Effects of Sex and Early Rearing Condition on Adult Behavior, Health, and Well-Being in Captive Chimpanzees (*Pan troglodytes*)

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Abstract

Scientific evaluation of management strategies for captive species is part of the establishment of best practices for animal welfare. Here we report the effects of sex, rearing, and a sex-by-rearing interaction on adult, captive chimpanzees' (*Pan troglodytes*) behavior, health, well-being, personality, and orientation towards humans based on multiple methods (observation, animal records, and surveys). Chimpanzees raised in three conditions, mother-reared (MR), standard nursery (ST) and an experimental nursery (RC), were assessed approximately 20 years after their differential rearing experiences concluded. Sex had a significant effect on behavior towards conspecifics (aggression [M>F]; affiliation [F>M]), on abnormal behavior (rocking [M>F]), and on likelihood of incurring at least one injury (between ages 6 and 10 [M>F]). Rearing condition had a significant impact on behavior towards humans (negative solicitation [RC=ST>MR=ST]; neutral behavior [RC>ST> MR], yawning (RC=ST>MR=ST), subjective well-being (MR=ST>RC=ST), and on GI illness frequency (RC>ST=MR). Sex interacted with rearing on aggression towards humans (for males, RC>MR=ST), frequency of upper respiratory infection (URI: for males RC>MR=ST)) and likelihood of at least one URI between the ages of 11 and 15 (RC males>ST males). Our findings support the conclusion that there are long-term effects of both early rearing and sex on captive adult chimpanzee welfare.

Abbreviations: AF-HO, Affiliative Human Orientation; AG-HO, Aggressive Human Orientation; F, females; GAW, Great Ape Wing; GI, gastro-intestinal infection; M, males; MR, mother-reared; RC, responsive care; ST, standard care; SWB, subjective well-being; URI, upper respiratory infection

Keywords: abnormal behavior; animal behavior; animal welfare; chimpanzee; health; sex factors

1.0 Introduction

Welfare is a multi-faceted concept, incorporating aspects of an organism's biology (Yamanashi et al. 2016), affective state (Boissy et al. 2007), behavior (Troisi 2002; Clubb and Vickery 2006), and environment (Olsson and Westlund 2007; Rushen and Passillé 1992). As the science of animal welfare has progressed, our understanding of the various factors which may affect and/or be indicative of welfare has also grown. Currently, we continue to discover, develop, and assess animal management practices toward the goal of optimal welfare (Mellor, Patterson-Kane, and Stafford 2009; Hemsworth et al. 2015). A broad approach to this continual assessment is recommended by the breadth of the existing, scientific literature (review of concepts and measurements related to welfare: Broom 1991; welfare concepts related to farm animals: Fraser and Broom 1990; scientific assessment of welfare: Hemsworth et al. 2015; animal welfare in zoos: Mallapur, Waran, and Sinha 2005; Maple and Perdue 2013; Marriner and Drickamer 1994; stereotypic behaviors and animal welfare: Mason 2006; Mason and Rushen 2008; animal welfare science: Mellor, Patterson-Kane, and Stafford 2009; biology, stress, and animal welfare: Moberg 2000).

Managing captive animals toward providing the best possible welfare outcomes is further complicated by the multitude of factors, which impact any individual animal's well-being. For example, an animal's individual traits, such as temperament (Clarke and Boinski 1995; Heath-Lange, Ha, and Sackett 1999; Mason 2000), can have significant impact across the lifespan, as does early environment (e.g. rearing experience: Andrews and Rosenblum 1994; Belsky 2005; Bloomsmith et al. 2003; Bogart et al. 2014). Indeed, individual characteristics may interact with early experience to impact an animal's response to the environment, and these responses may in turn become organized in ways that continue to have significant impact through adulthood (e.g. attachment strategy: Clay et al. 2015; Crawford et al. 2007; Grossmann and Grossmann 1991). Rearing environments, for animals and for humans, have been

[1]AF-HO: Affiliative Human Orientation; [2]AG-HO: Aggressive Human Orientation; [3]F: Females; [4]GAW: Great Ape Wing; [5]GI: Gastro-Intestinal Infection; [6]M: Males; [7]MR: Mother-reared; [8]RC: Responsive care; [9]ST: Standard care; [10]SWB: Subjective Well-being; [11]URI: Upper Respiratory Infection

shown to significantly impact adult behavior and biology in many specific ways (e.g. depression: Gilmer and McKinney 2003; sexual behavior: King and Mellen 1994; neuroendocrine system: Ladd et al. 2000; ability to adapt: Sackett, Novak, and Kroeker 1999; Sroufe, Egeland, and Kreutzer 1990; behavior: Suomi 1997; cognitive functioning: Vorria et al. 2003; cortical organization: Bogart et al. 2014). If we wish to responsively attend to and maximize the welfare of animals in our care, we need to be aware of the ways in which early experience impacts those animals both short-term and long-term and to explore as many areas of potential impact as possible. As we learn, we also need to modify, and continue to scientifically evaluate our short-term and long-term management practices to maximize the welfare of individual animals. In this paper, we report findings for the long-term effects of early rearing differences in captive chimpanzees (*Pan troglodytes*). We applied scientific analyses to a variety of data, including behavior, health, personality, and subjective well-being, and compared adult chimpanzees from three different early rearing environments on these measures. We hope that these data will generate further exploration and objective assessment of best practices for the early rearing of captive chimpanzees, particularly those who cannot be raised by their biological, conspecific mother.

During the first year of life the effects of early rearing were assessed for chimpanzees, some of which were born and raised at the Yerkes National Primate Research Center. Chimpanzees raised under two different nursery conditions, Standard Care (consisting of peer-rearing and limited human contact) and Responsive Care (an intervention designed to improve coping and species-typical communication in nursery-raised chimpanzees), and mother-raised chimpanzee infants were tested on various measures (the mother-reared infants were tested less often and, in some cases at other facilities, during brief separations from their mothers: (Hallock, Worobey, and Self 1989). The results of these assessments have been reported in detail elsewhere but here, we summarize those relevant to sex and rearing. The two nursery groups differed in emotional profiles, as newborns (in expressing anger versus distress, and in displaying vocal greetings during standardized testing: Bard 2003), and in the first year of life (in

ratings of amount and quality of positive emotions and fearful emotions: Bard, Bakeman, et al. 2014; Bard and Gardner 1996; and in fussing and crying: Bard 2000). RC[8] infant chimpanzees expressed more active, prosocial, positive emotions, and less fussing & crying than did ST[9] infants (Bard 2000; Bard, Bakeman, et al. 2014). As 30-day-old newborns, MR[7] chimpanzees differed from the nursery groups in orientation to animate (humans) and inanimate objects (MR exhibited lower levels), motor performance (MR were less mature), arousal (higher in MR), and regulation of behavioral state (MR less regulated: Bard et al. 2011). In the first 3 months of life, MR and nursery-reared chimpanzees differed in amount and intensity of fussing and crying (MR less: Bard 2000). RC and ST 9-month-old infants differed in hand use during standardized testing: RC used their left hands to hold onto caregivers while grasping objects with their right hand, whereas ST used their right hand to hold on and their left to grasp objects (Bard 1998). Across the first year of life, there were significant differences between ST and RC chimpanzees in joint attention, cooperativeness, and attachment: RC improved both types of triadic performance (Bard, Bakeman, et al. 2014) and decreased dysfunctional attachments (van IJzendoorn et al. 2009). Infant chimpanzees with dysfunctional attachments were significantly more likely to show abnormal rocking and clutch towels rather than caregivers for self-comfort (Bard, Dunbar, et al. 2014; van IJzendoorn et al. 2009). Interactions between sex and rearing were found in the nursery-reared infants: in smiling in the first 30 days of life (Bard et al. 2005) and in hand-to-mouth self-calming in the first 3 months of life (Bard 1998). In both these cases, there were significant differences between males and females raised in ST, but no sex differences in chimpanzees raised in RC. The interpretation was that sex differences were negated when care was more responsive to individual needs (as in RC versus ST).

Chimpanzees have a long lifespan and a relatively long period of dependence on their mothers (Bard 1994; Bloomsmith et al. 2003; Goodall 1986). Rearing environment has an impact on captive chimpanzees' adult behavior (Bloomsmith et al. 2002; Bloomsmith et al. 2006; Brent 2001; Davenport and Rogers 1970; Dienske and Griffin 1978; Freeman and Ross 2014) and biology (e.g. Bogart et al. 2014;

Yamanashi et al. 2016). In chimpanzees, some long-term outcomes of early rearing have been shown to be modified by sex (Nash et al. 1999) and by individual differences in attachment strategies (Bard et al. 2005; Clay et al. 2015; van IJzendoorn et al. 2009). It is important to note that RC and ST rearing environments differed only from birth through the first year of age; thereafter, both groups experienced the ST nursery environment. In contrast, the environment remained consistent for MR individuals from birth through adulthood. As older infants or juveniles, both ST and RC chimpanzees were moved out of the nursery environment, to share the physical environments of the MR chimpanzees and usually to live in social groups containing nursery-reared and mother-reared individuals. Since we know that early rearing experiences impact emotional, cognitive, and social outcomes in young chimpanzees, we investigate here the extent to which they might impact welfare outcomes in adult chimpanzees such as stress levels, social behavior and health. Here we present findings regarding the relative impact of sex and early rearing on the behavior, well-being, personality, human orientation and health of adult chimpanzees.

2.0 Methods

2.1 Statement of Ethical Compliance

All research reported here was conducted in accordance with the Guidelines for the Use of Animals in Research (Guidelines for the use of animals in research 1991) and with the Guide for the Care and Use of Laboratory Animals (*Guide for the Care and Use of Laboratory Animals* 2011).

2.2 Early Rearing Environments

Infants whose mothers exhibited adequate maternal behaviors were raised by their biological mothers typically from birth until maturity. Veterinary personnel evaluated each case of inadequate maternal care before deciding to place any infant into nursery care, balancing the desire to keep each

148 infant with the mother and maintaining the health of the infant. Therefore, infants were placed in the
149 nursery only when it was decided to be crucial for infant survival. The responsive care nursery was
150 designed in 1990 (Bard, 1996), and was given to infants that arrived in the nursery when they were less
151 than 24 hours old, between 1991 and 1995. All other infants placed in the nursery between 1987 and
152 1995, and arriving after 1 day of age, received standard nursery care.
153 2.2.1 Standard Care Nursery: The Standard Care (ST) nursery at Yerkes consisted of institutional
154 routines for the chimpanzees and for their human caretakers. Infant chimpanzees were placed in
155 incubators for their first 30 days of life and were handled by caretakers every 2 hours when they were
156 fed, had their diapers changed, and received various health checks, such as measurement of
157 temperature. After about 30 days, nursery chimpanzees were housed in cages with same-aged
158 conspecifics and rolled up towels (for padding and clinging). Human caretakers provided feeding and
159 health checks every 4 hours, spending about 10 minutes with the chimpanzees. At about 7 months of
160 age, nursery chimpanzees spent much of the day in a larger nursery room with play structures and toys.
161 After reaching a year of age, bottles were replaced by cups, towels were removed (van IJzendoorn et al.
162 2009), and the chimpanzees spent some time in outdoor play yards. Milk was still given during morning
163 and evening hours, but around lunch time, juice and food were delivered by a caretaker, who often
164 remained (up to an hour) to play with the chimpanzees. Between the ages of 1 to 5 years the young
165 chimpanzees were moved out of the nursery and onto the Great Ape Wing, where they were often
166 introduced to at least one adult chimpanzee. For nursery-reared subjects assessed here (N = 24;
167 14M[6]:10F[3]; 10RC:14ST), the mean age when moved to the GAW[4] was 3.33 years (SD = .96). A univariate
168 ANOVA found no significant difference between males and females in age moved, between RC and ST
169 condition, or a sex-by-rearing interaction.
170 2.2.2 Responsive Care Nursery: The Responsive Care (RC) nursery-reared chimpanzees were cared for
171 along with ST chimpanzees for all but 20 hours per week. For 4 hours every weekday, RC chimpanzees

were provided care by research assistants who had been trained to emulate some aspects of chimpanzee mothering behavior (Bard 1996). These researchers provided species-typical grooming, play with species-typical communicative gestures, and feeding as appropriate for the chimpanzees' age (Bard, Dunbar, et al. 2014). During the 4 hours RC chimpanzees spent with research assistants the ratio of caregiver to chimpanzee infant was 1:2, much reduced from the ratio of 1:12 while in Standard Care (Bard, Bakeman, et al. 2014). This aspect of the responsive care program ended shortly after each infant reached 1 year of age. Thereafter RC infants experienced the same nursery environment and caretaking practices as did ST infants, including leaving the nursery and moving onto the Great Ape Wing (van IJzendoorn et al. 2009).

2.2.3 Mother-rearing environment: Infants were raised by their biological mothers at the Yerkes Research Center, given that their mothers had adequate maternal behaviors. Infants were in constant physical contact with their mothers for the majority of the first 3 months of life, 70% of the time simply being cradled, but 30% of the time experiencing additional maternal behaviors of grooming, playing, holding, and other interactive behaviors (Bard 1994). MR infants nurse on demand. From 4 to 12 months of age, MR infants experienced nurturing of social and communicative skills, between 3 and 8 minutes per hour (Bard, Dunbar, et al. 2014), and also experienced nurturing of motor skills, and independence (Bard 1996). . Mother-reared chimpanzees included in this study (N = 11) lived in social groups averaging 8 individuals (M = 8.18, SD = 3.67, RANGE = 3 – 15) during their first year of life. Nine of the MR subjects spent their first year in large indoor/outdoor runs on the Yerkes GAW; two spent their first year at the Yerkes Field Station, where they were housed in a combination of indoor/outdoor runs and large, open-air yards. Like the nursery-reared chimpanzees, MR chimpanzees typically lived in a number of different social groups over the course of their lives. MR subjects were housed with their mothers for an average of 9.64 years (SD = 6.39, RANGE = 2 – 18 years), with any separations lasting less than 2 months. A univariate ANOVA found no significant difference in group-size for MR males versus

196 females (Males, N = 3; Females, N = 8). Similarly, a univariate ANOVA found no significant sex-based
197 difference in age separated from mother.

