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3 Long-term Effects of Infant Attachment Organization on Adult Behavior and Health in

4 Nursery-reared, Captive Chimpanzees (*Pan troglodytes*)

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## Abstract

41 This research traces the long-term effects on health, well-being, personality, and behavior of  
42 adult chimpanzees as a function of their attachment to a primary human caregiver assessed when  
43 they were 1 year of age (van IJzendoorn, Bard, Bakermans-Kranenburg & Ivan, 2009). Of the 46  
44 chimpanzees assessed at 1 year of age, we assessed health in 43 individuals, adult behavior in 20  
45 individuals, and adult well-being and personality in 21 individuals. Attachment disorganization  
46 was found to be a significant predictor of stereotypic rocking in adult chimpanzees ( $F(1,18) =$   
47  $7.50, p = .013$ ). For those subjects ( $N = 24$ ) with a full 20 years (birth through age 20) of health  
48 data available, both rearing experience and disorganized attachment were found to be significant  
49 predictors of upper respiratory infection frequency ( $F(2,21) = 8.86, p = .002$ ). Chimpanzees with  
50 disorganized attachment exhibited average subjective well-being as adults, whereas chimpanzees  
51 with organized strategies exhibited higher than average subjective well-being as adults. These  
52 results support the findings of human attachment research and are in line with attachment-based  
53 predictions for chimpanzees, such that the consequences of an early history of disorganized  
54 attachment may be adverse and long lasting.

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

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

59        Attachment theory was described first by Bowlby (1969, 1973, 1979, 1980), made testable  
60 by Ainsworth (Ainsworth, Blehar, Waters & Wall, 1978), and has since been studied  
61 extensively. Studies on various primates served both to validate attachment as an analogous  
62 construct in nonhuman primates and to clarify the effects of disrupted attachment bonds on  
63 physiological and behavioral systems (Laudenslager & Boccia, 1996). In humans, the quality of  
64 attachment to a primary caregiver, as assessed in the Strange Situation Procedure (SSP:  
65 Ainsworth, 1985a, 1985b, 1989), has been shown to have long-term consequences. Likewise,  
66 one-year-old, nursery-reared chimpanzees tested with the SSP were found to exhibit  
67 disorganization in their attachment system in proportions similar to those of human infants  
68 raised in poor quality orphanages (van IJzendoorn et al., 2009). Disorganized classification is  
69 distinct from Ainsworth's original three types of organized behavioral responses of secure,  
70 insecure-avoidant, and insecure-resistant (Ainsworth et al., 1978; Ainsworth, 1985a, 1985b,  
71 1989), and is exemplified by infants either exhibiting inconsistency or lacking a coordinated  
72 strategy for seeking comfort after being distressed (Main & Solomon, 1986; van IJzendoorn et  
73 al., 2009). Here we investigate the extent to which there are long-term consequences of early  
74 attachment classifications in chimpanzees. If the attachment system functions similarly in  
75 chimpanzees and in humans, we would expect to find poorer long-term outcomes in those  
76 chimpanzees with disorganized classifications than in those with any of the organized  
77 attachment classifications.

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

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

92 Studies of attachment in nonhuman primates have been conducted primarily with macaques  
93 (e.g. Mason & Green, 1962; Suomi, 2004; Suomi, Van der Horst & Van der Veer, 2008), titi  
94 monkeys (Hoffman, Mendoza, Hennessy & Mason, 1995), and squirrel monkeys (Hennessy,  
95 Kaplan, Mendoza, Lowe & Levine, 1979), and typically involve periods of separation (30  
96 minutes to an hour) which result in an immediate and significant increase in plasma cortisol  
97 levels. For titi monkeys, this adrenocortical response can persist through longer periods of  
98 separation (e.g. for a number of days or weeks: Mendoza, Capitanio & Mason, 2000).

99 Separations of infant macaques from their mothers cause disruptions of physiological systems,  
100 such as cardiac regulation, sleep rhythms, circadian rhythms, pituitary-adrenal systems,  
101 immunological systems, and cerebral spinal fluid. Additionally, during separation there are  
102 behavioral indicators of distress, such as increased vocalization and searching behaviors

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

107 In chimpanzees, attachment responses are equivalent to those seen in human infants and  
108 other nonhuman primate species (Bard & Nadler, 1983; Inoue, Hikami & Matsuzawa, 1992;  
109 Inoue & Hikami, 1993; van IJzendoorn et al., 2009). Characteristics of the rearing  
110 environments, such as the amount and quality of caregiver interactions with infants, have a  
111 significant impact on chimpanzee attachment patterns. Chimpanzees reared in a nursery  
112 environment in which caregivers spent relatively little time with infants (standard nursery care  
113 [ST] with 60 minutes per 24 hours: Bard, Bakeman, Boysen & Leavens, 2014a) exhibited a  
114 preponderance of disorganized attachment patterns, similar to those seen in humans raised in  
115 orphanages with minimal staff contact (van IJzendoorn et al., 2009). In contrast, chimpanzees  
116 reared in a responsive care [RC] nursery, in which human researchers spent four hours per  
117 weekday in continuous contact with infants and nurtured species-typical communication (Bard,  
118 1996; Bard et al., 2014b), were significantly less likely to exhibit disorganized attachment at  
119 one year of age (van IJzendoorn et al., 2009). It is clearly not desirable to deliberately place  
120 human or chimpanzee infants in non-optimal nurseries, but these comparative studies are  
121 extremely useful for understanding the importance of early experiences on the development of  
122 attachment in both species.

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

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

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

149 behavior (Mason, 2006; Mason & Rushen, 2008). However, in most circumstances, the  
150 presence of abnormal behavior is still an indicator that the animal's welfare is or has been poor.  
151 It is common wisdom that the number and/or frequency of abnormal behavior are an index of  
152 the degree to which that animal's welfare is compromised. For example, a greater variety and  
153 higher frequency of abnormal behaviors are associated with restrictive rearing (Davenport &  
154 Menzel, 1963; Davenport, Menzel & Rogers, 1966; Davenport, Rogers & Rumbaugh, 1973)..  
155 Behaviors documented as abnormal for chimpanzees include rocking or other stereotyped whole  
156 body movements, eye-poking, regurgitation and reingestion of foodstuffs, eating or  
157 manipulating feces, urophagy, stereotyped self-manipulation of body parts, thumb-sucking, etc.  
158 (Baker, 1997; Dieneske & Griffin, 1978; Fritz, Nash & Alford, 1992; Mallapur & Choudhury,  
159 2003; Martin, 2002). If disorganized attachment has long-term ramifications in chimpanzees,  
160 similar to those seen in humans, then such chimpanzees should exhibit impaired welfare as  
161 adults as measured by a higher frequency and/or a greater diversity of abnormal behavior.

