Long-term Effects of Infant Attachment Organization on Adult Behavior and Health in Nursery-reared, Captive Chimpanzees (*Pan troglodytes*)

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Abstract

This research traces the long-term effects on health, well-being, personality, and behavior of adult chimpanzees as a function of their attachment to a primary human caregiver assessed when they were 1 year of age (van IJzendoorn, Bard, Bakermans-Kranenburg & Ivan, 2009). Of the 46 chimpanzees assessed at 1 year of age, we assessed health in 43 individuals, adult behavior in 20 individuals, and adult well-being and personality in 21 individuals. Attachment disorganization was found to be a significant predictor of stereotypic rocking in adult chimpanzees ($F(1,18) = 7.50$, $p = .013$). For those subjects (N = 24) with a full 20 years (birth through age 20) of health data available, both rearing experience and disorganized attachment were found to be significant predictors of upper respiratory infection frequency ($F(2,21) = 8.86$, $p = .002$). Chimpanzees with disorganized attachment exhibited average subjective well-being as adults, whereas chimpanzees with organized strategies exhibited higher than average subjective well-being as adults. These results support the findings of human attachment research and are in line with attachment-based predictions for chimpanzees, such that the consequences of an early history of disorganized attachment may be adverse and long lasting.

Keywords: Attachment theory, comparative development, disorganized attachment, abnormal behavior.

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Attachment theory was described first by Bowlby (1969, 1973, 1979, 1980), made testable by Ainsworth (Ainsworth, Blehar, Waters & Wall, 1978), and has since been studied extensively. Studies on various primates served both to validate attachment as an analogous construct in nonhuman primates and to clarify the effects of disrupted attachment bonds on physiological and behavioral systems (Laudenslager & Boccia, 1996). In humans, the quality of attachment to a primary caregiver, as assessed in the Strange Situation Procedure (SSP: Ainsworth, 1985a, 1985b, 1989), has been shown to have long-term consequences. Likewise, one-year-old, nursery-reared chimpanzees tested with the SSP were found to exhibit disorganization in their attachment system in proportions similar to those of human infants raised in poor quality orphanages (van IJzendoorn et al., 2009). Disorganized classification is distinct from Ainsworth's original three types of organized behavioral responses of secure, insecure-avoidant, and insecure-resistant (Ainsworth et al., 1978; Ainsworth, 1985a, 1985b, 1989), and is exemplified by infants either exhibiting inconsistency or lacking a coordinated strategy for seeking comfort after being distressed (Main & Solomon, 1986; van IJzendoorn et al., 2009). Here we investigate the extent to which there are long-term consequences of early attachment classifications in chimpanzees. If the attachment system functions similarly in chimpanzees and in humans, we would expect to find poorer long-term outcomes in those chimpanzees with disorganized classifications than in those with any of the organized attachment classifications.

Attachment classifications of secure, insecure-avoidant, and insecure-resistant, represent the three types of organized behavioral responses in the SSP. Historically, all infant attachment

classifications were forced into one of these three categories, despite the poor fit for some subjects who lacked organized responses, especially prevalent in abused or neglected infants (e.g. Carlson, Cicchetti, Barnett & Braunwalk, 1989). Main and Solomon (1986) first presented the case that some infants exhibited a distinct set of behavioral responses to separation and reunions, which they described as 'disorganized or disoriented'. Long-term effects of disrupted attachment have been found for human infants raised in poor quality orphanages (in which infants spent up to 20 hours a day unattended) as the majority of them are disorganized in attachment (Zeanah, Smyke, Koga & Carlson, 2005), and many suffer long-term cognitive and behavioral deficits (Chugani et al., 2001; Vorria et al., 2003). However, when these infants were placed in environments in which more care was provided (e.g., Romanian infants adopted before 6 months and, to a lesser extent, those adopted at 6 months or older), they recovered cognitively and physically to near-normal by 4 years old (Rutter, 1998).

Studies of attachment in nonhuman primates have been conducted primarily with macaques (e.g. Mason & Green, 1962; Suomi, 2004; Suomi, Van der Horst & Van der Veer, 2008), titi monkeys (Hoffman, Mendoza, Hennessy & Mason, 1995), and squirrel monkeys (Hennessy, Kaplan, Mendoza, Lowe & Levine, 1979), and typically involve periods of separation (30 minutes to an hour) which result in an immediate and significant increase in plasma cortisol levels. For titi monkeys, this adrenocortical response can persist through longer periods of separation (e.g. for a number of days or weeks: Mendoza, Capitanio & Mason, 2000). Separations of infant macaques from their mothers cause disruptions of physiological systems, such as cardiac regulation, sleep rhythms, circadian rhythms, pituitary-adrenal systems, immunological systems, and cerebral spinal fluid. Additionally, during separation there are behavioral indicators of distress, such as increased vocalization and searching behaviors

followed by huddled, withdrawn posture and reduced activity. Consequences of these separations early in life include compromised immune function into adulthood (Laudenslager, Capitanio & Reite, 1985; Laudenslager & Boccia, 1996), and deficits in social and reproductive behaviors (e.g., Suomi, 2004).

In chimpanzees, attachment responses are equivalent to those seen in human infants and other nonhuman primate species (Bard & Nadler, 1983; Inoue, Hikami & Matsuzawa, 1992; Inoue & Hikami, 1993; van IJzendoorn et al., 2009). Characteristics of the rearing environments, such as the amount and quality of caregiver interactions with infants, have a significant impact on chimpanzee attachment patterns. Chimpanzees reared in a nursery environment in which caregivers spent relatively little time with infants (standard nursery care [ST] with 60 minutes per 24 hours: Bard, Bakeman, Boysen & Leavens, 2014a) exhibited a preponderance of disorganized attachment patterns, similar to those seen in humans raised in orphanages with minimal staff contact (van IJzendoorn et al., 2009). In contrast, chimpanzees reared in a responsive care [RC] nursery, in which human researchers spent four hours per weekday in continuous contact with infants and nurtured species-typical communication (Bard, 1996; Bard et al., 2014b), were significantly less likely to exhibit disorganized attachment at one year of age (van IJzendoorn et al., 2009). It is clearly not desirable to deliberately place human or chimpanzee infants in non-optimal nurseries, but these comparative studies are extremely useful for understanding the importance of early experiences on the development of attachment in both species.

Disorganized attachment in humans and chimpanzees is manifest when infants lack a strategy for balancing comfort and exploration when distressed by separation and are subsequently reunited with their attachment figures (van IJzendoorn et al., 2009). In human

infants, disorganized behaviors include freezing, stereotyped behaviors, misdirected behaviors (e.g., seeking comfort from the stranger), and/or fear of the attachment figure at reunion (van IJzendoorn, Schuengel & Bakermans-Kranenburg, 1999). The chimpanzee infants classified as disorganized tended to rock stereotypically, freeze, and/or clutch a towel when reunited with their favorite caregiver rather than approach and seek contact to alleviate their distress. In humans, disorganized attachment has been found to be significantly associated with: (a) elevated cortisol levels long after separation episodes (Lyons-Ruth, 1996; Spangler & Grossman, 1999); (b) aggressive behavior in kindergarten-aged children (Lyons-Ruth, Alpern & Repacholi, 1993; Lyons-Ruth, 1996); (c) less effective cognitive functioning at 7 – 17 years old (Jacobsen, Edelstein & Hofmann, 1994); (d) problematic stress management in infancy, and (e) dissociative behavior in adults (Liotti, 2004; van IJzendoorn et al., 1999). Since there are similarities in attachment behavior between human and chimpanzee infants, we expect adult chimpanzees and humans that experienced disorganized attachment to react similarly. These reactions may be manifested in measures of personality, sociality, and individual welfare (e.g., abnormal behaviors, stress responses, poor well-being, and poor health).

