ATTACHMENT AND EARLY REARING: LONGITUDINAL EFFECTS IN CHIMPANZEES (PAN TROGLODYTES)

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ATTACHMENT AND EARLY REARING: LONGITUDINAL EFFECTS IN CHIMPANZEES (PAN TROGLODYTES)

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To John Bowlby, Mary Ainsworth, and Harry Harlow

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LIST OF SYMBOLS AND ABBREVIATIONS

U	Mann Whitney U Score
τ	Kendall's Tau
χ^2	Chi Square
φ	Phi (effect size for Chi Square)
HPA	Hypothalamic-Pituitary-Adrenal Axis
ST	Standard Care
RC	Responsive Care
SW	Southwestern
NBAS	Neonatal Behavioral Assessment Scale
BSID	Bayley Scales of Infant Development
MDI	Mental Development Index
MR	Mother-reared
DA	Disorganized Attachment
ND	Non-disorganized Attachment
LA	Late Arrival Standard Care
EA	Early Arrival Standard Care
MWU	Mann Whitney U
URI	Upper Respiratory Infection
DIA	Diarrhea Incidence
INJ	Injury Incidence
NR	Nursery-Reared
NRC	Non-Responsive Care Nursery

SUMMARY

Between the years of 1987 and 1995, two different chimpanzee nursery rearing strategies were employed by caregivers and research staff at the Yerkes National Primate Research Center. One of these strategies included, in addition to the basic care provided by both nurseries, an additional 4 hours of human contact for 5 days each week. This human contact was provided by caregivers instructed in the behavior of chimpanzee mothers toward their offspring and required to emulate that behavior as much as possible. Various measures of cognitive and motor development were taken during the first year of the nursery-reared chimpanzees' lives; additionally, a modified version of the Strange Situation Test, used to measure attachment, was used to assess the chimpanzees' attachment style to their primary human caregiver. Based on these measures, chimpanzees reared in the standard care nursery (without the additional human contact) were significantly more likely to exhibit disorganized attachment styles towards their human caregiver; additionally, the standard care chimpanzees displayed less advanced motor and cognitive development. The responsive care chimpanzees (reared with the additional human contact) developed cognitively and in terms of motor function at a faster rate than the standard care chimpanzees; they also exhibited less coping skills. After one year of rearing in these two nurseries, all the chimpanzees were reared in conspecific social groups and the differential nurseries were terminated. In 2011-2012, 22 out of 49 of the original chimpanzee subjects were reassessed in an attempt to determine if long term effects of these differential rearing styles could still be

detected. Adult chimpanzees that were identified as exhibiting disorganized attachment at one year of age exhibited significantly higher rates of abnormal behavior as compared to those that did not exhibit a disorganized attachment style at one year of age; they were also more likely to experience an upper respiratory illness during ages 0 - five. Disorganized individuals were also more likely to be viewed as less intelligent and less purposeful, significantly more likely to be viewed as unperceptive in social interactions as compared to non-disorganized individuals. Adult chimpanzees from both responsive care and standard care exhibited significantly higher rates of abnormal behavior and attendance to humans as compared to chimpanzees that were mother-reared. Additionally, chimpanzees reared in either of the two nurseries were rated by survey respondents as exhibiting significantly higher human orientation and significantly lower subjective well- being as compared to mother-reared chimpanzees. Responsive care chimpanzees exhibited significantly more solicitation behaviors towards humans as compared to mother-reared chimpanzees; standard care chimpanzees did not significantly differ from mother-reared chimpanzees on this measure. Responsive care chimpanzees exhibited significantly higher rates of attending towards humans, negatively soliciting humans, and higher rates of aggressing on humans as compared to standard care chimpanzees. Survey respondents scored responsive care chimpanzees as significantly less calm, significantly less equable, significantly more dependent, significantly less unemotional, significantly more fearful, and more vulnerable than standard care chimpanzees. Finally, consistent trends in the data, while not significant, indicate that responsive care

chimpanzees may be seen as exhibiting lower subjective well-being as compared to standard care chimpanzees, soliciting help from humans more often than standard care chimpanzees, and experiencing anxiety more than standard care chimpanzees. Chimpanzees reared in both nurseries were at significantly higher risk for illness than those that were mother- reared; responsive care chimpanzees were at significantly higher risk for illness as compared to nursery-reared chimpanzees that were not in responsive care. Further research should be conducted to explore welfare-related issues as related to mother versus nursery rearing and as related to differential nursery rearing strategies for chimpanzees.

CHAPTER 1

INTRODUCTION

The role of early experience in long-term development of primates has been studied extensively over the past 50 years. Once an emphatically psychological field, the role of biology has become clear and now plays a highly relevant role in studies of the effects of social separation, of maternal deprivation, or otherwise stressful early experiences. Attachment theory, as developed by John Bowlby and delineated by Mary Ainsworth, is perhaps the more psychologically-oriented area of study, and over time, studies of attachment have been expanded to include multiple cultures, multiple species, and to include longitudinal effects. Studies of nonhuman primates have allowed for many experimental studies of attachment behaviors in various monkey species (D. Maestripieri, 2003) and have also allowed for a deeper delving into the biological effects of stressful early life experiences. This has led to a better understanding of the biological determinants of human depression (Gilmer & McKinney, 2003), the biology of parental responsiveness, variation in parenting styles, and the biological determinants of infant abuse and neglect (Dario Maestripieri, 1999; D. Maestripieri, 2006; D. Maestripieri & Carroll, 1998). Studies of multiple species and multiple human cultures have allowed for a better understanding of the danger of espousing one attachment or rearing style as 'normative' (Hinde, 1991), and studying nonhuman primates in particular has allowed for experimental studies of attachment behavior that could never have been possible with humans (Hinde, 1991). Finally, nonhuman primates have proven an invaluable resource in determining the neurobiological substrates that play a part in attachment processes,

possibly leading to a better understanding of human disorders such as autism (Insel, 1997).

Of course, studies with nonhuman primates not only have implications for humans, but also for nonhuman primates, themselves. As we manage various species in captivity, it is critical to understand the way that early life experiences effect the long-term development of individual animals in our care. Stressful early life experiences have been found to effect many species, not just primates (Ladd, Owens, & Nemeroff, 1996). Understanding the responses of different species to various types of early life stressors, such as maternal separation or social isolation, is a critical part of understanding not only the human species, but also the many different animal species for which we are responsible both in captivity and, increasingly, in the wild. Chimpanzees (*Pan troglodytes*) reared in captivity provide an excellent opportunity not just for measuring the effects of early rearing during the first few years of life, but also for evaluating the long-term effects of differential rearing.

CHAPTER 2

ATTACHMENT RESEARCH

Human Attachment Research

The theory of attachment as relevant to human bonds and socio-emotional development was first developed by John Bowlby. Bowlby initially formulated his theory based on observations he made about juvenile delinquents and the relatively high number of them reporting maternal separation, particularly as compared with a matched control group of non-delinquents (Ainsworth & Bowlby, 1991; Bowlby, 1944). Bowlby's theories contributed to the abandonment of the view that feeding an infant was of chief importance to the development and maintenance of the mother-infant relationship, and also led to important changes such as allowing parents to visit their infants when in hospitals (Hinde & Stevenson-Hinde, 1991). As Bowlby's career progressed, he developed the theory of attachment as a response to his own beliefs that early childhood events had a long-term effect on human development, and ultimately came to publish a series of books that described his theory in detail (Bowlby, 1969, 1973, 1979, 1980). Initially, however, Bowlby's statements regarding maternal separation and later outcome were largely theoretical, and he did not have the experimental data to explain his findings regarding the importance of the mother-infant bond.

Mary Ainsworth became fascinated with Bowlby's research and determined to further develop his theory (Ainsworth & Bowlby, 1991). Ultimately, while Bowlby developed relationships with noted nonhuman primate researchers such as Harry Harlow and Robert Hinde, developing more thoroughly his theoretical perspective on attachment, Ainsworth became the source of empirical validation for his theory (Ainsworth & Bowlby, 1991;

Hinde & Stevenson-Hinde, 1991). Current studies are coming to terms with other possible determinants of attachment, such as temperament (Stevenson-Hinde, 2005), and also with the influence of culture on attachment behaviors and 'norms' for development (Hinde & Stevenson-Hinde, 1991). Studies of maternal responsiveness as related to human infant security have also been generated, supporting the hypothesis that mothers that are more sensitive (as indicated by affectionate holding and quick responses to infant crying) also have infants that are more secure, crying less at 2, 6, and 10 months and vocalizing happily more often at 6 and 10 months than infants with less sensitive mothers (K. Grossmann, Grossmann, Spangler, Suess, & Unzner, 1985; K. E. Grossmann & Grossmann, 1991). Furthermore, maternal responsiveness and attachment style have been predicted to interact with temperament (defined as early appearing individual differences) such that behaviorally inhibited children are likely to be particularly negatively affected by anxious attachments to their mothers (Stevenson-Hinde, 2005).

Bowlby's theory always allowed for a combination of genetic and environmental forces as critical to human development. He initially proposed that a series of hard-wired behaviors that were displayed by human infants were responsible for the attachment bond formation and that these behaviors were modified as the infant matured. The most salient of these behaviors, Bowlby claimed, were clinging and following. Bowlby stated that these behaviors were active and were aimed towards a biological function for the child: protection from harm. In this way, he integrated evolutionary theory and biology into his psychological perspective (Ainsworth & Bowlby, 1991; Bowlby, 1969, 1973, 1979, 1980; Hinde & Stevenson-Hinde, 1991). Attachment bonds were proposed as distinct from other relationship bonds as they are characterized by proximity seeking, in which

the child seeks to remain in the protective range of his or her parents, particularly in threatening situations (a "secure base" effect). The presence of the attachment figure leads to more confident and secure behavior on the part of the infant or child, and also leads to separation protest, in which any threat to the child's accessibility of the attachment figure is met with protest and active attempts to ward off separation (R. S. Weiss, 1991).

Ainsworth, meanwhile, collected data and developed the Strange Situation test to assess the quality of a child's attachment to his or her mother. The Strange Situation test findings (as well as data collected from previous studies) led Ainsworth to classify infants as secure or insecure, and within the insecure category, as either avoidant or ambivalent-resistant. The test itself consisted of a series of manipulations of mother and infant separation and introduction of a 'stranger' to the infant. Measurements of various reactions of the child and attachment behaviors (clinging, for example) were made, and based on these measurements, Ainsworth was able to classify the subjects into one or the other attachment 'style' categories (Ainsworth, 1978, 1985). Various criticisms of attachment theory and it's continued developments have been levied, of course (Belsky, 1997). For example, one study found that though maternal responsiveness predicted security of attachment in the Strange Situation test, a temperamental variable, labeled 'proneness to distress,' better predicted resistance, a behavior measured in the Strange Situation test and an indicator of insecure attachment (Goldsmith & Alansky, 1987). However, for the most part, attachment theory has been highly generative for research, and the addition of physiological data has allowed for greater clarification of the effects

that attachment bonding and disruption of attachment bonds have on the brain (Leckman et al., 2005).

The basis of the Strange Situation test lies in the expectation that attachment behaviors, such as seeking proximity with the primary caregiver, usually the mother, are most likely to be emitted when the infant or child is in a situation that invokes fear or uncertainty (Ainsworth, 1985). The test itself lasts 20 minutes, and is aimed at intensifying attachment behaviors, as previously mentioned. To achieve this goal, a series of events occurs: first, the infant is brought into an unfamiliar environment; second, a stranger enters the environment; and third, there are two brief separations and reunions with the mother. Observations of the resulting behavior of the infant allowed classification into one of three different primary patterns as noted during the study. Pattern A babies were typically explorative of the environment under all conditions, not highly agitated by separation from the mother, and avoidant of the mother after reunions. These babies were called "anxious/avoidant." Pattern B babies were explorative when mother was present, less explorative when she was not, and quickly sought proximity to the mother during reunion events, neither angry nor avoidant. These babies were called "secure." Pattern C babies were wary of the stranger, extremely agitated by separation from mother, and both seeking proximity and expressing anger toward the mother after reunion. These babies were called "anxious/ambivalent (Ainsworth, 1978, 1985)."

Correlating differences in infant behavior were observed at home, such that Pattern A and Pattern C babies tended to cry more, were more likely to get upset about brief, everyday separations from mother and to cry when reunited, were less positively responsive to physical contact with mother and protested more when contact ended, were

less compliant and expressed more anger. Mothers of A and C babies were less responsive than mothers of B babies, slower to respond to crying, and less tender and affectionate when holding the baby. Mothers of A babies were more rejecting than mothers of C babies, however, expressing more irritability and frustration, and were more likely to kiss their babies than to cuddle or hug them in a comforting manner, suggesting that these mothers were actually averse to physical contact with their babies Mothers of C babies were not rejecting or negative, but tended to either ignore their infants more or interfere with them more, and were inconsistent in their responsivity to infant cries or bids for contact, often seeking contact with the infant when it was not sought for by the baby (Ainsworth, 1978, 1985; Tracy & Ainsworth, 1981).

Pattern B babies cried less, were less upset by brief separations, were more positively responsive to physical contact and to the cessation of that contact, and were more cooperative with their mothers. Mothers of Pattern B babies were more likely to be quickly responsive to infant cries and requests for contact, interfered and rejected less, and generally were more accurate in reading infant signals and responding promptly and appropriately (Ainsworth, 1978, 1985; Tracy & Ainsworth, 1981).

Bowlby and Ainsworth's theories and hypotheses have generated and continue to generate a large body of research regarding attachment styles. Confirmation of the various attachment styles and later correlations with infant crying amounts was found, for example, in a study focusing on mother-infant dyads in Pennsylvania. The same study did not confirm previous claims that anxious (or 'insecure') infants received less physical contact, though they were confirmed to receive less responsive care (Belsky, Rovine, & Taylor, 1984). Other studies have focused more on various interactions between mothers

and infants, such as the degree of general affective behavior expressed by infants when with mothers versus with peers, found to be higher in the presence of mothers (Adamson & Bakeman, 1985). And, of course, as the ability to examine physiological effects of responsive care has increased, studies have confirmed neurological changes associated with degrees of responsive care. For example, in an extreme case, infants raised in Romanian orphanages, institutions in which infants spent up to 20 hours a day unattended, have been shown to suffer long-term cognitive and behavioral deficits (Chugani et al., 2001)

Non-human Primate Attachment Research

History of Non-human Primate Attachment Research

Animal species have long been of interest to psychologists and behavioral researchers, both because they can be tested experimentally in ways that humans cannot and also because of the comparative value in understanding various psychological or behavioral phenomenon. For example, postnatal manipulation of the early lives of various mammal species, such as rodents, cattle, horses, monkeys, or even apes, can allow for better understanding of the way that certain life events affect later neurobiology, physiology, and behavior (Nelson & Panksepp, 1998; Pryce et al., 2005). Of course, nonhuman primates, and particularly apes, are likely to be a better model for assessing the effects of early rearing environments on humans. For example, a study comparing peer-reared rhesus macaques with mother-reared rhesus macaques found that peer-reared monkeys had higher cortisol levels during social separations and consumed more alcohol during separations than the mother-reared monkeys (Fahlke et al., 2000). Additionally, it is of value to captive animals, such as chimpanzees, for us to understand

in particular how early environments might affect their long-term welfare in laboratories, research facilities, and in zoos. Many studies focus on parenting, with implications for both nonhuman and human primates. For example, it has been found that various nonhuman primate species make poor mothers when they are younger (Fairbanks, 2003), and when it is their first offspring (Fairbanks, 2003). Such findings may influence management of apes and monkeys in captivity to wait until animals are older to allow them to breed, and may also influence our understanding of teenage parenthood in humans (Fairbanks, 2003). Greater understanding of the ways in which humans are similar to, or different from, close primate relatives such as chimpanzees and bonobos also has implications for research regarding rearing effects as we make comparisons between species and use one as a model for the other (Hare, 2007).

The beginnings of this area of research can certainly be said to lie in the work of Harry Harlow. Harlow sought to understand what variables were of greatest importance to infant development – the breast and suckling, as had been purported by psychoanalysts, or physical contact, as had been suggested to be very important by John Bowlby (Harlow, 1958). Harlow suggested using a monkey (rhesus macaque, *Macaca mulatta*) as a model for studying these variables experimentally due to the faster maturation of the monkey, experimental control possible, and also the similarity to humans in basic responses relating to affection and exploration. Initial observations Harlow and his colleagues made regarding the attachment of human-reared infant monkeys to the cloth diapers used in their cages led Harlow to conclude that the monkeys were expressing attachment similar to other human and nonhuman primate species, and, additionally, the failure to thrive of monkeys that did not have such cloth items available indicated to Harlow that

this was a very important variable in development (Harlow, 1958). From there, Harlow began his famous cloth-versus-wire mother studies, showing that infant monkeys would preferentially cling to a cloth-covered wire mother over a wire mother, regardless of having all feedings take place on the wire mother, and that this response was stronger in times of stress or fear. Additionally, the monkeys explored their environments with more confidence when the cloth mother was present, reacting with enormous distress if she was not, even if the wire mother was presented. Tests of the persistence of this bond indicated that it did not wane, even five months after separation from the cloth mother, with only brief, infrequent contact reinforcement (Harlow, 1958). Harlow also engaged in studies of social and maternal deprivation and its long term effect on macaque behavior. For example, one study found that providing very young, socially isolated monkeys with normal peer cage-mates when the isolates were 6 months of age and the peers 3 months of age seemed to allow for a near complete recovery of social abilities, a better result than had been found in studies in which the peers were the same age as the isolates (Harlow & Suomi, 1971). The result was also better than when the isolates were introduced to and allowed to bond to a cloth surrogate, and then socialized with other similarly housed isolates. Animals in that case did engage in social play and exploration, albeit with interspersed periods of disturbed activity (Harlow & Suomi, 1971). Manipulations of the temperature of surrogate mothers showed that when the surrogates where cold, infants developed significantly more abnormal behaviors, such as rocking, self-clasping, and huddling, than infants for whom the surrogate mother was warmed (Baysinger, Plubell, & Harlow, 1973). Comparisons of monkeys raised on fur-covered, mobile but inanimate ‘hobby horses’ to monkeys raised on living dogs showed that these

two rearing methods were, in many ways, comparable to each other (W. A. Mason & Capitanio, 1988). Later work showed that the cloth mothers were more effective when made to 'rock' and, later still, that cloth mothers that were hung like mobiles were more effective even then rocking mothers, leading to higher exploration levels and faster development of gross motor skills (Dettmer, Ruggiero, Novak, & Suomi, 2006). Even surrogate cloth mothers that were simply in motion for 50% of the time from 5 a.m. until midnight significantly reduced the odds of rocking behavior and also reduced emotional responsiveness in rhesus infants as compared to those infants with consistently stationary surrogates (W. A. Mason & Berkson, 1975).

Extensive research regarding the various attachment bonds formed by rhesus macaques in captivity has included, for example, 7 years of research that indicated that the strength of dyadic attachments was dependent on rearing experience, age, length of time together, and the sex of the two individuals involved (G. Mitchell, Maple, & Erwin, 1979; G. D. Mitchell, 1968). Other studies have focused on the nature of periodic separations from the mother using different barriers, such as a wire mesh or a thick, clear plastic wall, finding that when contact through the wire mesh was allowed, there was less protest and despair exhibited by the infant monkey than in separation situations which precluded contact (Suomi, Collins, Harlow, & Ruppenthal, 1976). Additionally, some studies comparing feral (and mother-reared) rhesus to nursery-reared rhesus have shown that mother-reared monkeys will respond more appropriately to other social stimuli, such as rats provided as cagemates, while also confirming that nursery-reared, not mother-reared monkeys will exhibit abnormal self-directed behaviors when isolated in a novel environment (W. A. Mason & Green, 1962).

Physiological studies of the way that separation from an attachment figure affects various monkey species have shown, for example, that in species that have demonstrated an attachment bond, such as titi and squirrel monkeys, separation results in an immediate and significant increase in plasma cortisol levels. For titi monkeys, this adrenocortical response can persist through long periods of separation (Mendoza, Capitanio, & Mason, 2000). Separation of infant macaques from their mothers have revealed disruptions of various physiological systems such as cardiac regulation, sleep rhythms, circadian rhythms, pituitary-adrenal systems, immunological systems, and cerebral spinal fluid along with behavioral indicators of distress, such as increased vocalization and searching behaviors followed by huddled, withdrawn posture and reduced activity (M. Laudenslager & Boccia, 1996)

However, because there are differences between species in regards to attachment behaviors and 'norms,' phylogenetic relationships are important to consider when one is attempting to generalize the results of a study of one species to another species, even within family groups (Suomi, et al., 1976; Swartz, 1982). The continued development of objective measures of attachment for different species, such as a scale of attachment relationships for capuchin monkeys, may allow for more interspecies comparisons to be made (Weaver & de Waal, 2002).

Chimpanzees (*Pan troglodytes*) and Attachment Research

Due to the lack of research on attachment behaviors in the other great apes, the amount of literature regarding rearing history, enculturation, and development of chimpanzees (*Pan troglodytes*) seems quite extensive. Chimpanzees are by far the most numerous of all the great apes in captivity, and perhaps also the most studied in their

natural habitat (Boesch & Boesch-Achermann, 2000; Brent, Bramblett, Bard, Bloomsmith, & Blangero, 1997; Goodall, 1986; McGrew, 1989; Sugiyama, 1989; Tomasello, Davis-Dasilva, Camak, & Bard, 1987). Because of their close genetic similarity to humans, they are also excellent models for comparative research. Studies of long-term behavioral differences based on rearing history are therefore highly informative to the study of such differences in humans, and also are critical to our management of this ape in captivity. While some improvement in captive management is indicated by research showing that chimpanzees reared in complex social groups until sexual maturity exhibit behavioral development very similar to that seen in free-ranging chimpanzees (M.A. Bloomsmith, Alford, & Pazol, 1991; M.A. Bloomsmith, Pazol, & Alford, 1994), many chimpanzees are still reared, for various reasons, in less complex social settings, or by human caregivers. Fortunately, current nursery-rearing practices for chimpanzees have advanced a great deal, and many of the detrimental results of early rearing practices seem to be ameliorated in some degree by greater complexity of caging, by increased social interaction with conspecifics and/or human caregivers or even other species, such as dogs. Additionally, it has been shown to be helpful to include better training for human caregivers in chimpanzee behavior and expression. Recent studies regarding personality structure and development compared laboratory-housed and zoo-housed chimpanzees and found more similarities than differences, again a positive finding in terms of captive management, but laboratory housed chimpanzees did score significantly lower on the factors of extroversion, conscientiousness, and agreeableness (A. Weiss, J. E. King, & W. D. Hopkins, 2007a). This is informative in that it implies a continued need to address captive management of chimpanzees in laboratory

environments. Studies of captive chimpanzees are also informative for attachment theory. For example, chimpanzees aged 18 – 24 months and housed with either one or two other same-aged cagemates exhibited many of the same attachment behaviors as human toddlers when separated from attachment figures (protest and despair); those chimps housed in triads responded to separation from one of the three apes by clinging to each other, mitigating some of these separation-distress behaviors (K. A. Bard & Nadler, 1983).

Specific studies of attachment behavior in chimpanzees have been conducted, primarily seeking to compare chimpanzee attachment styles and human attachment styles (K. A. Bard, 1991, 2007; Inoue & Hikami, 1993; Inoue, Hikami, & Matsuzawa, 1992). If attachment bonds are part of our human evolutionary heritage, then it stands to reason that attachment behaviors would exist in chimpanzees, as well. In fact, chimpanzees should show attachment behaviors that are similar to our own. Research indicates that they do: Chimpanzees reared in nursery environments in which they had limited human contact exhibited attachment classification patterns similar to those seen in human children raised in Greek or Romanian orphanages (assessed using Ainsworth's Strange Situation Procedure). Chimpanzees reared in nurseries in which they had greater durations of interaction with their human caregivers and in which human caregivers used chimpanzee gestures, facial expression, and vocalizations during their interactions with the chimpanzee infants were less likely to exhibit disorganized attachment to their human caregivers and less likely to exhibit object attachment as compared to chimpanzees in the limited-contact nursery (M. H. Van IJzendoorn, Bard, Bakersmans-Kranenburg, & Ivan, 2008). Generally, attachment bonds in chimpanzees seem to follow similar patterns to

those of humans, including increased explorative play in the presence of a primary attachment figure (Miller, Bard, Juno, & Nadler, 1986), attenuation of fearful response to novel objects and novel humans in the presence of a primary attachment figure (Miller, et al., 1986; Miller, Bard, Juno, & Nadler, 1990), and exhibition of protest response to separation from the primary attachment figure (M. H. Van IJzendoorn, et al., 2008). For chimpanzees, as well as humans, it seems that sensitive maternal care is necessary for the formation of secure attachment bonds. This conclusion is further supported by similar studies which found that having a secure attachment figure, be it human or chimpanzee, correlates with reduced abnormal behaviors as compared to chimpanzees reared without a secure attachment figure (Maki, Fritz, & England, 1993a).

Similarity in attachment response between chimpanzee and human indicates some basic biological or psychophysiological similarity, as well. Attachment response similarities between human and chimpanzee are strong enough that it implies the emotional experience of a chimpanzee in relation to his or her attachment figure is perhaps similar to that of a human. Finally, if we consider that this primary attachment relationship can have such strong impact on long-term development in humans, then it is unreasonable to assume any different for a highly related species which exhibits similar attachment relationships and behaviors. It has been suggested that, for example, the highly emotional relationships of attachment style bonds could have a high impact on the behavioral flexibility (ability to modify behavior to adapt to varying situations) of an individual primate, human or nonhuman (Aureli & Whiten, 2003).

Many chimpanzees have been reared in nursery-environments, relying on human caregivers rather than conspecifics. Much research has been conducted to evaluate the

long-term effects of various nursery-rearing protocols and neonatal environments without specifically attempting to address attachment bonds (Baker & Bloomsmith, 2001; K. A. Bard, 1992, 1996; K. A. Bard, Gardner, & Fort, 1993; Conlee, 1997; Howell et al., 2006). A study comparing chimpanzees reared for the first two years in restricted laboratory environments to wild born chimpanzees all of whom had shared an environment since ages 3 – 4 found that the lab-reared chimpanzees were inferior in cognitive skills (Davenport, Rogers, & Rumbaugh, 1973). Other studies have compared the longitudinal effects of early rearing for continually mother-reared chimpanzees, chimpanzees reared by mother for 2 years before transfer to alternate social environments, and chimpanzees continually reared in nursery environments, finding that at 6 years of age, nursery-reared chimpanzees displayed less social play, less sexual behavior, and more abnormal behavior than chimpanzees reared by their mothers for at least the first two years. Chimpanzees that were continually mother-reared exhibited more solitary play than the other two groups of chimps (M. Bloomsmith, Baker, Ross, & Pazol, 2002). Other studies have indicated that among mother-reared chimpanzees, those that are allowed to remain with their mothers longer (at least 3 years) exhibit less protest, despair, and depression when separated from their mothers (Howell, et al., 2006). Abnormal behaviors in chimpanzees such as self-clasping and body-rocking have been suggested to be behaviors that would be directed towards a mother or primary caretaker (providing a body to clasp to and a source of locomotion for an infant), now redirected towards the self as a result of under-stimulating nursery care (Dienske & Griffin, 1978). Among various hand-rearing protocols, only the one protocol that did not include much interaction with humans or other primary caregivers led to chimpanzees exhibiting significantly higher levels of

abnormal behavior as compared to mother-reared chimpanzees (Maki, Fritz, & England, 1993b).

Another long term study followed up chimpanzees reared either by their mothers with a social group of conspecifics, with conspecifics but not with their mothers, or reared apart from mother and any conspecifics for some portion of infancy. This last group exhibited, compared to the others, significantly more abnormal behavior in terms of quantity and in quality when they were younger, but as socially-housed adults, these chimps were indistinguishable on this count from the other chimpanzees (J. E. Martin, 2002). These same groups of chimpanzees were measured in terms of personality ratings as adults. Chimpanzees that were not reared with their mothers were not distinguishable from mother-reared chimpanzees by personality rating, though inter-rater reliability scores for non-mother-reared chimpanzees were much lower than those for mother-reared chimpanzees (J. E. Martin, 2005). Chimpanzees which were removed from their mothers less than one week after birth, however, have been shown to exhibit markedly higher rates of atypical social behavior (tandem walking, embracing) and lower rates of sexual and play behavior when observed in conspecific social groups at 4 – 5 years of age; they also interacted with significantly fewer social partners as compared to mother-reared chimpanzees (S. R. Ross, Bloomsmith, & Lambeth, 2003). Other studies have shown that chimpanzees reared in various nursery conditions (with peers, without peers, etcetera) showed significantly reduced rates of stereotypic body rocking when housed with a canine companion, showing that unconventional techniques can ameliorate some of the negative effects of rearing chimpanzees in human-caretaker environments (Pazol & Bloomsmith, 1993; M. A. Thompson, Bloomsmith, & Taylor, 1991).

Finally, a study comparing the success in introducing adult chimpanzees into social groups according to gender and to rearing history found that wild-born male chimps were actually the least successful in integrating into new social groups as compared to nursery-reared males and females, mother-reared males and females, and wild-born females. This same study noted that some nursery-reared males seemed to interpret submissive gestures of other chimpanzees inaccurately, leading to continued aggressive displays on the part of the males (Brent, 2001).

CHAPTER 3

ANIMAL WELFARE

Captive Animal Welfare

Considering the long-term ramifications of early environmental experience on behaviorally flexible species such as humans, nonhuman primates, and some other species, it is imperative that we manage the early environments of captive apes, paying much attention to the social and emotional bonding that is provided. It is certainly not a stretch to imagine that insecure or disorganized attachment styles for chimpanzee infants may be just as detrimental to the chimpanzee's long-term development as they can be for humans. We already know of various environmental stressors for captive held animals, whether or not the animals are held in laboratories (Balcombe, Barnard, & Sandusky, 2004; Novak & Suomi, 1988) or zoological parks (Hosey, 2005). Many of these stressors are either based on human activity, or can be ameliorated by positive animal-caretaker relationships (Balcombe, et al., 2004; Waitt, Buchanan-Smith, & Morris, 2002). Some are created by breaking mother-infant bonds (Newberry & Swanson, 2008). We have experimented with ways to improve environmental complexity and create structural responsivity in captive animal environments (Markowitz & Line, 1990; Schapiro, Bloomsmith, Suarez, & Porter, 1996, 1997). Such responsivity is theorized to encourage greater self-confidence in macaques reared on inanimate, but structurally responsive, structures, similar in this case to the responsivity of sensitive mothers (W. A. Mason, 2000). We know that providing captive animals with control over their early environment is important to socioemotional development (Mineka, Gunnar, & Champoux, 1986). We know that taking individual differences is important in assessing

and managing primate welfare (Suomi & Novak, 1991). The body of research on attachment and rearing effects in nonhuman primates, informed by research on attachment and early environmental effects in humans should also inform our management strategies for captive primates.

Physiology, Stress, and Early Development

The stress response is one far-reaching physiological system which has been heavily researched. The stress response is a wide network of physiological and behavioral effects associated with an animal attempting to adapt to environmental challenges; these effects include changes within the central nervous system (cognition, sensory processing, hypothalamic and pituitary function), changes in neurotransmitters and neurosteroids, changes in the limbic system (amygdala, hippocampus) changes in HPA (hypothalamic – pituitary – adrenal) axis and changes in circulating metabolites (Cook, Mellor, Harris, Ingram, & Matthews, 2000). Complications arise when an animal's attempts to cope with an environmental stressor, such as activation of the stress response and/or engaging in various behaviors, do not succeed in alleviating the stressor. At this point, the biological cost of engaging in what might otherwise be adaptive behavior or physiology become taxing and harmful, reducing the welfare of the animal (Hemsworth & Barnett, 2000). The interactions of the body, mind, and behavior with the stress response system are extensive. For example, research has shown that humans experiencing subjectively pleasurable stimuli (odors and pictures) show a decrease in salivary cortisol, a stress hormone, and an increase in secretory immunoglobins (Barak, 2006). The immune system and the relationship between stress and immune function has also been studied heavily, albeit the relationship is exceedingly complex (Blecha, 2000). It has been

observed that when cattle are shipped by truck, disease rates due to stress climb significantly; this increase in disease correlates with a significant decrease in lymphocyte proliferation (Blecha, 2000). In studies with pigs, social status interacted with the stress of shipping in effects of elevated cortisol (Blecha, 2000). Other studies have not found direct relationships between cortisol levels, environmental stressors, and immune function (Lund et al., 1998). Measurement of these various effects can be complicated, for one, by handling of the animal, which can be a stressor and thus affect the very system being sampled. Remote blood sampling devices have been utilized with some animals and have indicated less effect on plasma cortisol due to sampling than either catheter-sampling of penned animals or sampling obtained by restraint of the animal (Cook, et al., 2000).

That said, it is still a matter of concern if animals in captivity show reduced immune function, and it is clear that stress, in general, has negative effects on the immune system, even if the details of that interaction are still muddied quite a bit (Blecha, 2000). Studies of leukocyte levels in squirrel monkeys have been utilized as indicators of immune state and, thus, of psychological well-being, for example (Coe & Scheffler, 1989). Generally, stress' effect on the immune system becomes negative when the stress response itself is prolonged. An acute environmental stressor triggers the release, by the adrenal glands, of adrenaline, noradrenaline, and glucocorticoids; these substances then trigger the breakdown of fat and increased metabolism of glucose to allow for greater available energy. Ultimately, prolonged exposure to environmental stressors will tax out this system; this can lead to a multitude of health problems, including diabetes, hypertension, and heart disease (Francis, Champagne, Liu, & Meaney, 1999; Francis & Meaney, 1999).

In other cases, as has been demonstrated in monkey species, levels of glucocorticoids may actually be chronically low, which can result in additional health problems (Mendoza, et al., 2000). Additionally, because during response to a stressor attentional processes are focused on the stressor, memory can be negatively affected.

While aspects of the stress responses are, in short term, beneficial, they are not beneficial when sustained, and, due to the implications for alteration of the animal's neurological and physiological systems, experiences of even short term, acute stress during early rearing may have long term detrimental effects (Francis, et al., 1999). The early effects of stressors that increase stress reactivity ultimately result in greater exposure to stress hormones (like corticosteroids) and, thus, greater vulnerability for stress related illnesses and dysfunction (Francis & Meaney, 1999). Various stressors related to early rearing, such as separation from mother in rats and monkeys, can lead to effects such as altered serotonergic and noradrenergic systems, which could create a lifelong susceptibility to depression (Francis & Meaney, 1999). Environmental stressors which cause stress in the mother can also lead to decreased parental care and, ultimately, greater stress reactivity for their infants over the course of their lifespan (Rosenblum, Forger, Noland, Trost, & Copland, 2001).

Early social experiences of neonatal mammals have been implicated as having far reaching effects on physiology. Evidence is building for the argument that very early social experiences can have long lasting effects on the animal's sensitivity to neuropeptides (e.g., oxytocin and vasopressin) and neurohormones (e.g., estrogen), both of which have implications for an animal's ability to modulate stress and social interactions, including parental behavior, over the long term. Oxytocin and vasopressin

are both important to the formation of attachment bonds (Cushing & Kramer, 2005), and additionally, disruption of that bond can lead to profound physiological and behavioral effects (Kalin & Carnes, 1984). Oxytocin administrations to human subjects increase feelings of trust; fMRI studies have confirmed that oxytocin effectively reduces activation in the amygdala, which is associated with fear and anxiety, and also leads to a decoupling of the amygdala to various other regions of the brain that are involved in behavioral manifestations of fear (Kirsch et al., 2005). So, any overwhelming stressors present during early development may lead to impairment of the formation of attachment bonds, along with various other physiological and behavior impairments. Additionally, specific stressors related to disruption of the attachment bond may alone lead to long term physiological and behavioral problems. In one study, adult pigtail macaques (five years old) that had experienced a 10 – 14 day separation from maternal and/or peer animals during their first year of life exhibited reduced immunological responses as compared to age-matched animals without separation experiences (M. L. Laudenslager, Capitanio, & Reite, 1985). Social stressors have in fact been shown to be particularly effective in leading to chronic impairment of the stress response system, including prolonged alteration of the HPA axis (Mendoza, et al., 2000).

Stress and Welfare

One difficulty in assessing stress response related variables as a means for measuring welfare is that there are many different kinds of stress and many different ways in which stress may manifest. For example, some positive environmental stimuli activate the stress response system: sex, novel and exciting experiences, challenging physical activities, and encounters with novel locations or objects can all elicit a stress response.

Even mild stressors related to frustration, like encountering a new cognitive task or puzzle (Leavens, Aureli, & Hopkins, 2001), may be positive in effect. Lack of response to environmental stressors can in fact be, in some cases, considered a detriment. Chronic fatigue, chronic pain, and hyperinflammation, for example, are thought to result at least in part from insufficient activation of defensive responses to stressors (Parent et al., 2005). However, severe and/or chronic stressors inarguably lead to negative effects, including chronically enhanced emotional arousal, persistent increases in blood sugars and blood fats, disruption of sleep and of normal cognitive function (Parent, et al., 2005), reduced cardiac health, increased risk of diabetes (Seeman & McEwen, 1996), increased risk of upper respiratory infection (Cohen et al., 1997), altered brain structures (Kaufman & Charney, 2001; Kaufman, Plotsky, Nemeroff, & Charney, 2000) and reduced immunological function (Coe, 1993). These and other effects clearly impair welfare.

The difficulty is in distinguishing welfare-impairing stressors from those that are acceptable, even positive for the animal to encounter (Moberg, 2000). This might be thought of as the problem of distinguishing stress from distress. In cases where an animal suffers from chronic distress, welfare is certainly impaired: abnormal growth and development, abnormal behaviors, and other long term dysfunctional physiological effects are observed (Moberg, 2000). Acute stressors can also lead to distress if they divert an organism's energy from other, critical, biological tasks (Moberg, 2000). In the short term, acute stressors can cause changes in blood serum values which could be harmful of experienced frequently (Lambeth, Hau, Perlman, Martino, & Schapiro, 2006). Because many of these critical biological tasks are undergone during early development, acute stressors experienced during early life may lead to greater distress than they might

if experienced later. This has important implications for captive management of animals with long developmental periods, such as primates, particularly great apes. One researcher, in summarizing a vast body of literature on rearing effects for captive animals, delineated the various reported long-term physiological effects and proposed, ultimately, that because early experience differences can be associated with differences in dopamine systems, those early experiences could result in alteration of dopamine mediated behavioral patterns, thus leading to lack of acquisition of some 'normal' patterns of behavior or the development of abnormal patterns of behavior, such as stereotypies (Toates, 2000).

In dolphins, a highly social mammal species, stressful social situations such as instable hierarchies, changes in group dynamics, and intense competition for resources have been correlated with the development of various physiological and psychological problems that are often associated with chronic stress. These problems included gastric ulcers and loss of appetite (Waples & Gales, 2002). Many social primates have been demonstrated to exhibit dysfunctional social behaviors as a result of nursery rearing (Winslow, Noble, Lyons, Sterk, & Insel, 2003) or even brief periods of maternal separation (M. L. Laudenslager, et al., 1985). These effects of adverse early rearing extend, again, to the physiological, reflected in the size of various brain structures and the reactivity of the stress-response (Sanchez, Hearn, Do, Rilling, & Herndon, 1998; Sanchez, Ladd, & Plotsky, 2001; Sanchez et al., 2005; Sanchez, Young, Plotsky, & Insel, 1999) Dysfunctional social skills might be assumed to create distress for an animal living in a social group of conspecifics. Generally, it can be concluded that management of captive animals during early development is of critical importance towards later welfare.

Animal Psychopathology

In rats, pups that were deprived of contact with their mother developed abnormalities in neurological function that have been proposed as analogues to human schizophrenic brain abnormalities (Ellenbroek & Cools, 2002). Macaques subject to repeated maternal separations between 3 and 6 months of age exhibited short term and long term changes in HPA axis function and also exhibited an increased startle response to acoustic stimuli; these patterns of physiological and behavioral response are similar to those observed in humans diagnosed with mood or anxiety disorders (Sanchez, et al., 2005). Analysis of risk factors predictive of development of self-injurious and self-abuse behaviors in rhesus macaques has indicated that nursery rearing, as opposed to mother rearing, is one of the primary factors that can be linked to these destructive pathologies (Lutz, Well, & Novak, 2003; Novak & Suomi, 1988; Rommeck, Anderson, Heagarty, Cameron, & McCowan, 2009; Rommeck, D.H., Strand, & McCowan, 2009). Similar results have been found for pigtail macaques (Bellanca & Crockett, 2002). Great apes have been shown to exhibit behavioral abnormalities including stereotypies (Davenport & Menzel, 1963), self-mutilation, excessive aggression, and excessive fearfulness in patterns very similar to those exhibited by humans diagnosed with post-traumatic stress disorder, depression, eating disorder, or anxiety disorder (Brune, Brune-Cohrs, & McGrew, 2004; Brune, Brune-Cohrs, McGrew, & Preuschoft, 2006; Turner, Davenport, & Rogers, 1969). Often these states of psychopathology in great apes can be attributed, at least in part, to the separation of infants from their mothers, solitary housing, and other adverse experiences during early development (Brune, et al., 2006; Davenport & Menzel, 1963; Mallapur & Choudhury, 2003; Turner, et al., 1969). Chimpanzees reared in isolation for the first few

years have, for example, become anorexic, exhibited higher susceptibility to disease, a higher mortality rate, and a variety of other behavioral abnormalities (Davenport, Menzel, & Rogers, 1961, 1966). In some cases, behavioral problems have been shown to be ameliorated by application of behavioral conditioning programs or environmental enrichment; however, this rarely includes such full social integration of the ape that he or she is able to successfully mate or raise offspring (Brune, et al., 2006). It has been noted that some chimpanzees reared for their first three years in total isolation were, however, able to learn to copulate successfully if they had an experienced partner; in fact, animals reared in isolation performed better in this regard than chimpanzees that had been reared by humans (Turner, et al., 1969). Similarly, a study comparing zoo-born, zoo-living chimpanzees based on their rearing histories and copulation success found that human-reared chimpanzees were the least likely to be sexually competent adults as compared to peer-reared chimpanzees, chimpanzees reared with peers and at least one adult conspecific, and mother-reared chimpanzees (King & Mellen, 1994). Interestingly, one study found that for chimpanzees that are successful copulators, abnormal behaviors such as body-rocking are increased as compared to non-copulators (Fritz, Nash, & Alford, 1992).

Severe behavioral deficits highlight the importance of successful, positive management of great apes during their early development, which includes, of course, rearing conditions (Davenport & Menzel, 1963; Mallapur & Choudhury, 2003). Maternal deprivation either in part due to inadequate maternal care or in full due to separation from the mother has been linked, specifically, to abnormal behavior in primates, farm animals, and even companion animals (Latham & Mason, 2008; Sanchez, et al., 2001). The

severity of effect of maternal deprivation has been shown to be affected by the timing of deprivation, length of time of deprivation, and the abruptness of the separation (Latham & Mason, 2008). The range of effects can include stereotypies (Spiijkerman, Dienske, van Hooff, & Jens, 1994) or other frustration-induced motor behaviors, but also may include long-lasting and pervasive effects on temperament (e.g., reactivity) (Latham & Mason, 2008). In one study detailing various environmental and historical factors' influence on stereotypic behavior in various zoo-housed monkey and ape species, rearing environments were, in fact, found to be most predictive of the development of abnormal behavior (Marriner & Drickamer, 1994). However, it seems that the specific abnormal behavior an animal exhibits is important to consider; a large sample of captive chimpanzees (140 female, 128 male) from various rearing and developmental backgrounds was assessed for various behaviors as a function of sex, rearing, and current or previous environments (zoo housed, laboratory housed, kept as a pet or used as a performer). Behavioral abnormalities such as coprophagy were found to be associated more with mother-reared animals than human-reared. Stereotypies such as rocking and self-sucking were found more in human-reared animals (Nash, Fritz, Alford, & Brent, 1999).

Attachment and Welfare

Based on a thorough review of the attachment literature from human developmental research and related research in mammal and, specifically, nonhuman primate development, it seems clear that rearing conditions are critically important for the management of great ape species, such as chimpanzees, in captivity. Currently, there are 269 chimpanzees housed in North American zoos alone ("The chimpanzee SSP," 2005).

Nearly 1,000 chimpanzees are currently housed in laboratories, and several hundred in sanctuaries. Perhaps 200 chimpanzees are still bred for use as pets or in the entertainment industry. Chimpanzees are long-lived animals; currently there are 11 zoo housed chimpanzees over the age of 45; one of these is estimated to be 70 years old ("The chimpanzee SSP," 2005). Chimpanzees are still sometimes raised in deficient early environments, and there are still cases in which chimpanzees must be removed from their biological mothers for rearing purposes. As long as these conditions continue to exist, it is critical to the long term management of the species to investigate the effects of various rearing practices, particularly when they need to be applied by human caretakers. Early studies of two differential human-rearing protocols have revealed that there are differences between young chimpanzees human-reared in different contexts (K. A. Bard, 1992, 1996, 2005; K. A. Bard, 2007; K. A. Bard & Leavens, in press). A natural follow up to this study would include a current assessment of individual chimpanzees who were tested in the original study, all of whom are now adults, and might add chimpanzees whose rearing histories are otherwise known in detail.

Research such as this would not only add to the literature regarding chimpanzee development, but would inform captive management strategies and also provide insight to human development research. For example, it is possible that chimpanzees reared in one specific environment might be better or worse adapted for living, as adults, in large social groups of conspecifics versus living in small social groups (2 – 3 individuals) in laboratory settings. This outcome could be considered analogous to differential cultural rearing practices in humans and adaptation to long-term cultural environments. Currently, in the United States, human infants are often expected to sleep alone and engage in self-

soothing behaviors starting at a very young age; they spend time in daycare facilities, often up to 8 or 9 hours a day, as their parents both work fulltime. This is not the environment in which human behavior and physiology evolved. However, any argument that current rearing practices in this country are not adaptive is sure to be thwarted by mention of the end goal of rearing American children: to be successful American adults. American adult culture is also very different from the adult culture of our evolutionary ancestors. As cognitively advanced primates, we are assumed to be behaviorally flexible; however, all species have limits on their flexibility. It would be informative to know how flexible our ape cousins are in terms of rearing and long term outcomes. That is, if a chimpanzee reared in one captive, and thus inherently non-natural, situation is better adapted to a particular non-natural cultural end goal than a chimpanzee reared in another captive situation, then this implies that humans, also, should be better adapted for non-natural long-term environments based on particular, and perhaps also non-natural, rearing practices. Future research should illuminate these theoretical and practical issues.

CHAPTER 4

PREVIOUS RESEARCH

Differential Rearing in Laboratory-Housed Chimpanzees

The first 30 days

As reported in various cited research publications, chimpanzees at the Yerkes National Primate Research Center from years 1987 to 1995 were reared in either one of two nursery conditions if their biological mothers did not provide sufficient care (W. A. Mason & Mendoza, 1998). This research was supported by National Institute of Health grants to investigate bio-behavioral responsiveness, cognition, and emotional development in chimpanzees. Chimpanzees that were removed from their mothers on day one were assigned to either the "Standard Care" or "Responsive Care" nursery. In the Standard Care (ST) nursery, chimpanzee newborns were placed in incubators for the first 30 days of life so that body temperatures were properly regulated. Caregivers were dressed in white laboratory coats over white clothes and washed with soap before any direct contact with the chimpanzee infants. Formula was provided in bottles, starting every 2 hours and then eventually moving to every 4 hours. When bottles were given, caregivers held the chimpanzees in their laps, sometimes seated in rocking chairs. During these scheduled contact times, diapers were changed and health checks were conducted. In the Responsive Care (RC) nursery, which was conducted from 1987 through 1995, chimpanzee infants were kept in the same conditions at ST chimpanzees for most of the first 30 days of life. However, RC chimpanzees were provided with an

additional 4 hours of caregiver contact on Monday – Friday (5 days per week). During this additional contact time, a human caregiver trained to provide support, feeding, grooming, and parenting in a similar fashion to that provided by chimpanzee mothers would be with the chimpanzee infant and in constant cradling contact. Feeding, diaper changing, and playing were all provided as needed and not on a timed schedule. Caregivers stayed physically active, walking with the infants and exposing them to the sights and sounds of various areas of the Yerkes center, including visual and auditory access to adult chimpanzees and to other humans.

