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Prevalence and characteristics of hair plucking in captive bonobos (*Pan paniscus*) in North American zoos

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When primates exhibit hair loss and are observed to engage in self or social hair plucking (a rapid jerking away of the hair shaft and follicle by the hand or mouth, often accompanied by inspection, and consumption) the altered appearance, and behavior patterns are thought to reflect individual physiological, and psychological well-being. Hair loss and hair plucking occur in many captive primate species, including all of the great apes. We present the first survey of this behavior among captive bonobos (N = 88; 50 females and 38 males) in seven zoos in the United States. We found that 43% of the population engaged in this behavior pattern and discounting youngsters (who are not observed to hair pluck until the age of five), 58% of individuals hair plucked. Of the individuals who hair plucked, 97% engaged in social plucking, whereas 46% engaged in self-directed plucking. We regressed the occurrence of hair plucking with multiple predictor variables using binary logistic regression and multimodel inference to determine which predictors best explained the prevalence of self-directed and social plucking. We also analyzed publicly available data on hair plucking in captive chimpanzees. We found that the occurrence of another abnormal behavior, age, origin, and pelage condition best explained self-directed plucking in bonobos. Social plucking was explained by age, origin, pelage, and sex. Our analysis of chimpanzee hair plucking revealed that plucking is strongly influenced by rearing and sex. This study demonstrates that hair plucking is more prevalent in captive bonobos compared to captive chimpanzees and gorillas, however, the covariates associated with hair plucking for each species are different. Our data suggest a potential link between self-directed plucking and well-being. However, the higher prevalence and etiology of social hair plucking is more difficult to explain.

KEYWORDS

abnormal behavior, alopecia, hair pulling, welfare

1 | INTRODUCTION

Abnormal behaviors are defined as any behavior pattern that: 1) is atypical of a species or 2) occurs at different frequencies between captive and wild populations (Erwin & Deni, 1979). These behaviors occur in both captive and wild settings and are often considered a

proxy for the physical and/or psychological well-being of the individuals engaging in these patterns. Among captive populations, the occurrence of these behaviors has largely been considered a response, or coping mechanism to a past or present suboptimal environment (Mason, 1991). Abnormal behaviors vary across species and some patterns may result in self-injury or dramatically alter an

individual's appearance. One such behavior is hair plucking (or hair pulling): A rapid jerking away of the hair shaft and follicle by the hand or mouth, often accompanied by inspection, and consumption (Brand & Marchant, 2015).

Hair plucking is reported to occur in a number of captive primate species, including rhesus macaques (Heagerty, Wales, Prongay, Gottlieb, & Coleman, 2017; Lutz, Coleman, Worlein, & Novak, 2013; Reinhardt, Reinhardt, & Houser, 1986), and all the great apes (Birkett & Newton-Fisher, 2011; Brand & Marchant, 2015; Edwards & Snowdon, 1980; Hill, 2004; Jacobson, Ross, & Bloomsmith, 2016; Less, Kuhar, & Lukas, 2013; Miller & Tobey, 2012; Nash, Fritz, Alford, & Brent, 1999; Pizzutto, 2007). The behavior has been observed to be both self-directed and directed toward conspecifics (Heagerty et al., 2017). In captive macaques, the occurrence of hair plucking is related to a number of variables including sex, age, dominance rank, and reproductive status. Reinhardt et al. (1986) reported that females were more likely to hair pluck than males whereas Lutz et al. (2013) found that males were more likely to hair pluck. Adolescents were reported to have an increased likelihood of hair plucking compared to adults (Reinhardt et al., 1986). When directed toward conspecifics, hair pulling has been reported to be directed toward lower-ranking individuals in two different studies (Heagerty et al., 2017; Reinhardt et al., 1986) although the nature of social hair plucking was different. Reinhardt and colleagues (1986) found the behavior to be agonistic, resulting in behavioral responses in the recipients reflecting fear, and pain. In contrast, a recent study found social hair plucking to be independent of both aggression as well as grooming (Heagerty et al., 2017). Finally, female reproductive state may be related to the occurrence of hair plucking in captive macaques. Pregnant females were observed to pluck more frequently following parturition (Reinhardt et al., 1986). The degree of alopecia (partial or complete absence of hair from one or more body regions) is also reported to be significantly greater among expectant females (Beisner & Isbell, 2009) although the link between alopecia and hair plucking in captive macaques is contested. Lutz et al. (2013) argue that hair pulling played only a “small role” in alopecia among the macaques in their study, yet Heagerty et al. (2017) found a significant relationship between social hair pulling and alopecia.