In humans and other animals, the presence of abnormal behaviors are indicators of poor welfare, i.e., poor adaptation to the current or previous environment (Mason, 2006). Abnormal behavior is defined as behavior that differs in "pattern, frequency, or context from that which is shown by most members of the species in conditions that allow a full range of behavior" (Fraser & Broom, 1990, p. 385). Some abnormal behaviors have been shown to increase the release of endogenous endorphins (Mason & Rushen, 2008), perhaps reducing an animal's experience of suffering. In certain circumstances, animals exhibiting stereotypic behavior have been found to have improved welfare compared to animals in equivalent conditions who do not express the

behavior (Mason, 2006; Mason & Rushen, 2008). However, in most circumstances, the presence of abnormal behavior is still an indicator that the animal's welfare is or has been poor. It is common wisdom that the number and/or frequency of abnormal behavior are an index of the degree to which that animal's welfare is compromised. For example, a greater variety and higher frequency of abnormal behaviors are associated with restrictive rearing (Davenport & Menzel, 1963; Davenport, Menzel & Rogers, 1966; Davenport, Rogers & Rumbaugh, 1973).. Behaviors documented as abnormal for chimpanzees include rocking or other stereotyped whole body movements, eye-poking, regurgitation and reingestion of foodstuffs, eating or manipulating feces, urophagy, stereotyped self-manipulation of body parts, thumb-sucking, etc. (Baker, 1997; Dienske & Griffin, 1978; Fritz, Nash & Alford, 1992; Mallapur & Choudhury, 2003; Martin, 2002). If disorganized attachment has long-term ramifications in chimpanzees, similar to those seen in humans, then such chimpanzees should exhibit impaired welfare as adults as measured by a higher frequency and/or a greater diversity of abnormal behavior.

Humans with disorganized attachment as infants have poor ability to cope with stress as adults (Liotti, 2004). Thus, chimpanzees with disorganized attachment may exhibit more behaviors associated with acute stress than those with organized attachment styles. Behaviors commonly interpreted as related to acute stressors in chimpanzees and other nonhuman primates include rough scratching (Baker & Aureli, 1997; Troisi, 2002) and yawning (Castles & Whiten, 1998). Chronic stress has been shown to affect physiological systems (Cohen et al., 1997; Fahlke et al., 2000; Mendoza et al., 2000). Chronic stress can be observed as impaired immune response (Blecha, 2000), which, for example, has been linked with increased susceptibility to upper respiratory infection in nonhuman primates (Cohen et al., 1997). The ability to cope with stressful stimuli is an important component of welfare and well-being assessment (Maple &

Perdue, 2013; Mason, 2006) and we predict that early disorganized attachment will affect the ability of chimpanzees to cope effectively with stressful situations.

The well-being of captive chimpanzees has been assessed through a survey (Weiss et al., 2009). Assessing welfare subjectively (as with a survey) is useful (e.g., due to the speed of data collection), particularly when survey results correlate with more objective welfare measurements (such as counting the number or frequency of abnormal behaviors). We predict that disorganized chimpanzees will be perceived as having lower levels of well-being than organized chimpanzees, based on the human research indicating disorganized attachment in infancy is predictive of decreased welfare for adults (Liotti, 2004; van IJzendoorn et al., 1999).

One indirect way to measure aggression in nonhuman primates, particularly if observation of the group is impractical, is to record rates of wounding (Crockett & Pope, 1988). Higher wounding rates for disorganized chimpanzees could be interpreted as an indirect measure of aggression, predicted because aggression is found in disorganized humans (van IJzendoorn et al., 1999). In a study on chimpanzee wounding, adolescent males were found to be more likely than other age/sex classes to receive injuries, though they were no more likely to injure others. It was concluded that adolescent males may lack the social skills to avoid injury during agonistic encounters with other chimpanzees (Ross, Bloomsmith, Bettinger & Wagner, 2009). Similarly, we may tentatively conclude that a socially inept chimpanzee may be injured more often than a socially adept chimpanzee. If substantiated, this would parallel findings that school-aged children with disorganized attachment systems exhibit inconsistent and less socially successful behavior towards their peers (Jacobvitz & Hazen, 1999). Socially successful behavior may be evident in lower rates of aggression, higher rates of affiliation, higher rates of submission, or the presence of particular social behaviors, such as species-typical greetings. If

we obtain evidence of increased wounding in disorganized individuals, we could possibly distinguish the cause (e.g., as having poor social skills or displaying heightened aggression) with these independent behavioral data.

Personality in chimpanzees has been assessed and, to date, found to be generally consistent across variable environments on at least four of six factors extracted from chimpanzee personality inventories (Weiss, King & Hopkins, 2007; Weiss et al., 2009). Researchers are still divided as to the relative contributions of genetics and experience to human or nonhuman primate personality structure (and to the difference or lack of difference between temperament and personality as constructs) (for a review see Freeman & Gosling, 2010). Attachment has not been assessed in relation to personality structure in chimpanzees. In humans, one study found that attachment style was associated with aspects of personality in adults (particularly if attachment was categorized as secure or insecure without distinguishing between different insecure strategies) (Shaver & Brennan, 1992). To the authors' knowledge, there has been no assessment of organized versus disorganized attachment style in relation to non-clinical personality structure in adult humans or in nonhuman primates (van IJzendoorn et al., 1999). It is of interest to explore the possibility that organization of attachment style (or lack of) could be associated with personality structure (in this case, for chimpanzees).

As reported in van IJzendoorn et al. (2009), a sample of 46 nursery-reared 1-year-old chimpanzees was assessed with the SSP (22 females, 24 males; 29 raised under Standard Care (ST) and 17 raised in Responsive Care (RC)). All nursery-reared chimpanzees were housed in the Yerkes nursery and from as early as 30 days were raised in same-aged peer groups of 4 to 6 individuals. The experiences of Standard Care chimpanzees differed from those of Responsive Care chimpanzees in the first year of life, however, in that RC chimpanzees spent an additional

4 hours each weekday with humans who were trained to nurture social development, motor development, and species-typical communication in a manner similar to that provided by chimpanzee mothers (Bard et al., 2014b; Bard et al., 2014a). A large percentage of these nursery-reared chimpanzee infants, especially in ST, were determined to be disorganized in their attachment (72% of ST; 41% of RC). As in van IJzendoorn et al. (2009), the chimpanzee infants that were unclassifiable (n = 3) were grouped together with the disorganized group, because they did not display organized attachment systems. Individuals that exhibited organized attachment (i.e., secure, insecure-avoidant, insecure-resistant) were categorized together primarily because there were small numbers of individuals in each category, and secondarily, because long-term research on attachment indicates that the most substantial differences in long-term consequences are found between those classified as disorganized and those classified as organized (van IJzendoorn et al., 1999). In comparison to the chimpanzees with an organized attachment system, the 1-year-old chimpanzees in the disorganized group exhibited significantly more rocking, spent significantly more time clutching towels, and spent significantly less time touching their attachment figure during both reunion episodes of the SSP (Figures 4 & 5 in van IJzendoorn et al., 2009).

