

# The Impact of Atypical Early Histories on Pet or Performer Chimpanzees

It is widely accepted that an animal's early history, including but not limited to its rearing history, can have a profound impact on later behavior. In the case of captive animals, many studies have used categorical measures such as mother reared or human reared that do not account for both the influence of human *and* conspecific interaction. In order to account for the influence of both human and conspecific early exposure to later behavior, we collected 1385 hours of data on 61 chimpanzees, of which 36 were former pets or performers, currently housed at accredited zoos or sanctuaries. We developed a unique metric, the Chimpanzee-Human Interaction (CHI) Index that represented a continuous measure of the proportion of human and chimpanzee exposure subjects experienced and here focused on their exposure during the first four years of life. We found that chimpanzees who experienced less exposure to other chimpanzees as infants showed a lower frequency of grooming and sexual behaviors later in life which can influence social dynamics within groups. We also found chimpanzees who experienced more exposure to other chimpanzees as infants showed a higher frequency of coprophagy, suggesting coprophagy could be a socially-learned behavior. These results help characterize some of the long-term effects borne by chimpanzees maintained as pets and performers and may help inform managers seeking to integrate these types of chimpanzees into larger social groups, as in zoos and sanctuaries. In addition, these results highlight the necessity of taking into account the time-weighted influence of human and conspecific interactions when assessing the impact that humans can have on animals living in captivity.

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## 5 Introduction

6 Early life experiences have a significant impact on the behavioral development or the way  
7 in which individuals, both human and non-human, learn to interact with their environment (e.g.  
8 humans, Kagan, 1996; Fox & Henderson, 1999; non-human primates, Parker & Maestripieri,  
9 2011). Outcomes of early life experiences have uncovered a broad range of potential impacts  
10 including those falling in both the social and non-social realms. Non-social variables include the  
11 impact of the physical environment on development (rats, Leshem & Schulkin, 2012), as well as  
12 physiological factors such as genetics (primates Barr et al., 2003; Suomi, 2011) or hormones  
13 (primates, Saltzman & Maestripieri, 2011) that influence maternal care. Studies of social effects,  
14 including both maternal and non-maternal influences, have focused primarily on the impact of  
15 conspecifics in an infant's environment and the subsequent effect on behavior expressed later in  
16 life (humans, Sroufe, 2005; rodents & primates, Pryce et al., 2005; primates, Suomi, 1997).  
17 Even animals typically considered less social in nature, such as lizards, seem vulnerable to the  
18 effects of atypical and impoverished social histories (Cissy, Richard & Mats, 2014).

19 A range of circumstances in captivity might require infants to be raised by humans rather  
20 than by peers or their mothers. For instance, a biological mother may be unable to care for her  
21 offspring due to illness or disinterest leading to neglect; in these circumstances, human  
22 intervention may be warranted. Studies investigating the impact of these atypical rearing  
23 situations on primates – notably with rhesus macaques and chimpanzees – have used categorical  
24 classifications, such as mother-reared and human-reared, and reported a range of substantive  
25 impacts on developmental trajectories (Anderson & Mason, 1974; Maki, Fritz & England, 1993;  
26 Suomi, 2011). In the most extreme cases of social deprivation, there are a range of impacts  
27 including behaviors such as self-clutching, excessive rocking, and self-mutilation (Harlow,  
28 Dodsworth & Harlow, 1965). In laboratory settings, peer-reared chimpanzees (with no maternal  
29 contact) tended to be less dominant and less active and often showed more abnormal rocking and

30 less social play behavior (Rosenblum & Kaufman, 1968; Bloomsmith, Lambeth & Alford, 1991;  
31 Spijkerman et al., 1994; Spijkerman, 1996). Alternatively, a recent study assessing orphaned and  
32 mother-reared chimpanzees in African sanctuaries found that orphaned chimpanzees engaged in  
33 more social play compared with those classified as mother-reared. However, the play periods of  
34 the orphaned chimpanzees were shorter and more often led to aggression (Van Leeuwen,  
35 Mulenga, & Chidester, 2014). The effects of these early rearing histories may have long-term  
36 effects as well: studies of laboratory-housed chimpanzees that were raised exclusively by humans  
37 exhibited more abnormal behaviors later in life in comparison to peer-reared chimpanzees who  
38 were raised with other chimpanzees (Martin, 2002; Martin, 2005). In sum, the results of these  
39 studies show human-reared chimpanzees seem particularly prone to both short- and long-term  
40 negative impacts on their behavior and likely their wellbeing.

