Journal of Comparative Psychology, 116, 93-106.

Weaver, A., & de Waal, F.B.M. (2003). The mother-offspring relationship as a template in
social development: reconciliation in captive brown capuchins (Cebus apella).
Journal of Comparative Psychology, 117, 101-110.

Wells, D.L. (2005). A note on the influence of visitors on the behavior and welfare of zoo-

enterprise. In A. Whiten (Ed.), Natural Theories of Mind: evolution, development,


APPENDIX A: BIOGRAPHICAL PROFILE TEMPLATE

Subject #
Species:
Sex:
Age:
Wild or Captive Born:

Sections A and B include questions about the subject’s early experiences from birth through 6 months of age. Section C involves questions about the remainder of the subject’s infancy through the present. The period of infancy in bonobos, chimpanzees, and western lowland gorillas lasts from birth to approximately 5 years of age (Bard, 1995; van Lawick-Goodall, 1968; Kano, 1986; Robbins et al., 2004). The period of infancy in orangutans lasts from birth until 7 years of age (van Noordwijk & van Schaik, 2005).

START HERE
Was the subject raised by his/her biological mother continually from birth through 6 months of age? [Temporary separations for routine medical care do not constitute a break in continual care by the biological mother].
Yes, go to Section A.
No, go to section B.

SECTION A

1. Select the attributes that best describe the mother’s general pattern of care for the subject during the first 6 months of life.
   a. Species-appropriate, responsive care behavior towards infants during the first 6 months, such as frequent direct physical contact with the infant (almost constant direct physical contact, especially in the first 3 months); frequent acceptance of infant-initiated approaches; frequent and appropriate cradling and transporting of the infant; general allowance of nursing on infant demand; inspection of the infant’s body and encouragement of motor skills through direct physical contact; allowance of infant exploration of its environment at appropriate age levels, but physically comforting the infant if he/she became distressed; and frequent acceptance/initiation of play behavior with the infant
   b. Adequate care behavior towards infants during the first 6 months, including moderate to relatively little direct physical contact with the infant; moderate to frequent rejection of infant-initiated approaches; moderate to relatively little cradling and transporting of the infant; occasional inappropriate carrying/handling of the infant; moderate to frequent rejection of nursing on infant demand; moderate to relatively little inspection of the infant’s body and encouragement of motor skills through direct physical contact; moderate to relatively little physical comfort provided to the infant if he/she became distressed; moderate to little play behavior; and/or some play behavior, but
2. Did the subject have 24 hour access to its mother?
   a. Yes.
   b. No. Please explain.

3. Describe the types of conspecific social partners to whom the subject had access (besides its mother) during the first 6 months of life. Include the level of access (e.g., direct, through mesh, visual, olfactory). If the subject did not have any access to conspecifics, please explain.

4. Describe the level of interaction the mother-subject dyad had with animal care staff.
   a. None, except during feeding.
   b. Some, including time outside of feeding.
   c. Routine contact.

You have completed Section A. Please proceed directly to Section C.

SECTION B.

1. Why were the infant and biological mother separated? If the infant was diagnosed with a medical problem which necessitated separation, describe the condition in detail.

2. How old was the infant at the time of separation?

3. Who raised the subject after this separation?
   a. A conspecific surrogate (go to Section A)
   b. A surrogate from another nonhuman great ape species (go to Section A)
   c. Human surrogate(s) (go to number 4)

4. How many human caregivers raised the infant after separation from the biological mother?

5. Describe the level of interaction between the human caregiver(s) and the infant.
   a. Direct physical contact primarily in the context of feeding.
   b. Some direct physical contact outside of routine feeding sessions.
   c. A high amount of direct physical contact during the day.
   d. Virtually 24 hour direct physical contact.

6. What types of social partners did the infant have access to (besides the human caregivers)? Include the type of access (e.g., direct, through mesh, visual, olfactory).

7. How long were the infant and his/her biological mother separated?
a. The infant and the biological mother were reunited. List the age of the subject when this occurred.
b. The infant and biological mother were never reunited (i.e. having direct physical access). Please explain in detail.

You have completed Section B. Please proceed directly to Section C, #3.

SECTION C
The following section involves questions about the subject after 6 months of age through the present.

1. Are the mother and subject still housed together (i.e., do they have direct physical access to each other?)?
   a. Yes, go to number 3.
   b. No, go to number 2.

2. How old was the subject when he/she no longer had direct physical access to its mother? What was the reason for the separation?

3. Did the subject experience any major events after the first 6 months of age through the present?

4. Did the subject live with conspecific social partners after the first 6 months of age through the present?
   a. Yes. Describe the composition of the group(s).
      6 mos-5 yrs
      6 yrs-10 yrs
      11 yrs-present
   b. No. Please explain.