Here we assess abnormal behaviors, affiliative behaviors, aggressive behaviors, submissive behaviors, personality, health, and well-being in adult chimpanzees that were assessed with the SSP as 1-year-olds. If we find that chimpanzees identified as disorganized in attachment tests at one year of age are: 1) more likely to exhibit abnormal or stress-related behaviors; 2) more likely to experience illness; 3) are wounded at a higher rate or 4) have poorer subjective well-being than those chimpanzees classified as having organized attachments, then we may conclude that disorganized attachment in young chimpanzees is predictive of later behavioral

and physiological health similar to that found in humans. The three sections that follow provide the methods and results for the behavioral observations, health assessments, and survey, respectively.

Methods

Note about Study Subjects

Note that of the 46 individuals tested with the SSP at one year of age, only 20 remained at Yerkes into adulthood and were available for the behavioral assessments, and only 21 for the personality and subjective well-being assessments. Health was assessed in 43 chimpanzees, of whom 24 had a full 20 years of health and injury data available. Individuals selected for relocation were not chosen at random (though the criteria for relocation differed depending on the transfer location), so the subjects of this study cannot be considered randomly selected.

Study One: Behavioral Observations

Study One Subjects. From the 46 chimpanzees previously assessed with the SSP (van IJzendoorn, et al., 2009), behavioral observations were conducted on the 20 adults (between 17 and 25 years of age) that remained housed at the Yerkes National Primate Research Center. As adults, the nursery-reared chimpanzees lived in small groups of between 2 and 6 individuals. The sample comprised 10 chimpanzees (3 females and 7 males, ages 19 - 22) that had previously been classified as disorganized (DA), and 10 (6 females and 4 males, ages 17 - 25) that had previously been classified as organized (OA). Unlike the ratios found at 1 year of age, here the two attachment groups were comprised of equivalent ratios of ST to RC infants: OA group included 4 ST and 6 RC chimpanzees and the DA group included 6 ST and 4 RC chimpanzees. We hypothesized that, as adults, chimpanzees that had been classified as

disorganized at one year of age would be more likely to exhibit abnormal or stress-related behaviors.

Study One Methods. Behavioral observations were conducted in 1 hour time blocks balanced between 8 a.m. and 3 p.m., and totaled 6 – 10 hours per chimpanzee. In each 60-second interval the presence or absence of seven categories of events were recorded: abnormal behavior, stress-related behavior, affiliative behavior, aggressive behavior, submissive behavior, sexual behavior and environmental events (loud noise, approach of a human within 5 feet, displays or loud vocal chimpanzees in area, approach of vehicle within 15 feet). The mean total intervals observed for DA chimpanzees was 516.0 (MIN = 420.0, MAX = 600.0, SD = 51.99); the mean total intervals observed for the OA group was 569.5 (MIN = 475.0. MAX = 600.0, SD = 64.50). There was no significant difference in total intervals observed between the two attachment groups ($F(1,18) = 4.17$, $p = .056$). However, given there was a trend, we choose to use proportions, rather than totals, as summary measures.

Of primary interest to this report were seven abnormal behavior categories (urophagy; feces-related; stereotypic rocking; stereotypic manipulation of body parts; regurgitation/reingestion of edible substances; hair plucking; other abnormal: Appendix A) and two stress-related behavior categories (rough scratching; yawning) (Baker & Aureli, 1997; Castles & Whiten, 1998; Troisi, 2002). Data were collected using an iPaq recorder and Noldus Observer software. All statistical results reported were based on two-tailed probability tests. For the complete ethogram, see Appendix A.

Study One Data summary. There were no incidences of urophagy scored, and so this category was eliminated from analysis. We were interested in attachment group differences in each of the remaining six abnormal behavior categories, as well as the total amount of abnormal

behavior. Summary scores were computed for the two stress-related behaviors, the five affiliative behaviors, the six aggressive behaviors, the four submissive behaviors, and the four sexual behaviors (masturbation was not included as this is not a social behavior: for details of all behaviors see Appendix A). Environmental events were considered individually. Proportions were calculated by dividing the total number of intervals in which behaviors or events occurred by total number of intervals observed. A Kendall's Tau correlation test was conducted to assess whether there was any relation between environmental events and the behaviors of interest. This was important because environmental events were recorded, but not controlled, and thus could differ in rate of occurrence between the two test groups. A Kendall's Tau test was more appropriate than more traditional statistics for the small sample size and in conjunction with the MWU tests used for group comparisons. All probability values reported are corrected for ties as is usually recommended for small sample size.

Study One Results. Because environmental events were scored, but not controlled, it was important: 1) to determine if there was any relation between these events and scored behaviors and 2) to ensure that groupwise differences in exposure to environmental events were accounted for statistically if a relation was found. A significant positive correlation was found between the mean proportional occurrence of human approach and the mean proportional occurrence of stress-related behavior ($\tau = .392$, N = 20, $p = .001$), between mean proportion of human approach and mean proportion of affiliative behavior ($\tau = .275$, N = 20, $p = .026$) and between mean proportion of human approach and mean proportion of sexual behavior ($\tau = .333$, N = 20, $p = .013$). A significant negative correlation was found between the mean proportional occurrence of chimp vocalizations in the area and mean proportional occurrence of stress-related behavior ($\tau = -.300$, N = 20, $p = .015$), between mean proportion of chimp vocalization

and submissive behavior (τ = -.253, N = 20, p = .054) and between mean proportion of chimp vocalization and sexual behavior (τ = -.269, N = 20, p = .045). However, the mean proportion of intervals in which human approach was scored was nearly identical in the two attachment groups (.038 for OA and .039 for DA), as was the mean proportion of intervals in which chimp vocalization was scored (.065 for OA and .072 for DA). A MWU test confirmed no significant groupwise difference in mean proportion of human approach (p = .970) or chimp vocalization (p = .650). Therefore, any differences in stress behavior, affiliative behavior, submissive behavior and/or sexual behavior between groups cannot be attributed to group differences in human approaches or chimp vocalizations. There were no significant correlations found between any other of the environmental events and chimpanzee behaviors.

Rearing and attachment. Table 1 lists the means and standard deviations of attachment group differences in the behavioral variables. A stepwise multiple regression, with attachment classification and rearing as predictors, was conducted on each of the dependent variables. Significant effects were found only for stereotypic rocking; neither attachment or rearing were significant predictors for any of the other behavioral variables. Attachment group accounted significantly for 30% (26% adjusted) of the variance in rocking (F(1,18) = 7.50, p = .013). Rearing did not add significantly to the equation at step 2 (t = -1.48, p = .156). The disorganized group of adult chimpanzees exhibited significantly more rocking than the organized group.

Study Two: Health Assessments

Study Two Subjects. From the 46 chimpanzees previously assessed with the SSP (van IJzendoorn et al., 2009), health was assessed in the 43 chimpanzees that had records available. Details about each individual's environment during years for which data were available were not provided. However, all subjects assessed were living at Yerkes in roughly equivalent

enclosures (indoor/outdoor runs) and social situations (groups of 2 – 6 total individuals) for however many years they were housed at the facility, especially once they had been moved from the nursery. Records were available from birth to at least 5 years of age for 43 of the 46 individuals, from birth to 10 years of age for 37 of 46 individuals, and from birth to 15 years of age for 30 of 46 individuals. Only 24 subjects had records available from birth through 20 years of age. The chimpanzees for which records were not available at all or were not available through 20 years of age were largely animals transferred to other facilities, though some were deceased (2 OA died, and 4 DA died).