41         Although previous studies have noted both short - and long-term impacts on chimpanzees  
42 who were human-reared, past research on human-reared chimpanzees has not taken into account  
43 differences in the degree and amount of human interaction in early development and how this  
44 influences later behavior. However, social influences may vary depending on an individual's  
45 living situation, so a strict categorical classification may not be adequate in many cases. For  
46 example, the largely unstudied population of privately-owned chimpanzees – those living as  
47 personal pets and as trained performers in the entertainment industry – often includes individuals  
48 who have experienced a mix of human and chimpanzee influences. A continuous metric that  
49 allows researchers to account for variation in social influences at different stages of an  
50 individual's life may be more apt than a categorical metric, so that a wide variety of potential  
51 influences can be assessed.

52         Chimpanzees bred for the pet industry are typically removed from their mother soon  
53 after birth to facilitate human handling. They are sold to members of the general public, who  
54 most often have no experience or training to care for this species. These pet chimpanzees are

55 likely to have relatively little exposure to conspecifics early in life and during key developmental  
56 periods. Many are essentially raised as humans, with related traditions such as eating at a table  
57 and wearing clothes, until they grow to be too large and dangerous to be kept in the home.  
58 Performing chimpanzees have a more variable trajectory and though they may spend some  
59 proportion of their time with other chimpanzees, they are also highly exposed to humans (trainers  
60 and audiences) until they too typically grow to be unmanageable in adolescence. The categorical  
61 designations of “human-raised”, “peer-raised”, or “mother-raised” do not encompass the actual  
62 experience of a chimpanzee such as those who performed and spent significant time in full  
63 contact with both humans and other chimpanzees. There is growing consensus that privately-  
64 owned chimpanzees represent significant human health and safety risks (McCann et al., 2007).  
65 In the case of entertainment chimpanzees, these practices produce additional consequences such  
66 as negative public perceptions that can impact conservation efforts (Ross et al., 2008; Ross,  
67 Lonsdorf & Vreeman, 2011; Schroepfer et al. 2011). However, here we focus on the long-term  
68 outcomes of these practices and the degree to which the atypical early histories experienced by  
69 these chimpanzees influence their behavioral development.

70         In the current study, we used a novel approach to assess the impact of atypical early  
71 histories experienced by pet and performing chimpanzees and the subsequent outcomes for  
72 behavioral development. We employed a long-term continuous measure, chimpanzee-human  
73 index (CHI), that accounts for both the amount of time spent with humans as well as the amount  
74 of time spent with other conspecifics. We examined how differential human/conspecific exposure  
75 during the infant period or the first four years of life impacted current behavioral patterns for ex-  
76 pet and ex-performer chimpanzees now living in accredited zoos and sanctuaries. Although our  
77 question revolved around chimpanzees without early exposure to conspecifics, we also studied  
78 the behavioral patterns of chimpanzees who have lived their entire lives in their natal group to  
79 provide a comparison group. These zoo-born chimpanzees may also have a range of

80 human/conspecific exposure early in life; however, most have never had full contact with humans  
81 and have always lived with other chimpanzees. In the current study, we focused on the first four  
82 years of life because this is considered to be a particularly influential period for behavioral and  
83 socio-cognitive development for this species (Tomasello, Kruger & Ratner, 1993; Bard, 1995;  
84 Bard et al., 2014). We predicted that chimpanzees with atypical early histories (high human  
85 exposure, low conspecific exposure) would differ behaviorally compared with those having more  
86 species-typical histories. We projected these differences would be most pronounced in areas of  
87 social, sexual and abnormal behaviors and ultimately reflect our hypothesis that these atypical  
88 early histories can result in a long-term decrease in species-typical developmental trajectories .