In addition to the Yerkes nursery infants, infants cared for in the nursery of the Southwest Foundation for Biomedical Research were also included in some comparative studies. These infants were also in incubators and also received contact every 2 hours at first and then every 4 hours. However, as compared to the Yerkes ST nursery, Southwest infants (SW) were cared for by humans that wore, in addition to lab coats and uniforms, masks on their faces and gloves on their hands as well as hair nets on their heads. Bottles were sometimes propped inside the incubators rather than fed by hand and infants were at times placed inside a mechanical rocker (designed to provide vestibular stimulation). Contact with people was minimized for SW infants (K. A. Bard, 2005; W. A. Mason & Mendoza, 1998).

Finally, some chimpanzees were mother-reared and then separated on specific days of development for cognitive and behavioral testing purposes. Other than very short separations (30 minutes or under) from their mothers for testing, these infants were in 100% contact with their mothers for the first 30 days and thus assumed to experience the

normal playing, grooming, motor stimulation and grooming that mother chimpanzees provide (K. A. Bard, 2005; W. A. Mason & Mendoza, 1998).

During this first 30 days of life, chimpanzees from both Yerkes nursery conditions were tested every other day using the Brazelton's Neonatal Behavioral Assessment Scale (Brazelton, 1984). SW chimpanzee infants were tested at 2, 14, and 30 days using the same scale. On Day 2 and Day 30 of life, mother-reared chimpanzee infants were also tested using the NBAS during brief separations from their mothers. The Neonatal Behavioral Assessment Scale (NBAS) is designed to measure neurobehavioral integrity during a semi-structured 25 minute assessment conducted by individuals that have been certified to use the NBAS to a certain standard. The test measures how well an infant manages behavioral state changes (state regulation), response to environment and social partners (orientation), sensitivity to stimuli (range of state) and maturity of the motor system (motor). The results of these tests indicated that the ST infants were fairly similar to the RC infants on most measures, but that ST infants were able to self-quiet more easily than RC infants based on the results of day-to-day tests (W. A. Mason & Mendoza, 1998). Based on Day 2 and Day 30 measures, both ST and RC infants self-quieted more easily than mother-reared infants. Measures of emotional expression during the day-to-day NBAS tests indicated that while 14% of the ST chimpanzees expressed anger, 88% of the RC expressed anger; 67% of the ST infants vocalized greetings as compared to 94% of the RC infants (K. Bard, 2003; K. A. Bard, 2005). Based on tests on Day 2 and Day 30, it was concluded that more cradling time, regardless of the species providing cradling, led to less motor development, higher arousal state, and less self-regulatory or coping ability on the part of the infants. Similarly, Day 2 and Day 30 tests indicated that

the more human exposure had occurred (thus greatest for RC, then for ST, then SW, and, lastly, for mother-reared infants), the higher a chimpanzees' orientation scores, the more social smiles the chimpanzee exhibited, and the greater the chimpanzees' autonomic nervous system stability (K. Bard, 2003; K. A. Bard, 2005).

The first year

Standard Care (ST) infants at Yerkes past the first 30 days received socialization with other peer-aged chimpanzees, usually 4 to 6 other chimps, and continued health-related care as provided by human caregivers. About 15 – 20 chimpanzees were usually in nursery care and about 4 human caregivers assigned to provide care to those chimpanzees. Typically, caregivers spent about 15 – 20 minutes with the chimpanzees every 4 hours, feeding bottles and changing diapers or otherwise monitoring the infants' health. From about 4 p.m. until 10 a.m., most of the chimpanzees' time was spent, once they graduated from incubators, in padded cages with other chimpanzees and with rolled towels to cling to and provide extra padding. At first, single cages of about 1 meter in length, height and width were used to house the grouped infants; by about 3 or 4 months, when the chimpanzees were crawling, they were moved to double or triple cages. At the age of 4 months, chimpanzees were housed from 10 a.m. until 4 p.m. in playpens (with their peers). At 5 months, the playpen was put into a large room. At 7 months, the playpen was removed and a plastic climbing structure was added to the room. At 8 or 9 months, the chimpanzees were moved to a larger room during the day. Starting at around 6 or 7 months of age, a human caregiver would come to the play area for an hour of play after lunch. At 1 year of age, the chimpanzees stopped receiving bottles, were no longer

wearing diapers, had all towels removed from the area, and were soon transferred into larger outdoor enclosures (M. H. Van IJzendoorn, et al., 2008).

Chimpanzees in Yerkes' Responsive Care (RC) nursery continued to receive, as they did for the first 30 days, 4 hours per weekday (Monday through Friday) of human caregiver attention. From 1 p.m. to 5 p.m., all the chimpanzees in the RC group were given attention appropriate to their age by a specially trained research assistant; this consisted of play, grooming, and feeding at approximately the same levels as that provided to mother-raised infants (by their mothers) at the Yerkes facility (K. A. Bard & Gardner, 1996; M. H. Van IJzendoorn, et al., 2008). There were typically three assistants at any given time working with from three to five chimpanzees. For the first three months, assistants focused on encouraging motor development. From three to six months, primary focus was on encouraging proper social behavior with conspecifics and with humans; from six months on, the focus was encouraging the chimpanzees to cope with novelty and to regulate fear and distress responses (M. H. Van IJzendoorn, et al., 2008).

Chimpanzees in both Yerkes nurseries were tested using the Bayley Scales for Infant Development (Bayley, 1969). The Bayley Scales (BSID) test was designed to assess the developmental functioning of human infants and children from ages 3 to 42 months. The BSID can be used to compute a Mental Development Index (MDI) which represents cognitive, language, and personal-social development. At 9 months of age, chimpanzees in the Yerkes nurseries were tested using the BSID-MDI. Results indicated that the ST chimps were significantly lower in cognitive development than the RC chimpanzees. Additionally, object attachment assessments during testing sessions revealed that 59% of

the ST chimps displayed attachment to inanimate objects (typically a cloth towel) while only 12% of the RC chimps displayed these attachments. Finally, at the age of 12 months, all nursery chimpanzees were tested using the Strange Situation Procedure (Ainsworth, 1978) as adapted for use with the chimpanzees. The attachment bond between chimpanzee and the chimpanzee's favorite caregiver was measured; the testing room was a novel setting for the chimpanzee, and the 'stranger' was a human adult that was not familiar with the chimpanzee. Based on these tests, chimpanzees were classified into four different categories: securely attached (chimpanzees who actively sought proximity with their caregiver after reunion, showed feelings of distress openly, but calmed down after being reassured by the caregiver and then resumed exploration); insecure-avoidant (chimpanzees who ignored or avoided the caregiver after reunion); insecure-ambivalent (chimpanzees who both exhibited proximity seeking behaviors and resisted actual contact and who were not consolable nor resumed exploration after reunion); and disorganized (chimpanzees who exhibited no organized attachment strategy but instead engaged in inconsistent and contradictory behaviors). Chimpanzees categorized as disorganized also exhibited significantly more rocking behavior during separation episodes and during reunions and also clutched towels more often during separation and reunion. Significantly more chimpanzees from the ST nursery were classified as disorganized (72%) as compared to RC chimpanzees (41%) (M. H. Van IJzendoorn, et al., 2008). Additionally, tests at 3 and at 9 months revealed that rearing condition (ST versus RC) accounted for 33% of the variance in lateral bias in grasping objects, suggesting some neurophysiological response based on rearing environment (K. A. Bard, 2000).

Early Stress Chimpanzees

While most chimpanzees in the ST or RC nurseries were placed in one of the two environments immediately due to the mother not cradling the infant, some chimpanzees stayed longer with their mothers; six infants remained with their biological mothers less than 30 days after birth while three chimpanzees remained with their mothers up to 12 weeks. These latter two categories of chimpanzees (totaling 9 infants) were classified as 'late arrival' or 'early stress' chimpanzees and were added to the Standard Care nursery; early stress group chimpanzees had typically suffered more extensive trauma than those removed from their mothers immediately. Trauma included bitten fingers, lips, and/or feet, dehydration, overgrooming and general poor health (M. H. Van IJzendoorn, et al., 2008). Late arrival chimpanzees were found to differ from all other nursery chimpanzees on some measures. For example, between 3 and at 12 months of age, all ST and RC chimpanzees were tested for social cooperation with human examiners. Standard Care chimpanzees were accepting of examiner requests at both 3 and 12 months; however, Responsive Care chimpanzees improved from accepting at 3 months to enjoying the give and take of objects at 12 months. Early stress chimpanzees, on the other hand, were accepting at 3 months, more often rated as refusing to cooperate with examiner at 6 months, and were rated as significantly less cooperative at 12 months as compared to RC infants. Additionally, early stress chimpanzees tested as significantly worse than the human norm for performance on the BSID-MDI cognition scales at 9 months of age while the other ST chimps tested about on par with human infants and RC chimps tested significantly better than human infants. Tests of social and emotional responsiveness revealed RC chimps to be happiest and least fearful, ST chimps to be in the mid-range,

and early stress chimps to be the least happy and most fearful. Interestingly, while ST chimps remained at midway levels on social and emotional responsiveness tests from 3 to 12 months, the RC group showed an increase in happiness and decrease in fearfulness across this time span and the early stress group showed a peak in fearfulness at about 6 months along with a pronounced dip in happiness, both of which resolved to be similar to ST levels by about 12 months of age (K. A. Bard & Leavens, in press).

CHAPTER 5

PROPOSAL FOR CURRENT STUDY

Introduction

Based on a body of data collected by Bard and colleagues (e.g. Bard, 1991; Bard, 2000; Bard, 2001; Bard et al., 1991; Bard et al., 1993), groups of chimpanzees specific to this study were reared in different environments and shown to exhibit various behavioral differences through the first year of life. These differences have been summarized, complete descriptions provided of the protocols of rearing in these differential environments, and a study will now be proposed to determine what of these early detectable differences still exist in these same chimpanzees much later (circa 20 years). I hypothesize that early stressors on chimpanzees will have impacted chimpanzee neurophysiological systems to a degree that should still be manifest in dysfunctional stress response such that these effects will be detectable in physiological and behavioral measures. Additionally, the inclusion of other chimpanzees that were reared either in standard nursery conditions or mother-reared will allow for greater power in examining the long-term effects of early rearing experiences on physiological health and social/behavioral development.

Study Subjects

Between 33 and 115 chimpanzees made up the subject pool for the different components of this study. Primary comparison groups include the Responsive Care group (RC); the Standard Care group (ST); and the Mother-reared group (MR). Different groupings made up of these same chimpanzees and compared on particular measures

include chimpanzees previously identified as exhibiting a disorganized attachment pattern (DA) or not (ND). A second grouping for comparison on particular measures includes standard care, late arrival chimpanzees (LA) (referred to previously as 'early stress' chimpanzees), and standard care, early arrival chimpanzees (EA). Mother-reared animals living in comparable social groupings at the Yerkes Main Center will be used for comparison purposes and in some cases animals raised at Yerkes and known to be either mother or nursery-reared will be used for broader comparisons. It should be noted that 22 out of 49 of the original nursery-reared subjects assessed by Bard and colleagues were available for this project; the other 27 have been moved to other facilities or, in a few cases, have passed away. Using attachment styles such as disorganization as were assessed for responsive care and some standard care chimpanzees in their first few years by using an adaptation of Ainsworth's Strange Situation test is considered reasonable due to the correlation of behaviors associated with the different attachment styles in these chimpanzees with behaviors typically correlated to human attachment styles. For example, studies of attachment bonding as related to social referencing in these chimpanzees at the age of 1-year found that using gaze as a communicative and referential strategy in assessing a 'novel' human interactant varied in correlation with established attachment styles between the chimpanzees and their preferred human caregivers much in the same way patterns of gaze referencing in humans vary in correlation with established attachment styles (Scott, Bard, van IJzendoorn, & Bakermans-Kranenburg, 2005).

General Predictions

Attachment and Later Development

Theories of attachment were eventually expanded to include predictions for long-term development. Once Bowlby's theories had taken hold, many institutions tried to alter the way orphaned children were cared for, and it had become of great interest to research to follow children into their fourth, fifth, and sixth years to monitor any long-lasting behavioral effects of institutionalization and often inconsistent or detached caregiving. For example, one such study in 1975 compared four-year-olds that had been consistently reared in an institution with four-year-olds of a comparable working class that had been reared at home and another set of four-year-olds that had spent their first 2 years in institutions and then been adopted or restored to their natural parents. The primary observations made by researchers included a fair equivalence between the groups in regards to overall prevalence of behavior problems in the children, but also noted that for the institutionalized children, problems reported included clinginess, temper tantrums, and poor peer relations, while working class children's problems were generally of a disciplinary nature. Generally, institutionalized children were described as clingy, attention-seeking, and not overly attached to care-staff (Tizard, 1975) – descriptions similar to those used by Ainsworth in regards to 'anxious' attachment styles. A more recent study following the behavior of children from Romanian orphanages that were adopted into Canadian families determined that when compared to Canadian children (never institutionalized) and to Romanian children that would have gone to the orphanage had they not been adopted before 4 months of age, the post-orphanage children were observed to have more behavioral problems. Additionally, it was found that length of time in the orphanage correlated positively with an increase in various problems such as eating disorders, medical issues, and stereotypical behaviors (Fisher, Ames, Chisholm, &

Savoie, 1997). The predictive value of attachment styles as assessed by the SST has been demonstrated by studies in which, for example, it was shown that children at 15 months of age that were classified as secure (using the SST) were more likely than those similarly classified as insecure to be considered socially competent and effective at age 3 ½ years (Waters, Wippman, & Sroufe, 1979). According to attachment theory, this demonstrates a continuity of development based on how the infant initially organizes his or her behavior towards the principal attachment figure, leading in a predictable manner to later behaviors (Ainsworth, 1985). Similar predictions include the better mental development of securely attached infants as they exhibit better affect during test situations, better cooperation with examiners, and more exploration of their environment (Ainsworth, 1985). Accordingly, it was found that security of attachment at 12 months did predict exploratory behavior, social behavior, cognitive development and language development at 21 months of age. More securely attached toddlers performed better on the Bayley Mental Scale (Bayley, 1969), had a larger observed vocabulary, were more playful, and were more attentive to features of a puzzle presented during testing (Main, 1983). For example, two case studies that were part of the Minnesota study showed the potential for secure infant attachment to ultimately override the effects of negative life events, and the potential for insecure infant attachment to ultimately predict a poor adult outcome regardless of positive indicators during later childhood (L. A. Sroufe, Egeland, Carlson, & Collins, 2005).

Of course, the ultimate goal in most child development studies such as these is to better understand what sort of rearing situations lead to the most healthy, effective, adapted child and, later, adult. Severe situations like those encountered in Romanian

orphanages in past decades have, for example, stimulated research aimed at determining the long-term effects of the deprivation infants and children have experience in Romanian institutionalized care. Such studies have revealed physiological and behavioral effects on deprived children, including altered patterns of cortisol secretion indicative of reduced stress responsivity and altered social behavior, and have included initial steps toward developing programs to minimize such damage (Carlson & Earls, 1997). Similar studies following children adopted out of Romanian orphanages have confirmed that early neurological effects persist years after removal from deprived environments, though for some children in the sample,the damage seemed to be reversible (Rutter, O'Connor, & Team, 2004). Based on similar results, some researchers have concluded that children have individual adaptabilities that allow some to recover from past poor functioning, while others do not show the same measurable amount of adaptability (L. Alan Sroufe, Egeland, & Kreutzer, 1990). Reviews of attachment literature have reported multiple longitudinal studies in which correlations between attachment classifications in infancy and antisocial behaviors, such as aggression, were significant; secure-attached children generally are reported to indicate greater empathy and less bullying behavior than anxious-attached children (M.H. Van IJzendoorn, 1997).

Disorganized Attachment

In the past two decades, a fourth attachment style has been parsed out from the previously mentioned styles; this style is labeled ‘disorganized attachment’ (Main & Solomon, 1990). Disorganized attachment is characterized by inconsistency in behaviors during the Strange Situation test; behaviors may include approach and also avoidance of the attachment figure during reunion episodes, apprehension, helpless or depressed

behaviors, or otherwise unpredictable mixes of the three organized attachment style behaviors (Main & Solomon, 1990). Infants classified as disorganized also have been found to exhibit cardiac arousal as compared to securely attached infants during the Strange Situation test (Spangler & Grossmann, 1993). Various meta-analyses of research regarding disorganized attachment have found, for example, that infants classified as disorganized exhibit elevated cortisol levels after separation episodes as compared to infants in organized attachment categories (Lyons-Ruth, 1996a; Spangler & Grossmann, 1993). Additionally, longitudinal studies have indicated that disorganized attachment as identified in infancy is a predictor for aggressive behavior in kindergarten (Lyons-Ruth, 1996a) and for less effective cognitive functioning in Icelandic children aged 7 – 17 years (Jacobsen, Edelstein, & Hofmann, 1994). In another meta-analysis of disorganized attachment research, classification of individuals into the category has been found to be relatively stable and to be predictive of problematic stress management (increased reactivity to stressful situations), aggressive behavior, and dissociative behaviors (e.g., intrusive thoughts, sudden lack of continuity during conversation, thoughts of behavior of which the person is unaware) later in life (Liotti, 2004; M. H. Van IJzendoorn, C. Schuengel, & M. J. Bakermans-Kranenburg, 1999). It has also been suggested that biological insults to specific areas of the right hemisphere occur during very early life if abuse is present, and that these insults are responsible for the later dissociative or hyper-arousal behaviors observed in disorganized-classified infants and older children (Schore, 2002). In a related study of rhesus macaques, reduction in cross-hemispheric connections in the corpus callosum, correlating with impaired cognitive function, has been found for nursery-reared rhesus as compared to mother-reared, group-housed rhesus (Sanchez, et

al., 1998). Measurements of various early-stress-related neuroanatomical structures is now possible due to advanced technology, such as structural magnetic resonance imaging (MRI) (Hopkins & Marino, 2000). Findings include reduced hippocampal size, reduced amygdala size, and reduced volume of the corpus callosum in various nonhuman primates and other mammals (Kaufman & Charney, 2001) as well as reduced anterior cingulated gyrus, altered frontal cortex regions, and, in some cases, increased amygdala size in humans and animals exposed to early life stressors (Lupien, McEwen, Gunnar, & Heim, 2009; Teicher et al., 2003). If disorganization in early life is correlated with early stress, then it is perhaps these biological effects that lead to the long-term effects associated with disorganized attachment.

CHAPTER 6

CURRENT STUDY

Experiment One: General Behavioral Observations

Experiment Subjects

All subjects are currently located at Yerkes Main Center or Field Station in small groups (2 – 6 animals) and between the ages of 15 and 30 years (see Table 1, page 47). Rearing group totals are as follows: 1) Mother-reared: 8 females, 3 males; 2) Responsive care: 6 females, 4 males; 3) Standard care: 4 females, 8 males. Within this same subject pool, there were 6 female and 4 male chimpanzees in the non-disorganized group (ND) and 3 females, 7 males in the disorganized group (DA). Only chimpanzees that were tested in the Strange Situation Test 20 years ago were considered as subjects for the attachment comparisons portion of the study; though disorganization is often seen at higher rates in individuals that are separated from their mothers, assuming that, for example, all mother-reared chimpanzees would be non-disorganized would be inappropriate. In fact, research supports the idea that some individuals raised by their mothers still exhibit a disorganized attachment. In addition, other attachment classifications were not considered because 1) the disorganization classification seems to be the most predictive of long-term effect and 2) there were not enough individuals in each of Ainsworth's secure/insecure categories to allow for comparison.

Table 1: Subjects for Experiment One: Behavioral Observations

(Specific rearing divides nursery into responsive vs. standard; General rearing combines responsive and standard into simply nursery; Early vs. Late Arrival standard further divides standard nursery into early and late arrival groups; NA = not applicable for this comparison)

Name	Sex	Age	Specific Rearing	General Rearing	Early vs. Late Arrival Standard	Disorganized Yes or No
Agatha	F	19	mother	mother	mother	NA
Amanda	F	21	responsive	nursery	responsive	N
Artemus	M	21	standard	nursery	standard - early arrival	Y
Arthur	M	21	responsive	nursery	responsive	Y
Callie	F	21	responsive	nursery	responsive	N
Christa	F	17	mother	mother	mother	NA
Drew	M	19	responsive	nursery	responsive	N
Duff	M	22	standard	nursery	standard - early arrival	N
Edwina	F	21	standard	nursery	standard - late arrival	Y
Elvira	F	23	mother	mother	mother	NA
Elwood	M	22	standard	nursery	standard - early arrival	Y
Evelyne	F	20	responsive	nursery	responsive	N
Faye	F	20	responsive	nursery	responsive	N
Fiona	F	17	mother	mother	mother	NA
Frannie	F	19	standard	nursery	standard - early arrival	Y
Fritz	M	24	standard	nursery	standard - early arrival	Y
Jewelle	F	20	mother	mother	mother	NA
Jolson	M	19	mother	mother	mother	NA
Julie	F	17	responsive	nursery	responsive	N
Justin	M	25	standard	nursery	standard - early arrival	NA

Table 1 continued

Katrina	F	24	standard	nursery	standard - early arrival	N
Lamar	M	24	standard	nursery	standard - late arrival	N
Lucas	M	19	responsive	nursery	responsive	Y
Luther	M	22	standard	nursery	standard - early arrival	Y
Lux	M	30	mother	mother	mother	NA
Melinda	F	29	mother	mother	mother	NA
Patrick	M	19	responsive	nursery	responsive	Y
Rebecca	F	21	responsive	nursery	responsive	Y
Rowena	F	23	standard	nursery	standard - late arrival	NA
Scott	M	25	standard	nursery	standard - early arrival	N
Suwanee	F	27	mother	mother	mother	NA
Sylvia	F	19	mother	mother	mother	NA
Travis	M	22	mother	mother	mother	NA

Hypotheses

1. Higher rates of abnormal and stress-related behaviors should be exhibited by individuals in the ST versus MR reared group.
2. Higher rates of abnormal and stress-related behaviors should exhibited by the DA animals versus ND (non-disorganized) animals.
3. Higher rates of solicitation directed towards humans should be observed for RC and ST versus MR individuals.
4. Higher rates of solicitation directed towards humans should be observed for RC versus ST individuals.

Methods

The ethogram detailed in Appendix A (page #) was used to record behavioral data. Observations were conducted in one hour blocks spread equally between the hours of 8:00 a.m. and 3:00 p.m. A total of between 6 and 10 hours of data were collected for each chimpanzee. Chimps were watched in their social groups using 1-0 sampling with intervals of 60 seconds to record behaviors and environmental events; proximity to other chimpanzees was recorded using scan sampling every 60 seconds. Data was collected using an iPaq recorder and Noldus Observer.

Data Analysis

Planned comparisons based on the listed hypotheses were conducted using a one-tailed Mann Whitney U test. Where data indicated it was appropriate, additional comparisons were made using a two-tailed Mann Whitney U. Kendall's Tau was used to assess possible correlations (two-tailed). This was decided to be the most appropriate test as it is based on ranks and the MWU is also based on ranks; this allows for a more consistent method of analysis. Abnormal behavior consisted of urophagy, feces related behaviors, idiosyncratic movement or manipulation of body parts, regurgitation/reingestion, and hair plucking. Stress-related behavior consisted of long, heavy, audible scratching and yawning. Both of these categories were collapsed for analysis.

Results

Because the ratio of females to males differed between the three rearing groups and the two disorganization groups, all statistics to be tested were initially compared using a Mann Whitney U between male and female subjects. These results did not indicate any significant differences between the subjects in the categories of attention toward humans, aggression toward humans, general solicitation of humans, positive solicitation of humans, negative solicitation of humans, abnormal behaviors or stress-related behaviors.

Additionally, because rates of humans approaching chimpanzee subjects were recorded but not controlled during data collection, possible correlations between the above mentioned behavioral categories and human approach required investigation. Kendall's Tau was not significant for any correlations except for the correlation between human approach and stress-related behaviors, $\tau = .459$, N = 33, $p = .000$ (two-tailed) (see Figure 1, page 50).

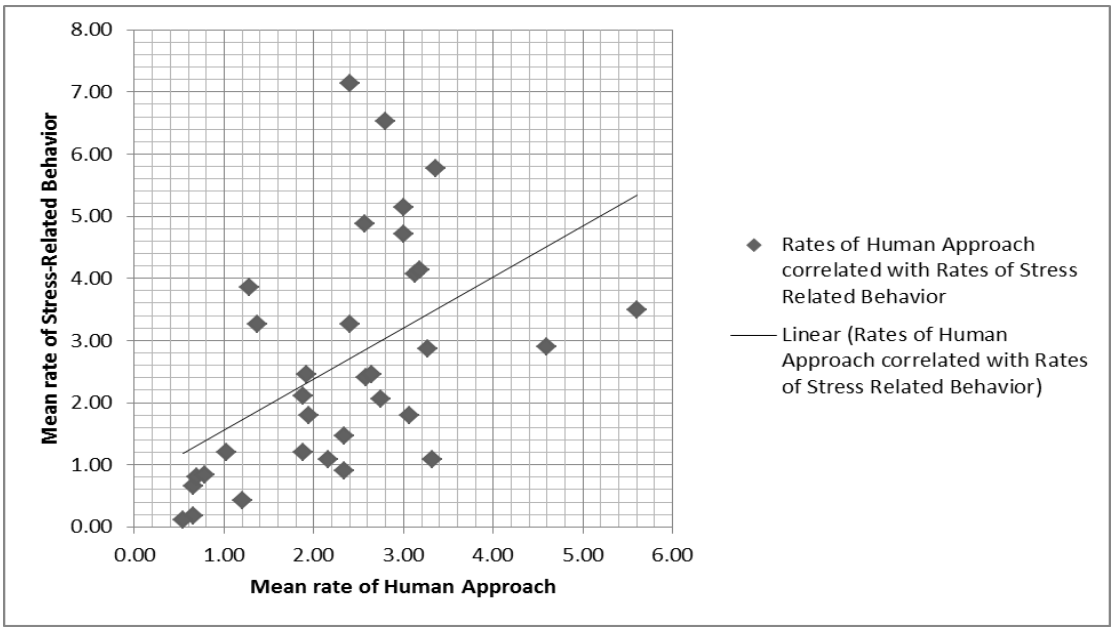
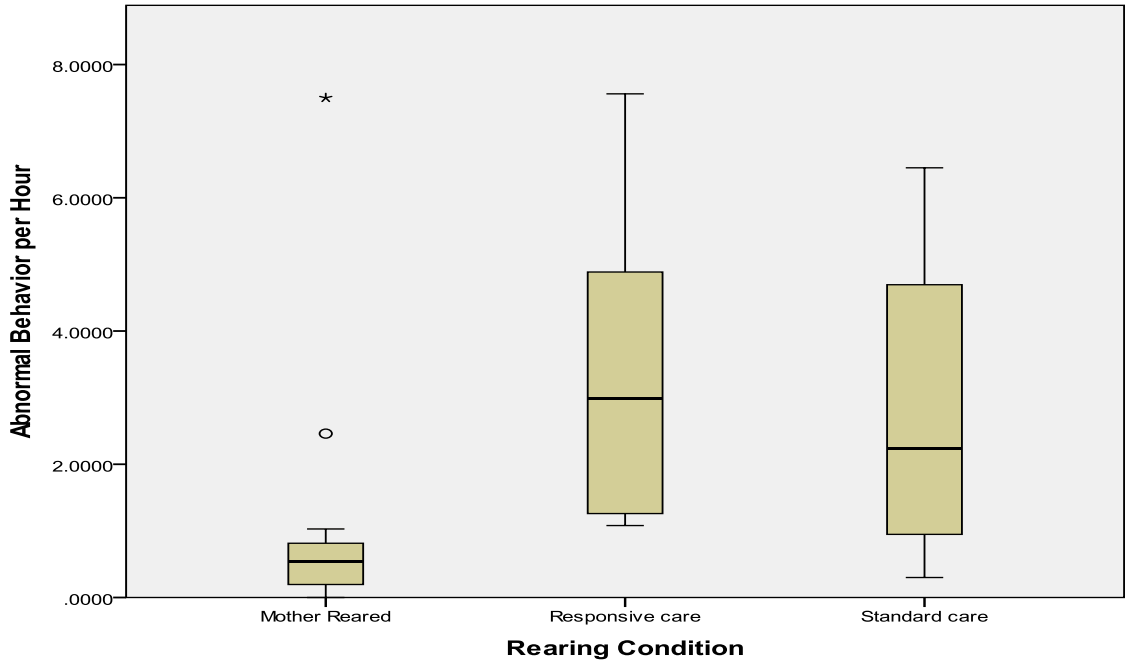


Figure 1: Correlation of Human Approach and Stress-Related Behavior (Rates per Hour)

Hypothesis Testing

1. Higher rates of abnormal and stress-related behaviors should be exhibited by individuals in the ST versus MR reared group.
    a. Standard care subjects exhibited significantly higher rates of abnormal behavior, $U = 30.0$, $N_{ST} = 12$, $N_{MR} = 11$, $p = .013$ (one-tailed).
    b. Standard care subjects did not exhibit significantly higher rates of stress-related behavior, $U = 56.0$, $N_{ST} = 12$, $N_{MR} = 11$, $p = .283$ (one-tailed).
    c. Responsive care subjects were also tested. Responsive care subjects, like standard care subjects, exhibited significantly higher rates of abnormal behavior as compared to mother-reared subjects, $U = 14.0$, $N_{RC} = 10$, $N_{MR} = 11$, $p = .004$ (two-tailed).
    d. Responsive care subjects did not exhibit significantly higher rates of stress-related behavior, $U = 33.0$, $N_{RC} = 10$, $N_{MR} = 11$, $p = .121$ (two-tailed).
    e. Only partial support was found for this hypothesis (see Figures 2a and 2b, page 52).
2. Higher rates of abnormal and stress-related behaviors should exhibited by the DA animals versus ND (non-disorganized) animals.
    a. Disorganized subjects did exhibit significantly higher rates of abnormal behavior, $U = 23.0$, $N_{ND} = 10$, $N_{DA} = 10$, $p = .021$ (one-tailed).
    b. Disorganized subjects did not exhibit significantly higher rates of stress-related behavior, $U = 39.0$, $N_{ND} = 10$, $N_{DA} = 10$, $p = .203$ (one-tailed).
    c. Only partial support was found for this hypothesis (see Figures 3a and 3b, page 53)

a.



b.

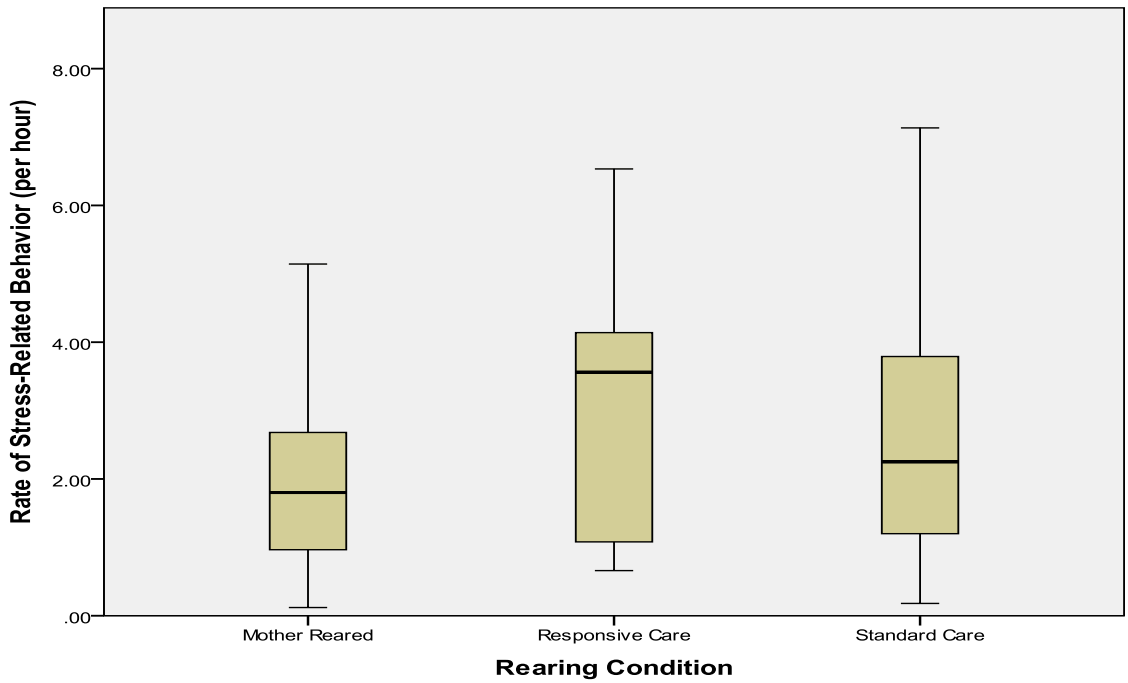


Figure 2: Rearing Group effects on rates of Abnormal and Stress Related Behavior

a. Abnormal Behavior by Rearing Condition

b. Stress-Related Behavior by Rearing Condition

a.

b.

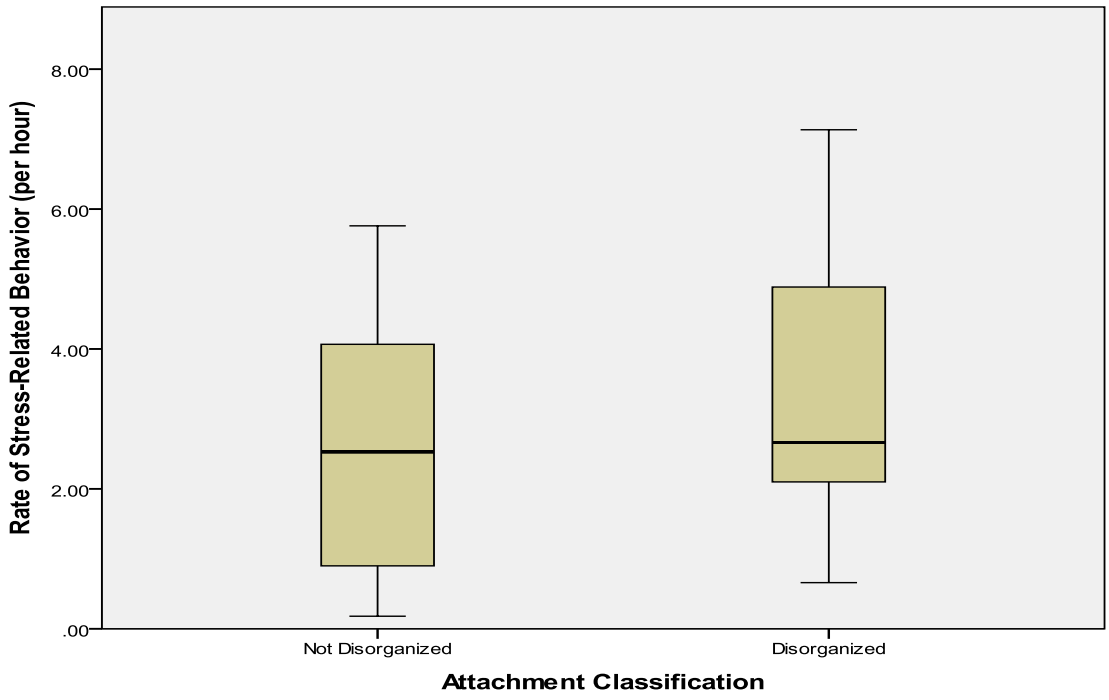


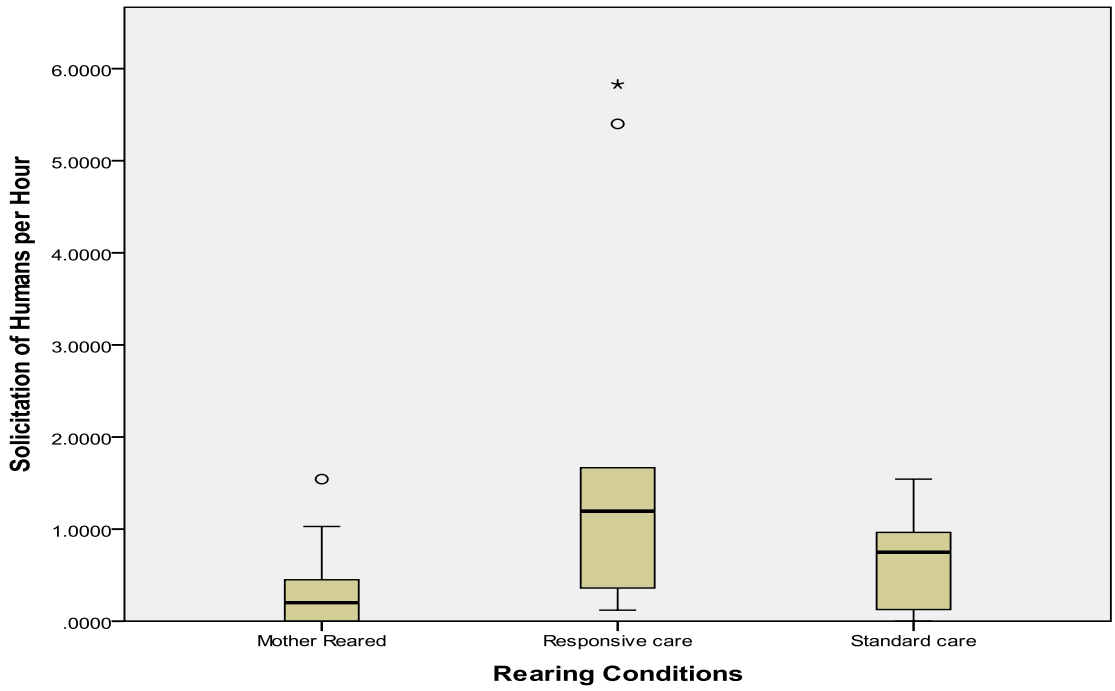
Figure 3: Disorganization effects on rates of Abnormal and Stress Related Behavior

a. Abnormal Behavior by Attachment Classification

b. Stress-Related Behavior by Attachment Classification

3. Higher rates of solicitation directed towards humans should be observed for RC and ST versus MR individuals.
    a. Responsive care subjects solicited human attention at a significantly higher rate as compared to mother-reared subjects, U = 20.5, N_{RC} = 10, N_{MR} = 11, p = .007 (one-tailed).
    b. Standard care subjects did not solicit human attention at a significantly higher rate than mother-reared subjects, U = 41.0, N_{ST} = 12, N_{MR} = 11, p = .065 (one-tailed).
    c. Only partial support was found for this hypothesis (see Figure 4a, page 55).
    d. Solicitation was recorded generally as solicitation of humans, but was also recorded as either positive or negative solicitation.
        i. Positive solicitation comparisons revealed significantly higher rates of positive solicitation for responsive care versus mother-reared subjects, U = 22.5, N_{RC} = 10, N_{MR} = 11, p = .022 (two-tailed) (Figure 4b, page 55).
        ii. Additionally, responsive care subjects negatively solicited humans at a significantly higher rate than mother-reared subjects, U = 23.5, N_{RC} = 10, N_{MR} = 11, p = .003 (two-tailed) (Figure 4c, page 56).
        iii. Standard care subjects did not significantly differ from mother-reared subjects on these measures (positive solicitation, U = 42.0, N_{ST} = 12, N_{MR} = 11, p = .137, two-tailed; negative solicitation, U = 61.0, N_{ST} = 12, N_{MR} = 11, p = .599, two-tailed)

a.



b.

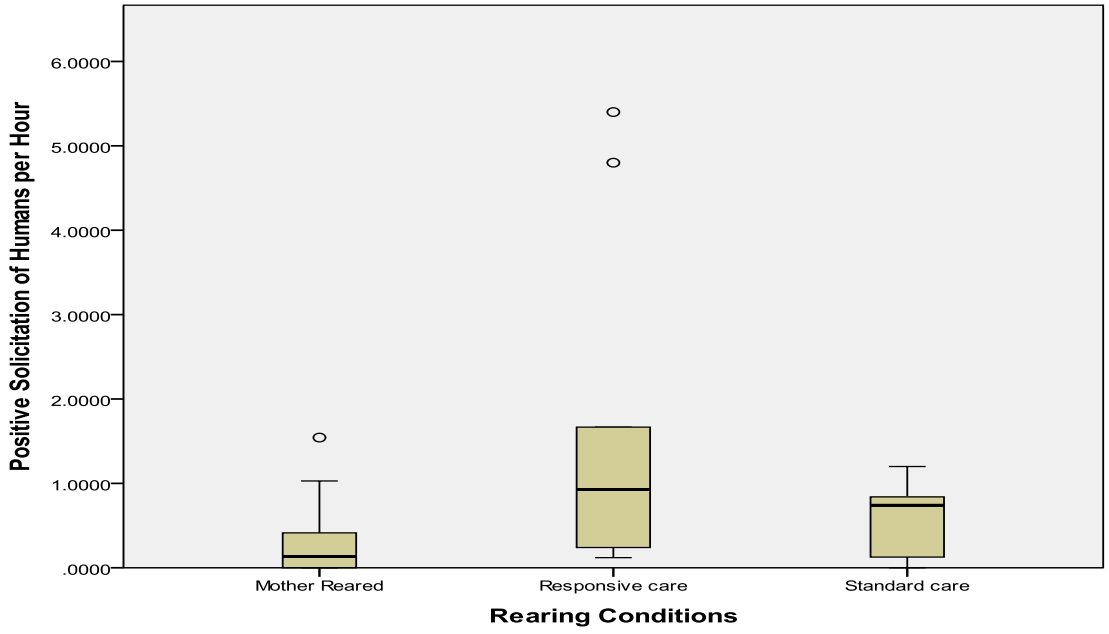


Figure 4: Rearing Group effects on rates of Human Directed Behavior

a. Overall Solicitation

b. Positive Solicitation

c.

d.

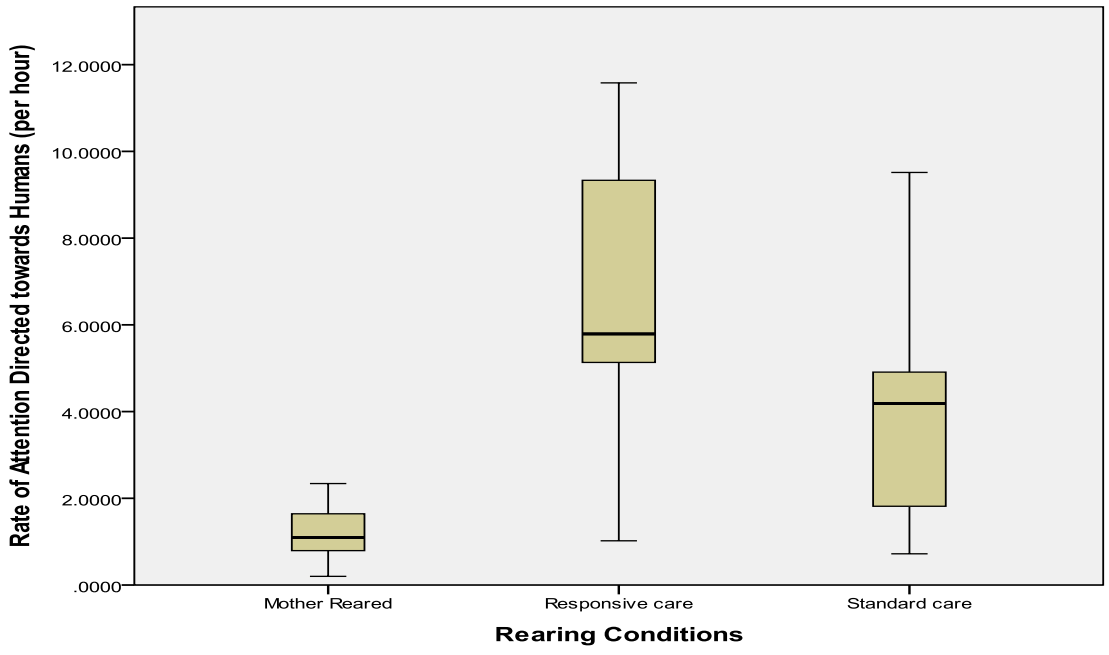


Figure 4: Rearing Group effects on rates of Human Directed Behavior

c. Negative Solicitation

d. Attention Directed towards Humans/Human Activity

4. Higher rates of solicitation directed towards humans should be observed for RC versus ST individuals.
    a. Responsive care subjects did not exhibit significantly higher rates of solicitation towards humans as compared to standard care subjects, $U = 39.0$, $N_{RC} = 10$, $N_{ST} = 12$, $p = .082$ (one-tailed).
    b. Support was not found for this hypothesis (See Figure 4a, page 55).
    c. Solicitation was recorded generally as solicitation of humans, but was also recorded as either positive or negative solicitation. Positive solicitation rate differences between the two nursery groups were not significantly different, $U = 41.5$, $N_{RC} = 10$, $N_{ST} = 12$, $p = .222$ (two-tailed) (Figure 4b, page 55).
    d. However, responsive care subjects did negatively solicit humans at a significantly higher rate than standard care subjects, $U = 23.5$, $N_{RC} = 10$, $N_{ST} = 12$, $p = .008$ (two-tailed) (Figure 4c, page 56).
    e. Though support was not found for the initial hypothesis, some exploratory analysis did reveal partial support for the hypothesis, but only regarding negative solicitations, not positive solicitations.
5. Exploratory analyses comparing rearing groups in terms of the amount of attention they focused on humans and human activity revealed significant differences between the groups (see Figure 4d, page 56).
    a. Standard care subjects attended to humans and human activity at a significantly higher rate than mother-reared subjects, $U = 20.0$, $N_{ST} = 12$, $N_{MR} = 11$, $p = .005$ (two-tailed).

b. Responsive care subjects attended to humans and human activity at a significantly higher rate than mother-reared subjects, U = 7.0, N_{RC} = 10, N_{MR} = 11, p = .001 (two-tailed).

c. Responsive care subjects also attended to humans and human activity at a significantly higher rate than standard care subjects, U = 25.0, N_{RC} = 10, N_{ST} = 12, p = .021 (two-tailed).

Experiment Two: Retrospective Health Analysis

Experiment Subjects

Subjects were 115 chimpanzees total though not all were included in each analysis. All subjects have spent most of their lives in roughly equivalent social situations at the Main Center or in Field Station runs or small group areas. Only records from the time animals lived at Yerkes were utilized. Animals that have since relocated to other facilities served as subjects only for the time spans for which they were present at Yerkes. All subjects are listed in Table 2 (page 59) with rearing and attachment categories defined.