198 2.3 General Methods for Adult Assessments

199 When RC, ST, and MR chimpanzees were approximately 20 – 25 years old, their behavior was
200 assessed, and they were rated on their personality, well-being, and human orientation. Additionally,
201 data concerning their health (serious illnesses and wounding) were obtained from the Animal Records
202 System from their first 20 years of life. Comparisons were made based on rearing condition and sex.
203 Previously, we reported main effects of attachment on these dependent measures for a small (N = 20)
204 subset of our sample, and the relative impact of RC and ST nursery rearing and attachment on several
205 health-related measures (Clay et al. 2015). Here we report the relative impact of sex and rearing on all
206 measures for a larger sample (N = 35), in particular including MR chimpanzees (N = 11).

207 Where assumptions were met, we conducted a series of univariate ANOVAs to assess the impact of
208 sex, rearing, and a sex-by-rearing interaction on our dependent measures. We considered p values $<.05$
209 to be significant, but additionally report results with $p <.06$ as nonsignificant trends. Tukey's tests were
210 used to compare differences across rearing groups, when significant rearing differences were found.
211 When the sex-by-rearing interaction was significant, males and females were assessed in separate One-
212 way ANOVAs, and Tukey's post-hoc tests were used to compare the rearing groups. In some cases, the
213 nature of the data and/or the size of our sample necessitated the use of nonparametric statistics. We
214 consider the breadth of this study and the exploratory nature of our measures to preclude the use of an
215 adjusted alpha level, choosing to protect our Type II error probability (false negative) over decreasing
216 the likelihood of a Type I error (false positive) (for a discussion of this rationale, see Sinclair, Taylor, and
217 Hobbs 2013). However, we recommend that our findings be considered cautiously as a result,
218 particularly given our small sample size.

2.3.1 Additional Methods for Health Measures: The Yerkes Animal Records System (ARS) provided information on the health and wounding history of 35 chimpanzees from birth through 20 years of age. Subjects assessed here were the same as those assessed by survey and also included the 33 chimpanzees assessed behaviorally. We assessed the chimpanzees for incidence of upper respiratory infection (URI[11]), gastro-intestinal illness (GI[5]), and wounding across their first 20 years of life. Veterinary technicians noted incidences of illness or injury based on their daily visual inspections of the chimpanzees. Injuries were generally not recorded in ARS unless considered severe enough to require treatment and/or continued monitoring. Each incidence of URI, GI or injury was counted once for our analyses. Injuries noted to have occurred due to nonsocial causes were not included in analyses. The number of male and female chimpanzees in each rearing condition is included in Tables A.1, B.1 and C.1. Each subject's total number of incidents per category (URI, GI or injury) was divided by their age to get an incident-per-year rate for analysis.

We also wanted to assess the likelihood of experiencing URI, GI or wounding as a function of age, so we assessed 35 subjects across five year age intervals (0 – 5 years, 6 – 10 years, 11 – 15 years and 16 – 20 years) using a simple yes/no dependent measure (yes, subject experienced at least one URI/GI/wound or no, subject did not). We used Chi-square tests to assess the number of individuals with the health problem within each age interval to assess whether there was any association with rearing condition, sex, and sex by rearing. If a significant interaction was found, then a relation with rearing condition was assessed for males and females separately. Fisher's Exact Tests are reported in those cases when there were high frequencies of expected cell sizes of less than five. Statistics are reported as significant when $p < .05$, and reported as nonsignificant trends for $p < .06$.

2.3.2 Additional Methods for Behavioral Measures: Behavioral data were collected on 33 adult chimpanzees, between 16 and 24 years ($M = 19.4$, $SD = 2.61$), in 2011 as part of a dissertation project (Clay 2012). Data were collected using a 1-0 interval method with intervals of 60 seconds each. Six to

10 hours of data were collected per chimpanzee, balanced for time of day (Mean 60 second intervals per chimpanzee = 517.6, SD = 86.3). A Univariate ANOVA was conducted to test for any difference in observation time based on sex, rearing, or sex-by- rearing interaction. There were no significant main effects of sex ($F(1) = 3.61$, $p = .068$) or rearing ($F(2) = .18$, $p = .840$). The interaction was significant ($F(2) = 3.99$, $p = .030$. MR males were observed for longer than MR females, but there were no significant sex differences for RC and ST observations. For this reason, the observational data are reported as proportions of total time observed. A single, experienced observer recorded all behavioral data; the observer was aware of the various rearing conditions but generally not cognizant of each chimpanzee's rearing history during collection of behavioral data. All subjects were living in small groups (2 – 5 individuals) in large indoor/outdoor runs at the Yerkes main center at the time of this study. We had 33 subjects for whom we could assess the effect of sex and rearing on behavior (see Tables D.1 – D.2 for details).

Social and nonsocial behaviors were assessed using a previously published ethogram (see Clay et al. 2015). Social behaviors include categories of Aggression, Submission, Neutral, Affiliation, Sex, and Solicitation. Aggressive behaviors, e.g., aggressive contact, displays, and pant hoots, were computed separately for behaviors directed at conspecifics and behaviors directed at humans. Two summary scores, one for behavior directed towards conspecifics and one for behavior directed towards humans, were also computed for submissive behaviors, e.g., pant grunting and presenting, for neutral behaviors, e.g., approaching, following, or looking at other individuals, and for affiliative behaviors, e.g., grooming, playing, or touching. A single summary score was computed for sexual behaviors, e.g., genital inspection, masturbation. Four summary scores were computed for soliciting: positive soliciting behavior (gesture, vocalizations, eye contact) and negative soliciting behavior (spitting, throwing feces, slamming/banging mesh), based on whether the behavior was directed toward a conspecific or a human.

Nonsocial behaviors recorded consisted of abnormal behavior and stress-related behavior. Abnormal behaviors recorded were abnormal fecal (e.g. coprophagy or feces painting), hair plucking of self or other, abnormal body manipulation (e.g., nipple-tweaking, repetitive self-grooming, lip-sucking), abnormal rocking, regurgitation/reingestion, and an 'other' category for idiosyncratic abnormal behaviors not previously categorized. Stress-related behaviors recorded were rough scratching and yawning. Nonsocial behaviors were analyzed independently, because of suggestions that different abnormal behaviors may have different etiologies (te Boekhorst, de Weerth, and van Hooff 1991; Easley, Coelho, and Taylor 1987; Troisi et al. 1991; Hopper, Freeman, and Ross 2016; Nash et al. 1999).

Environmental events were also recorded, including the approach of a motorized cart, close-by chimpanzees displaying, humans' near approach, loud noise, and close-by chimpanzee vocalization. Environmental events were assessed for correlation with social and nonsocial behaviors and compared between groups where significant correlations were found to ensure they did not introduce confound. We also assessed the impact of environmental events on stress-related behaviors, such as scratching and yawning. This was achieved by considering the environmental events as opportunistic stress tests. Animals who engaged in a higher ratio of intervals containing scratching behavior but did not experience a higher ratio of intervals containing a potentially stressful environmental event, for example, might be considered to be more reactive to stressful events.

2.3.3 Additional Methods for Survey Measures: Thirty-five chimpanzees (the same subjects as assessed for health) were assessed by survey measures including a personality inventory, a subjective well-being assessment (SWB[10]), and a human orientation assessment (for complete SWB and personality survey see appendices previously published in Clay et al. 2015). Mean age of the subjects was 19.7 years (Range: 16 – 24; SD: 2.72). Respondents included researchers, animal care providers, veterinary staff, and behavioral management staff who had worked with the chimpanzees on a regular basis for at least one year. These respondents were generally not aware of the two nursery conditions that had existed at

Yerkes prior to 1995, but some were aware of the basic rearing history of most subjects as nursery or mother-reared. None of the respondents were involved in rearing the chimpanzees. The personality inventory and SWB assessments included items from previous studies (Weiss 2002; Weiss et al. 2009; Weiss, King, and Enns 2002; Weiss, King, and Hopkins 2007). Because Weiss et al.'s (2007) study results were based on a larger sample of Yerkes chimpanzees it was decided to use the items and unit-weights from that study to calculate four factors (Dominance, Extraversion, Conscientiousness and Agreeableness). The human orientation section of the survey was designed to assess the degree to which the chimpanzees directed behavior towards humans (items listed in Appendix A). All survey items asked the respondents to use a 7-point Likert scale to assess the degree to which a chimpanzee exhibits a certain trait (1 = least amount, 4 = average amount, 7 = most amount). 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 0.75 (ICC scores ranging from 0.57 to 0.89). Multiple scores for each item for each chimpanzee were averaged for a composite score prior to further analysis.

The nine items designed to measure human orientation were entered into a PCA Factor Analysis with Varimax rotation (Table F). Rotation converged in 3 iterations. Two components with Eigenvalues greater than one were extracted, component 1 with an Eigenvalue of 3.76, accounting for 47.0% of the variance, and component 2 with an Eigenvalue of 3.16, accounting for 39.5% of the variance. Examination of the scree plot confirmed that there were two principal components underlying all of the human orientation items. Items were assigned to whichever of the two components they loaded onto most strongly (see Table F for loading scores). One item, which was designed to assess compliance with human demands, loaded weakly and also fairly equally onto both components, so that item was dropped from analysis (see Appendix A, item 9). For each subject, the mean ratings for items loading onto each factor were averaged. The first component was labeled Affiliative Human Orientation based on the factors loading onto it (AF-HO[1]: interest in humans, solicitation of humans, affiliative human

attention seeking, affiliative human orientation) and the second Agonistic Human Orientation (AG-HO[2]: aggressive towards humans, moodiness towards humans, agonistic human attention seeking, agonistic human orientation). For each component, higher scores indicate a rating judgment of a stronger orientation towards humans. Higher AG-HO scores would indicate a rating judgment that the chimpanzee interacted with humans in an agonistic manner more frequently; higher AF-HO scores would indicate a rating judgment that a chimpanzee interacted with humans in an affiliative manner more frequently.

3.0 Results

3.1 Health Measures

3.1.1 Injury Age 0 – 20: For injury count, a main effect of rearing was found, ($F(2,29) = 3.51$, $p = .043$, partial $\eta^2 = .20$), whereas neither sex nor the interaction were significant. None of the post-hoc tests were significant, but a nonsignificant trend ($p = .059$) was found indicating MR chimpanzees experienced more injuries than RC whereas ST did not differ from either MR or RC (Table A.1). In the analysis of number of chimpanzees incurring at least one injury, significantly more males than females were injured during this age span (χ^2 (1) = 6.81, F.E. = .018; M: 94.1%, F: 55.6%). There was not a significant difference in likelihood of incurring at least one injury due to rearing.

3.1.1.1 Injury Age 0 – 5: Neither sex nor rearing nor interaction significantly affected the number of chimpanzees injured during this age span.

3.1.1.2 Injury Age 6 – 10: There was no effect of rearing or interaction for this age span, but there was a significant effect of sex (χ^2 (1) = 6.29, F.E. = .018). Males were significantly more likely to experience at least one injury during this age span (M: 41.2%; F: 5.6%).

3.1.1.3 Injury Age 11 – 15: A main effect of rearing was found for number of chimpanzees injured between the ages of 11 and 15 years (χ^2 (2) = 6.74, F.E. = .026). RC subjects were significantly more likely to be injured than ST subjects, whereas MR subjects did not significantly differ from RC or ST (MR: 27.3%; RC: 40.0%; ST: 0.0%). There was not a significant main effect of sex, but there was a nonsignificant trend (p = .059) for an interaction of sex and rearing. For females, there was no significant impact of rearing on likelihood of experiencing at least one injury during this age span, but there was for males (χ^2 (2) = 8.38, F.E. = .011). RC males were significantly more likely than ST males to experience at least one injury between 11 and 15 years of age whereas MR males did not differ from either nursery group (MR/M: 33.3%; RC/M: 75.0%; ST/M: 0.0%).

3.1.1.4 Injury Age 16 – 20: There was no main effect of sex or rearing on likelihood of experiencing at least one injury between ages 16 and 20 years. There was also not a significant interaction. See Table A.2 for a summary of age-interval results.

3.1.2 GI Tract Illnesses Age 0 – 20: For number of GI tract illnesses, a main effect of rearing was found ($F(2,29) = 22.60$, p = .002, partial $\eta^2 = .36$). Post-hoc tests determined that RC chimpanzees experienced a significantly higher number of GI tract illnesses than either MR or ST chimpanzees. MR and ST chimpanzees did not significantly differ (Table B.1). In the analysis of number of chimpanzees incurring at least one GI illness, RC was significantly more likely than MR to have at least one GI tract illness across years 0 – 20 whereas ST did not differ from either group (χ^2 (2) = 12.30, F.E. = .001; MR: 27.3%, RC: 100.0%, ST: 57.1%). There was no significant sex difference in likelihood of at least on GI illness across this age span.

3.1.2.1 GI Tract Illnesses Age 0 – 5: Between 0 and 5 years, there was no main effect of sex but there was a main effect of rearing (χ^2 (2) = 17.74, F.E. < .001). RC chimpanzees were significantly more likely to experience at least one GI tract illness than either ST or MR chimpanzees whereas ST did not significantly differ from either group (MR: 18.2%; RC: 100.0%; ST: 28.6%). The interaction was also

significant. For females (χ^2 (2) = 10.57, F.E. = .002), RC were significantly more likely to experience one or more GI illness than MR whereas ST did not significantly differ (MR/F: 12.5%; RC/F: 100.0%; ST/F: 50.0%). For males (χ2 (2) = 7.15, F.E. = .023), RC were significantly more likely to experience one or more GI illness than ST whereas MR did not significantly differ from either group (MR/M: 33.3%; RC/M: 100.0%; ST/M 20.0%).

