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 their rearing history, can have a profound impact on later behavior. In the case of captive animals, many studies have used categorical measures that do not account for both the influence of human and conspecific interaction. To enable a more holistic evaluation of early life experiences, we collected 1385 hours of data on 60 chimpanzees, of which 35 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 social and sexual behaviors later in life. 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.

2 Hani D. Freeman and Stephen R. Ross

3 Lester E. Fisher Center for the Study and Conservation of Apes, Lincoln Park Zoo, IL, USA

4 Correspondence should be sent to Stephen Ross, sross@lpzoo.org

Introduction

Early life experiences have a significant impact on the behavioral development of human and non-human animals and the expression of those behaviors later in life (e.g. humans, Fox & Henderson, 1999; Kagan, 1996; non-human primates, Parker & Maerstripieri, 2011) outcomes of early life experiences have uncovered a broad range of potential impacts including those falling in both the social and non-social realms. Non-social variables include the impact of the physical environment on development (rats, Leshem & Schulkin, 2012), as well as physiological factors, such as genetics (primates Barr et al., 2003; Suomi, 2011) or hormones (primates, Saltzman & Maestripieri, 2011), that influence maternal care. Studies of social effects, including both maternal and non-maternal influences, have focused primarily on the impact of conspecifics in an infant's environment, and the subsequent effect on behavior expressed later in life (humans, Sroufe, 2005, rodents & primates, Pryce et al., 2005, primates, Suomi, 1997). Even animals typically not thought of as being as social, such as lizards, seem vulnerable to the effects of atypical and impoverished social histories (Cissy et al., 2014).

Previous studies investigating early life experiences in primates have focused on the influence of the mother. Mothers are particularly important for social development and this is especially true for primate species such as chimpanzees (Lonsdorf & Ross, 2012). Interactions with the mother help infants develop skills such as tool-use (Goodall, 1986; Lonsdorf, 2005; Nishida, 1968), but also important social skills. A study assessing wild chimpanzees found that orphaned chimpanzees displayed higher levels of anxiety and less play behavior compared to those who were raised by their mothers (Botero et al., 2013). Although maternal influences are integral to their offsprings' development, it is well documented that other relatives and non-related group members can play important roles (Boesch et al., 2010; Muller & Thompson, 2012; van Noordwijk, 2012). For example, older female siblings may play an important allo-parenting role; a behavior which can serve to strengthen bonds between family members (Nishida, 1983).

As in their natural environment, captive primates rely heavily on the presence of both their mother and other conspecifics for their development. A range of circumstances, planned and unplanned, may however, result in situations that prevent appropriate socialization in captivity and require the need of alternative rearing methods such as human-rearing or peer-rearing. Studies investigating the impact of these atypical situations on primates – notably with rhesus macaques and chimpanzees – have reported a range of substantive impacts on developmental trajectories (Suomi, 2011; Anderson & Mason, 1974). Macaques raised in the most extreme lack of appropriate early socialization, demonstrated high levels of abnormal behaviors, such as self-clutching, excessive rocking and self-mutilation, illustrating the severe behavioral consequences of these social deficiencies despite the necessary care provided by human caregivers (Harlow, Dodsworth & Harlow, 1965). Other early studies revealed that mother-raised rhesus macaques tended to show more social play and grooming and fewer abnormal behaviors later in life compared with infants raised by "artificial mothers" (Harlow & Zimmerman, 1959; Harlow, Dodsworth & Harlow, 1965). Some studies of chimpanzees focused on less severe environments in which chimpanzees were reared in groups composed of like-aged conspecifics. Though chimpanzees reared in these peer-groups were also affected by their lack of appropriate socialization, the developmental consequences were less evident that those observed in primates raised without any exposure to conspecifics. Nonetheless, these peer-reared chimpanzees were clearly differentiated from those raised in larger social groups and with their biological mother: they were less dominant and less active and often showed more abnormal rocking and less social play behavior (Bloomsmith, Lambeth & Alford, 1991; Rosenblum & Kaufman, 1968; Spijkerman et al., 1994; Spijkerman, 1996). A recent study assessing orphaned and mother-reared chimpanzees in African sanctuaries, found that orphaned chimpanzees engaged in more social play compared with those living in typical social groups with their mother and conspecifics, but that the play periods were shorter and more often led to aggression (Van