Among chimpanzees and gorillas, the presence or absence of hair plucking has largely been studied using survey methods (Jacobson et al., 2016; Less et al., 2013). Surveys provide rapid assessment of the prevalence of this behavioral pattern and may identify potential influencing factors. Less et al. (2013) found that hair plucking was relatively rare among captive gorillas (37 institutions, $N = 240$); only 15% of the individuals in the sample were reported to hair pluck. This analysis found that early familiarity with the behavior (e.g., an individual was housed with another individual who hair plucked) significantly predicted its occurrence later in life. Other factors, such as sex, age, type of social group (i.e., bachelor group, mixed sex group), were not related to the behavior. Jacobson et al. (2016) surveyed a sample of captive chimpanzees (26 institutions, $N = 165$) for a number of abnormal behaviors, including hair plucking, which occurred in 32% of the individuals in the sample. Specifically, this analysis examined the

effects of sex, rearing (mother- or non-mother-reared), and origin (lab, private, wild, or zoo). Among abnormal behaviors other than coprophagy, the only significant predictor was rearing; that is non-mother-reared individuals were more likely to exhibit abnormal behaviors. The authors note that factors, such as social isolation, may facilitate the development of some abnormal behaviors, while other behaviors (including hair plucking) may be explained by heredity, and social learning (see also Less et al., 2013; Nash et al., 1999). Collectively, these studies highlight how rearing and early familiarity may predispose captive apes to exhibit hair plucking later in life.

Recently, hair plucking has been studied among captive bonobos (*Pan paniscus*). One study highlighted inter-individual differences in hair plucking among captive bonobos ($N = 17$) at a single institution (Brand & Marchant, 2015). This study found that 21% of grooming bouts involved hair plucking, 53% of the group members hair plucked, and social hair plucking was more frequent than self-directed plucking. There was no sex difference, although adolescent males plucked significantly more than adult males. The effects of the social and physical environment on hair plucking were also investigated. Party size was found to significantly influence daily plucking rates in some individuals. However, there were no significant difference in hair plucking by location (indoor vs. outdoor) or the number of visitors present (Brand & Marchant, 2015).

Brand and Marchant (2015) did find differences in the occurrence of hair plucking based on rearing; wild-born individuals were never observed to hair pluck. However, in a comparative study of hair plucking in another bonobo group at another institution, Findley, Marchant, and Brand (2015) found that the only subject who was wild-born plucked more frequently than any other individual, and that his plucking was all self-directed. Thus, rearing may not consistently explain the presence or absence of this behavioral pattern. In a related study, Brand et al. (2016) investigated the etiology of hair plucking in the same group of bonobos reported on in the Brand and Marchant (2015) paper. Urinary cortisol levels showed a significant positive correlation between mean cortisol and self-directed plucking for females ($r = 0.88$, $P < 0.05$) but not for males ($r = -0.73$, $P = 0.09$). This suggests multiple etiologies for hair plucking: Some individuals, particularly females, may hair pluck themselves in response to stress, whereas stress did not explain self-directed hair plucking in males. Thus, hair plucking may manifest for reasons other than stress in captive bonobos, including social transmission (Brand et al., 2016).

It seemed useful to investigate more widely the patterns of hair plucking among bonobos. We chose to differentiate between self-directed and social hair plucking given the potential functional differences (see Brand et al., 2016). The study reported here had three objectives. First, we sought to assess the prevalence of hair plucking in captive bonobos housed in U.S. zoos. We define prevalence as the number of individuals that engage in a behavior pattern, regardless of frequency. Prevalence has been previously documented at two institutions, with hair plucking shown by 53% and 83% respectively of those individuals (Brand & Marchant, 2015; Findley et al., 2015). We sought to test whether these percentages were representative of the larger U.S. captive population of bonobos. We also aimed to compare

our results with a recent, large study on captive chimpanzees where 32% of individuals exhibited hair plucking (Jacobson et al., 2016), as well as a survey on captive gorillas in which 15% of individuals hair plucked (Less et al., 2013). Differences in the prevalence of hair plucking among these three species may reflect species differences in biology and/or behavior. Our second objective was to identify covariates of bonobo hair plucking and compare these results with those of captive chimpanzees and gorillas. If self-directed plucking is related to welfare, we predicted non-mother reared individuals to more frequently engage in the behavior, consistent with abnormal behavior in non-mother reared chimpanzees (Jacobson et al., 2016). Additionally, other abnormal behavior should co-occur with self-directed plucking (Birkett & Newton-Fisher, 2011; Less et al., 2013). We did not anticipate a sex difference in the prevalence of self-directed plucking as hair plucking overall did not previously vary between females and males (Brand & Marchant, 2015). We did not anticipate any differences in social plucking according to sex, age, origin, rearing, or the occurrence of abnormal behavior. We predicted that self-directed hair plucking and coat condition were negatively correlated, that is individuals who engaged in self-directed hair plucking would be more likely to exhibit hair loss. We did not predict a relationship between social plucking and pelage. Our third and final objective was to characterize the prevalence of other abnormal behaviors in this population. In order to meet our objectives, we surveyed the entire population of zoo-housed bonobos in North America. This survey allowed for the rapid accumulation of a comparatively large, and for this taxon, exhaustive dataset for zoo-housed bonobos in North America. While it is the case that surveys have limitations, such as sampling over time (see also Jacobson et al. (2016) and Less et al. (2013)), surveys represent an important approach at revealing the dimensions of a behavioral phenomenon.