## 89 **Materials and Methods**

90 This research was conducted at three sanctuaries that are members of the North American  
91 Primate Sanctuary Alliance (NAPSA: Center for Great Apes, Chimps, Inc., and Save the Chimps)  
92 and six zoos accredited by the Association of Zoos and Aquariums (AZA: Houston Zoo, Dallas  
93 Zoo, Lincoln Park Zoo, Lion Country Safari, North Carolina Zoo, and Oakland Zoo). Each of  
94 these facilities adheres to high standards of chimpanzee care including housing chimpanzees in  
95 social groups and providing nesting material and various forms of enrichment. All animals were  
96 observed in their home cages during observations. All subjects had *ad libitum* access to water  
97 and at no time were the subjects ever food or water deprived. Subjects were provided daily with  
98 primate chow and fruit and/or vegetable food enrichment at each of the facilities. This study was  
99 approved by and complied with protocols approved by the Chimpanzee Species Survival Plan  
100 (SSP) management group as well as animal care committees at each of the institutions that  
101 participated in this study.

## 102 **Subjects**

103           The subjects were 60 chimpanzees (25 males, 35 females, mean age = 21 years, range: 6 –  
104 54 years) that varied widely in the degree of human and conspecific exposure they experienced  
105 early in their lives (Figure 1, Tables S1 in Online Supplementary Materials). Though many of  
106 them were formerly housed as personal pets or performers, all were evaluated in their current  
107 housing at NAPSA sanctuaries or AZA zoos. The number of subjects studied at each institution  
108 ranged from four to 12. The subjects had been at his/her respective facilities between one month  
109 and 54 years before the study. The average amount of time that each subject spent at his/her  
110 respective facility before the study was nine and a half years. Data were collected at three  
111 NAPSA-accredited sanctuaries as well as six AZA-accredited zoos. None of the NAPSA  
112 sanctuaries were open to the public, but the AZA zoos all had public access with daily visitors.  
113 All of the subjects were socially housed, with between one and 25 other chimpanzees (average  
114 group size was seven chimpanzees). All of the chimpanzees in the study were captive-born, and  
115 none had lived in a laboratory environment.

## 116 **Behavioral Assessments**

117           Behavioral data on the chimpanzees were collected with a modified version of an  
118 ethogram used for Lincoln Park Zoo's long-term behavioral monitoring studies of great apes  
119 (Ross et al., 2011). The ethogram included six primary behavioral categories (social (e.g.  
120 grooming, playing, begging, embrace) sexual, agonism, solitary, inactivity and abnormal), which  
121 were comprised of 21 behaviors (provided in the Online Supplementary Materials). Behavioral  
122 data were collected using a combination of all occurrence and scan sampling. Data were collected  
123 with handheld computers (Pocket Observer 2.0, Noldus Observer, Noldus Information  
124 Technology, Wageningen, The Netherlands) in 30-min focal samples with a 30-sec intersample  
125 interval for the scan samples. When more than one focal sample was collected on the same  
126 individual in one day, there was at least a one hour period between each of the samples collected  
127 for that individual. Observations were conducted between 9 am and 5 pm by a single observer

128 (HF) at eight of the nine study sites. The data collected at the ninth site (Lincoln Park Zoo) were  
129 collected by observers who had previously achieved 85% reliability on the ethogram. HF  
130 conducted a *post hoc* inter-rater reliability assessment with a researcher at the Lincoln Park zoo  
131 and was found to have 90% reliability on the ethogram. An equal number of observations were  
132 collected in the morning and afternoon for each chimpanzee. The order of the observations was  
133 randomly selected ahead of time. Feeding and enrichment times varied at each of the study sites,  
134 and data were collected to cover each of these periods. Observations were conducted from a safe  
135 and approved area from where the chimpanzees could be easily seen but would not be unduly  
136 affected by the presence of the observer. Between 14.5 and 30 hours of data were recorded on  
137 each subject, over a period ranging from three to eight weeks between November 2011 and  
138 November 2012, for a total of 1385 hours of behavioral data. The number of hours varied due to  
139 time constraints and the number of subjects on which data were collected at each institution. The  
140 range in the number of hours collected on each subject was factored into the analyses.