Leeuwen et al., *in press*). The effects of these early rearing histories may have long-term effects as well: studies of laboratory-housed chimpanzees that were raised exclusively by humans exhibited more abnormal behaviors later in life in comparison to chimpanzees with conspecific involvement in rearing (Martin, 2002; Martin, 2005). In sum, captive chimpanzees with an absence of typical early histories with biological mothers and conspecifics seem particularly prone to both short- and long-term negative impacts on their behavior and likely, their wellbeing.

Closely associated with the influence of conspecifics, captive chimpanzees are clearly affected by the presence of humans in their social environment. In the most extreme circumstances, some chimpanzees are exposed broadly and extensively to a wide range of human culture, including language and tools (Tomasello, Kruger & Ratner, 1993). These "enculturated" chimpanzees tend to be more successful at human-designed cognitive tasks, and have better human perspective-taking abilities, compared to chimpanzees with less exposure to humans (Buttelmann et al., 2007; Furlong, Boose & Boysen, 2008; Hayes & Hayes, 1952; Russell et al., 2011). Less, however, is known about the degree to which limited conspecific and high human social influences (hereafter termed "atypical" because these are not practices endorsed by current mainstream accredited facilities) affects developmental trajectories in chimpanzees, and ultimately their ability to living in large and dynamic groups of conspecifics.

These questions are perhaps most relevant in considering the largely unstudied population of privately-owned chimpanzees – those living as personal pets and as trained performers in the entertainment industry. Chimpanzees bred for the pet industry are typically removed from their mother soon after birth to facilitate human handling. They are sold to members of the general public, who lack any formal husbandry training, and these chimpanzees are likely not to encounter any conspecifics throughout their key developmental stages. Many are essentially raised as humans, in human households and with human traditions, until they grow to be too large and dangerous to be maintained in free contact with their owners. Performing chimpanzees, in

the entertainment industry, have a more variable trajectory, and though they may spend some proportion of their day with other chimpanzees in small groups, they are also highly exposed to humans (both trainers and audiences) at high frequencies until they typically grow to be unmanageable in adolescence. There is growing consensus that privately-owned chimpanzees represent significant human health and safety risks (McCann et al., 2007), and in the case of entertainment chimpanzees, produce additional consequences such as negative public perceptions that can impact conservation efforts (Ross et al., 2008; Ross, Lonsdorf & Vreeman, 2011; Schroepfer et al. 2011). However, here we focus on the ontogenetic outcomes of these practices and the degree to which the atypical early histories experienced by these chimpanzees influence their behavioral development.

In the current study, we used a novel and holistic approach to assess the impact of atypical early histories experienced by pet and performing chimpanzees and the subsequent outcomes for behavioral development. We employed a long-term continuous measure that accounts for both the amount of time spent with humans as well as the amount of time spent with other conspecifics. We examined how differential human/conspecific exposure during the first four years of life impacted current behavioral patterns for ex-pet and ex-performer chimpanzees now living in accredited zoos and sanctuaries. We acknowledge that the impact of these different early histories could vary for chimpanzees entering various environments, where more human interaction is typical. Although our question revolves around chimpanzees without early exposure to conspecifics, we also studied the behavioral patterns of chimpanzees who have lived their entire lives in their natal group in a zoo setting, in order to assess a broader range of human/conspecific interactions. These zoo-born chimpanzees may also have a range of human/conspecific exposure early in life. In the current study we focused on the first four years of life because this is broadly considered to be the particularly influential infant period for this species (Bard, 1995). We predicted that chimpanzees with atypical early histories (high human

exposure, low conspecific exposure) would differ behaviorally compared with those having more species-typical histories. We projected these differences would be most pronounced in areas of social, sexual and abnormal behaviors and ultimately reflect our hypothesis that these atypical early histories can result in detrimental developmental trajectories and compromised wellbeing.