Study Two Methods. The Yerkes electronic Animal Records System (ARS) was used to count incidents of upper respiratory system infection (URI), diarrhea (DIA), and injury (INJ) in each subject's medical history when they were aged 0 – 5, 6 – 10, 11 – 15, and 16 – 20 years. These age categories were based roughly on developmental stages of the chimpanzee (infant/young juvenile: 0 – 4/6; juvenile ~5 – 10; adolescent ~11 – ~15; adult ~16 and older: (Zihlman, Bolter & Boesch, 2007). Veterinary procedures (medication, surgery, or other treatments) and concerns (e.g., illnesses, injuries) were routinely recorded in ARS by Yerkes veterinary staff. Veterinarians assess all chimpanzees housed on Yerkes Great Ape Wing on a daily basis, but entries into ARS were made only for non-routine interventions. Counts did not include injuries that were known to have occurred due to a non-social event (e.g., a chimpanzee was seen to have cut himself accidentally on the caging). Illnesses that did not require any intervention (e.g., that did not require treatment) were not included in counts.

Chi-square tests were conducted to compare the disorganized and organized groups as either having or not having an incident of URI, DIA, or INJ during the relevant age span (yes/no in the 5-year period). Fisher's exact test was used as some expected cell values were less than five. A

stepwise multiple regression was conducted to assess the relation between attachment strategy, rearing condition, and the overall frequency of URI, DIA and INJ across the 0 – 20 year age span (rather than presence/absence of URI, DIA or INJ).

Study Two Results. Results are organized by age span categories.

Ages 0 – 5. In the DA group for ages 0 - 5, there were 26 subjects. In the OA group, there were 17 subjects. There was a significant association between attachment and veterinary intervention for URI for chimpanzees ages 0 – 5 (χ^2 (1) = 6.87, p = .016, φ = .40). During this period, 85% of the DA subjects experienced veterinary care for an URI, but only 47% of OA subjects experienced at least one URI. No relation between attachment group and health was found for incidence of veterinary intervention for DIA or INJ in the span of 0 – 5 years.

Ages 6 – 10. There were 20 individuals in the DA group for this age span. There were 17 individuals in the OA group. No significant relation was found between attachment group and DIA, URI or INJ for years 6 – 10.

Ages 11 – 15. There were 17 individuals in the DA group for this age span. There were 13 individuals in the OA group. There were no significant associations between attachment group and any of the dependent variables (URI, DIA, INJ).

Ages 16 – 20. There were 13 chimpanzees in the DA group and 11 chimpanzees in the OA group for this age span. There were no significant associations between attachment group and any of the dependent variables (URI, DIA, INJ).

Ages 0 – 20. There were 13 adult chimpanzees in the DA (4 RC, 9 ST) group and 11 in the OA (6 RC, 5 ST) group with data available for their first 20 years. The multiple regression revealed significant effects for frequency of URI and of DIA. Attachment and rearing each contributed uniquely and significantly to the variance in overall frequency of URI across the

first 20 years of life. Rearing accounted significantly for 30% (27% adjusted) of the variance ($F(1,22) = 9.37$, $p = .006$) in URI frequency in step 1, and attachment group accounted for an additional 16% ($F(2,21) = 8.86$, $p = .002$) of the variance when added to the model in step 2. Responsive care and disorganized attachment were associated with higher frequency of URI incidence across the first 20 years of life. Only rearing was a significant predictor of DIA frequency (years 0-20), accounting for 28% (25% adjusted) of the variance in DIA with no further predictors added past step 1 ($F(1,22) = 8.61$, $p = .008$). Adult chimpanzees from the RC nursery experienced a higher frequency of DIA bouts across the first 20 years of life as compared to the ST individuals.

Attachment group was not a significant predictor of variance in INJ frequency (years 0 – 20) at step 1 of analysis ($F(1,22) = 4.18$, $p = .053$), although it accounted for 16% (12% adjusted) of the variance in INJ frequency. Rearing group was not a significant predictor of INJ frequency at step 2 ($t = 1.01$, $p = .326$).

Study Three: Survey Assessments

Study Three Subjects. From the 46 chimpanzees previously assessed with the SSP (van IJzendoorn et al., 2009), personality and well-being surveys were conducted with 21 adult chimpanzees between the ages of 16 – 29 years, all living at Yerkes in similar enclosures and in social groups of 2 – 6 animals. In the DA group, there were 4 RC and 6 ST chimpanzees. In the OA group, there were 6 RC and 5 ST chimpanzees.

Study Three Methods. Researchers, animal care providers, veterinary staff, and behavioral management staff that worked with the chimpanzees on a regular basis for at least one year completed surveys on the adult chimpanzees. No respondents were aware of previous attachment categorizations, nor were they involved in the rearing of the chimpanzees. Survey

sections related to personality (59 items) and to subjective well-being (4 items), and were based on previous surveys (Weiss et al., 2007; Weiss et al., 2009). Personality and subjective well-being (SWB) items ask the respondents to use a 7-point Likert scale to assess the degree to which a chimpanzee exhibits a certain trait (1 = least amount, 7 = most amount). Items and the traits the items are intended to measure are listed in Appendix B. Surveys were completed using surveymonkey.com. Four to 9 respondents completed surveys for each chimpanzee. Inter-rater reliability was calculated as a mixed-model two-way interclass coefficient for each subject on each item resulting in an average inter-rater reliability of .74 (ICC scores ranging from .57 to .87), with no difference in reliability scores between the two attachment groups (U = 42.0, p = .360). Multiple scores for each individual were averaged for a composite score before being entered into factor analysis. The two survey sections (Subjective Well-Being and Personality) were analyzed and reported in separate sections.

Study Three Results.

Subjective Well-Being (SWB). A PCA Factor Analysis confirmed that the 4 SWB items correlated heavily and that one underlying factor accounted for 78.9% of the variance (see Table 2 for loading scores). Item scores were therefore averaged to create a single composite SWB score for each individual that would still map onto the original Likert ratings (e.g., a rating of 4 indicates average well-being). No significant difference was found between the two attachment groups in SWB (Mann Whitney U = 45.0, p = .510). However, while the OA group confidence interval (CI [4.03, 5.01]) was above (and did not include) the average SWB score of 4, the DA group confidence interval did contain the average SWB score (CI [3.81, 4.60]: Figure 3). This result indicates that the OA group mean SWB score was significantly higher than average, whereas the DA group mean SWB score was not.