162 Humans with disorganized attachment as infants have poor ability to cope with stress as  
163 adults (Liotti, 2004). Thus, chimpanzees with disorganized attachment may exhibit more  
164 behaviors associated with acute stress than those with organized attachment styles. Behaviors  
165 commonly interpreted as related to acute stressors in chimpanzees and other nonhuman primates  
166 include rough scratching (Baker & Aureli, 1997; Troisi, 2002) and yawning (Castles & Whiten,  
167 1998). Chronic stress has been shown to affect physiological systems (Cohen et al., 1997;  
168 Fahlke et al., 2000; Mendoza et al., 2000). Chronic stress can be observed as impaired immune  
169 response (Blecha, 2000), which, for example, has been linked with increased susceptibility to  
170 upper respiratory infection in nonhuman primates (Cohen et al., 1997). The ability to cope with  
171 stressful stimuli is an important component of welfare and well-being assessment (Maple &



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

174 The well-being of captive chimpanzees has been assessed through a survey (Weiss et al.,  
175 2009). Assessing welfare subjectively (as with a survey) is useful (e.g., due to the speed of data  
176 collection), particularly when survey results correlate with more objective welfare  
177 measurements (such as counting the number or frequency of abnormal behaviors). We predict  
178 that disorganized chimpanzees will be perceived as having lower levels of well-being than  
179 organized chimpanzees, based on the human research indicating disorganized attachment in  
180 infancy is predictive of decreased welfare for adults (Liotti, 2004; van IJzendoorn et al., 1999).

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

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

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

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

218 4 hours each weekday with humans who were trained to nurture social development, motor  
219 development, and species-typical communication in a manner similar to that provided by  
220 chimpanzee mothers (Bard et al., 2014b; Bard et al., 2014a). A large percentage of these  
221 nursery-reared chimpanzee infants, especially in ST, were determined to be disorganized in their  
222 attachment (72% of ST; 41% of RC). As in van IJzendoorn et al. (2009), the chimpanzee  
223 infants that were unclassifiable ( $n = 3$ ) were grouped together with the disorganized group,  
224 because they did not display organized attachment systems. Individuals that exhibited  
225 organized attachment (i.e., secure, insecure-avoidant, insecure-resistant) were categorized  
226 together primarily because there were small numbers of individuals in each category, and  
227 secondarily, because long-term research on attachment indicates that the most substantial  
228 differences in long-term consequences are found between those classified as disorganized and  
229 those classified as organized (van IJzendoorn et al., 1999). In comparison to the chimpanzees  
230 with an organized attachment system, the 1-year-old chimpanzees in the disorganized group  
231 exhibited significantly more rocking, spent significantly more time clutching towels, and spent  
232 significantly less time touching their attachment figure during both reunion episodes of the SSP  
233 (Figures 4 & 5 in van IJzendoorn et al., 2009).

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

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

244

245

## Methods

### 246 Note about Study Subjects

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

### 253 Study One: Behavioral Observations

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

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

266 **Study One Methods.** Behavioral observations were conducted in 1 hour time blocks  
267 balanced between 8 a.m. and 3 p.m., and totaled 6 – 10 hours per chimpanzee. In each 60-  
268 second interval the presence or absence of seven categories of events were recorded: abnormal  
269 behavior, stress-related behavior, affiliative behavior, aggressive behavior, submissive behavior,  
270 sexual behavior and environmental events (loud noise, approach of a human within 5 feet,  
271 displays or loud vocal chimpanzees in area, approach of vehicle within 15 feet). The mean total  
272 intervals observed for DA chimpanzees was 516.0 (MIN = 420.0, MAX = 600.0, SD = 51.99);  
273 the mean total intervals observed for the OA group was 569.5 (MIN = 475.0. MAX = 600.0, SD  
274 = 64.50). There was no significant difference in total intervals observed between the two  
275 attachment groups ( $F(1,18) = 4.17, p = .056$ ). However, given there was a trend, we choose to  
276 use proportions, rather than totals, as summary measures.

277 Of primary interest to this report were seven abnormal behavior categories (urophagy; feces-  
278 related; stereotypic rocking; stereotypic manipulation of body parts; regurgitation/reingestion of  
279 edible substances; hair plucking; other abnormal: Appendix A) and two stress-related behavior  
280 categories (rough scratching; yawning) (Baker & Aureli, 1997; Castles & Whiten, 1998; Troisi,  
281 2002). Data were collected using an iPaq recorder and Noldus Observer software. All  
282 statistical results reported were based on two-tailed probability tests. For the complete  
283 ethogram, see Appendix A.

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

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

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

310 and submissive behavior ( $\tau = -.253$ ,  $N = 20$ ,  $p = .054$ ) and between mean proportion of chimp  
311 vocalization and sexual behavior ( $\tau = -.269$ ,  $N = 20$ ,  $p = .045$ ). However, the mean proportion  
312 of intervals in which human approach was scored was nearly identical in the two attachment  
313 groups (.038 for OA and .039 for DA), as was the mean proportion of intervals in which chimp  
314 vocalization was scored (.065 for OA and .072 for DA). A MWU test confirmed no significant  
315 groupwise difference in mean proportion of human approach ( $p = .970$ ) or chimp vocalization ( $p$   
316  $= .650$ ). Therefore, any differences in stress behavior, affiliative behavior, submissive behavior  
317 and/or sexual behavior between groups cannot be attributed to group differences in human  
318 approaches or chimp vocalizations. There were no significant correlations found between any  
319 other of the environmental events and chimpanzee behaviors.