Methods

This research was conducted at three sanctuaries that are members of the North American Primate Sanctuary Alliance (NAPSA: Center for Great Apes, Chimps, Inc., and Save the Chimps) and six zoos accredited by the Association of Zoos and Aquariums (AZA: Houston Zoo, Dallas Zoo, Lincoln Park Zoo, Lion Country Safari, North Carolina Zoo, and Oakland Zoo). Each of these facilities adheres to high standards of chimpanzee care including housing chimpanzees in social groups, providing nesting material and various forms of enrichment. All animals were observed in their home cages and were not confined to a specific area of their enclosures during observations. All subjects had *ad libitum* access to water and at no time were the subjects ever food or water deprived. Subjects were supplemented daily with primate chow and fruit and/or vegetable food enrichment at each of the facilities. This study was approved by and complied with protocols approved by the Chimpanzee Species Survival Plan (SSP) management group as well as animal care committees at each of the institutions that participated in this study. This study was fully funded by a grant through the Arcus Foundation (1102-34).

Subjects

The subjects were 60 chimpanzees (25 males, 35 females, mean age = 21 years, range: 6 – 54 years) that varied widely in the degree of human and conspecific exposure they experienced early in their lives (Figure 1, Tables S1 in Online Supplementary Materials). Though many of them were formerly housed as personal pets or performers, all were evaluated in their current housing at NAPSA sanctuaries or AZA zoos. The number of subjects studied at each institution

ranged from four to twelve. All of the subjects were socially-housed, with between 1 and 25 other chimpanzees (average group size was 7 chimpanzees). All of the chimpanzees who participated in the study were captive-born and none had lived in a laboratory environment.

Behavioral Assessments

Behavioral data on the chimpanzees were collected with a modified version of an ethogram used for Lincoln Park Zoo's long-term behavioral monitoring studies of great apes (Ross et al., 2011). The ethogram included six primary behavioral categories (social (e.g. grooming, playing, begging, embrace) sexual , agonism, solitary, inactivity and abnormal), which were comprised of 21 behaviors (provided in the Online Supplementary Materials). Data were collected with handheld computers (Pocket Observer 2.0, Noldus Observer, Noldus Information Technology, Wageningen, The Netherlands) in 30-min focal samples with a 30-sec intersample interval. When more than one focal sample was collected on the same individual in one day there was at least a one hour period between each of the samples collected for that individual. Observations were conducted between 9 am and 5 pm by a single observer (HF) at eight of the nine study sites. The data collected at the ninth site (Lincoln Park Zoo) were collected by observers who had previously achieved 85% reliability on the ethogram. HF conducted a *post hoc* inter-rater reliability assessment with a researcher at the Lincoln Park zoo and was found to have 90% reliability on the ethogram. An equal number of observations were collected in the morning and afternoon for each chimpanzee. The order of the observations was randomly selected ahead of time. Feeding and enrichment times varied at each of the study sites and data were collected to cover each of these periods. Observations were conducted from a safe and approved area from where the chimpanzees could be easily seen, but would not be unduly affected by the presence of the observer. Between 14.5 and 30 hours of data were recorded on each subject, over a period ranging from three to eight weeks, for a total of 1385 hours of behavioral data.

Chimpanzee Human Interaction Index

In order to characterize the variable degree of exposure to potential influences (conspecifics and humans), we developed a novel, continuous measure, the Chimpanzee Human Interaction (CHI) index. We used management records acquired from past and current holding institutions and calculated the proportion of time per day that each chimpanzee spent in each of three categories: full exposure to conspecifics, full exposure to humans and mixed exposure to both conspecifics and humans. Each day was weighted based on these three categories of exposure. For instance, a chimpanzee living exclusively within a large social group with only minimal exposure to humans (such as chimpanzees living in large social groups at a safari park where there is only marginal influence by human caretakers and distant zoo visitors) would have a proportion of 1/1 for the day, indicating they spent 100% of their time with other chimpanzees. Likewise, a pet chimpanzee raised exclusively with a human family, without any exposure to other chimpanzees would have a proportion of 0/1 for that same day. A performing chimpanzee with relatively equal exposure to small groups of conspecifics and full contact with human trainers and audiences would have a proportion of .5/1. CHI is calculated as the sum of these variable exposure periods over a particular timeframe given that many chimpanzees have experienced variation in the degree of human and conspecific exposure across their lifetimes. For this analysis, we chose to focus specifically on the infant period: the first four years of life (see Figure 1 for a histogram of the infant CHI_i distribution and Table S1 in Online Supplementary Materials for details about each subject), however the CHI index could be utilized to characterize human/conspecific exposure across any particular timeframe or across the entire lifetime.

