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Characterizing abnormal behavior in a large population of zoo-housed chimpanzees: Prevalence and etiologies

Sarah L Jacobson, Stephen R Ross, Mollie A Bloomsmith

Abnormal behaviors in captive animals are generally defined as behaviors that are atypical for the species and are often considered to be indicators of poor welfare. While some abnormal behaviors have been empirically linked to conditions related to elevated stress and compromised welfare in primates, others have little or no evidence on which to base such a relationship. The objective of this study was to investigate a recent claim that abnormal behavior is endemic in the captive population by surveying a broad population of chimpanzees (*Pan troglodytes*), while also considering the etiologies of some of these behaviors. We surveyed animal care staff from 26 institutions to assess the prevalence of abnormal behavior in a large population of zoo-housed chimpanzees in the United States for which we had information on origin and rearing history. Our results demonstrated that 64% of this population were reported to engage in some form of abnormal behavior in the past two years and 48% of chimpanzees engaged in abnormal behavior other than coprophagy. Logistic regression models were used to analyze the historical variables that best predicted the occurrence of all abnormal behavior, any abnormal behavior that was not coprophagy, and coprophagy. The resulting models support previous claims that coprophagy has a fundamentally different etiology than the other abnormal behaviors. Rearing had opposing effects on the occurrence of coprophagy and the other abnormal behaviors such that mother-reared individuals were more likely to perform coprophagy, whereas non-mother-reared individuals were more likely to perform other abnormal behaviors. These results support the assertion that coprophagy is best classified separately when assessing abnormal behavior and the welfare of captive chimpanzees. This robust evaluation of the prevalence of abnormal behavior in the U.S. zoo population also demonstrates the importance of considering the contribution of historical variables to present behavior in order to better understand the causes of these behaviors and any potential relationship to psychological wellbeing.

Characterizing abnormal behavior in a large population of zoo-housed chimpanzees: Prevalence and etiologies

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Abstract

Abnormal behaviors in captive animals are generally defined as behaviors that are atypical for the species and are often considered to be indicators of poor welfare. While some abnormal behaviors have been empirically linked to conditions related to elevated stress and compromised welfare in primates, others have little or no evidence on which to base such a relationship. The objective of this study was to investigate a recent claim that abnormal behavior is endemic in the captive population by surveying a broad population of chimpanzees (*Pan troglodytes*), while also considering the etiologies of these behaviors. We surveyed animal care staff from 26 institutions to assess the prevalence of abnormal behavior in a large population of zoo-housed chimpanzees in the United States for which we had information on origin and rearing history. Our results demonstrated that 64% of this population were reported to engage in some form of abnormal behavior in the past two years and 48% of chimpanzees engaged in abnormal behavior other than coprophagy. Logistic regression models were used to analyze the historical variables that best predicted the occurrence of all abnormal behavior, any abnormal behavior that was not coprophagy, and coprophagy. The resulting models support previous claims that coprophagy has a fundamentally different etiology than the other abnormal behaviors. Rearing had opposing effects on the occurrence of coprophagy and the other abnormal behaviors such that mother-reared individuals were more likely to perform coprophagy, whereas non-mother-reared individuals were more likely to perform other abnormal behaviors. These results support the assertion that coprophagy is best classified separately when assessing abnormal behavior and the welfare of captive chimpanzees. This robust evaluation of the prevalence of abnormal behavior in the U.S. zoo population also demonstrates the importance of considering the contribution of historical variables to present behavior, in order to better understand the causes of these behaviors and any potential relationship to psychological wellbeing.