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

## 328 **Study Two: Health Assessments**

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

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

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

353 Chi-square tests were conducted to compare the disorganized and organized groups as either  
354 having or not having an incident of URI, DIA, or INJ during the relevant age span (yes/no in the  
355 5-year period). Fisher's exact test was used as some expected cell values were less than five. A



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

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

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

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

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

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

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

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

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

### 392 **Study Three: Survey Assessments**

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

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

402 sections related to personality (59 items) and to subjective well-being (4 items), and were based  
403 on previous surveys (Weiss et al., 2007; Weiss et al., 2009). Personality and subjective well-  
404 being (SWB) items ask the respondents to use a 7-point Likert scale to assess the degree to  
405 which a chimpanzee exhibits a certain trait (1 = least amount, 7 = most amount). Items and the  
406 traits the items are intended to measure are listed in Appendix B. Surveys were completed  
407 using surveymonkey.com. Four to 9 respondents completed surveys for each chimpanzee.  
408 Inter-rater reliability was calculated as a mixed-model two-way interclass coefficient for each  
409 subject on each item resulting in an average inter-rater reliability of .74 (ICC scores ranging  
410 from .57 to .87), with no difference in reliability scores between the two attachment groups ( $U =$   
411  $42.0, p = .360$ ). Multiple scores for each individual were averaged for a composite score before  
412 being entered into factor analysis. The two survey sections (Subjective Well-Being and  
413 Personality) were analyzed and reported in separate sections.

#### 414 **Study Three Results.**

415 ***Subjective Well-Being (SWB).*** A PCA Factor Analysis confirmed that the 4 SWB items  
416 correlated heavily and that one underlying factor accounted for 78.9% of the variance (see Table  
417 2 for loading scores). Item scores were therefore averaged to create a single composite SWB  
418 score for each individual that would still map onto the original Likert ratings (e.g., a rating of 4  
419 indicates average well-being). No significant difference was found between the two attachment  
420 groups in SWB (Mann Whitney  $U = 45.0, p = .510$ ). However, while the OA group confidence  
421 interval (CI [4.03, 5.01]) was above (and did not include) the average SWB score of 4, the DA  
422 group confidence interval did contain the average SWB score (CI [3.81, 4.60]: Figure 3). This  
423 result indicates that the OA group mean SWB score was significantly higher than average,  
424 whereas the DA group mean SWB score was not.

425        **Personality.** A previous study compared a sample of Yerkes chimpanzees to a much larger  
426 sample of zoo-living chimpanzees and found congruency on four extracted factors (two factors  
427 extracted from zoo populations were not found to be congruent with the Yerkes sample) (Weiss  
428 et al., 2007). Because Weiss et al.'s (2007) study results were based on a larger sample it was  
429 decided to use the items and unit-weights used in that study to calculate the same four factors  
430 (Dominance, Extraversion, Conscientiousness and Agreeableness). We concluded based on a  
431 Levene's test for homogeneity of variance that it was possible to use a parametric ANOVA test  
432 for analyses. No significant differences were found between the two attachment groups on any  
433 of the four personality factors (Figure 4). Agreeableness correlated significantly and positively  
434 with Conscientiousness ( $r = .656$ ,  $N = 21$ ,  $p = .001$ ) and Extraversion ( $r = .707$ ,  $N = 21$ ,  $p =$   
435  $.000$ ). Dominance correlated significantly and inversely with Conscientiousness ( $r = -.562$ ,  $N =$   
436  $21$ ,  $p = .008$ ). Stepwise regression analyses did not find either rearing or attachment group to be  
437 significant predictors for SWB or any of the Personality factors.

438        **Correlates with Behavior.** For the subjects that had data available, correlations were  
439 conducted to assess relations between the personality factors, SWB, and behaviors (abnormal  
440 behavior, affiliative behavior, aggressive behavior, submissive behavior, sexual behavior and  
441 stress behavior). Significant positive correlations were found between SWB and the personality  
442 factors Agreeableness ( $r = .646$ ,  $N = 21$ ,  $p = .002$ ) and Extraversion ( $r = .734$ ,  $N = 21$ ,  $p < .001$ ).  
443 Significant negative correlations were found between SWB and the means for abnormal  
444 behavior ( $r = -.510$ ,  $N = 20$ ,  $p = .021$ ) and stress behavior ( $r = -.486$ ,  $N = 20$ ,  $p = .011$ ).  
445 Agreeableness significantly and inversely correlated with abnormal behavior ( $\tau = -.368$ ,  $N = 20$ ,  
446  $p = .030$ ). Submissive behavior correlated significantly and inversely with Dominance ( $r = -$   
447  $.642$ ,  $N = 20$ ,  $p = .002$ ) and significantly and positively with Agreeableness ( $r = .681$ ,  $N = 20$ ,  $p$

448 = .001). Affiliative behavior correlated significantly and positively with abnormal behavior ( $r =$   
449 .665,  $N = 20$ ,  $p = .001$ ). No other significant correlations were found.

### 450 **Discussion**

451 We found long-term effects in the behavior and health of adult chimpanzees based on  
452 attachment tests conducted when the chimpanzees were one year of age (van IJzendoorn et al.,  
453 2009). Our findings were analogous to those for humans raised in poor quality orphanages  
454 (van IJzendoorn et al., 1999), thus providing support for attachment as an organizing feature of  
455 human and nonhuman primates during development. Specifically, chimpanzees identified as  
456 disorganized in infancy exhibited higher proportions of stereotypic rocking behavior as adults,  
457 and a higher incidence of health problems, including veterinary interventions for upper  
458 respiratory infections, than chimpanzees identified as organized. However, the two groups did  
459 not differ in stress-related behavior, social behaviors, or personality ratings. Therefore, the  
460 attachment system in chimpanzees likely functions in a similar way to that of humans; when this  
461 system has broken down in the infant, there can be long-term negative consequences into  
462 adulthood (Liotti, 2004; Lyons-Ruth, 1996; van IJzendoorn et al., 1999).