Categorical Groups

Although our CHI index was developed to be used as a continuous variable, CHI_i values in this study revealed a tri-modal distribution of the data (Figure 1). This was likely a result of

relatively low variability in conspecific/human exposure over the first four years of life. Therefore, we analyzed the data using categorical groupings by early history experience: with subjects categorized as having only or primarily human exposure (CHI_i index: 0-0.30, n = 6), exposure to both chimpanzees and humans (CHI_i index: 0.31 – 0.70, n = 32), or primarily chimpanzee experience (CHI_i index: .71 – 1.0, n =21) (see Table S1 in the Online Supplementary Materials for each subject's rating). Future analyses across broader timeframes will likely provide the increased variability necessary to utilize CHI as a continuous variable.

Data Analysis

Data analyses were conducted in IBM SPSS 20 (IBM Corp., 2011). A false discovery rate correction was performed on the results to control for multiple comparisons and a corrected p-value based on this correction of less than .01 was considered to be significant.

MANOVA Calculations

In order to assess differences between the three categories of early history during the infant period ("human", "mixed", and "chimpanzee"), we performed a one-way multivariate analysis of variance (MANOVA) using each of the 22 behaviors as dependent variables and the behavioral categories as a fixed factor.

Results

MANOVA Analysis

One-way MANOVA analysis revealed there was a statistically significant difference in the proportion of time the chimpanzees spent engaging in different behaviors based on their early exposure history (F (44, 70) = 3.180, $p < .00005$, Wilks' Lamda = .111, partial $\eta^2 =$ .667). A series of one-way ANOVA's on each of the 22 dependent variables was conducted as follow-up tests to the MANOVA. An examination of the data revealed that for the following behaviors, the

homogeneity of variance assumption was violated: social sex, masturbation, abnormal movement, coprophagy, abnormal body posturing and abnormal plucking. In these cases, we ran a Welsh test on the data to look at the significance of the ANOVA test. The ANOVA tests revealed that in four (social, sexual, inactivity, abnormal) out of six behavioral categories (social, sexual, agonism, solitary, active, and abnormal) a significant relationship was found between the categories of early history based on the CHI_i values and the proportion of time the chimpanzees were observed engaging in each behavior (the results of the MANOVA between proportion of behaviors and categories can be seen in Table 1). In addition, a series of post-hoc analyses (Bonferonni) were performed to examine individual mean difference comparisons across the three levels of CHI_i values and each of the behaviors found to be significant with the MANOVA. The specific results are outlined below.

Social Behavior

The individual ANOVA analyses revealed that early exposure categories influenced frequencies of grooming behavior later in life. Specifically, post-hoc analyses revealed that subjects with high amounts of chimpanzee exposure early in life groomed significantly more than those with mixed or minimal early exposure to conspecifics (F (2, 56) = 10.13, p = .0001). They also received grooming significantly more than those with mixed or minimal early exposure to conspecifics (F (2,56) = 9.22, p = .0001). There was not a significant relationship between early exposure category and frequencies of social play or other prosocial behaviors ($p > .01$).

Sexual Behavior

Frequencies of sexual behavior were influenced by the category of early exposure such that chimpanzees with high amounts of early exposure to conspecifics demonstrated higher frequencies of mounting and sexual exploration compared to chimpanzees with low exposure to

conspecifics (F (2, 56) = 4.98, p = .01). There was not a significant difference found between chimpanzees with high exposure to conspecifics and those with mixed exposure (p > .01). There was not a significant relationship found between the category of early exposure and rates of masturbation (p > 0.01).