3.1.2.2 GI Tract Illnesses Age 6 – 10, 11 – 15, and 16 – 20: There was no significant relation between sex, rearing, or the interaction and GI tract illness during any of these age intervals. See Table B.2 for a summary of age-interval results.

3.1.3 URI (Overall Frequency for Age 0 – 20): For Upper Respiratory infections, sex ($F(1,29) = 18.45$, $p < .001$, partial $\eta^2 = .39$), rearing ($F(2,29) = 13.12$, $p < .001$, partial $\eta^2 = .48$), and the sex-by-rearing interaction ($F(2,29) = 5.58$, $p = .009$, partial $\eta^2 = .28$) were all significant. The analysis was thus split between males and females to determine the effects of rearing for each sex on this measure. Females from the different rearing groups were not found to differ significantly on URI count, but males did ($F(2,14) = 27.06$, $p < .001$). RC males experienced significantly more upper respiratory infections than either MR or ST males whereas ST males experienced significantly fewer URI than MR males (see Table C.1). In the analysis of number of chimpanzees incurring at least one URI across this age span, there was no rearing or sex effect.

3.1.3.1 URI Age 0 – 5: For chimpanzees age 0 – 5 years, RC were significantly more likely to be treated for at least one upper respiratory illness than MR animals, whereas ST did not significantly differ from RC or MR ($\chi^2(2) = 8.14$, F.E. = .015; MR: 9.1%, RC: 70.0%, ST: 42.9%). There also a significant difference in likelihood for males versus females between the ages of 0 – 5 ($\chi^2(1) = 4.88$, F.E = .041 (M: 58.8%, F: 22.2%). The interaction was not significant.

3.1.3.2 URI Age 6 – 10: Chi square was not significant, so there was not a relation between number of individuals with a URI and sex, rearing, or sex-by-rearing between the ages of 6 and 10.

3.1.3.3 URI Age 11 – 15: Between 11 and 15 years of age, RC chimpanzees were significantly more likely to be treated for at least one upper respiratory illness than ST chimpanzees whereas MR chimpanzees were not significantly different from RC or ST ($\chi^2(2) = 6.74$, F.E. = .026; MR: 27.3%, RC: 40.0%, ST: 0.0%). No main effect of sex was found, but there was a significant interaction such that for females, rearing did not significantly impact likelihood of at least one URI between 11 and 15, but for males, it did ($\chi2(2) = 8.38$, F.E. = .011). RC males were significantly more likely than ST males whereas MR males did not significantly differ (MR/M: 33.3%, RC/M: 75.0%, ST: 0.0%).

3.1.3.4 URI Age 16 – 20: There was a significant interaction of sex-by-rearing for likelihood of experiencing at least one URI between ages 16 and 20 years. For females, there was no significant difference in likelihood based on rearing experience, but MR males were more likely than ST to experience at least one URI during this interval; RC did not differ significantly ($\chi^2(2) = 6.53$, F.E. = .022; MR/M: 66.7%; RC/M: 0.0%; ST/M: 0.0%). There was no main effect of rearing or sex. See Table C.2 for a summary of age-interval results.

3.2 Behavioral Measures

3.2.1 Social Behaviors

3.2.1.1 Social behavior toward conspecifics: There was a significant main effect of sex on the category of affiliative behavior towards conspecifics, ($F(1,27) = 6.00$, $p = .021$, partial $\eta^2 = .18$). Females exhibited significantly more affiliative behavior than males (Males: M = .024, SD = .018; Females: M = .048, SD = .033: Figure 1.1). There was not a significant effect of rearing or of the sex-by-rearing interaction on this behavior.

There was a significant effect of sex on aggressive behavior towards conspecifics ($F(1,27) = 24.83$, $p < .001$, partial $\eta^2 = .48$). Males exhibited more aggressive behavior towards conspecifics than females (Males: M = .041, SD = .025; Females: M = .008, SD = .006: Figure 1.1). There was not a significant effect of rearing or of the sex by rearing interaction on this behavior.

Neutral behavior towards conspecifics was significantly affected by rearing with a moderately large effect size ($F(2,27) = 3.96$, $p = .031$, partial $\eta^2 = .23$). RC chimpanzees exhibited significantly more neutral behavior towards conspecifics than ST chimpanzees, whereas MR chimpanzees did not differ from RC or ST on this measure (MR: M = .049, SD = .022; RC: M = .068, SD = .034; ST: M = .040, SD = .015: Figure 1.2). There was not a significant main effect of sex or a significant sex by rearing interaction on neutral behavior toward conspecifics.

No significant effects for sex, rearing or sex by rearing were found for submissive behavior directed towards other chimpanzees, positive soliciting of conspecifics, or negative soliciting of conspecifics. Additionally, there were no significant effects of sex, rearing, or sex-by-rearing on the measure of sexual behavior (this behavior was only analyzed as directed towards other chimpanzees as there were no human-directed sexual behaviors recorded).

3.2.1.2 Social behavior toward humans: There were significant effects of sex ($F(1,27) = 9.33$, $p = .005$, partial $\eta^2 = .26$), rearing ($F(2,27) = 10.54$, $p < .001$, partial $\eta^2 = .44$) and the interaction ($F(2,27) = 3.49$, $p = .045$, partial $\eta^2 = .21$) on aggressive behavior towards humans. Although females exhibited significantly less aggressive behavior toward humans than did males, this is qualified by the significant sex-by-rearing interaction. There was no significant effect of rearing for females, but for males, RC exhibited significantly more aggressive behavior towards humans than did MR males or ST males ($F(2,12) = 7.52$, $p = .008$). MR males and ST males did not differ significantly from each other (Males/MR: M = .001, SD = .001; Males/RC: M = .012, SD = .005; Males/ST: M = .004, SD = .004: Figure 2.1).

Neutral behavior directed towards humans was significantly affected by rearing ($F(2,27) = 13.64$, $p < .001$, partial $\eta^2 = .50$), but not by sex or by the interaction. RC chimpanzees exhibited significantly higher proportions of neutral behavior towards humans than did either MR or ST chimpanzees. ST chimpanzees also exhibited significantly more neutral behavior to humans than did MR chimpanzees (MR: M = .026, SD = .012; RC: M = .127, SD = .055; ST: M = .074, SD = .044: Figure 2.2).

For positive soliciting behaviors, there was no significant effect found for sex or interaction. There was a nonsignificant trend for a main effect of rearing ($F(2,27) = 3.16$, $p = .059$, partial $\eta^2 = .19$). Tukey's post-hoc found RC engaged in significantly more positive solicitation than MR, though ST did not differ significantly from MR or RC (MR: M = .006, SD = .008; RC: M = .028, SD = .033; ST: M = .010, SD = .008).

For negative soliciting, we found a significant main effect of rearing ($F(2,27) = 3.45$, $p = .046$, partial $\eta^2 = .20$). RC chimpanzees exhibited negative soliciting behavior in significantly more intervals than MR chimpanzees with the ST group not differing significantly from MR or RC (MR: M = .000, SD = .001; RC: M = .004, SD = .004; ST: M = .001, SD = .004: Figure 2.3).

No significant effects for sex, rearing or sex-by-rearing were found for affiliative behavior directed towards humans. There were no significant effects for sex, rearing or sex-by-rearing on submissive behavior directed towards humans.

3.2.2 Abnormal and Stress-related Behavior: We found a nonsignificant trend for a sex-by-rearing effect for abnormal body manipulation,($F(2,27) = 3.30$, $p = .052$, partial $\eta^2 = .20$). There was no significant difference across rearing groups for males, but there was for females ($F(2,15) = 4.68$, $p = .026$). RC females exhibited abnormal body manipulation in significantly more intervals than MR females. ST females were not significantly different from either MR or RC females on this measure (Table D.1).

Males rocked significantly more than females ($F(1,27) = 4.92$, $p = .035$, partial $\eta^2 = .15$: Figure 3). There was also a nonsignificant trend for a rearing effect ($F(2,27) = 3.25$, $p = .054$, partial $\eta^2 = .19$). RC chimpanzees exhibited abnormal rocking in significantly more intervals than MR chimpanzees, whereas ST chimpanzees did not differ significantly from either RC or MR chimpanzees (Table D.2).

No significant effects (main or interaction) were found for the remaining abnormal behavior measures of abnormal feces behavior, abnormal hair plucking (self or other), regurgitation and reingestion, or other abnormal behaviors.

There were no significant effects of sex, rearing or sex-by-rearing on scratching. There was a significant main effect of rearing found for yawning ($F(2,27) = 3.73$, $p = .037$, partial $\eta^2 = .22$) . RC chimpanzees yawned in significantly more intervals than MR chimpanzees. ST chimpanzees did not differ from either RC or MR chimpanzees on yawning (MR: M = .005; SD = .005; RC = .017, SD = .014; ST: M = .012; SD = .011: Figure 4).

3.2.3 Environmental Events: We recorded, but did not control, a number of environmental events which were informally observed to impact the chimpanzees' behavior. Because these events had been observed to have impact on the chimpanzees' behavior, we needed to assess any differences per rearing group or sex group in exposure to these events. We found no significant differences based on sex, rearing, or sex-by-rearing for approach of a cart, close-by chimpanzee displays, human approach or loud noise. We did find a significant effect of sex on proportion of intervals containing close-by chimpanzee vocalizations ($F(1,27) = 8.92$, $p = .006$, partial $\eta^2 = .25$). Males (M = .08, SD = .02) experienced more close-by vocalizations than females (M = .06, SD = .02).

Since the impact of these events had been observed and reported informally, we also checked our data to see if they support an impact of these events on behavior. Positive significant correlations between environmental events and assessed behaviors were found for scratching with human approach ($r = .43$, $p = .014$) and for affiliative behavior towards conspecifics with human approach ($r = .41$, $p = .018$). Inverse significant correlations were found for scratching with close-by chimpanzee vocalizations ($r = -.42$, $p = .014$), submissive behavior towards conspecifics with close-by chimpanzee displays ($r = -.40$, $p = .021$), and submissive behavior towards conspecifics with close-by chimpanzee vocalizations ($r = -.50$, $p = .003$).

3.2.4 Unplanned Environmental Events as Opportunistic Stress-Tests: We could not conduct stress tests on the chimpanzees in this study due to ethical concerns, so we had very little ability to determine if our subjects exhibited differential response to observed stressors based on rearing or sex. Events which

typically occurred in the chimpanzees' environment, however, could be assessed. Therefore, where we found a significant correlation between environmental events and stress-related scratching, we assessed the strength of that correlation for each rearing group and each sex separately. For MR chimpanzees, only the correlation between scratching and close-by vocalizations remained significant ($r = -.61$, $p = .047$, $N = 11$). For RC chimpanzees, only the correlation between scratching and human approach remained significant ($r = .68$, $p = .032$, $N = 10$). Neither correlation with scratching remained for ST chimpanzees. By sex, neither correlation remained significant for females, but both were significant for males (scratching with close-by vocalizations: $r = -.64$, $p = .011$, $N = 15$; scratching with human approach: $r = .62$, $p = .014$, $N = 15$).

3.3 Survey Results

3.3.1 Subjective Well-being (SWB): There was a significant main effect of rearing on SWB rating ($F(2,29) = 3.63$, $p = .039$, partial $\eta^2 = .20$). Post-hoc tests indicated that RC chimpanzees were rated significantly lower on SWB than MR chimpanzees, whereas ST chimpanzees did not differ significantly from either rearing group. Notably, the means for all three rearing groups were above the rating of 4.0 which was associated on the Likert scale with 'average' well-being (MR: M = 4.88, SD = .30; RC: M = 4.18, SD = .29; ST: M = 4.52, SD = .75: Figure 5).

3.3.2 Personality: There were no significant effects found for sex, rearing, or sex by rearing on dominance, extraversion or agreeableness as personality factors. There was a significant effect of rearing ($F(2,29) = 6.39$, $p = .005$, partial $\eta^2 = .31$) on conscientiousness with neither sex nor the interaction factor significant (MR: M = -1.57, SD = .48; RC: M = -2.35, SD = .74; ST: M = -2.43, SD = .56: Figure 6). Post-hoc tests indicated that RC and ST chimpanzees did not differ significantly, but both were significantly lower on conscientiousness than MR chimpanzees. Interestingly, all groups were rated negatively on conscientiousness, indicating less predictability and more erratic, irritable, impulsive traits

(chimpanzees scored as high on traits related to predictability or low on traits related to irritability, for example, might have had a positive conscientiousness rating).

3.3.3 Human Orientation: For both Aggressive Human Orientation (AG-HO: $F(2,29) = 6.92$, $p = .003$, partial $\eta^2 = .32$) and Affiliative HO (AF-HO: $F(2,29) = 5.30$, $p = .011$, partial $\eta^2 = .27$) rearing had a significant main effect, but not sex or the interaction factor. ST chimpanzees were rated significantly higher on AG-HO than MR chimpanzees but RC chimpanzees did not differ significantly from MR or ST (MR: M = 2.45; SD = .46; RC: M = 3.26; SD = 1.09; ST: M = 3.50; SD = .89: Figure 7). Both RC and ST were rated significantly higher on AF-HO than were MR chimpanzees, but RC and ST were not significantly different from each other (MR: M = 4.09, SD = .80; RC: M = 5.45, SD = .53; ST: M = 5.03, SD = 1.03) (Figure 7).

3.4 Correlations between Measures

3.4.1 SWB as Welfare: SWB scores were assessed for correlation with all three health measures (number of injuries, upper respiratory infections and GI tract illness between ages 0 and 20), all observed behaviors (towards humans and towards chimpanzees), all four personality factors, and both human orientation ratings (Figures 8 and 9). SWB was found to be significantly inversely correlated with number of GI tract illness ($r = -.35$, $p = .039$, $N = 35$), time spent rocking ($r = -.40$, $p = .021$, $N = 33$), yawning (r -.38, $p = .028$, $N = 33$), submissive behavior towards humans ($r = -.41$, $p = .017$, $N = 33$), and neutral social behavior towards humans ($r = -.41$, $p = .017$, $N = 33$). SWB was significantly and positively correlated with agreeableness ($r = .54$, $p = .001$, $N = 35$), conscientiousness ($r = .36$, $p = .031$, $N = 35$) and extraversion ($r = .60$, $p < .001$, $N = 35$). None of the other correlations with SWB were significant.