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Introduction

Abnormal behaviors in primates have been generally defined as behaviors that are atypical of the species and/or occur at different frequencies in captivity than in the wild (Erwin & Deni, 1979; Walsh, Bramblett, & Alford, 1982). These behaviors can result from both proximate and past exposure to chronic aversive stimuli, including environments that limit the ability to perform species-typical behaviors, repeated stressful procedures such as sedations for clinical procedures (Lutz, Well, & Novak, 2003), and/or atypical early social experiences such as reduced or absent maternal care (Brent, Lee, & Eichberg, 1989; Kalcher et al., 2008; Freeman & Ross, 2014). Other intrinsic factors such as sex, species, and animal temperament (Vandeleest, McCowan, & Capitanio, 2011; Gottlieb, Capitanio, & McCowan, 2013) can also influence the expression of some abnormal behaviors. In part because of the association with suboptimal social and physical environments, abnormal behaviors are often considered to be reliable indicators of psychological distress and as such, poor welfare (Mason, 1991; Garner, 2005). Studying the etiology and persistence of these behaviors in captive environments is critical to better understanding the factors contributing to the wellbeing of captive primates.

Despite its importance to improving the captive management of primates, the study of abnormal behavior can be quite challenging for several reasons. The first is a lack of consistency in the types and definitions of behaviors considered to be atypical. Walsh, Bramblett, and Alford (1982) developed one of the most widely-used ethograms of abnormal behaviors in chimpanzees (*Pan troglodytes*), but there are a variety of others for this species that differ in important ways

(see Nash et al., 1999; Hook et al., 2002; Birkett & Newton-Fisher, 2011). While some classifications distinguish between behaviors that are pathological and harmful (e.g. self-injurious behavior) and those that are less severe (e.g. repetitive motions) (Bayne & Novak, 1998), others do not (Birkett & Newton-Fisher, 2011) treating a variety of abnormal behaviors as functionally equivalent in terms of impact on the animal. A second challenge relates to the interpretation of the context in which particular behaviors are performed. In some cases, behaviors can occur in both a species-typical context as well as those that may be more likely tied to an underlying distressful state. For example, some researchers have recognized this difficulty and advised that caution be used when categorizing rocking as an abnormal behavior because of the difficulties in distinguishing instances when the behavior is communicative in chimpanzees (Fritz et al., 1992; Ross & Bloomsmith, 2011). These types of definitional incongruities can lead to difficulties interpreting and comparing results of abnormal behavior studies.

Perhaps the broadest challenge related to the study of abnormal behavior is related to the interpretation of behaviors and their potential underlying etiologies. While some behaviors have been empirically linked to conditions related to elevated stress and compromised welfare, others have little or no evidence on which to base such a relationship. Many stereotypies are commonly used as indicators of reduced wellbeing, but this relationship is convoluted due to the complex mechanisms underlying stereotypic behaviors. Mason & Latham (2004) suggest that some stereotypies develop as coping mechanisms for animals and with repetition shift into an automatic behavior that is not necessarily reflective of their current environment. Particularly the relationship between stereotypy and self-injurious behavior is not well understood, since some self-directed stereotypies can cause injury while the same behavior can occur without injury. The

88 classification of depilation and regurgitation and reingestion as problematic behaviors is also
89 debated (Baker & Easley, 1996; Hosey & Skyner, 2007). Novak et al. (2006) advocated for
90 further study of the biological bases of these categories of behavior to determine whether they
91 represent different manifestations of the same underlying mechanism. Clearly, a better
92 understanding of the etiologies of those behaviors classified as abnormal will be critical to
93 determining which can be used as reliable indicators of negative welfare in captive primates.

94 One of the most comprehensively studied factors influencing the development of abnormal
95 behaviors is early social experience and in particular, the rearing history of captive primates.
96 Early maternal separation in captive macaques and chimpanzees has repeatedly been shown to
97 lead to stereotypies, self-injurious behavior, and incompetent social and reproductive behavior
98 (Harlow & Harlow, 1965; Rogers & Davenport, 1969; Fritz et al., 1992; Nash et al., 1999;
99 Martin, 2002). Stress physiology has also supported this connection, demonstrating a
100 dysregulation of the hypothalamic-pituitary-adrenocortical axis in primates that are separated
101 from their mothers early in life, along with elevated expression of abnormal behaviors (Feng et
102 al., 2012). In contrast, some abnormal behaviors in chimpanzees, such as coprophagy, have been
103 seen to be more prevalent in those reared by their mothers than those raised by humans (Nash et
104 al., 1999; Bloomsmith et al., 2006). Although not all primates who have experienced maternal
105 separation demonstrate behavioral abnormalities, the rearing history of individual primates
106 remains an important consideration in any attempt to determine the factors influencing the
107 expression of abnormal behavior.