Agonistic Behavior

There was no difference in the expression of agonistic behaviors, including displays, non-contact, and contact aggression given or received in relation to categories of early exposure (p > .01).

Solitary Behavior

We found no relationship between frequencies of solitary behaviors including self-grooming and self-play in relation to categories of early exposure (p > .01).

Inactivity

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

Abnormal Behavior

We examined four forms of abnormal behavior: coprophagy, abnormal movement, abnormal body posturing, and hair plucking. The ANOVA revealed that chimpanzees with high amounts of early exposure to conspecifics demonstrated the highest frequencies of coprophagy later in life than those with either mixed early exposure or primarily human exposure early in life

(F (2, 56) = 14.99, p = .0001). There was not a significant difference in rates of coprophagy between chimpanzees from primarily human or mixed early exposure histories. There were not significant differences in rates of the other forms of abnormal behavior when comparing the three early exposure categories (p > .01).

Discussion

The primary aim of this study was to use a novel and holistic approach to assess the long-term behavioral impact of variable early life exposure to both conspecifics and humans on captive chimpanzees. To achieve this, we focused on a rarely studied population, former pet and performer chimpanzees that now live in accredited zoos and sanctuaries. We also studied individuals who had experienced more typical early life histories for captive chimpanzees, living in their natal group with multiple conspecifics, in accredited zoo environments throughout their lifetime. In general, supportive of our hypotheses, we found that chimpanzees raised in "human" or "mixed" exposure groups tended to exhibit lower frequencies of grooming compared with those in the "chimpanzee" group. In addition, chimpanzees raised in the "human" exposure group exhibited lower frequencies of social sexual behavior later in life, compared with those in the "chimpanzee" group. Lastly, chimpanzees in the "mixed" exposure group exhibited higher frequencies of inactivity compared with the "human" or "chimpanzee" groups. The results of this study suggest that high human exposure early in a chimpanzee's life, and/or reduced conspecific exposure, is related to observable differences in behavioral development which are sustained throughout their life and have the potential to be related to animal management and welfare measures.

While it is possible that variability in current living environments may represent a confound to the conclusions of this study (due in part to the relatively limited number of institutions caring for chimpanzees with such atypical backgrounds), it is important to note that the demonstrated effects are unlikely to be solely the result of current physical or social

environments. All subjects were socially housed and all were managed under similar contemporary management systems.

The behavioral differences observed across chimpanzees in different groups based on CHI_i index values support previous findings in chimpanzees, and other non-human primates, looking specifically at the impact of rearing history (i.e. mother-reared individuals compared to isolated individuals, Harlow & Suomi, 1971; Kalcher et al., 2008; Rogers & Davenport, 1970; Turner et al., 1969). For example, several studies have found that human-reared primates often have lower rates of reproductive success, possibly indicative of less appropriate sexual behavior (Ryan, Thompson & Roth, 2002). The evidence for a developmental influence of rearing on later chimpanzee behavior is mixed. While some studies report a lack of rearing effect in social behavior (Bloomsmith et al., 2002; Howell et al., 2006; van Ijzendoorn et al., 2009) more recent analyses (Clay, 2012) and the results of our analyses suggest the possibility that these effects might not be evident until much later in life. Duration of exposures might also be a particularly important factor; Martin et al. (2005) assessed behavior in chimpanzees that were reared in a variety of contexts and found no statistical effect of rearing, however the authors were unable to account for the duration of time spent in each of the rearing categories.

We also noted differential effects of one form of abnormal behavior relating to early experiences: coprophagy. This behavior has been suggested to be socially-learned– as opposed to an individually-developed response indicative of stress – and thus animals with the broad social exposure may be more likely to adopt these behaviors. Previous studies have found that mother-reared chimpanzees engage in coprophagy more often than non-mother reared individuals (Bloomsmith et al., 2005; Nash et al., 1999), which suggests that coprophagy may be functionally distinct from other abnormal behaviors. Future studies should involve investigation regarding the welfare concerns associated with different types of abnormal behaviors in order to determine

294 which behaviors are performed only during times of stress compared with times of boredom or
295 during routine times.