2 | METHODS

2.1 | Study questionnaire

We designed and disseminated an online study questionnaire using the software Qualtrics (Provo, UT). The survey was approved and endorsed by the Bonobo Species Survival Plan and subsequently sent to all zoos in the United States ($N = 7$) that currently house the species. We asked each institution to identify an individual to complete our survey who had the professional knowledge to answer our questions about each individual bonobo's behavior and appearance (such individuals included curators or head keepers). It may be the case, however, that survey takers varied in the amount of time they knew the subjects resulting in a potential underestimate of the prevalence of hair plucking. Questionnaire respondents answered a series of questions for each individual bonobo currently housed at the facility. Our questionnaire was modeled after that of Less et al. (2013) in order to allow for comparison between the studies.

Questions included specifying each individual's age and sex. We asked about the origin of each individual (captive-born or wild-born) and his or her rearing history. For captive-born individuals, rearing

categories included: Mother-reared, human-reared, or reared by another bonobo. We decided to combine these last two categories as non-mother-reared. Survey respondents were asked to score whether or not each individual had ever been observed, or was known to hair pluck themselves, and whether or not an individual had ever been observed, or was known to hair pluck others. Thus, our one-zero sampling does not account for differences in frequency (e.g., one individual hair plucks daily versus an individual who has hair plucked once in the last year). See Jacobson et al. (2016) for further discussion on this limitation. We asked about the general appearance of each bonobo's pelage and asked respondents to rank an individual's coat condition from 0–2 (0 = none: No hair missing, 1 = moderate: One patch of hair missing, 2 = severe: Two or more patches of hair missing) or "other" to allow respondents to explain categories not listed. We used this scoring system to compare our results with those of Less et al. (2013). We later condensed these categories into 0 = no hair loss and 1 = any hair loss. Finally, we asked participants to report which other abnormal behaviors an individual exhibited, including coprophagy, regurgitation and reingestion (R&R), rocking, urophagy, and/or another behavior, in which the respondent was asked to specify the behavior(s).

As the focus of the survey was on individual covariates associated with hair plucking, we did not ask participants about specific housing or social conditions that may influence hair plucking. However, all individuals had access to the outdoor enclosures at some point during the year, contingent on temperature, and weather.

2.2 | Study subjects

We received responses between May 2016 and January 2017 from seven U.S. zoos ($N = 88$), which represents the entire population of zoo-housed bonobos in North America. The population consists of 50 females and 38 males (56.8% female). The population has a median age of 13.5 years, ranging from 0–49 years of age. Five individuals were wild-born while the rest were captive-born. Of the captive-born individuals, 70 individuals were mother-reared, 10 individuals were human-reared, one was reared by another bonobo female, and two were of unknown rearing.

Respondents could not state for certain whether or not seven individuals engaged in self-directed hair plucking and if eight individuals engaged in social hair plucking. Additionally, rearing status was unknown for two females included in our analysis of social plucking. Therefore, we excluded these individuals from our statistical analyses. Our resulting bonobo sample ($N = 81$) for self-directed plucking ranged in age from 0 to 49 and included 45 females (55%), 76 individuals that were captive-born, five individuals who were wild-born, 70 individuals that were mother-reared, and 11 individuals that were non-mother-reared. Our sample for social hair plucking in bonobos ($N = 78$) also ranged in age from 0 to 49 and included 44 females (56%), 73 individuals that were captive-born, five that were wild-born, 69 individuals that were mother-reared, and nine that were non-mother-reared.