Personality. A previous study compared a sample of Yerkes chimpanzees to a much larger sample of zoo-living chimpanzees and found congruency on four extracted factors (two factors extracted from zoo populations were not found to be congruent with the Yerkes sample) (Weiss et al., 2007). Because Weiss et al.'s (2007) study results were based on a larger sample it was decided to use the items and unit-weights used in that study to calculate the same four factors (Dominance, Extraversion, Conscientiousness and Agreeableness). We concluded based on a Levene's test for homogeneity of variance that it was possible to use a parametric ANOVA test for analyses. No significant differences were found between the two attachment groups on any of the four personality factors (Figure 4). Agreeableness correlated significantly and positively with Conscientiousness ($r = .656$, $N = 21$, $p = .001$) and Extraversion ($r = .707$, $N = 21$, $p = .000$). Dominance correlated significantly and inversely with Conscientiousness ($r = -.562$, $N = 21$, $p = .008$). Stepwise regression analyses did not find either rearing or attachment group to be significant predictors for SWB or any of the Personality factors.

Correlates with Behavior. For the subjects that had data available, correlations were conducted to assess relations between the personality factors, SWB, and behaviors (abnormal behavior, affiliative behavior, aggressive behavior, submissive behavior, sexual behavior and stress behavior). Significant positive correlations were found between SWB and the personality factors Agreeableness ($r = .646$, $N = 21$, $p = .002$) and Extraversion ($r = .734$, $N = 21$, $p < .001$). Significant negative correlations were found between SWB and the means for abnormal behavior ($r = -.510$, $N = 20$, $p = .021$) and stress behavior ($r = -.486$, $N = 20$, $p = .011$). Agreeableness significantly and inversely correlated with abnormal behavior ($\tau = -.368$, $N = 20$, $p = .030$). Submissive behavior correlated significantly and inversely with Dominance ($r = -.642$, $N = 20$, $p = .002$) and significantly and positively with Agreeableness ($r = .681$, $N = 20$, p

= .001). Affiliative behavior correlated significantly and positively with abnormal behavior (r = .665, N = 20, *p* = .001). No other significant correlations were found.

Discussion

We found long-term effects in the behavior and health of adult chimpanzees based on attachment tests conducted when the chimpanzees were one year of age (van IJzendoorn et al., 2009). Our findings were analogous to those for humans raised in poor quality orphanages (van IJzendoorn et al., 1999), thus providing support for attachment as an organizing feature of human and nonhuman primates during development. Specifically, chimpanzees identified as disorganized in infancy exhibited higher proportions of stereotypic rocking behavior as adults, and a higher incidence of health problems, including veterinary interventions for upper respiratory infections, than chimpanzees identified as organized. However, the two groups did not differ in stress-related behavior, social behaviors, or personality ratings. Therefore, the attachment system in chimpanzees likely functions in a similar way to that of humans; when this system has broken down in the infant, there can be long-term negative consequences into adulthood (Liotti, 2004; Lyons-Ruth, 1996; van IJzendoorn et al., 1999).

At Yerkes, one-year old, nursery-reared chimpanzees that were classified as disorganized exhibited more stereotypic rocking behavior during the separation episodes of the SSP than those classified as having an organized attachment with their primary caregivers. Since the short separations of the SSP are designed to stress the attachment system (Ainsworth et al., 1985), this indicates that one year old chimpanzees with disorganized attachment exhibit abnormal behavior when they experience moderate, acute stress (van IJzendoorn et al., 2009). Previous research has found that abnormal behavior in nursery-reared chimpanzees can be reduced by housing with canine companions (Pazol & Bloomsmith, 1993; Thompson,

Bloomsmith & Taylor, 1991). We suggest that having an organized attachment system may reduce stereotypic rocking in chimpanzees (van IJzendoorn, 1995; van IJzendoorn et al., 1999), whether that attachment is to a canine companion or to a human caregiver. It should be noted that although there was significantly less disorganization in the responsive care group, both nursery protocols produced a substantial proportion of infant chimpanzees with disorganized attachment (41% in responsive care; 72% in standard care). It is likely that peer rearing and relatively low amounts of caretaker contact time with infants lead to high levels of disorganized attachments in nursery-reared chimpanzees, as both factors contribute to disorganization in human infants (van IJzendoorn et al., 2009). It could also be that genetic differences combined with environmental conditions in early development affect susceptibility to attachment disorders. This is somewhat controversial in human research, but there are indications that polymorphism in a serotonin transporter gene combines with low maternal responsiveness to increase the likelihood of disorganized attachment in human infants (Spangler, Johann, Ronai & Zimmermann, 2009).

Stress-related behaviors in the adult chimpanzees did not differ as a function of their infant attachment classification. It should be noted, however, that the behaviors observed for this study measure acute, not chronic stress (Elder & Menzel, 2001). Stress-related behaviors were were not frequently observed here (averaging 5% of the recorded intervals), but the rate was comparable scratching in wild baboons (Castles & Whiten, 1998: 2.1 bouts per hour) and less than stress-related behaviors in other studies of laboratory-housed chimpanzees (Baker & Aureli, 1997: approximately 5 bouts per hour). Another aspect of the stress system is stress-reactivity, usually measured by placing individuals in a stressful situation and assessing the speed or variability in their reactions (Bard & Nadler, 1983; Koolhaas et al., 1999; Nachmias,

Gunnar, Mangelsdorf, Parritz & Buss, 1996; Pardon et al., 2002). We found that adult chimpanzees exhibited higher proportions of stress behavior when there were more instances of humans approaching their enclosures, but these reactive behaviors (indices of acute stress) did not differ with attachment group. Future studies could collect baseline and reactive cortisol and immune system measures (e.g., salivary cortisol, blood serum values, fecal cortisol, and/or hair cortisol) that might allow detection of stress-reactivity, and importantly, chronic stress (Boinski, Swing, Gross & Davis, 1999; Fahlke et al., 2000; Reinhardt, Cowley, Scheffler, Vertein & Wegner, 1990; Winslow, Noble, Lyons, Sterk & Insel, 2003).

The number of injuries was low for both attachment groups (a median of 1 in the 0 to 20 year period for chimpanzees with a history of organized attachment, and 2 in the 20 year period for adult chimpanzees with a history of disorganized attachment: Figure 2). Although there was a nonsignificant trend for total number of injuries to differ between DA and OA chimpanzees (p = .053), this was associated with a large effect size (16% of the variance accounted for), which we consider to be a noteworthy result, particularly in our small sample. A higher frequency of injury for chimpanzees with a disorganized attachment history indicates that these chimpanzees received more aggression from conspecifics, because only injuries resulting from social interactions were considered for this study. Humans and rhesus monkeys with a history of disorganization show higher rates of aggressive behavior, rather than any change in received aggression (Suomi, 2004; van IJzendoorn et al., 1999). In the chimpanzees, we did not find significant differences in aggressive behavior towards conspecifics based on attachment classification. Nevertheless, the higher incidence of wounding in the chimpanzees with disorganized attachment may point to problems in negotiating harmonious social relationships at a more subtle level than we assessed in this study.

We also found that disorganized attachment in infancy was associated with reduced health during development. In infant humans, disorganized attachment has been associated with greater stress-reactivity (Lyons-Ruth, 1996; Spangler & Grossman, 1999). Chronic stress, associated with greater stress-reactivity, is clearly responsible for reduced immune function (Coe & Scheffler, 1989; Coe, 1993; Cohen et al., 1997), and this may reduce an animal's ability to deal with various viruses, infections, and parasites. Indeed, nonhuman primates under chronic stress are particularly susceptible to upper respiratory illnesses (Cohen et al., 1997). We suggest poor health outcomes of disorganized chimpanzees may be due, in part, to the chronic stress associated with the lack of an organized attachment relationship with a primary caregiver during infancy.