5. Has the subject ever copulated? If not, please explain.

6. Has the subject produced offspring?
   a. Yes. List the number and indicate whether the mother raised the infant (if applicable).
   b. No. Please explain (e.g., too young, not paired with potential mate, etc.).

7. Describe the level of interaction the subject had with animal care staff after 6 months of age through the present.
   a. None, except during feeding.
   b. Some, including time outside of feeding.
   c. Routine contact.
   d. A combination of different levels of interaction over time.
      6 mos-5 yrs
      6 yrs-10 yrs
      11 yrs-present
APPENDIX B: SOCIAL BEHAVIOR CATALOG

SOCIAL BEHAVIORS

Affiliative Social Behavior

Social Play
Non-aggressive interactions between two or more individuals that may include behaviors such as wrestling, play-biting, mouthing, playful approach, playful falling (e.g., an individual hanging from mesh drops onto the floor in the presence of a conspecific), and play face (open mouth, teeth may be visible). An individual may use objects to initiate and sustain play behavior, such as covering a conspecific’s head with a sheet.

Sex
Sexual interactions including presenting, oral-genital manipulation, manual-genital manipulation, intromission, and ejaculation.

Contact
Direct physical contact between two or more individuals that occurs outside of sexual behavior or social play; may include physical inspection of a conspecific’s body in a nonsexual context (e.g., mother’s inspection of infant’s body (including genitalia), grooming, etc.), or simply sitting or lying in direct contact.

Agonistic Social Behavior

Display
May include swaying, throwing, rocking, stomping, chest-beating, pilo-erection, running and/or vocalizing in the context of a display; may include manipulation of an object during the display (e.g., swaying and then throwing a barrel around an enclosure).

Displaced
An individual moves out of proximity of a conspecific (1 meter or more) as a result of the conspecific’s behavior. Behaviors may include simply walking past, or moving towards, the individual or may include display behaviors.

Displace
Behaviors that cause a conspecific or conspecifics to move out of proximity of that individual. Behaviors may include simply walking past, or moving towards, the individual or may include display behaviors.

Agonistic Contact
Agonistic direct physical contact that may include hitting, biting, grabbing, slapping, aggressive hair pulling.
SOLITARY BEHAVIORS

Solitary Play
Non-social play behaviors that may include rolling, spinning, falling down, swinging

Solitary Rest
Non-social behaviors while at rest which exclude solitary play, but include sitting or lying down; may include foraging; may include self-inspection in which any part of the body is investigated with hands, other appendages, and/or using external objects

Masturbation
Self-manipulation of an individual’s genitals which may be achieved with or without the use of an external object

OTHER

Not visible
The focal animal is not visible
ACKNOWLEDGEMENTS

There are many individuals to whom I am indebted for their assistance with the current study. First, I would like to thank the members of my committee: Dr. Jill Pruetz, Dr. Nancy Coinman, Dr. Mack Shelley, and Dr. Robert Shumaker. Second, this research could not have been completed without the support from the following individuals and institutions: Great Ape Trust of Iowa, Bill Fields, Director of Bonobo Research, Dr. Robert Shumaker, Director of Orangutan Research; Henry Doorly Zoo, Daniel Cassidy, General Curator, Dan Houser, Primate Supervisor; Lincoln Park Zoo, Dr. Sue Margulis, Curator of Primates, Steve Ross, Supervisor of Behavioral and Cognitive Research, and the remaining members of the Lincoln Park Zoo Research Committee; Smithsonian National Zoological Park, Lisa Stevens, Curator of Primates and Giant Pandas; Toledo Zoological Gardens, Dr. Peter Tolson, Director of Conservation and Research, Dr. Randi Meyerson, Curator of Large Mammals, and Beth Stark-Posta, Curator of Behavioral Husbandry and Research. A special thank you is due to the following staff from the above institutions for research assistance: Teresa Anderson, Andy Antilla, Peter Clay, Tine Geurts, Suzanne Husband, Jackie Mack, Becky Malinsky, Sandra Palencia, Melissa Pollock, Liz Pugh, Chris Schumacher, Erin Stromberg, Takashi Yoshida, and Mark Zajac. I would also like to additional staff from Great Ape Trust for their guidance and assistance: Dr. Benjamin Beck, Director of Conservation, Dr. Serge Wich, Visiting Scientist, and Kristina Walkup, Research Assistant. Dr. Karyl Swartz, Scientist, Great Ape Trust, deserves special recognition for her mentorship and support throughout this process. I am greatly indebted to Ms. Pat Sass, whose long term experience and knowledge of great apes was invaluable. I am especially appreciative of the statistical support from Man-Yu Yum, Research Assistant, Iowa State University. Finally, I would like to extend my
deepest gratitude to Dr. Robert Shumaker, whose respect and admiration for great apes inspired me to pursue a career studying these incredible beings.