2.3 | Statistical analysis

While this study includes data on bonobos who are housed at different facilities, we analyzed this population as an aggregate. We fitted generalized linear mixed models (GLMMs) with a binomial error structure and logit link to examine the effects of our predictor variables on the occurrence of self-directed and social hair plucking. We used R version 3.3.1 (R Core Team, 2015) for all statistical analyses and the package “lme4” (Bates, Maechler, Bolker, & Walker, 2015) to run our GLMMs. We included sex, age, origin, rearing, pelage condition, and the occurrence of other abnormal behaviors as predictor variables. We decided to categorize rearing status as mother-reared or non-mother reared, combining individuals that were hand reared, and one infant raised by another female. We considered only main effects because small sample size did not allow for all possible combinations across sex, origin, and rearing. Facility was included as a random effect as this improved AICc scores for our models (data not shown). We selected top model sets from possible model combinations based on AICc comparison and included models with $\Delta\text{AICc} < 2$ in the top model set (Burnham & Anderson, 2002; Grueber, Nakagawa, Laws, & Jamieson, 2011). Models were further considered by model weight and we employed model averaging when there was no obvious best model (weight > 0.90) (Burnham & Anderson, 2002). We averaged models using the zero method (Burnham & Anderson, 2002), which decreases the effect sizes of predictors from models with small model weights. Following Nakagawa and Freckleton (2010), we used this method rather than the natural average method because we were interested in which predictors best explained the prevalence of hair plucking rather than the effects of specific predictors of interest. We averaged models using the package “MuMIn” (Bartoń, 2009). Post-estimation plots for relevant explanatory predictors were constructed using the package “sjPlot” (Lüdtke, 2017).

We also present descriptive statistics on the prevalence of other abnormal behaviors in this population.

2.4 | Comparative analysis

In addition to the data on gorilla hair plucking from Less et al. (2013), we compared our results to data on abnormal behavior among a sample of captive chimpanzees generously provided by Jacobson et al. (2016) (available at <https://doi.org/10.7717/peerj.2225/supp-1>). Their study examined the effects of covariates on the occurrence of multiple abnormal behaviors including hair plucking. We ran the same GLMMs used in our study on the chimpanzee hair plucking data including sex, origin, and rearing as predictor variables and facility as a random effect. However, we could not include age or pelage condition as independent variables as these data were not collected for that study.

3 | RESULTS

Forty-three percent of the population exhibited hair plucking. When we excluded infants and juveniles under five years of age (who groom infrequently and were never reported to hair pluck), this number rose to 58%. Of individuals who hair plucked, 45.5% engaged in

self-directed hair plucking, while all but one individual plucked socially (96.9%).

We did not include rearing as a predictor in our models for self-directed plucking because there was no variation in the occurrence of self-directed plucking among non-mother-reared individuals; non-mother-reared bonobos never engaged in self-directed plucking. Supplement 1 lists the models, AICc values, ΔAICc values, and model weights for our analysis of self-directed and social hair plucking. The top model set for self-directed plucking included abnormal behavior, age, origin, and pelage condition as predictor variables (Table 1). Individuals that exhibited at least one other abnormal behavior were 9.75 times more likely to pluck themselves than those individuals that did not. Self-directed plucking increased with age although we note that this predictor was the least important. Wild-born individuals were 27.48 times more likely than captive-born individuals to pluck themselves and individuals with at least one patch of hair missing were 39.90 times more likely to engage in self-directed plucking (Figures 1–4).

Social hair plucking was best explained by age, origin, pelage, and sex (Table 2). Social hair plucking was positively associated with age, such that likelihood of social plucking increases as an individual ages. Wild-born individuals were only marginally less likely to engage in social hair plucking. Bonobos that had at least one patch of hair missing from their coat were 87.84 times more likely to socially hair pluck. Finally, females were 59.2 times more likely to engage in social hair plucking than males. Postestimation plots for these predictors are presented in Figures 5–8.

3.1 | Other abnormal behavior

The prevalence of other abnormal behaviors is reported in Table 3. Of the 88 bonobos in this study, 32 (36.4%) were reported to engage in another abnormal behavior other than hair plucking. When we exclude

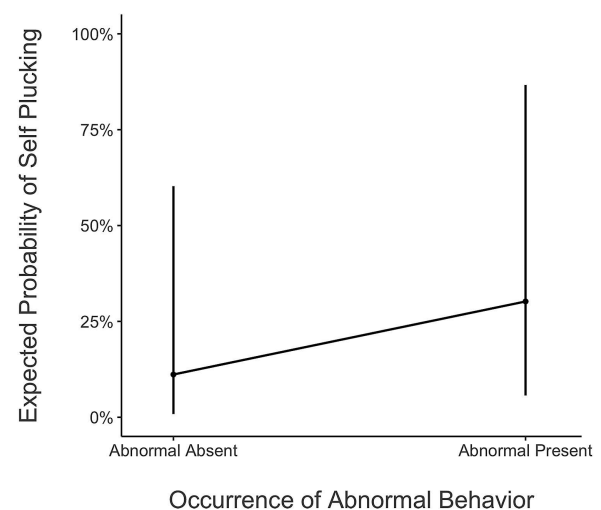


FIGURE 1 Estimated probability of self-directed hair plucking based on the occurrence of other abnormal behaviors with 95% confidence intervals

TABLE 1 Fixed-effect estimates, odds ratio, and relative importance after model averaging for self-directed hair plucking in bonobos

	β	SE	OR	RI
Intercept	-5.677	2.42		
Abnormal: Present	1.852	1.52	9.75	0.81
Age	0.007	0.03	1.04	0.18
Origin: Wild-born	2.086	2.22	27.48	0.63
Pelage: Hair loss	3.686	1.55	39.90	1.00

β , standardized coefficient for predictor; SE, adjusted standard error; OR, odds ratio, RI, relative importance of each parameter to other parameters in final model.

the number of infants and young juveniles (individuals under the age of 5), who have not yet developed abnormal behaviors, this percentage rises to 44%. The most prevalent behavioral pattern was R&R ($N = 24$), followed by coprophagy ($N = 12$).