Interestingly, higher incidences of upper respiratory infections (URIs) were associated with disorganized attachment both in the first 5 years (measured by presence/absence) and over the 0 – 20 year period (measured by total frequency). The frequency of these infections over the 0 – 20 period was significantly associated with both attachment classification (21%) and rearing condition (27%). As expected, the 11 adult chimpanzees classified as disorganized had 1.3 incidences of URI compared to the 0.8 incidences for those 13 adults classified as organized. Counter to expectations, the ten chimpanzees raised in responsive care that remained at Yerkes as adults exhibited a total of 1.7 incidences of URI in 20 years, compared to the 0.6 incidences of URI exhibited by the 14 adult chimpanzees that had been raised in the standard care nursery. It is possible that chimpanzees with disorganized attachment responses were more vulnerable to infection compared to those with organized attachment responses. It is also possible that being in the responsive care nursery, which increased time in contact with humans as part of the protocol, simply increased the number of inadvertent exposures to infection. It is an alternative

possibility that illness was simply reported more frequently in responsive care due to the greater presence of human caregivers. This might explain why most of the incidences of URI occurred when the chimpanzees were still in the nursery (12 of the 17 adult chimpanzees with at least one incident of URI had 100% of the incidents in the first 5 years of life). We will address these questions further with a larger sample of chimpanzees, comparing the two nursery conditions and mother rearing, to allow greater understanding of the effect of rearing history on health.

We did not find attachment-based differences in personality structure, supporting findings that personality may be relatively more heritable (e.g. Jang, Livesley & Vemon, 1996), whereas attachment (organized and disorganized) is relatively more environmentally determined (Bokhorst et al., 2003). We presented inter-trait correlations for personality factors since these results can inform about evolutionary foundations of personality structures (e.g., 3 vs 5 trait models: Zuckerman, Kuhlman, Joireman, Teta & Kraft, 1993). The manner in which subjective well-being may be related to attachment and personality is a current topic of research. Thus far, studies have focused primarily on well-being among organized attachment strategies (secure, insecure-anxious and insecure-avoidant: Wei, Liao, Ku & Shaffer, 2011).

In our data, we found the well-being ratings of the organized chimpanzees were significantly above the average score, whereas the well-being scores of the disorganized chimpanzees were not different from average. A number of behavioral measures correlated significantly with the subjective well-being score, and thus support the validity of our well-being assessment (see Appendix B based on Weiss et al., 2009). Both abnormal behaviors and stress behaviors significantly increased as well-being scores decreased, for example. The well-being survey is recommended for future studies with chimpanzees since it is short, easy for caregivers to complete and correlates strongly with observed behaviors.

Conclusions

Disorganized attachment in infancy can have a strong and negative impact on long-term development in humans, monkeys, and in chimpanzees. With the current study, we show that adult chimpanzees with disorganized attachment in infancy have significantly increased stereotypic rocking, more health problems, and only average well-being when compared to those adult chimpanzees with organized attachment in infancy. These results provide support for the notion that attachment is an important organizing feature of primates during development (e.g., Bowlby, 1980; Suomi, 2004). Our research findings support results in humans, particularly those raised in abusive or neglectful situations, that indicate people with organized attachment styles are distinguishable from those with disorganized attachment past early childhood (van IJzendoorn et al., 1999). Larger samples for chimpanzees could allow researchers to determine if, as in human research, these long-term differences eclipse the long-term differences between secure and insecure attachment styles (van IJzendoorn et al., 1999).

Further research should be conducted to ascertain the extent to which disorganized attachment exists in chimpanzee infants raised with their biological mothers, which would further validate the evolutionary basis of attachment, and could be useful to facilitate the design of appropriate interventions or to enable long-term prognosis. These further investigations could rely on behavioral observations such as the Q sort test (Tartabini & Simpson, 1991; Waters, 1987) so that separations between infants and mothers could be avoided. Follow-up studies are needed of the long-term consequences of early rearing and infant attachment styles on adult behavior and well-being in great apes. Such studies could improve captive management procedures for great apes, which is particularly relevant as the number of orphan great apes being raised in rescue, rehabilitation, and release sanctuaries continues to increase.

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Tables

Table 1

Means (M) and Standard Deviations (SD) for Abnormal Behaviors based on Raw Proportions of Scored Behaviors for Organized and Disorganized Attachment groups

	ORGANIZED ATTACHMENT IN INFANCY		**DISORGANIZED ATTACHMENT IN INFANCY**	
ADULT BEHAVIOR	MEAN	SD	MEAN	SD
Aberrant Fecal	.001	.002	.000	.000
Hair Pluck	.018	.037	.004	.008
Stereotypic Body Manipulation	.005	.006	.002	.002
Stereotypic Rocking	.022*	.024	.065*	.043
Reingest and Regurgitate	.004	.007	.001	.002
Other Abnormal	.004	.006	.010	.013
Abnormal (TOTAL)	.055	.061	.082	.037
Affiliative (TOTAL)	.031	.024	.031	.031
Aggressive (TOTAL)	.027	.026	.030	.030
Submissive (TOTAL)	.009	.015	.003	.008
Sexual (TOTAL)	.001	.002	.001	.001
Stress (TOTAL)	.047	.034	.062	.042

Table 1: *denotes a significant group difference at $p<.050$

816 Table 2

817 *Salient Factor Loadings for Confirmatory Factor Analysis of Subjective Well-being Inventory*

Item	SWB
Happiness of Chimpanzee	+.86
Sociability of Chimpanzee with Conspecifics	+.94
Effectiveness of Chimpanzee	+.79
Would be Happy to be the Chimpanzee	+.95

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820 **Figures**

821 Figure 1: Proportions of Stereotypic Rocking Behavior by Attachment Categorization
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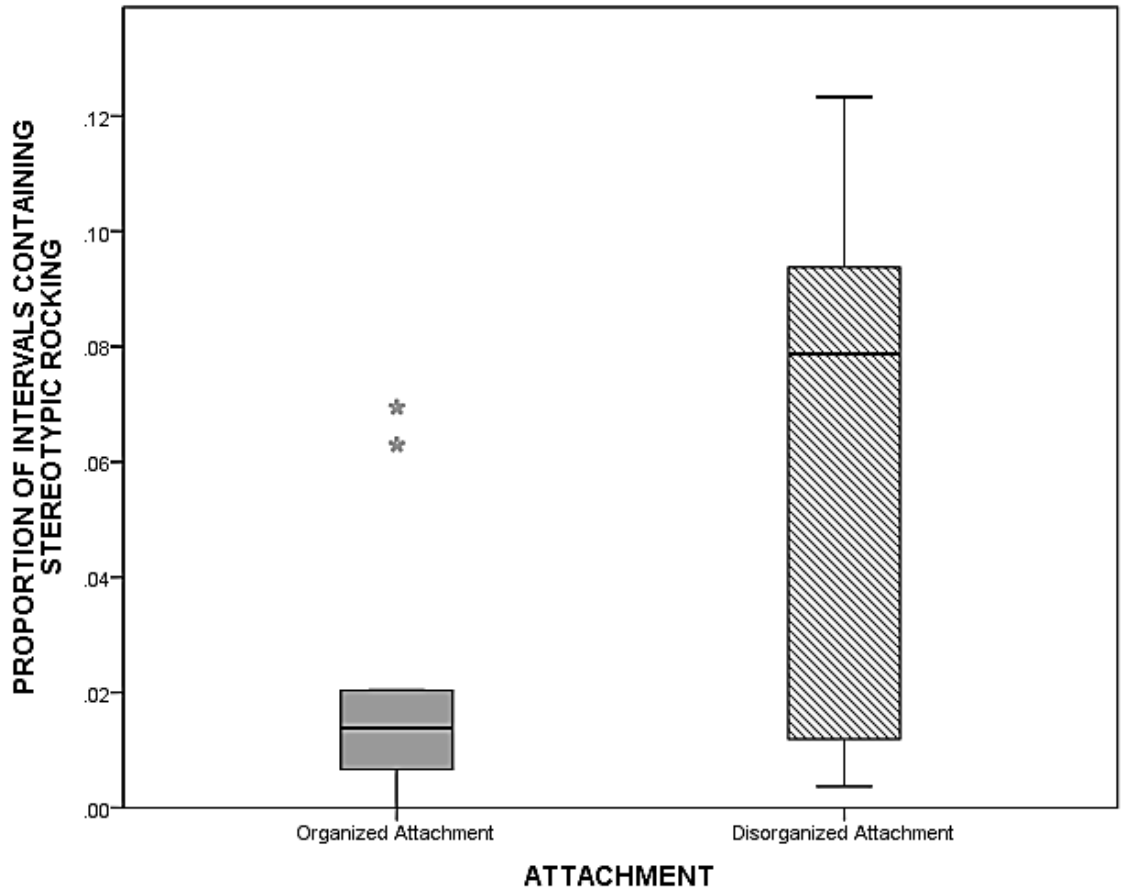