3.4.2 Relationship between Stress-related Behaviors and Human-directed Behaviors: We assessed the strength of correlation between stress-behaviors and human-directed behaviors (aggression, submission, affiliative, neutral, positive solicitation and negative solicitation) in an effort to further explore possible links between human orientation and welfare. Rates of yawning increased significantly

as neutral behavior directed towards humans increased ($r = .52$, $p = .002$: Figure 10), but no other significant correlations were found for yawning. No significant correlations were found for scratching.

3.4.3 Social behavior as a Function of Social Partner: We first assessed whether the ratings of AG-HO and AF-HO correlated with the observed social behavior measures ($N = 33$). AG-HO ratings did not correlate significantly with any observed social behaviors. AF-HO ratings (Figure 11) correlated significantly and positively with neutral behavior towards humans ($r = .65$, $p < .001$), affiliative behavior towards humans ($r = .48$, $p = .004$), and surprisingly, with negative solicitation of humans ($r = .35$, $p = .047$). No other correlations between AF-HO and social behavior towards chimpanzees or humans were significant.

We next assessed whether social behavior toward humans correlated with social behaviors toward chimpanzees. We found a significant correlation only for aggressive behavior ($r=.55$, $p<.01$): individuals that were higher in aggression toward chimpanzee partners tended to be higher in aggression toward human partners, and vice versa. For the rest of social behaviors, however, there was no correlation between proportions of time spent in social behavior directed toward humans and that same social behavior as directed toward chimpanzees, which supports our decision to assess these behaviors separately.

4.0 Discussion

4.1 Is there evidence of poor welfare in these chimpanzees?

Overall there were few injuries (an average of less than 2 over 20 years per individual), and very infrequent illness that required veterinary attention (on average each chimpanzee had approximately 1 gastrointestinal illness and 1 upper respiratory infection over a 20 year span). Although some abnormal behavioral patterns were evident (hair plucking, abnormal body manipulation, regurgitation), most

552 occurred at levels fairly equivalent to those reported for other captive chimpanzees (for most abnormal
553 behaviors, approximately 1 interval every 2 hours); only rocking occurred more frequently
554 (approximately 2 intervals per hour) (for comparison see: 'non-oral abnormal behavior': Baker 1997;
555 'stereotypy' and 'self-directed behavior': Clarke, Juno, and Maple 1982). There were also some signs of
556 more acute but mild stress: rough scratching occurred during 2.5 intervals per hour and yawning
557 occurred about once every 2 hours. These rates are also equivalent to those found for other captive
558 chimpanzees (Baker and Aureli 1997; Vick and Paukner 2010). These chimpanzees were rated as having
559 average subjective well-being. We found meaningful differences between males and females, and
560 between rearing groups on many of these measures, but we conclude that there was no evidence of
561 poor welfare in these chimpanzees.

562 4.2 What is the relationship between rearing and/or sex and welfare?

563 4.2.1 Welfare and Health

564 *4.2.1.1 Injury*: There is a suggestion that long term frequency of wounding may differ as a function of
565 rearing group, with a nonsignificant trend for MR chimpanzees to show a higher frequency of injury than
566 RC chimpanzees (with ST not differing from either group). Although we found that more MR than
567 nursery-reared subjects were injured in the 11-15 age interval, when we considered the number of
568 individuals who were injured during the 0-20 year period, there was no effect of rearing. This suggests
569 that the higher frequency of injury found for MR chimpanzees across the 20 years might be due to
570 individual MR chimpanzees receiving multiple injuries. Perhaps some MR chimpanzees were more likely
571 to persist in social conflicts (e.g., seeking higher rank) or some MR individuals experienced more social
572 conflicts (in part due to being in larger social groups) than RC individuals, and incurred more wounds as
573 a result. Although there have been reports suggesting that nursery-reared chimpanzees may exhibit less,
574 or less appropriate, social behavior towards conspecifics than MR (play and sexual behavior:
575 Bloomsmith et al. 2002; sexual and maternal behavior: Bloomsmith et al. 2006; initiation of grooming:

Freeman and Ross 2014; rates of social behavior for MR captive chimpanzees: Bloomsmith, Pazol, and Alford 1994), we did not find any rearing group differences in frequencies of either affiliative or aggressive behavior toward conspecifics. Therefore, our data support a tentative conclusion that mother-reared chimpanzees incur more injuries, and that this is not due to any obvious group differences in social engagement.

It is notable that there was no sex-based difference in frequency of injury between birth and 20 years of age, but there was a significant sex difference in likelihood of being injured at least once across this age period. It could be that males have an increased risk of injury due to more aggressive behavior (e.g. Nishida 1970; Sugiyama 1969). Although males were found to exhibit higher levels of aggressive behavior here, there was no correlation between frequency of injury across ages 0 - 20 and levels of aggressive behavior observed in these chimpanzees as adults. It is possible that aggression at other ages relates to frequency or likelihood of injury at those ages, as levels of aggressive behavior vary across age and sex (Kraemer et al. 1982). We did find that the number of males and females injured (at least once) differed significantly only during early adolescence, between 6 and 10 years, but unfortunately there are no data concerning their level of aggression during this age period. At other captive facilities, adolescent male chimpanzees received more wounding than females or males of other age groups (Ross et al. 2009).

4.2.1.2 GI Tract Illness: RC chimpanzees were treated for an average of 2.5 GI illnesses between birth and 20 years of age, significantly higher than the average of 0.9 for ST and 0.3 for MR chimpanzees. These results may be due to GI illnesses treated between birth and 5 years of age since there were no significant effects for the other age intervals, though our results should be considered with caution due to the small sample size. It is possible that increased human contact allowed for increased reporting of GI illness (i.e., RC caregivers were able to observe diarrhea more often and therefore reported it more often). It is also possible that the extended hours of human contact in RC actually exposed these infants

to more infectious agents. These retrospective data do not allow us to distinguish between these possibilities, but it is notable that GI illness was found more rarely in chimpanzees older than 5 years of age.

4.2.1.3 URI: Male chimpanzees experienced 1.2 upper respiratory infections (URI) compared to 0.7 URIs experienced by females across the 20 year period. For males, there was also a significant effect of rearing, with 2.8 URIs for RC males, 1.7 for MR males, and only 0.5 for ST males. Whereas some studies indicate that females (human and other vertebrate species) experience better immune function than males (e.g. see review of literature in Nunn et al. 2009), we are not aware of any findings regarding sex differences in immune function for chimpanzees. It could be that the differences observed between rearing groups were due to some sex-based difference in immune function interacting with rearing, since we found rearing effects interacting with sex in the number of chimpanzees who exhibited URI at ages 11-15 and at 16-20. Long-lasting dysregulation of the stress response system can occur due to early life stress, and one observed effect of this dysregulation, for primates, can be increased risk of upper respiratory illness (Cohen et al. 1997). However, in both the frequency across 20 years measure, and the number of chimpanzees at some age intervals, male chimpanzees appear to be more compromised than females, but only under certain rearing conditions.

4.2.1.4 Summary of Welfare & Health: Although rearing appeared to impact all three measures of physical health, the effects differed across measures. For GI illness and URI, immune function might be the root cause, or alternatively the differences might be attributable to the ease of identification of the illness or increased human exposure. It may be that long-lasting effects of sex and/or rearing on immune function are more detectable through URI symptoms than GI illness symptoms in adult chimpanzees, perhaps due to social housing leading to difficulty in identifying specific individual animals responsible for abnormal stool observed in an enclosure. In contrast, it is likely that more exogenous factors are responsible for health effects measured by injury. Larger samples in future research might

be able to provide more definitive evidence of the likely mechanisms. Thus, our study highlights the importance of using multiple measures of health to assess their impact on welfare.

4.2.2 Welfare and Behavior

4.2.2.1 Abnormal Behavior: In contrast to physical health, in the six categories of abnormal behavior, we found no significant effects of rearing and only one significant effect of sex. Males and females differed in the abnormal behavior of rocking. Rocking was significantly higher for males, which is consistent with the literature (Nash et al. 1999).

There was a nonsignificant trend for more rocking in the RC than the MR group, although ST did not differ from either group. Previously, we found that nursery-reared chimpanzees categorized with a disorganized attachment strategy rocked significantly more than nursery-reared chimpanzees with an organized attachment both as infants and as adults (Clay et al. 2015; van IJzendoorn et al. 2009). Attachment strategy, developed in infancy, might be linked with our results, but since we do not have attachment ratings for MR subjects, we cannot discern the degree to which quality of attachment is affecting rocking in the chimpanzees of the current study.

There was a nonsignificant trend for an interaction between sex and rearing for abnormal behavior body manipulation. Abnormal body manipulation included stereotypies such as repetitive touching, squeezing, or stroking of some part of their own body. Rearing group appeared to affect body manipulation in females, but not in males. Specifically RC females engaged in this abnormal behavior more often than MR females, although ST females did not differ from either group. It is important to note that there was a relatively high number of chimpanzees that did not exhibit this abnormal behavior (11 of 11 MR; 3 of 10 RC; and 5 of 12 ST), perhaps accounting for the nonsignificant trend. However, a study of nursery-reared chimpanzees at a different institution found that females exhibited more abnormal self-clinging than males (Fritz, Nash, and Alford 1992).

4.2.2.2 Stress-related Behavior: Yawning and rough scratching are well-accepted as measures of acute, mild stress in nonhuman primates (e.g. Elder and Menzel 2001). Although rough scratching occurred more often than yawning, only yawning differed significantly as a function of rearing. RC chimpanzees exhibited more yawning than MR, with ST not differing from either MR or RC. Most findings regarding yawning in primates link it to particular stressors, such as dominance or social ranking (te Boekhorst, de Weerth, and van Hooff 1991; Troisi 2002), but we were not able to link it with any specific stressor in this study. Only a particular morphological form of yawning has been linked to increased arousal for captive chimpanzees (Vick and Paukner 2010), but we did not distinguish between different forms of yawning. We did find a link between yawning and the number of lifetime URIs, and between scratching and proportion of nonspecific abnormal behaviors, providing some support that these stress-related behaviors measured some aspect of less-than-optimal welfare in our sample of chimpanzees.

For males and RC individuals, more scratching was associated with more human approach. For males and MR individuals, less scratching was associated with more close-by chimpanzee vocalizations. Our interpretation here is limited because while we recorded environmental events and scratching, we did not analyze our data sequentially, so we cannot be at all certain that scratching increased as a function of human approach or decreased as a function of vocalizations. If human approach was a strong trigger of scratching for RC subjects, but not for any other group, we should likely have found differences between rearing groups in scratching, but we did not, and this cannot be attributed to differences in rate of human approach. Similarly, we cannot attribute lack of difference between rearing groups to a difference in close-by vocalizations, though there may be an impact for sex. Due to our small sample size, these results, while interesting, do not provide strong support for a rearing difference or sex difference in stress-related scratching.

4.2.2.3 Subjective Well-Being (SWB): SWB is a widely accepted measure of welfare (Weiss 2002; Weiss et al. 2009; Weiss, King, and Enns 2002; King and Landau 2003) and we found that it was significantly

higher in MR than in RC chimpanzees, although ST did not differ from either group. MR chimpanzees' mean score was nearly 5 ("displays greater than average amounts of the trait") and RC chimpanzees' mean score was just above 4 ("displays about average amounts of the trait"). The difference between any two consecutive points on the Likert scale is equivalent to about 17% of the full scale, so this difference is meaningful.

The subjective well-being of zoo-living chimpanzees was rated between 4.1 and 4.2, similar to our sample of chimpanzees rated as 4.5 (King and Landau 2003). Thus, we may conclude that well-being was not compromised for the Yerkes chimpanzees relative to other captive-living chimpanzees. Raters appear to be basing their SWB judgments on the chimpanzees' submissive behavior and personality characteristics, in part (King and Landau 2003; Weiss, King, and Enns 2002), but also on welfare. We found significant links between SWB and health (frequency of GI illness), SWB and abnormal behavior (amount of rocking), and SWB and stress (yawning), which expands the concept subjective well-being to include aspects of welfare. Rocking has been associated with early rearing stressors such as nursery-rearing (Fritz, Howell, and Selchow-Burr 1994; Fritz, Nash, and Alford 1992; Pazol and Bloomsmith 1993; Spiijkerman et al. 1994) and yawning is a widely used measure for stress (Elder and Menzel 2001; Vick and Paukner 2010); immune function is also affected by stress, particularly chronic stress (Cohen et al. 1997; Lay 2000; Mendoza, Capitanio, and Mason 2000; Olsson et al. 1999). So, our findings support a conclusion that SWB is a valid measure of welfare in captive chimpanzees.

4.2.3 Human Exposure and Stress: Based on the health, abnormal behavior, stress-related behavior, and SWB results from this study, we suggest that chronic stress levels, such as typically have impact on immune functioning, are influenced by both early rearing condition and sex. It is possible that increased human exposure during early life contributes to stress in adulthood through changing physiological and/or immunologic functioning. It may be that exposure to humans indirectly impacts adult stress through a path of increasing human orientation. Human orientation might increase stress levels,

perhaps due to a frustrated desire either for human attention or for interaction with people. For example, one study has found that chimpanzees who exhibit negative solicitation of humans do so due to the positively reinforcing value of human attention, no matter the valence of that attention (Martin et al. 2011). In support of this possibility, we found a significant relationship between one category of behavior directed towards humans (neutral) and one stress behavior (yawning). Assessment of chronic stress through physiological measures such as urinary, fecal, or hair cortisol, would be highly informative in this case (Clarke 1993; Kalin et al. 1998; Yamanashi et al. 2016). If orientation towards humans correlates with chronic or acute stress levels, an individualized approach to welfare-management might allow us to improve the welfare of human-oriented adult chimpanzees.