3.2 | Chimpanzee data

Our analysis of the chimpanzee hair plucking data resulted in three models with an AICc score difference of less than two, one of which included the null model (Supplement 1). However, the top model set included both rearing and sex as predictors (Table 4). Non-mother-reared chimpanzees were more likely to hair pluck than mother-reared individuals and females were more likely to pluck than males. Postestimation plots for these predictors are presented in Supplement 2.

4 | DISCUSSION

This survey demonstrates the surprisingly high prevalence of hair plucking among captive bonobos. Plucking in captive bonobos is more prevalent (43%) than in captive chimpanzees (32%) or gorillas (15%) (Jacobson et al., 2016; Less et al., 2013). Interestingly, in contrast to the

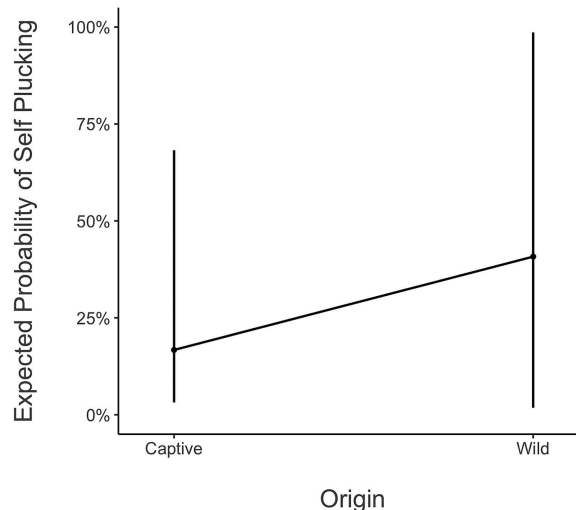


FIGURE 3 Estimated probability of self-directed hair plucking based on origin with 95% confidence intervals

Less et al. (2013) description of gorilla behavior, where 83% of individuals who engaged in hair plucking exhibited self-directed hair plucking, 6% plucked socially, and 11% engaged in both self-directed, and social plucking, our results demonstrate a different pattern. All but a single individual engaged in social hair plucking, whereas less than half of our sample plucked themselves. This difference may represent species differences in biology, management practices, how the pattern is propagated, or respondent recall error.

We found that the occurrence of self-directed hair plucking was influenced by age, origin, pelage condition, and the occurrence of other abnormal behaviors. It is rather unsurprising that individuals who are more likely to engage in self-directed plucking have coats with missing hair. As hair plucking occurs almost exclusively during grooming (Brand & Marchant, 2015), the relationship between age and self-directed plucking is understandable as young bonobos engage in self grooming

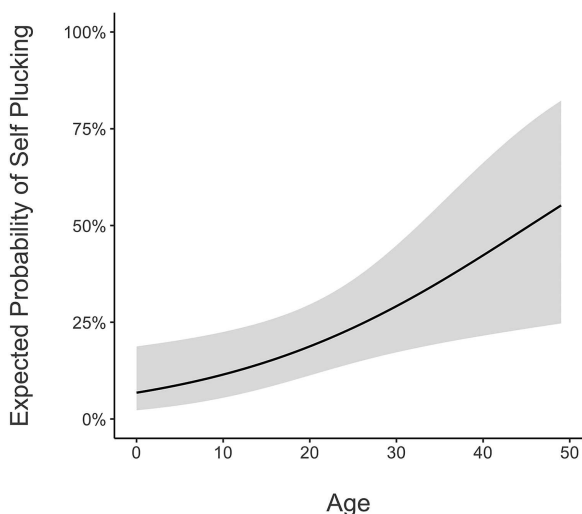


FIGURE 2 Estimated probability of self-directed hair plucking based age with 95% confidence intervals