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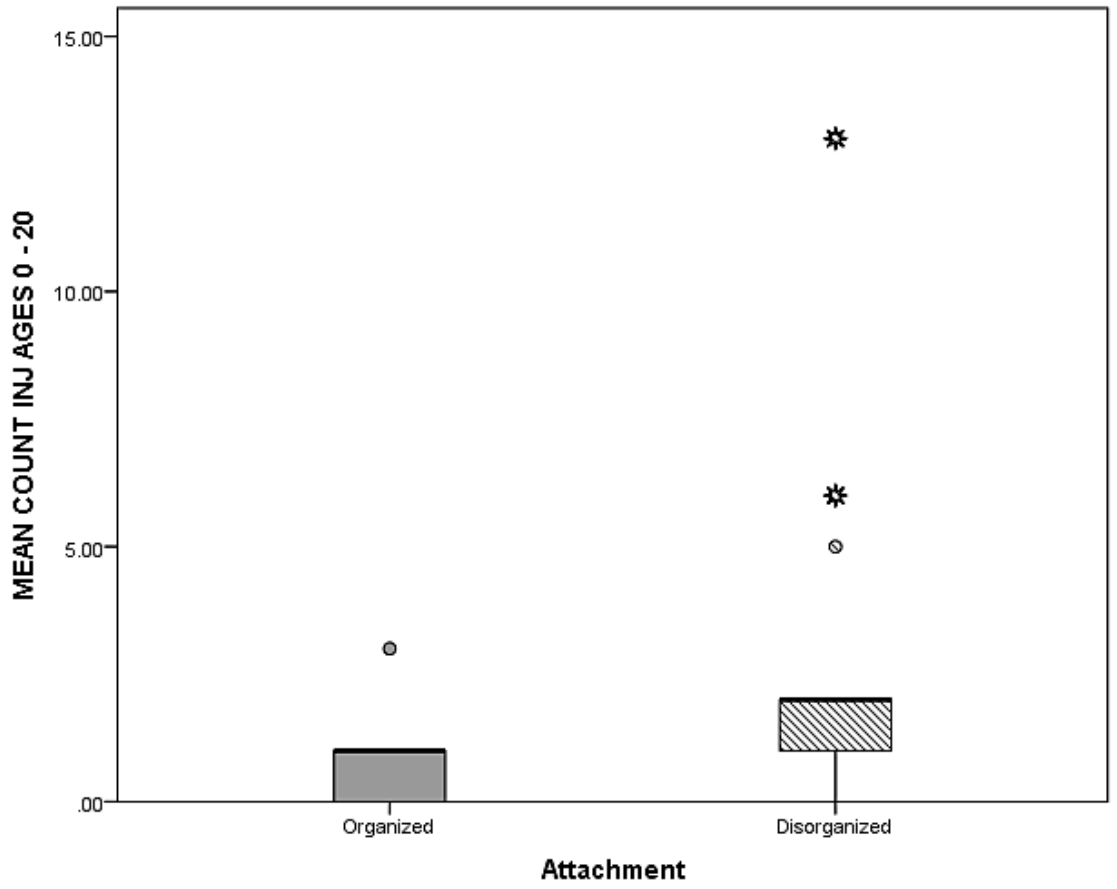
825 *Figure 1*: Central bar = median, lower box = 25th percentile, upper box = 75th percentile,

826 whiskers = highest and lowest values of the data set that are within 1.5 times the inter-quartile

827 range of the boxes, * = extreme outliers.

828 Figure 2: Total INJ Incidents Across 0 - 20 years by Attachment Categorization



829
830

831 *Figure 2*: Central bar = median, lower box = 25th percentile, upper box = 75th percentile,

832 whiskers = highest and lowest values of the data set that are within 1.5 times the inter-quartile

833 range of the boxes, ° = outliers, * = extreme outliers.

Figure 3: Average Subjective Well-Being Ratings based on 7 point Likert Scale (1 = lowest rating, 7 = highest rating)