Table 2: Subjects for Experiment Two: Health Assessments

(Specific rearing divides nursery into responsive vs. standard; General rearing combines responsive and standard into simply nursery; Early vs. Late Arrival standard further divides standard nursery into early and late arrival groups; NA = not applicable for this comparison)

Chimp name	Sex	Specific Rearing	General Rearing	Early vs. Late Arrival Standard	Disorganized Yes or No
Abby	F	mother	mother	mother	NA
Agatha	F	mother	mother	mother	NA
Alicia	F	mother	mother	mother	NA
Amanda	F	responsive	nursery	responsive	N
Amos	M	mother	mother	mother	NA
Andi	F	responsive	nursery	responsive	N
Anja	F	mother	mother	mother	NA
Artemus	M	standard	nursery	standard - early arrival	Y
Arthur	M	responsive	nursery	responsive	Y
Artica	F	standard	nursery	NA	NA
Augusta	F	standard	nursery	NA	NA
Azalea	F	mother	mother	mother	NA
Barbara	F	mother	mother	mother	NA
Barbi	F	mother	mother	mother	NA
Barney	M	standard	nursery	standard late arrival	N
Bjorn	M	mother	mother	mother	NA
Brandy	F	standard	nursery	NA	NA
Brodie	F	standard	nursery	NA	NA
Brooks	M	responsive	nursery	responsive	N
Bunny	F	standard	nursery	standard - early arrival	Y
Callie	F	responsive	nursery	responsive	N
Carl	M	standard	nursery	NA	NA
Carole	F	standard	nursery	standard - early arrival	Y
Cathy	F	mother	mother	mother	NA
Chip	M	standard	nursery	standard - early arrival	Y

Table 2 continued

Chrissy	F	standard	nursery	standard - early arrival	Y
Christa	F	mother	mother	mother	NA
Cissie	F	standard	nursery	NA	NA
Cynthia	F	mother	mother	mother	NA
Daisey	F	mother	mother	mother	NA
Dara	F	standard	nursery	NA	NA
David	M	standard	nursery	NA	NA
Debbie	F	standard	nursery	standard - early arrival	NA
Dona	F	mother	mother	mother	NA
Donald	M	standard	nursery	standard - early arrival	N
Drew	M	responsive	nursery	responsive	N
Duff	M	standard	nursery	standard - early arrival	N
Edwina	F	standard	nursery	standard - late arrival	Y
Elvira	F	mother	mother	mother	NA
Elwood	M	standard	nursery	standard - early arrival	Y
Evelyne	F	responsive	nursery	responsive	N
Faye	F	responsive	nursery	responsive	N
Fiona	F	mother	mother	mother	NA
Frannie	F	standard	nursery	standard - early arrival	Y
Fritz	M	standard	nursery	standard - early arrival	Y
Gelb	M	standard	nursery	NA	NA

Table 2 continued

Jarred	M	standard	nursery	standard - late arrival	Y
Jason	M	standard	nursery	standard - late arrival	Y
Jencie	F	mother	mother	mother	NA
Jewelle	F	mother	mother	mother	NA
Jolson	M	mother	mother	mother	NA
Jones	M	standard	nursery	standard - late arrival	Y
Josh	M	standard	nursery	standard - early arrival	Y
Julianne	F	mother	mother	mother	NA
Julie	F	responsive	nursery	responsive	N
Justin	M	standard	nursery	NA	NA
Kasey	F	standard	nursery	NA	NA
Katrina	F	standard	nursery	standard - early arrival	N
Kengee	F	standard	nursery	standard - late arrival	Y
Kerri	F	mother	mother	mother	NA
Kevin	M	mother	mother	mother	NA
Lamar	M	standard	nursery	standard - late arrival	N
Lindsey	F	responsive	nursery	responsive	Y
Liza	F	mother	mother	mother	NA
Lizzie	F	standard	nursery	standard - early arrival	Y
Lucas	M	responsive	nursery	responsive	Y
Luther	M	standard	nursery	standard - early arrival	Y
Lux	M	mother	mother	mother	NA
Lyons	M	standard	nursery	NA	NA
Magnum	M	standard	nursery	standard - late arrival	NA
Marietta	F	standard	nursery	NA	NA
Melinda	F	mother	mother	mother	NA

Table 2 continued

Melissa	F	standard	nursery	NA	NA
Merlin	M	responsive	nursery	responsive	N
Missy	F	mother	mother	mother	NA
Morgan	M	mother	mother	mother	NA
Mortimer	M	standard	nursery	NA	NA
Moses	M	responsive	nursery	responsive	Y
Patrick	M	responsive	nursery	responsive	Y
Pericles	M	mother	mother	mother	NA
Puddin	M	standard	nursery	NA	NA
Ranette	F	mother	mother	mother	NA
Rebecca	F	responsive	nursery	responsive	Y
Reid	M	mother	mother	mother	NA
Rita	F	mother	mother	mother	NA
Rosemary	F	responsive	nursery	responsive	Y
Rowena	F	standard	nursery	standard - late arrival	NA
Sabrina	F	standard	nursery	NA	NA
Samantha	F	mother	mother	mother	NA
Scott	M	standard	nursery	standard - early arrival	N
Sean	M	mother	mother	mother	NA
Sheena	F	standard	nursery	standard - early arrival	Y
Sheila	F	mother	mother	mother	NA
Shirley	F	standard	nursery	NA	NA
Sierra	F	standard	nursery	standard - early arrival	Y
Socrates	M	mother	mother	mother	NA
Steward	M	mother	mother	mother	NA
Storer	M	mother	mother	mother	NA
Suwanee	F	mother	mother	mother	NA

Table 2 continued

Sylvia	F	mother	mother	mother	NA
Tank	M	standard	nursery	NA	NA
Tara	F	mother	mother	mother	NA
Travis	M	mother	mother	mother	NA
Valerie	F	standard	nursery	NA	NA
Virginia	F	mother	mother	mother	NA
Vivienne	F	standard	nursery	NA	NA
Waga	F	mother	mother	mother	NA
Wilma	F	mother	mother	mother	NA
Wilson	M	responsive	nursery	responsive	N
Winston	M	standard	nursery	standard - early arrival	N
Zana	F	standard	nursery	standard - early arrival	Y

Hypotheses

1. Individuals categorized as disorganized should exhibit more frequent illnesses (respiratory infections, diarrhea) as compared to non-disorganized individuals due to impaired stress regulation.
    a. Disorganized subjects: 13 females, 13 males
    b. Non-disorganized subjects: 7 females, 10 males
2. Individuals in the standard care (late arrival) group should exhibit more frequent illnesses (respiratory infections, diarrhea) as compared to standard care (early arrival) individuals due to impaired stress regulation.

a. Early arrival subjects: 10 females, 10 males
b. Late arrival subjects: 3 females, 6 males

3. Individuals in the standard care rearing group should exhibit higher risk for wounding due to both conspecific aggression and self-wounding as compared to mother-reared individuals. This effect should be especially pronounced for standard care (late arrival) animals.
    a. Mother-reared subjects: 34 females, 13 males
    b. Standard care subjects: 13 females, 16 males
        i. Early arrival subjects: 10 females, 10 males
        ii. Late arrival subjects: 3 females, 6 males
4. Overall, nursery-reared animals should exhibit more frequent illnesses (respiratory infections, diarrhea) and increased wounding as compared to mother-reared animals.
    a. Mother-reared subjects: 34 females, 13 males
    b. Nursery-reared subjects: 35 females, 33 males

Methods

Subject animals' records from the Animal Records System (ARS) at Yerkes National Primate Research center were accessed for purposes of this study. Each animal's records were organized into reports from age 0 – 5, 6 – 10, 11 – 15, and 16 – 20 years. Incidents of upper respiratory infection, diarrhea, and injury were recorded and then compared between different rearing groups and different attachment categories, where available, as determined during previous research (M. H. Van IJzendoorn, et al., 2008).

Data Analysis

The mean number of incidents for each experimental group (e.g. nursery, standard care, disorganized, etc.) was compared using nonparametric tests. MWU tests were used for hypothesis testing using a one-tailed test in the direction of the stated hypothesis. In addition to comparing the mean number of incidents in each category during each age category (e.g., upper respiratory illnesses between ages 0 – 5), frequencies of each category of incident across years 0 - 20 were compared using the same nonparametric tests as previously described. This resulted in comparisons using overall frequencies of illness due to upper respiratory infection or diarrhea or frequencies of injury across the 20 year age span; an additional test was run to look at overall frequencies of illness based on a combination of data regarding upper respiratory infection and diarrhea. These tests were conducted only for individuals for whom a full 20 years of data was available. Finally, tests were run to check for sex bias across categories, particularly as the number of males and females in each comparison group were not always equivalent. Not all animals had data available for all 20 years; animals' data included in comparisons across the different age spans is indicated in Table 3 (page 66).

Table 3: Incident Data from ARS (Animal Records System)

(URI = upper respiratory infection; INJ = injury; DIA = diarrhea; NA = no data available)

Name	Age 0 - 5			Age 6 - 10			Age 11 - 15			Age 16 - 20		
	URI	INJ	DIA	URI	INJ	DIA	URI	INJ	DIA	URI	INJ	DIA
Abby	0	0	0	0	1	0	0	1	0	NA	NA	NA
Agatha	0	0	0	0	0	0	1	0	0	NA	NA	NA
Alicia	1	0	0	0	0	0	0	0	0	NA	NA	NA
Anja	0	0	0	0	0	0	0	3	0	0	2	0
Azalea	0	0	1	0	0	0	0	1	0	NA	NA	NA
Barbara	0	0	0	0	0	0	0	0	0	0	0	0
Barbi	0	0	0	0	0	0	0	0	0	0	1	0
Cathy	2	0	0	0	2	0	1	1	0	0	0	0
Christa	0	0	0	0	1	0	1	0	0	NA	NA	NA
Cynthia	0	0	0	0	0	0	0	0	0	1	0	0
Daisey	0	0	0	0	0	1	0	0	0	0	1	0
Dona	1	1	0	0	2	0	0	0	0	0	3	1
Elvira	0	0	0	1	0	1	0	0	0	0	0	0
Fiona	0	0	1	0	0	0	0	1	0	NA	NA	NA
Georgia	0	0	0	0	0	0	1	1	0	0	1	0
Jacqueline	0	0	0	0	0	0	0	0	0	0	1	0
Jaimie	0	0	0	1	1	0	0	2	0	NA	NA	NA
Jencie	0	0	0	0	0	0	0	0	0	0	0	0
Jewelle	0	1	0	0	0	0	0	0	0	0	0	0
Julianne	0	0	0	0	0	0	1	1	0	NA	NA	NA
Kerri	0	0	0	1	0	0	0	0	1	NA	NA	NA
Liza	0	0	0	0	2	0	0	3	0	NA	NA	NA
Melinda	0	0	0	0	0	0	0	2	0	0	0	0
Missy	0	0	0	0	1	1	0	0	0	NA	NA	NA
Ranette	0	0	0	0	4	0	0	0	0	0	0	0
Rita	0	0	0	0	0	0	0	0	0	0	1	0

Table 3 continued

Samantha	0	0	0	0	1	0	0	0	0	NA	NA	NA
Sheila	0	0	0	0	0	0	0	0	0	0	0	0
Suwanee	0	0	0	0	0	0	0	1	0	NA	NA	NA
Sylvia	0	0	0	0	0	0	0	0	0	NA	NA	NA
Tara	0	0	1	0	0	0	0	0	0	0	0	0
Virginia	0	0	1	0	1	0	0	1	0	0	2	0
Waga	0	0	0	0	0	0	0	0	0	0	0	0
Wilma	0	0	0	0	0	0	NA	NA	NA	NA	NA	NA
Amos	0	0	0	0	0	0	0	2	0	0	2	0
Bjorn	0	1	0	0	0	0	0	1	0	0	14	0
Jolson	1	0	0	0	0	0	0	0	0	NA	NA	NA
Kevin	0	0	0	0	0	0	0	3	0	NA	NA	NA
Lux	0	0	0	0	2	0	0	0	0	1	1	0
Morgan	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	NA
Pericles	0	0	0	0	0	0	NA	NA	NA	NA	NA	NA
Reid	2	0	0	1	0	0	NA	NA	NA	NA	NA	NA
Sean	0	0	0	1	1	0	NA	NA	NA	NA	NA	NA
Socrates	0	0	0	0	7	0	0	9	0	0	10	0
Steward	0	0	0	0	0	0	0	1	0	NA	NA	NA
Storer	0	0	0	1	0	0	0	0	0	1	0	0
Travis	0	1	1	1	1	0	1	1	0	0	0	0
Amanda	0	0	4	0	0	0	0	0	0	0	1	0
Andi	0	0	7	0	0	0	NA	NA	NA	NA	NA	NA
Callie	0	0	1	0	0	0	0	0	0	1	1	0
Evelyne	0	0	2	0	0	0	0	0	0	0	0	0
Faye	2	0	3	0	0	0	0	0	0	0	0	0
Julie	1	0	2	0	0	0	1	0	0	NA	NA	NA
Lindsey	1	0	2	0	0	0	NA	NA	NA	NA	NA	NA

Table 3 continued

Rebecca	1	0	4	0	0	0	0	0	0	0	0	0
Rosemary	2	1	2	0	0	0	NA	NA	NA	NA	NA	NA
Arthur	1	0	1	0	2	0	2	0	0	0	0	0
Brooks	2	1	1	0	0	0	NA	NA	NA	NA	NA	NA
Drew	1	1	1	1	0	0	1	0	0	NA	NA	NA
Lucas	2	1	1	0	0	0	0	0	0	NA	NA	NA
Merlin	1	2	4	0	0	0	NA	NA	NA	NA	NA	NA
Moses	2	4	1	NA	NA	NA	NA	NA	NA	NA	NA	NA
Patrick	2	0	6	0	0	0	1	0	0	NA	NA	NA
Wilson	1	0	1	0	0	0	NA	NA	NA	NA	NA	NA
Artica	0	0	0	0	0	0	0	0	0	0	0	0
Augusta	0	0	0	0	0	0	0	0	0	0	0	0
Brandy	0	0	0	0	0	0	0	1	0	NA	NA	NA
Brodie	0	0	0	0	0	0	0	0	0	0	1	0
Bunny	1	0	2	NA	NA	NA	NA	NA	NA	NA	NA	NA
Carole	1	1	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
Chrissy	0	0	1	NA	NA	NA	NA	NA	NA	NA	NA	NA
Cissie	0	0	0	0	0	0	0	0	0	0	1	0
Dara	0	0	0	0	0	0	1	0	0	0	0	0
Debbie	1	3	1	0	0	0	0	0	0	NA	NA	NA
Edwina	0	1	2	0	0	0	0	0	0	0	1	0
Frannie	1	0	2	0	0	0	0	1	0	0	1	0
Kasey	0	0	0	0	1	1	0	0	0	NA	NA	NA
Katrina	0	0	0	0	0	0	0	0	1	0	0	0
Kengee	1	2	0	0	0	0	0	0	0	0	0	0
Lizzie	1	0	0	0	1	1	0	0	0	NA	NA	NA
Marietta	0	0	0	0	0	0	0	0	0	1	0	0

Table 3 continued

Melissa	0	0	0	0	0	0	0	0	0	0	0	0
Rowena	0	0	0	1	0	0	0	0	0	0	0	0
Sabrina	0	0	0	0	0	0	0	0	0	0	0	0
Sheena	1	0	1	0	0	1	0	0	0	NA	NA	NA
Shirley	0	0	0	0	0	0	0	0	0	0	0	0
Sierra	1	1	1	NA	NA	NA	NA	NA	NA	NA	NA	NA
Valerie	0	0	0	0	0	0	NA	NA	NA	NA	NA	NA
Vivienne	0	0	0	0	0	0	0	0	0	0	0	0
Zana	1	2	2	1	0	0	0	0	0	NA	NA	NA
Artemus	1	3	1	0	0	1	0	1	0	0	2	0
Barney	1	1	2	0	2	0	0	0	0	NA	NA	NA
Carl	0	0	0	0	1	1	0	0	0	0	0	0
Chip	1	2	1	0	2	0	0	5	0	0	4	0
David	0	0	0	0	0	0	0	0	0	0	2	0
Donald	0	1	0	0	2	0	0	1	0	NA	NA	NA
Duff	0	1	0	0	0	0	0	0	0	0	0	0
Elwood	1	0	0	0	1	0	0	0	0	0	0	0
Fritz	1	1	0	0	1	0	0	0	0	0	0	0
Gelb	0	0	0	0	0	0	0	1	0	0	0	0
Hunter	0	0	0	0	0	0	0	0	0	0	2	0
Jarred	1	1	0	0	1	0	0	0	0	0	3	0
Jason	0	0	3	0	0	0	NA	NA	NA	NA	NA	NA
Jones	0	1	1	NA	NA	NA	NA	NA	NA	NA	NA	NA
Josh	1	1	3	0	0	0	0	0	0	NA	NA	NA
Justin	0	0	0	0	0	0	0	1	1	0	0	0
Lamar	0	0	0	0	0	0	0	0	0	0	1	0
Luther	1	1	2	0	0	1	0	0	0	0	0	0
Lyons	0	0	0	1	0	0	0	0	0	0	1	0
Magnum	1	0	2	0	0	0	0	3	0	NA	NA	NA

Table 3 continued

Mortimer	0	0	0	0	0	0	0	0	0	0	0	0
Puddin	0	0	0	0	0	0	0	0	0	0	0	0
Scott	0	0	0	0	1	0	0	0	1	0	0	0
Tank	0	0	0	0	0	1	0	0	0	NA	NA	NA
Winston	1	0	0	0	0	0	0	0	0	0	0	0

Results

An initial MWU was conducted to compare the sexes in each age category, each incident category. There were two significant differences found. In both the upper respiratory age 0 – 5 category and the injury 0 – 5 category, males were found to have a significantly higher mean count of incidents (p_{URI} = .030, two-tailed; p_{INJ} = .003, two-tailed). Based on these results, differences found in these two age categories where the sex ratio across groups is not similar may be driven by sex bias. Cases where this might be a problem are indicated with an 'a' superscript. Overall frequencies across the 20 year life span for diarrhea, upper respiratory infection, and injury were not affected by a sex bias.

Hypothesis Testing

1. Individuals categorized as disorganized should exhibit more frequent illnesses (respiratory infections, diarrhea) as compared to non-disorganized individuals due to impaired stress regulation. Disorganized individuals were identified in previous research on these chimpanzees (M. H. Van IJzendoorn, et al., 2008).
    a. Using non-parametric tests, disorganized individuals (N_{DA}) were compared to non-disorganized individuals (N_{ND}) in each category of incident (upper

respiratory infection (URI), diarrhea, and injury) in each specific age span. Mann Whitney U tests revealed two categories in which significant difference between these subject pools existed in the predicted direction (See Figure 5, page 72):

i. Disorganized individuals had a significantly higher mean incidence of upper respiratory infection (URI) between the ages of 0 and 5 as compared to non-disorganized individuals, $U = 144.0$, $N_{DA} = 26$, $N_{ND} = 17$, $p = .016$, one-tailed.

ii. Disorganized individuals had a significantly higher mean incidence of diarrhea between the ages of 6 and 10 as compared to non-disorganized individuals, $U = 136.0$, $N_{DA} = 20$, $N_{ND} = 17$, $p = .027$, one-tailed.

iii. In all other age span categories, supporting data for the hypothesis was not found. However, in 7 out of 12 age/incident categories, disorganized subjects did have higher frequency of incidents as compared to non-disorganized subjects. Of the remaining 5 age/incident categories, 1/5 was equal across the two groups and 4/5 were categories in which non-disorganized subjects had higher frequencies of incidents.

b. Further tests compared disorganized subjects to non-disorganized subjects in terms of overall frequencies of upper respiratory illnesses, diarrhea, and injury, each considered separately. Mann Whitney U tests were used to conduct planned comparisons according to the hypothesis. These tests

determined that if looking at the entire available age span for subjects who had 20 years of data available, neither the frequency of overall illness (URI + DIA) nor the frequency of diarrhea alone was significantly different between the two groups. However:

i. The frequency of injury was significantly different in the hypothesized direction, U = 2.0, N_{DA} = 11, N_{ND} = 9, p = .000 (two-tailed), as was:

ii. The frequency of upper respiratory infection was significantly different in the hypothesized direction, U = 18.0, N_{DA} = 11, N_{ND} = 9, p = .010 (two-tailed) (see Figure 6, page 73).

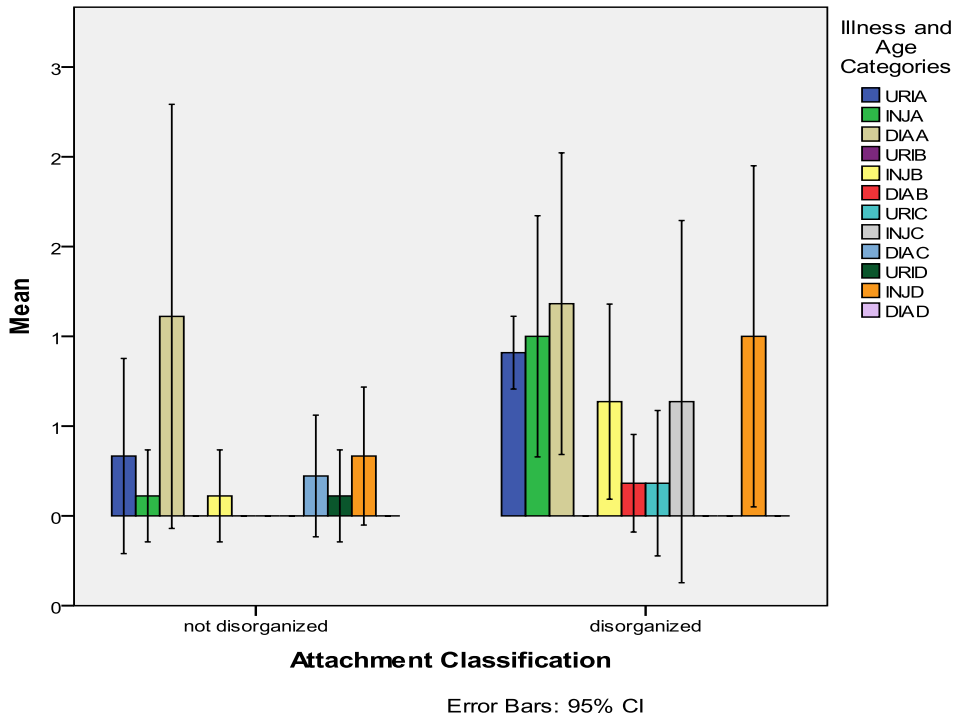


Figure 5: Disorganized versus Non-disorganized subjects: Incidences of upper respiratory infection (URI), diarrhea (DIA), and injury (INJ) in different age categories (A = 0 – 5, B = 6 – 10, C = 11 – 15, D = 16 – 20)

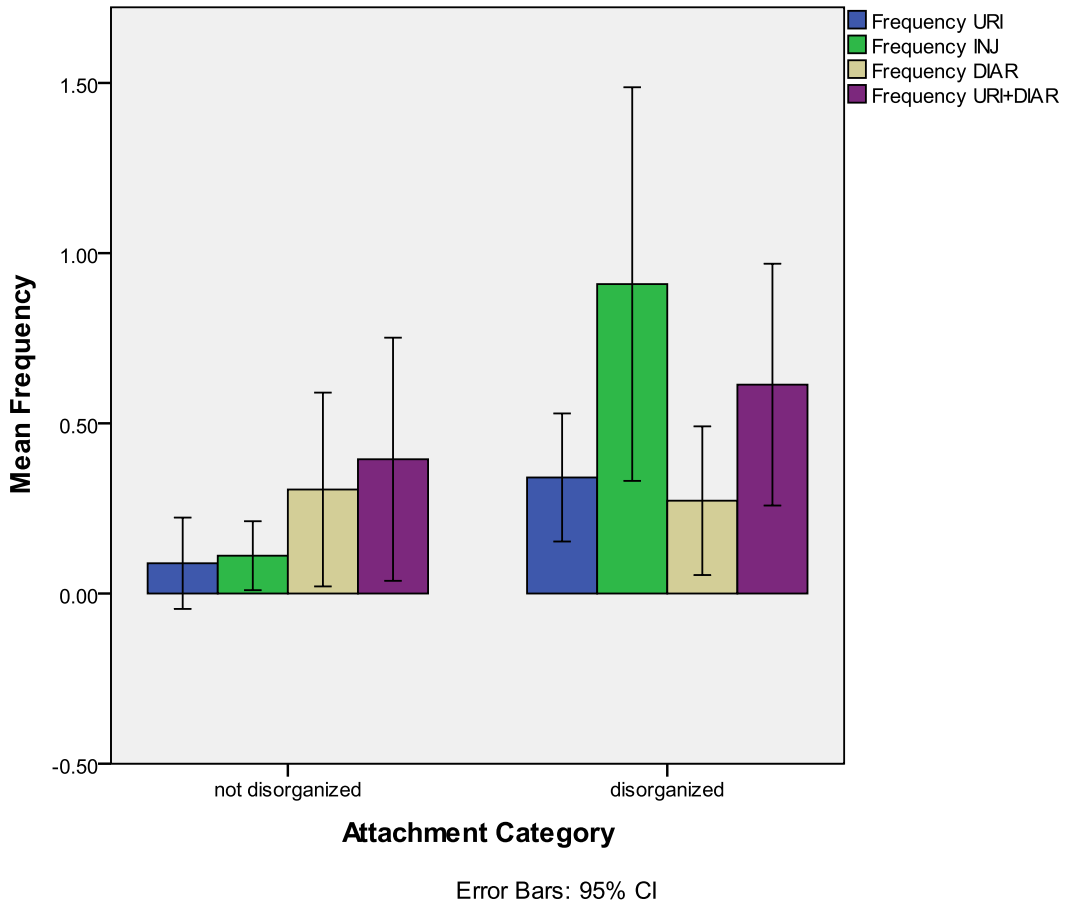


Figure 6: Disorganized versus Non-disorganized subjects: Incidences of upper respiratory infection (URI), diarrhea (DIA), injury (INJ), and overall illness (URI + DIA) across ages 0 – 20

2. Individuals in the standard care (late arrival) group should exhibit more frequent illnesses (respiratory infections, diarrhea) as compared to standard care (early arrival) individuals due to impaired stress regulation. For these tests, only subjects previously assessed by Bard and her colleagues were compared. Other

individuals known to be reared in the standard nursery but whose time of arrival is not known were not included (Figure 7, page 75).

a. MWU tests comparing the frequency of specific incident types in the different age span categories revealed no significant differences between the two groups of standard care chimpanzees[a].

b. Mann Whitney U tests revealed no significant difference between the two groups in the categories of overall frequency of upper respiratory infection, diarrhea, or overall frequency of illness (upper respiratory and diarrhea incidents combined)[a] (Figure 8, page 76).

c. The hypothesis was not supported by the data. In only 3 out of 12 age/incident categories was there a trend in the hypothesized direction; in 6 out of 12 age/incident categories, early arrival standard care subjects actually had a higher mean frequency of incidents than the late arrival subjects; in 3 age/incident categories there was no difference found[a].

d. Any sex bias driven effects should have increased the likelihood of higher scores for late arrival subjects; early arrival subjects consisted of 10 females and 10 males, but there were 3 females and 6 males in the late arrival group. However, since so few categories showed higher scores for late arrival subjects, none of them significant, any sex bias should not be relevant here.

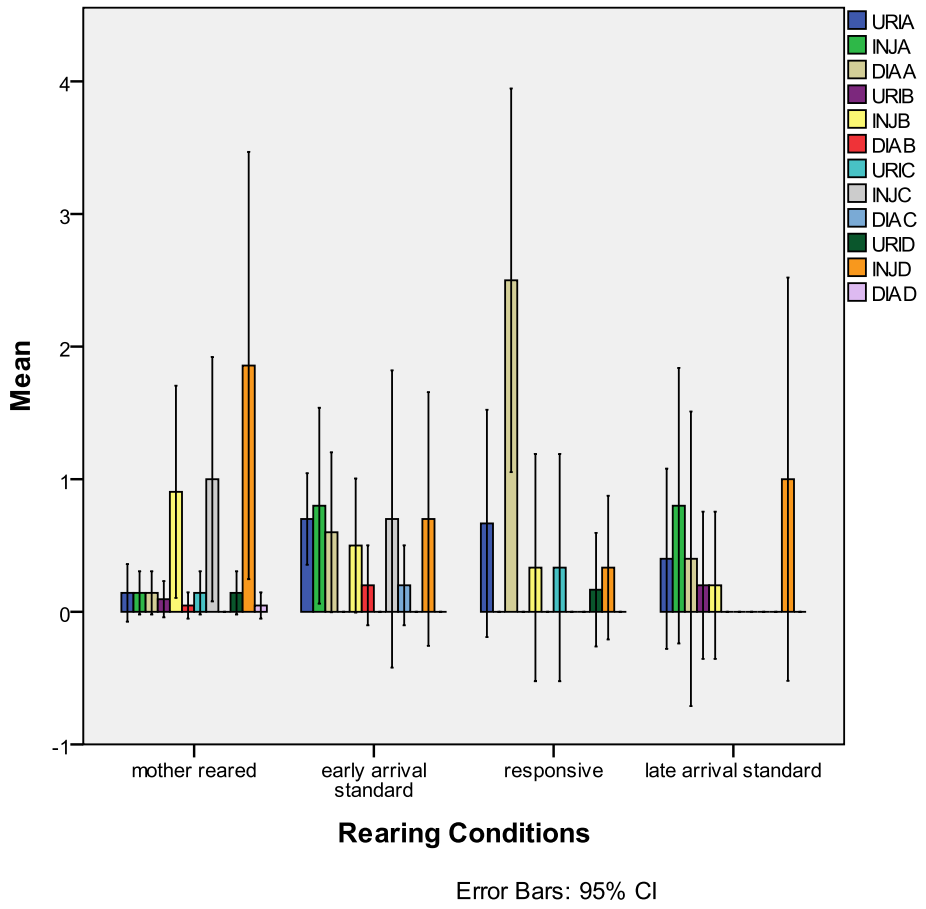


Figure 7: Mother-Reared, Responsive Care, Early and Late Arrival Standard Nursery subjects: Incidences of upper respiratory infection (URI), diarrhea (DIA), and injury (INJ) in different age categories (A = 0 – 5, B = 6 – 10, C = 11 – 15, D = 16 – 20)

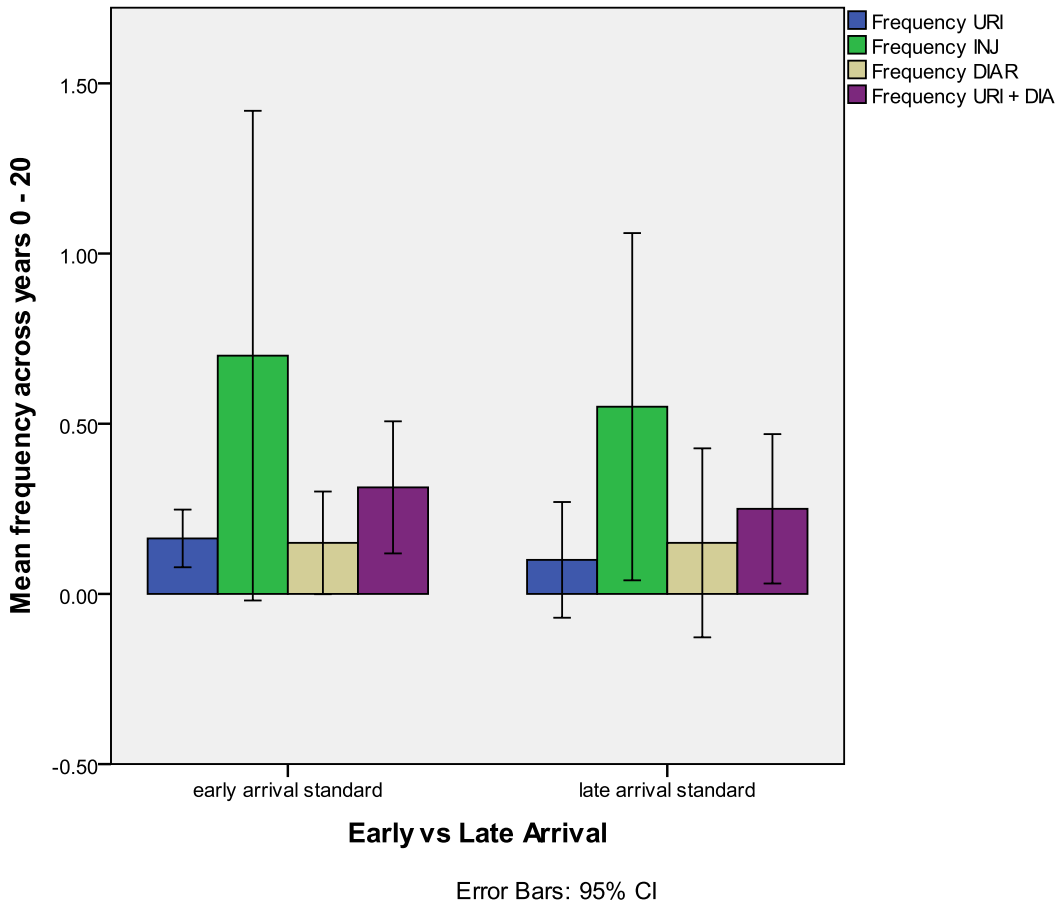


Figure 8: Early versus Late Arrival Standard Nursery: Frequency of upper respiratory infection (URI), diarrhea (DIA), injury (INJ) and overall illness (URI + DIA) across ages 0 – 20

3. Individuals in the standard care rearing group should exhibit higher risk for wounding due to both conspecific aggression and self-wounding as compared to mother-reared individuals. This effect should be especially pronounced for standard care (late arrival) animals. For these tests, only subjects previously assessed by Bard and her colleagues were compared. Other individuals known to

be reared in the standard nursery but whose time of arrival is not known were not included.

a. Individuals raised in the standard care nursery from the day of birth (EA) had a significantly higher frequency of injury as compared to mother-reared (MR) individuals during the years 0 – 5, U = 208.5, N_{EA} = 18, N_{MR} = 41, p = .000 (one-tailed)[a] (Figure 7, page 75).
b. Individuals known to have arrived at least 3 weeks post-birth to the standard care nursery (LA) exhibited a significantly higher frequency of injury during the years 0 – 5 as compared to mother-reared (MR) individuals, U = 94.00, N_{LA} = 9, N_{MR} = 41, p = .000 (one-tailed)[a] (Figure 7, page 75).
c. There was no significant difference found between late arrival and early arrival chimpanzees in terms of injury frequency in the different age categories or across the entire age span (0 – 20 years)[a] (Figure 8, page 76).
d. Generally the data could be interpreted as support for the hypothesis. However, the data only support the hypothesis for the years 0 – 5; past the fifth year, there is no support for the hypothesis. Additionally, there are concerns due to sex biases.
e. Effects of sex bias may be a concern for comparisons between early arrival chimpanzees and mother-reared chimpanzees; early arrival chimpanzees were balanced between male and female, but the mother-reared group contained more than twice as many females as males, which could have reduced incident scores for ages 0 – 5 in upper respiratory and injury categories. Thus support for the hypothesis found in 3a is weakened. Similarly, because late

arrival chimpanzees were 3 females and 6 males, scores for this group for upper respiratory or injury categories in ages 0 – 5 could be elevated by the sex bias, weakening hypothesis support for 3b.

4. Overall, nursery-reared animals should exhibit more frequent illnesses (respiratory infections, diarrhea) and increased wounding as compared to mother-reared animals. Nursery subjects (NR) in this case include all animals known to have been nursery-reared at Yerkes for whom ARS incident data was available. Similarly, all animals known to be mother-reared (MR) were included in these comparisons.

   a. Nursery-reared subjects were found to have a significantly higher frequency of upper respiratory illness during the years 0 – 5 as compared to mother-reared (MR) subjects, U = 1033.0, N_{NR} = 68, N_{MR} = 47, p = .000 (one-tailed)[a] (Figure 12, page #) .

   b. Nursery-reared subjects were found to have a significantly higher frequency of diarrhea during the years 0 – 5 as compared to mother-reared (MR) subjects, U = 945.0, N_{NR} = 68, N_{MR} = 47, p = .000 (one-tailed) (Figure 9, page 80).

   c. Nursery-reared subjects were found to have a significantly higher frequency of injury during the years 0 – 5 as compared to mother-reared (MR) subjects, U = 1203.0, N_{NR} = 68, N_{MR} = 47, p = .000 (one-tailed)[a] (Figure 9, page 80).

   d. In the age 11 – 15 category, mother-reared subjects had a significantly higher frequency of injury as compared to nursery-reared animals, U = 809.5, N_{NR} = 54, N_{MR} = 42, p = .002, (two-tailed) (Figure 9, page 80).

e. There was no significant difference between mother-reared and nursery-reared subjects in frequency of upper respiratory illness, diarrhea, injury, or a combined illness (URI + DIA) category across the 0 – 20 year age span (Figure 10, page 81).

f. Support was found for the hypothesis for years 0 – 5; however, support for years 6 – 20 was minimal, and injury data actually revealed differences, sometimes significant, in the opposite direction from what was predicted for these later years.

g. Additionally, sex bias may influence the results for incidents of injury and of upper respiratory illness during years 0 - 5, so only the results for diarrhea incidents can be considered as good support for the hypothesis. Sex bias could have effectively lowered mean scores for the mother-reared group due to a higher ratio of females to males; the nursery-reared group was well balanced between the sexes. Support for the hypotheses indicated by 4a, 4c and 4e are weakened by this possibility.

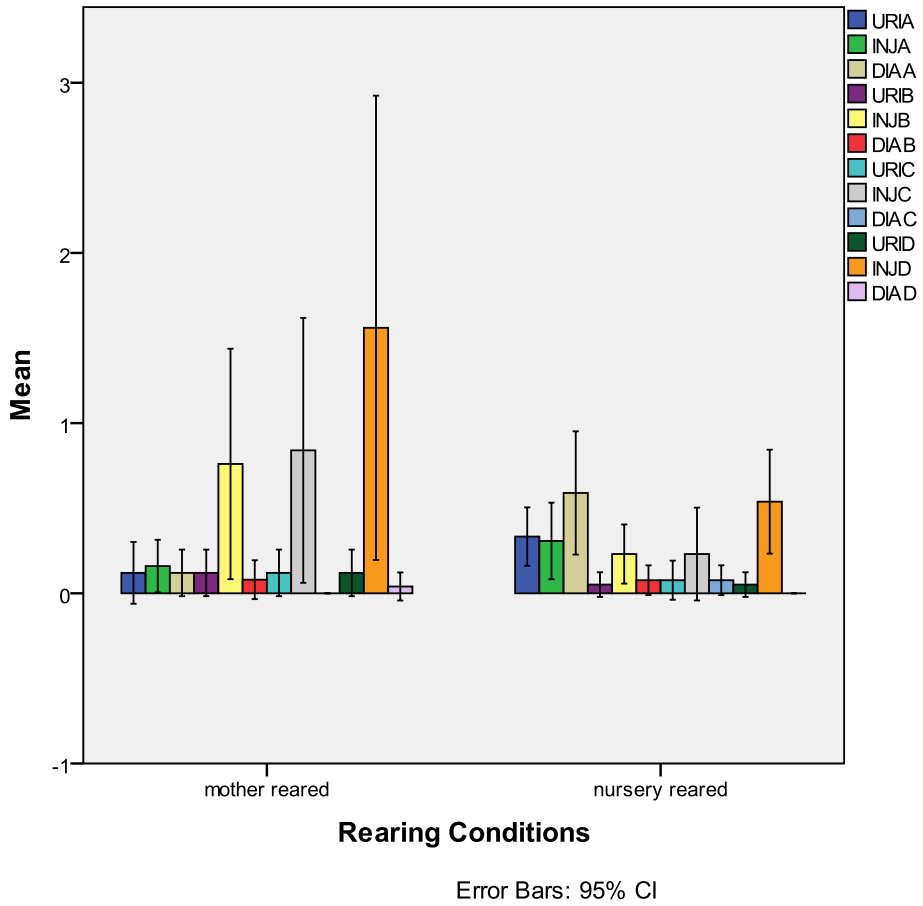


Figure 9: Mother-reared vs. Nursery-reared subjects: Incidences of upper respiratory infection (URI), diarrhea (DIA), and injury (INJ) in different age categories (A = 0 – 5, B = 6 – 10, C = 11 – 15, D = 16 – 20)

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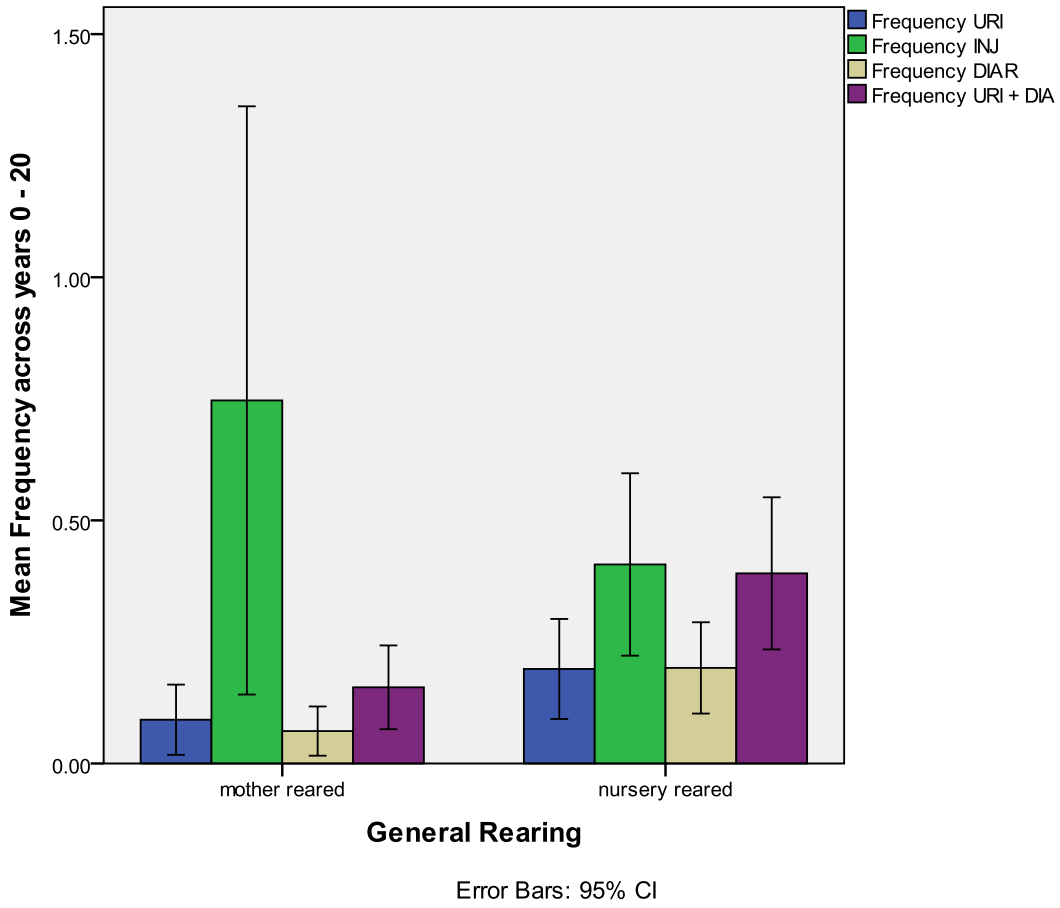

Figure 10: Mother-reared vs. Nursery-reared subjects: Frequency of upper respiratory infection (URI), diarrhea (DIA), injury (INJ) and overall illness (URI + DIA) across ages 0 – 20

Experiment Three: Personality, Well-being, and Human Orientation Survey

Experiment Subjects

Subjects for this study included animals raised in Bard and colleagues' responsive care nursery, animals raised in the standard nursery that served as subjects for Bard's original studies, and animals known to be mother-reared at Yerkes (Table 4, page 82). A total of 35 animals served as subjects, all between the ages of 16 – 29, all housed at Yerkes Main Center. Respondents included researchers, animal care providers,

veterinary staff, and behavioral management staff that work with the chimpanzees on a regular basis. A total of 4 – 9 surveys were collected for each chimpanzee. Respondents were not generally familiar with rearing conditions of the chimpanzees, particularly of the differential nursery conditions or even that there was a responsive care nursery for a period of time around 20 years ago; therefore, bias was not concluded to be a problem in regards to these results. Sample sizes for the differential rearing comparison groups were as follows: 1) Standard Care: 10 males, 4 females; 2) Responsive Care: 4 males, 6 females; 3) Mother-reared: 3 males, 8 females. Sample sizes for attachment comparison groups were as follows: 1) Disorganized: 7 males, 3 females; 2) Non-disorganized: 5 males, 7 females.

Table 4: Subjects for Experiment Three: Survey

(NA = not applicable for this comparison)

Chimpanzee	**Sex**	**Age**	**Rearing**	**Disorganization**
Agatha	F	18	Mother-reared	NA
Amanda	F	20	Responsive Care	N
Callie	F	20	Responsive Care	N
Christa	F	16	Mother-reared	NA
Edwina	F	20	Standard Care	Y
Elvira	F	23	Mother-reared	NA
Evelyne	F	20	Responsive Care	N
Faye	F	19	Responsive Care	N
Fiona	F	17	Mother-reared	NA
Frannie	F	19	Standard Care	Y
Jewelle	F	19	Mother-reared	NA
Julie	F	17	Responsive Care	N
Melinda	F	29	Mother-reared	NA

Table 4 continued

Rebecca	F	20	Responsive Care	Y
Rowena	F	23	Standard Care	NA
Suwanee	F	26	Mother-reared	NA
Sylvia	F	18	Mother-reared	NA
Artemus	M	21	Standard Care	Y
Arthur	M	20	Responsive Care	Y
Carl	M	25	Standard Care	NA
Drew	M	18	Responsive Care	N
Duff	M	22	Standard Care	N
Elwood	M	22	Standard Care	Y
Fritz	M	23	Standard Care	Y
Jolson	M	19	Mother-reared	NA
Justin	M	25	Standard Care	NA
Lamar	M	23	Standard Care	N
Lucas	M	18	Responsive Care	Y
Luther	M	22	Standard Care	Y
Lux	M	29	Mother-reared	NA
Patrick	M	18	Responsive Care	Y
Scott	M	24	Standard Care	N
Travis	M	22	Mother-reared	NA
Winston	M	25	Standard Care	N

Hypotheses

1. Individuals in the mother-reared (MR) group should exhibit better subjective well-being than those raised in the standard care nursery (ST) and those raised in the responsive care nursery (RC); similarly, individuals in the disorganized (DA)

group should exhibit lower subjective well-being than those not categorized as disorganized (ND).

2. Traits associated with dominance or social effectiveness should be exhibited at higher levels for mother-reared subjects as compared to standard care subjects.
3. Mother-reared animals should generally exhibit greater well-being than those that are nursery-reared (NR).
4. Mother-reared animals should generally exhibit lower human orientation scores than nursery-reared animals.

Methods

Surveys were sent to respondents using SurveyMonkey.com to enable quick and easy response and collection of results. The surveys themselves were designed to assess each chimpanzee in terms of relevant personality traits, subjective well-being, and human orientation. The personality and subjective well-being portions of the survey were based on surveys previously used on a number of occasions to assess chimpanzee traits (A. Weiss, 2002; A. Weiss et al., 2009; A. Weiss, et al., 2007a). Survey questions are reported in Appendix B (page #).

Data Analysis

Results were analyzed using a factor analysis with Varimax rotation to extract components. After extraction and loading of factor scores, individuals in the various rearing and attachment groups were compared using one-tailed Mann Whitney U tests for planned comparisons in the relevant categories as identified using the factor analysis. Traits associated with each extracted factor and the associated Eigen scores for each factor are listed in Table 5 (page 85). Traits with loading scores below an absolute value

of .30 on a factor were not included in analysis (DiStefano, Zhu, & Mindrila, 2009; Introduction to SAS; Walker & Maddan, 2009).