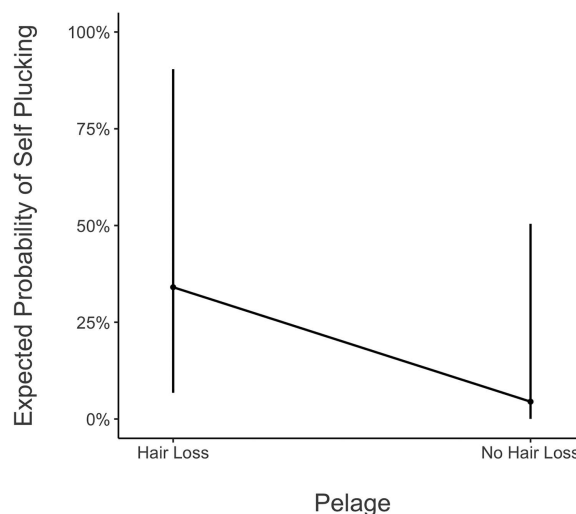


FIGURE 4 Estimated probability of self-directed hair plucking based on pelage condition with 95% confidence intervals

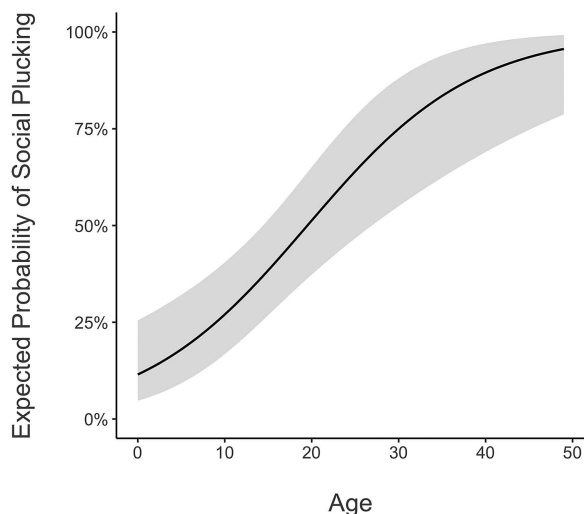
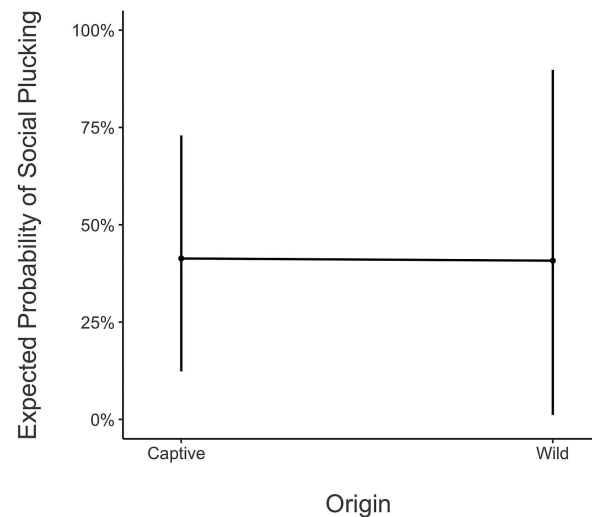
TABLE 2 Fixed-effect estimates, odds ratio, and relative importance after model averaging for social hair plucking in bonobos

	β	SE	OR	RI
Intercept	-10.086	4.32		
Age	0.338	0.15	1.40	1.00
Origin: Wild-born	-3.024	3.61	0.00	0.58
Pelage: Hair loss	4.477	1.67	87.94	1.00
Sex: Females	4.081	2.09	59.20	1.00

β , standardized coefficient for predictor; SE, adjusted standard error; OR, odds ratio; RI, relative importance of each parameter to other parameters in final model.

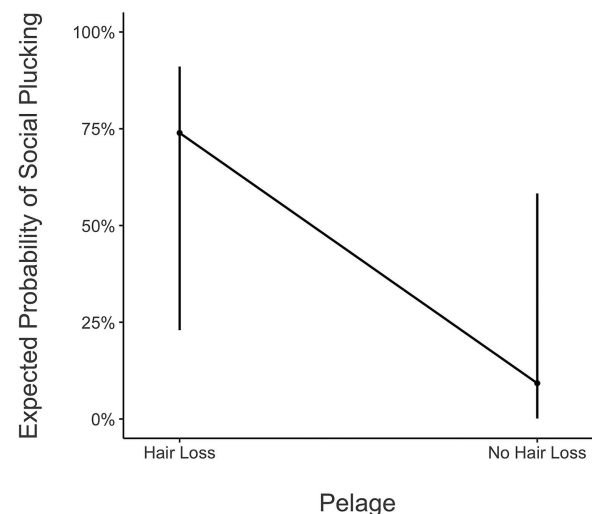
far less than other individuals until they are a few years of age. While origin was present in our averaged model, we draw attention to our small size for wild-born individuals ($N = 5$). However, further tests of this effect are not possible as captive apes are no longer acquired from the wild. The co-occurrence of hair plucking and other abnormal behaviors provides support for the hypothesis that self-directed hair plucking is tied to individual welfare, at least in some individuals. There was no sex difference and contrary to our predictions and the findings of Jacobson et al. (2016), non-mother-reared bonobos engaged in self-directed hair plucking.