#### 141 **Chimpanzee Human Interaction Index**

142 In order to characterize the variable degree of exposure to potential influences  
143 (conspecifics and humans), we developed a novel, continuous measure, the Chimpanzee Human  
144 Interaction (CHI) index. We used management records acquired from past and current holding  
145 institutions and calculated the proportion of time per day that each chimpanzee spent in each of  
146 three categories: full exposure to conspecifics, full exposure to humans, and mixed exposure to  
147 both conspecifics and humans. Each day was assigned a numerical value based on these three  
148 categories of exposure. For instance, chimpanzees living exclusively within a large social group  
149 in a zoo with only minimal exposure to humans would have a proportion of 1/1 for the day,  
150 indicating they spent 100% of their time with other chimpanzees. Likewise, a pet chimpanzee  
151 raised exclusively with a human family, without any exposure to other chimpanzees, would have

152 a proportion of 0/1 for that same day. A performing chimpanzee with relatively equal exposure to  
153 small groups of conspecifics and full contact with human trainers and audiences would have a  
154 proportion of 0.5/1. CHI is calculated as the sum of these variable exposure periods over a  
155 particular timeframe given that many chimpanzees have experienced variation in the degree of  
156 human and conspecific exposure across their lifetimes. For this analysis, we chose to focus  
157 specifically on the infant period: the first four years of life (see Figure 1 for a histogram of the  
158 infant CHI<sub>i</sub> (CHI<sub>i</sub> refers to the CHI value of chimpanzees during the infant period) distribution  
159 and Table S1 in Online Supplementary Materials for details about each subject), however the CHI  
160 index could be utilized to characterize human/conspecific exposure across any particular  
161 timeframe or across the entire lifetime.

## 162 **Categorical Groups**

163 Although our CHI index was developed to be used as a continuous variable, CHI<sub>i</sub> values  
164 in this study revealed a non-normal distribution of the data with clear peaks (Figure 1). This was  
165 likely a result of relatively low variability in conspecific/human exposure over the first four years  
166 of life. Therefore, we analyzed the data using categorical groupings by early history experience:  
167 with subjects categorized as having only or primarily human exposure (CHI<sub>i</sub> index: 0-0.30, n =  
168 6), exposure to both chimpanzees and humans (CHI<sub>i</sub> index: 0.31 – 0.70, n = 32), or primarily  
169 chimpanzee experience (CHI<sub>i</sub> index: .71 – 1.0, n =21) (see Table S1 in the Online Supplementary  
170 Materials for each subject's rating).

## 171 **Data Analysis**

172 Data analyses were conducted in IBM SPSS 20 (IBM Corp., 2011). A false discovery rate  
173 correction was performed on the results to control for multiple comparisons, and a corrected  
174 alpha value of p less than or equal to .01 was considered to be significant for all tests. We  
175 controlled for the difference in the number of hours spent observing each chimpanzee by

176 calculating the proportion of time out of the total that an individual spent engaging in a particular  
177 behavior compared to the total number of hours of observations on the individual.

178 In order to assess differences between the three categories of early history during the  
179 infant period (“human,” “mixed,” and “chimpanzee”), we performed a one-way multivariate  
180 analysis of variance (MANOVA) using each of the 21 behaviors as dependent variables and the  
181 early history categories as a fixed factor.

## 182 **Results**

183 One-way MANOVA analysis revealed there was a statistically significant difference in the  
184 proportion of time the chimpanzees spent engaging in different behaviors based on their early  
185 exposure history ( $F(44, 70) = 3.180, p < .00005$ , Wilks' Lambda = .111, partial  $\eta^2 = .667$ ).