4.3 Do the chimpanzees show species-typical personality traits and behavior?

4.3.1 Personality:

We did not find significant differences on most of our personality measures, but there was a significant difference found between the nursery groups and MR chimpanzees for the factor of conscientiousness. Because a number of the survey items which load on this factor relate to behavior towards other chimpanzees, there may be some unintended effect of social orientation which impacts ratings on this factor. For example, items such as helpfulness (see survey reported in Clay et al., 2015) specifically indicate chimpanzees as the target of any helpful behavior, and items such as considerate/kind focus on consolation behaviors which would likely only be possible to express to conspecific group members. All of the chimpanzees assessed here scored negatively on conscientiousness, which could have negative implications for overall welfare for all three groups. It could also simply be that captive chimpanzees are generally not very conscientious. In some other cases where captive chimpanzees were assessed for personality conscientiousness did not emerge as a factor (King and Landau 2003). One study using the same inventory to assess personality in orangutans reported that there was no conscientiousness factor extracted, and that this may be due to

719 conscientiousness being a more recently evolved trait, perhaps more exclusively observed in humans
720 and, to a lesser degree, in chimpanzees (Weiss, King, and Perkins 2006). It is also possible that our
721 sample of chimpanzees exhibited less conscientiousness than would chimpanzees in a different setting,
722 either in captivity or in their natural habitat. This would be consistent with one previous study in which
723 laboratory chimpanzees scored lower on conscientiousness than a sample of zoo-living chimpanzees;
724 the authors in that case suggested several possible causes for this, including founder effect and less
725 knowledgeable survey respondents at the lab (Weiss, King, and Hopkins 2007).
726 4.3.2 Social Behavior towards Conspecifics: In our sample, females engaged in more affiliative behavior
727 towards conspecifics, whereas males engaged in more aggressive behavior towards conspecifics. These
728 results are at least partially in line with previous studies of chimpanzees in the wild (e.g. Goodall 1986;
729 Sugiyama 1969), particularly with regard to sex differences in aggression (e.g., Muller 2002). Wild male
730 chimpanzees are typically more aggressive than females (Muller 2002), for example. However, while
731 some studies report higher affiliative behavior for wild females (Goodall 1986), others report wild males
732 as more social (Nishida and Hiraiwa-Hasegawa 1987). The more neutral behaviors of looking,
733 approaching, and following were significantly impacted by rearing but not by sex. Looking, in our
734 ethogram, requires a target be separated from the subject by a mesh partition. Approaching and
735 following, in this case, would almost exclusively apply to social group partners. Because these different
736 components of neutral behavior towards conspecifics apply in part to behavior within the social group
737 and in part to behavior directed outside the subjects' social group, it is difficult to interpret our results.
738 Overall, rearing did not seem to have much impact on these chimpanzees' social behavior directed
739 towards other chimpanzees. Sex differences in social behaviors, when we found them, did not differ
740 much from wild chimpanzees.
741 4.4 What is the relationship between behavior directed towards humans and welfare?

742 RC chimpanzees engaged in significantly more neutral behavior towards humans than did ST subjects,
743 and ST engaged in significantly more neutral behavior than MR chimpanzees. For this behavior, the
744 amount of human exposure experienced by the chimpanzees during their early rearing could fully
745 account for adult behavior. Although we found significant rearing effects in two other social behaviors
746 directed towards humans (aggression and negative solicitation), and in the human orientation ratings
747 (AF-HO and AG-HO), as well as a nonsignificant trend towards rearing effects on positive solicitation of
748 humans, we did not find this same pattern of group differences. For these other behaviors, rearing
749 group only impacted males (aggression) or only one nursery group differed from the MR group (RC in
750 positive and negative solicitation, but ST for AG-HO). When the pattern is that ST and RC differ from
751 MR, we can conclude that something about nursery-rearing that is not present in mother-rearing
752 impacts adult outcomes. However, we find here that while RC differed from MR on four of these
753 measures, ST differed from MR only on one, and on only one behavior (neutral) was there a significant
754 difference between RC and ST as well as a significant difference between each nursery-condition and
755 MR. While human exposure alone may account for neutral behavior, it does not fully account for our
756 results. In addition to human exposure, there are likely other variables involved here (e.g. increased
757 nurturing behavior from RC caregivers and MR mothers compared to that provided by ST caregivers).
758 Thus, we conclude that human exposure during infancy may accounts for some, but not all, of the
759 observed group differences in human orientation in adulthood.
760 The effects of rearing, other than amount of human exposure, still need to be identified and explored
761 with greater detail, especially concerning the types of experiences which may differ. One recent study
762 categorized privately-owned chimpanzees in terms of the amount of human exposure versus the
763 amount of conspecific exposure experienced during their early life (Freeman and Ross 2013) and this
764 type of classification may be useful in future research. Additionally or alternatively, other studies focus
765 on the amount of nurturing experiences during early life (e.g., nurturing for the development of

766 communicative skills, nurturing of motor development), as we know that these experiences differ with
767 different types of rearing, impact short-term outcomes (Bard, Bakeman, et al. 2014; Bard, Dunbar, et al.
768 2014), and therefore, might have an impact on adult behavior, as well.

769 The outcome of increased orientation towards humans is unknown, and could have different impacts
770 on chimpanzee welfare. Increased orientation to humans appears to influence some outcomes
771 positively (e.g., chimpanzees with more extensive human exposure have been shown to do better on
772 some cognitive tests: Leavens and Hopkins 1998) and influence other outcomes in a more negative
773 fashion (e.g., in this study, male chimpanzees with higher human exposure in the first year of life
774 behaved more aggressively to humans in adulthood than those with less human exposure). We did find
775 a significant positive correlation between yawning and neutral behavior towards humans, which could
776 be interpreted as support for human orientation as a stressor, but our methodology for data collection
777 did not allow for more informative analyses on this point.

778 Likely the impact of human orientation on welfare is also moderated by the environment in which the
779 chimpanzee currently lives. For example, a highly human-oriented chimpanzee would receive benefits
780 in a facility where there is a premium on good communication with humans, but that same chimpanzee
781 would be at a disadvantage in a setting where human-chimpanzee interaction is discouraged or less
782 available. A better understanding of time budget profiles would assist in exploring further the impact of
783 human orientation on well-being. The amount of time spent watching humans and human activity may
784 not be a problem if the subjects also spend a good deal of time spent engaging with conspecifics, but it
785 would be a problem if it interfered with attention to chimpanzees and chimpanzee activity. It would be
786 important to investigate chimpanzees' behavior towards humans and towards chimpanzees as a
787 function of social context (e.g., on-going social conflicts, invitations to grooming, calm situations).

788

789 5.0 Conclusion

The strongest form of the prediction that the extent of human exposure predicts poor welfare would be that highest levels of welfare would be found in MR group and lowest welfare found in RC group, with the ST group in between, but significantly better than RC. This pattern was found in only one of the 31 measures taken in this study (neutral social behavior to humans), and this measure does not have clear relation with adult chimpanzee welfare. A less strong form of the prediction would suggest that there may be a critical value of human exposure that relates to poor welfare (above which there is no worse impact). There are two conclusions possible from this premise: (1) that an average of 60 minute per day is the cut-off value (so that RC=ST < MR, that is the MR group shows better welfare, and that the nursery-reared groups are not different from one another but show poorer welfare than MR); or (2) that some value more than 60 minutes is cutoff so that RC < MR=ST; that is, poor welfare is found in the RC group, but the MR group is not different from ST. The first form of this pattern was found in only two of the 31 measures (AFF-HO and Conscientiousness), neither of which is explicitly linked with welfare. The second form was found in three of the 31 measures (GI illness, URI, aggression to humans), but for two of these, rearing only affected males (URI, aggression to humans).

In five additional measures in which significant rearing group effects were found, one nursery-reared group was indistinguishable statistically from both the MR group and the other nursery group, making it impossible to specify human exposure as the key variable. In three of these measures, RC was significantly different from MR, and two have strong welfare implications (yawning, SWB). On one of these measures ST was significantly different from MR (AG-HO), and one measure RC was significantly different from ST (neutral behavior toward humans), but these behaviors do not have a clear relation with welfare. Finally, there was one health variable (number of treatments for injury) in which it appeared that MR chimpanzees had poorer outcomes than RC whereas ST was not distinguishable from

813 either. Although we are hesitant to conclude that RC is a protective factor with regard to injuries, this
814 unexpected finding requires further investigation.

815 There are other factors that contribute to our findings. For example, we found sex effects for five
816 variables, including two with implications for welfare (i.e., URI and abnormal rocking). We found that
817 males had more welfare issues than female chimpanzees. Our hypothesis is that there are multiple
818 factors, including human exposure, other aspects of early rearing, experiences beyond the first year of
819 life, and sex that impact welfare outcomes in adult chimpanzee. Moreover, the impact of these
820 variables differs for different welfare outcomes, with some variables interacting for some outcomes
821 (e.g., males with RC rearing experiences are more aggressive to humans than males with ST or MR
822 experiences). There is a great deal of individual variability. We also must recognize that there could
823 have been some pre-existing conditions which resulted in subjects being reared by their mothers, or in
824 nurseries. For example, there may be some genetic difference between chimpanzee mothers with
825 adequate and those with inadequate maternal skills, and this inherited difference might have some
826 impact on measures of health, social behavior, or welfare as assessed in this study.

827 It is critical that we continue to employ scientific evaluation methods in assessing the effects of
828 changes which occur for many chimpanzees in captive care. This should include assessments of
829 individual chimpanzees' responses as they are moved from facility to facility or into new and larger
830 social groups or into redesigned enclosures. Management choices should focus on individual
831 differences, and collaboration between facilities may allow us to better assess individual differences.
832 Findings in the current study indicated that small and often overlooked differences in early rearing
833 environments may have a lasting impact on the behavior and health of adult chimpanzees. As we
834 envision and put into action our 'best practice' plans for managing captive chimpanzee care, and define
835 programs for optimal welfare, we must attend to large individual differences among chimpanzees.
836

Acknowledgments

Funding: This project was funded by the National Center for Research Resources [P51RR000165] to the Yerkes National Primate Research Center. The Yerkes Center is currently supported by the Office of Research Infrastructure Programs/OD [P51OD011132]. Data collection and analysis of the early rearing projects were funded, in part, by NIH grants, RR-00165 (to the Yerkes Center), RR-03591 (to R.B. Swenson), RR-06158 (to K.A. Bard), and HD-07185 (to K. A. Bard), by The Leverhulme Trust, F/00678/O (to K.A. Bard), and the European Commission, FP6, IST-045169 (to L. Canamero). The Yerkes Center is fully accredited by the Association for Assessment and Accreditation of Laboratory Animal Care, International.

Tables

Table A: Number of Injuries Incurred between Ages 0 – 20 years

Table A.1: Sample characteristics, Means, and Standard Deviations

Means and Standard Deviations	N	Mother-reared		Responsive Care		Standard Care		Means for Sex Groups (MR + RC + SC)	
N		11 (3M, 8F)		10 (4M, 6F)		14 (10M, 4F)			
		Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Males	17	3.33	.58	1.75	.96	1.50	1.65	1.88	1.50
Females	18	2.13	2.10	.33	.52	1.00	1.16	1.28	1.67
Means for Rearing Groups (Males + Females)		2.45^{a}	1.86	$.90^{b}$	1.00	$1.36^{a,b}$	1.50		

^{ab} superscripts for rearing groups indicate where post-hoc Tukey's test found nonsignificant differences at $p < .06$ such that groups with the same subscripts were not found to be different from each other

Table A.2: Summary of Significant Chi-Square results for Age Intervals

Proportion of sample with at least one Injury		MR	RC	ST	Main Effect of Sex	Main Effect of Rearing	Interaction of Sex by Rearing
Age 0 – 5	**Males**	1/3	2/4	4/10	-	-	-
	Females	1/8	0/6	1/4			
Age 6 - 10	**Males**	2/3	1/4	4/10	m > f	-	-
	Females	1/8	0/6	0/4			
Age 11 - 15	**Males**	1/3	3/4	0/10	-	RC > ST	RC-m > ST-m
	Females	2/8	1/6	0/4			
Age 16 - 20	**Males**	2/3	2/4	2/10	-	-	-
	Females	3/8	2/6	2/4			

- indicates non-significant; m=male, f=female; RC= Responsive Care nursery; ST = Standard Care Nursery; MR = mother-reared

Table B: Number of GI tract Illness between Ages 0 – 20 years

Table B.1: Sample characteristics, Means, and Standard Deviations

Means and Standard Deviations	**N**	**Mother-reared**		**Responsive Care**		**Standard Care**		**Means for Sex Groups (MR + RC + SC)**	
N		11 (3M, 8F)		10 (4M, 6F)		14 (10M, 4F)			
		Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Males	17	.33	.58	2.25	2.50	.80	1.03	1.06	1.52
Females	18	.25	.46	2.67	1.21	1.25	.96	1.28	1.36
Means for Rearing Groups (Males + Females)		.27[a]	.47	2.50[b]	1.72	.93[a]	1.00		

[ab] superscripts for rearing groups indicate where post-hoc Tukey's test found significant differences at p < .05 such that groups with the same subscripts were not found to be significantly different from each other

Table B.2: Summary of Significant Chi-Square results for Age Intervals

Proportion of sample with at least one GI illness		**MR**	**RC**	**ST**	**Main Effect of Sex**	**Main Effect of Rearing**	**Interaction of Sex by Rearing**
Age 0 – 5	**Males**	1/3	4/4	2/10	-	RC > ST=MR	RC-f > MR-f; RC-m > ST-m
	Females	1/8	6/6	2/4			
Age 6 - 10	**Males**	0/3	0/4	3/10	-	-	-
	Females	1/8	0/6	0/4			
Age 11 - 15	**Males**	0/3	0/4	2/10	-	-	-
	Females	0/8	0/6	1/4			
Age 16 - 20	**Males**	0/3	0/4	0/10	-	-	-
	Females	0/8	0/6	0/4			

- indicates non-significant; m=male, f=female; RC= Responsive Care nursery; ST = Standard Care Nursery; MR = mother-reared

Table C: Number of Upper Respiratory Infections between Ages 0 – 20 years

Table C.1: Sample characteristics, Means, and Standard Deviations

Means and Standard Deviations	**N**	**Mother-reared**		**Responsive Care**		**Standard Care**		**Means for Sex Groups (MR + RC + SC)**	
N		11 (3M, 8F)		10 (4M, 6F)		14 (10M, 4F)			
		Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Males	17	1.67[a]	.58	2.75[b]	.50	.50[c]	.53	1.24	1.09
Females	18	.50	.54	1.00	.89	.50	.58	.67	.69
Means for Rearing Groups (Males + Females)		.82	.75	1.70	1.16	.50	.52		

A significant sex by rearing group interaction is depicted; for males, [abc] superscripts indicate where post-hoc Tukey's test found significant differences at $p < .05$ such that groups with the same subscripts were not found to be significantly different from each other; for females there was no difference across groups.