Social plucking was best explained by age, origin, pelage condition, and sex. As noted above, the relationship between age and social plucking is likely explained by the ontogeny of grooming. Again, our sample size for individuals of wild-born origin is small so we cautiously consider the effect of origin on social plucking. The association between pelage condition and social plucking is perplexing. Plucking others should not result in the denuding of the individual engaging in that behavior pattern unless they also engage in self-directed plucking or are a frequent recipient of allogrooming, during which hair plucking

**FIGURE 5** Estimated probability of social hair plucking based on age with 95% confidence intervals**FIGURE 6** Estimated probability of social hair plucking based on origin with 95% confidence intervals

may occur. The observed sex difference is also interesting but may be explained by the sociality of this particular taxon. Bonobo males are less bonded with each other and are often peripheral to the core social group in both the wild and in captivity (Franz, 1999; Furuichi, 1989; White, 1988). However, while female-female bonds are well documented, male-female relationships appear to play an equally important role in bonobo sociality, including mother-son relationships (Furuichi, 1989; Kano, 1992; Stevens, Vervaecke, De Vries, & Van Elsacker, 2006; Surbeck, Mundry, & Hohmann, 2011; White, 1996). We speculate that differences in the sociality of bonobo males and females may explain the sex difference in social plucking prevalence.

We found that rearing and sex explained hair plucking in chimpanzees. As we do not know whether this was self-directed or social plucking, we make tentative comparisons here. Rearing was not

**FIGURE 7** Estimated probability of social hair plucking based on pelage condition with 95% confidence intervals

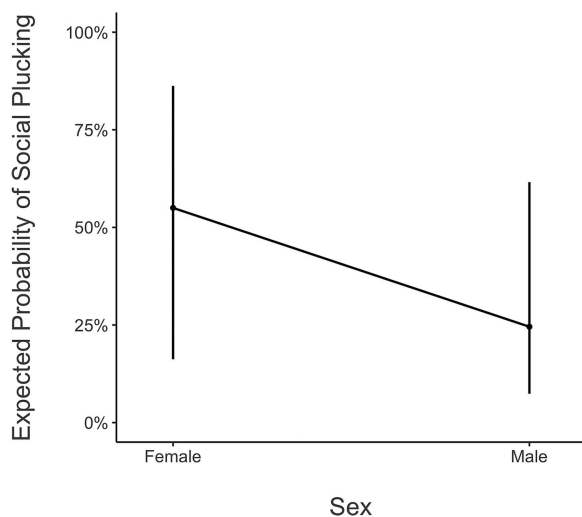


FIGURE 8 Estimated probability of social hair plucking based on sex with 95% confidence intervals

an important predictor for either self-directed or social plucking in our bonobo sample yet was an important predictor for chimpanzees. This difference may be attributed to the significant differences between the individuals in the present study and those in the Jacobson et al. (2016) study. The chimpanzee sample consisted of some animals that were former pets and former laboratory subjects. Additionally, this sample had roughly equivalent numbers of individuals who were mother reared and should be non-mother-reared. This is in strong contrast to the bonobo population, in which the majority of individuals are captive-born and mother-reared. Thus, the greater heterogeneity of the chimpanzee population may explain differences in hair plucking in these two sister taxa. Sex helped explain hair plucking in both species, although this was only true for social plucking in bonobos. As aforementioned, high rates of social plucking in females are not unexpected for bonobos, however, this result is harder to explain for chimpanzees especially given that we cannot know if this hair plucking is self-directed or social.

In this survey, in addition to hair plucking, of the seven other reported abnormal behaviors, R&R stands out as the most prevalent

TABLE 3 Prevalence of other abnormal behaviors in the North American zoo-housed bonobo population

Abnormal behavior	Prevalence of behavior (N)	% of total population (N = 88)
Regurgitation and reingestion (R&R)	24	27.3
Coprophagy	12	13.6
Rocking	2	2.3
Fecal smearing	2	2.3
Fecal throwing	1	1.1
Spinning	1	1.1
Urophagy	1	1.1

(approximately 27%), followed by coprophagy (14%) (Table 3). The remaining five patterns are represented by one or two individuals. It is worth noting that the three most prevalent abnormal behavioral patterns (hair plucking, R&R, coprophagy) all have a pronounced oral component to the behavior. Among zoos that house bonobos there is considerable variation in the prevalence of R&R. Our combined sample reports 27% of the total population engaging in this behavior but one report indicates 71.4% of individuals at one zoo exhibited R&R (Miller & Tobey, 2012). In contrast, in the Jacobson et al. (2016) study, chimpanzees are rarely reported to exhibit this pattern (7.3%). Captive gorillas show the highest prevalence of R&R with 50% of individuals reported to show R&R (Less et al., 2013).