108 The physical environment experienced by captive primates may also play a role in the
109 development of abnormal behaviors, as the absence of appropriate sensory and motor stimulation
110 can lead to stereotypies in primates in captivity (Berkson, Mason, & Saxon, 1963; Harlow &

Harlow, 1965). When captive environments fail to provide adequate opportunities for natural behavior patterns, some atypical behaviors such as rocking or pacing may develop as a form of self-stimulation (Walsh, Bramblett, & Alford, 1982). Further evidence for the importance of physical environments comes from studies that demonstrate reductions in abnormal behaviors following a move to a more natural or enriched environment (Pfeiffer & Koebner, 1978; Brent, Lee, & Eichberg, 1989; Schapiro & Bloomsmith, 1994; Novak et al., 1998; Ross et al., 2011). Given this broad support for a link between a primate's current and past physical and social environments, it seems imperative to consider a wide range of potential factors when investigating the etiologies of expressed abnormal behaviors.

In this study, we surveyed animal care staff to assess the prevalence of abnormal behaviors in a broad population of chimpanzees living in accredited zoological parks and to evaluate potential links between historical variables and abnormal behaviors. Although many primates exhibit abnormal behavior, chimpanzees are a particularly relevant species with which to investigate these phenomena. Chimpanzees are members of a socially and cognitively complex species, and they perform a wide variety of abnormal behaviors in a variety of settings (Nash et al., 1999; Birkett & Newton-Fisher, 2011). Indeed, the captive chimpanzee population in North America provides a unique opportunity to investigate factors influencing the development of abnormal behavior, in part because of the inherent variety of rearing and housing conditions experienced by these individuals. Chimpanzees living in accredited zoos come from a broad diversity of backgrounds including those born and raised in zoos, those born in the wild and imported (many years ago) to North America, and those born in other captive settings such as research laboratories or those privately owned as pets or performers, and later moved to zoos.

A recent study of abnormal behavior in chimpanzees attempted to quantify the prevalence and diversity of abnormal behaviors in the zoo setting (Birkett & Newton-Fisher, 2011) and concluded that abnormal behavior is endemic to zoo population despite living in enriched enclosures. The study included chimpanzees at only six institutions to arrive at this conclusion. Here, we use a broader sampling of the zoo-housed chimpanzee population to assess the prevalence of these behaviors, surveying animal staff at 26 accredited zoos to collect data on 165 chimpanzees. Furthermore, we used information on their rearing and birthplace investigate the factors influencing the expression of these behaviors with the intention of informing our characterization of these populations and influencing future management practices.

Methods

Data Collection

To assess the prevalence of abnormal behavior of a large population of chimpanzees housed in accredited zoos in the United States, we surveyed animal care staff who were familiar with those individuals. We administered an online questionnaire to the Institutional Representatives to the Chimpanzee Species Survival Plan (SSP) at all participating institutions as part of the 2013 Chimpanzee SSP Annual Planning Survey using PMCTrack software (2016). These individuals were curators and zookeepers who worked regularly with the chimpanzees and were responsible for their care and management. Respondents were asked to note, for each individual chimpanzee at their institution, which abnormal behaviors were displayed at least once in the previous two-year period. The list of abnormal behavior categories (Figure 1) was

154 developed in part from Birkett & Newton-Fisher (2011) to facilitate comparisons with the results
155 of that study.

156

157 Figure 1. The definitions of abnormal behavior categories for chimpanzees used in this study

Coprophagy	Ingestion of feces
Hair Pluck	Pulling out hair on self or another
Rock	Repetitive and sustained swaying movement without piloerection
Regurgitation & Reingestion	The deliberate regurgitation of food and subsequent consumption of the food
Self-injurious Behavior	Biting, picking, or scratching at own body to cause injury
Pacing	Locomoting repetitively along the same path with no clear objective
Other	Any other behavior deemed abnormal, space to describe

158

159 Historical variables

160 Information about the chimpanzees, including their sex, rearing and origin, was drawn
161 from the North American Regional Studbook for Chimpanzees (Ross, 2015) and individual
162 taxon reports from each zoo. Rearing was simply categorized as mother-reared or non-mother-
163 reared as distinguishing between subtle forms of alternative rearing was difficult with some
164 records. The origin of individuals was defined as where the chimpanzee was born, and therefore
165 the environment where it spent at least some of its early developmental period. The different
166 origins were categorized as zoo, laboratory, wild, and private. The private designation included
167 chimpanzees that were kept as pets or performers and therefore had significant human interaction
168 during their development (Freeman & Ross, 2014).