Table C.2: Relation of URI incidence by age interval with sex and rearing

Proportion of sample with at least one URI		**MR**	**RC**	**ST**	**Main Effect of Sex**	**Main Effect of Rearing**	**Interaction of Sex by Rearing**
Age 0 – 5	**Males**	1/3	4/4	5/10	m > f	RC > MR	-
	Females	0/8	3/6	1/4			
Age 6 - 10	**Males**	1/3	1/4	0/10	-	-	-
	Females	1/8	0/6	1/4			
Age 11 - 15	**Males**	1/3	3/4	0/10	-	RC > ST	RC-m > ST-m
	Females	2/8	1/6	0/4			
Age 16 - 20	**Males**	2/3	0/4	0/10	-	-	MR-m > ST-m
	Females	1/8	1/6	0/4			

- indicates non-significant; m=male, f=female; RC= Responsive Care nursery; ST = Standard Care Nursery; MR = mother-reared

Table D: Sample Characteristics, Means, and Standard Deviations for Behavioral Measures

Table D.1: Proportion of Observed Intervals Containing Abnormal Body Manipulation

Means and Standard Deviations	**N**	**Mother-reared**		**Responsive Care**		**Standard Care**		**Means for Sex Groups (MR + RC + SC)**	
N		11 (3M, 8F)		10 (4M, 6F)		12 (8M, 4F)			
		Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Males	15	.000	.000	.001	.002	.004	.004	.002	.003
Females	18	.000[a]	.000	.006[b]	.007	.001[a,b]	.001	.002	.005
Means for Rearing Groups (Males + Females)		.000	.000	.004	.006	.003	.003		

[ab] superscripts for rearing groups indicate where post-hoc Tukey's test found significant differences at p < .05 such that groups with the same subscripts were not found to be significantly different from each other

Table D.2: Proportion of Observed Intervals Containing Abnormal Rocking

Means and Standard Deviations	**N**	**Mother-reared**		**Responsive Care**		**Standard Care**		**Means for Sex Groups (MR + RC + SC)**	
N		11 (3M, 8F)		10 (4M, 6F)		12 (8M, 4F)			
		Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Males	15	.018	.024	.066	.031	.052	.040	.049*	.037
Females	18	.011	.020	.040	.046	.004	.006	.019*	.032
Means for Rearing Groups (Males + Females)		.013[a]	.020	.050[b]	.041	.036[a,b]	.040		

* indicates significant differences found at p < .05 for sex

[ab] superscripts for rearing groups indicate where post-hoc Tukey's test found significant differences at p < .05 such that groups with the same subscripts were not found to be significantly different from each other

Table E: Component Matrix Loading Scores for Human Orientation Survey

Human Orientation Survey Items	Factor 1 (AF-HO)	Factor 2 (AG-HO)
HO7: Interest in Humans	**.951***	.209
HO6: Aggression towards Humans	.071	**.940***
HO2: Moodiness towards Humans	-.030	**.931***
HO3: Solicitous of Humans	**.930***	.190
HO8: Negative Human Orientation	-.152	**.927***
HO1: Positive Human Orientation	**.896***	-.310
HO4: Positive Attention Seeking	**.893***	.009
HO5: Negative Attention Seeking	.370	**.776***

AF-HO = Affiliative Human Orientation

AG-HO = Aggressive Human Orientation

** Loaded onto factor at +1/-1 unit weight*

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Figure 1: ***Social Behavior towards Conspecifics (*p < .05, **p < .001)***

