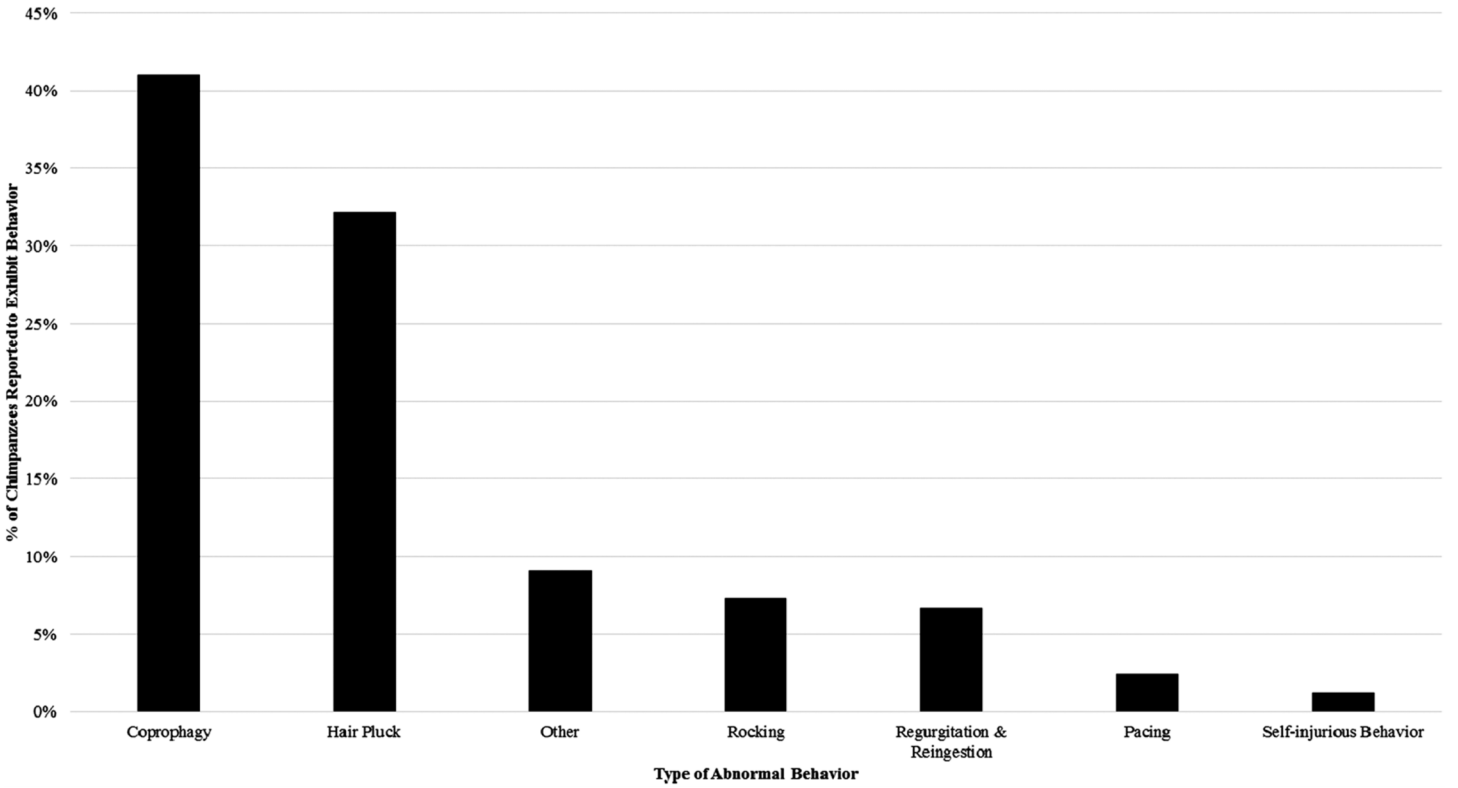

Figure 1 **The percentage of the study sample reported to engage in each category of abnormal behavior at least once from 2011–2013.**

Table 3 **Logistic regression model for any abnormal behavior (ABN-ALL) with predictor variables and constant.**

	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

Note:
Significant variables are bolded. R^2 = 0.03 (Hosmer-Lemeshow); 0.04 (Cox-Snell); 0.05 (Nagelkerke). Model $X^2(2)$ = 6.49; p = 0.04.

3.18 times more likely to exhibit ABN-XC than those who were mother-reared. The other variables included did not contribute significantly to the model.