463 At Yerkes, one-year old, nursery-reared chimpanzees that were classified as disorganized  
464 exhibited more stereotypic rocking behavior during the separation episodes of the SSP than  
465 those classified as having an organized attachment with their primary caregivers. Since the  
466 short separations of the SSP are designed to stress the attachment system (Ainsworth et al.,  
467 1985), this indicates that one year old chimpanzees with disorganized attachment exhibit  
468 abnormal behavior when they experience moderate, acute stress (van IJzendoorn et al., 2009).  
469 Previous research has found that abnormal behavior in nursery-reared chimpanzees can be  
470 reduced by housing with canine companions (Pazol & Bloomsmith, 1993; Thompson,

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

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

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

502       The number of injuries was low for both attachment groups (a median of 1 in the 0 to 20 year  
503 period for chimpanzees with a history of organized attachment, and 2 in the 20 year period for  
504 adult chimpanzees with a history of disorganized attachment: Figure 2). Although there was a  
505 nonsignificant trend for total number of injuries to differ between DA and OA chimpanzees ( $p =$   
506  $.053$ ), this was associated with a large effect size (16% of the variance accounted for), which we  
507 consider to be a noteworthy result, particularly in our small sample. A higher frequency of  
508 injury for chimpanzees with a disorganized attachment history indicates that these chimpanzees  
509 received more aggression from conspecifics, because only injuries resulting from social  
510 interactions were considered for this study. Humans and rhesus monkeys with a history of  
511 disorganization show higher rates of aggressive behavior, rather than any change in received  
512 aggression (Suomi, 2004; van IJzendoorn et al., 1999). In the chimpanzees, we did not find  
513 significant differences in aggressive behavior towards conspecifics based on attachment  
514 classification. Nevertheless, the higher incidence of wounding in the chimpanzees with  
515 disorganized attachment may point to problems in negotiating harmonious social relationships  
516 at a more subtle level than we assessed in this study.

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

527 Interestingly, higher incidences of upper respiratory infections (URIs) were associated with  
528 disorganized attachment both in the first 5 years (measured by presence/absence) and over the 0  
529 – 20 year period (measured by total frequency). The frequency of these infections over the 0 –  
530 20 period was significantly associated with both attachment classification (21%) and rearing  
531 condition (27%). As expected, the 11 adult chimpanzees classified as disorganized had 1.3  
532 incidences of URI compared to the 0.8 incidences for those 13 adults classified as organized.  
533 Counter to expectations, the ten chimpanzees raised in responsive care that remained at Yerkes  
534 as adults exhibited a total of 1.7 incidences of URI in 20 years, compared to the 0.6 incidences  
535 of URI exhibited by the 14 adult chimpanzees that had been raised in the standard care nursery.  
536 It is possible that chimpanzees with disorganized attachment responses were more vulnerable to  
537 infection compared to those with organized attachment responses. It is also possible that being  
538 in the responsive care nursery, which increased time in contact with humans as part of the  
539 protocol, simply increased the number of inadvertent exposures to infection. It is an alternative



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

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

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

### 563 **Conclusions**

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

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

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808

809

**Tables**

810 Table 1

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

813

ADULT BEHAVIOR	ORGANIZED ATTACHMENT IN INFANCY		DISORGANIZED ATTACHMENT IN INFANCY	
	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

814

815 *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

818

819

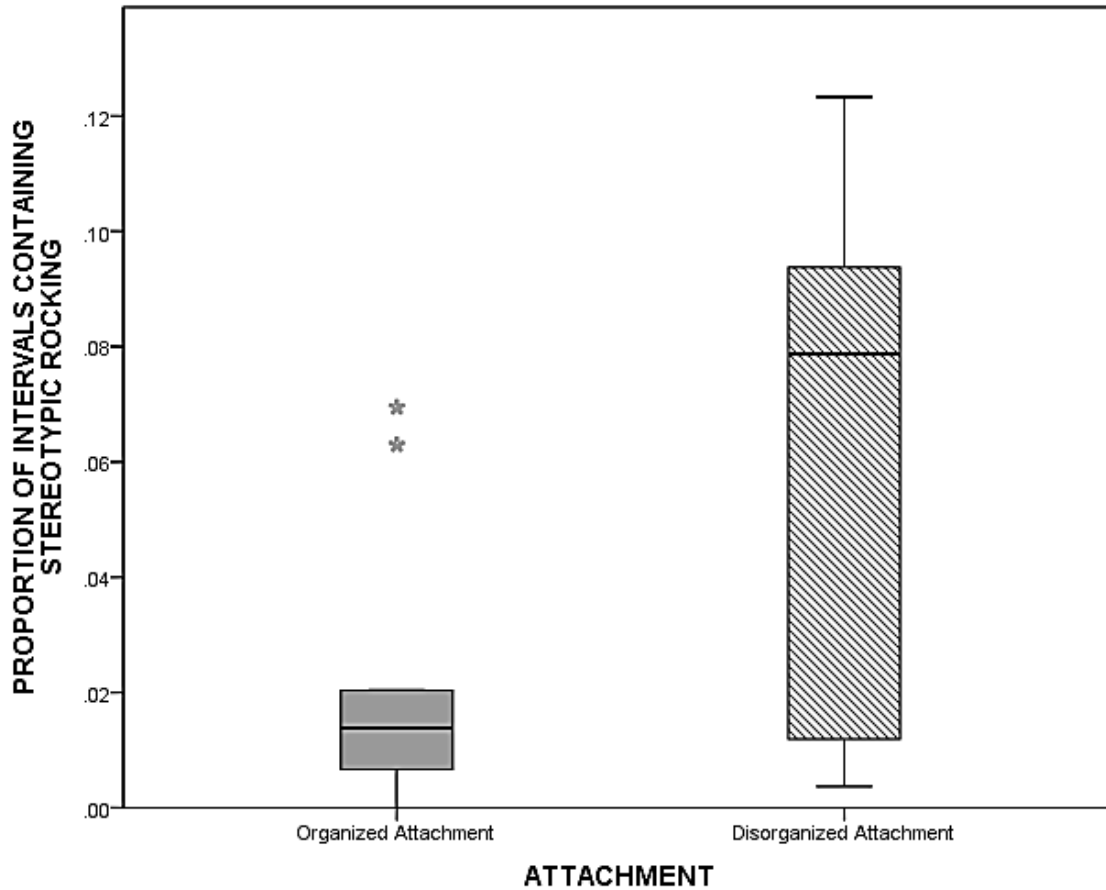
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**Figures**