169

170 Facilities and Subjects

171 We received surveys on 181 chimpanzees, but not all were complete. After removing
172 incomplete surveys and excluding chimpanzees with unknown historical variables, our study
173 population consisted of 165 chimpanzees (see Figure 2a & 2b for population breakdown of
174 independent variables). Chimpanzees ranged in age from 2-78 years old and were all socially
175 housed at one of 26 zoos accredited by the Association of Zoos and Aquariums (AZA). Though
176 there was some variability in physical environments and management practices, all individuals
177 lived under the regulatory framework provided by AZA and care was guided by the principles in
178 the AZA Chimpanzee Care Manual (AZA Ape Tag, 2010). The population was 38% male and
179 62% female, which matches the overall sex distribution of the entire AZA population (Ross,
180 2015).

181 Figure 2a. Chimpanzees in study population with each rearing history

Rearing	Number of individuals	Percentage of population
Mother-reared	64	61 %
Non-mother-reared	41	39%

182

183 Figure 2b. Chimpanzees in study population from each origin category

Origin	Number of individuals	Percentage of population
Laboratory	13	12%
Private	8	8%
Wild	19	18%
Zoo	65	62%

184

185

186 Analysis

187 We calculated the proportion of individuals who were reported to engage in any form of
188 abnormal behavior, hereafter ABN-ALL. Additionally, due to the reported ambiguity of
189 coprophagy as a reliable indicator of welfare (Hopper, Freeman, & Ross, 2016), we calculated
190 both the proportion of individuals that were reported to engage in coprophagy specifically
191 (ABN-C), as well as the proportion of individuals who were reported to engage in any form of
192 abnormal behavior *except* for coprophagy (ABN-XC).

193 The association between the historical variables and sex with the prevalence of abnormal
194 behavior was assessed using binary logistic regression modeling. The variable of sex was
195 considered in this analysis due to inconsistent results evaluating its effect on abnormal behavior
196 in past studies (Fritz et al., 1992; Nash et al., 1999). Analyses were conducted in R (R Core
197 Team, 2015). The reference variable for sex was female, for rearing was mother-reared, and for
198 origin was wild. A separate model was run for each of the dependent variables: ABN-ALL,
199 ABN-C and ABN-XC. For all analyses an alpha value of $p \leq 0.05$ was considered significant.