Table 5: Factor Analysis Results

Varimax Rotated Component Matrix*												
Traits	**Factors**											
	Affiliative Orientation	Aggressive Orientation	Dominance	Human Orientation	Purposeful -ness	Subjective Well-being	Activity Orientation	Neuroticism	Stinginess	Depression	Sexual Well-being	Excitability
Eigen values	20.165	14.720	9.833	5.636	2.552	2.258	1.902	1.556	1.523	1.407	1.151	1.089
Protective	.856											
Kindness	.821	-.320										
Sympathetic	.808	-.366										
Helpful	.798	-.393										
Affiliative	.768					.350						
Friendly	.765					.412						
Social Ineptness	-.756									.313		

Table 5 continued

Irritability	Negative Orientation/ Humans	Aggressive/ Humans	Moody/ Humans	Erratic	Cool	Equable	Eccentricity	Solitary	Autistic
-.403				-.559	.591	.611	-.662	-.710	-.749
.787	.871	.913	.914	.426		-.424			
					.407				
					-.326				
				-.474				-.310	
							.353		
						-.441			

Table 5 continued

Reckless	Manipulative	Predictability	Defiance	Gentleness	Negative Solicitation/ Humans	Impulsive	Mischievous	Moodiness	Deceptive
-.468		.545		.498		-.343		-.470	
.512	.547	-.550	.637	-.645	.666	.677	.693	.703	.757
.342	.377		.353	-.390					
					.427				
	.366		.337				.351		.407
.375									
	.484		.346						

Table 5 continued

Cautious	SWB/ Effective	Fearfulness	Vulnerabilit-y	Dependence	Dominance	Timid	Submissive	Jealous	Relaxed
								-.332	.470
								.472	-.479
-.746	.784	-.798	-.844	-.845	.852	-.863	-.884	.345	
								.384	
									.392
								.326	
								.363	
					.332				

Table 5 continued

Positive Solicitation /Humans	Positive Orientation /Humans	Solicitous/ Humans	Interest/ Humans	Human orientation	Independence	Anxious	Aggression	Boldness	Bullying
						-.464			
	-.304						.391	.507	.358
					.639	-.683	.701	.706	.724
.824	.854	.912	.938	.943					
					-.319				
							.371		.324
						.315			

Table 5 continued

Intelligence	Distractibility	Methodic	Imitative	Unemotion-al	Playfulness	Excitability	Quitting	Curiosity
.371				.397	.347	-.306		
						.355		
			-.383					
			.482	-.485	.573	.598	-.656	.670
.779	-.811	.918	.467				-.467	.430
			.413					
					.505	.367		
							.312	
	.365			-.413				.304

Table 5 continued

	Activity	SWB/Social Happiness	SWB/Happy	SWB/Want to be	Disorganization	Persistent	Inventive	Unperceptive	Decisiveness
		.550	.392	.488	-.482			-.347	
			-.335						.407
	.375					.459	.504		
			.310		-.584	.612	.616	-.663	.719
		.552	.611	.651					
	.799								
					.416				
								.390	

Table 5 continued

Laziness				-.481			-.737					
Awkward					-.329			.794				
Caring						.444		-.682				
Tractability/ Humans		-.429		.394				-.450			-.388	
Stinginess	-.315		.393						.690			
Depression	-.320				-.351	-.349				.491		
Sexuality	.344										.764	
Extraction Method: Principal Component Analysis. Rotation Method: Varimax with Kaiser Normalization.												
*Rotation converged in 17 iterations.												

Results

Factor Analysis

Factor analysis extracted 12 components with Eigenvalues greater than 1.000. This study did not rely on factors previously identified by investigators looking at chimpanzee

personality because the goal was to identify factors based on not just personality surveys but, in addition, subjective well-being and human orientation. Factors and trait loading scores onto each factor are reported in Table 5 (page 85). Based on the traits loading onto each factor, Factor 1 was labeled Affiliative Orientation, Factor 2 labeled Aggressive Orientation, Factor 3 labeled Dominance, Factor 4 labeled Human Orientation, Factor 5 labeled Purposefulness, Factor 6 labeled Subjective Well-being, Factor 7 labeled Activity Orientation, Factor 8 labeled Neuroticism, Factor 9 labeled Stinginess, Factor 10 labeled Negative Orientation, Factor 11 labeled Sexual Well-being, and Factor 12 labeled Excitability (Figure 11, page 94). Loading scores from the Rotated Component Matrix obtained through Varimax rotation were multiplied by each animal's mean score on the various traits loading higher than an absolute value of .30 onto the relevant factor. Rotation is often recommended especially for small sample sizes as it clarifies between overlapping categories ("Construction of Composite Indicators: Step 6. Weighting; Garrett-Mayer, 2006). Weighting scores is recommended for small sample sizes as well as it allows for more power in investigating differences between groups in that small sample; the scores obtained through weighting are not as generalizable, but exact factor scores (as derived from weighting) may be preferred when using factor scores on the same sample as that from which they were derived, especially when sample size is relatively small, which applies in this case (Grice & Harris, 1998). Because the goal of this study was to look for differences between groups in this particular sample, weighted scores were used. Once these calculations were made, the resulting scores for each trait as contributing to the relevant factor were summed for each subject. Means of these sum scores on factors were then compared between the different

study groups using Mann Whitney U tests to evaluate hypotheses. Factors 10 – 12 were not assessed for purposes of this study; visual evaluation of a scree test confirmed that this choice was valid.

Testing for Sex-Related Effects

Because there were unequal ratios of males to females in the different study groups, a MWU test was conducted to assess any main effect of sex on any of the tested factors; there were significant effects of sex on the category of Purposefulness (U = 61.0, N_F = 18, N_M = 17, p = .002, two-tailed), females exhibiting significantly higher scores on Purposefulness as compared to males, and significant effects of sex on Activity Orientation (U = 92.0, N_F = 18, N_M = 17, p = .044, two-tailed), males exhibiting significantly higher scores on Activity Orientation as compared to females. There were no other significant effects of sex on factor scores.

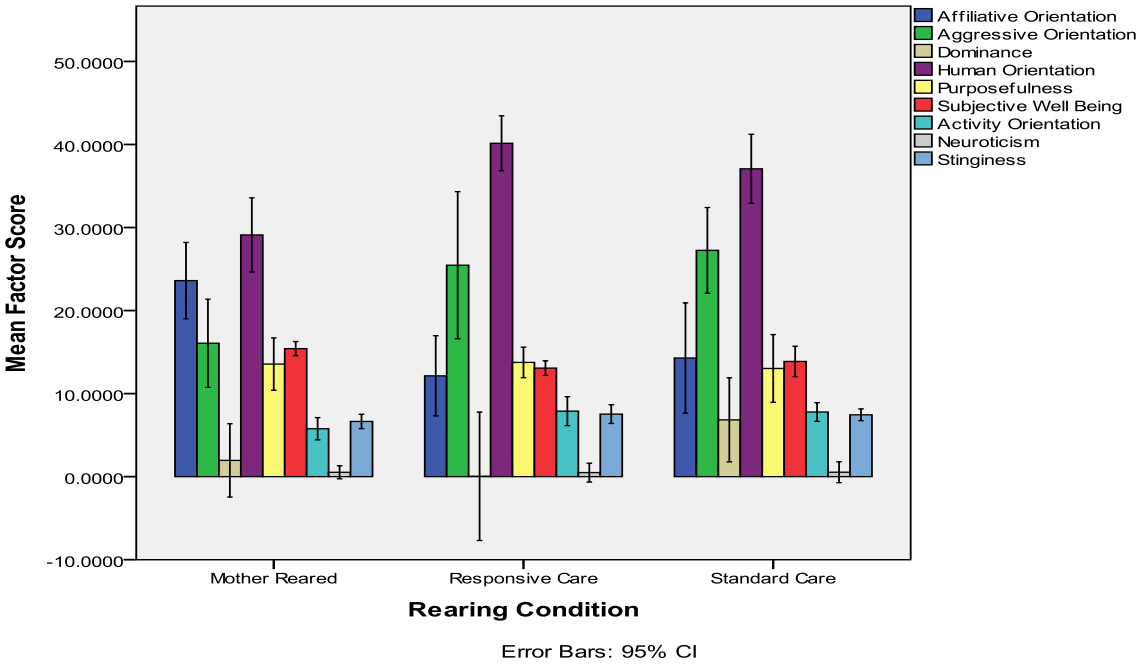

Figure 11: Survey Factors 1 – 9, Rearing Group Mean Scores

Hypothesis Testing

1. Individuals in the mother-reared (MR) group should exhibit better subjective well-being than those raised in the standard care nursery (ST) or responsive care nursery (RC); similarly, individuals in the disorganized (DA) group should exhibit lower subjective well-being than those not categorized as not-disorganized (ND).
    a. Mother-reared subjects exhibited significantly higher scores on the Factor of Subjective Well-being as compared to standard care subjects, $U = 45.0$, $N_{MR} = 11$, $N_{ST} = 14$, $p = .040$ (one-tailed) (see Figure 12, page 95).
    b. Mother-reared subjects exhibited significantly higher scores on the Factor of Subjective Well-being as compared to responsive care subjects, $U = 9.0$, $N_{MR} = 11$, $N_{RC} = 10$, $p = .001$ (one-tailed) (see Figure 12, page 96).
    c. No significant difference was found in regards to Subjective Well-being for disorganized versus non-disorganized subjects (see Figure 13, page 96).
    d. There was strong support found for the first part of this hypothesis but weak to no support found for the second part of the hypothesis.

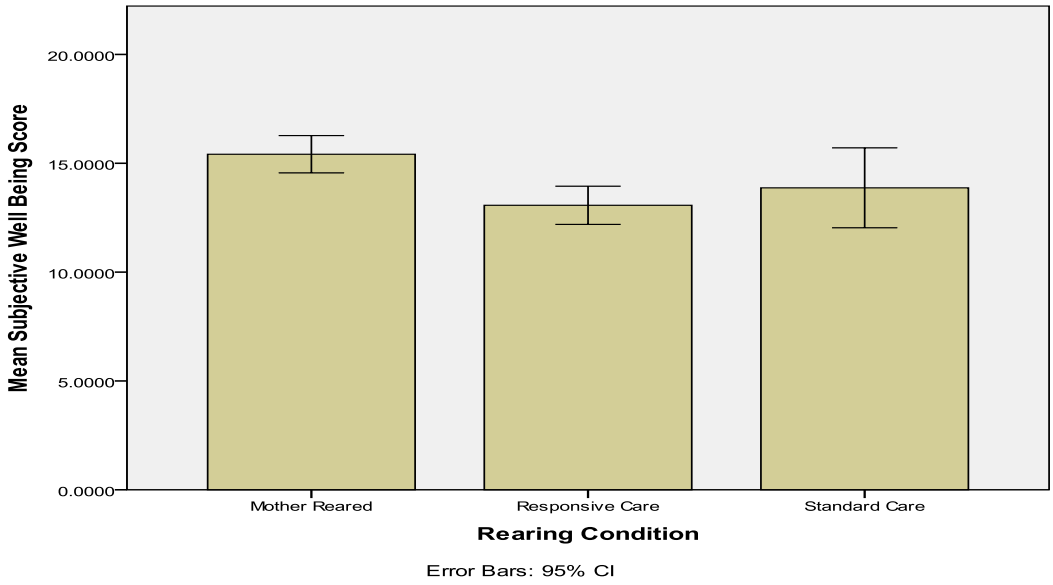

Figure 12: Mean Subjective Well-Being by Rearing Condition (mother versus responsive care versus standard care)

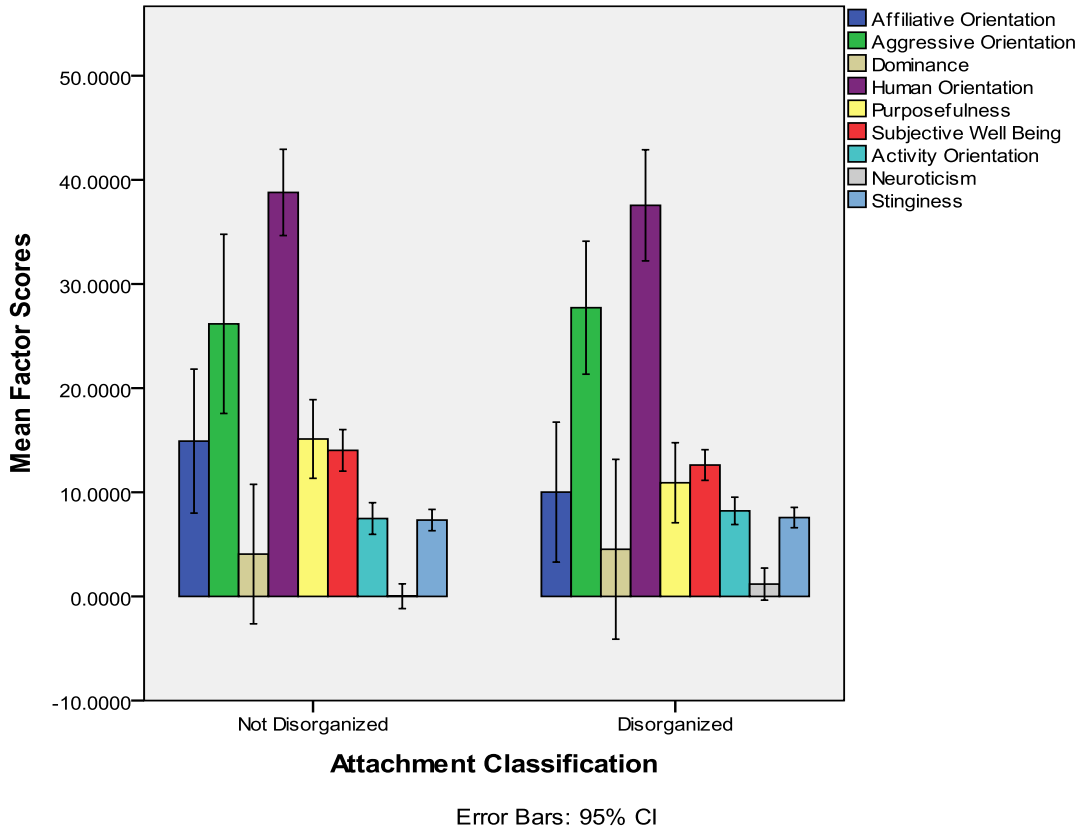

Figure 13: Survey Factors 1 – 9, Disorganized and Non-disorganized Mean Scores

2. Traits associated with dominance or social effectiveness should be exhibited at higher levels for mother-reared subjects as compared to standard care subjects.
    a. There was no significant difference found between these two groups in regards to the Dominance factor, U = 47.0, N_{ST} = 14, N_{MR} = 11, p = .101 (two-tailed) (Figure 11, page 94).
    b. No support was found for this hypothesis.
3. Mother-reared animals should generally exhibit greater well-being than those that are nursery-reared (NR).
    c. Mother-reared animals scored significantly higher on scores of Subjective Well-being as compared to nursery-reared subjects (NR, standard care and responsive care subjects combined), U = 54.0, N_{MR} = 11, N_{NR} = 24, p = .003 (one-tailed) (Figure 14, page 97).
    d. Strong support was found for this hypothesis.

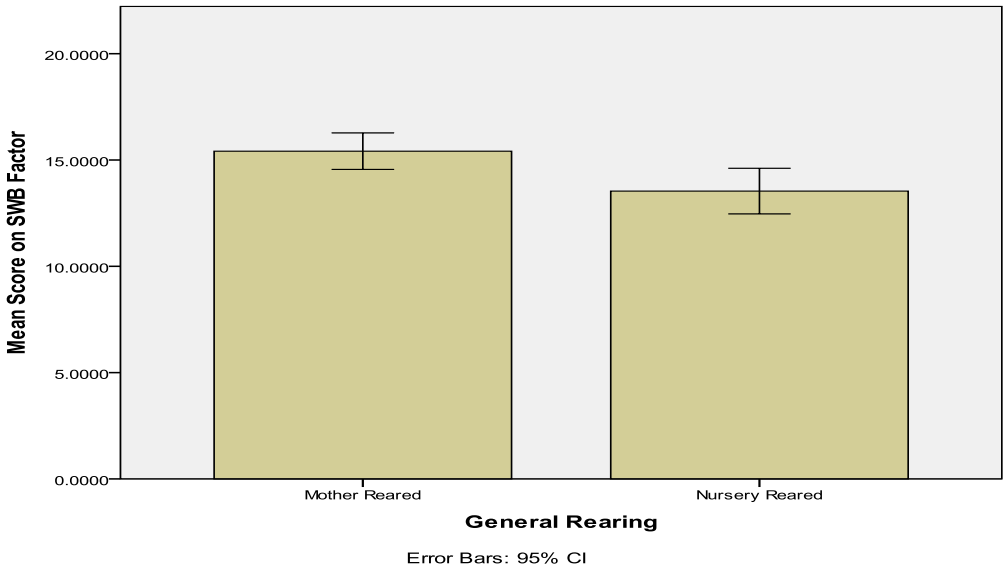

Figure 14: Mean Subjective Well-Being Factor Scores by Rearing Condition (mother versus general nursery)

4. Mother-reared animals should generally exhibit lower human orientation scores than nursery-reared animals.
    a. Mother-reared animals scored significantly lower on Human Orientation scores as compared to nursery-reared subjects, U = 41.0, N_{MR} = 11, N_{NR} = 24, *p* = .001 (one-tailed) (Figure 15, page 98).
    b. Strong support was found for this hypothesis.

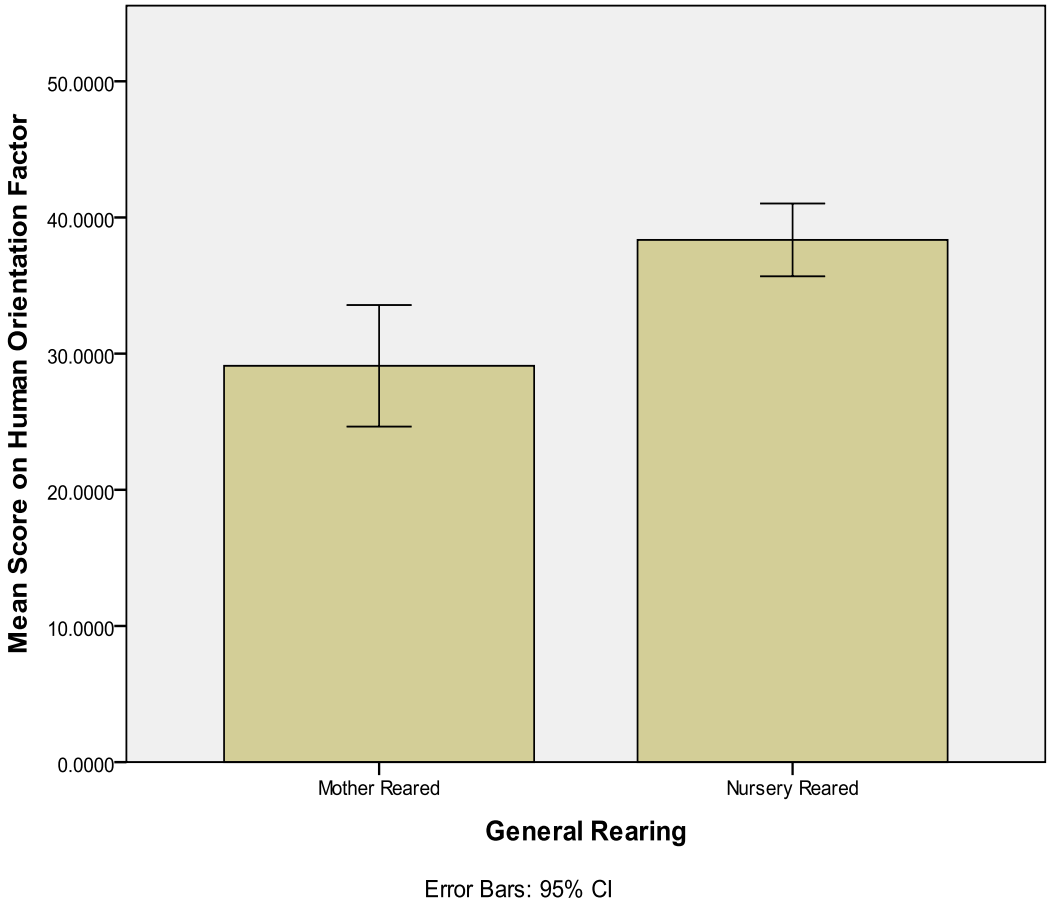

Figure 15: Mean Human Orientation Factor Scores by Rearing Condition (mother versus general nursery)

Trends in the Data

Responsive versus Standard Care

A consistent trend indicating possible differences between the RC and ST nursery groups pointed towards the need for further exploration. Additional MWU tests were conducted where appropriate to explore non-hypothesis related results.

1. Behavioral data:
    a. Aggressive behavior towards humans: Responsive care subjects aggressed on humans at a near-significant higher rate than standard care subjects, U = 31.50, N_{RC} = 10, N_{ST} = 12, p = .058 (two-tailed) (Figure 16, page 100).
    b. There was no significant difference between the two groups regarding abnormal behavior (p = .391, two-tailed) or stress-related behavior (p = .391, two-tailed).

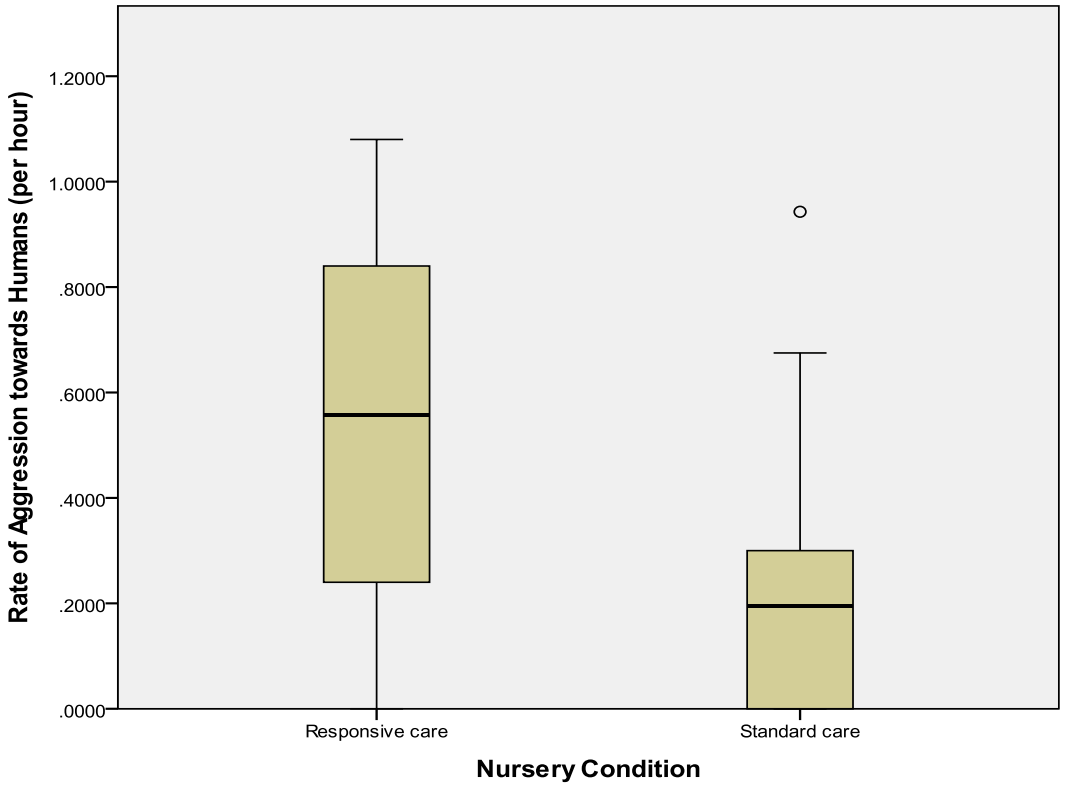

Figure 16: Rate of Aggressive Behavior towards Humans: Responsive versus Standard Care

2. Health-related data: nursery categorization was slightly different for health data analysis; please see data analysis following this section of the paper for results.
3. Survey data:
    a. MWU tests were run to compare scores on Subjective Well-Being questions (B1 – B4) between responsive and standard care subjects (see Appendix B for the specific questions). Though in all cases standard care subjects had higher mean scores than responsive care subjects, none of these differences were significant based on two-tailed MWU scores (see Figure 17, page 101).

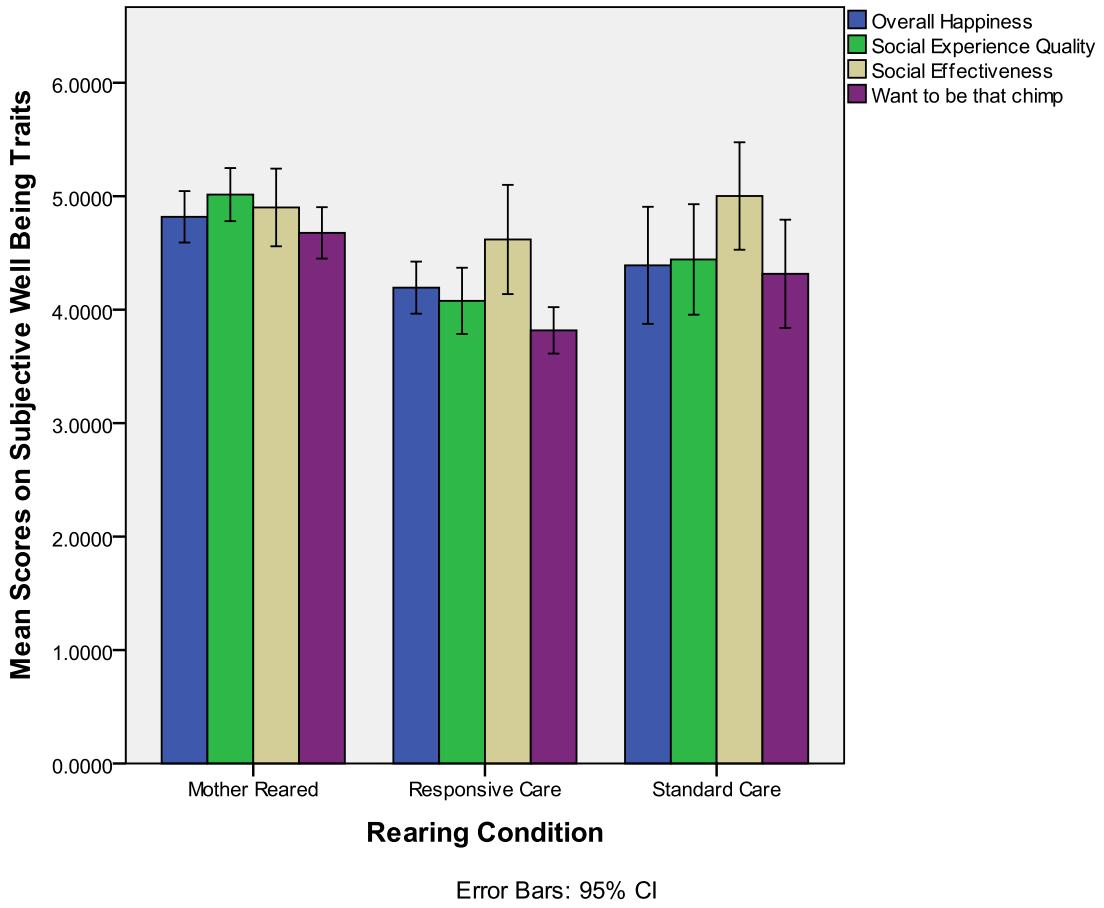

Figure 17: Subjective Well-Being Trait Scores by Rearing Condition (mother versus responsive care versus standard care)

b. MWU tests were run to explore differences on various personality survey items from the survey; notable differences are reported here:

   i. The RC chimps had near-significant higher mean scores than ST chimps on question C5 (perceived anxiety of the chimpanzee), U = 31.50, N_{RC} = 10, N_{ST} = 12, p = .060 (two-tailed) (see Figure 18, page 102).

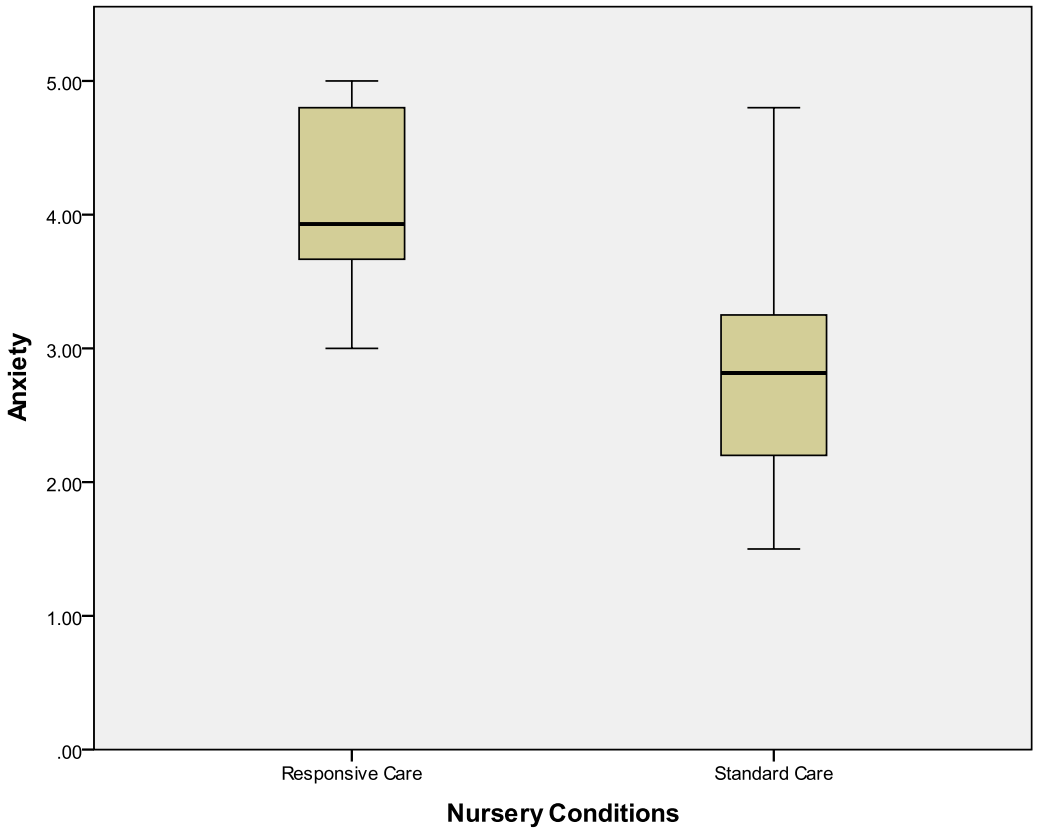

Figure 18: Mean Scores on survey question C5 (perceived anxiety of the chimpanzee)

ii. The RC chimps had significantly lower mean scores than ST chimps on question C9 (perceived equability of the chimpanzee), U = 29.50, N_{RC} = 10, N_{ST} = 12, p = .044 (two-tailed) (see Figure 19, page 103).

iii. The RC chimps had significantly lower mean scores than ST chimps on question C13 (perceived calm of the chimpanzee), U = 27.50, N_{RC} = 10, N_{ST} = 12, p = .032 (two-tailed) (see Figure 20, page 103).

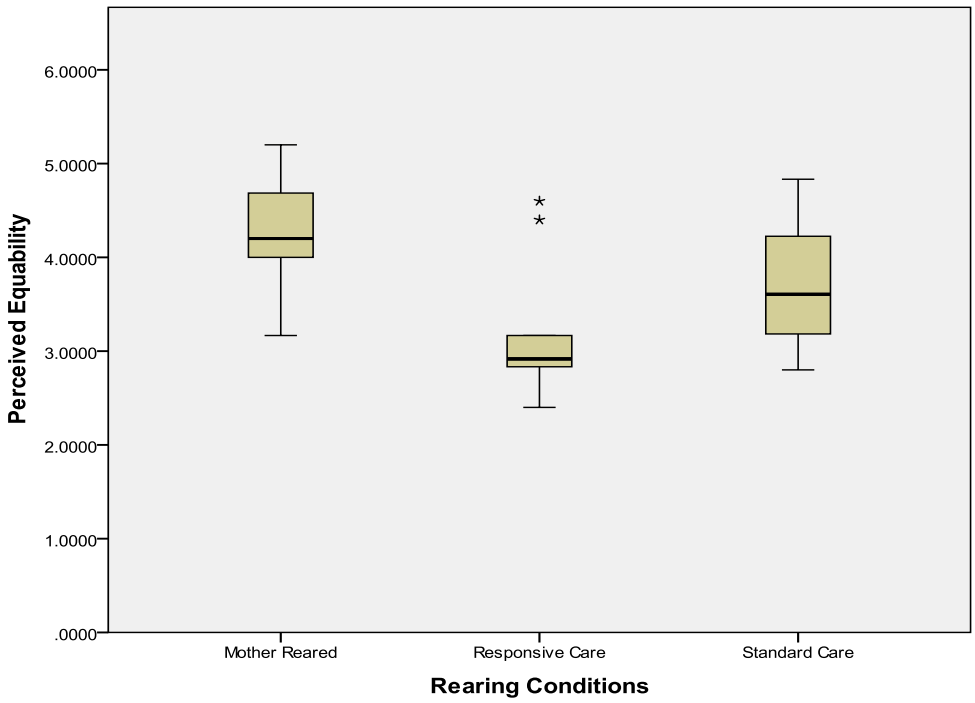

Figure 19: Mean Scores on survey question C9 (perceived equability of the chimpanzee)

Figure 20: Mean Scores on survey question C13 (perceived calmness of the chimpanzee)

iv. The RC chimps had significantly higher mean scores than ST chimps on question C17 (perceived dependence on others), U = 25.50, N_{RC} = 10, N_{ST} = 12, p = .023 (two-tailed) (see Figure 21, page 104).

Figure 21: Mean Scores on survey question C17 (perceived dependency of the chimpanzee)

v. The RC chimps had significantly higher mean scores than ST chimps on question C25 (perceived fearfulness), U = 22.50, N_{RC} = 10, N_{ST} = 12, p = .013 (two-tailed) (see Figure 22, page 105).

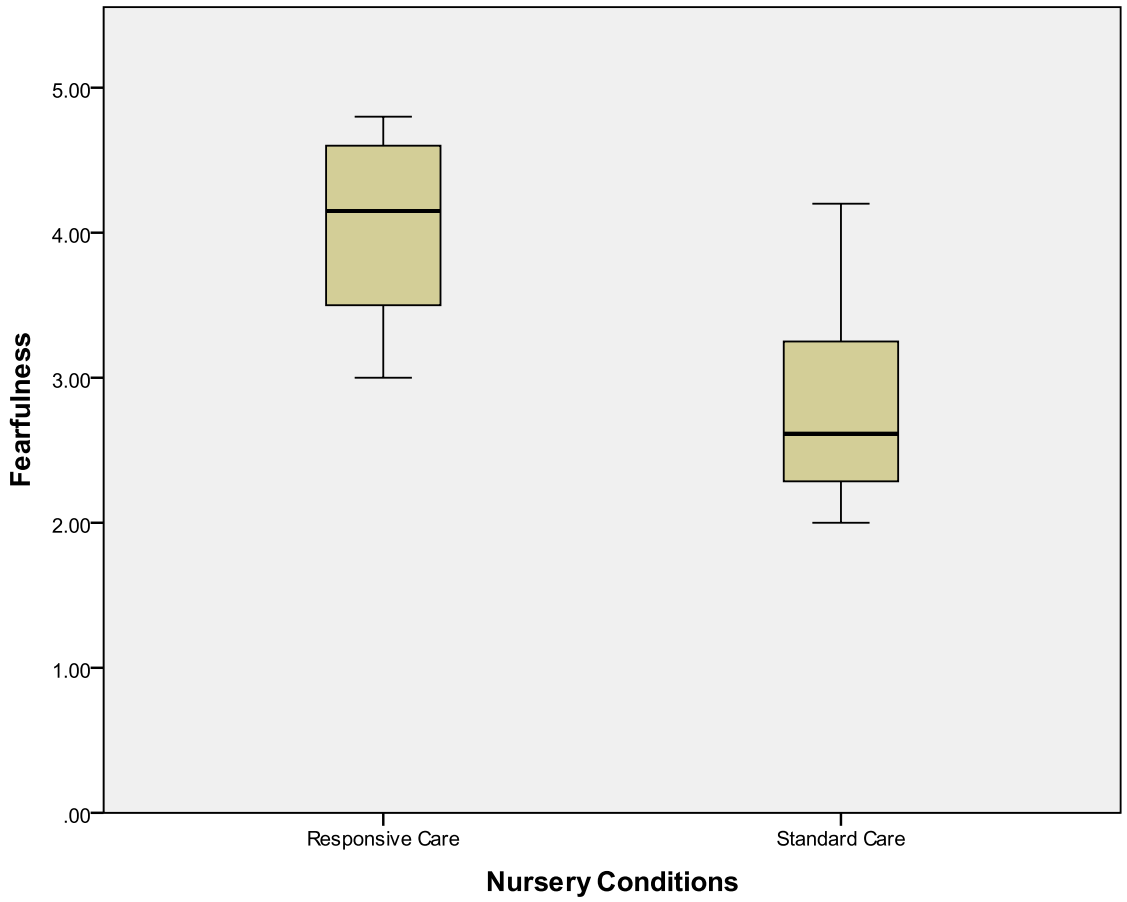

Figure 22: Mean Scores on survey question C25 (perceived fearfulness)

vi. The RC chimps had significantly lower mean scores than ST chimps on question C57 (perceived un-emotionality), U = 15.00, N_{RC} = 10, N_{ST} = 12, p = .003 (two-tailed) (see Figure 23, page 106).

vii. The RC chimps had near-significant higher mean scores than ST chimps on question C59 (perceived vulnerability), U = 30.50, N_{RC} = 10, N_{ST} = 12, p = .051 (two-tailed) (see Figure 24, page 106).

Figure 23: Mean Scores on survey question C57 (perceived un-emotionality of the chimpanzee)

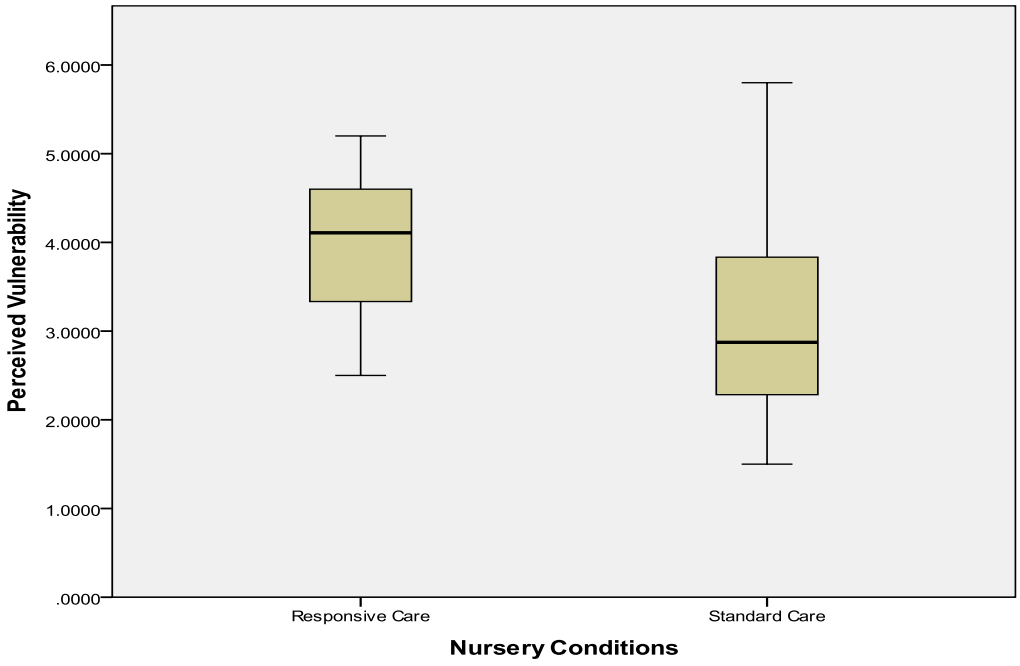

Figure 24: Mean Scores on survey question C59 (perceived vulnerability of the chimpanzee)

Mother-reared versus Nursery-reared

1. Survey data
    a. Mother-reared subjects scored significantly higher than responsive care subjects on scores compiled from respondents' answers to 3/4 questions (B1, B2, and B4) related to subjective well-being and higher on scores to 1/4 of these questions (B3), though this difference was not significant (Figure 17, page 101).
        i. B1: This question is designed to assess the respondent's opinion about the animal's general happiness, higher scores indicating greater happiness. Mother-reared subjects scored significantly higher than responsive care subjects, $U = 10.5$, $N_{MR} = 11$, $N_{RC} = 10$, $p = .002$ (two-tailed).
        ii. B2: As stated above, this question assesses the respondent's opinion about the animal's general social experience with other chimpanzees, higher scores indicating higher quality of social experience. Mother-reared subjects scored significantly higher than responsive care subjects, $U = 5.0$, $N_{MR} = 11$, $N_{RC} = 10$, $p = .000$ (two-tailed).
        iii. B3: This question assesses the respondent's opinion about the subject's social effectiveness. Mother-reared subjects scored higher than responsive care subjects on this measure but the difference was not significant, $U = 41.5$, $N_{MR} = 11$, $N_{RC} = 10$, $p = .341$ (two-tailed).

iv. B4: This question assesses the respondent's opinion regarding how happy the respondent would be if they were the target chimpanzee for one week; higher scores indicate greater happiness. Mother-reared chimpanzees scored significantly higher on this measure than responsive care chimpanzees, U = 0.0, N_{MR} = 11, N_{RC} = 10, p = .000 (two-tailed).

b. Mother-reared subjects scored significantly higher than standard care subjects (U = 37.5, N_{MR} = 11, N_{ST} = 14, p = .030, two-tailed) on scores compiled from respondents' answers to question B2 (quality of subject's social experience with other chimpanzees) of the survey. There was no significant difference between the groups on questions B1, B3 or B4 (Figure 17, page 101).

c. MWU tests (two-tailed) comparing all mother-reared to all nursery-reared subjects also revealed significant differences between the two groups as regards scores on questions B1, B2, and B4. Based on these results and the above stated results, it seems that the responsive care subjects largely drive this overall result, particular on questions B1 and B4 (Figure 25, page 109).

   i. B1: Mother-reared subjects scored significantly higher than nursery-reared subjects, U = 66.00, N_{MR} = 11, N_{NR} = 24, p = .019 (two-tailed).

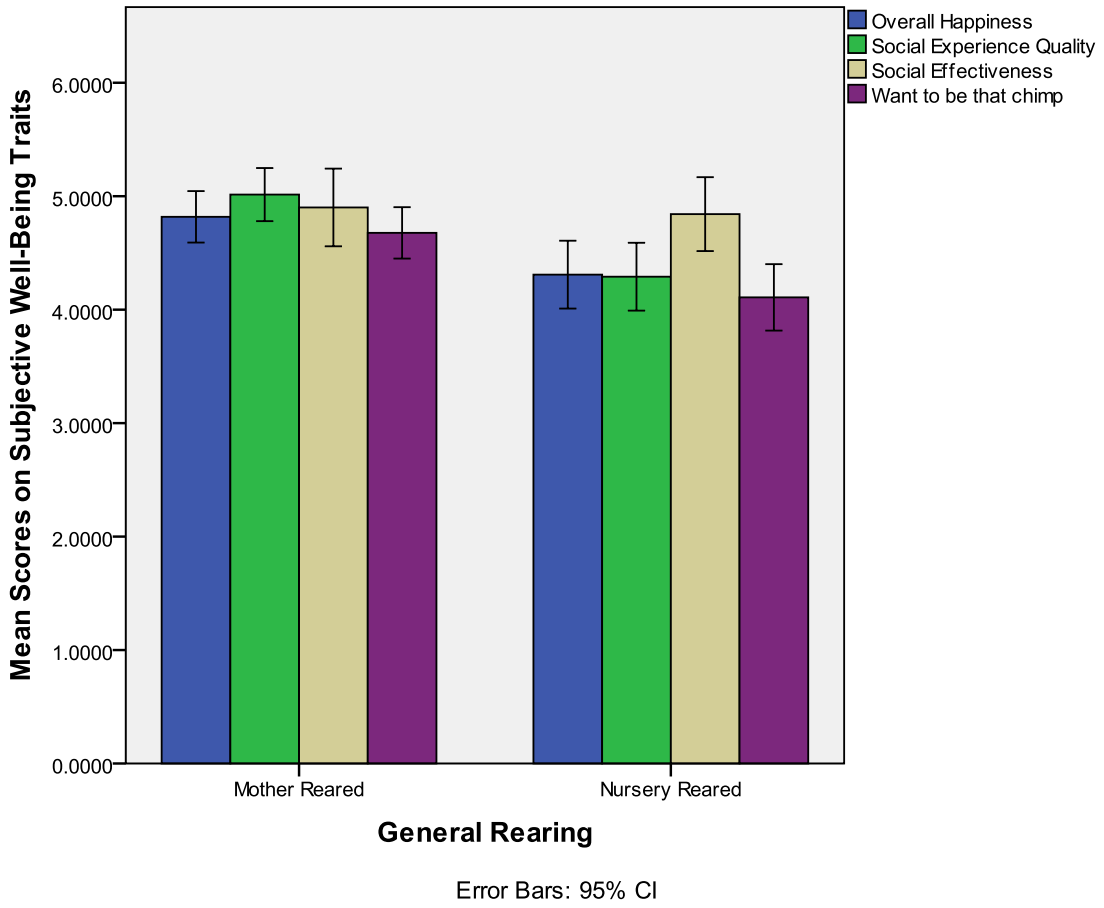

Figure 25: Mean scores on Individual SWB items (B1 – B4), Mother versus Nursery-reared

ii. B2: Mother-reared subjects scored significantly higher than nursery-reared subjects, U = 42.50, N_{MR} = 11, N_{NR} = 24, p = .001 (two-tailed).

iii. B3: Mother-reared subjects did not score significantly higher than nursery-reared subjects, U = 131.00, N_{MR} = 11, N_{NR} = 24, p = .972 (two-tailed).

iv. B4: Mother-reared subjects scored significantly higher than nursery-reared subjects, U = 56.00, N_{MR} = 11, N_{NR} = 24, p = .007 (two-tailed).

d. MWU tests (two-tailed) were run to check for possible gender effects on each of these four questions (B1 – B4); no significant effects of gender were found.

Further Exploration

Stress-related Behavior Correlations

1. Exploratory analyses investigating correlations with stress- related behavior found that not only did stress-related behavior vary positively and significantly with rates of human approach, but it also varied positively and significantly with:
    a. Rates of solicitation of human attention, both overall (τ = .277, N = 33, p = .026, two-tailed) and just in terms of positive solicitation (τ = .248, N = 33, p = .046, two-tailed) (see Figure 26, page 111).
    b. Rates at which subjects attended to humans and human activity, τ = .335, N = 33, p = .006, two-tailed (see Figure 27, page 111).