186 Separate analyses revealed that sex, age, potential number of social partners, and time spent at  
187 current location did not significantly change the results ( $p > .05$  for all behaviors after controlling  
188 for the effect of early history). A series of one-way ANOVA's on each of the 21 dependent  
189 variables was conducted as follow-up tests to the MANOVA. An examination of the data revealed  
190 that for the following behaviors, the homogeneity of variance assumption was violated: social  
191 sex, masturbation, abnormal movement, coprophagy, abnormal body posturing, and abnormal  
192 plucking. In these cases, we ran a Welsh test on the data to look at the significance of the ANOVA  
193 test. The results of the Welsh test revealed that for the behaviors of abnormal movement and  
194 abnormal plucking, the F-value, which was significant in the original ANOVA test, was not  
195 significant after correcting for unequal variances. However, the ANOVA tests for the remaining  
196 behaviors revealed that in four (social, sexual, inactivity, abnormal) out of six behavioral  
197 categories a significant relationship existed between categories of early history and the proportion  
198 of time subjects were observed engaging in each behavior. The results of the individual ANOVA  
199 tests between proportion of behaviors and categories can be seen in Tables 1, 2 and 3. In addition,

200 a series of post-hoc analyses (Dunnett's T3 assuming unequal variances) were performed to  
201 examine individual mean difference comparisons across the three levels of CHI<sub>i</sub> values and each  
202 of the behaviors found to be significant with the MANOVA at  $p < .05$ . The specific results are  
203 outlined below.

#### 204 **Social Behavior**

205 The individual ANOVA analyses revealed that early exposure categories influenced frequencies  
206 of grooming behavior later in life. The ANOVA revealed a significant difference between groups  
207 in frequency of giving grooming ( $F(2,56) = 10.13, p = 0.0001$ ). Post-hoc analyses revealed that  
208 subjects with high amounts of chimpanzee exposure early in life groomed significantly more than  
209 those with mixed ( $p = 0.012$ ) or minimal exposure to conspecifics ( $p = 0.002$ ).

210 There was also a significant difference between groups in frequency of grooming received  
211 ( $F(2,56) = 9.22, p = .0001$ ). Post-hoc analyses revealed that the subjects with high amounts of  
212 chimpanzee exposure early in life groomed significantly more than those with mixed ( $p <$   
213  $0.0001$ ) or minimal exposure to conspecifics ( $p = 0.003$ ). There was not a significant relationship  
214 between early exposure category and frequencies of social play or other prosocial behaviors ( $p$   
215  $> .01$ ).

#### 216 **Sexual Behavior**

217 The ANOVA revealed a significant difference between groups in frequency of sexual  
218 behavior ( $F(2, 56) = 4.98, p = .01$ ). The post-hoc analyses revealed that chimpanzees with high  
219 amounts of early exposure to conspecifics demonstrated higher frequencies of mounting and  
220 sexual exploration compared to chimpanzees with low exposure to conspecifics ( $p = .02$ ). There  
221 was not a significant difference found between chimpanzees with high exposure to conspecifics

222 and those with mixed exposure ( $p > .01$ ). There was not a significant relationship found between  
223 the category of early exposure and rates of masturbation ( $p > 0.01$ ).

#### 224 **Agonistic and Solitary Behaviors**

225 There was no difference in the expression of agonistic or solitary behaviors, including  
226 displays, non-contact, contact aggression given or received, self-grooming or self-play in relation  
227 to categories of early exposure ( $p > .01$ ).

#### 228 **Inactivity**

229 The ANOVA analyses revealed significant differences in frequencies of inactivity between  
230 the early history categories ( $F(2, 56) = 7.72, p = .001$ ). Post-hoc tests revealed that chimpanzees  
231 with mixed early exposure demonstrated higher rates of inactivity than those with either primarily  
232 human ( $p < .0001$ ) or primarily conspecific exposure early in life ( $p = .002$ ).

#### 233 **Abnormal Behavior**

234 We examined four forms of abnormal behavior: coprophagy, abnormal movement,  
235 abnormal body posturing, and hair plucking. The ANOVA analysis revealed significant  
236 differences in frequencies of coprophagy between the early history categories ( $F(2, 56) = 14.99,$   
237  $p = .0001$ ). The post-hoc tests revealed that chimpanzees with high amounts of early exposure to  
238 conspecifics demonstrated the highest frequencies of coprophagy later in life than those with  
239 either mixed early exposure ( $p = .040$ ) or primarily human exposure early in life ( $p = .001$ ). There  
240 was not a significant difference in rates of coprophagy between chimpanzees from primarily  
241 human or mixed early exposure histories. The ANOVA analysis found there was not a significant  
242 difference between the three categories in rates of the other forms of abnormal behavior ( $p > .$   
243  $01$ ).