821

Figure 1: Proportions of Stereotypic Rocking Behavior by Attachment Categorization

822



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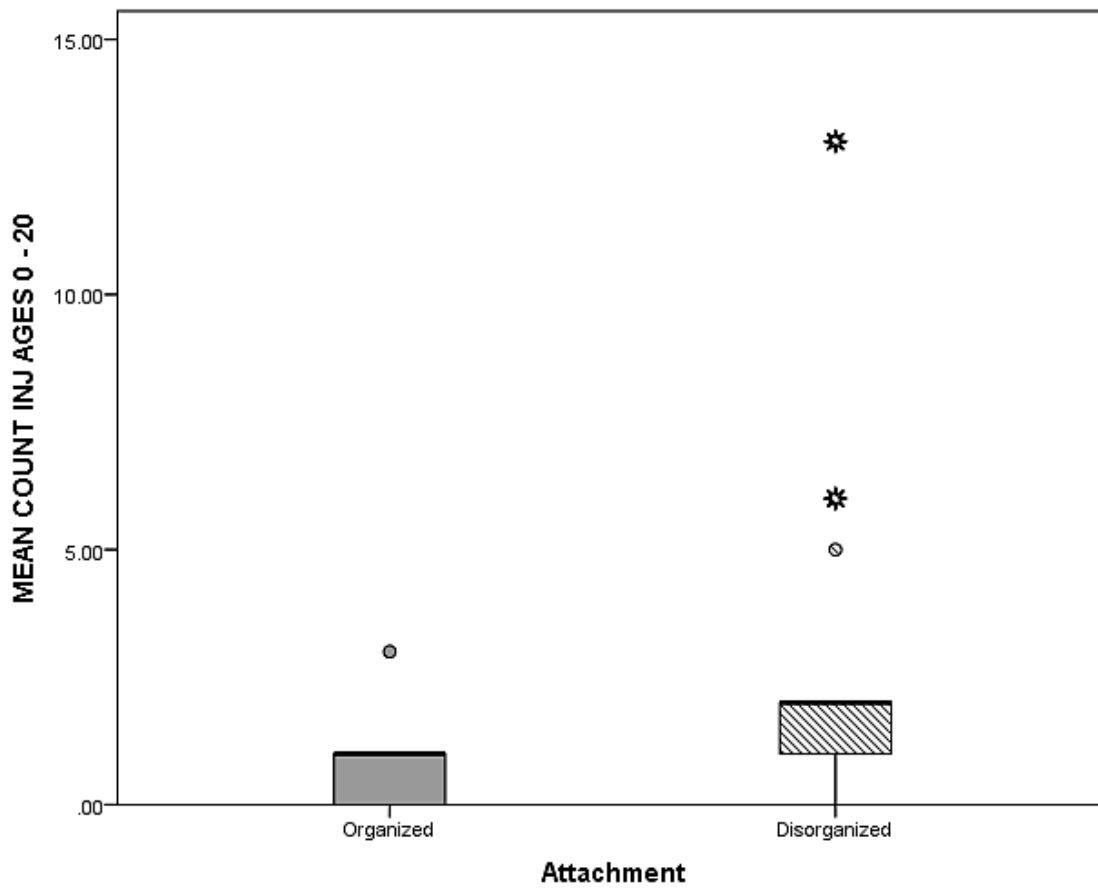
824