296 Despite the breadth of the data used for this investigation, there remain a number of
297 limitations that reflect the complexity of a multi-institutional study and require additional
298 consideration. The first is the potential confound between a chimpanzee's current housing
299 locations with their early history exposure. Chimpanzees from particular backgrounds tended to
300 cluster at specific institutions and as a result, there was relatively little intra-institutional variation
301 in early histories among the chimpanzees housed within single groups. Fortunately, the variation
302 in current housing conditions, and management styles, was relatively low, at least in comparison
303 to the wide variety of physical and social environments from which many of these chimpanzees
304 originated. All current housing was either at AZA-accredited zoos or NAPSA member
305 sanctuaries; all of which maintain consistently high standards of care in terms of diet, enrichment
306 and housing. Additionally, subjects were housed in different social groupings (ranging from 2 –
307 26 chimpanzees per group), and in some cases, this was an outcome of their atypical early
308 histories and difficult socialization histories.

309 We must also consider the potential limitations of our measure of human and conspecific
310 exposure including both the CHI index and categories based on this index. In this analysis, we
311 utilized a subset of the CHI index (CHI_i), specific to a relatively narrow time frame from birth to
312 age 4, within which there is inherently less variation across individuals in comparison to that
313 observed across the entire lifetime. Therefore, we used a categorical analysis based on the CHI_i
314 values. There were only six individuals out of the 60 chimpanzees who had only human exposure
315 during their first four years of life compared with 33 and 21 in the other categories. We felt it was
316 still important to compare these individuals to the other groups, because of the lack of any
317 conspecific exposure. However, it is possible that there were other differences in behavior
318 between the categories that were not detected because of the small sample size. We also

acknowledge that it is possible that similar CHI index values may reflect differential patterns of exposure to conspecifics and humans. Further refinement of this index may help address this potential limitation.

Overall, the results of this study suggest that adolescent and adult chimpanzee behavior is associated with early life experiences and that individuals exposed to more human-centric environments may express behavioral deficits later in life related to grooming and sexual behavior. It is possible that the consequences of these developmental trajectories may differ considerably for chimpanzees living in situations with greater regular exposure to humans, such as in laboratory settings. Research on how the CHI index relates to differences in personality, cognitive performance, cortisol levels and health histories is likely to give a more comprehensive representation of how these effects are manifested and possibly further confirmation of the directionality of these factors. Finally, care should be taken to consider the substantive variation in how these early histories affected individuals. Not every chimpanzee who had a low CHI_i score and was in the "human" category showed deficits in social and sexual behaviors, as evidenced by the wide-ranging standard deviations, and future studies should help identify what variables lead to better social resilience in order to aid chimpanzees who struggle more with social integration. The reduced (or absent) exposure to conspecifics and full contact exposure to humans that these chimpanzees experienced, especially during the first four years, may have especially profound and long-term behavioral outcomes. Given the known public safety concerns surrounding pet chimpanzee ownership and the negative perception and conservation impacts of inappropriate media portrayals of privately-owned "actor" chimpanzees (McCann et al., 2007; Ross et al., 2008; Ross et al., 2011), we now add empirical evidence of the potentially negative welfare effects on the chimpanzees themselves as important considerations in the discussion of privately-owned chimpanzees. We promote further use of these and other evidence-based

methods to further inform policy and legislative change that protects chimpanzees, and other important non-human animals that are subject to conservation and welfare threats.

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Author Contributions

This study was designed by SRR in collaboration with HDF. HDF collected the behavioral data at each of the facilities except for the Lincoln Park Zoo. HDF analyzed the data. Both authors contributed to the writing of this article.