200

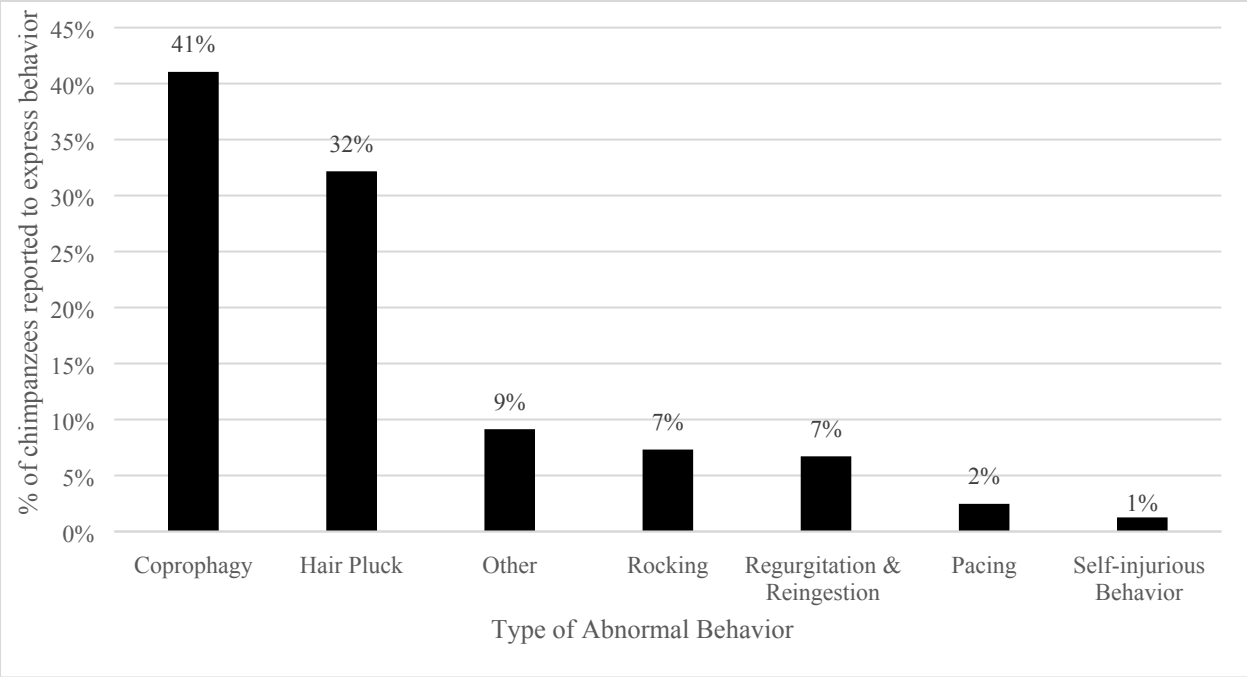
201 **Results**

202 Our survey indicated that 64% of the 165 chimpanzees had been seen to exhibit some
203 form of abnormal behavior (ABN-ALL) at least once in the previous 2 years. Coprophagy
204 (ABN-C) was the most prevalent abnormal behavior, with 41% of chimpanzees reported as
205 engaging in the behavior. Hair plucking was also fairly common, with 32% of the population
206 reported to engage in this behavior. Other behaviors were far less commonly reported (see Figure

207 3). When removing chimpanzees that only exhibited coprophagy, 48% of the 165 chimpanzees
208 exhibited abnormal behavior (ABN-XC).

209

210 Figure 3. The percentage of the study population reported engaging in each category of abnormal
211 behavior at least once from 2011-2013



212

213 Logistic regression models were created using all combinations of the three historical
214 variables (sex, rearing, and origin) to determine which combination of these best predicted each
215 of the dependent variables: ABN-ALL, ABN-C and ABN-XC. The best fit model was chosen
216 through AIC comparison for each dependent variable (Symonds & Moussalli, 2011). When
217 multiple models were statistically equivalent, the model that included the most variables was
218 chosen in order to assess the influence of more factors on the chimpanzees' behavior. The best fit
219 model for ABN-ALL included sex and rearing (not origin) as predictor variables and was

220 statistically significant, $X^2(2)=6.49$, p=0.04. Figure 4 reports the regression coefficients and the
221 odds ratios for the model. The model explained 5.3% (Nagelkerke R^2) of the variance in ABN-
222 ALL and correctly classified 61.8% of cases. The variable sex had a negative relationship with
223 ABN-ALL such that male chimpanzees were 2.04 times less likely to exhibit abnormal behavior
224 than females. Rearing was not a significant predictor of ABN-ALL in this model.

225

226 Figure 4. Logistic regression model for any abnormal behavior (ABN-ALL). Significant
227 variables are bolded. R^2= 0.03 (Hosmer-Lemeshow), 0.04 (Cox-Snell), 0.05 (Nagelkerke).
228 Model $X^2(2)=6.49$, p=0.04

	β(SE)	p	95% CI for odds ratio		
			Lower	Odds Ratio	Upper
Constant	0.68 (0.24)	0.01			
Sex (Male)	**-0.71 (0.34)**	**0.03**	**0.25**	**0.49**	**0.94**
Rearing (Non-mother)	0.48 (0.35)	0.17	0.82	1.62	3.29

229

230 The best-fit model for ABN-XC included all three predictor variables and was
231 statistically significant ($X^2(5) = 19.18$, $p<0.01$). Figure 5 reports the regression coefficients and
232 odds ratios for this model. The model explained 14.6% (Nagelkerke R^2) of the variance in ABN-
233 XC and correctly classified 64.2% of cases. Rearing had a positive relationship with ABN-XC
234 such that chimpanzees who were not mother-reared were 3.18 times more likely to exhibit ABN-
235 XC than those who were mother-reared. The other variables included, sex and origin, did not
236 contribute significantly to the model.