Figure 1.1 Aggressive and Affiliative Behaviors towards Conspecifics

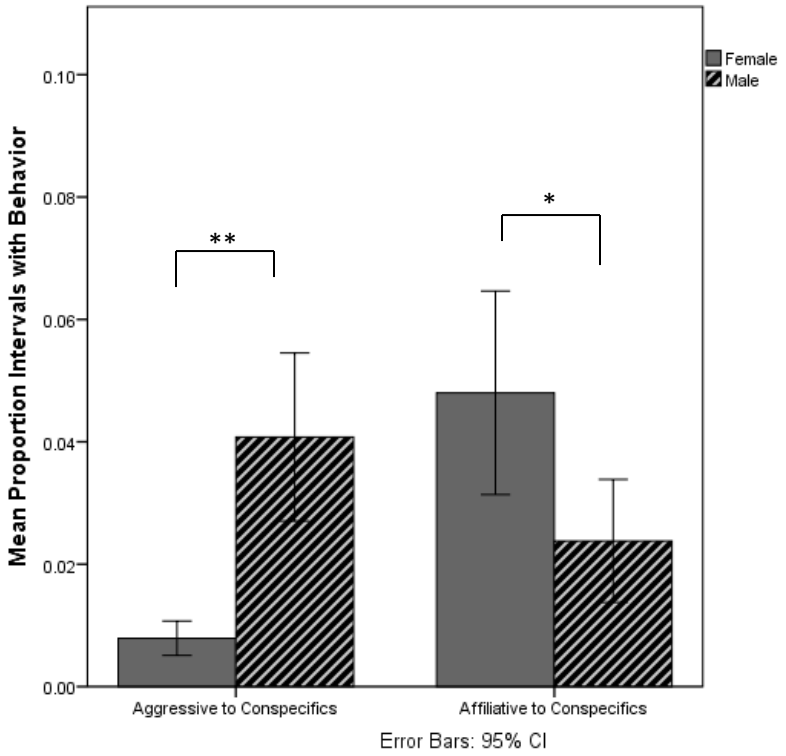


Figure 1.2 Neutral Behaviors towards Conspecifics

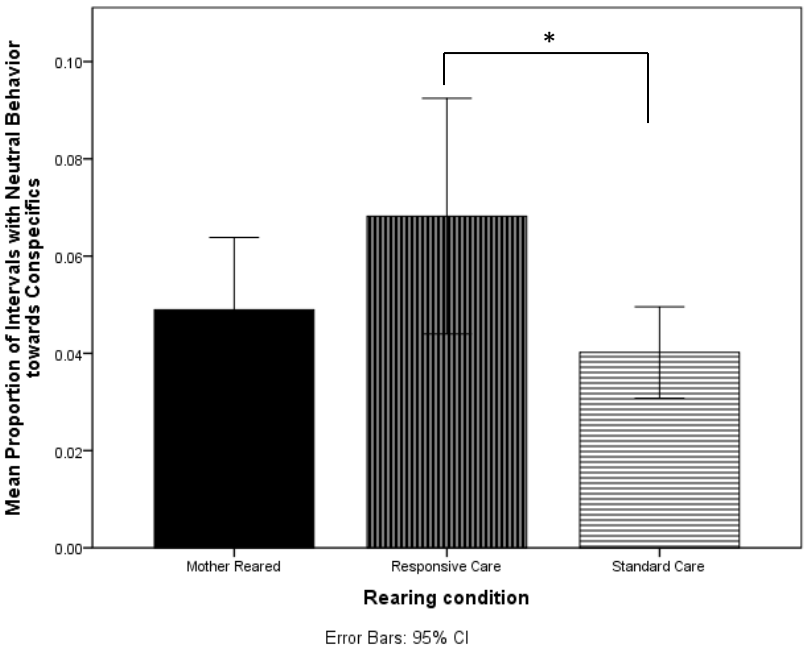


Figure 2: ***Social Behavior towards Humans (*p < .05, **p < .001)***

Figure 2.1 Aggressive Behaviors towards Humans

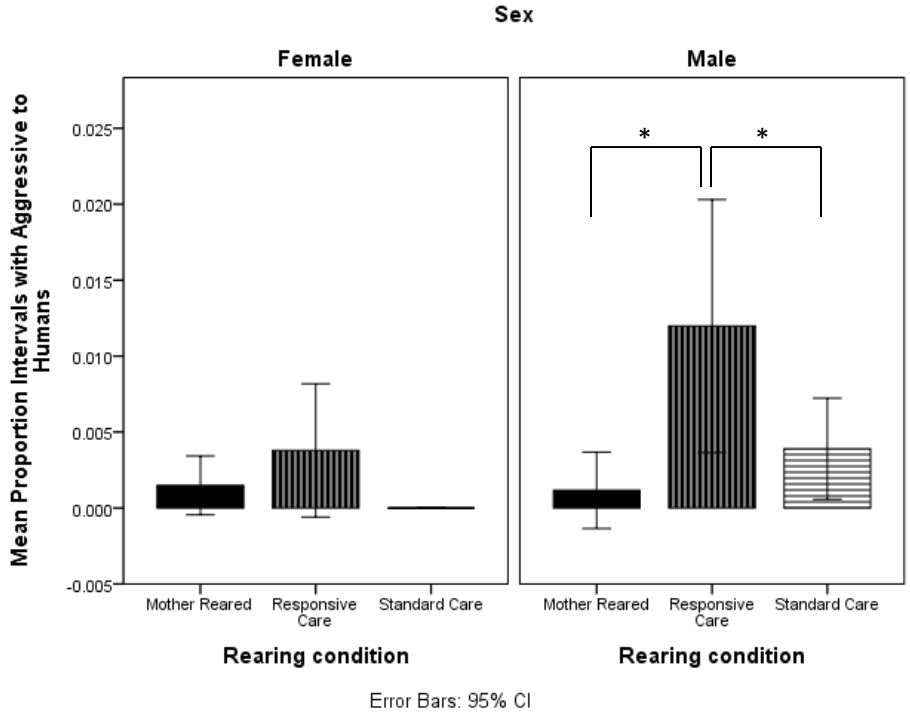


Figure 2.2 Neutral Behaviors towards Humans

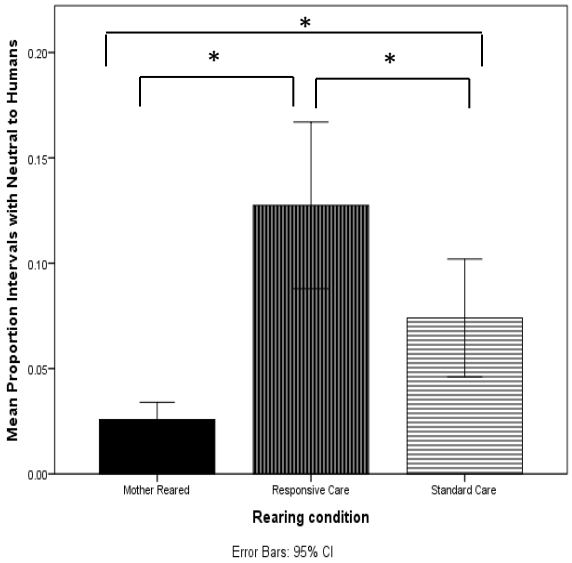


Figure 2.3 Negative Solicit Behaviors towards Humans

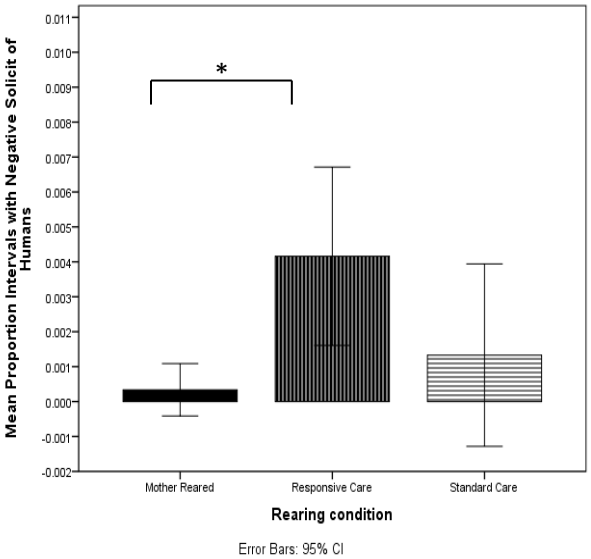


Figure 3: ***Abnormal Rocking (*p < .05)***

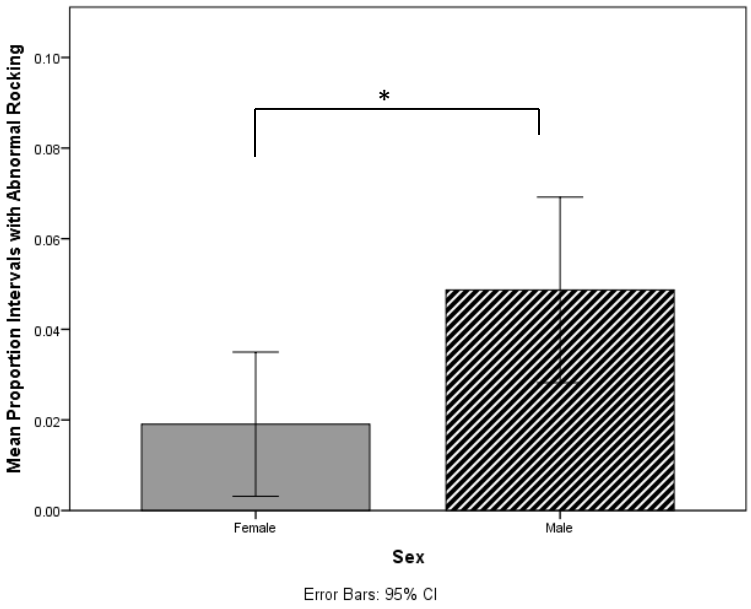


Figure 4: ***Stress Behaviors (*p < .05)***

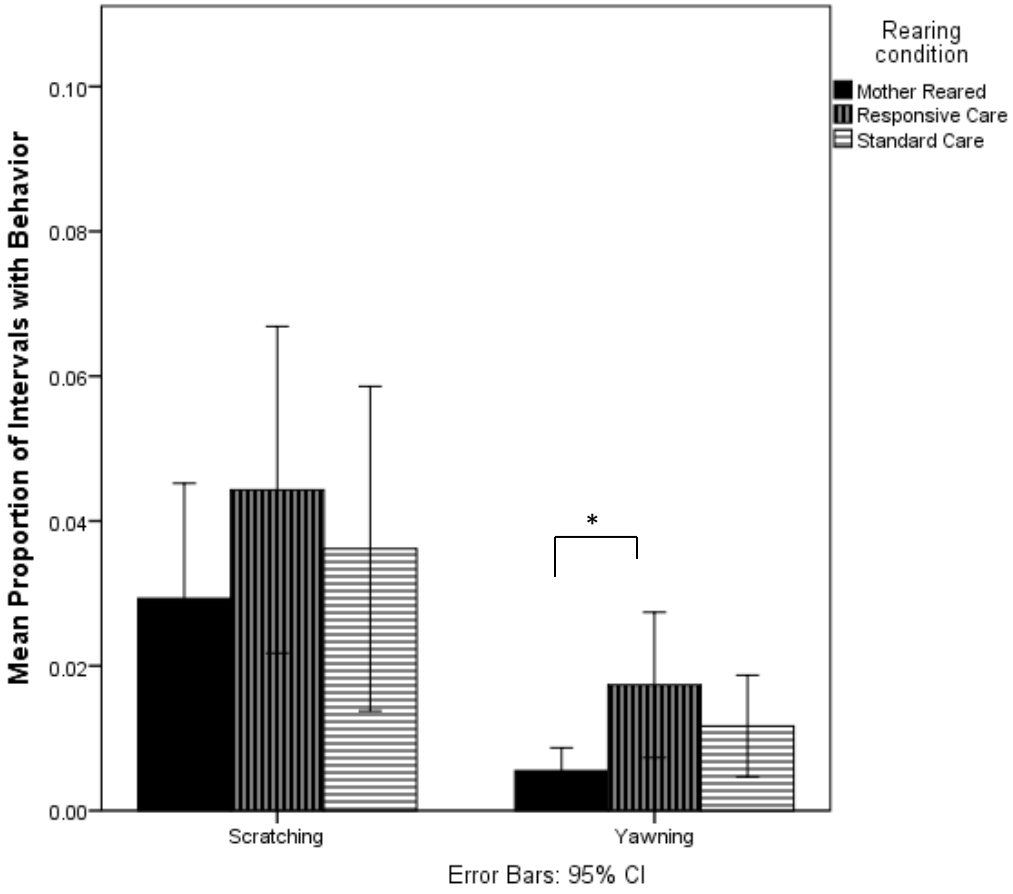


Figure 5: ***Subjective Well-Being (*p < .05)***

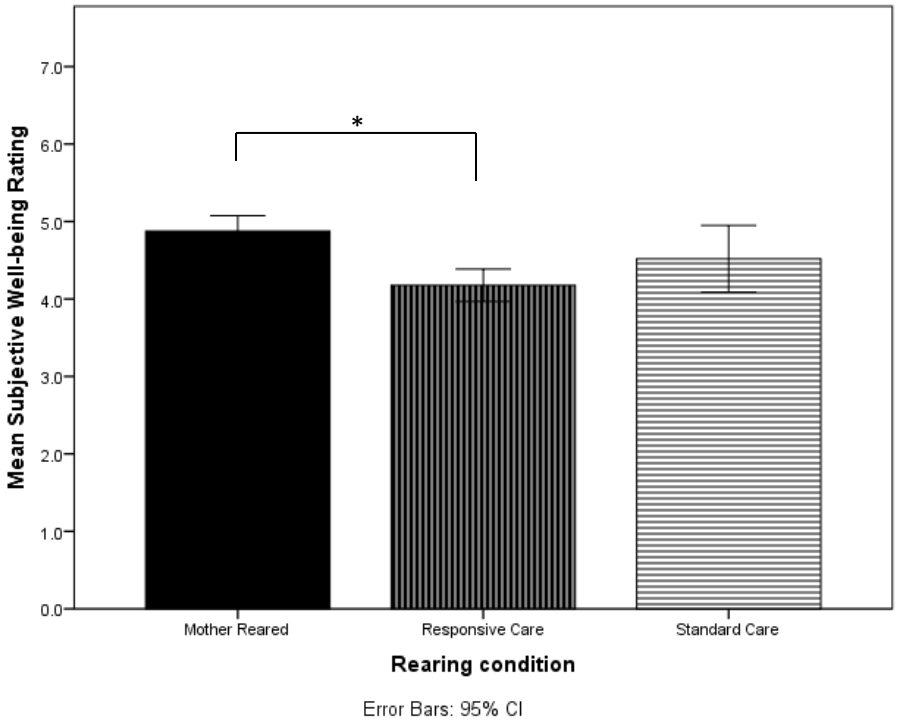


Figure 6: ***Personality (*p < .05)***

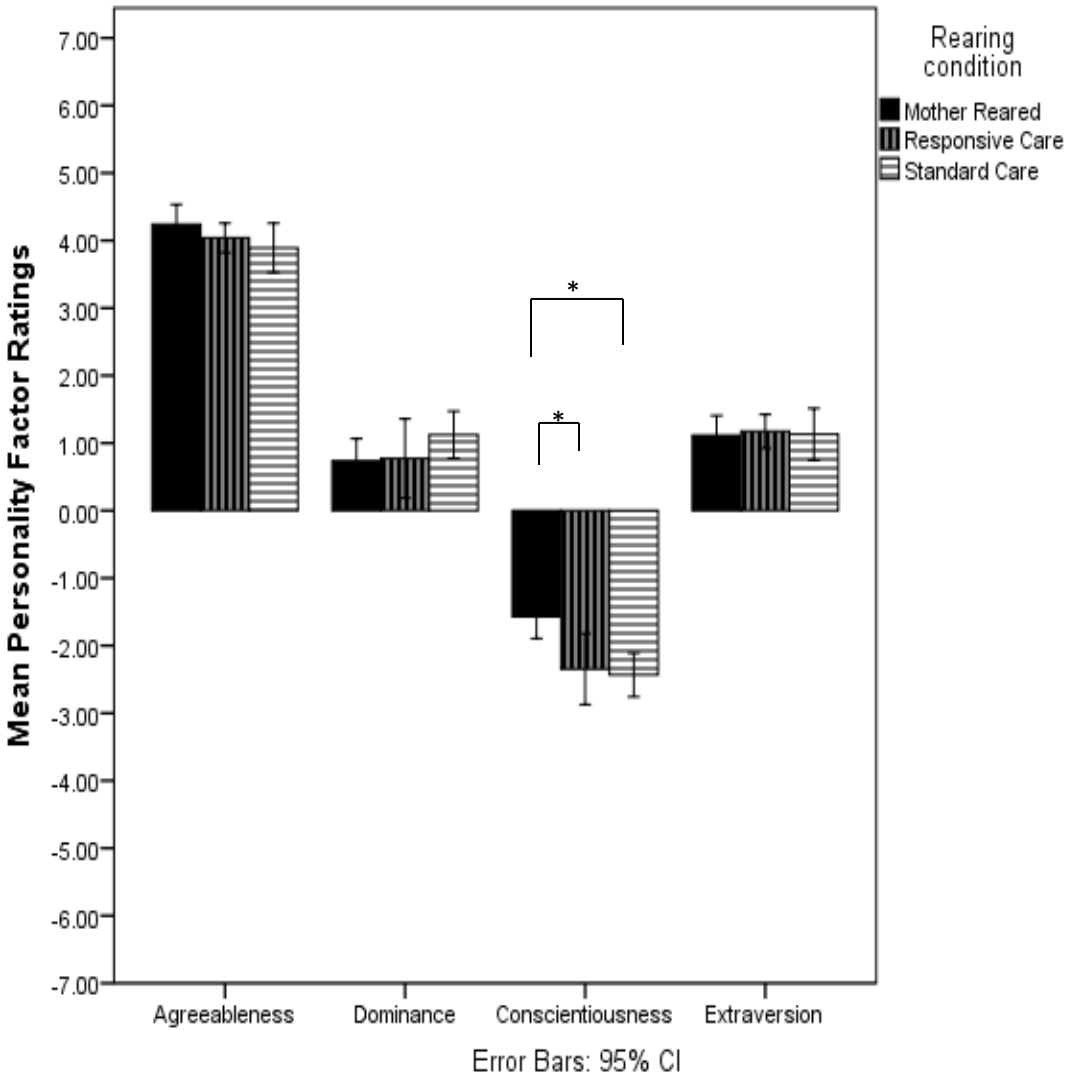


Figure 7: ***AG-FO and AF-HO (*p < .05)***

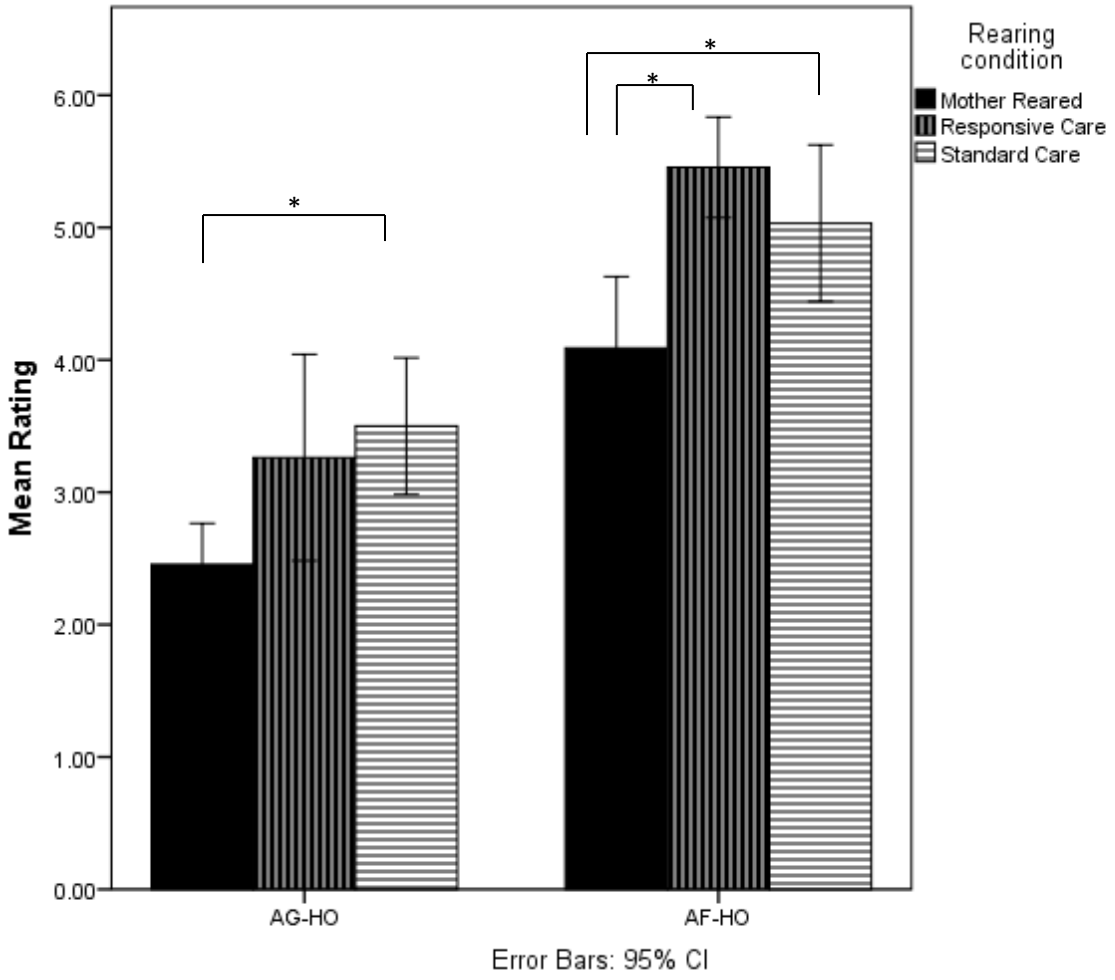


Figure 8: *Subjective Well-being, Health and Behavior*

Figure 8.1 SWB and GI Illness
(r = -.35, p < .05)

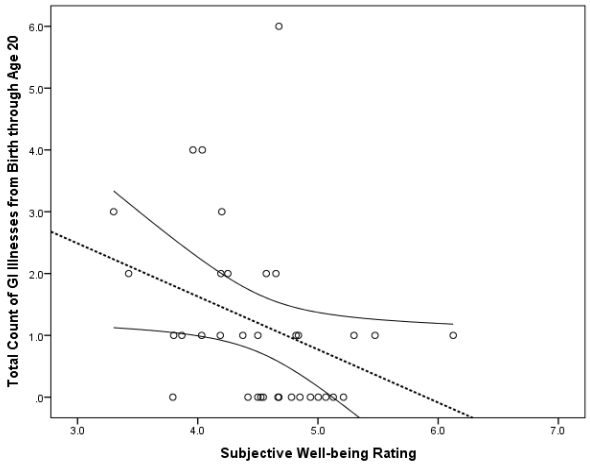


Figure 8.1 SWB and Neutral towards Humans
(r = -.41, p < .05)