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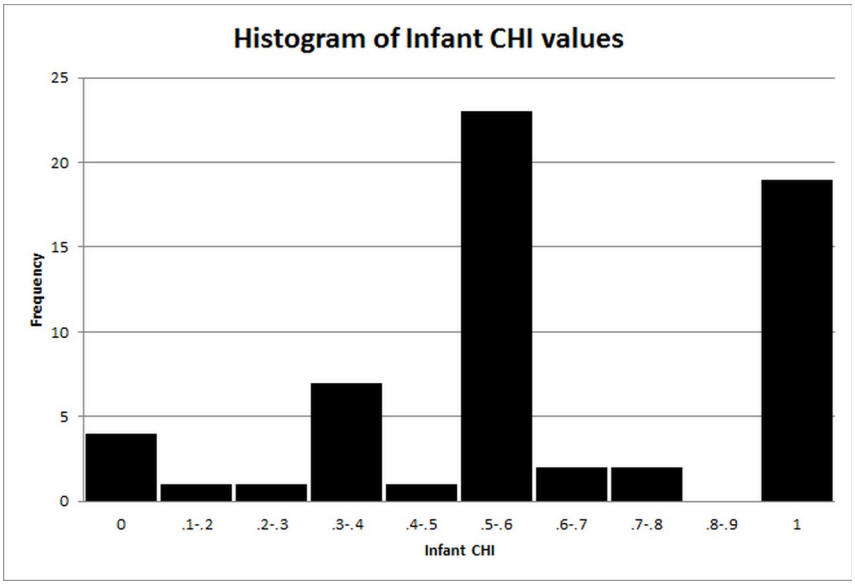
Figure 1
Histogram of Infant CHI Values
Distribution of CHI values across chimpanzees in the study.



Manova Test with Paired Comparisons for Behaviors and Early History Categories Based on Infant CHI Values

Detailed statistical results comparing Behaviors in Early History Categories based on Infant CHI values

	Behavior	Early History Category	Mean Percentage of Time Engaged in Behavior	SD	Early History Differences	F-value	Tukey's HSD Pairwise comparisons
Social	Groom give	Human	2.40	3.27	H-M	10.132	.930
		Mixed	3.20	3.65	H-C		.002*
		Chimpanze	8.61	5.73	M-C		.012*
		e					
	Groom receive	Human	1.5	1.54	H-M	9.219	.227
		Mixed	3.1	3.20	H-C		.000*
		Chimpanze	6.5	3.70	M-C		.003*
		e					
	Social Play	Human	.42	.46	H-M	1.114	.188
		Mixed	.98	1.26	H-C		.018
		Chimpanze	1.54	1.48	M-C		.392
		e					
	Prosocial	Human	.14	.15	H-M	4.983	.986
		Mixed	.16	.13	H-C		.162
		Chimpanze	.37	.44	M-C		.138
		e					
Sexual	Social sex	Human	.00	.00	H-M	3.496	.054
		Mixed	.14	.22	H-C		.020
		Chimpanze	.54	.76	M-C		.084*
		e					
	Sex masturbate	Human	.00	.00	H-M	3.946	.014
		Mixed	.11	.00	H-C		.997
		Chimpanze	.00	.00	M-C		.011
		e					

Agonism	Display	Human	.33	.50	H-M	1.945	.937
		Mixed	.23	.23	H-C		.682
		Chimpanzee	.13	.19	M-C		.218
	NC Aggression receive	Human	.00	.00	H-M	.097	.1.00
		Mixed	.00	.00	H-C		.969
		Chimpanzee	.00	.00	M-C		.996
	C Aggression receive	Human	.00	.00	H-M	.270	1.00
		Mixed	.00	.00	H-C		.973
		Chimpanzee	.00	.00	M-C		.872
	NC Aggression give	Human	.00	.00	H-M	.064	.999
		Mixed	.00	.00	H-C		.991
		Chimpanzee	.00	.00	M-C		.985
	C Aggression give	Human	.00	.00	H-M	1.157	1.00
		Mixed	.00	.00	H-C		.764
		Chimpanzee	.00	.00	M-C		.350
Solitary	Self play	Human	.11	.11	H-M	.579	.402
		Mixed	.29	.71	H-C		.968
		Chimpanzee	.14	.40	M-C		.696
	Self groom	Human	17.46	.07	H-M	2.821	.586
		Mixed	13.87	.05	H-C		.329
		Chimpanzee	12.40	.03	M-C		.422