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

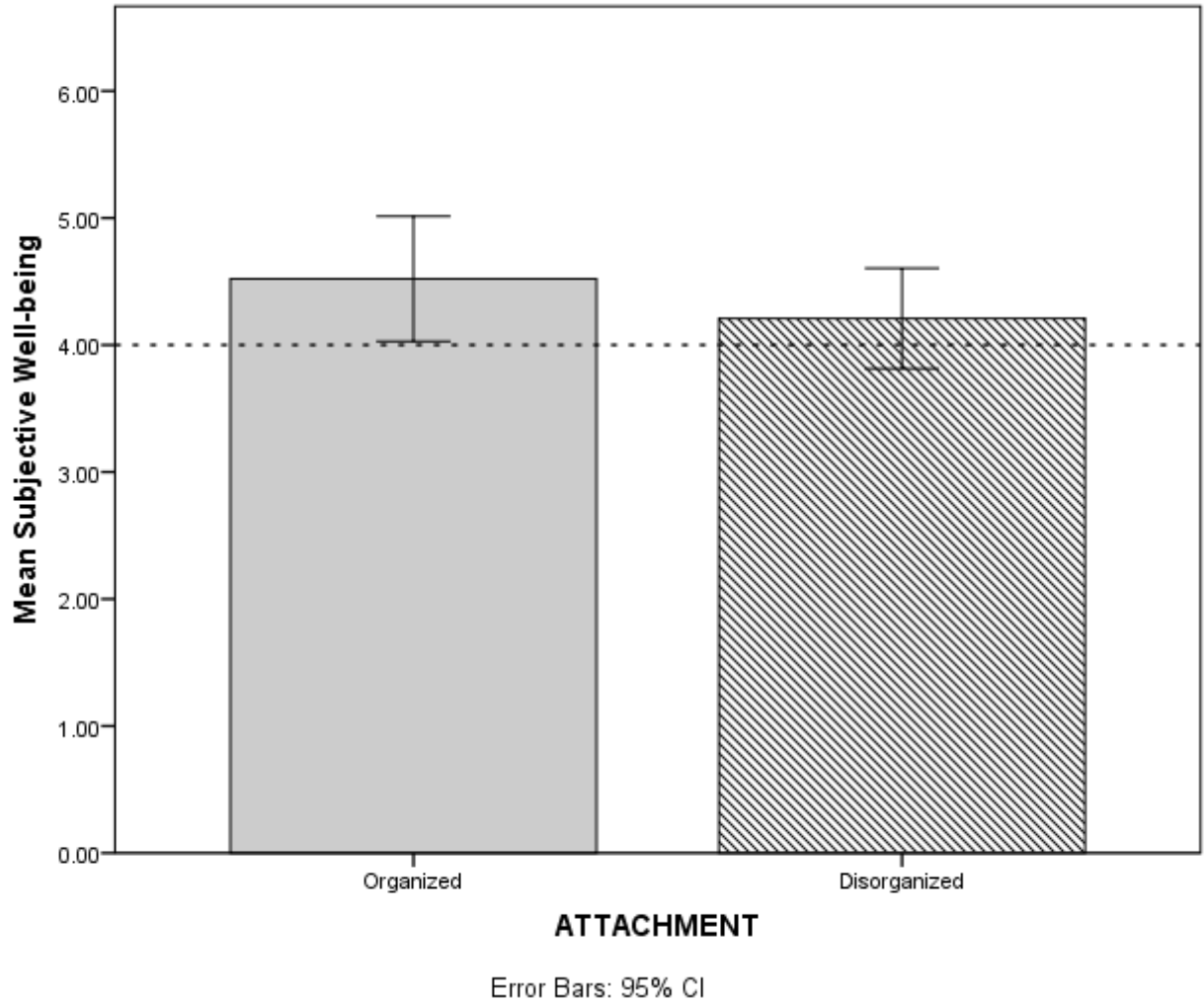


829  
830

831 *Figure 2: Central bar = median, lower box = 25<sup>th</sup> percentile, upper box = 75<sup>th</sup> 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.*



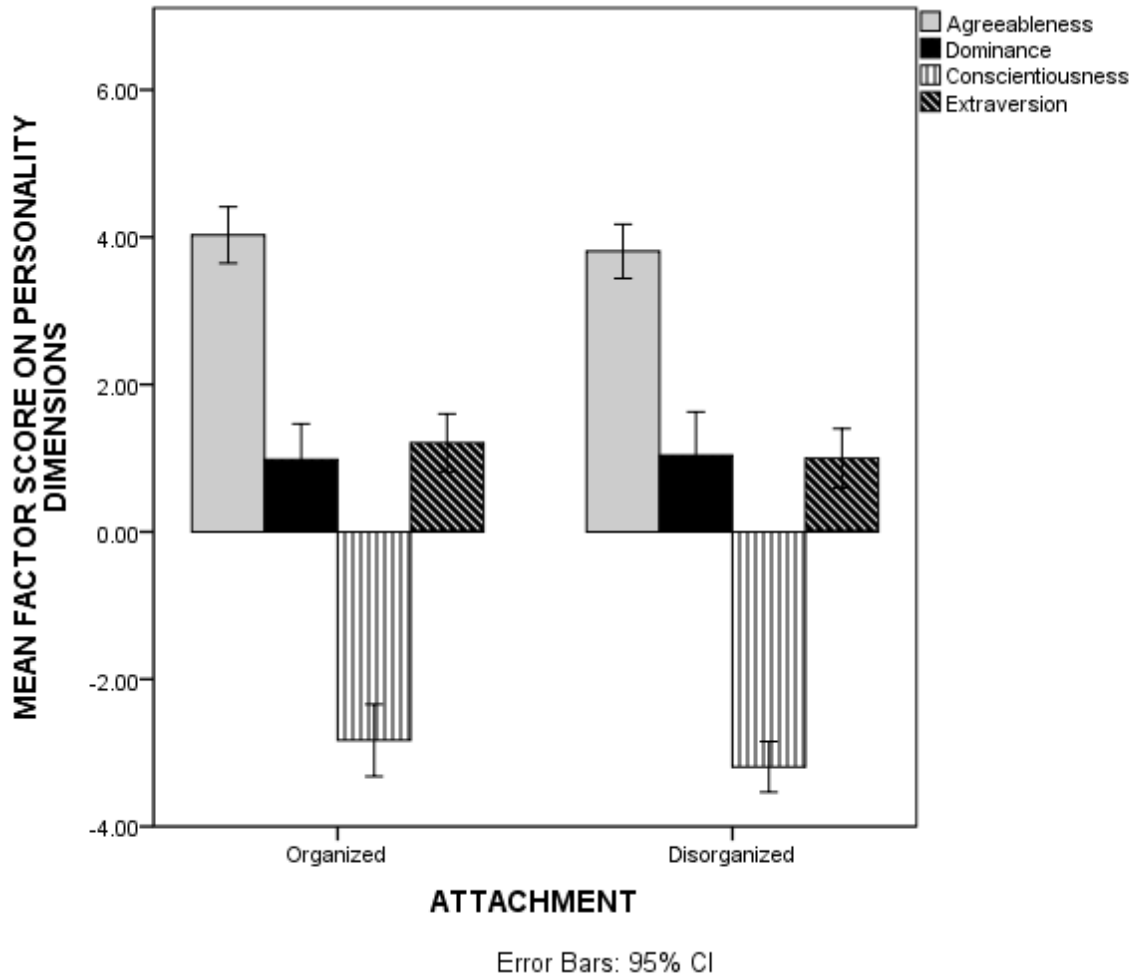
834 Figure 3: Average Subjective Well-Being Ratings based on 7 point Likert Scale (1 = lowest  
835 rating, 7 = highest rating)



836

837 *Figure 3: Error Bars = 95% Confidence Interval for the Mean; Reference line = Average Rating*  
838 *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.



841

842

843 **Appendix A: Ethogram**

844 Instructions: Record priority behavior in each category if it occurs during interval being scored  
845 (for each animal in observation group). Behaviors in each category are listed in order of priority  
846 (1-0 sampling, intervals are 60 seconds for all behaviors and environmental events).

847 **Social Behaviors**

848 ***Agonistic-aggressive behaviors:***

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

855 ***Agonistic-submissive behaviors***

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

862 ***Affiliative behavior:***

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

- 866 3. Play with partner: wrestling, tickling, chasing, and etcetera; may be accompanied by play  
867 face and laughing.
- 868 4. Play Chase: one individual runs after another group member playfully.
- 869 5. Watch/stare: one individual actively watching another group member, often within a few  
870 inches of one another.
- 871 6. Other affiliative: non-agonistic social behavior not defined elsewhere.

872 ***Sexual behavior:***

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

883 ***Abnormal behaviors:***

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

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

895 ***Stress-related behaviors:***

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

899 **Environmental Events:**

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

906 **Appendix B: Survey Questionnaire**

## 907 A. Section 1: Demographic Information

908 1. Please enter your name here:

909 2. Name of chimpanzee you are rating:

910 3. Location where you work with the chimpanzee:

911 4. How long have you worked with this chimpanzee?