## 244 **Discussion**

245           The primary aim of this study was to use a novel approach to assess the long-term  
246 behavioral impact of variable early life exposure to both conspecifics and humans on captive  
247 chimpanzees. To achieve this, we focused on a rarely studied population, former pet and  
248 performer chimpanzees that now live in accredited zoos and sanctuaries with other chimpanzees.  
249 We also studied individuals who had experienced more typical early life histories for captive  
250 chimpanzees, living in their natal group with multiple conspecifics, in accredited zoo  
251 environments throughout their lifetime. In general, supportive of our hypotheses, we found that  
252 chimpanzees raised in “human” or “mixed” exposure groups tended to exhibit lower frequencies  
253 of grooming compared with those in the “chimpanzee” group. In addition, chimpanzees raised in  
254 the “human” exposure group exhibited lower frequencies of social sexual behavior later in life as  
255 compared with those in the “chimpanzee” group. Lastly, chimpanzees in the “mixed” exposure  
256 group exhibited higher frequencies of inactivity compared with the “human” or “chimpanzee”  
257 groups. The results of this study suggest that high human exposure early in a chimpanzee’s life,  
258 and/or reduced conspecific exposure, is related to observable differences in behavior in  
259 adulthood. Grooming and sexual behavior are important components to the dynamics of social  
260 groups in chimpanzees. Decreases in these behaviors could have the potential to be related to  
261 animal management and welfare issues connected with social interactions between chimpanzees.

262           While it is possible that variability in current living environments may represent a  
263 confound to the conclusions of this study (due in part to the relatively limited number of  
264 institutions caring for chimpanzees with such atypical backgrounds), it is important to note that  
265 the demonstrated effects are unlikely to be solely the result of current physical or social  
266 environments. All subjects were socially housed, and all were managed under similar  
267 contemporary management systems.

268           The behavioral differences observed between early-history groups are consistent with  
269 previous findings in chimpanzees and other non-human primates (i.e. mother-reared individuals  
270 compared to isolated individuals, Turner, Davenport & Rogers, 1969; Davenport & Rogers, 1970;  
271 Harlow & Suomi, 1971; Kalcher et al., 2008). For example, several studies have demonstrated  
272 that human-reared primates often have lower rates of reproductive success, possibly indicative of  
273 less appropriate sexual behavior (Ryan, Thompson & Roth, 2002). The evidence for a  
274 developmental influence of rearing on later chimpanzee behavior is mixed. While some studies  
275 report a lack of rearing effect in social behavior (Bloomsmith et al., 2002; Howell et al., 2006;  
276 van Ijzendoorn et al., 2009) more recent analyses (Clay, 2012) and the results of our analyses  
277 suggest the possibility that these effects might not be evident until much later in life. Duration of  
278 exposures of chimpanzees to humans or conspecifics might also be a particularly important  
279 factor. Martin (2005) assessed behavior in chimpanzees that were reared in a variety of contexts  
280 and found no statistical effect of rearing; however, the authors were unable to account for the  
281 duration of time spent in each of the rearing categories.

282           We also noted differential effects of early experiences on coprophagy, a behavior typically  
283 categorized as abnormal (Walsh, Bramblett & Alford, 1982; Nash et al., 1999). We found that  
284 chimpanzees with more conspecific exposure engaged in coprophagy more frequently compared  
285 to those in the “mixed” or “human” groups. This behavior is likely socially learned (as opposed  
286 to an individually-developed response indicative of stress) and thus animals with broad social  
287 exposure may be more likely to adopt these behaviors. Previous studies have found that mother-  
288 reared chimpanzees engage in coprophagy more often than non-mother-reared individuals (Nash  
289 et al., 1999; Bloomsmith et al., 2005), which suggests that coprophagy may be functionally  
290 distinct from other abnormal behaviors. Future studies should involve investigating potential  
291 welfare concerns associated with different types of abnormal behaviors in order to determine  
292 which behaviors are performed only during times of stress compared with other times. Despite