Figure 5. Logistic regression model for non-coprophagy abnormal behavior (ABN-XC) with predictor variables and constant. Significant variables are bolded. R^2= 0.08 (Hosmer-Lemeshow), 0.11 (Cox-Snell), 0.15 (Nagelkerke). Model $X^2(5)=19.18$, $p<0.01$

	β(SE)	p	95% CI for odds ratio		
			Lower	Odds Ratio	Upper
Constant	-0.45 (0.37)	0.22			
Rearing (Non-mother)	**1.16 (0.44)**	**0.01**	**1.37**	**3.18**	**7.65**
Sex (Male)	-0.09 (0.35)	0.80	0.46	0.92	1.81
Origin (Lab)	1.50 (0.90)	0.09	0.89	4.50	34.5
Origin (Private)	-0.52 (0.78)	0.50	0.13	0.60	2.76
Origin (Zoo)	-0.05 (0.43)	0.91	0.41	0.95	2.26

The best fit model for ABN-C included all three predictor variables and was statistically significant, $X^2(5)= 17.59$, $p<0.01$. The regression coefficients and odds ratios are reported in Figure 6. The model explained 13.6% (Nagelkerke's R^2) of the variance in the exhibition of coprophagy and correctly classified 67.3% of cases. The variable sex was negatively related to coprophagy such that male chimpanzees were 3.57 times less likely to exhibit coprophagy than female chimpanzees. The laboratory origin variable had a positive relationship with coprophagy such that chimpanzees that were born in a laboratory were 5.33 times more likely to exhibit coprophagy than those born in the wild.

Figure 6. Logistic regression model for coprophagy (ABN-C) with predictor variables and constant included. Significant variables are bolded. R^2= 0.08 (Hosmer-Lemeshow), 0.10 (Cox-Snell), 0.14 (Nagelkerke). Model $X^2(5)=17.59$, $p<0.01$

	β(SE)	p	95% CI for odds ratio		
			Lower	Odds Ratio	Upper
Constant	-0.30 (0.38)	0.38			
Sex (Male)	**-1.24 (0.37)**	**<0.01**	**0.14**	**0.29**	**0.59**
Origin (Lab)	**1.67 (0.76)**	**0.03**	**1.24**	**5.33**	**24.99**
Origin (Private)	1.17 (0.84)	0.16	0.61	3.21	16.84
Origin (Zoo)	0.63 (0.45)	0.16	0.79	1.87	4.63
Rearing (Non-mother)	-0.88 (0.46)	0.056	0.16	0.42	0.99

Discussion

Our survey results revealed a lower prevalence of abnormal behavior in the zoo-housed chimpanzee population compared to the most recent published evaluation (Birkett & Newton-Fisher, 2011) which reported these behaviors as "endemic" and present in 100% of the zoo-housed subjects they sampled. Using similar categories of these behaviors in survey form, our data suggests that a more modest prevalence of 64% of the zoo-housed chimpanzee population have been observed engaging in some type of abnormal behavior over a two-year period. While methodological differences may account for some of these differences, we assert that the current evaluation is a broader assessment of the prevalence of abnormal behavior in this population. The current study draws from a substantially larger sample of zoos (26 institutions compared to 6) and subsequently surveys a broader range of individuals (165 subjects compared to 40). This

is an important consideration given that, in this study and others, these behaviors are often linked to early rearing histories, which should be adequately represented in the study population.