Less et al. (2013) demonstrated that early exposure to hair plucking predicted the occurrence of the behavior later in life among captive gorillas supporting the hypothesis that hair plucking is a learned behavior and socially transmitted in at least some individuals. Indeed, one recent study of captive chimpanzees have suggested that another abnormal behavior, coprophagy, is a socially transmitted behavior (Hopper, Freeman, & Ross, 2016). These authors assert that if these behaviors are learned, their occurrence may not accurately reflect an individual animal's well-being or welfare (see also Nash et al., 1999). Our previous analysis of hair plucking in captive bonobos highlighted that while stress may explain the behavior in some individuals, particularly females, it did not explain its occurrence in others (Brand et al., 2016). These data suggest that among bonobos, hair plucking may result from multiple etiologies including stress and/or social transmission. The data for self-directed plucking in the present study appear to support a link between this behavior and individual well-being. This idea would be better supported by a more comprehensive study examining the relationship between the behavior and biomarkers of stress (Brand et al., 2016). However, the occurrence of social hair plucking and its higher prevalence in this population compared to self-directed plucking is harder to explain.

Our ability to ask questions about the potential social transmission of hair plucking in bonobos is limited as there is at least one individual reported to hair pluck at all seven zoos. In contrast, examining the data made available by Jacobson et al. (2016) of the 26 institutions surveyed, nine report no hair plucking. It may well be that some individuals at those zoos have never been exposed to individuals transferred from another zoo that hair pluck or that the environments those chimpanzees are housed in do not stimulate the behavior. With fewer institutions housing bonobos, the probability increases that individuals will be exposed to hair plucking and the behavior will be propagated.

Furthermore, differences in management style may facilitate the transmission of hair plucking in bonobos. Some groups of captive bonobos are either housed in social groups that change in composition every few days, emulating their fission-fusion social system (Brand & Marchant, 2015). It may be that a higher probability of encountering a stranger, and/or a unique management style, may facilitate the widespread and rapid social transmission of particular behavior patterns in this population, including hair plucking. Indeed, if social transmission explains some hair plucking in this population of captive

TABLE 4 Fixed-effect estimates, odds ratio, and relative importance after model averaging for hair plucking in chimpanzees

	β	SE	OR	RI
Intercept	-1.182	0.454		
Rearing: Non-mother	0.079	0.272	0.73	1.00
Sex: Male	-0.073	0.252	1.40	1.00

β , standardized coefficient for predictor; SE, adjusted standard error; OR, odds ratio; RI, relative importance of each parameter to other parameters in final model.

bonobos, as well as perhaps behaviors in other species (e.g., coprophagy in captive chimpanzees), then a reconsideration of these behaviors as an indicator of ape well-being is warranted (Hopper et al., 2016; Nash et al., 1999). Alternatively, bonobos may be inherently more sensitive to developing hair plucking in a captive environment compared with other primates.

While hair plucking is an abnormal behavior, the consequences for ape health have yet to be studied (Brand & Marchant, 2015). It is obvious in nature that hair is important for thermoregulation and the same ought to be true for captive primates. However, management practices sometimes provide heat sources and apes and other primates may spend part of their day in indoor facilities that provide heating and cooling. These management practices may buffer the consequences of hair loss in these apes. Nonetheless, visitor perception of ape health may be unduly influenced by coat appearance. This results in attempts at ameliorating this behavior with limited success. In captive gorillas, increased foraging opportunities and increased keeper attention resulted in a modest reduction in hair plucking (Hill, 2004; Pizzutto, 2007). There are few other studies that report efforts, successful or not, at reducing the frequency of this behavior. If it can be demonstrated that an abnormal behavior is the result of identifiable stress, it is potentially possible to manipulate the source of that stress, environmental or social, to achieve a reduction in the occurrence of the behavior. However, if the origin of an abnormal behavior is tied to social transmission, this presents a far more challenging problem for zoo management. Because hair plucking is assumed to not present an immediate challenge to the health status of captive apes and may not be an indicator of individual well-being, reducing or eliminating this pattern of behavior has not been a significant priority in captive management.

To conclude, this research project demonstrates the efficacy of survey-based methods. We also see the complementarity of direct observation to assess the duration, frequency, and periodicity of hair plucking and other behaviors that provide insight into the lives of these complex apes. Hair plucking is more prevalent in captive bonobos compared to captive chimpanzees and gorillas. Age, origin, pelage condition, and the presence of other abnormal behavior best explained self-directed hair plucking in this population. The plucking of conspecifics was related to age, origin, pelage condition, and sex. Another recent study found a strong link between alopecia and social hair plucking in captive rhesus macaques (Heagerty et al., 2017). These data provide the foundation for the continued testing of hypotheses to better understand and potentially mitigate abnormal behavioral patterns like hair plucking among captive primates.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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