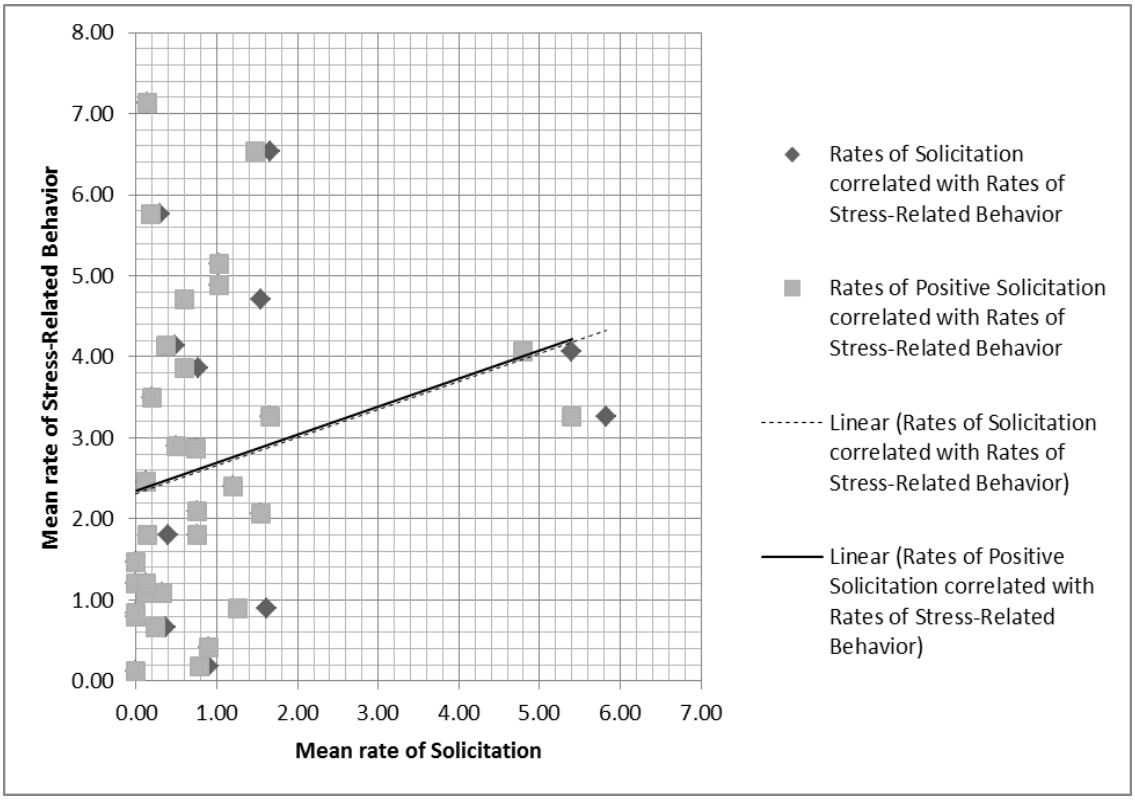

Figure 26: Correlation of Solicitation and Stress-related Behavior (Rates per Hour)

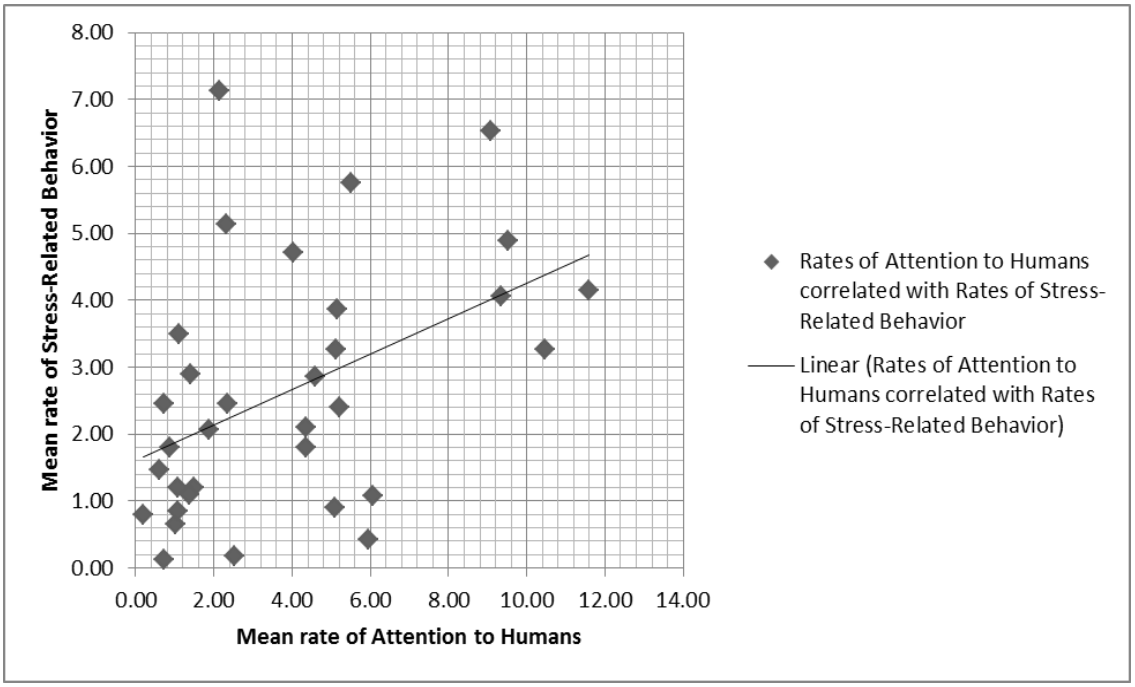

Figure 27: Correlation of Attention to Humans and Stress-Related Behavior (Rates per Hour)

2. Stress-related behavior varied negatively and significantly with:

    a. Mean Subjective Well Being score, τ = -.268, N = 33, p = .029, two-tailed (Figure 28, page 112).

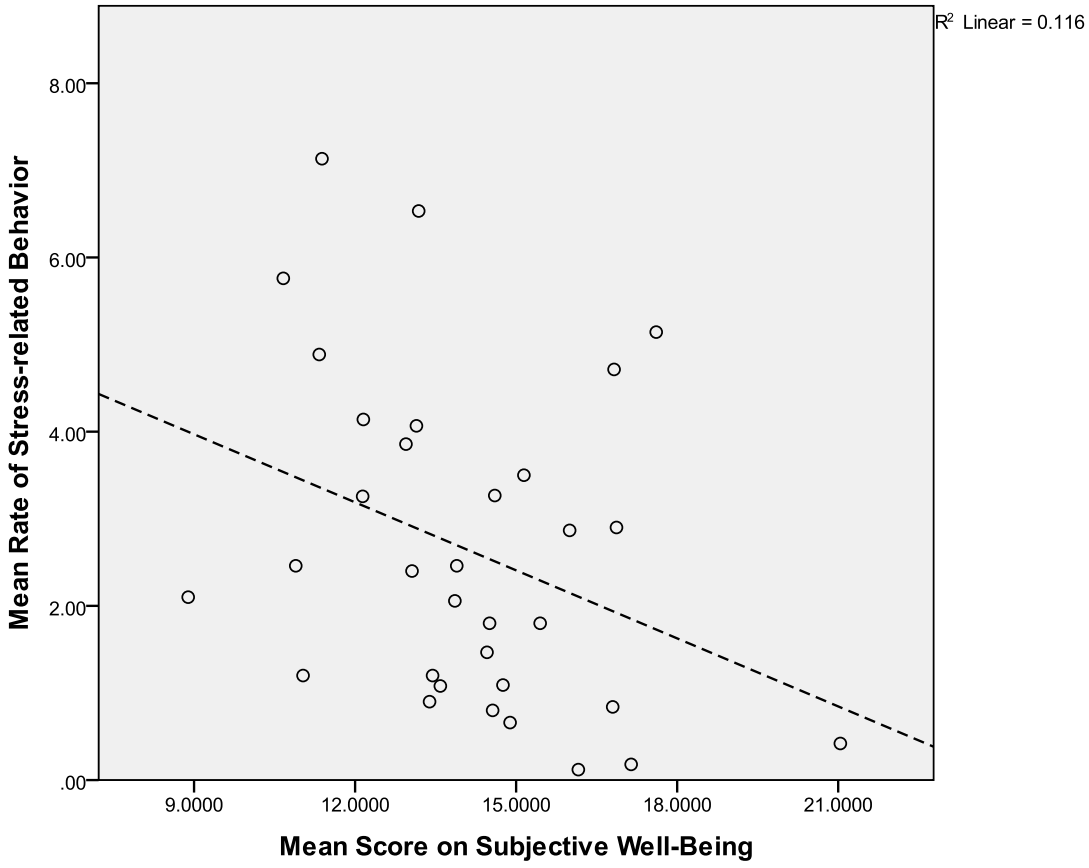

Figure 28: Correlation of Mean Rate of Stress-Related Behavior with Mean Score on Subjective Well-Being Factor

    b. Two of the individual trait scores that loaded on the SWB Factor:

        i. Score on the quality of the target chimpanzee's social experience (question B2), τ = -.312, N = 33, p = .012, two-tailed (Figure 29, page 113).

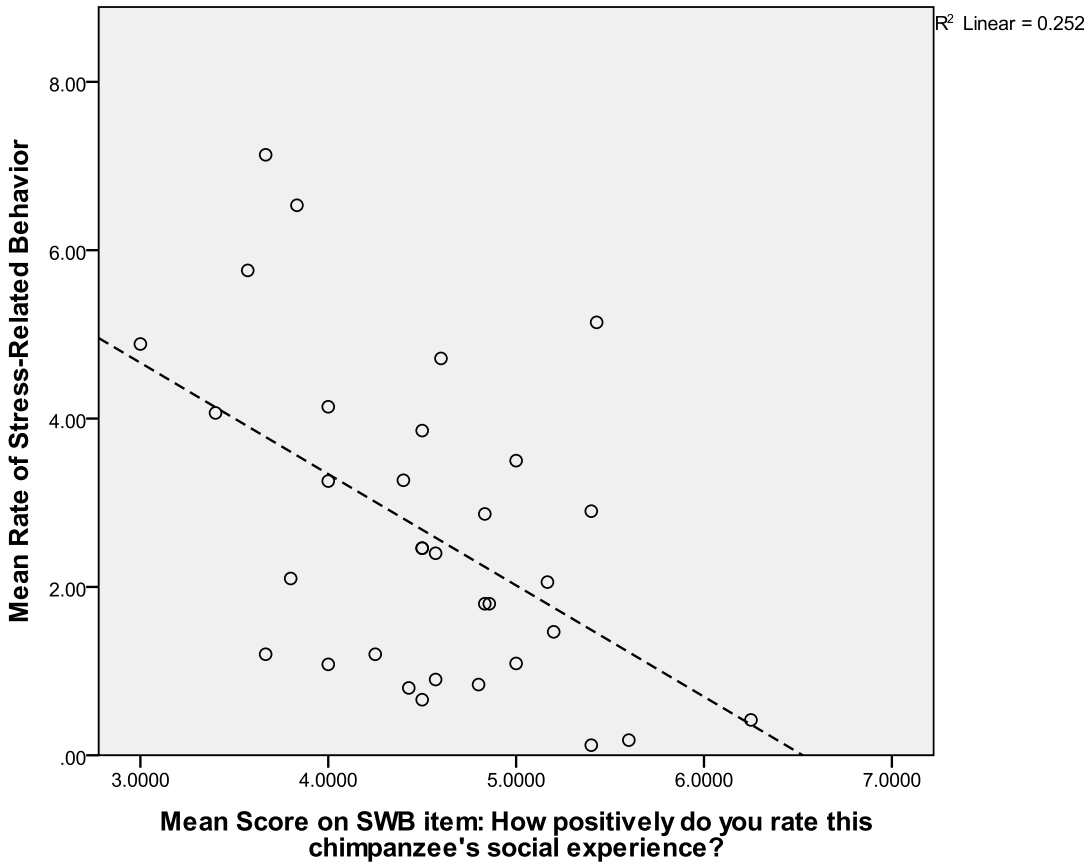

Figure 29: Correlation of Mean Rate of Stress-Related Behavior with Mean Score on SWB item: How positively do you rate this chimpanzee's social experience?

ii. Degree to which the respondent would like to be that chimpanzee (question B4), τ = -.271, N = 33, p = .029, two-tailed (Figure 30, page 114).

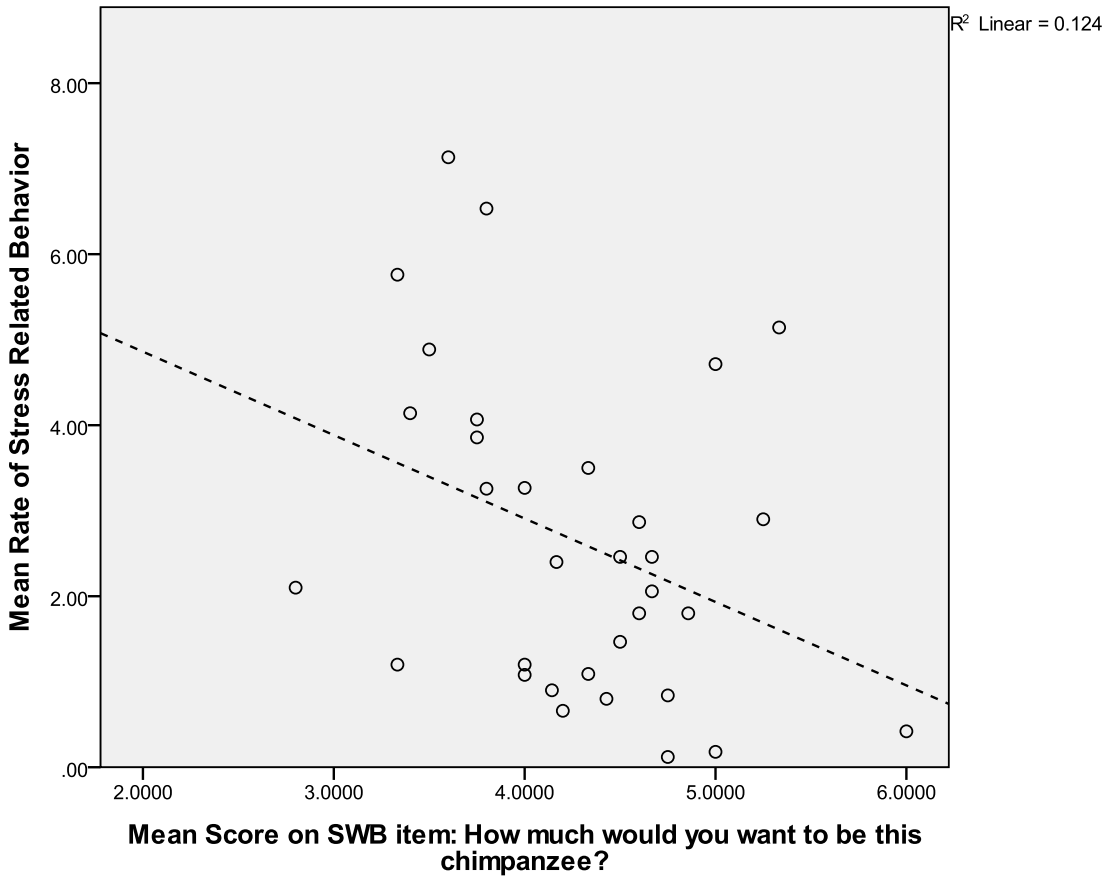

Figure 30: Correlation of Mean Rate of Stress-Related Behavior with Mean Score on SWB item: How much would you want to be this chimpanzee?

3. Due to variables related to the measurement of human approach rates, a MWU was conducted to ensure that rates of human approach did not significantly differ between the different rearing groups (MR, RC, and ST); there was no significant difference found (Figure 31, page 115).

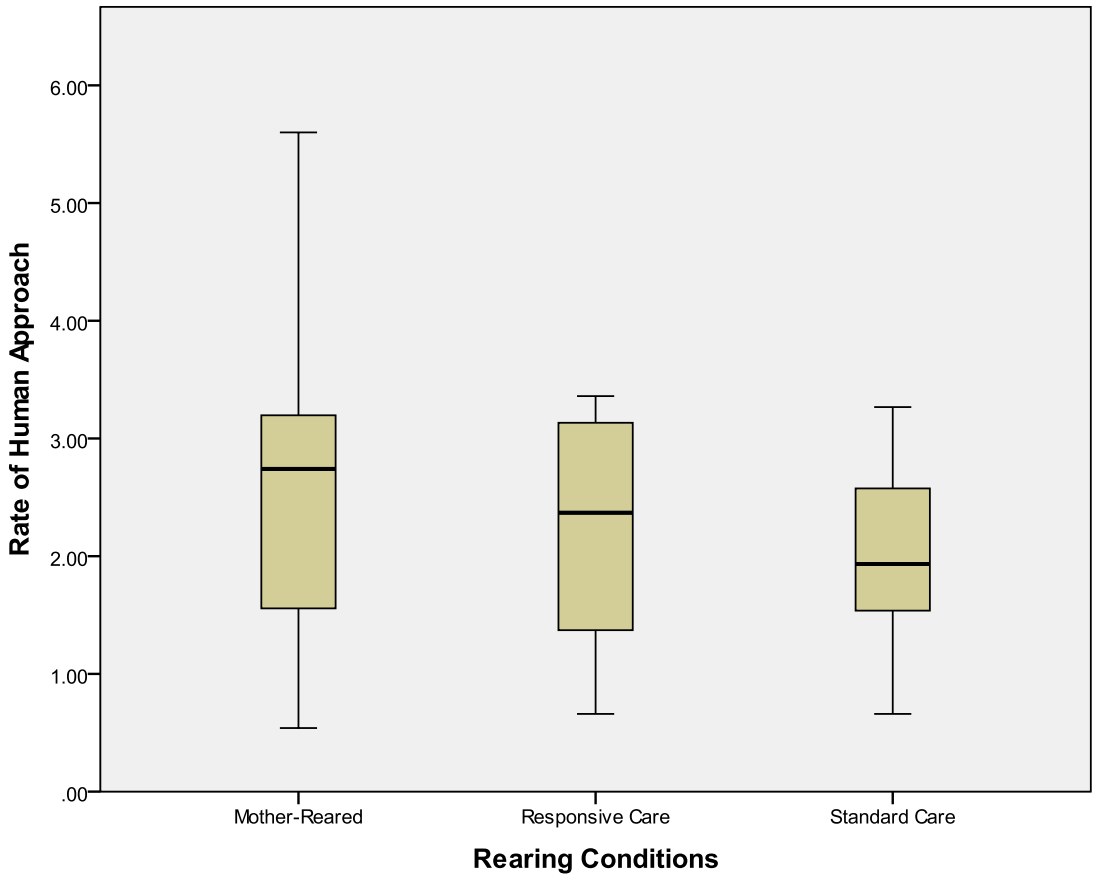

Figure 31: Rates of Human Approach for the different Rearing Groups

Abnormal Behavior Correlations

1. Abnormal Behavior correlated significantly and negatively with:
    a. Mean scores on the Subjective Well-Being factor, τ = -.356, N = 33, p = .004 (two-tailed) (Figure 32, page 116);
    b. Mean scores on SWB item (B1): Rate the happiness of this chimpanzee, τ = -.386, N = 33, p = .002 (two-tailed) (Figure 33, page 116);

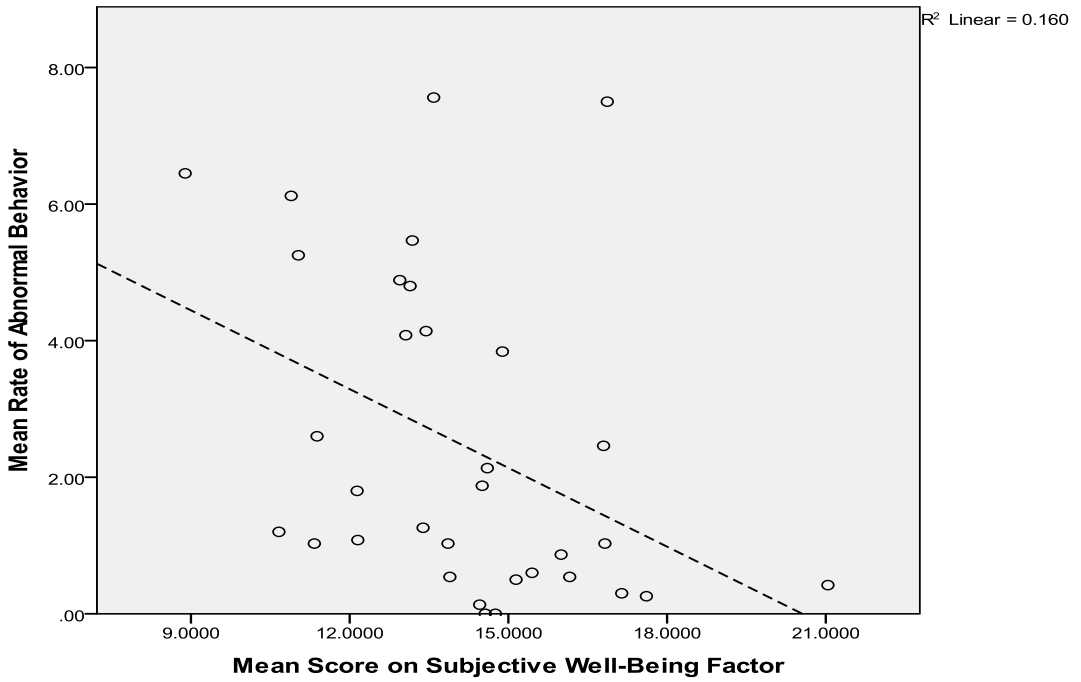

Figure 32: Correlation of Mean Rate of Abnormal Behavior with Mean Score on Subjective Well-being Factor

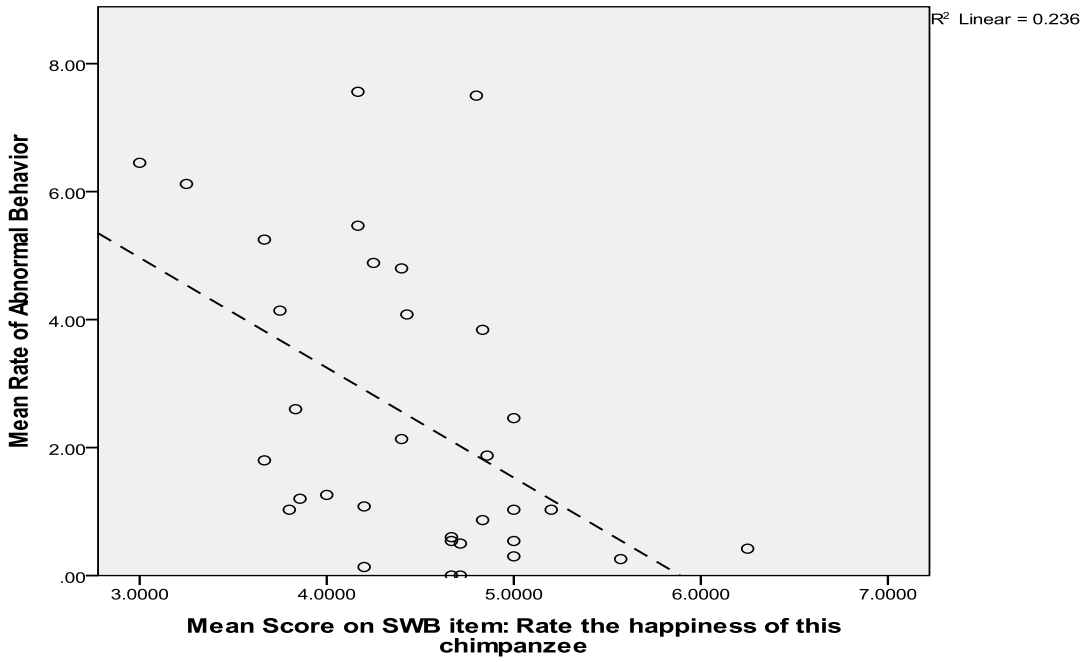

Figure 33: Correlation of Mean Rate of Abnormal Behavior with Mean Score on SWB item: Rate the happiness of this chimpanzee.

c. Mean scores on SWB item (B2): Rate the quality of this chimpanzee's social experience, τ = -.384, N = 33, p = .002 (two-tailed) (Figure 34, page 117);

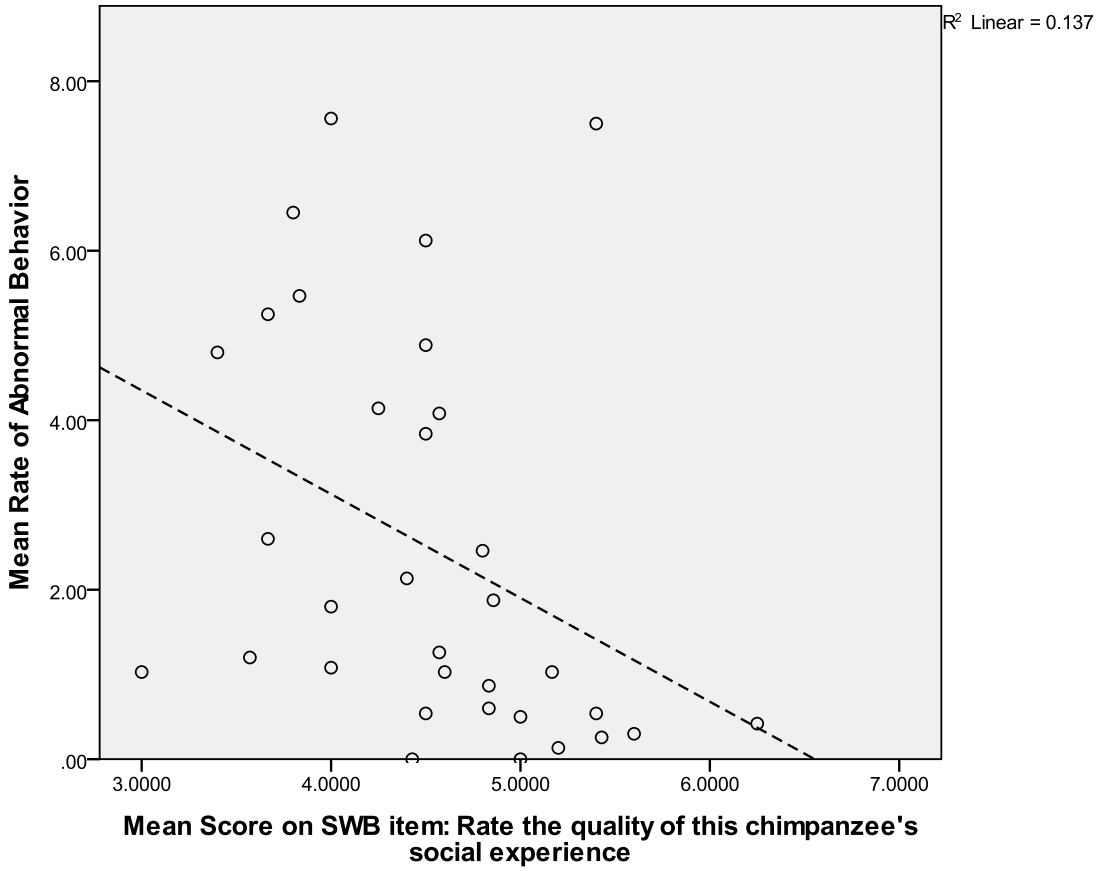

Figure 34: Correlation of Mean Rate of Abnormal Behavior with Mean Score on SWB item: How positively do you rate this chimpanzee's social experience?

d. Mean scores on SWB item (B4): Rate the degree to which you would want to be this chimpanzee, τ = -.291, N = 33, p = .019 (two-tailed) (Figure 35, page 118).

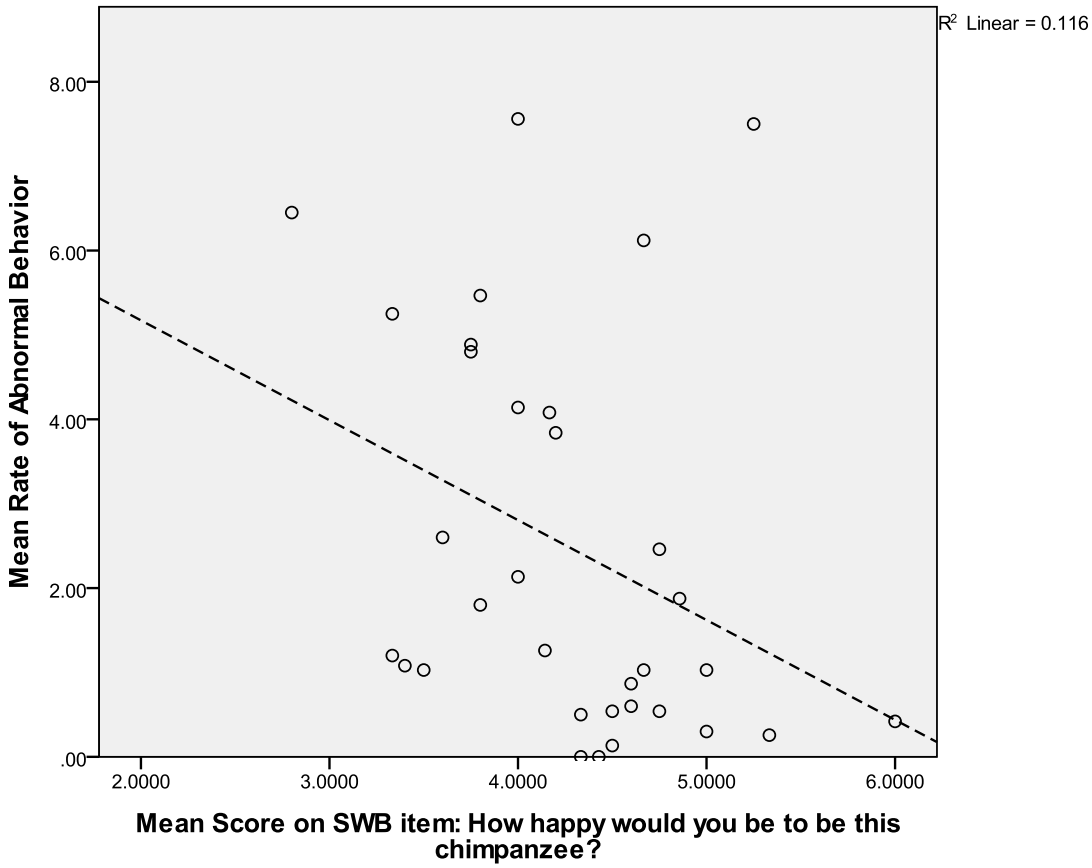

Figure 35: Correlation of Mean Rate of Abnormal Behavior with Mean Score on SWB item: How much would you want to be this chimpanzee?

Health Assessments

The primary goal for investigating animals' health records was to determine if there were any long-term effects on health as a function of differential rearing, early trauma, or attachment classification. Because of the many zeroes found in the data, it was determined that using a simple yes/no category for presence or absence of URI, DIA, or INJ during each age category would be a better statistical test. Data was reorganized and re-analyzed using a chi-square test.

It is important to point out that for this study, animals that are considered 'standard care' are not only those chimpanzees that were reared in the Yerkes general nursery during the years 1987 – 1995; for this study, many chimpanzees that were reared in the Yerkes general nursery were considered for comparison with the responsive care chimpanzees. Therefore, rather than referring to these animals as 'standard care', they will be referred to here as non-responsive care or NRC chimpanzees. Nursery conditions at Yerkes varied to some extent, sometimes focusing on peer-group rearing and other times on larger group rearing, but there was always a much lower contact time with humans for animals in the general nursery and the responsive care nursery was the only nursery at Yerkes that focused on emulating mother chimpanzee behaviors and which provided extensive human contact to the chimpanzees.

1. Ages 0 – 5:
    a. Checking for main effects of gender:
        i. In the upper respiratory category (URI), a significant relationship between gender and URI was detected, χ^2 (1) = 4.489, N_F = 69, N_M = 46, p = .034 (two-tailed), φ = .20. A higher proportion of males (43.5%) than females (24.6%) were reported to experience at least one case of upper respiratory infection between birth and five years of age (see Figure 36a, page 120).

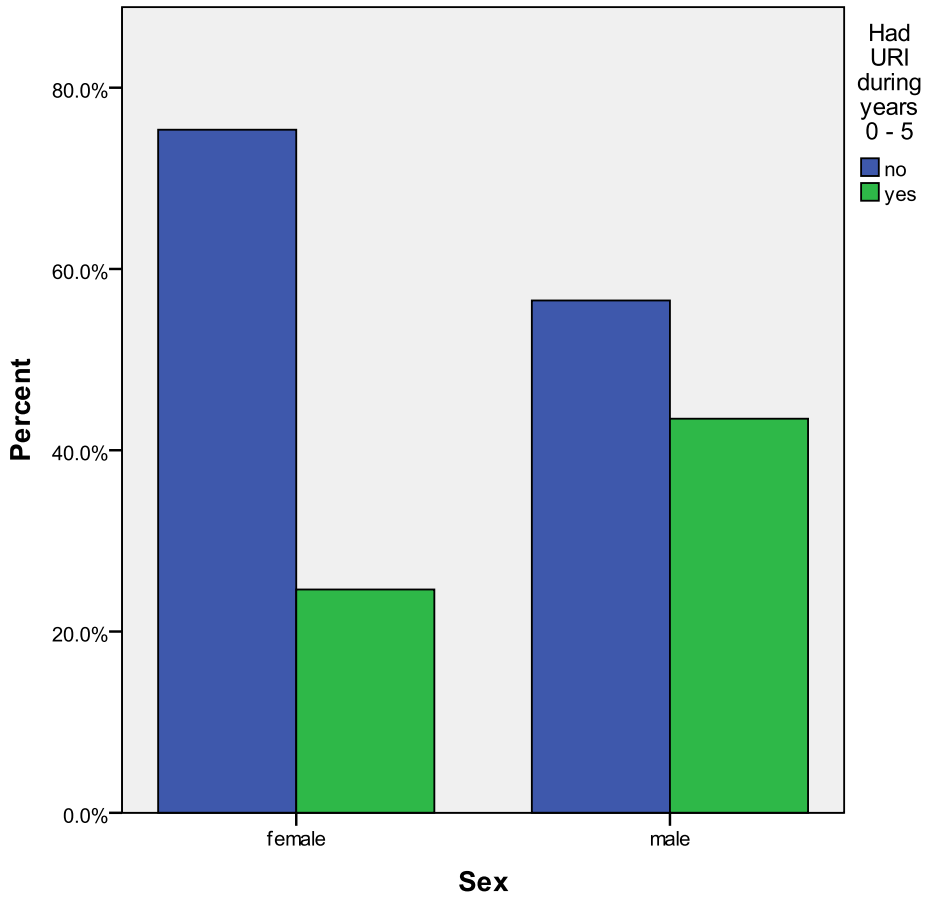

Figure 36:

a. Proportion of URI (upper respiratory infections) for Males vs. Females ages 0 – 5 years

ii. In the diarrhea category (DIA), no significant relationship between gender and diarrhea was detected (p = .466, two-tailed).

iii. In the injury category (INJ), a significant relationship between gender and injury was detected, χ^2 (1) = 9.020, N_F = 69, N_M = 46, p = .003 (two-tailed), φ = .28. A higher proportion of males (37.0%) than females (13.0%) were reported to experience at least one wounding incident between birth and five years of age (see Figure 36b, page 121).

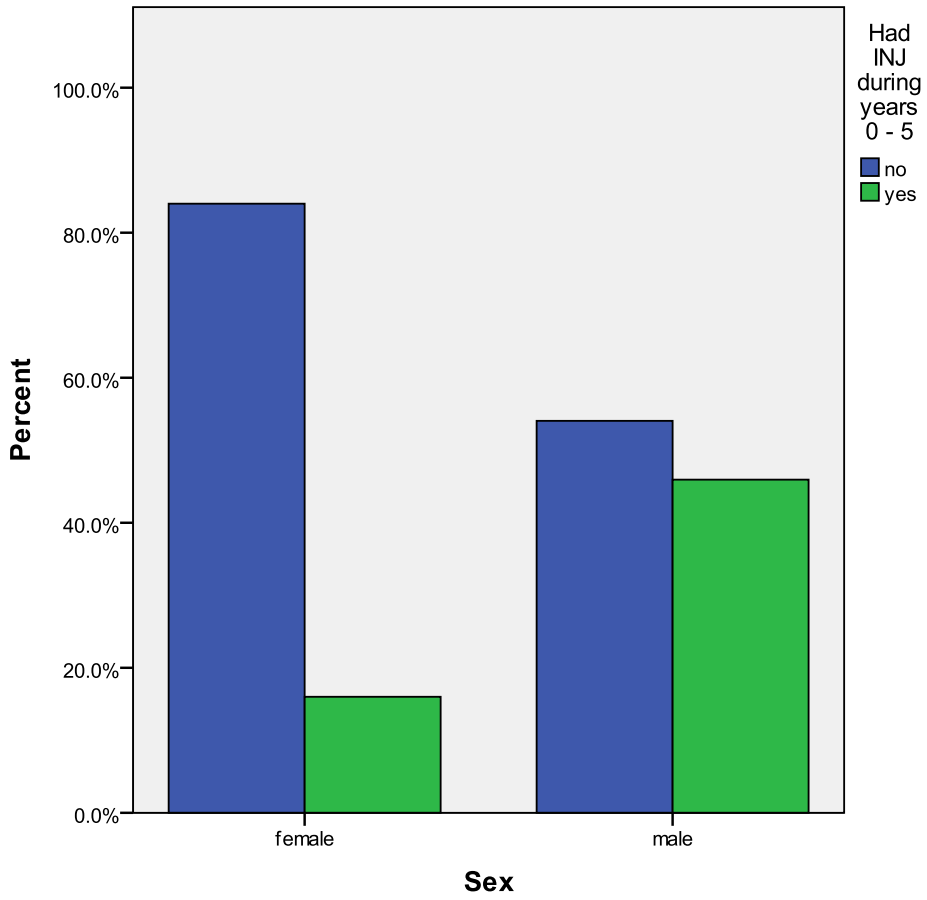

Figure 36:

b. Proportion of INJ (injury) incidence for Males vs. Females ages 0 – 5 years

b. Checking for main effects of rearing:

i. Mother-rearing, responsive care, and standard care comparisons:

1. A chi square test for relationship between rearing (mother, responsive nursery, or non-responsive care nursery) and upper respiratory infection did reveal a significant relationship between rearing and URI, $\chi^2(2) = 25.878$, $N_{MR} = 47$, $N_{RC} = 17$, $N_{NRC} = 51$, $p = .000$ (two-tailed), $\varphi = .47$. Seventy-seven

percent of individuals in the responsive care nursery experienced at least one URI during years 0 – 5 while only 37 percent of individuals in the non-responsive care nursery and 11 percent of the individuals that were mother reared experienced at least one URI during that same age span (see Figure 37, page 122). The effect size for this relationship is large at .47 and the effect size for the relationship between URI and gender is fairly small at .20 so that the relationship between rearing and URI is likely still meaningful.

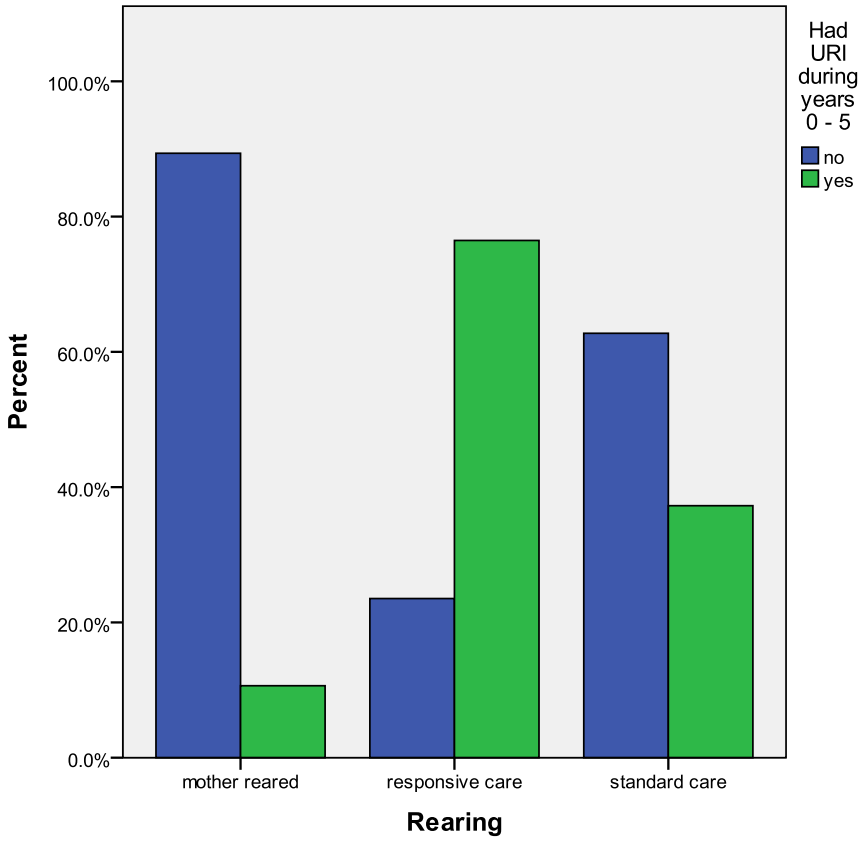

Figure 37: Proportion of URI (upper respiratory infections) for Different Rearing Groups during ages 0 – 5 years (mother versus responsive care versus non-responsive care)

2. A chi square test for relationship between rearing (mother, responsive nursery or non-responsive care nursery) and incidence of diarrhea revealed a significant relationship between rearing and DIA, $\chi^2(2) = 45.176$, $N_{MR} = 47$, $N_{RC} = 17$, $N_{NRC} = 51$, $p = .000$ (two-tailed), $\varphi = .63$. One hundred percent of the individuals in the responsive care nursery experienced at least one bout of diarrhea during years 0 – 5 while only 31 percent of individuals in non-responsive care and 11 percent of individuals that were mother-reared experienced at least one round of diarrhea during that same age span (see Figure 38, page 124). The effect size for this relationship is large, indicating a robust effect.

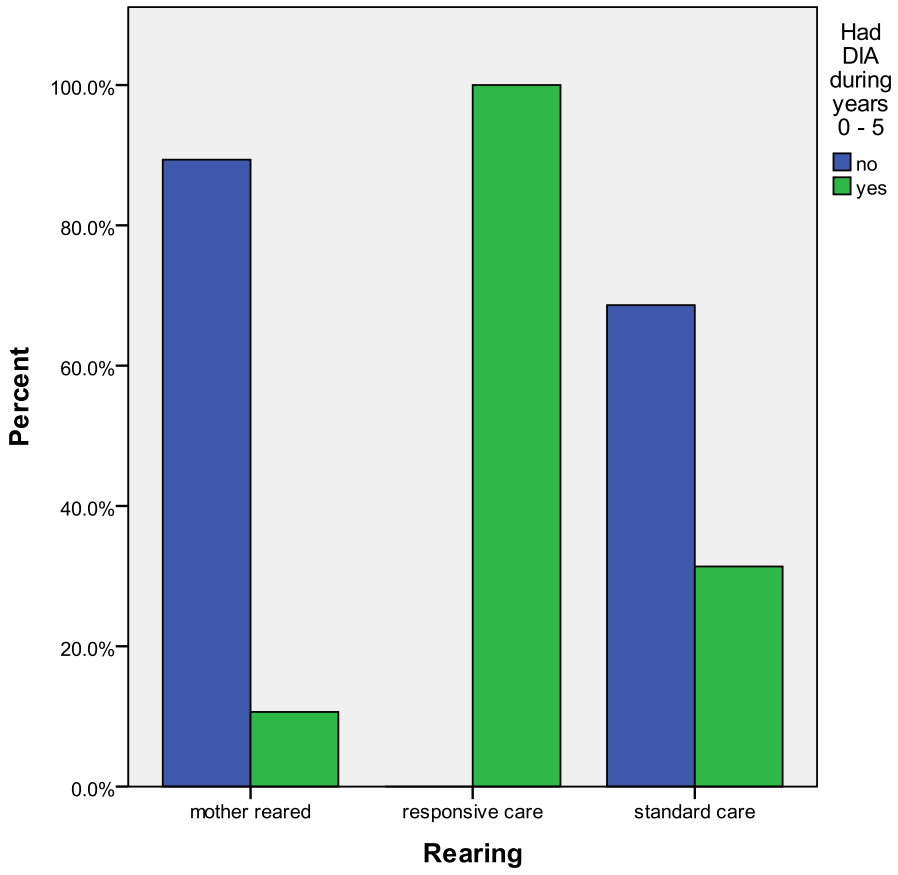

Figure 38: Proportion of DIA (diarrhea) incidence for Different Rearing Groups during ages 0 – 5 years (mother versus responsive care versus non-responsive care)

3. A chi square test for relationship between rearing (mother, responsive nursery or non-responsive care nursery) and incidence of injury revealed a significant relationship between rearing and INJ, $\chi^2(2) = 9.141$, $N_{MR} = 47$, $N_{RC} = 17$, $N_{NRC} = 51$, $p = .000$ (two-tailed), $\varphi = .28$. A proportion of 35.3% of the individuals in the responsive care nursery experienced at least one injury during years 0 – 5 while 31.4 percent of individuals in non-responsive care and 8.5 percent of individuals that were

mother-reared experienced at least one injury during that same age span (see Figure 39, page 125). The effect size for this result is not large, and is no bigger than the effect size for gender difference in this category. There was a balanced ratio of males to females in both nursery categories (ST: 25M, 26F; RC 8M, 9F) but in the mother-reared category there was a much higher proportion of females (13M, 34F), so rearing differences detected here are likely not robust.

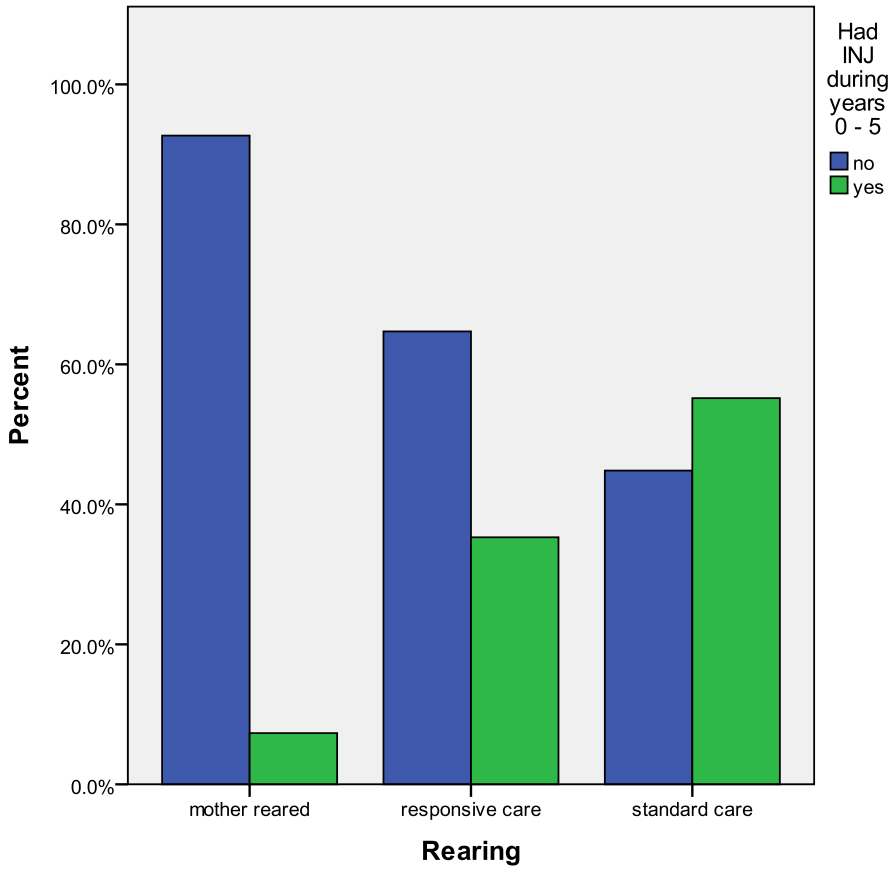

Figure 39: Proportion of INJ (injury) incidence for Different Rearing Groups during ages 0 – 5 years (mother versus responsive care versus non-responsive care)

ii. Mother-rearing versus nursery rearing (RC + NRC):

1. Chi square tests indicated that there was a significant relationship between rearing (mother-reared versus a collapsed nursery-reared category) and upper respiratory infection during years 0 – 5, χ^2 (1) = 16.893, N_{MR} = 47, N_{NR}= 68, *p* = .000 (two-tailed), φ = .38. Forty-seven percent of individuals that were nursery-reared experienced at least one bout with URI between the ages of 0 – 5 while only 11 percent of mother-reared individuals experienced an URI during that same age span (see Figure 40, page 127). The effect size for this relationship is fairly large at .38 and the effect size for the relationship between URI and gender is fairly small at .20 so that the relationship between rearing and URI is likely still meaningful.