912  0 – 1 year913  2 – 5 years914  6 – 10 years915  More than 10 years

916 5. How many hours per week, on average, do you spend working around this chimpanzee?

917 This includes working around the animal if you are cleaning, or otherwise working in the  
918 proximate area of the animal. This does not include DIRECT INTERACTION with the  
919 animal (this will be asked about later)

920  0 – 1 hour921  Between 1 and 5 hours922  More than 5 hours

923 6. How much time per week, on average, do you spend interacting directly with the

924 animals? This includes feeding, giving enrichment, doing veterinary procedures (while  
925 animal is awake), conducting research with the animal, training the animal using positive  
926 reinforcement, etcetera.

927  0 – 1 hour928  Between 1 and 5 hours

929           ○ More than 5 hours

930       7. In what capacity do you work with the chimpanzee? Mark as many as apply.

931           ○ Veterinarian

932           ○ Biomedical researcher

933           ○ Cognitive or behavioral researcher

934           ○ Caretaker

935           ○ Behavioral management (training, enrichment)

936           ○ Other (please specify):

937       8. If this animal receives positive reinforcement training, please indicate the average amount  
938           of time per week the animal is trained (it does not require that you be the trainer).

939           ○ Does not receive training

940           ○ Less than 30 minutes

941           ○ Between 30 minutes and 1 hour

942           ○ Between 1 and 2 hours

943           ○ Between 2 and 5 hours

944           ○ More than 5 hours

945       9. If this animal receives positive reinforcement training, how long has the animal been  
946           getting training?

947           ○ Does not receive training

948           ○ Less than three months

949           ○ Between 3 and 6 months

950           ○ Between 6 and 12 months

951           ○ More than one year

- 952 B. Section II: Subjective Well-being (adopted from A. Weiss, et al., 2009) Instructions: This  
953 part of the questionnaire has four questions, all relating to the subjective well-being of the  
954 chimpanzee you are rating. Each asks about a different personality dimension or trait  
955 relating to subjective well-being. The following scale should be used to make your ratings.  
956 Please do not discuss your rating of any particular chimpanzee with anyone else! This is  
957 necessary to obtain valid reliability coefficients for the traits. Please give a rating for each  
958 item even if your judgment seems to be based on purely subjective impression of the  
959 chimpanzee and you are somewhat unsure about it. Ratings: 1 = displays either total absence  
960 or negligible amounts of the trait or state (least); 2 = displays small amounts of the trait on  
961 infrequent occasions; 3 = displays somewhat less than average amounts of the trait; 4 =  
962 displays about average amounts of the trait; 5 = displays greater than average amounts of the  
963 trait; 6 = displays considerable amounts of the trait on frequent occasions; 7 = displays  
964 extremely large amounts of the trait (most).
- 965 1. Estimate the amount of time the chimpanzee is happy, contented, enjoying itself, or  
966 otherwise in a positive mood. Assume that at other times the chimpanzee is unhappy,  
967 bored, frightened, or otherwise in a negative mood.
  - 968 2. Estimate the extent to which social interactions with other chimpanzees are satisfying,  
969 enjoyable experiences as opposed to being as source of fright, distress, frustration, or  
970 some other negative experience. It is not the number of social interaction that should be  
971 estimated, but the extent to which social interactions that do occur are a positive  
972 experience for the chimpanzee. Use as many social interactions as you can recall as a  
973 basis for your judgment.
  - 974 3. Estimate, for this chimpanzee, the extent to which it is effective or successful in



975 achieving its goals or wishes. Examples of goals would be achieving desired locations,  
976 devices, or materials in the enclosure. Keep in mind that each chimpanzee will  
977 presumably have its own set of goals that may be different from other chimpanzees.

978 4. Imagine how happy you would be if you were that chimpanzee for a week. You would  
979 be exactly like that chimpanzee. You would behave the same way as that chimpanzee,  
980 and would feel things the same way as that chimpanzee.

981 C. Section III: Personality Trait Assessment (adopted from combination of (Weiss et al., 2007;  
982 Weiss et al., 2009). Instructions: Chimpanzee personality assessments can be made with this  
983 questionnaire by assigning a numerical score for all of the personality traits listed below.  
984 Make your judgments on the basis of your own understanding of the trait guided by the short,  
985 clarifying definition following the trait. Each chimpanzee's own behaviors and interactions  
986 with other chimpanzees should be the basis for your numerical ratings. Use your own  
987 subjective judgment of typical chimpanzee behavior to decide if the chimpanzee you are  
988 scoring is above, below, or average for a trait. Please give a rating for each trait even if you  
989 are unsure if your judgment seems to be based on a purely subjective impression of the  
990 chimpanzee and you are somewhat unsure about it. Please do not discuss your rating of any  
991 particular chimpanzee with anyone else. This is to make sure we obtain valid reliability  
992 coefficients for the traits. Ratings: 1 = displays either total absence or negligible amounts of  
993 the trait or state (least); 2 = displays small amounts of the trait on infrequent occasions; 3 =  
994 displays somewhat less than average amounts of the trait; 4 = displays about average  
995 amounts of the trait; 5 = displays greater than average amounts of the trait; 6 = displays  
996 considerable amounts of the trait on frequent occasions; 7 = displays extremely large  
997 amounts of the trait (most).

- 998 1. Active: spends little time idle and seems motivated to spend considerable time either  
999 moving around or engaging in some overt, energetic behavior.
- 1000 2. Affectionate/Friendly: seems to have a warm attachment or closeness with other  
1001 chimpanzees. This may entail frequent grooming, touching, embracing, or lying next  
1002 to others.
- 1003 3. Affiliative/Agreeable/Sociable: Appears to like the company of others. Seeks out  
1004 social contact with, or showing preference for, another animal; for example, playing,  
1005 walking next to, or sitting with another animal.
- 1006 4. Aggressive: Often initiates fights or other menacing and agonistic encounters with  
1007 other chimpanzees.
- 1008 5. Anxious: Hesitant, indecisive, tentative, jittery.
- 1009 6. Autistic: does not make eye contact, and/or not well integrated into the social group.
- 1010 7. Bold: Daring, not restrained or tentative. Not timid, shy, or coy.
- 1011 8. Bullying: Overbearing and intimidating towards younger or lower ranking  
1012 chimpanzees.
- 1013 9. Calm: Equable, restful; reacts to others in an even, calm way; is not easily disturbed  
1014 or agitated.
- 1015 10. Cautious: Exhibits a careful, measured approach to investigating things.
- 1016 11. Clumsy: Subject is relatively awkward or uncoordinated during movements including  
1017 but not limited to acrobatics, walking, and play.
- 1018 12. Considerate/Kind: Often consoles others in distress to provide reassurance.
- 1019 13. Cool: Subject seems unaffected by emotions and is usually undisturbed, assured, and  
1020 calm.