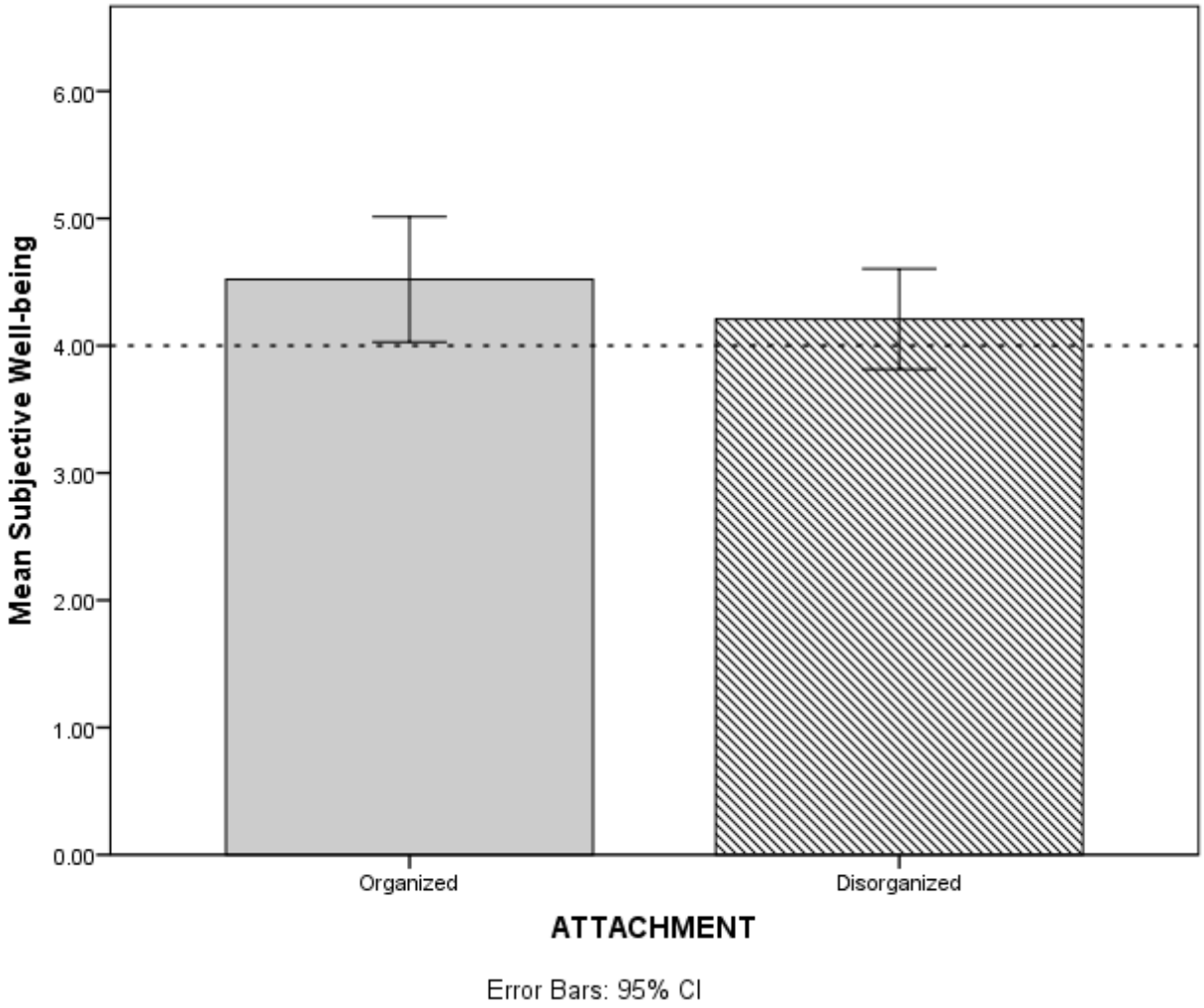
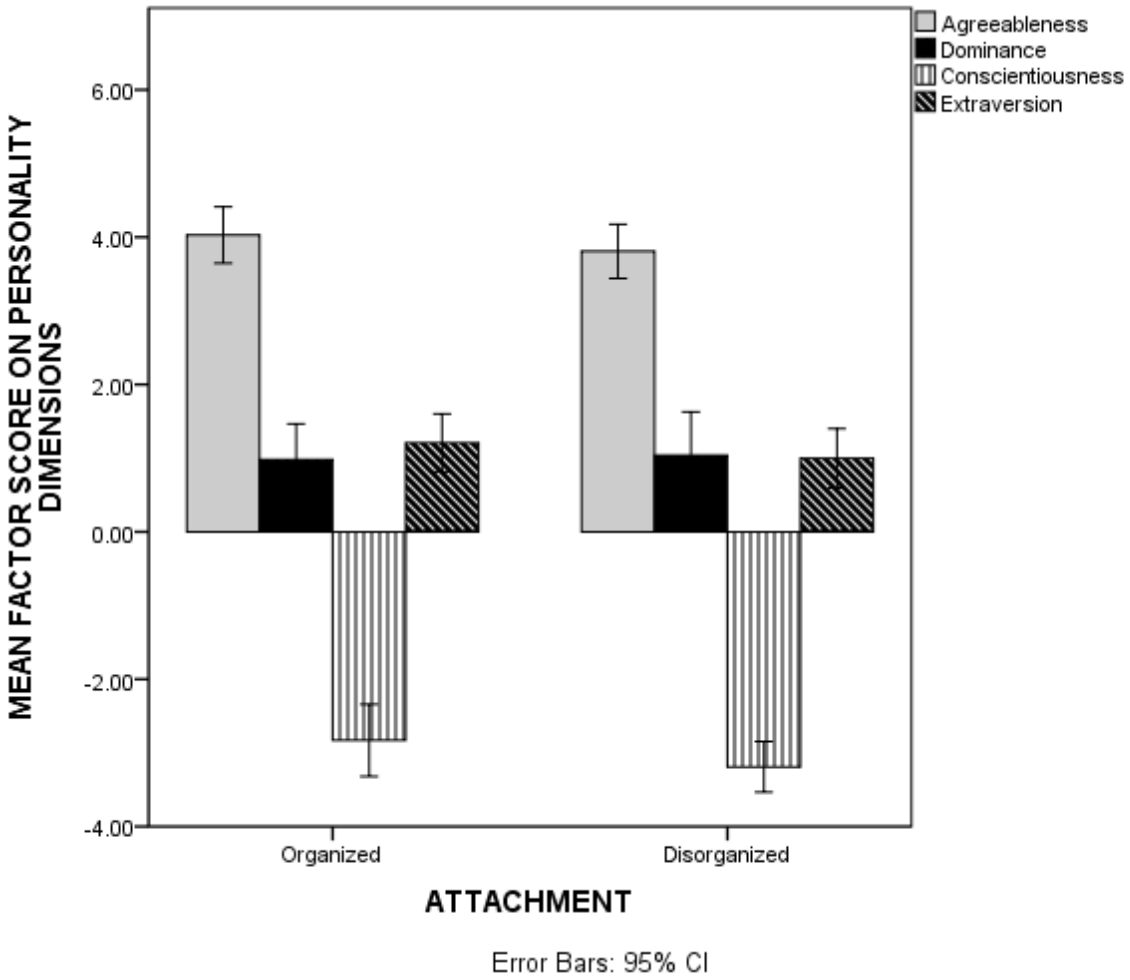


Figure 3: Error Bars = 95% Confidence Interval for the Mean; Reference line = Average Rating for Subjective Well-Being

839 Figure 4: Mean Scores on Personality Factors after Unit Weighting, Summing, and Averaging

840 across items loading on to that Factor.



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Appendix A: Ethogram

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).

Social Behaviors

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.

Affiliative behavior:

1. Touch/embrace: one individual extends hands or arms and gently makes contact with another individual.
2. Groom: picking through hair or at skin, removing debris with hand or mouth.

3. Play with partner: wrestling, tickling, chasing, and etcetera; may be accompanied by play face and laughing.
4. Play Chase: one individual runs after another group member playfully.
5. Watch/stare: one individual actively watching another group member, often within a few inches of one another.
6. 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.

Cart: cart or other vehicle approaches within 20 feet in front of the cage.

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. Ratings: 1 = displays either total absence or negligible amounts of the trait or state (least); 2 = displays small amounts of the trait on infrequent occasions; 3 = displays somewhat less than average amounts of the trait; 4 = displays about average amounts of the trait; 5 = displays greater than average amounts of the trait; 6 = displays considerable amounts of the trait on frequent occasions; 7 = 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 (Weiss et al., 2007; Weiss et al., 2009). 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. Ratings: 1 = displays either total absence or negligible amounts of the trait or state (least); 2 = displays small amounts of the trait on infrequent occasions; 3 = displays somewhat less than average amounts of the trait; 4 = displays about average amounts of the trait; 5 = displays greater than average amounts of the trait; 6 = displays considerable amounts of the trait on frequent occasions; 7 = 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 group. 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. Mischievous: 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.