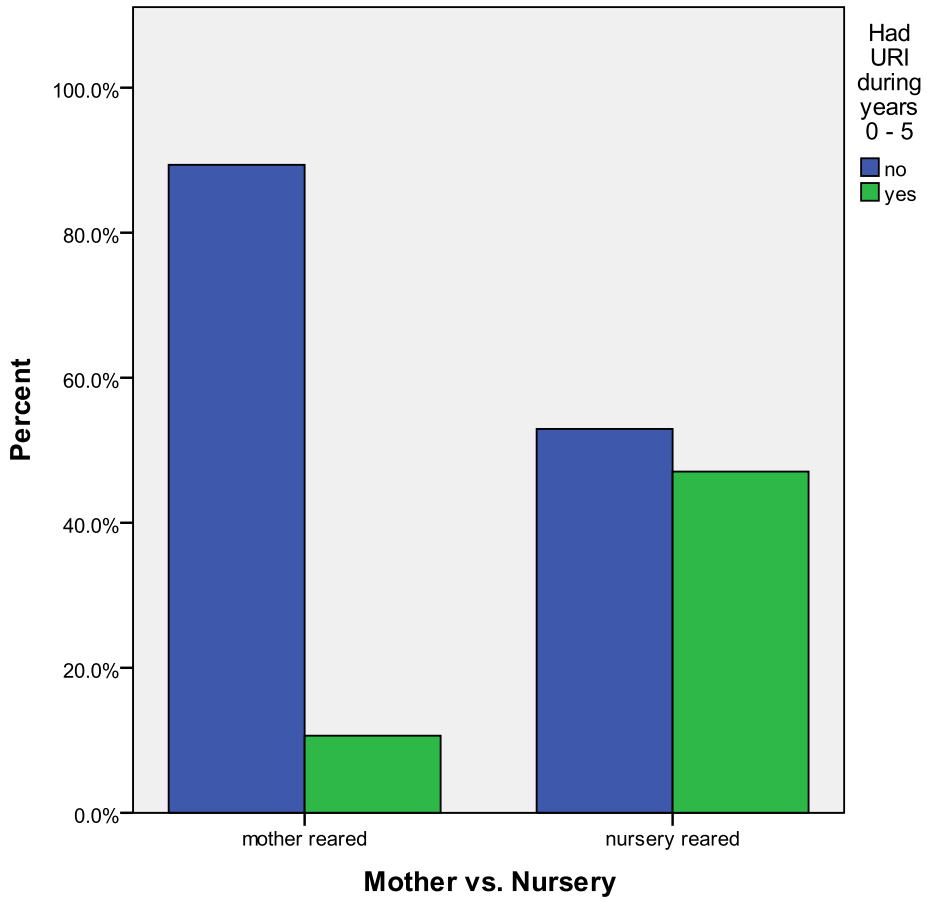

Figure 40: Proportion of URI (upper respiratory infections) for Mother versus Nursery-reared during ages 0 – 5 years

2. Chi square tests also indicated that there was a significant relationship between rearing (mother-reared versus a collapsed nursery-reared category) and diarrhea during years 0 – 5, χ^2 (1) = 18.035, N_{MR} = 47, N_{NR}= 68, p = .000 (two-tailed), φ = .40. Forty-nine percent of individuals that were nursery-reared experienced at least one bout of diarrhea during years 0 – 5 while only 11 percent of mother-reared individuals experienced a bout of diarrhea during this age span (see Figure 41, page

128). This is a medium to large Phi value indicating a fairly robust effect.

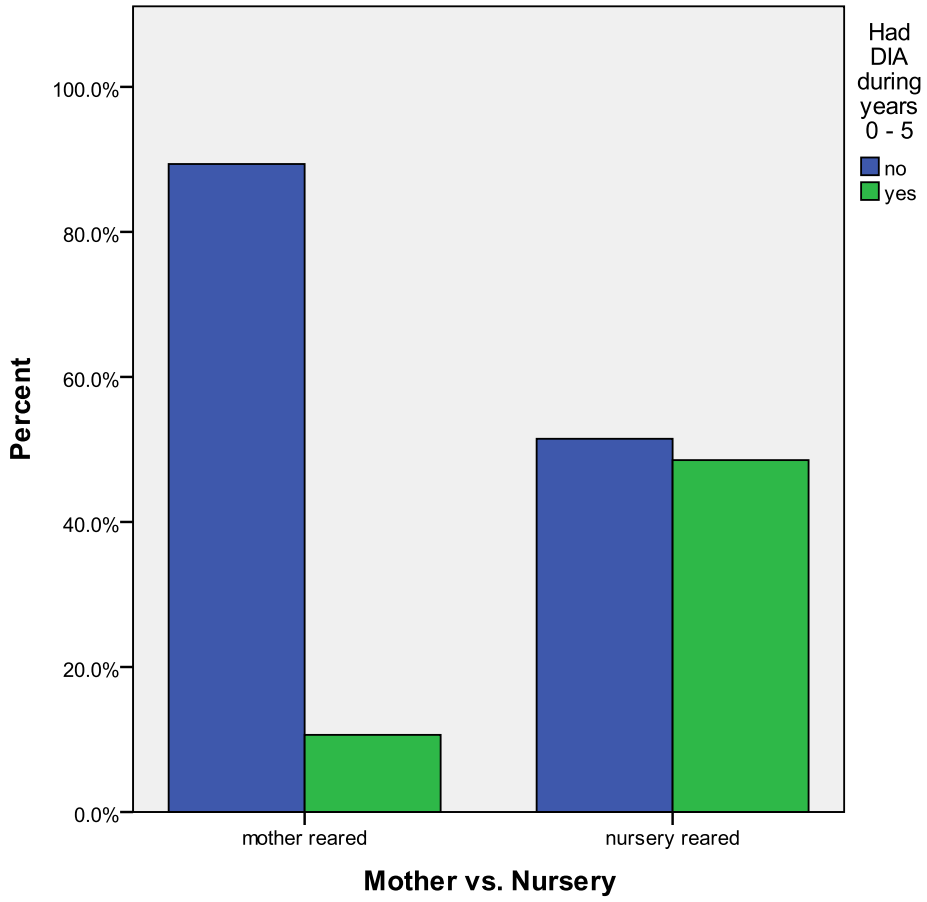

Figure 41: Proportion of DIA (diarrhea) incidence for Mother versus Nursery-reared during ages 0 – 5 years

3. A chi square test for relationship between rearing (mother-reared versus a collapsed nursery-reared category) and incidence of injury revealed a significant relationship between rearing and INJ, $\chi^2(2) = 9.029$, $N_{MR} = 47$, $N_{RC} = 17$, $N_{NR} = 68$, $p = .003$ (two-tailed), $\varphi = .28$. Thirty-two percent of the individuals in the nursery experienced at least one injury

during years 0 – 5 while only 8.5 percent of individuals that were mother-reared experienced at least one injury during that same age span (see Figure 42, page 129). Again, however, we have a problem with non-equivalent sex ratios and similar effect sizes, rendering this result less meaningful.

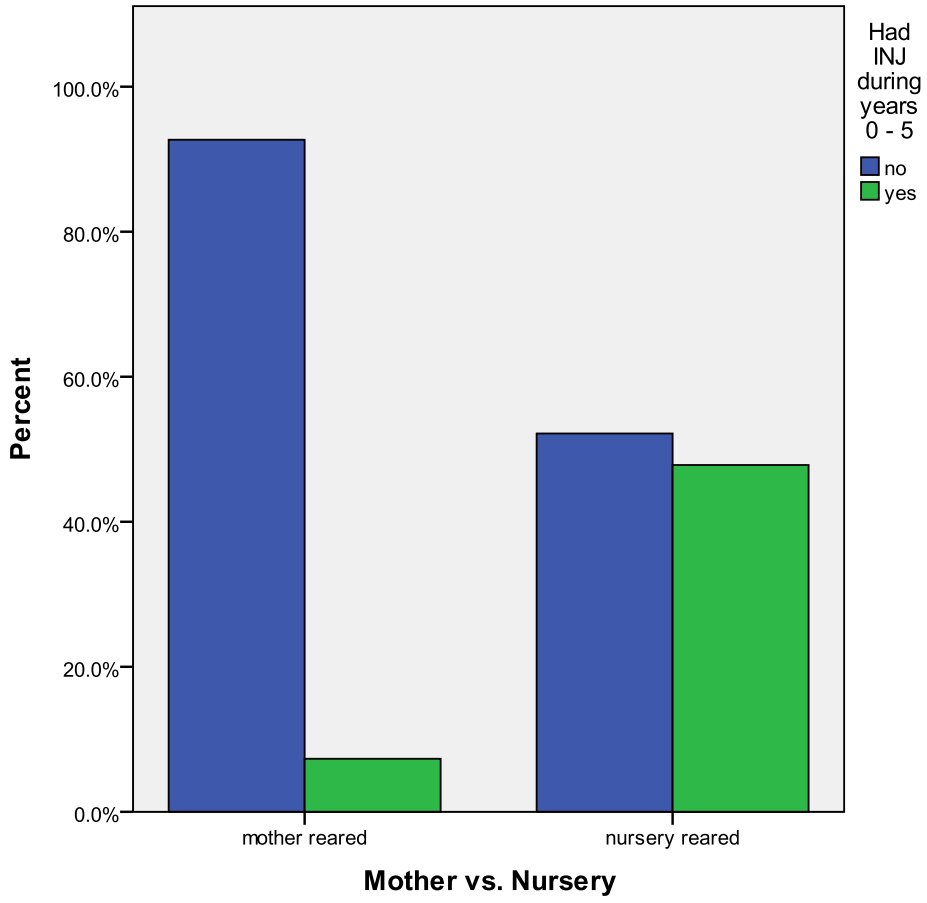

Figure 42: Proportion of INJ (injury) incidence for Mother versus Nursery-reared during ages 0 – 5 years

iii. Responsive versus non-responsive care:

1. Chi square tests also indicated there was a significant relationship between the type of nursery rearing (non-

responsive care vs. responsive) and URI incidence during years 0 – 5, χ^2 (1) = 7.870, N_{NRC} = 51, N_{RC}= 17, p = .005 (two-tailed), φ = .34. Seventy-seven percent of individuals in the RC group experienced at least one bout with URI between the ages of 0 – 5 while only 37 percent of individuals in the NRC group experienced an URI during that same age span (Figure 43, page 130). The effect size for this relationship is fairly large at .34 and the ratios of males to females in both groups are equivalent (ST: 25M, 26F; RC: 8M, 9F) so that the sex bias should not effect this result.

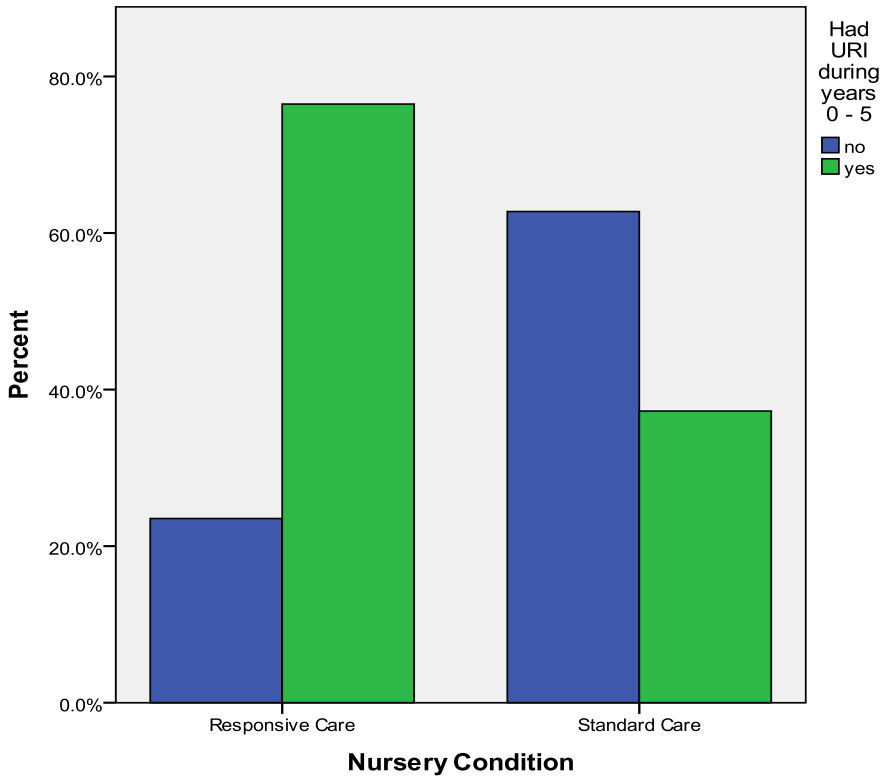

Figure 43: Proportion of URI (upper respiratory infections) for Responsive versus Non-Responsive Care during ages 0 – 5 years

2. Chi square tests also indicated there was a significant relationship between the type of nursery rearing (non-responsive vs. responsive) and DIA incidence during years 0 – 5, χ^2 (1) = 24.040, N_{NRC} = 51, N_{RC}= 17, p = .000 (two-tailed), φ = .60. One hundred percent of individuals in the RC group experienced at least one bout with DIA between the ages of 0 – 5 while only 31 percent of individuals in the NRC group experienced DIA during that same age span (see Figure 44, page 131). The effect size for this relationship is large at .60 indicating this result is rather robust.

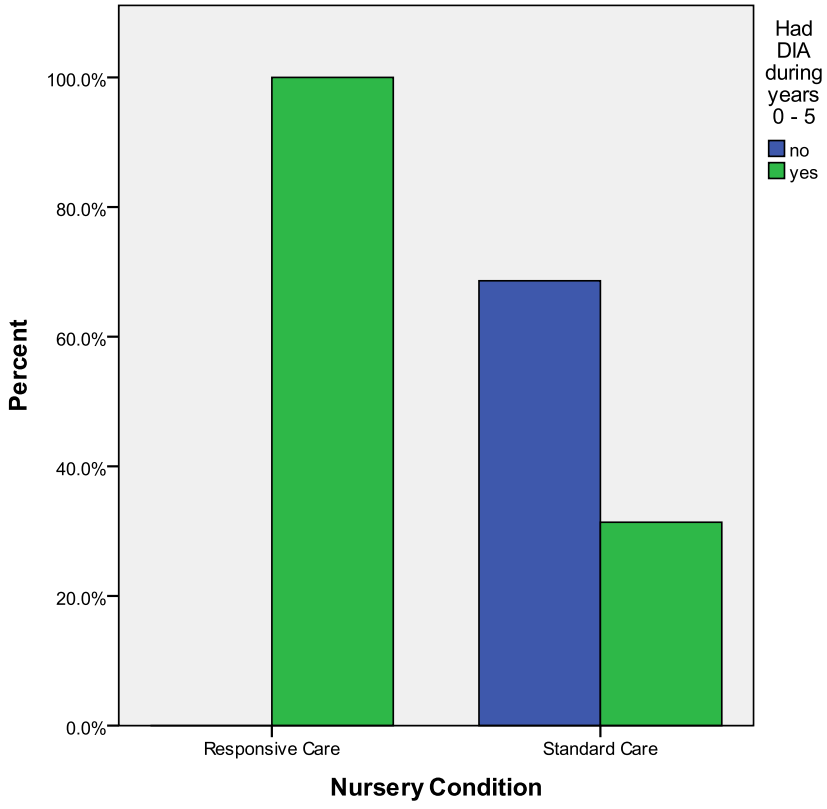

Figure 44: Proportion of DIA (diarrhea) incidence for Responsive versus Non-Responsive Care during ages 0 – 5 years

3. Chi square tests detected no significant difference between the two nursery types and incidence of injury between ages 0 and 5, $p = .765$ (two-tailed).

iv. Early arrival versus late arrival standard care:

1. There were no significant differences found between the two standard care groups during ages 0 - 5 for URI ($p = .109$, two-tailed), DIA ($p = .978$, two-tailed) or INJ ($p = .978$, two-tailed)

c. Checking for main effects of attachment classification:

v. There was a significant relationship between attachment classification (disorganized vs. non-disorganized) and upper respiratory infection during years 0 – 5, χ^2 (1) = 6.874, $N_{DA} = 26$, $N_{ND} = 17$, $p = .009$ (two-tailed), $\varphi = .40$. A proportion of 85% of disorganized individuals experienced an upper respiratory infection during years 0 – 5 while only 47% of non-disorganized individuals did so (see Figure 45, page 133). There is not an issue with sex bias here as the two groups were balanced with each other in ratio of males to females. At a Phi value of .40, this is a fairly robust effect.

vi. There was not a significant relationship between attachment classification (disorganized vs. non-disorganized) and diarrhea ($p = .383$, two-tailed) or injury ($p = .151$, two-tailed) during years 0 – 5.

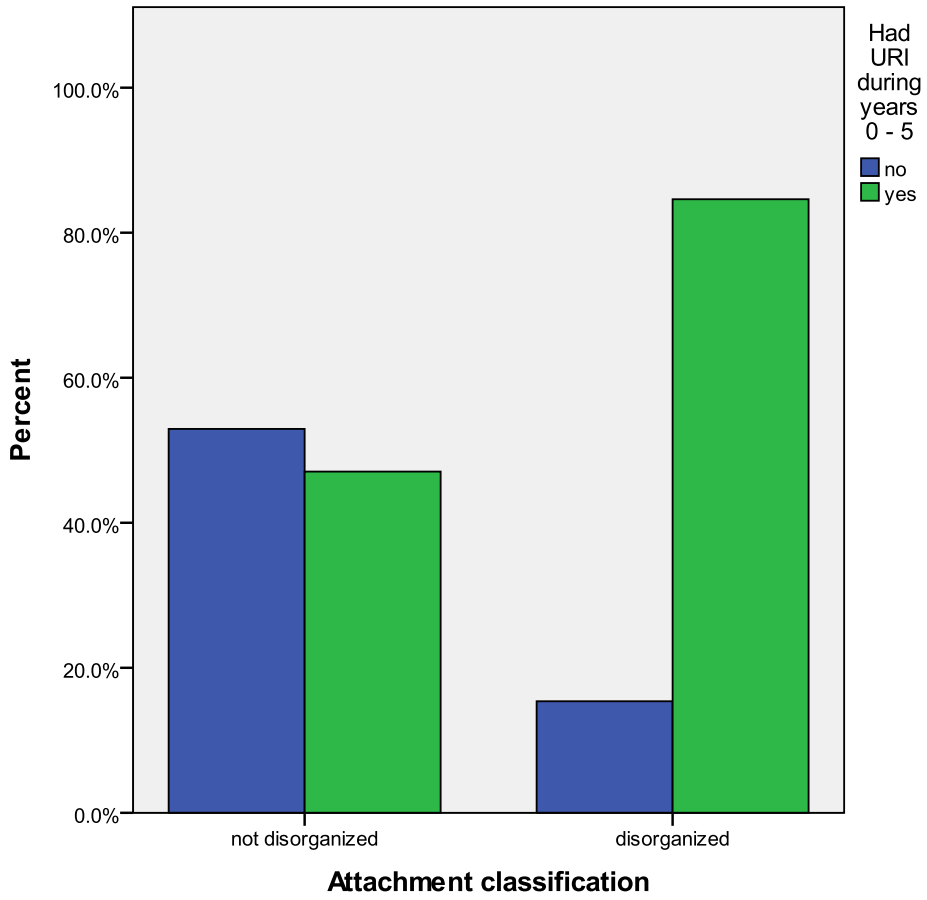

Figure 45: Proportion of URI (upper respiratory infections) for Disorganized versus Non-Disorganized during ages 0 – 5 years

2. Ages 6 – 10:
    a. Checking for main effects of gender:
        i. No significant relationship was found between gender and incidence of URI during the age span 6 - 10 according to chi square tests (p = .292, two-tailed).
        ii. No significant relationship was found between gender and incidence or DIA during the age span 6 - 10 according to chi square tests (p = .156, two-tailed).

iii. No significant relationship was found between gender and incidence or DIA during the age span 6 - 10 according to chi square tests (p = .990, two-tailed).

b. Checking for main effects of rearing:

i. Mother-rearing, responsive care, and non-responsive care comparisons:

1. There was no significant relationship between these three rearing categories at ages 6 – 10 for URI (p = .330, two-tailed), INJ (p = .136, two-tailed) or DIA (p = .136, two-tailed).

ii. Mother-rearing versus nursery rearing (RC + NRC):

1. There was no significant relationship between these two rearing categories at ages 6 – 10 for URI (p = .136), INJ (p = .122) or DIA (p = .398).

iii. Responsive versus non-responsive care:

1. There was no significant relationship between these two rearing categories at ages 6 – 10 for URI (p = .970), INJ (p = .162) or DIA (p = .098).

iv. Early arrival versus late arrival standard care:

1. There were no significant differences found between the two standard care groups during ages 6 – 10 for URI (p = .602), DIA (p = .121) or INJ (p = .540)

c. Checking for main effects of attachment classification:

i. There was not a significant relationship between attachment classification (disorganized vs. non-disorganized) and URI (p = .906, two-tailed) or INJ (p = .383, two-tailed) during years 6 – 10.

ii. There was a near-significant difference for the two groups in the DIA category, χ^2 (1) = 3.812, N_{DA} = 20, N_{ND} = 17, p = .051 (two-tailed); 20% of the DA subjects experienced at least one bout of diarrhea between the ages of 6 – 10 while zero of the ND subjects experienced a bout of diarrhea during that age span (Figure 46, page 135).

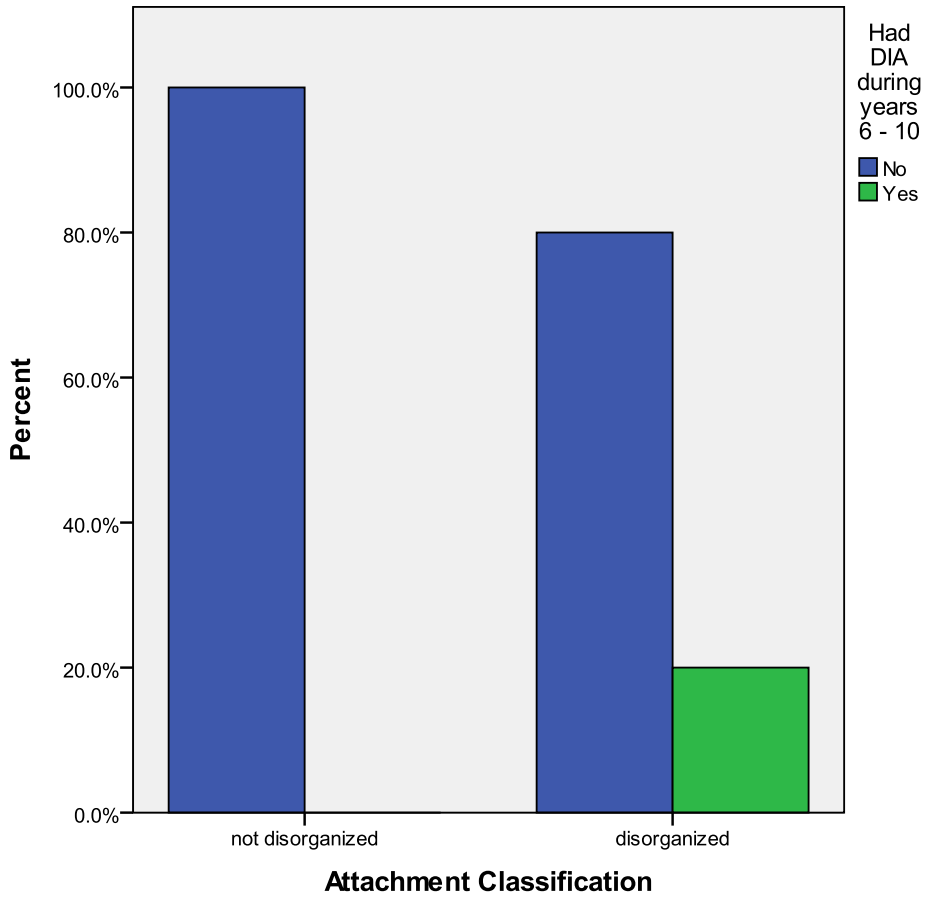

Figure 46: Proportion of DIA (diarrhea) incidence for Disorganized versus Non-Disorganized during ages 6 - 10 years

3. Ages 11 – 15:

   a. Checking for main effects of gender:

      i. No significant relationship was found between gender and incidence of URI during the age span 11 - 15 according to chi square tests (p = .934, two-tailed).

      ii. No significant relationship was found between gender and incidence of DIA during the age span 11 – 15 according to chi square tests (p = .598, two-tailed).

      iii. No significant relationship was found between gender and incidence of INJ during the age span 11 – 15 according to chi square tests (p = .143, two-tailed).

   b. Checking for main effects of rearing:

      i. Mother-rearing, responsive care and standard care:

         1. A chi square test for relationship between rearing (mother, responsive nursery, or non-responsive care nursery) and upper respiratory infection did reveal a significant relationship between rearing and URI, $\chi^2(2) = 12.020$, $N_{MR} = 42$, $N_{RC} = 10$, $N_{NRC} = 44$, $p = .002$ (two-tailed), $\varphi = .35$. Forty percent of individuals in the responsive care nursery experienced at least one URI during years 11 - 15 while only 2 percent of individuals in the non-responsive care nursery and 14 percent of the individuals that were mother-reared experienced at least one URI during that same age span (see Figure 47, page 137).

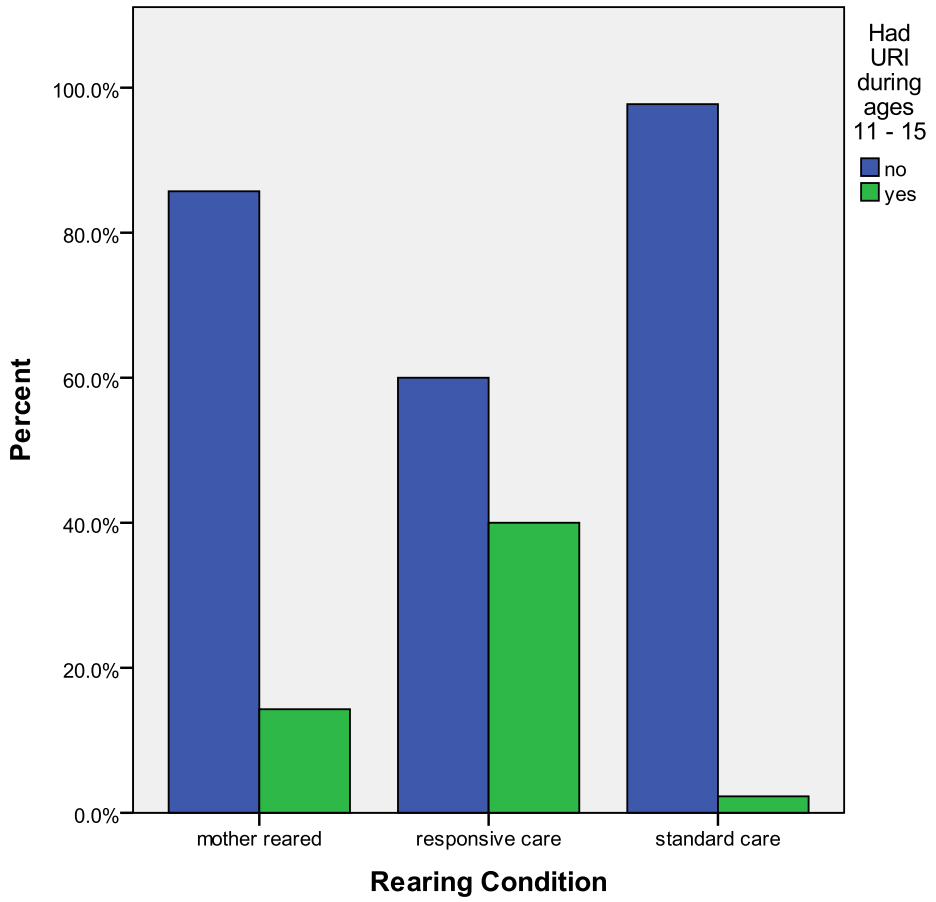

Figure 47: Proportion of URI (upper respiratory infections) for Different Rearing Groups during ages 11 – 15 years (mother versus responsive care versus non-responsive care)

2. A chi square test for relationship between rearing (mother, responsive nursery or non-responsive care nursery) and incidence of diarrhea revealed no significant relationship between rearing and DIA (p = .462, two-tailed) during years 11 - 15.
3. A chi square test for relationship between rearing (mother, responsive nursery, or non-responsive care nursery) and

incidence of injury did reveal a significant relationship between rearing and INJ, $\chi^2(2) = 10.771$, $N_{MR} = 42$, $N_{RC} = 10$, $N_{NRC} = 44$, $p = .005$ (two-tailed), $\varphi = .34$. Zero percent of individuals in the responsive care nursery experienced at least one INJ during years 11 - 15 while 18 percent of individuals in the non-responsive care nursery and 43 percent of the individuals that were mother-reared experienced at least one injury during that same age span (see Figure 48, page 138).

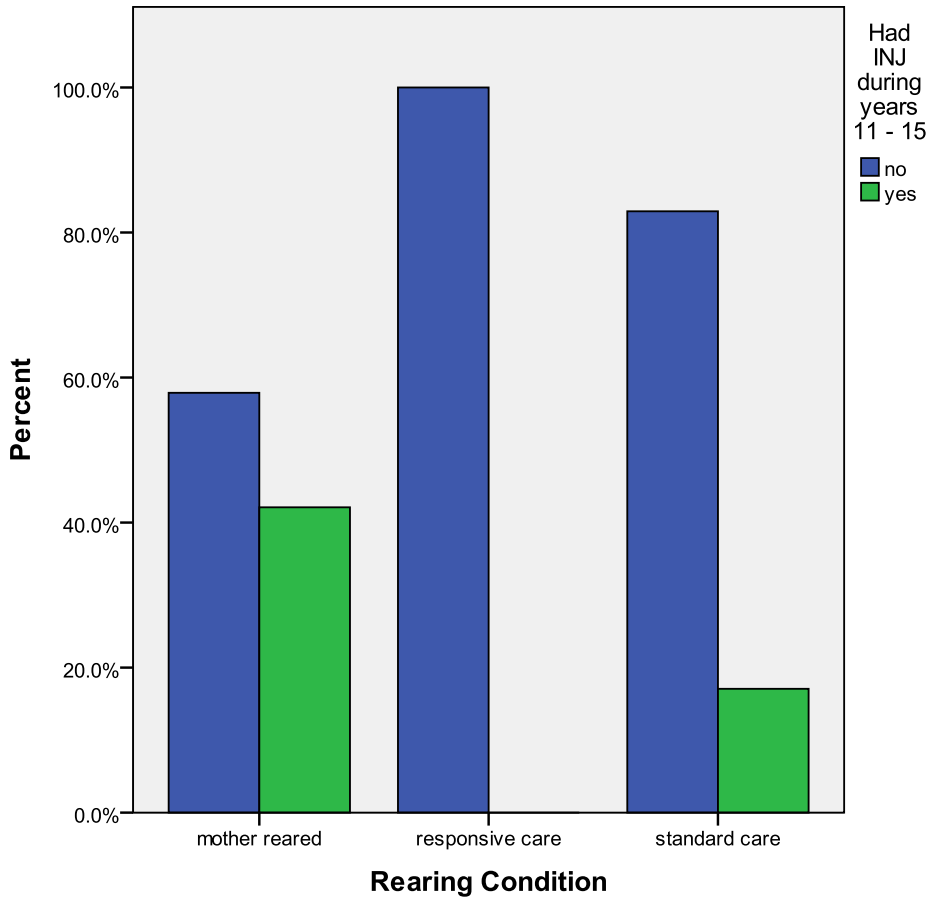

Figure 48: Proportion of INJ (injury) incidence for Different Rearing Groups during ages 11 – 15 years (mother versus responsive care versus non-responsive care)

ii. Mother-rearing versus nursery-rearing (NRC + RC):

1. Chi square tests indicated that there was no significant relationship between rearing (mother-reared versus a collapsed nursery-reared category) and upper respiratory infection during years 11 – 15 (p = .443, two-tailed) or between rearing and DIA during that age span (p = .440, two-tailed).
2. Chi square tests indicated that there was a significant relationship between rearing (mother-reared versus a collapsed nursery-reared category) and INJ during years 11 – 15, χ^2 (2) = 9.407, N_{MR} = 42, N_{NR} = 54, p = .002 (two-tailed), φ = .31. Fifteen percent of individuals raised in nurseries experienced at least one INJ during years 11 - 15 while 43 percent of the individuals that were mother-reared experienced at least one injury during that same age span (see Figure 49, page 140).

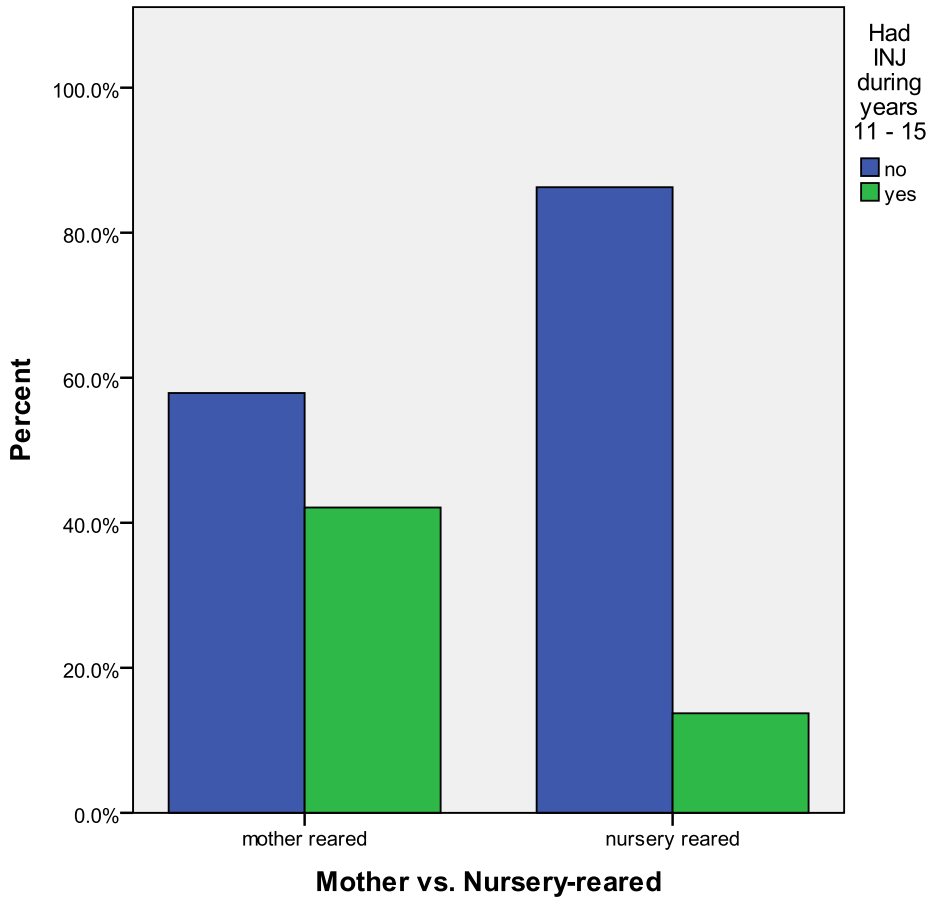

Figure 49: Proportion of INJ (injury) incidence for Mother versus Nursery-reared during ages 11 – 15 years

iii. Responsive versus non-responsive care:

1. Chi square tests indicated there was a significant relationship between the type of nursery rearing (non-responsive care vs. responsive) and URI incidence during years 11 - 15, χ^2 (1) = 13.804, N_{NRC} = 44, N_{RC}= 10, p = .000 (two-tailed), φ = .51. Forty percent of individuals in the RC group experienced at least one bout with URI between the ages of 11 - 15 while only 2 percent of individuals in the NRC group experienced an URI

during that same age span (see Figure 50, page 141). This is a robust effect at a Phi value of .51.

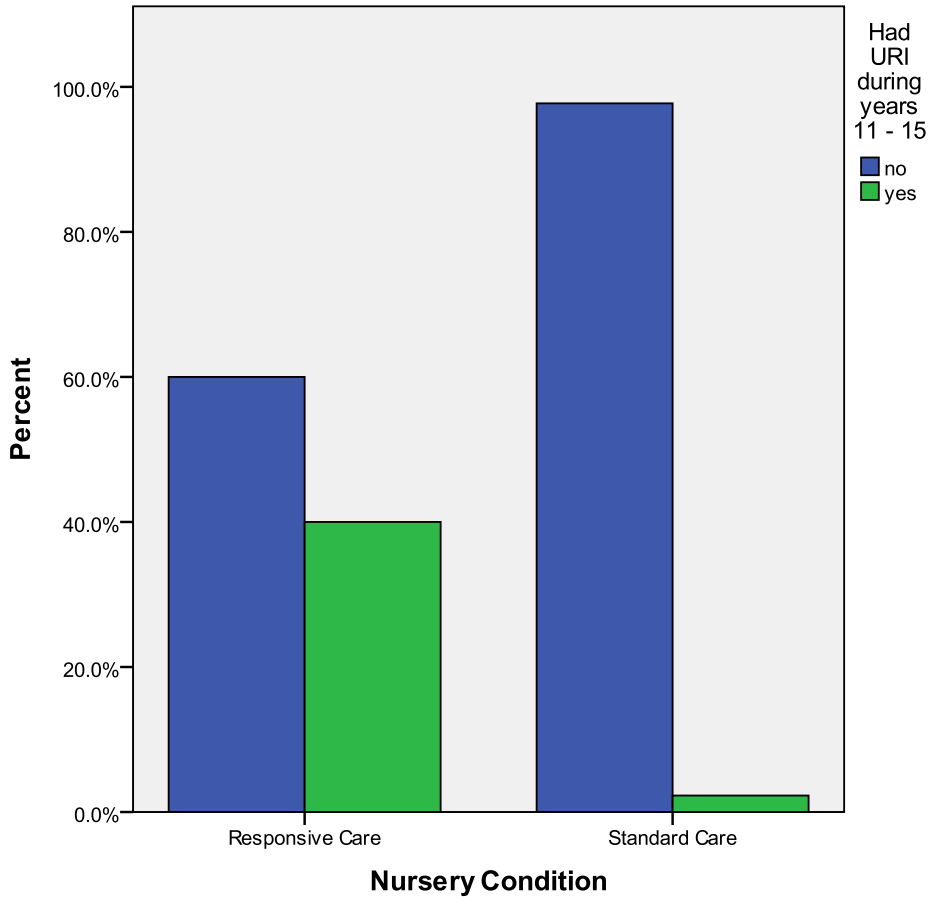

Figure 49: Proportion of INJ (injury) incidence for Responsive versus Non-Responsive Care during ages 11 – 15 years

2. Chi square tests indicated there was not a significant relationship between type of nursery rearing and DIA incidence (p = .396, two-tailed) or incidence of injury (p = .144, two-tailed) during years 11 – 15.

c. Checking for main effects of attachment classification:

i. There was not a significant relationship between attachment classification (disorganized vs. non-disorganized) and upper respiratory infection during years 11 - 15, $p = .773$ (two-tailed).

ii. There was not a significant relationship between attachment classification (disorganized vs. non-disorganized) and diarrhea during years 11 - 15, $p = .094$ (two-tailed).

iii. There was not a significant relationship between attachment classification (disorganized vs. non-disorganized) and injury during years 11 - 15, $p = .427$ (two-tailed).

d. Checking for main effects of early trauma:

i. Of the individuals who were known to have arrived at the standard care nursery on the first day (Early Arrival) and those known to have arrived later (Late Arrival), there were no incidences of upper respiratory infection reported during years 11 – 15.

ii. There was no significant difference between these two groups in regards to incidence of injury, $p = .678$ (two-tailed).

iii. There was no significant difference between the two groups in regards to incidence of diarrhea, $p = .364$ (two-tailed).

4. Ages 16 - 20:

a. Checking for main effects of gender:

i. No significant relationship was found between gender and incidence of URI during the age span 16 - 20 according to chi square tests ($p = .964$, two-tailed).

ii. No significant relationship was found between gender and incidence of DIA during the age span 16 - 20 according to chi square tests (p = .420, two-tailed).

iii. No significant relationship was found between gender and incidence of INJ during the age span 16 - 20 according to chi square tests (p = .517, two-tailed).

b. Checking for main effects of rearing:

i. Mother-rearing, responsive care and non-responsive care (NRC):

1. Chi square tests for relationships between rearing (mother, responsive nursery or non-responsive care nursery) and incidence of diarrhea (p = .453, two-tailed), upper respiratory infection (p = .315, two-tailed) or injury (p = .679, two-tailed) revealed no significant relationship between rearing and these categories during years 16 - 20.

ii. Mother-rearing versus nursery-rearing (NRC + RC):

1. Chi square tests indicated that there was no significant relationship between rearing (mother-reared versus a collapsed nursery-reared category) and upper respiratory infection during years 16 - 20 (p = .318, two-tailed), between rearing and DIA (p = .208, two-tailed) or between rearing and INJ (p = .241, two-tailed) during that age span.

iii. Responsive versus Non-responsive care:

1. Chi square tests indicated there was no significant relationship between the type of nursery rearing (non-responsive care vs. responsive) and URI incidence (p = .164, two-tailed) or INJ (p = .627, two-tailed) during years 16 – 20.
2. There were no incidences of diarrhea reported for either of these two groups during years 16 – 20.

c. Checking for main effects of attachment classification:
   i. There was not a significant relationship between attachment classification (disorganized vs. non-disorganized) and upper respiratory infection during years 16 - 20, p = .257 (two-tailed).
   ii. There were no cases of diarrhea reported for any of the animals in either group during this time span.
   iii. There was not a significant relationship between attachment classification (disorganized vs. non-disorganized) and injury during years 11 - 15, p = .582 (two-tailed).

d. Checking for main effects of early trauma:
   i. Of the individuals who were known to have arrived at the standard care nursery on the first day (Early Arrival) and those known to have arrived later (Late Arrival), there were no incidences of upper respiratory infection reported during years 16 - 20.
   ii. There was no significant difference between these two groups in regards to incidence of injury, p = .264 (two-tailed).

iii. There were no reported incidences of diarrhea for animals in these groups during years 16 – 20.

5. Frequencies of illness and injury over the 0 – 20 life span for responsive versus non-responsive care (Figure 51, page 146):
   a. There were no significant differences found between the two groups in terms of overall frequency of upper respiratory infection (p = .079, two-tailed) or injury (p = .601, two-tailed).
   b. Responsive care had a significantly higher frequency of diarrhea across the 0 – 20 age span as compared to non-responsive care, U = 18.0, N_{RC} = 6, N_{ST} = 33, p = .000 (two-tailed).
   c. Responsive care had a significantly higher frequency of overall illness (URI + DIA) across the 0 – 20 age span as compared to non-responsive care, U = 18.0, N_{RC} = 6, N_{ST} = 33, p = .001 (two-tailed).
   d. There was no significant effect of gender on age span frequencies in any of these categories.

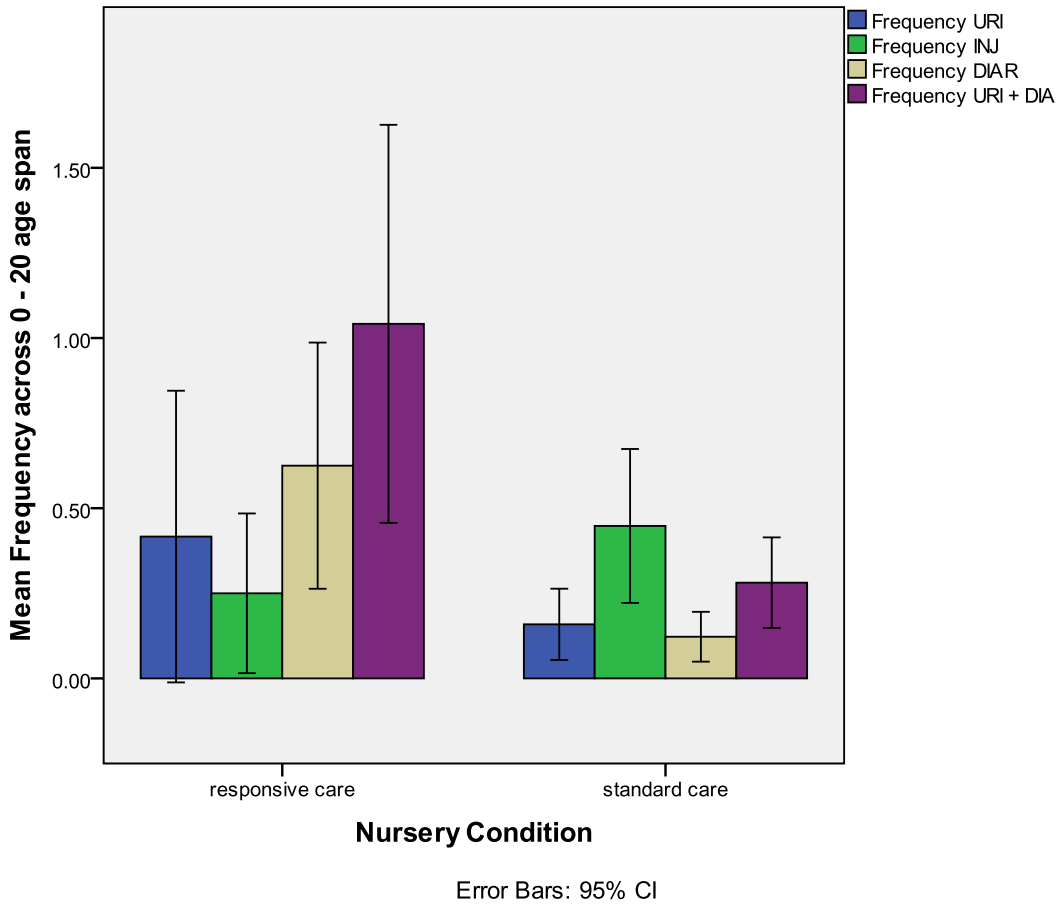

Figure 51: Overall Mean Frequency of URI (upper respiratory infections), INJ (injury), DIA (diarrhea), and overall illness (URI + DIA) for Responsive versus Non-Responsive Care during ages 0 – 20 years

Attachment Differences

MWU tests were conducted to determine if any non-hypothesis related differences existed between disorganized and non-disorganized chimpanzees in regards to response measures; there were very few differences between the groups but notable results are listed here:

1. Disorganized subjects were scored, on average, as less intelligent both socially and outside of social situations) than non-disorganized subjects, U = 25.5, N_{DA} =

10, N_{ND} = 12, p = .064 (two-tailed); this result was near significant (see Figure 52, page 147).