293 the breadth of the data used for this investigation, there remain a number of limitations that  
294 reflect the complexity of a multi-institutional study and require additional consideration. The  
295 first is the potential confound between a chimpanzee's current housing locations with his/her  
296 early history exposure. Chimpanzees from particular backgrounds tended to cluster at specific  
297 institutions. As a result, there was relatively little intra-institutional variation in early histories  
298 among the chimpanzees housed within single groups. Fortunately, the variation in current  
299 housing conditions and management styles was relatively low, at least in comparison to the wide  
300 variety of physical and social environments from which many of these chimpanzees originated.  
301 All current housing was either at AZA-accredited zoos or NAPSA member sanctuaries; all  
302 maintain consistently high standards of care in terms of diet, enrichment, and housing.  
303 Additionally, subjects were housed in different social groupings (ranging from 2 – 26  
304 chimpanzees per group), and in some cases, this was an outcome of their atypical early histories  
305 and difficult socialization histories. In addition, some of the chimpanzees were genetically related  
306 to each other; however, because of the amount of variability in the degree of relatedness both  
307 within and across institutions, we could not account for it given our current sample size.

308 We must also consider the potential limitations of our measure of human and conspecific  
309 exposure, including both the CHI index and categories based on this index. In this analysis we  
310 utilized a subset of the CHI index ( $CHI_i$ ), specific to a relatively narrow time frame from birth to  
311 age 4. During this timeframe, there is inherently less variation across individuals in comparison  
312 to that observed across the entire lifetime. For instance, chimpanzees with low conspecific  
313 exposure were usually maintained in those conditions across those first four years, but across  
314 their lifetime they may experience a wider array of social conditions. Subsequently, we chose to  
315 use a categorical analysis. Only six of the 60 chimpanzees had solely human exposure during  
316 infancy but including this category in the analyses was important to draw comparisons among  
317 those individuals who lacked exposure to conspecifics. Inclusion of this small sample group

318 comes with limitations including the possibility of failing to detect some behavioral effects (type  
319 II errors). We also acknowledge that it is possible that individuals with similar CHI values may  
320 in fact have experienced very different patterns of exposure to conspecifics and humans. Further  
321 refinement of this index may help address these potential limitations.

322 Overall, the results of this study suggest that adolescent and adult chimpanzee behavior is  
323 associated with early life experiences and that individuals exposed to more human-centric  
324 environments may express behavioral deficits later in life in relation to grooming and sexual  
325 behavior. It is possible that the consequences of these developmental trajectories may differ  
326 considerably for chimpanzees living in situations with greater regular exposure to humans, such  
327 as in laboratory settings. Research on how the CHI index relates to differences in personality,  
328 cognitive performance, stress levels (as measured through cortisol), and health histories is likely  
329 to give a more comprehensive representation of how these effects are manifested. Finally, care  
330 should be taken to consider the substantive variation in how these early histories affected  
331 individuals. Not every chimpanzee who had a low CHI score showed deficits in social and  
332 sexual behaviors, as evidenced by the wide-ranging standard deviations. Future studies should  
333 help identify what variables lead to better social resilience in order to aid chimpanzees who  
334 struggle more with social integration. The results of this research suggest that future research  
335 should focus on developing the best management strategies for how to care for chimpanzees with  
336 a variety of early histories in order to meet their social needs. The reduced (or absent) exposure to  
337 conspecifics and full contact exposure to humans that these chimpanzees experienced, especially  
338 during the first four years, may have especially profound and long-term behavioral outcomes.  
339 Given the known public safety concerns surrounding pet chimpanzee ownership and the negative  
340 perception and conservation impacts of inappropriate media portrayals of privately-owned  
341 “actor” chimpanzees (McCann et al., 2007; Ross et al., 2008; Ross, Lonsdorf & Vreeman, 2011),

342 we now add empirical evidence of the potentially negative welfare effects on the chimpanzees  
343 themselves as important considerations in the discussion of privately-owned chimpanzees. We  
344 promote further use of these and other evidence-based methods to further inform policy and  
345 legislative change that protects chimpanzees and other important non-human animals that are  
346 subject to conservation and welfare threats.