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 Table 5. 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

Table 4 Logistic regression model for non-coprophagy abnormal behavior (ABN-XC) with predictor variables and constant.

	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

Note:
Significant variables are bolded. R^2 = 0.08 (Hosmer-Lemeshow); 0.11 (Cox-Snell); 0.15 (Nagelkerke). Model $X^2(5)$ = 19.18; $p < 0.01$.

Table 5 Logistic regression model for coprophagy (ABN-C) with predictor variables and constant.

	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

Notes:
Significant variables are bolded. R^2 = 0.08 (Hosmer-Lemeshow); 0.10 (Cox-Snell); 0.14 (Nagelkerke). Model $X^2(5)$ = 17.59; $p < 0.01$.

were born in a laboratory were 5.33 times more likely to exhibit coprophagy than those born in the wild.

DISCUSSION

Our survey results revealed a lower prevalence of abnormal behavior in zoo-housed chimpanzees 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 lower prevalence of 64% of zoo-housed chimpanzees were observed to engage in some type of abnormal behavior over a two-year period. Although 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 the zoo-housed chimpanzee population. The current study draws from a substantially larger sample of zoos (26 institutions compared to six) 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 sample.

One clear similarity in the results of these two assessments is the prevalence of coprophagy as the most commonly reported abnormal behavior: 41% of the sample was reported to engage 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 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*). Though a socially-learned behavior could still be an indicator of negative welfare, it can likely be distinguished from those behaviors that are more directly tied to environmental or social inadequacies. Our analysis of the variables that predict the occurrence of coprophagy in this sample 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 3.57 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 may 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 2.38 times more likely than non-mother-reared chimpanzees to exhibit coprophagy, though this finding did not reach 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 learn this behavior socially may be heightened. In addition, mother-reared chimpanzees typically have more developed social skills than those raised in nurseries or by humans (*Spijkerman et al., 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 sample, 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 further evaluated.

Laboratory origin was also a significant predictor of coprophagy; chimpanzees born in research laboratory settings were 5.33 times more likely to exhibit coprophagy than

chimpanzees born in the wild. It is unclear why this 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 reported less in this chimpanzee sample; rocking and self-injurious behavior were reported in fewer than 10% of chimpanzees. Overall, when we remove the occurrences of coprophagy, the prevalence of abnormal behaviors in the sample decreases to about half of the sample (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 heredity and 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 past studies have shown, rearing is associated with 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 3.18 times more likely to exhibit abnormal behavior (excluding coprophagy) than mother-reared chimpanzees. This rearing result is in the opposite direction as the trend revealed by our coprophagy-only model, again demonstrating 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 approach allows for a larger statistical sample, there are several potential methodological weaknesses which should be considered. One limitation of a survey method is that our results only show the prevalence of these behaviors without any information about their frequency or duration. 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. Furthermore, we are also unable to determine the potential effect of other factors such as shifts in management protocols and social dynamics that may have influenced the expression of abnormal behaviors over that time period. Though more intensive observational studies could potentially address this weakness, they take considerably more time and resources to conduct adequately.

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. Although these are valid perspectives, 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*; *Less et al., 2012*). Furthermore, the survey methods used here are ultimately a conservative measure, as abnormal behaviors need only be observed once in a two-year period, and are therefore likely to be *overestimating* the prevalence of these behaviors.

We assert that these survey data represent a useful evaluation of the prevalence of abnormal behaviors in zoo-housed chimpanzees. This study provides a broad characterization of the occurrence of abnormal behavior in zoo-housed chimpanzees 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 associated differently with these factors. 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 calls into question *Birkett & Newton-Fisher's (2011)* assertion that abnormal behavior is pervasive in zoo-housed chimpanzees, but we join those authors in their support for work to assess and ultimately improve captive environments for chimpanzees. We acknowledge that we were unable to assess all of the many factors potentially associated with abnormal behaviors, and as a result, we encourage future research to include information on factors such as genetic relatedness, age, social exposure and more detailed early historical variables in order to refine our knowledge of these behaviors. 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.

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Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Sarah L. Jacobson analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Stephen R. Ross conceived and designed the experiments, performed the experiments, contributed reagents/materials/analysis tools, wrote the paper, reviewed drafts of the paper.
- Mollie A. Bloomsmith conceived and designed the experiments, wrote the paper, reviewed drafts of the paper.

Data Deposition

The following information was supplied regarding data availability:

The raw data has been supplied as Supplemental Dataset Files.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.2225#supplemental-information.

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