To validate our methods against those used by Birkett and Newton-Fisher (2011), we compared the prevalence of abnormal behaviors demonstrated by subjects who were likely to be subjects of both of those studies. We identified data from chimpanzees who (a) lived at one of three zoos who reported to have participated in the earlier study, (b) were present at that zoo during the data collection period (December 2008 to May 2010), and (c) for whom we had survey data as part of our analysis. All of these subjects (n=8) were reported to have demonstrated abnormal behavior in our survey data, matching the results of Birkett and Newton-Fisher (2011) and suggesting that results from these different methods are relatively comparable. This post-hoc finding indicates that some of the differences between the two analyses may indeed be related to differences in sampling moreso than the result of methodological variance.

One clear similarity in the results of these two assessments is the prevalence of coprophagy as the most commonly reported abnormal behavior: 41% percent of the current population was reported to have engaged in this behavior. The link between this behavior and its utility as an indicator of wellbeing however, has recently been brought into question (Nash et al., 1999; Hopper, Freeman, & Ross, 2016). There is growing evidence that coprophagy may be a socially-learned behavior and therefore may not be as relevant an indicator of negative welfare as some other abnormal behaviors (Nash et al., 1999; Hook et al., 2002; Freeman & Ross, 2014; Hopper, Freeman, & Ross, 2016). Our analysis of the variables that predict the occurrence of coprophagy in this population support this concept in a number of ways. First, we found a significant sex difference in the prevalence of coprophagy such that female chimpanzees were 3.6 times more likely than male chimpanzees to exhibit this behavior. This finding mirrors a past

assessment (Fritz et al., 1992) and may be linked to sex differences in social learning. A study by Lonsdorf (2005) has directly demonstrated the biased proclivity of female offspring to be the recipients of socially-transmitted tool-using behavior and we argue that coprophagy is likely to be learned similarly through cultural transmission (Hopper, Freeman, & Ross, 2016).

Another finding that would support the idea that coprophagy is indeed a socially-transmitted behavior is a link to rearing history. Indeed we found that mother-reared chimpanzees were 2.4 times more likely than non-mother-reared chimpanzees to exhibit coprophagy, though this finding fell just short of reaching statistical significance. Mother-reared chimpanzees are likely to have more exposure to other chimpanzees who display coprophagy than those chimpanzees raised in a human setting (nursery or privately owned individuals typically live in smaller groups and their companions are less likely to show coprophagy), so the opportunity to socially learn this behavior may be heightened. In addition, mother-reared chimpanzees typically have more developed social skills than those raised in nurseries or by humans (Spijkerman, 1997; Baker et al., 2000; Kalcher-Sommersguter et al., 2011) which may allow them to better learn behaviors from their mothers and others in their social groups. For these two reasons we would expect these individuals to be more likely to learn a behavior like coprophagy. Also, given what we know about the negative welfare outcomes for non-mother-reared chimpanzees (Fritz et al., 1992; Nash et al., 1999; Martin, 2002; Kalcher-Sommersguter et al., 2011), if coprophagy was an indicator of negative welfare, we would expect to see these chimpanzees exhibit more of this behavior. Indeed the opposite trend is true in our population, suggesting that coprophagy rates have relatively little to do with welfare. These results reinforce the established relationship between mother-rearing and elevated coprophagy (Nash et al., 1999; Bloomsmith et al., 2006;

Hopper, Freeman, & Ross, 2016) and the idea that the link between welfare and this behavior should be scrutinized.

Laboratory origin was also a significant predictor of coprophagy; chimpanzees born in research laboratory settings were 5.3 times more likely to exhibit coprophagy than chimpanzees born in the wild. Of note is the fact that there were no significant interactions between rearing and origin that would suggest that differential rearing strategies in laboratory settings were the explanation. It is unclear why relationship exists; further work is needed to compare the effects of different physical and management environments on the behavior of captive chimpanzees.