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359 This study was designed by SRR in collaboration with HDF. HDF collected the behavioral data  
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**Table 1** (on next page)

Significant ANOVA Tests with Posthoc Paired Comparisons for Behaviors between Early History Categories During the Infant Period

Behavior	Early History Category	Mean Percentage of Time Engaged in Behavior	SD	Early History Differences	F-value	Dunnett's T3 Pairwise comparisons
Groom give	Human	2.40	3.27	H-M	10.132	.930
	Mixed	3.20	3.65	H-C		.002*
	Chimpanzee	8.61	5.73	M-C		.012*
Groom receive	Human	1.5	1.54	H-M	9.219	.227
	Mixed	3.1	3.20	H-C		.000*
	Chimpanzee	6.5	3.70	M-C		.003*
Social sex	Human	.00	.00	H-M	4.983	.054
	Mixed	.14	.22	H-C		.020*
	Chimpanzee	.54	.76	M-C		.084
Inactive	Human	20.30	4.06	H-M	7.716	<.001*
	Mixed	33.22	12.20	H-C		.886
	Chimpanzee	22.10	10.20	M-C		.002*
Abnormal Coprophagy	Human	.12	.30	H-M	14.994	.888
	Mixed	.04	.12	H-C		.040*
	Chimpanzee	.60	.58	M-C		.001*

**Table 2**(on next page)

Non-Significant ANOVA Tests for Agonism and Abnormal Behaviors between Early History Categories During the Infant Period

	Behavior	Early History Category	Mean Percentage of Time Engaged in Behavior	SD	F-value
Agonism	Display	Human	.33	.50	1.945
		Mixed	.23	.23	
		Chimpanzee	.13	.19	
	NC Aggression receive	Human	.00	.00	.097
		Mixed	.00	.00	
		Chimpanzee	.00	.00	
	C Aggression receive	Human	.00	.00	.270
		Mixed	.00	.00	
		Chimpanzee	.00	.00	
	NC Aggression give	Human	.00	.00	.064
		Mixed	.00	.00	
		Chimpanzee	.00	.00	
C Aggression give	Human	.00	.00	1.157	
	Mixed	.00	.00		
	Chimpanzee	.00	.00		
Abnormal	Abnormal Movement	Human	6.08	8.60	3.492
		Mixed	1.63	4.22	
		Chimpanzee	.79	2.50	
	Abnormal Body	Human	.02	.03	.746
		Mixed	.05	.19	
		Chimpanzee	.00	.02	
	Abnormal Pluck	Human	2.10	3.45	6.471
		Mixed	.27	.45	
		Chimpanzee	.44	.80	

**Table 3**(on next page)

Non-Significant ANOVA results for Solitary, Social and Sexual Behaviors between Early History Categories During the Infant Period

	Behavior	Early History Category	Mean Percentage of Time Engaged in Behavior	SD	F-value
Solitary	Submissive	Human	.00	.00	3.947
		Mixed	.00	.00	
		Chimpanzee	.00	.00	
	Attention	Human	11.92	7.12	1.144
		Mixed	12.00	5.68	
		Chimpanzee	9.09	7.12	
	Self play	Human	.11	.11	.579
		Mixed	.29	.71	
		Chimpanzee	.14	.40	
Self groom	Human	17.46	.07	2.821	
	Mixed	13.87	.05		
	Chimpanzee	12.40	.03		
Locomotion	Human	.03	.01	1.655	
	Mixed	.03	.01		
	Chimpanzee	.03	.01		
Social	Social Play	Human	.42	.46	2.088
		Mixed	.98	1.26	
		Chimpanzee	1.54	1.48	
	Prosocial	Human	.14	.15	3.640
		Mixed	.16	.13	
		Chimpanzee	.37	.44	
Sexual	Sex masturbate	Human	.00	.00	3.946
		Mixed	.11	.00	
		Chimpanzee	.00	.00	

# Figure 1

## Histogram of Infant CHI Values

Distribution of CHI<sub>i</sub> values across chimpanzees in the study.