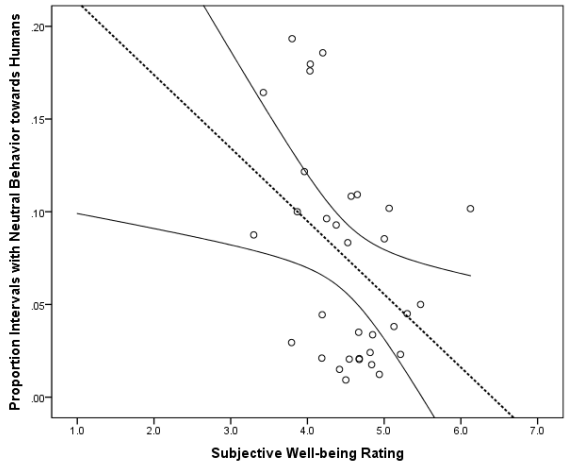


Figure 8.2 SWB and Submissive towards Humans
(r = -.41, p < .05)

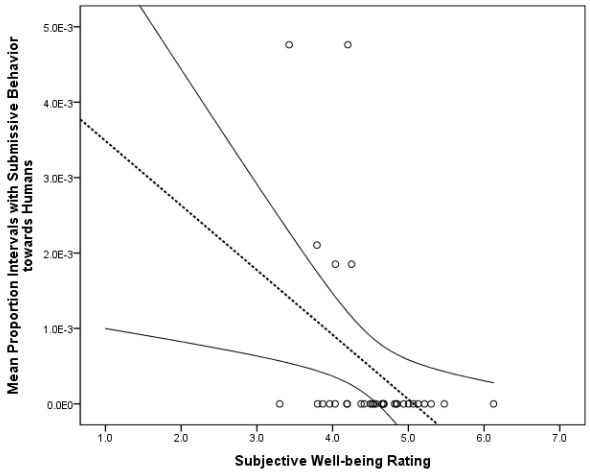


Figure 8.3 SWB and Rocking
(r = -.40, p < .05)

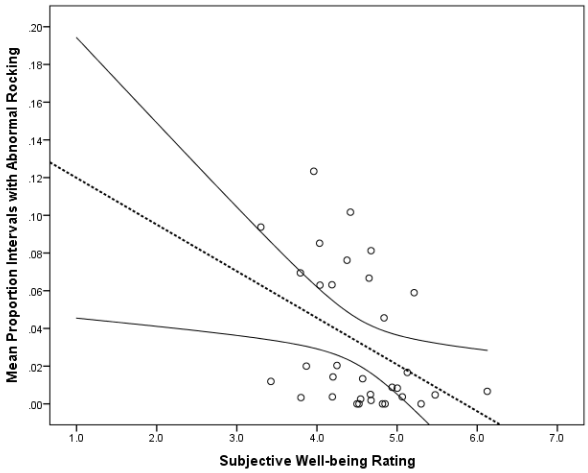


Figure 8.4 SWB and Yawning
(r = -.38, p < .05)

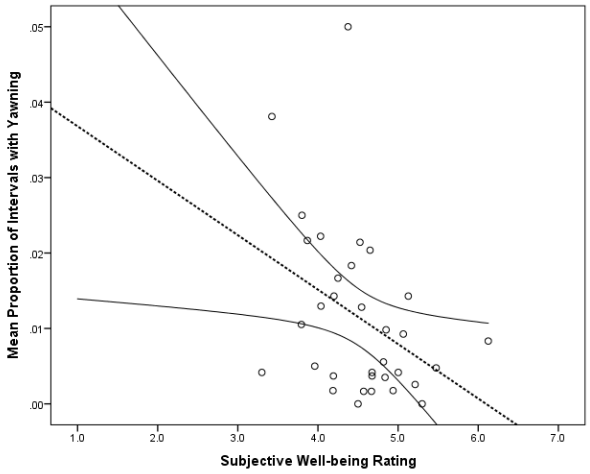


Figure 9: *SWB and Personality*

Figure 9.1 SWB and Agreeableness (r = .54, p < .001)

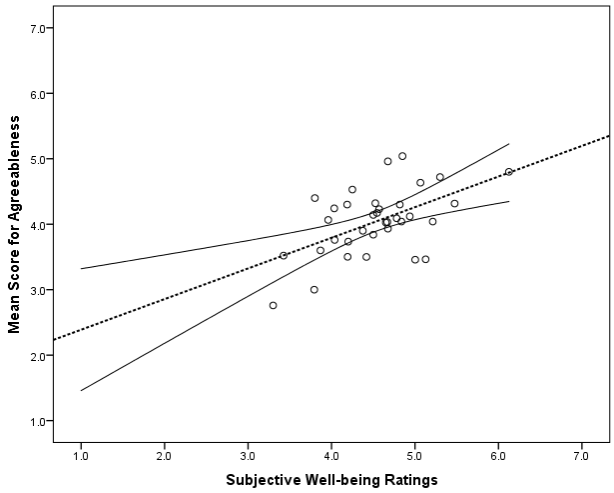


Figure 9.5 SWB and Conscientiousness (r = .36, p < .05)

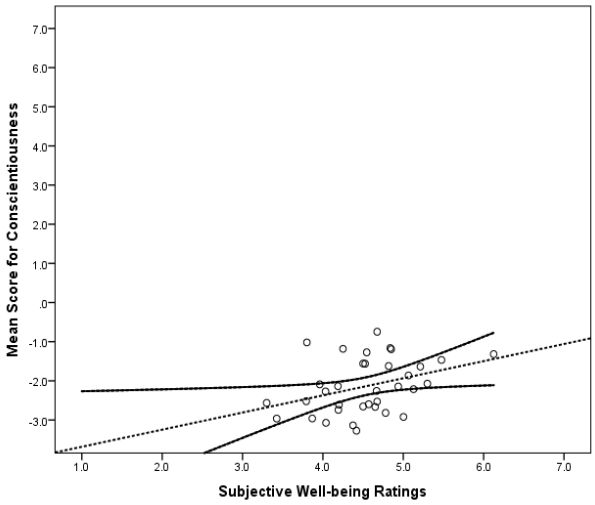


Figure 9.6 SWB and Dominance (r = .28, p = .100)

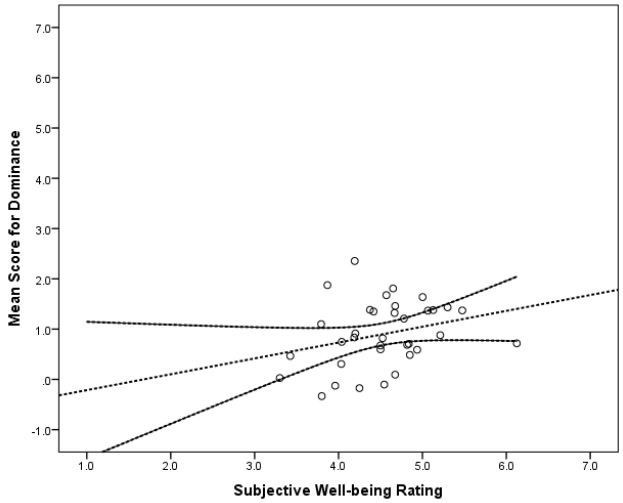


Figure 9.7 SWB and Extraversion (r = .60, p < .001)

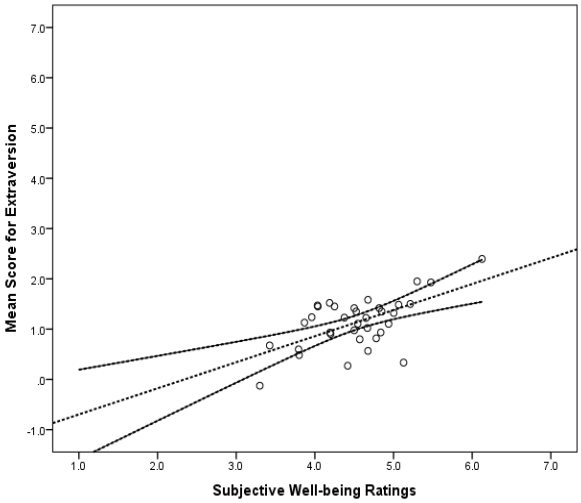
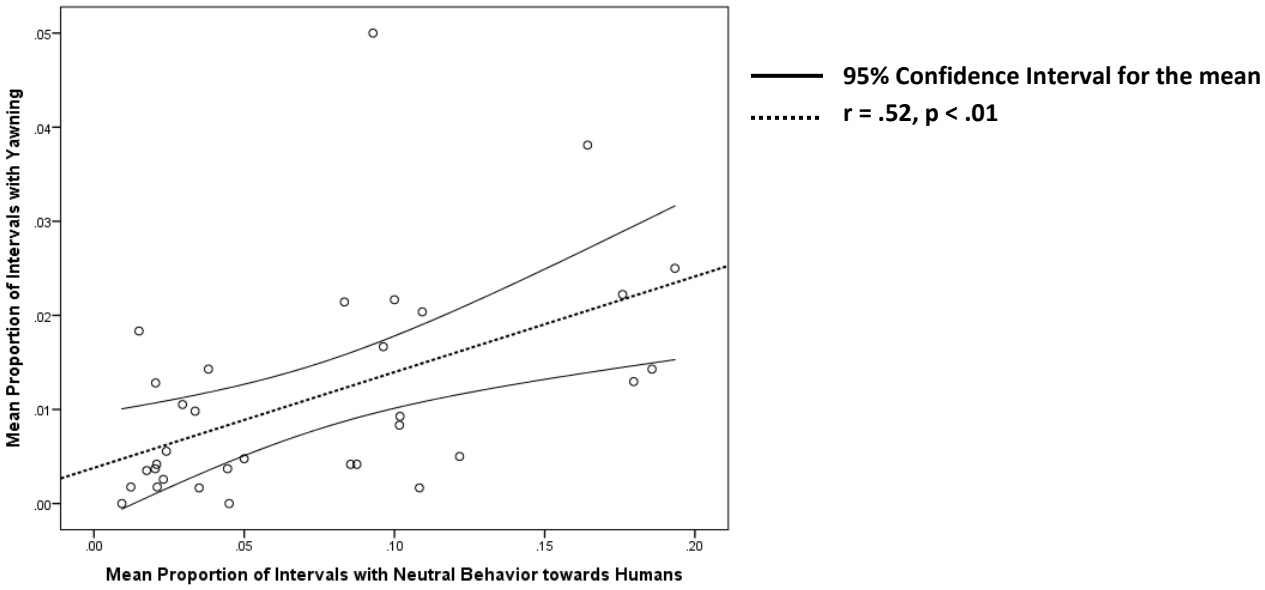
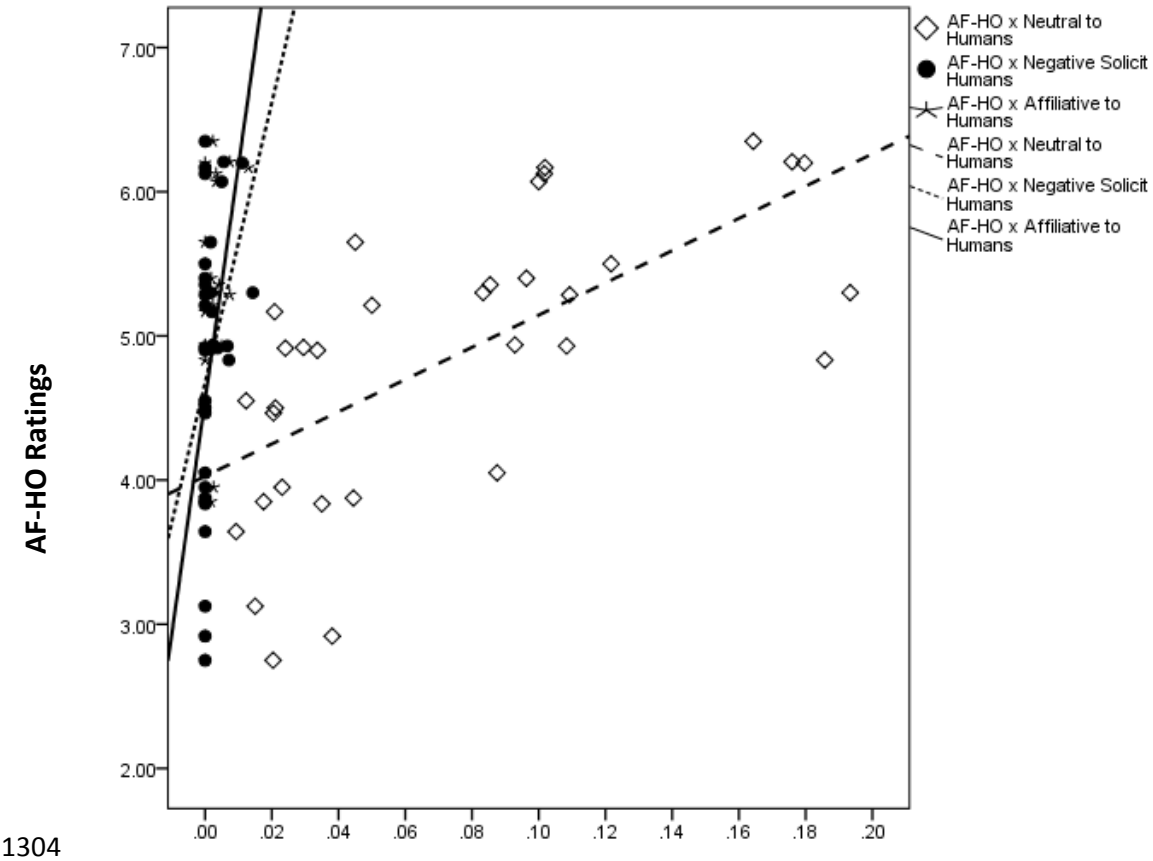


Figure 10: ***Correlation of Yawning and Neutral Behavior towards Humans***



1303 **Figure 11:** ***Correlations of AF-HO Ratings with Behavior***



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