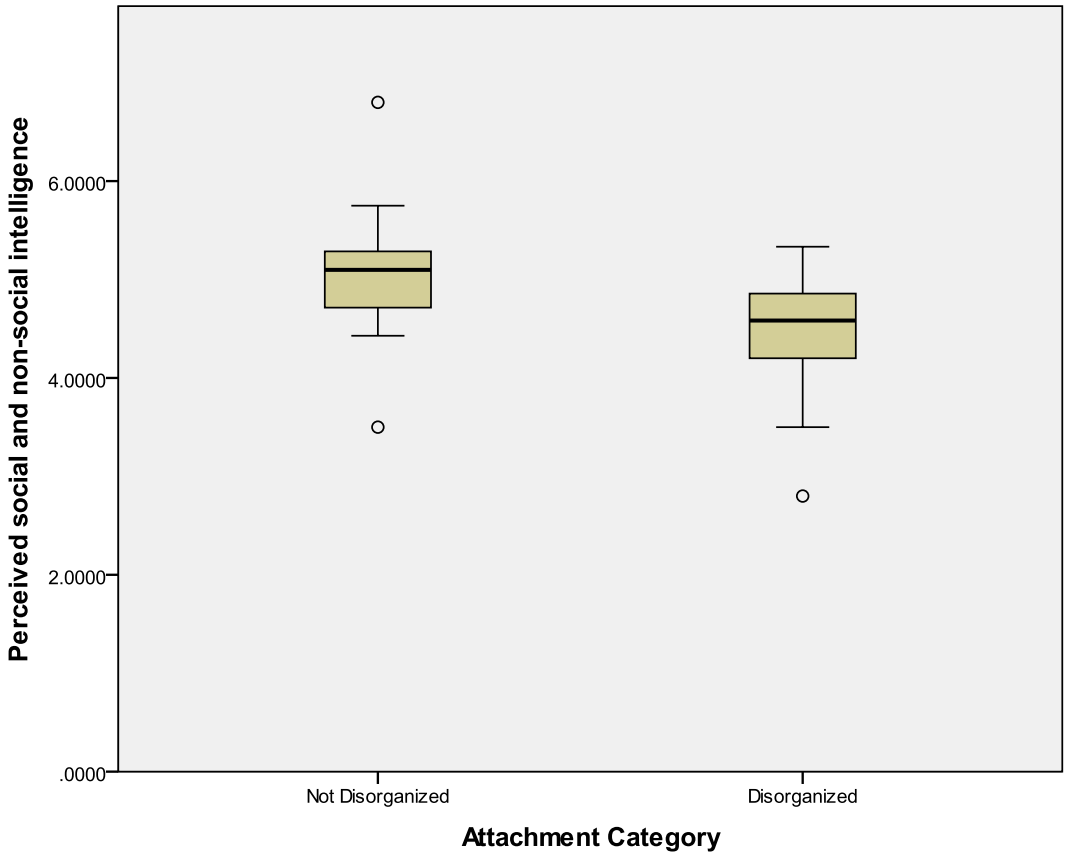

Figure 52: Mean Scores on survey question C33 (perceived social and non-social intelligence of the chimpanzee)

2. Disorganized subjects were scored, on average, as significantly more lacking in perceptive ability regarding social partners' moods as compared to non-disorganized subjects, U = 21.5, N_{DA} = 10, N_{ND} = 12, p = .031 (two-tailed) (see Figure 53, page 148).

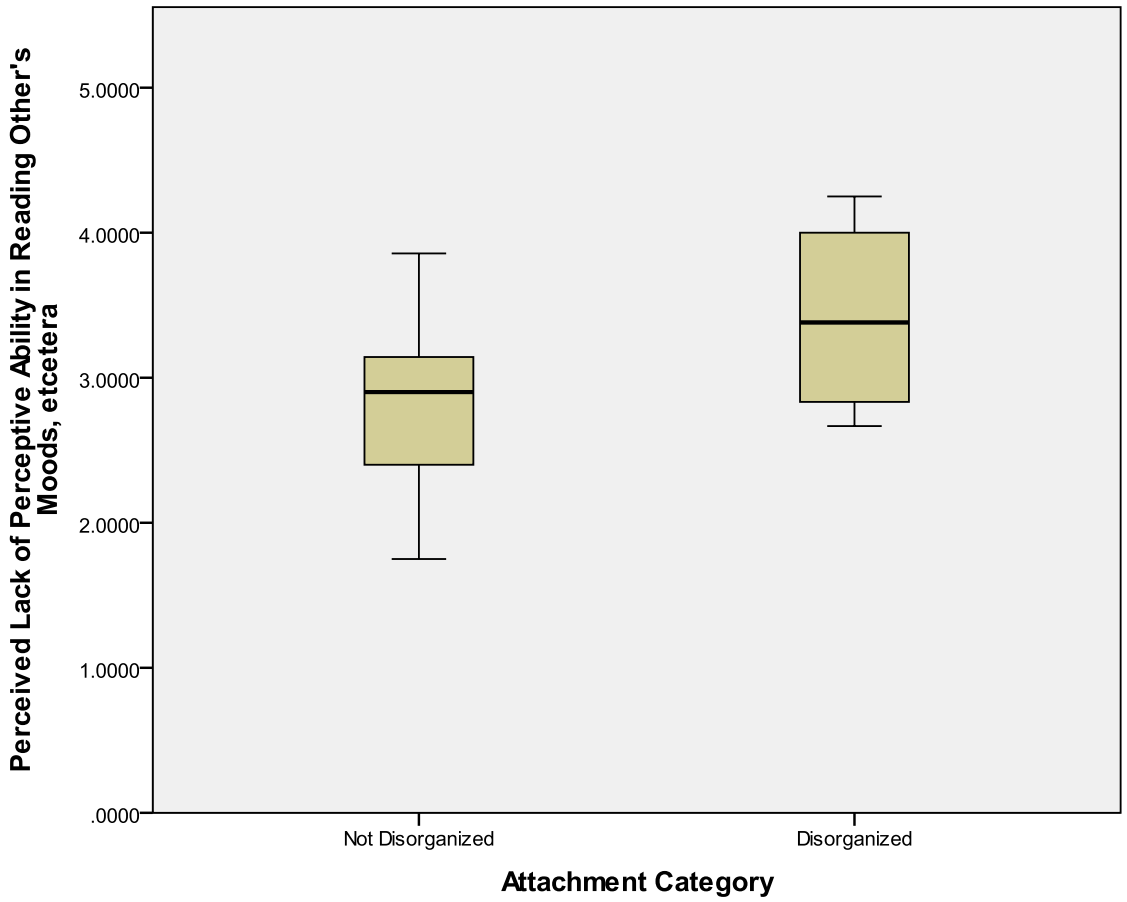

Figure 53: Mean Scores on survey question C58 (lack of perceptive ability in reading others' moods)

3. Disorganized subjects were scored lower, on average, on the Purposefulness Factor as compared to non-disorganized subjects, U = 25.0, N_{DA} = 10, N_{ND} = 12, p = .059 (two-tailed); this result was near significant (see Figure 54, page 149). These results must be viewed with some skepticism, however, due to the unequal sex ratios in the two groups (DA: 7M, 3F; ND: 5M, 7F). These ratios could bias the results slightly towards the ND group as they have more females than males while the DA group as more males than females.

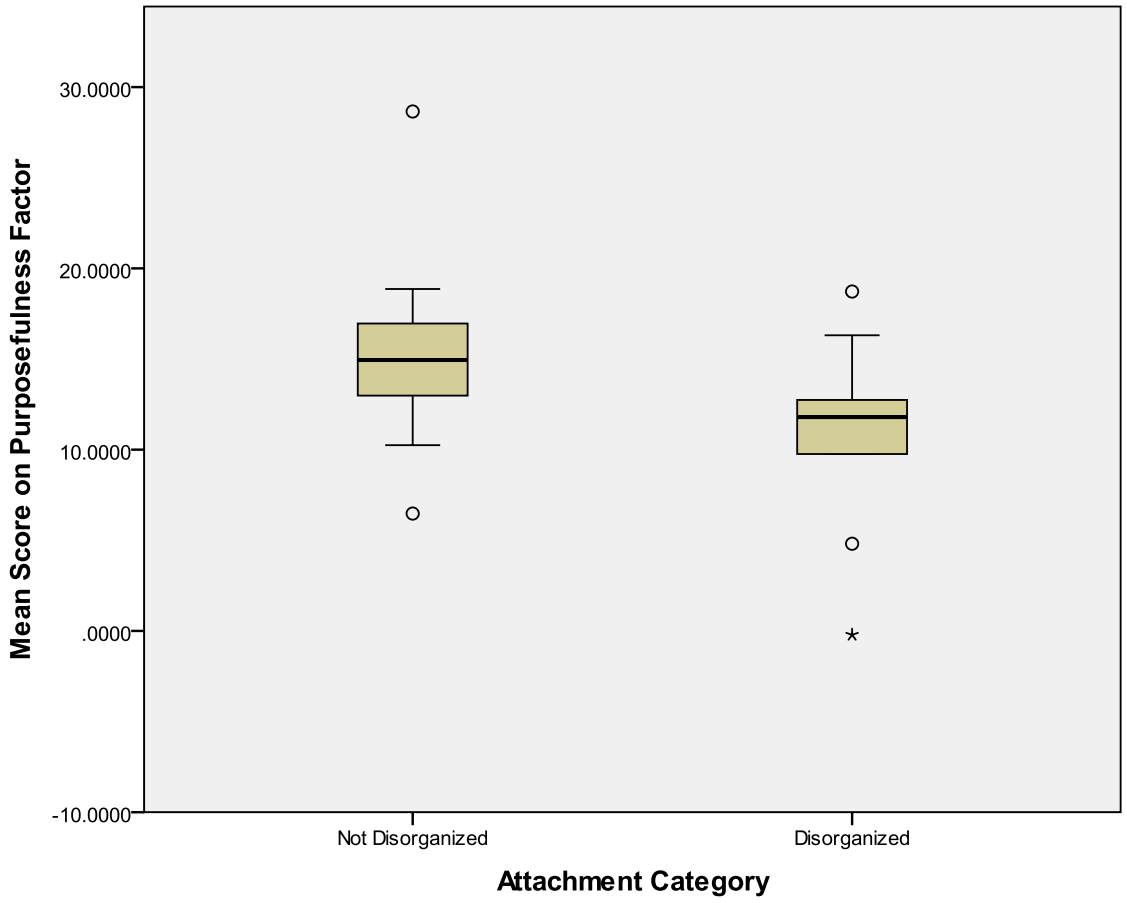

Figure 54: Mean Scores on Purposefulness Factor: Disorganized versus Non-Disorganized Subjects

CHAPTER 7

DISCUSSION

Experiment One: Behavioral Observations

Abnormal and Stress-related Behaviors due to Rearing Differences

Though both nursery groups exhibited higher rates of stress-related behavior as compared to the mother-reared group, neither of these comparisons was significant using a Mann Whitney U test. Stress-related behavior was found to be correlated with an uncontrolled but recorded environmental event (the approach of a human to within 5 feet of the caging). Therefore, it was important to determine that these groups did not experience varying rates of human approach; MWU tests confirmed that there was not a significant difference between any of the three groups in rate of human approach. Stress regulation both physiologically and psychologically is highly impacted by early rearing (Sackett, 1965; Sanchez, et al., 1998; Sanchez, et al., 2001; Sanchez, et al., 1999; Suomi, et al., 1976; Teicher, et al., 2003; Tizard, 1975; Turner, et al., 1969; Watson, 1996; Weary, Appleby, & Fraser, 1999; Young, Suomi, Harlow, & McKinney, 1973) and the differential effects found here might parsimoniously be considered to result from stress during the first few years of these chimpanzees' lives, but the lack of significant results indicates that either there truly are no differences between nursery-reared and mother-reared chimpanzees in terms of stress response regulation or it may indicate that measuring stress through general and basic behavioral observations is not sufficient to detect differences; stress is notoriously tricky to measure, both behaviorally and

physiologically, and even more difficult to assess as either positive or negative, acute or chronic by nature (Blecha, 2000).

Both nursery groups exhibited significantly higher rates of abnormal behavior as compared to the mother-reared group. This result is not surprising; other studies have found that abnormal behaviors are higher in nursery-reared chimpanzees as compared to mother-reared chimpanzees (M. Bloomsmith, et al., 2002). However, at least one study found that differences in the rate of abnormal behaviors disappeared when differentially reared chimpanzees reached adulthood (J. E. Martin, 2002). Another study found that only chimpanzees that did not have much interaction with humans (such as standard care chimpanzees from this study) continued to exhibit higher rates of abnormal behaviors than mother-reared chimpanzees (Maki, et al., 1993b). However, in this study, not only were nursery-reared chimpanzees found to exhibit higher rates of abnormal behavior into adulthood, but additionally, responsive care chimpanzees, who did have a substantial amount of interaction with primary caregivers, also exhibited these higher rates of abnormal behavior into adulthood. The contradictory results of these different studies suggest further research should be dedicated to determining what factors might predict long-lasting differences in the rate of abnormal behavior in captive chimpanzees. This might include comparisons that take into account social groupings with conspecifics, captive settings (laboratory or zoological institution), age at which human caregivers no longer interacted substantially with nursery-reared chimpanzees, age of reintroduction to social groups of chimpanzees, or perhaps temperament differences between individual chimpanzees. It is also going to be important to assess the amount of time infant

chimpanzees are with humans as relevant to abnormal behavior development and maintenance in adult chimpanzees.

Abnormal and Stress-related Behaviors due to Attachment Differences

Disorganized individuals did exhibit significantly higher rates of abnormal behaviors as compared to non-disorganized individuals. Stress related behaviors were not significantly different between the two groups. However, even if only abnormal behavior rates are considered, significant differences found between these two groups based on tests of attachment conducted over 20 years ago indicate some long-lasting differences between these two groups in essential ways.

Of all the attachment categories identified, disorganization has the worst long-term prognosis in humans (Lyons-Ruth, 1996b; M.H. Van IJzendoorn, C. Schuengel, & M. J. Bakermans-Kranenburg, 1999). In previous research, it was observed that chimpanzees reared in Bard's responsive care nursery were significantly less likely to be classified as disorganized (41% of the group) as compared to standard care chimpanzees (72% of the group). Organized attachment to a primary caregiver as was fostered in the responsive care environment was likely important for the chimpanzees' psychological health and perhaps prevented the development of some abnormal behaviors, such as rocking. Chimpanzees categorized as disorganized in previous research also exhibited significantly more rocking behavior during separation episodes and during reunions, and rocking was one of the highest scoring categories recorded under abnormal behaviors in this study (M. H. Van IJzendoorn, et al., 2008) (Figure 55, page 153). Adult chimpanzees in the non-disorganized group had a smaller proportion of abnormal behavior devoted to idiosyncratic movement (64%), which primarily consists of

rocking/swaying behaviors, as compared to disorganized chimpanzees (80%) (See Figures 56 - 58, pages 154 - 155).

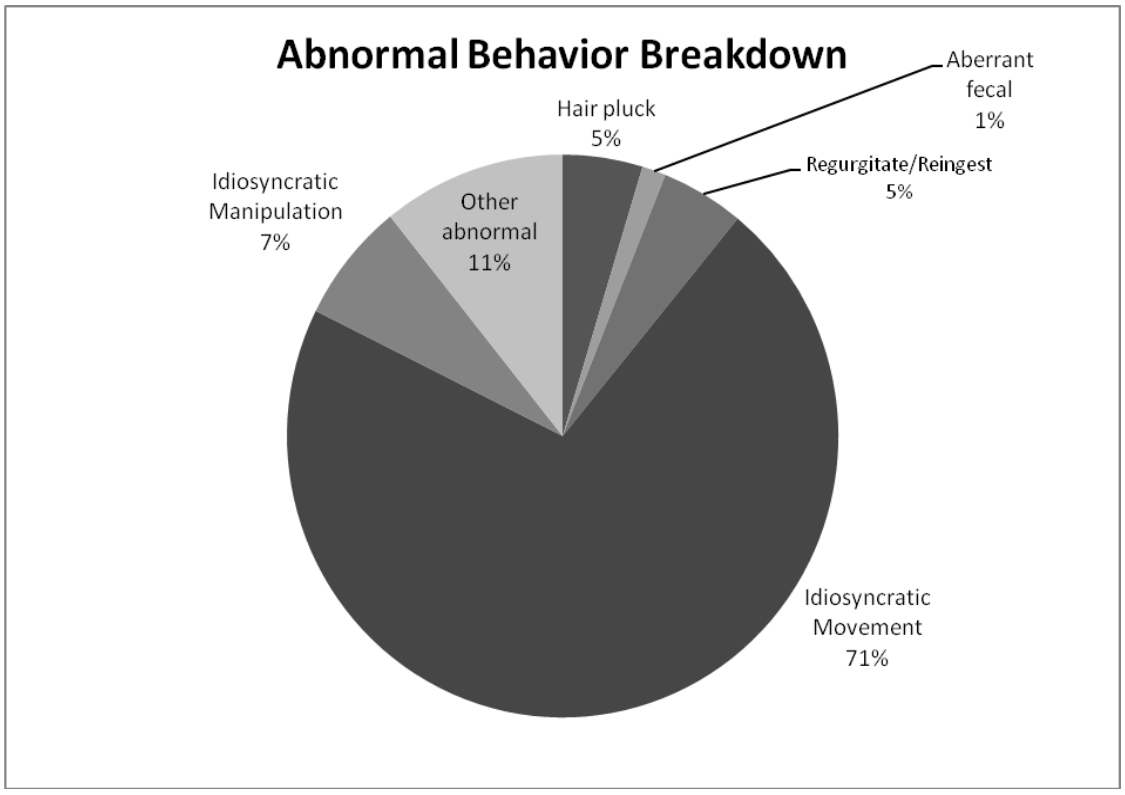

Figure 55: Breakdown of Abnormal Behavior Category into Percentages per Individual Behaviors (note: idiosyncratic movement includes rocking, stereotypic swaying, and head wagging)

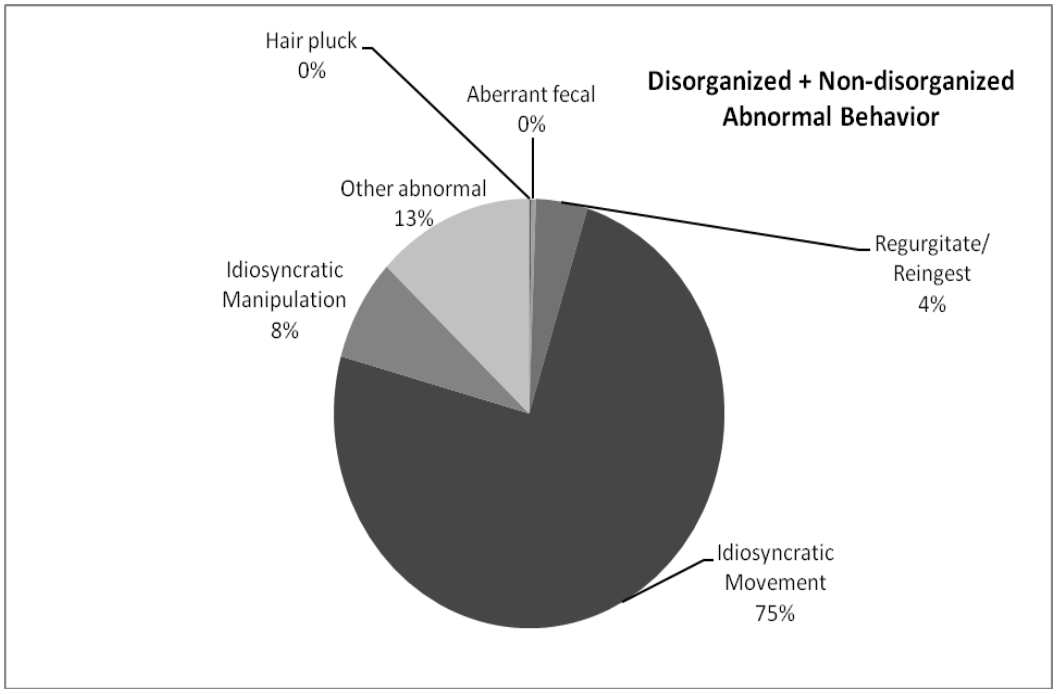

Figure 56: Breakdown of Abnormal Behavior Category into Percentages per Individual Behaviors (note: idiosyncratic movement includes rocking, stereotypic swaying, and head wagging): Disorganized + Non-Disorganized

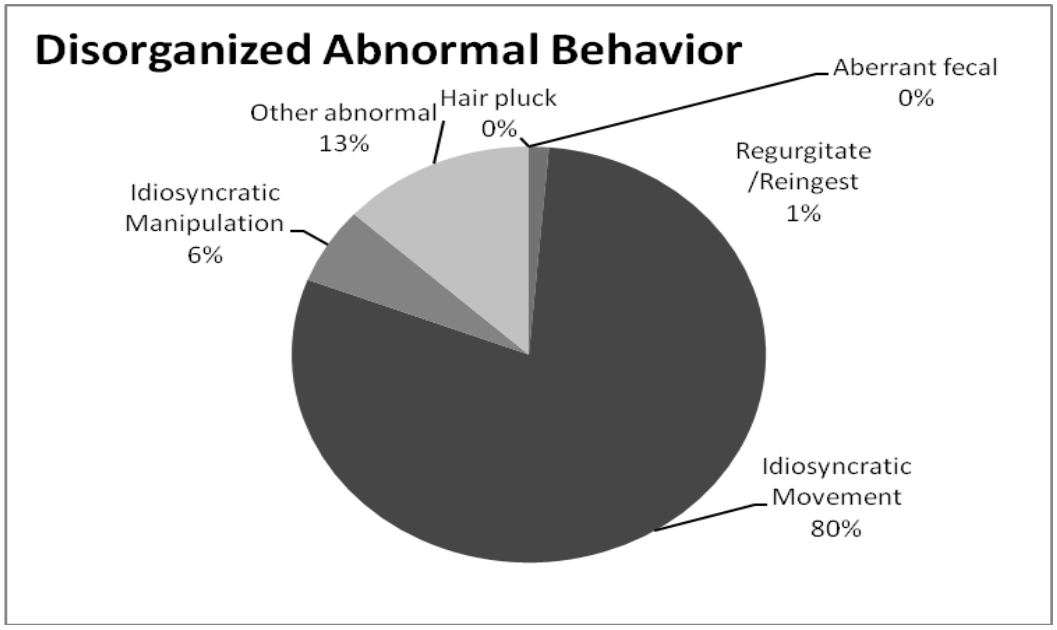

Figure 57: Breakdown of Abnormal Behavior Category into Percentages per Individual Behaviors (note: idiosyncratic movement includes rocking, stereotypic swaying, and head wagging): Disorganized Subjects

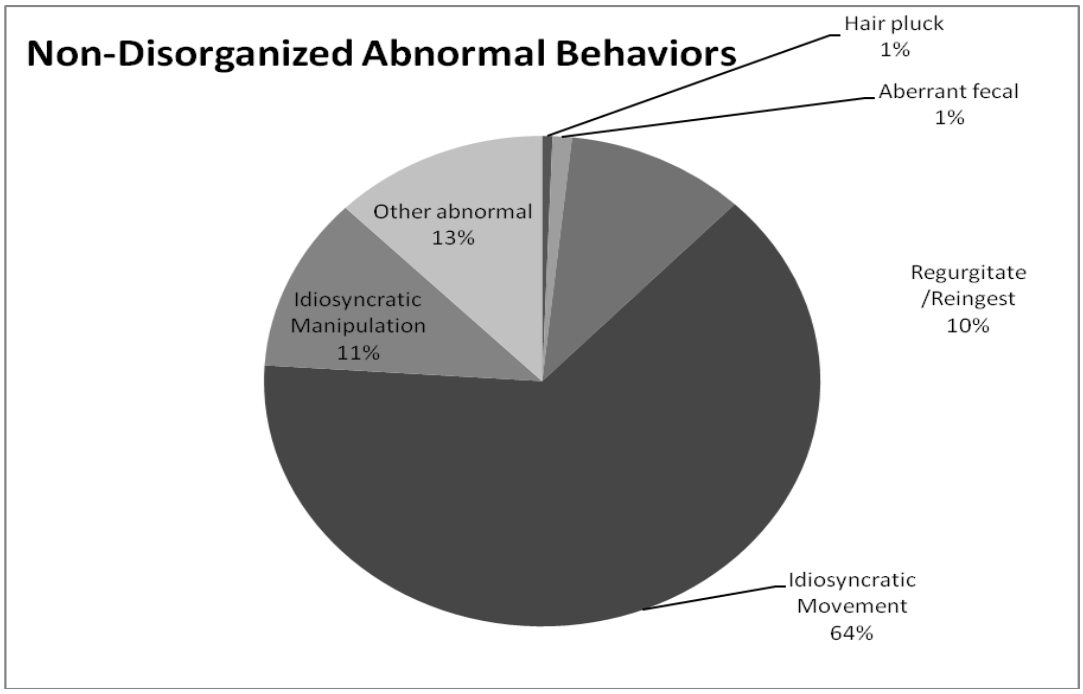

Figure 58: Breakdown of Abnormal Behavior Category into Percentages per Individual Behaviors (note: idiosyncratic movement includes rocking, stereotypic swaying, and head wagging): Non-Disorganized Subjects

Rocking has been suggested to occur in nursery chimpanzees as a result of absence of a mother to whom the infant would normally cling, and who would move around a lot, providing more motion to the infant than can be provided in the absence of a living adult to whom the infant can cling (Dienske & Griffin, 1978). Other studies have found that providing a canine companion to nursery-reared infant chimpanzees can significantly ameliorate rocking behaviors (Pazol & Bloomsmith, 1993; M. A. Thompson, et al., 1991). Therefore spending more time with humans that carried and held the infants in the responsive care nursery could be expected to ameliorate rocking for RC chimpanzees; this was the case when the two nursery groups were compared 20 years ago. Currently, the RC group exhibits a higher (though not significantly higher) rate of abnormal behavior as compared to the ST group; within that category of abnormal behavior,

rocking is by far the primary behavior (73 - 76%) observed for both groups (see Figures 59 and 60, page 157), but there is no significant difference in rates of rocking between the two groups (the RC group had a very slightly higher mean rate as compared to the ST group). The mother-reared group has a much smaller percentage (59%) of abnormal behavior devoted to rocking (see Figure 61, page 158). The two attachment groups (Disorganized and Non-Disorganized) were well balanced for standard versus responsive care subjects: the DA (disorganized) group was made up of 4 individuals from responsive care and 6 from standard care; the ND (non-disorganized) group was made up of 6 individuals from responsive care and 4 from standard care. In addition, based on the results of this study regarding abnormal behavior, there was no significant difference between the two nursery groups in terms of rocking behavior or abnormal behavior in general. Therefore the results indicating that chimpanzees identified as disorganized 20 years ago currently exhibit significantly higher levels of abnormal behavior as compared to chimpanzees identified as non-disorganized 20 years ago are fairly robust.

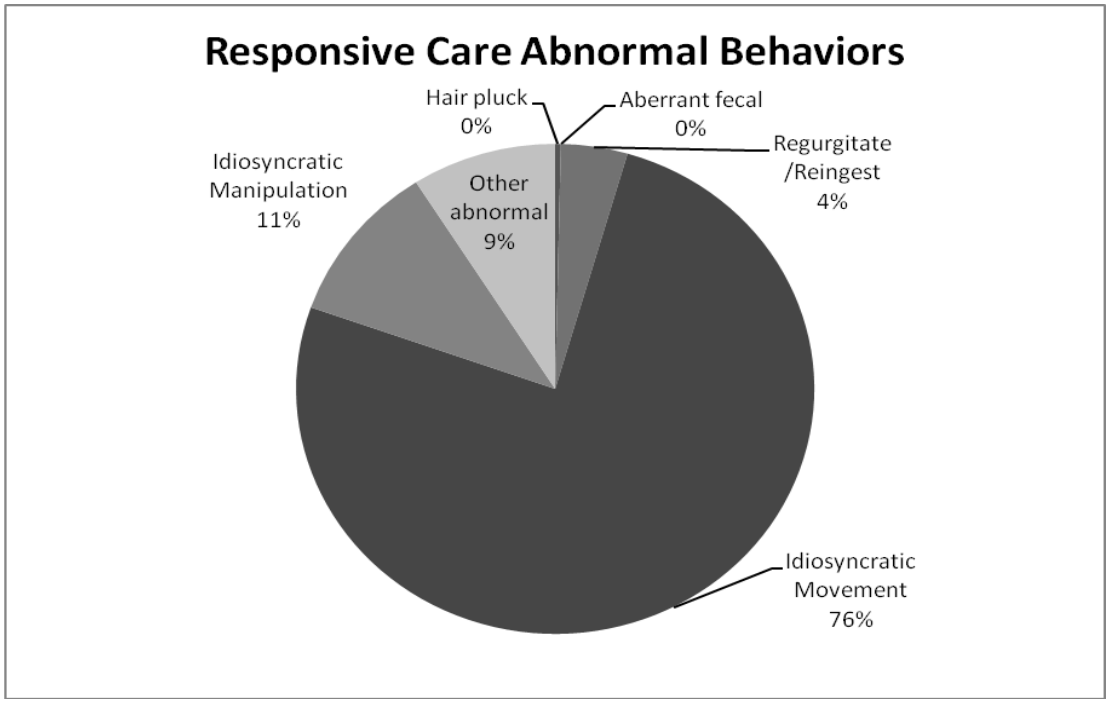

Figure 59: Breakdown of Abnormal Behavior Category into Percentages per Individual Behaviors (note: idiosyncratic movement includes rocking, stereotypic swaying, and head wagging): Responsive Care Subjects

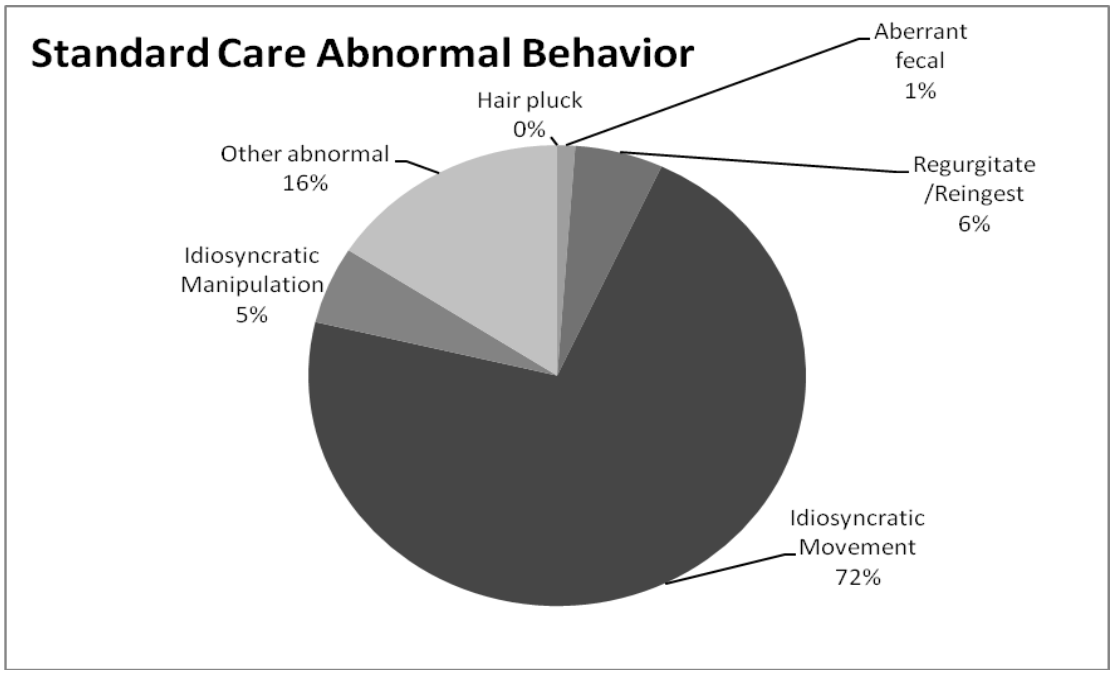

Figure 60: Breakdown of Abnormal Behavior Category into Percentages per Individual Behaviors (note: idiosyncratic movement includes rocking, stereotypic swaying, and head wagging): Standard Care Subjects

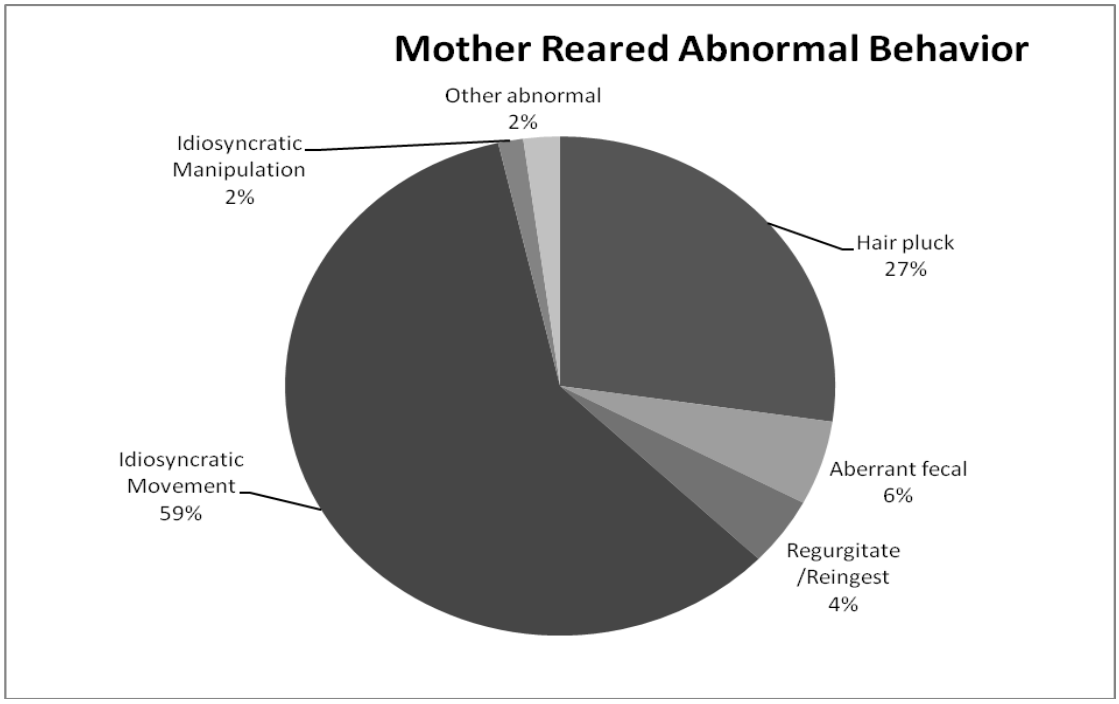

Figure 61: Breakdown of Abnormal Behavior Category into Percentages per Individual Behaviors (note: idiosyncratic movement includes rocking, stereotypic swaying, and head wagging): Mother-Reared Subjects

Solicitation Behaviors

For subjects of this portion of the study, rearing in the Yerkes nursery necessarily means more initial contact with humans than with other chimpanzees. Much of any infant's time in the nursery is, initially, incubator time. Responsive care chimpanzees, as compared to standard care chimpanzees, had a good deal more time interacting with other living beings, even during incubator time (K. A. Bard & Gardner, 1996; M. H. Van IJzendoorn, et al., 2008). These living beings, however, were humans, not chimpanzees. Tests of attachment conducted at one year of age revealed that the responsive care chimpanzees were more likely to exhibit organized attachment to their primary caregivers (humans) than standard care chimpanzees (M. H. Van IJzendoorn, et al., 2008). If

responsive care chimpanzees are, then, in some more organized fashion attached to their human caregivers, this could predict that these chimpanzees would be more likely to continue to depend on human caregivers to a greater extent than do standard care chimpanzees and, of course, mother-reared chimpanzees for which human contact was relatively minimal during infant years. It turns out that indeed responsive care chimpanzees as observed in this study solicit human attention at a higher rate than mother-reared chimpanzees do; standard care chimpanzees do not. Responsive care subjects also solicit human attention at higher rates than standard care subjects, though this difference was significant only in terms of negative solicitation. Taken together, the data suggest that chimpanzees reared in the responsive care nursery might require more human interaction and human contact than other chimpanzees, even other nursery-reared chimpanzees, in order to maximize their welfare as adults; certainly they require more than mother-reared chimpanzees. Non-Yerkes facilities that have utilized responsive care techniques to raise chimpanzee infants until reintroduction to conspecifics have found similar results: infants reintroduced at 9 months of age continued through 2 years of age to exhibit higher rates of human-directed behavior than a mother-reared, age-matched infant (Bashaw, Gullot, & Gill, 2010).

Positive versus Negative Solicitation

Responsive care chimpanzees solicited human attention at significantly higher rates than mother-reared chimpanzees whether in terms of negative solicitation (aggressive behavior, spitting, or throwing feces) or in terms of positive solicitation (raspberries, gestures, vocalizations, or eye contact). Standard care chimpanzees again did not significantly differ from mother-reared chimpanzees on these measures. Additionally,

responsive care chimpanzees solicited human attention at significantly higher rates than standard care chimpanzees in terms of negative solicitation. Negative solicitation of human attention through throwing feces has been determined, through functional analysis, to be maintained as a behavior if human attention, positive or negative, occurs as a result (A. L. Martin, Bloomsmith, Kelley, Marr, & Maple, 2011). Anecdotally, many chimpanzee caretakers and researchers acknowledge that negative solicitation often occurs more if chimpanzees that engage in this behavior receive attention as a result. Often it seems that chimpanzees who want attention and are not satisfied with the amount they have received are more likely to throw, spit, or otherwise attempt to gain a human's attention through negative means. The findings of this research indicate that responsive care chimpanzees may desire more human interaction than they currently receive, again supporting the idea that perhaps for animals raised with more extensive human contact, ongoing human attention and interaction may be required for better welfare. This conclusion is bolstered by the finding that responsive care chimpanzees exhibited a near-significant higher rate of aggressive behavior towards humans as compared to standard care chimpanzees (p = .058). Negative solicitation is, in fact, a form of aggressive behavior; the suggestion by Martin and colleagues (2011) that such behavior is an attempt to receive attention from humans and the data collected in the current study indicate that observed rates of aggression could be related to frustration. Interestingly, the survey-extracted factor of Aggressive Orientation was not significantly different for the two nursery groups (p = .792); this factor combines aggressive behavior towards humans and towards conspecifics.

Attention Directed Towards Humans

Findings regarding the rate at which chimpanzees in this study attended to humans and/or human activity support the previous conclusions. Both standard care and responsive care subjects attended to humans at a significantly higher rate than mother-reared subjects; additionally, responsive care subjects attended to humans at a significantly higher rate than standard care subjects. The higher the contact with humans during younger years, the higher the rate of attending to humans and human activity; this suggests again that there are long-lasting effects on the species orientation of chimpanzees as a result of early exposure to humans. Added to the above data, it seems that this greater orientation is associated with higher rates of solicitation, particularly negative solicitation, and possibly higher rates of aggression towards humans. More responsive care chimpanzees were reported to exhibit anger (88%) as compared to standard care chimpanzees (14%) when tested during the first year of life; they were also more likely to exhibit social greetings towards humans (94% for RC, 67% for ST) (K. Bard, 2003; K. A. Bard, 2005). The differences reported between the two nursery-reared groups during the first year of life seem to be analogous to some of the differences reported here.

Behavioral Data as a Whole

Generally the data support research with humans which suggests that disorganization classification can have long-term effects on stress regulation (M.H. Van IJzendoorn, et al., 1999), affecting abnormal behavior development. Additionally, the behavioral data collected indicates that the more exposure chimpanzees have to humans as youngsters (approximately ages 0 – 1 year), the more those chimpanzees exhibit attachment and

orientation towards humans as adults up to 20 years later. These findings are significant in that they support human research on disorganization effects and also suggest long lasting species orientation effects for animals that have been cross-reared. The latter finding has implications for animal welfare which will be discussed later in this paper.

Experiment Two: Health Assessments

Attachment Classifications

Disorganized individuals did exhibit significantly higher rates of upper respiratory infection through age 5 and diarrhea for ages 6 – 10, but there was not adequate support for any long-lasting ill effects on health due as corresponding to disorganization classification at a young age. Because there were so many zeros in the database, it was decided to reanalyze portions of the health data using a yes/no Chi Square test as described previously. A Chi Square test confirmed that there was a significant relationship between attachment classification and upper respiratory infection during years 0 – 5, 85% of disorganized individuals experiencing at least on URI during that time as compared to only 47% of non-disorganized individuals. Chi square also found that there was a near-significant relationship between attachment classification and incidence of diarrhea between ages 6 – 10, 20% of the DA subjects experiencing at least one episode of diarrhea during that time as compared to zero percent of ND subjects (p = .051, two-tailed). Taken with the MWU results, both of these results should be taken seriously. However, there was no difference between the two groups on measures related to illness between the ages 11 – 20, indicating that perhaps there are not long-term effects on health as associated with attachment style for chimpanzees. Overall frequency of upper respiratory infection did differ significantly between the two groups across the 0 –

20 life span, but this result may be primarily driven by the results from ages 0 – 5 years. However, it is relevant to this study that the records system accessed for information about the health of these chimpanzees is not entirely reliable. Incidents are not always recorded for all individuals and additionally may not specify a type of illness in all cases. Additionally, the truly informative physiological measures for assessing long term health effects in these animals are likely to be those that are not in the animals' records: Levels of different immunoglobins, for example, or levels of stress hormones as related to stressful environmental events. These measures should be used in future studies of this kind.

There was a significantly higher frequency of injury across the 0 – 20 age span for disorganized versus organized subjects. This implies more aggression from conspecifics and perhaps supports human research which has shown that higher rates of aggression at later ages, for example, have been correlated with disorganization classification in toddlers (M.H. Van IJzendoorn, et al., 1999). However, these results need to be viewed with some hesitation as it is not always recorded how an animal received an injury, even if it is known. Additionally, small wounds are often not recorded at all. Injury counts, if there are to be used to assess social effectiveness, should be assessed in a more systematic fashion.

Rearing and Early Stress Effects

There was no significant difference between late arrival (early stress) chimpanzees and early arrival chimpanzees in the standard care group for health-related measures at any age or across the age span; this was confirmed by Chi Square tests. There was a significantly higher rate of injury found for animals in both early and late arrival standard

care groups as compared to mother-reared individuals for ages 0 – 5, but this difference disappears past age 5 and, in addition, the results are uncertain due to a significant sex bias in this category and unequal sex ratios between the relevant groups. Similarly, though nursery-reared subjects (non-responsive combined with responsive care) as compared to mother-reared subjects exhibited higher rates of upper respiratory illness, diarrhea, and injury for ages 0 – 5, some of these results are again questionable due to the sex bias found for ages 0 – 5, though looking at chi square effect sizes indicates that the results are fairly robust despite the sex bias. The diarrhea results are completely clear as no sex bias was found for rate of diarrhea at any age; this does indicate some general effect of early nursery rearing on the immune system. However, there are no significant differences detectable past age five in terms of illness; mother-reared animals did experience significantly higher risk of injury during years 11 – 15 as compared to nursery-reared individuals. Overall, it seems, based on the results of this study, that differences as a result of nursery versus mother rearing may be negligible past age five.

Health scores for the different rearing groups were re-coded into yes/no dependent variables and analyzed using Chi Square tests as previously discussed. A main effect was again found for gender for the categories of URI and INJ during years 0 – 5, but the effect size for this finding was relatively small (.20). No gender effect was found in the category of DIA during years 0 – 5, just as was determined through MWU tests. There was no effect of gender found during any other age/health category. A chi square test found a significant relationship between rearing condition (mother, responsive nursery or non-responsive care nursery) and URI during years 0 – 5 and in this case there was a large effect at a Phi value of .47; considering these two effect sizes (gender and rearing)

together, there is likely some main effect of rearing condition on the presence of at least one URI during the relevant age span. Additionally, a significant relationship was found between these three rearing conditions and incidence of at least one case of diarrhea during years 0 – 5. There was a large effect size found for this finding as well (.60). In both of these cases, RC individuals had the highest proportion of animals that experienced at least one bout of the relevant illness, NRC individuals the next highest proportion, and MR individuals the lowest.

Chi squares were also conducted to compare the two different nursery conditions to each other. A significant relationship was found between nursery condition and both URI and DIA during years 0 – 5; again, the effect size for URI findings (.34) was larger for nursery conditions than for gender (.20). Additionally, the two nursery groups contained equivalent ratios of males to females, so that any sex bias should be controlled for. Near twice as many, proportionally, of the RC individuals experienced at least one URI incident during this age span as compared to the proportion of NRC individuals. The effect size for the DIA finding was large at .60 and indicates a robust effect. Taken together, the data support a significant difference between susceptibility to URI and DIA for the two different nursery conditions, responsive care subjects exhibiting the greater susceptibility. Additionally, this significant difference in risk of URI was found by a chi square test to exist 5 – 10 years later when these animals were 11 – 15 years of age, again a robust finding with a Phi value of .51. There was not, however, a significant relationship detected between the type of nursery an individual was reared in and the presence of diarrhea during years 11 – 15. Overall, gender comparisons confirmed no sex bias for the 0 – 20 year frequency of URI, DIA, INJ, or combined illness (URI +

DIA). MWU tests confirmed that the RC individuals experienced, during the 0 – 20 age span, a significantly higher frequency of diarrhea (p = .000, two-tailed) and a significantly higher overall rate of illness (URI + DIA), (p = .001, two-tailed). Given results for comparisons during the different age categories, this result is driven by early life differences more than continued, long-term effects. However, higher risk for URI for responsive care between the years 11 – 15 support the idea for some long term effects of early rearing in this case.

It is possible that record keeping in ARS was not thorough, but additionally, it is likely that looking at factors such as immune system response and brain structure size would be more helpful in determining biological factors related to early rearing experiences or disorganization classification. However, there is solid evidence in the data reported here for the existence of long term effects of differential rearing on the health of chimpanzees. Individuals reared in the responsive care nursery seem to be particularly susceptible to long term health effects as compared to those that were not reared in responsive care. This might indicate that these animals experience greater stress response dysfunction, but additional research should be conducted to confirm this. More extensive interaction with humans during that time could have allowed for a higher risk of spreading illness amongst the chimpanzees in responsive care. However, since responsive care chimpanzees were still spending a great deal of time with the chimpanzees and caregivers in the standard care nursery at that time, germs spread amongst RC chimps should have been spread to ST chimps as well. Preliminary results (personal communication, K. Bard) indicate that indeed the ST and RC chimps did not differ from each other in risk of illness during years 0 – 5; comparisons should be made between all the nursery chimps

during years 1987 – 1995 (the time span of the responsive care nursery) and other Yerkes nursery chimps both before and after that time period. In any case, though these variables could be contributing factors to the presence of increased illness during the first year of the nursery-reared chimpanzees' lives, they do not explain the long-term effects seen in this studies' data.

Experiment Three: Survey

Survey results did not indicate many notable significant differences between disorganized and non-disorganized subjects. However, disorganized chimps were rated significantly lower on social/non-social intelligence, significantly more lacking in social perceptive abilities, and lower to a point of near-significance on the Purposefulness factor. These results, taken together, may indicate that the disorganized chimpanzees are less socially adept than non-disorganized chimpanzees. There was strong support for the hypothesis that mother-reared subjects would be perceived as experiencing greater well-being as compared to either standard care or responsive care nursery-reared subjects. Additionally, strong support was found for the hypothesis that mother-reared subjects would be perceived as significantly less human oriented than nursery-reared chimpanzees. Based on the initial MWU test results, further tests were run to explore differences between the two nursery conditions and to explore the different survey items that loaded onto the Subjective Well-Being factor. MWU tests also revealed significant differences between the two nursery groups, RC animals scoring significantly higher on survey items regarding dependency on others and fearfulness; nearly significant higher scores on survey items regarding anxiety levels and vulnerability. Responsive care chimps scored significantly lower than ST group individuals on survey items regarding

emotional calmness, equability and degree of unemotionality. There was no significant difference between the two nursery groups in regards to tractability re: human requests (p = .974). This last item is interesting because one possible benefit of being human oriented in a human-controlled environment might be better ability to comply with human requests and understand human communication; if responsive care chimps do understand better, that does not seem to influence their willingness to comply.