- 1021 14. Decisive: Subject is deliberate, determined, and purposeful in its activities.
- 1022 15. Deceptive: Deceives others for own benefit.
- 1023 16. Defiant: Assertive or contentious in a way inconsistent with the usual dominance  
1024 order. Maintains these actions despite unfavorable consequences or threats from  
1025 others.
- 1026 17. Dependent: Often relies on other chimpanzees for leadership, reassurance, touching,  
1027 embracing, and other forms of social support.
- 1028 18. Depressed: Often appears isolated, withdrawn, sullen, brooding and has reduced  
1029 activity.
- 1030 19. Disorganized: Subject is scatterbrained, sloppy or haphazard in its behavior as if not  
1031 following a consistent goal.
- 1032 20. Dominant: Able to displace, threaten, or take food from other chimpanzees. Or  
1033 subject may express high status by decisively intervening in social interactions.
- 1034 21. Distractible: Subject is easily distracted and has a short attention span.
- 1035 22. Eccentric: Shows stereotypies or unusual mannerisms.
- 1036 23. Erratic: Subject is inconsistent, indefinite, and widely varying in its behavior and/or  
1037 moods.
- 1038 24. Excitable: Easily aroused to an emotional state.
- 1039 25. Fearful: Subject reacts excessively to real or imagined threats by displaying behaviors  
1040 such as screaming, grimacing, running away, or other signs of anxiety and distress.
- 1041 26. Gentle: Subject responds to others in an easy-going, kind, and considerate manner.  
1042 Subject is not rough or threatening.
- 1043 27. Helpful: Subject is willing to assist, accommodate, or cooperate with other

- 1044 chimpanzees.
- 1045 28. Human Oriented: Very interested in human activities around their enclosure. Solicits  
1046 support from humans.
- 1047 29. Imitative: Subject often mimics, or copies behaviors that it has observed in other  
1048 chimpanzees.
- 1049 30. Impulsive: Often displays some spontaneous or sudden behavior that could not have  
1050 been anticipated.
- 1051 31. Independent: Subject is individualistic and determines its own course of action  
1052 without control or interference from other chimpanzees.
- 1053 32. Inquisitive/Curious: Readily explores new situations, objects or animals.
- 1054 33. Intelligent: Quick and accurate in judging and comprehending both social and  
1055 nonsocial situations.
- 1056 34. Inventive: More likely than others to engage in novel behaviors, e.g. use new devices  
1057 or materials in their enclosure.
- 1058 35. Irritable: Often seems in a bad mood or is impatient and easily provoked to anger,  
1059 exasperation, and consequent agonistic behavior.
- 1060 36. Jealous/Attention-seeking: Often troubled by others who are in a desirable or  
1061 advantageous situation such as having food, a choice location or having access to  
1062 social group. May attempt to disrupt activities or make noise to get attention.
- 1063 37. Lazy: Subject is relatively inactive, indolent, or slow moving and avoids energetic  
1064 activities.
- 1065 38. Manipulative: Is able to get others to do things without using force.
- 1066 39. Methodical: Does things in a logical, organized manner following a consistent goal.

- 1067 40. Mischievous: Engages in activities or behavior with the goal of provoking a negative  
1068 reaction from someone or doing something that has previously been established as not  
1069 socially acceptable.
- 1070 41. Persistent: Tends to continue in a course of action, task, or strategy for a long time or  
1071 continues despite external interference.
- 1072 42. Playful: Is eager to engage in lively, vigorous, sportive or acrobatic behaviors with or  
1073 without other chimpanzees.
- 1074 43. Predictable: Behavior is consistent and steady over extended periods of time. Does  
1075 little that is unexpected or deviates from its usual behavioral routine.
- 1076 44. Protective: Shows concern for other chimpanzees and often intervenes to prevent  
1077 harm or annoyance from coming to them.
- 1078 45. Quitting: Subject readily stops or gives up activities that have recently been started.
- 1079 46. Reckless: Subject is rash or unconcerned about the consequences of its behaviors.
- 1080 47. Relaxed: Does not show restraint in postures and movements. Is not tense.
- 1081 48. Self-Caring: Shows high, but healthy level of self-grooming and cleanliness.
- 1082 49. Sexual: Engages in frequent copulations and/or masturbation.
- 1083 50. Socially-inept: Acts inappropriately in a social setting.
- 1084 51. Solitary: Prefers to spend considerable time alone not seeking or avoiding contact  
1085 with other chimpanzees.
- 1086 52. Stingy: Is excessively desirous or covetous of food, favored locations, or other  
1087 resources in the enclosure. Is unwilling to share these resources with others.
- 1088 53. Submissive: Subject often gives in or yields to another chimpanzee. Subject acts as if  
1089 it is subordinate or of lower rank than other chimpanzees.

- 1090            54. Sympathetic: Subject seems to be considerate and kind towards others as if sharing  
1091            their feelings or trying to provide reassurance.
- 1092            55. Temperamental/Moody: Inconsistent and wildly varying in moods and behaviors.
- 1093            56. Timid: Lacks confidence and is easily alarmed and is hesitant to venture into new  
1094            social or nonsocial situations.
- 1095            57. Unemotional: Subject is relatively placid and unlikely to become aroused, upset,  
1096            happy, or sad.
- 1097            58. Unperceptive: Subject is slow to respond to or understand moods, dispositions, or  
1098            behaviors of others.
- 1099            59. Vulnerable: Subject is prone to be physically or emotionally hurt as a result of  
1100            dominance displays, highly assertive behavior, aggression, or attack by another  
1101            chimpanzee.