For some abnormal behaviors in primates we have empirical evidence to link the behaviors to suboptimal environments such as social isolation and non-mother-rearing (rocking: Fritz et al., 1992; self-injurious behavior: Harlow & Harlow, 1965; Kraemer & Clarke, 1990). These behaviors were much less prevalently reported in this chimpanzee population; rocking and self-injurious behavior were reported in less than 10% of respondents. Overall, when we remove the occurrences of coprophagy, the prevalence of abnormal behaviors in the population decreases to about half of the population (48%). The most prevalent behavior after coprophagy was hair plucking (32%) which has been recognized as a relatively common abnormal behavior in many primate species (Nash et al., 1999; Lutz, Well, & Novak, 2003; Less, Kuhar, & Lukas, 2013; Brand & Marchant, 2015). However, the relationship between this behavior and psychological wellbeing is still unclear, as social learning may influence the expression of hair plucking (Nash et al., 1999; Hook et al., 2002; Less, Kuhar, & Lukas, 2013). When examining the factors that influence the expression of these abnormal behaviors, we find some substantive differences from those factors influencing the expression of coprophagy.

As many past studies have shown, rearing greatly affects the occurrence of abnormal behaviors, although these studies have generally been correlational (Harlow & Harlow, 1965; Rogers & Davenport, 1969; Fritz et al., 1992; Nash et al., 1999; Martin, 2002). Our model supported this idea, demonstrating that chimpanzees who were not mother-reared were 3.2 times more likely to exhibit abnormal behavior (excluding coprophagy) than mother-reared chimpanzees. This rearing result is in the opposite direction as the trend that was revealed by our coprophagy-only model, again demonstrating the differences in the ontogeny of these behaviors. We found no effect of sex, suggesting that in contrast to coprophagy, these behaviors are unlikely to be the result of social transmission and therefore may be more reliable indicators of individual welfare. The strong effect of rearing also emphasizes that welfare evaluation must consider the contribution of historical variables to present behavior, rather than solely focusing on proximate factors as the cause of all abnormal behavior.

Although this survey-based method allows for a more conservative measure of prevalence and a larger sample size, there are several potential weaknesses with this method that must be considered in interpreting these findings. One limitation of a survey method is that our results only show the prevalence of these behaviors without any information about frequency or duration of any of these abnormal behaviors. As such, individuals who perform these abnormal behaviors on a daily basis cannot be distinguished from those who engage much more rarely, perhaps only once over a two-year period. Obviously, more intensive, observational studies can address this weakness, but are considerably more time-consuming and expensive to conduct. Conversely, we argue that the prevalence findings here are relatively conservative in nature as a result of these methods. Raters only had to have witnessed the chimpanzee performing abnormal

behavior once over a two-year period for their response to be counted in this study and as such it is doubtful that we are underestimating the scope of these behaviors.

Another possible weakness is that these findings are based on reports from animal management staff working with the chimpanzees and may be vulnerable to subjective interpretation or even diminished opportunity to observe these behaviors. While these are valid criticisms of the methods used in this work, we assert that even direct observations result in a relatively minute fraction of a chimpanzee's daily activities and that more generalized observations taken over the course of several years may be as likely to produce accurate prevalence estimates (Whitham & Wielebnowski, 2009).

We assert that these data represent the most robust evaluation of the prevalence of abnormal behaviors in zoo-housed chimpanzees yet produced. This study provides a broader picture of the occurrence of abnormal behavior in this population and elucidates some of the variables in the life histories of chimpanzees that contribute to these behaviors. When considering our results and the effects of rearing, sex, and origin on the occurrence of coprophagy compared to the other abnormal behaviors, it is apparent that coprophagy, despite its prevalence, is fundamentally different in etiology. This supports previous proposals for coprophagy to be classified separately when assessing abnormal behavior and welfare of chimpanzees (Hopper, Freeman, & Ross, 2016). Overall, this study refutes the assertion that abnormal behavior is pervasive in zoo-housed chimpanzees (Birkett & Newton-Fisher, 2011), but we join those authors in their support for further work in this area to assess and ultimately improve captive environments for chimpanzees. Understanding not only the prevalence of abnormal behaviors but also focusing efforts on determining the causes of those behaviors most likely to inform us about chimpanzees' psychological states, should be a priority for managers and welfare scientists.

Acknowledgements

We would like to thank all the zoo staff that completed surveys as part of this study. We would also like to thank the staff of the Fisher Center for their assistance in data analysis and manuscript preparation.

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