Survey results are particularly informative if considered along with behavioral data indicating that nursery-reared subjects, particularly those reared in the responsive care nursery, solicit attention from and attend to humans at higher rates than mother-reared subjects. The nature of the relationship between subjective well-being and human orientation is further supported by the finding that mother-reared chimpanzees scored significantly lower on human orientation scores as compared to nursery-reared chimpanzees. More intensive exploration of the data revealed that if the specific questions related to subjective well-being were analyzed separately, mother-reared chimpanzees scored significantly higher than responsive care subjects on three out of four questions. Mother-reared chimpanzees scored significantly higher than standard care subjects on only one of these same four questions. Additionally, responsive care subjects scored lower on all four questions than standard care chimpanzees, though these differences were not significant. Taken as a whole, there is a strong suggestion that either one or both of the following relationships exist: 1) increased exposure to humans during early development correlates negatively with subjective well-being and positively with human orientation in adult captive chimpanzees; 2) decreased exposure to adult

chimpanzees during early development correlates positively with subjective well-being and negatively with human orientation in adult chimpanzees.

CHAPTER 8

CONCLUSION

Summary of Findings

To summarize, the primary findings of this study indicate the following:

1) Disorganization classifications as measured at one year of age in chimpanzees have some predictive value, similar to that seen for human children classified as disorganized: increased risk of injury and upper respiratory infection through 20 years of age, indicating less successful social interaction; increased risk of illness during years 0 – 10; and increased abnormal behavior during adulthood. Additionally, people perceive disorganized chimpanzees as less intelligent, significantly less socially perceptive, and less purposeful than non-disorganized chimpanzees. These findings support the validity of the disorganization classification for humans and for chimpanzees.
2) Nursery-reared chimpanzees in general exhibit a higher risk of illness due to upper respiratory infection and/or diarrhea than mother-reared chimpanzees. Chimpanzees reared in the responsive care nursery exhibited a significantly higher risk of illness due to diarrhea and upper respiratory infection between birth and age six as compared to chimpanzees reared in other Yerkes' nurseries; this elevated risk continued to be observed for chimpanzees between the ages of eleven and fifteen, at least for upper respiratory infection. They are also supported by results indicating significantly higher frequency of diarrhea and overall illness (URI + DIA) for RC versus NRC chimpanzees over the 0 – 20 year life span. These results indicate long-lasting disregulation of the stress response

system as can occur due to early stress and its impact on developing organisms, one effect of which can be increased risk of upper respiratory illness in primates (Cohen, et al., 1997).

3) Chimpanzees reared without conspecific mothers are likely to exhibit long-lasting behavioral differences as compared to chimpanzee-reared peers: increased rate of abnormal behavior; increased orientation toward humans which also continues into adulthood; and decreased subjective well-being as adults as assessed by individuals working regularly with those chimpanzees.

4) Some long-lasting behavioral differences between differentially reared chimpanzees do not seem to be ameliorated by exposing infant/toddler chimpanzees to more nurturing, responsive care as provided by humans. Indeed, current findings imply that chimpanzees reared in a more intensive human interactive and responsive nursery exhibit higher levels of human-directed negative solicitation behaviors and aggressive behaviors, higher levels of attention directed towards humans, higher levels of dependency and fearfulness, and lower levels of perceived emotional calm, equability and un-emotionality as compared to chimpanzees reared in minimal human contact nurseries.

5) Subjective well-being, which has important implications for the management of chimpanzees in captivity as well as for the chimpanzees' welfare, shows strong negative correlation with the rate at which chimpanzees engage in stress-related and, separately, abnormal behavior. Stress-related behavior varied strongly and positively with rates of solicitation of human attention and, separately, rates at which animals attended to humans and human activity.

Summary Discussion

The findings regarding chimpanzees identified as disorganized circa 20 years ago are interesting chiefly because of their relevancy to established theories of attachment as originally laid out by John Bowlby and Mary Ainsworth (Ainsworth, 1985, 1989; Bowlby, 1944, 1969, 1973, 1980). Studies of human children have indicated that those identified as disorganized through attachment tests such as the Strange Situation Test have been more likely to exhibit dysfunction as older children and young adults (M.H. van IJzendoorn, 1995; M.H. Van IJzendoorn, et al., 1999). The findings of this study provide support for attachment theory as of evolutionary importance as it validates that some attachment classifications established at a young age are predictive of aspects of later development in our closely related evolutionary cousins, the chimpanzees. It has been posited that organization of attachment type behaviors is of great importance for early and long-term development, and that it is this lack of organization that leads to a poorer long-term prognosis for disorganized individuals (L. A. Sroufe, et al., 2005; L. Alan Sroufe, et al., 1990; L. A. Sroufe & Waters, 1977). For chimpanzees identified as disorganized, the findings of this study indicate some long-term differences predicted by their earlier attachment classification which support these assertions. In addition, exploratory analyses did not find strong or significant effects of either secure classification vs. not secure or of classification into secure vs. Ainsworth's two defined insecure categories. Similar results observed in humans have been argued to occur partially because while a secure classification is typically more likely to predict positive adult attachment behaviors, that security can be negatively affected by intervening

events, such as sudden loss of a primary attachment figure (Bowlby, 1980; L. A. Sroufe, et al., 2005; L. Alan Sroufe, et al., 1990; L. A. Sroufe & Waters, 1977). Additionally, it has been argued that even less positive classifications, such as insecure-avoidant, may still indicate an organized set of attachment responses which may allow organized adult attachment and be less predictive of negative outcomes. In fact, it is this argument that led to the development of the disorganization classification, and as was supported by this research, disorganization seems to be more relevant to long-term outcome than insecure but organized classifications (L. A. Sroufe, et al., 2005; M. H. Van IJzendoorn, et al., 2008; M.H. Van IJzendoorn, et al., 1999).

This study reveals some other non-attachment related but important long-term effects of differential rearing on chimpanzees. Abnormal behavior levels provide some information about welfare (Bracke & Hopster, 2006; Broom, 1991), and as this study's findings regarding abnormal behavior are complemented and bolstered by survey findings indicating that nursery-reared animals are perceived as having lower well-being as compared to mother-reared animals, we can feel relatively confident in asserting that abnormal behaviors and well-being, at least as perceived by humans, are negatively correlated in chimpanzees. Indeed, significant negative correlations were found between rates of abnormal behavior and scores on the overall Subjective Well-being factor as well as ¾ items that loaded most heavily onto that factor. Stress-related behavior also correlated significantly and inversely with scores on the SWB factor and on 2/4 of the items that loaded most heavily onto that factor. These findings suggest that survey respondents' perception of a chimpanzee's well-being is linked significantly with behaviors regarded by the scientific community as indicators of poor welfare (Broom,

1991; Dawkins, 2004; Yeates & Main, 2008). While it should be pointed out that the scores for both nursery groups on SWB measures were slightly below average to above average (means ranging between 3 – 5 on a Likert scale for individual SWB items), mother-reared animals scored higher, with means ranging between 4 - 6 consistently. This may seem like a small difference, but the consistency of the trend that indicates that nursery-reared chimpanzees' welfare is negatively impacted by early experiences in nursery environments. That rates of human solicitation and rates of attending to human activity also vary positively and strongly with rates of stress-related behavior imply that increased human orientation is stressful, at least for chimpanzees at this particular institution, and especially for animals that are reared with more extensive human contact (remember that RC chimpanzees scored significantly higher on attention towards humans as compared to ST chimpanzees). Stressful conditions which cannot be dealt with effectively by an organism can become chronic stress and have detrimental effects on an organism's physiological and psychological health (Moberg, 2000; Morgan & Tromborg, 2007). The welfare of chimpanzees in captivity, particular in laboratory environments, is important for several reasons: 1) behavioral and/or biomedical studies which include welfare-impaired animals are not likely to result in sound results as poor welfare often corresponds to impaired immune response, behavioral abnormalities, and/or shortened life span; 2) it is the moral and financial responsibility of those that keep animals in captivity to ensure optimal welfare for those animals as it directly impacts not only the psychological well-being of those animals but also the quality of the research conducted at any facility; and 3) current hot topics in our nation do include controversy over

housing chimpanzees in laboratory facilities or any facilities whose chief objective is to use these animals as subjects for research, biomedical or behavioral.

Recent changes in the requirements for laboratories that house chimpanzees ("Chimpanzees in biomedical and behavioral research: Assessing the necessity," 2011) and the public attention this issue has garnered increase the necessity for not just maximizing the welfare of institutionally housed chimpanzees because it is a moral and scientific imperative, but also because the perception of captive, laboratory housed chimpanzee welfare is of increasing relevance to the continued ability to conduct research with chimpanzees. Leaving the issue of biomedical research aside for the moment, much of the research currently conducted in laboratory facilities is in fact noninvasive and focuses on behavioral and cognitive in nature; Yerkes itself currently conducts primarily behavioral and cognitive research in the chimpanzee colony. Many of these studies actually increase problem-solving opportunities and mental stimulation for the animals, which can improve captive welfare (Carlstead & Sheperdson, 2000; Chamove, 1989; Tarou & Bashaw, 2007; Tarou et al., 2002; Washburn, Rumbaugh, & Richardson, 1992). The goal of some of these studies is in fact to objectively assess animal welfare and methodically assess possible methods for improving welfare (M.A. Bloomsmith, Baker, Ross, & Lambeth, 2006; M. A. Bloomsmith & Lambeth, 1995; Novak & Drewson, 1989). However, many individuals that do not have any or perhaps have only a minimal amount of actual knowledge about the science of animal welfare, the psychological or physical needs of chimpanzees, the practices of specific laboratories, or the benefits of cognitive and/or behavioral science have had and will have strong opinions on the use of chimpanzees in research, be it biomedical or behavioral, and perhaps on the continuation

of housing chimpanzees in captivity for any purpose. For example, a PETA (People for the Ethical Treatment of Animals) website states that 'experimenters at Yerkes subject chimpanzees to neuroimaging, cognitive and motor testing, and invasive endocrine status tests in long-term studies on aging' ("Chimpanzees in laboratories," 2012). This statement implies that cognitive research is by definition harmful (despite a very wide range of solid research indicating that cognitive problem solving is beneficial to the welfare of captive chimpanzees), that motor testing is in all forms harmful (no specifics are noted as to if this is mere observation of motor movement, computerized and simulated motor movement assessments, or otherwise), makes no mention of how or why neuroimaging is harmful to the chimpanzee (for example, as it compares to other aspects of yearly physicals conducted on all chimpanzees to assess their health), and incorrectly qualifies the aging research conducted at Yerkes as invasive (in fact, the aging project is not invasive and consists, for the chimpanzees, primarily of positive reinforcement training to urinate into a urine collection wand. It is clearly highly relevant that human perception of an animal's welfare be positive, and that facilities that house chimpanzees work to improve this perception not only because of the impact of public opinion on legislative law, but also because we do have a moral obligation to enhance captive animal welfare. In this study it was found that as subjective well-being decreased, rates of abnormal behavior increased, for example. Thus it is not just a perception that welfare may be at risk for some of these animals but it is actually a probable reality because elevated abnormal behavior rates and impaired response to stress (e.g., elevated rates of stress-related behavior) are often an indication of poor welfare (Broom, 1991), at least at

some time in the organism's history (G. J. Mason & Latham, 2004; Yeates & Main, 2008).

The findings of this study also indicate that there are perhaps some notable drawbacks to increasing nursery chimpanzees' exposure to and, as a result, attachment to human caregivers. Initially, chimpanzees reared in the responsive care nursery at Yerkes exhibited positive developmental trends as compared to standard care chimpanzees (better motor coordination, longer attention spans, more exploration of novel objects, less object attachment, higher cognitive abilities, and less likelihood of exhibiting disorganized attachment) (K. Bard, 2003; K. A. Bard & Gardner, 1996; M. H. Van IJzendoorn, et al., 2008). This study, however, found no positive differences between the two nursery groups as adults; significantly higher rates of attending to humans, aggressing on humans, and negatively soliciting humans could indicate a negative difference, in fact. This difference could be a result of cross-species attachment. Generally, cross-species attachment is still not the ideal. Mother-reared chimpanzees are seemingly better adjusted, according to this study, and also are not as solicitous of or interested in human attention. Chimpanzees become extremely strong and can be unpredictable and aggressive; they cannot live as humans or in direct contact with humans safely. It is highly preferable that an infant chimpanzee be placed with a conspecific surrogate mother if his or her biological mother cannot raise the infant herself so that the chimpanzee's primary attachment figure will be a chimpanzee, not a human. Though in some environments human interaction is quite frequent (such as it is at the Yerkes Main Center), even that frequent interaction leaves the chimpanzees with only each other for company for the overwhelming majority of their time. Focus on humans

could easily impair a chimpanzee's continued ability to develop affiliative relationships with other chimpanzees – this aspect of what is considered a positive welfare indicator (Yeates & Main, 2008) needs to be assessed carefully. The results of this study accentuate the need for careful and critical planning for any institution that plans to breed chimpanzees; nursery rearing, even when it involves more dedicated and chimpanzee-savvy human caregivers, cannot replicate the benefits of mother rearing, and in fact it seems that some of our current practices (constant contact with a reduced number of human primary caregivers) could in fact be detrimental for the chimpanzee in the long run, though this needs to be more thoroughly investigated before any strong claims can be made.

It seems clear based on previous studies that nursery-reared chimpanzees provided with more extensive contact with primary caregivers do develop more secure, more organized attachment systems during their younger years, albeit with non-conspecifics (K. A. Bard & Leavens, in press; M. H. Van IJzendoorn, et al., 2008). Cross-species attachment has been studied and observed to occur in a number of mammals: simple imprinting, for example, has been observed to occur across species in geese and can affect sexual preference (Irwin & Price, 1999); lambs that were confined with canine companions exhibited strong attachment behaviors toward those canine companions (Cairns, 1966; Cairns & Johnson, 1965); rhesus monkeys paired with female baboons during infancy exhibited social attachment toward their non-rhesus partners after 6 months of cohabitation (Maple & Westlund, 1977). The effects of separation from a non-conspecific but primary attachment figure have been observed to be similar for many mammal species: rhesus macaques separated from inanimate surrogate mothers (Harlow,

1971); lambs separated from surrogate parent canines (Cairns, 1966; Cairns & Johnson, 1965); dogs separated from their human caregivers (Topal, Miklosi, Csanyi, & Doka, 1998); and, more pointedly, for many of the nursery-reared chimpanzees assessed during this study when separated from humans that served as their primary caregivers (K. A. Bard & Gardner, 1996; K. A. Bard, et al., 1993; M. H. Van IJzendoorn, et al., 2008). Thus we can parsimoniously assert that attachment to a non-conspecific is possible and can give rise to similar behaviors as attachment to a conspecific, including distress upon separation. Distress upon separation has been observed to occur for nonhuman primate species, and similar to other aspects of attachment observed in humans, the nonhuman primate response to separation is highly similar to the human response to separation from a primary attachment figure (W. A. Mason & Mendoza, 1998). Learning theorists have proposed models for assessing and predicting the degree to which a particular animate or inanimate surrogate might serve as a primary attachment figure for a mammal; highly relevant to this equation is the similarity of the surrogate to the 'natural' target for attachment – the conspecific parent, usually the mother, that is the primary caregiver to the infant (Cairns, 1966).

A human surrogate, for a chimpanzee, especially a human surrogate trained to exhibit chimpanzee-like behaviors (K. A. Bard, 1996), could hardly be a better target for primary attachment. And, in fact, attachment to human primary caregivers has been observed to occur in chimpanzees (M. H. Van IJzendoorn, et al., 2008). We can only assume that separation from this primary caregiver would elicit distress. Previous studies have found that chimpanzees allowed to stay with their mothers for at least 3 years express significantly less despair, protest, and depression as compared to those that were

separated earlier (Howell, et al., 2006); separation at 1 year from a primary attachment figure can be assumed to be similarly more disruptive than separation at 3 years of age, even if we ignore the variable of cross-species attachment. Chimpanzees reared in the responsive care nursery, though in more extensive contact with humans than chimpanzees in the standard care nursery did in fact live in the standard care nursery for all but five 4 hour periods each week. The sum of human interaction for standard care chimpanzees each day during that first year of life was 60 minutes; the sum for the responsive care individuals was, on five days a week, 300 minutes. Mother-reared chimpanzees were with their mothers, of course, 24 hours per day – a sum of 1440 minutes every day. All nursery-reared chimpanzees were housed more and more exclusively with peers and less and less exposed to humans as they aged, particularly once they reached one year of age. Chimpanzees reared by their mothers typically remain in bodily contact at all times with their mother for up to 12 months; weaning usually does not occur until around 4 or 5 years of age, and young chimpanzees will remain in close, affiliative contact with their mothers for several years afterward and, in some cases, up to ten years later (Pusey, 1983). The availability of the primary attachment figure for an infant chimpanzee reared by his or her mother is thus dramatically contrasted to the availability of the primary attachment figures to nursery-reared chimpanzees, even those raised in responsive care. It is not surprising, then, that nursery-reared chimpanzees in this study exhibited significantly higher rates of abnormal behavior along with significantly lower rates of subjective well-being as scored by human interactants when compared to mother-reared chimpanzees.

Abnormal behavior, in specific, is very resistant to change once it has been established. Much of the reinforcement for this behavior is internal and related to neurochemical reinforcers and reinforcement circuitry in the brain, such as the release of endorphins following a self-biting episode (T. Thompson, Symons, Delaney, & England, 1995). Attachment disruption, also, has effects on neurochemicals and brain circuitry, and these effects can be long-term (Kalin & Carnes, 1984; Kraemer, 1992, 1997; M. L. Laudenslager, et al., 1985; Leckman, et al., 2005). It could be that simply breaking the attachment bond that nursery-reared chimpanzees had to their human primary caregiver could have resulted in alteration of these individuals' physiology in a way that led to more abnormal behavior or other of the observed effects found in this study. This is not a stretch of the imagination, either; consider previous research in which one separation of 10 – 14 days during the first year of life was associated with lowered immune function in adult pigtail macaques (M. L. Laudenslager, et al., 1985).

It has been asserted by at least one researcher that chimpanzees reared extensively by humans have demonstrated a pronounced inability to repair psychologically following traumatic experience; this inability was attributed to the incompatibility of the chimpanzees' primary enculturation experience (human-based) with their eventual cultural surroundings (chimpanzee-based) (Bradshaw, Lindner, Capaldo, & Grow, 2009). This particular study cannot be considered of itself as informative, as these conclusions were based on a case study of one chimpanzee. However, some of the ideas posited by the researchers may be worth evaluating further. A number of different researchers refer to chimpanzees partially reared by humans and with rather extensive human experience as bicultural or enculturated (Bjorklund, Yunger, Bering, & Ragan, 2002; Povinelli,

Eddy, Hobson, & Tomasello, 1996; Tennie, Call, & Tomasello, 2006). Enculturation for chimpanzees and bonobos is usually correlated with better performance on cognitive tasks (Bjorklund, et al., 2002; Call & Tomasello, 1996), better understanding and use of human-based cues such as gaze orientation or pointing (Lyn, Russell, & Hopkins, 2010), and increased ability to comprehend and produce language (Savage-Rumbaugh, 1986). The vast body of research that supports the idea that enculturated apes perform better on these types of tasks indicates that perhaps enculturation with human caregivers does enhance apes' ability to perform on certain tasks, though there are those that argue this is too simplistic an explanation (Tomasello & Call, 2004). However, the effect of enculturation on the welfare of these animals is undetermined. Enculturation assumes much more extensive experience with human culture, behavior, and communication than either standard care or responsive care nurseries would have provided to chimpanzees at Yerkes, though the responsive care nursery, simply through increased exposure to humans, would have somewhat more closely approximated enculturation experiences in which apes are raised at least partially by humans and have near-continuous to continuous exposure to humans and human environments for some period of time (Savage-Rumbaugh, 1986; Savage-Rumbaugh & Lewin, 1994).

Nursery-reared chimpanzees at Yerkes were found to exhibit, as compared to mother-reared chimpanzees, higher rates of abnormal behavior, higher rates of human solicitation and attendance to human activity and lower rates of subjective well-being as scored by people that work with the chimpanzees regularly. In fact, in some cases, responsive care chimpanzees differed not only from the mother-reared chimpanzees but also, sometimes significantly, from standard care chimpanzees, indicating that it is possible that as

exposure to humans during early development increases, so does the risk of undesirable outcomes. For example, significant differences between the standard and responsive care nurseries at Yerkes include, for the responsive care chimpanzees, increased fearfulness, increased dependency on others, decreased equability, decreased calm, and increased emotionality as rated by human interactants. These and other possible results of cross-fostering infant apes onto human caregivers, encouraging ape-human cross-species orientation and attachment, and in some cases biculturally-rearing apes have not been investigated thoroughly.

There are three explanations for the findings of the current study: 1) the cross species attachment and orientation formed during early life has impacted the psychological development of these chimpanzees in a way that is not fully reversible once chimpanzees are confined, in their social groups, to life with conspecifics; this might lead to poor welfare for human oriented, human attached chimpanzees when they are old enough and strong enough that they need to live with other chimpanzees full time and do not have regularly available human interaction partners; 2) attachment bonds formed during early years to non-conspecifics were indeed very strong and as such, separation from these primary caregivers when it came was traumatic in a way that impacted development; in this case, human orientation might not be directly related to welfare but is just a symptom, much like elevated rates of abnormal behavior and lowered scores of subjective well-being, of poor adjustment after separation from an attachment figure; 3) it could be that intervening events between one year of age and the current age of the subjects have created these group-wise differences. Of course, it is not a given that separation was traumatic for the nursery-reared chimpanzees, and we cannot retroactively

test this possibility. It is unlikely that observed differences in these groups result from intervening events which continued to effect mothers of the individual nursery groups distinctively. For example, responsive care, mother-reared and standard care chimpanzees live in single social groups and have all lived in a variety of social groups over the course of their lives; they have not, in any group-wise differentiated fashion, differently experienced research protocols or social group differences or environmental differences. There has been extensive variation individually for these chimpanzees in terms of their experiences over the past 20 years; that we have found distinct differences between the groups as they were differentiated in the early 1990s indicates that there is a robust effect of nursery versus mother-rearing for chimpanzees raised at Yerkes over the past 20 years; additionally, the current study points to some interesting and significant differences between the two nursery groups. Finally, there is clearly an effect associated with attachment ratings for chimpanzees as assessed over 20 years ago.

Granted, there are some issues with the current study that need to be discussed. For one, the health data gathered for this study was not extensive or reliable in a fashion that makes these results conclusive. More studies should be done to discover the physiological health of the chimpanzees' stress responses, their immune systems, and to compare brain structure sizes as have been noted to differ in humans based on early rearing stress experiences. The behavioral data would be greatly complemented by information about the chimpanzees' social behavior with conspecifics. Though this data was recorded, the data turned out to be irretrievable due to a technological malfunction and as of yet has not been recovered. Having more data that allows analysis of the positive indicators of welfare might give us a more balanced view of the overall welfare

of these chimpanzees (Yeates & Main, 2008). Finally, the survey data was analyzed in a way that though it provides greater control and greater power in comparing the groups making up the study's sample does not allow for generalization. That is, should we extend the survey to include chimpanzees from other facilities or try to compare our results to previous personality survey results (A. Weiss, et al., 2009), it would be advisable to use the same factor structure as has been found for other chimpanzee studies to cover the personality survey and, separately, the subjective well-being part of the survey; the human interaction portion of the survey, developed for this project, would be assessed separately as well. Because for this particular study we sought to see how all portions of the survey correlated and to develop a factor model that explained our specific results regarding these specific chimpanzees, it was more appropriate to derive our own factor structure based on analysis of this body of data. Using weighed scores, in addition, allows us to analyze the relative contributions that some survey answers make to more than one identified factor. This degree of specification allowed for better and truer comparisons within the study group for this research, but it would be advisable to look at the results differently if comparing to chimpanzees outside this sample. For this study it was often desirable to look at individual questions and responses using original scores – this is one aspect of our results that would be immediately comparable to other personality inventories.

Future Directions and Recommendations

Future Research

Future research in this area should, for one, seek to determine exactly what factors might lead to the kind of results observed in this study. Possible differences that might

lead to long-term behavioral changes for the responsive care chimpanzees, for example, could include the time moving out of and then back into the standard nursery population, the break from a human primary attachment figure, something about the specific social dynamics in the chimpanzee group during that time, or effects of forming that attachment and then only having the attachment figure available part of the time during that first year. However, perhaps the emphasis should be on how to proceed, given the findings of this research, with a goal towards improving the welfare of captive housed chimpanzees and thus also benefiting researchers, laboratory facilities, and also the validity of research conducted on these chimpanzees. At the very least, the fact that no significant advantages were found for responsive care versus standard care chimpanzees indicates a need to evaluate the time and money required to create a more intensive nursery environment and determine what might make that investment more likely to pay off in terms of long-term development. It is clear that the responsive care animals benefited during their time in the nursery; however, this benefit has not been assessed since the animals were one year of age and returned to standard nursery conditions. Some differences seen in the two nursery groups during that first year seem to be still visible today – for example, the RC chimps were more likely to express anger during that first year and now are more likely to express aggression towards humans, significantly in the form of negative solicitation. However, during the first year, RC chimps were less likely to be fearful and in fact decreased in fearfulness between 3 and 12 months (K. A. Bard & Leavens, in press). Standard care chimpanzees did not show this same result and were more fearful than RC chimpanzees during that first year. Currently, RC chimps are

perceived as significantly more fearful than ST chimpanzees – this reversal in results warrants some attention.

Critical to the goal of improved welfare for captive chimpanzees is continued research into the best environments for rearing and housing chimpanzees throughout their lives. Part of reaching that goal will require people that work with adult chimpanzees to determine for each individual chimpanzee what 'better welfare' might mean. For some chimpanzees, increased human interaction might not be relevant to their welfare; for others it might be extremely beneficial. Following the current study, it seems that conducting some applied research to determine the behavioral effects of altered amounts of human interaction could be of value. For nursery-reared chimpanzees in particular, human orientation may be fixed to some degree and might require that those chimpanzees receive more human attention to maximize their well-being. Other options for increasing well-being might include using positive reinforcement training to enhance social relationships with conspecifics. Increasing welfare for captive chimpanzees, particularly those housed in laboratory settings, has always been of high importance for the chimpanzees; currently, it is of exponentially increasing importance to stakeholders in laboratory-based chimpanzee research. This should provide plenty of impetus to apply the findings of this project to future research.

Recommendations

For Breeding Facilities

Those facilities that still breed or may breed chimpanzees in the future will need to be cautious about human intervention. Diarrhea and other illnesses seem to be more likely for animals in nurseries, which is one reason to work to avoid nursery rearing young

apes. If it is unavoidable to raise an animal in a nursery, attempts should be made to find a surrogate conspecific to raise that infant as soon as possible. Reintroduction and successful surrogating has been possible for apes as young as 11 weeks (Hoff, Tarou, Horton, Mayo, & Maple, 2005) and for chimpanzees as young as 9 months (Bashaw, et al., 2010). This can sometimes require cooperation between facilities to match an infant with a surrogate and often requires some preparatory training both for the potential surrogate and for the infant. However, it is likely that these efforts are worth it in terms of the animal's eventual welfare. For chimpanzees, surrogate attempts have often failed (anecdotal information). It has been considered that perhaps due to the more aggressive nature of chimpanzees, on the whole, as compared to other apes, the protection provided by a surrogate mother (rarely as intense as that provided by a biological mother) is not adequate to protect the introduced infant. However, there are other options for improving conspecific attachment, such as early introduction to a group where peer age infants may reside with an older animal identified as a good 'auntie' type figure. These types of groupings seem to have been successful in many sanctuary settings, for example. Creating smaller social groups with reintroduced infants, surrogate mothers, and non-aggressive individual chimpanzees has also been successful as a midway resocialization until adult males, for example, were added back to the group (Bashaw, et al., 2010). A better program of identifying chimpanzee mothers at risk of being inadequate mothers and doing preparatory training with those females to enhance the likelihood that they might successfully rear their own infants should be developed and applied in any institution where breeding takes place; additionally, alternative options (possible

surrogates or aunty conspecifics, for example) should be developed and planned for in case an infant is rejected and requires human intervention.

When human caregiving is unavoidable, care should be taken to stimulate and socialize the chimpanzees with as little human intervention as possible. For example, using dogs to provide a mobile, animate being for an infant to cling to may be advantageous over having humans provide this service. Keeping the infants in areas where they have constant visual and auditory access to other chimpanzees should be a high priority. It might be better to rotate human caregivers often enough that there is no primary bonding to one human as an attachment figure. It also might be that chimpanzees are better off if they have less time overall with humans present and more time to bond only with other chimpanzees, even if they are peer aged (which is still less desirable than having an aunty or surrogate mother). Though many institutions have increased the amount of interaction young apes have with humans in an attempt to better care for them, this may not have the desired result. Studies have found, for example, that isolation-reared chimpanzees improved their ability to successfully copulate when placed with an experienced partner; this same improvement did not occur for human-reared chimpanzees (Turner, et al., 1969). Another study found that zoo-born, zoo-living chimpanzees that had been human-reared were the least likely to be sexually competent adults as compared to peer-reared chimpanzees, chimpanzees reared with peers and at least one adult conspecific, and mother-reared chimpanzees (King & Mellen, 1994). These studies suggest that human orientation as it develops amongst human-reared, human-bonded chimpanzees can be detrimental to normal adult social behavior for

chimpanzees. Finding a way to successfully rear chimpanzees without increasing human orientation may be critical to any facility that still breeds chimpanzees.

For Nursery-reared or Enculturated Apes currently living in Captivity

The results of this study should generate further research to assess the welfare of chimpanzees and other apes in captivity with a particular focus on those that have spent extensive time with humans. Studies should focus on both physiological and behavioral assessments and should attempt to determine the impact of human orientation on abnormal behavior, well-being, and sociality with conspecifics. In addition to making these assessments, applied research should investigate various methods of treatment for increasing the welfare of those apes that are observed to exhibit lower welfare and for whom human orientation may be a factor. Treatments that might be tested included increased human interaction time, increased positive reinforcement training in conjunction with conspecifics with a goal toward increasing conspecific-directed affiliative behavior, attempting different conspecific social partners, investigating the effects of different kinds of housing, social groupings, and habitat enrichment, and perhaps assessing the effects of creating predictable and extended time periods for human interaction. There are a number of ways in which we might impact the welfare of these animals and it is likely that different individuals will benefit from different treatments.

A probable first step is to assess human orientation, well-being, and abnormal behavior in different environments – other laboratory facilities, zoological institutions, sanctuaries, or any other facilities that house chimpanzees. Conducting a rather broad study to assess these factors would likely also suggest some possible methods for improving welfare and could guide research into those treatments. Chimpanzees in the

United States are still used in entertainment, are sometimes still held in private homes and pets, and are still bred in some facilities for the express purpose of conducting research. In addition, hundreds of chimpanzees that are currently adult-aged are housed in captive settings where their welfare is dependent on human care. While the public eye is directed towards biomedical laboratories, this is likely just the beginning of the scrutiny under which all labs, biomedical or behavioral, will now exist. If our own moral imperative to take as good care as possible of our evolutionary cousins is not enough, then public opinion might tip the balance.

APPENDIX A

ETHOGRAM

Developed from ethograms used by Cleveland Metroparks Zoo (Bettinger) and Lincoln Park Zoo (S. Ross & Lukas; S. K. Ross & Lukas, 2001).

Instructions: Record priority behavior in each category if it occurs during interval being scored (for each animal in observation group). Behaviors in each category are listed in order of priority (1-0 sampling, intervals are 60 seconds for all behaviors and environmental events; scan sampling every 60 seconds for proximity measures).

Social Behaviors (with modifiers)

Modifiers: record initiator of action and recipient of action (includes chimpanzee and human subjects).

Agonistic-aggressive behaviors:

1. Aggressive contact: one individual hits, kicks, bites, threatens another group member.
2. Aggressive Chase: one individual runs after another group member aggressively.
3. Displace: one individual moves away from another individual to allow them to take over their former location (animal that takes over the spot is the actor).
4. Other aggressive non-contact: aggressive behavior without contact not otherwise defined such as threat, lunge, or bark.

Agonistic-submissive behaviors

1. Avoid/flee: one animal walks speedily or runs from another individual.
2. Submissive present: female presents to another individual in submissive context.
3. Pant grunt: series of short guttural grunts given by subordinate animal to a higher ranking animal.
4. Other submissive: includes head bobbing, crouching, screaming, fear grimacing, any submissive behavior not otherwise defined.

Neutral behavior:

1. Approach: one animal deliberately walks or runs toward another group member.
2. Follow: one animal is deliberately walking behind another.
3. Pant hoot: vocalization.
4. Display: display behavior in context of aggression or non-directed.
5. Look out bars: animal is actively watching another individual through the bars for 5 or more seconds.

Affiliative behavior:

1. Solicit attention: attention getting behavior (gesture, vocalizations, eye contact, and etcetera) exhibited towards another individual (positive = gesture, vocalizations, eye contact; negative = spitting, throwing feces, aggression).
2. Touch/embrace: one individual extends hands or arms and gently makes contact with another individual.
3. Groom: picking through hair or at skin, removing debris with hand or mouth.
4. Play with partner: wrestling, tickling, chasing, and etcetera; may be accompanied by play face and laughing.
5. Play Chase: one individual runs after another group member playfully.

6. Watch/stare: one individual actively watching another group member, often within a few inches of one another.
7. Other affiliative: non-agonistic social behavior not defined elsewhere.

Sexual behavior:

1. Copulation: male mounts and thrusts a female.
2. Genital rub: female rubs her genitalia against another female's genitalia.
3. Inspect: an animal sniffs or probes the genitalia of another individual.
4. Masturbate: self-stimulation of the genitalia; should include modifier if individual is watching another individual while masturbating.
5. Mount: one individual mounts another but thrusting does not occur.
6. Present, sexual: female may crouch with genitalia directed to male or merely approach and orient genitalia in the male's line of vision.
7. Solicit sex: animal approaches another and solicits sexual behavior by presenting, head bobbing, swaying, penile display.

Abnormal behaviors:

1. Idiosyncratic movement or posture: sustained movement of body, such as rocking or head bobbing, with a definitive repetitive pattern.
2. Idiosyncratic body manipulation: repeated or sustained manipulation of a specific area of own body, such as eye-poking, self-patting or ear-covering.
3. Aberrant fecal: eating, manipulating or examining feces.

4. Regurgitation/reingestion: deliberate regurgitation accomplished by various methods including lowering head to the ground, bobbing head, or more subtle techniques. Vomitus may be retained in mouth or expelled into hand or substrate before being reingested.
5. Hair Pluck (actor, recipient modifier) pulling out own or another animal's hair; may be ingested.
6. Other abnormal: abnormal behaviors not categorized above such as urophagy or pacing.

Stress-related behaviors:

7. Scratch: raking of fingernails over skin; may be smaller movements of the hand or larger sweeping scratching involving arm movement.
8. Yawn: involuntary wide opening of mouth accompanied by deep inhalation.

Environmental Events:

1. Human approach: human approaches within 5 feet of enclosure or remains within 5 feet of enclosure.
2. Display in area: loud displaying by chimpanzees on the wing.
3. Vocal chimps: loud vocalizations (but no displaying) from chimpanzees on the wing.
4. Loud noise: loud noise in the area.
5. Cart: cart or other vehicle approaches within 20 feet in front of the cage.

Location (record nearest proximity of conspecific to each subject chimpanzee):

1. In contact.
2. Near: within 10 feet.
3. Far: 11 – 20 feet.
4. Distant: beyond 20 feet.
5. Out of view: Chimp is out of view, proximity unknown.

APPENDIX B

SURVEY QUESTIONNAIRE

A. Section 1: Demographic Information

1. Please enter your name here:
2. Name of chimpanzee you are rating:
3. Location where you work with the chimpanzee:
4. How long have you worked with this chimpanzee?
    - 0 – 1 year
    - 2 – 5 years
    - 6 – 10 years
    - More than 10 years
5. How many hours per week, on average, do you spend working around this chimpanzee? This includes working around the animal if you are cleaning, or otherwise working in the proximate area of the animal. This does not include DIRECT INTERACTION with the animal (this will be asked about later)
    - 0 – 1 hour
    - Between 1 and 5 hours
    - More than 5 hours
6. How much time per week, on average, do you spend interacting directly with the animals? This includes feeding, giving enrichment, doing veterinary procedures (while animal is awake), conducting research with the animal, training the animal using positive reinforcement, etcetera.

- 0 – 1 hour
- Between 1 and 5 hours
- More than 5 hours

7. In what capacity do you work with the chimpanzee? Mark as many as apply.
    - Veterinarian
    - Biomedical researcher
    - Cognitive or behavioral researcher
    - Caretaker
    - Behavioral management (training, enrichment)
    - Other (please specify):
8. If this animal receives positive reinforcement training, please indicate the average amount of time per week the animal is trained (it does not require that you be the trainer).
    - Does not receive training
    - Less than 30 minutes
    - Between 30 minutes and 1 hour
    - Between 1 and 2 hours
    - Between 2 and 5 hours
    - More than 5 hours
9. If this animal receives positive reinforcement training, how long has the animal been getting training?
    - Does not receive training
    - Less than three months

- Between 3 and 6 months
- Between 6 and 12 months
- More than one year

B. Section II: Subjective Well-being (adopted from (A. Weiss, et al., 2009)) Instructions: This part of the questionnaire has four questions, all relating to the subjective well-being of the chimpanzee you are rating. Each asks about a different personality dimension or trait relating to subjective well-being. The following scale should be used to make your ratings. Please do not discuss your rating of any particular chimpanzee with anyone else! This is necessary to obtain valid reliability coefficients for the traits. Please give a rating for each item even if your judgment seems to be based on purely subjective impression of the chimpanzee and you are somewhat unsure about it.

Displays either total absence or negligible amounts of the trait or state (least)	Displays small amounts of the trait on infrequent occasions	Displays somewhat less than average amounts of the trait	Displays about average amounts of the trait	Displays greater than average amounts of the trait	Displays considerable amounts of the trait on frequent occasions	Displays extremely large amounts of the trait (most)

1. Estimate the amount of time the chimpanzee is happy, contented, enjoying itself, or otherwise in a positive mood. Assume that at other times the chimpanzee is unhappy, bored, frightened, or otherwise in a negative mood.
2. Estimate the extent to which social interactions with other chimpanzees are satisfying, enjoyable experiences as opposed to being as source of fright, distress, frustration, or some other negative experience. It is not the number of social interaction that should be estimated, but the extent to which social interactions that do occur are a positive experience for the chimpanzee. Use as many social interactions as you can recall as a basis for your judgment.
3. Estimate, for this chimpanzee, the extent to which it is effective or successful in achieving its goals or wishes. Examples of goals would be achieving desired locations, devices, or materials in the enclosure. Keep in mind that each chimpanzee will presumably have its own set of goals that may be different from other chimpanzees.
4. Imagine how happy you would be if you were that chimpanzee for a week. You would be exactly like that chimpanzee. You would behave the same way as that chimpanzee, and would feel things the same way as that chimpanzee.

C. Section III: Personality Trait Assessment (adopted from combination of (A. Weiss, et al., 2009; A. Weiss, J. E. King, & W. E. Hopkins, 2007b)). Instructions: Chimpanzee personality assessments can be made with this questionnaire by assigning a numerical score for all of the personality traits listed below. Make your judgments on the basis of your own understanding of the trait guided by the short, clarifying definition following the trait. Each chimpanzee's own behaviors and interactions with other

chimpanzees should be the basis for your numerical ratings. Use your own subjective judgment of typical chimpanzee behavior to decide if the chimpanzee you are scoring is above, below, or average for a trait. Please give a rating for each trait even if you are unsure if your judgment seems to be based on a purely subjective impression of the chimpanzee and you are somewhat unsure about it. Please do not discuss your rating of any particular chimpanzee with anyone else. This is to make sure we obtain valid reliability coefficients for the traits.

Displays either total absence or negligible amounts of the trait or state (least)	Displays small amounts of the trait on infrequent occasions	Displays somewhat less than average amounts of the trait	Displays about average amounts of the trait	Displays greater than average amounts of the trait	Displays considerable amounts of the trait on frequent occasions	Displays extremely large amounts of the trait (most)

1. Active: spends little time idle and seems motivated to spend considerable time either moving around or engaging in some overt, energetic behavior.
2. Affectionate/Friendly: seems to have a warm attachment or closeness with other chimpanzees. This may entail frequent grooming, touching, embracing, or lying next to others.
3. Affiliative/Agreeable/Sociable: Appears to like the company of others. Seeks out social contact with, or showing preference for, another animal; for example, playing, walking next to, or sitting with another animal.

4. Aggressive: Often initiates fights or other menacing and agonistic encounters with other chimpanzees.
5. Anxious: Hesitant, indecisive, tentative, jittery.
6. Autistic: does not make eye contact, and/or not well integrated into the social group.
7. Bold: Daring, not restrained or tentative. Not timid, shy, or coy.
8. Bullying: Overbearing and intimidating towards younger or lower ranking chimpanzees.
9. Calm: Equable, restful; reacts to others in an even, calm way; is not easily disturbed or agitated.
10. Cautious: Exhibits a careful, measured approach to investigating things.
11. Clumsy: Subject is relatively awkward or uncoordinated during movements including but not limited to acrobatics, walking, and play.
12. Considerate/Kind: Often consoles others in distress to provide reassurance.
13. Cool: Subject seems unaffected by emotions and is usually undisturbed, assured, and calm.
14. Decisive: Subject is deliberate, determined, and purposeful in its activities.
15. Deceptive: Deceives others for own benefit.
16. Defiant: Assertive or contentious in a way inconsistent with the usual dominance order. Maintains these actions despite unfavorable consequences or threats from others.
17. Dependent: Often relies on other chimpanzees for leadership, reassurance, touching, embracing, and other forms of social support.

18. Depressed: Often appears isolated, withdrawn, sullen, brooding and has reduced activity.
19. Disorganized: Subject is scatterbrained, sloppy or haphazard in its behavior as if not following a consistent goal.
20. Dominant: Able to displace, threaten, or take food from other chimpanzees. Or subject may express high status by decisively intervening in social interactions.
21. Distractible: Subject is easily distracted and has a short attention span.
22. Eccentric: Shows stereotypies or unusual mannerisms.
23. Erratic: Subject is inconsistent, indefinite, and widely varying in its behavior and/or moods.
24. Excitable: Easily aroused to an emotional state.
25. Fearful: Subject reacts excessively to real or imagined threats by displaying behaviors such as screaming, grimacing, running away, or other signs of anxiety and distress.
26. Gentle: Subject responds to others in an easy-going, kind, and considerate manner. Subject is not rough or threatening.
27. Helpful: Subject is willing to assist, accommodate, or cooperate with other chimpanzees.
28. Human Oriented: Very interested in human activities around their enclosure. Solicits support from humans.
29. Imitative: Subject often mimics, or copies behaviors that it has observed in other chimpanzees.

30. Impulsive: Often displays some spontaneous or sudden behavior that could not have been anticipated.
31. Independent: Subject is individualistic and determines its own course of action without control or interference from other chimpanzees.
32. Inquisitive/Curious: Readily explores new situations, objects or animals.
33. Intelligent: Quick and accurate in judging and comprehending both social and nonsocial situations.
34. Inventive: More likely than others to engage in novel behaviors, e.g. use new devices or materials in their enclosure.
35. Irritable: Often seems in a bad mood or is impatient and easily provoked to anger, exasperation, and consequent agonistic behavior.
36. Jealous/Attention-seeking: Often troubled by others who are in a desirable or advantageous situation such as having food, a choice location or having access to social groups. May attempt to disrupt activities or make noise to get attention.
37. Lazy: Subject is relatively inactive, indolent, or slow moving and avoids energetic activities.
38. Manipulative: Is able to get others to do things without using force.
39. Methodical: Does things in a logical, organized manner following a consistent goal.
40. Mischevious: Engages in activities or behavior with the goal of provoking a negative reaction from someone or doing something that has previously been established as not socially acceptable.

41. Persistent: Tends to continue in a course of action, task, or strategy for a long time or continues despite external interference.
42. Playful: Is eager to engage in lively, vigorous, sportive or acrobatic behaviors with or without other chimpanzees.
43. Predictable: Behavior is consistent and steady over extended periods of time. Does little that is unexpected or deviates from its usual behavioral routine.
44. Protective: Shows concern for other chimpanzees and often intervenes to prevent harm or annoyance from coming to them.
45. Quitting: Subject readily stops or gives up activities that have recently been started.
46. Reckless: Subject is rash or unconcerned about the consequences of its behaviors.
47. Relaxed: Does not show restraint in postures and movements. Is not tense.
48. Self-Caring: Shows high, but healthy level of self-grooming and cleanliness.
49. Sexual: Engages in frequent copulations and/or masturbation.
50. Socially-inept: Acts inappropriately in a social setting.
51. Solitary: Prefers to spend considerable time alone not seeking or avoiding contact with other chimpanzees.
52. Stingy: Is excessively desirous or covetous of food, favored locations, or other resources in the enclosure. Is unwilling to share these resources with others.
53. Submissive: Subject often gives in or yields to another chimpanzee. Subject acts as if it is subordinate or of lower rank than other chimpanzees.

54. Sympathetic: Subject seems to be considerate and kind towards others as if sharing their feelings or trying to provide reassurance.
55. Temperamental/Moody: Inconsistent and wildly varying in moods and behaviors.
56. Timid: Lacks confidence and is easily alarmed and is hesitant to venture into new social or nonsocial situations.
57. Unemotional: Subject is relatively placid and unlikely to become aroused, upset, happy, or sad.
58. Unperceptive: Subject is slow to respond to or understand moods, dispositions, or behaviors of others.
59. Vulnerable: Subject is prone to be physically or emotionally hurt as a result of dominance displays, highly assertive behavior, aggression, or attack by another chimpanzee.

D. Section IV: Orientation towards Humans: Please answer the following questions using the rating scale and the descriptions for each behavior as given alongside the scale. Use your own subjective assessment of this particular chimpanzee as compared to chimpanzee behavior in general. Please do not discuss your ratings with anyone else.

Displays either total absence or negligible amounts of the trait or state (least)	Displays small amounts of the trait on infrequent occasions	Displays somewhat less than average amounts of the trait	Displays about average amounts of the trait	Displays greater than average amounts of the trait	Displays considerable amounts of the trait on frequent occasions	Displays extremely large amounts of the trait (most)

1. Positive human orientation: With familiar humans, the chimpanzee is generally positive (interested, friendly) in his/her orientation.
2. Moodiness: When interacting with familiar humans, the chimpanzee is prone to quick changes in attitude.
3. Solicitous: The chimpanzee often solicits support from familiar humans during times of low or high stress.
4. Positive attention-seeking: The chimpanzee often seeks attention from familiar humans in neutral (e.g., blowing raspberries) or positive (e.g., inviting to play) ways.
5. Negative attention-seeking: The chimpanzee often seeks attention from familiar humans by engaging in negative behaviors such as throwing feces, displaying aggressively, or spitting. The goal of seeking attention may not be clear.
6. Aggression: The chimpanzee is prone to behaving aggressively towards familiar humans.

7. Interest in humans: The chimpanzee is extremely interested in human activities around his or her enclosure.
8. Negative orientation: With familiar humans, the chimpanzee is generally negative (aggressive, threatening) in his/her orientation.
9. Tractable: The chimpanzee is generally cooperative with human requests to shift, allow another chimpanzee to approach, or other human requests.

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VITA

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Andrea Clay worked at the Georgia State University Language Research Center with chimpanzees and bonobos from 1992 – 1994 while completing her first B.S. in Biology. She was a zookeeper working with gorillas and orangutans for eight years before returning to school to earn her second B.S., this time in Psychology. She completed her Masters in Psychology at the Georgia Institute of Psychology in 2007 while working at the Yerkes National Primate Research Center. After serving as a graduate student teacher at Georgia Tech and a primary teacher for middle school science classes for several years, she returned to Yerkes and completed her PhD in Experimental Psychology in 2012. She started working full-time as a Behavioral Management Lead Technician focused on the chimpanzees at Yerkes in 2011. In her free time, she volunteers for a wildlife rehabilitation center, hikes wherever she can, and dabbles in photography, writing, and drawing.