



Hair plucking in captive bonobos (*Pan paniscus*)



Colin M. Brand^{a,*}, Linda F. Marchant^b

^a Department of Anthropology, University of Oregon, Eugene, OR, United States

^b Department of Anthropology, Miami University, Oxford, OH, United States

ARTICLE INFO

Article history:

Received 31 January 2015

Received in revised form 27 July 2015

Accepted 3 August 2015

Available online 10 August 2015

Keywords:

Bonobo

Pan paniscus

Hair plucking

Undesirable behavior

Well being

ABSTRACT

Both wild and captive studies of grooming in non-human primates emphasize the adaptive role of this behavior. Indeed, social grooming is frequently characterized as “social glue” in the life of primates. Grooming behavior is studied to reveal dominance, kin relations, and social networks. Many captive primates, including apes, are observed to over-groom which may result in denuding of individuals. This study focused on a discrete pattern of grooming, specifically hair plucking—a rapid jerking away of the hand or mouth to remove the hair and hair follicle, often accompanied by inspection and consumption of the hair and follicle. This pattern has never been reported for wild bonobos (*Pan paniscus*) but is routinely observed in many individuals in captive colonies. Subjects were 17 bonobos (4 wild-born and 13 captive-born) housed at the Columbus Zoo. Data on grooming behavior were collected using all-occurrence sampling. Approximately 21% of self-directed and dyadic grooming bouts involved hair plucking. The four wild-born individuals were never observed to hair pluck. While plucking was not significantly different between males and females, subadult males plucked significantly more than adult males. Self-directed plucking appears to be influenced by dominance—the dominant male and female showed the highest percent of self-directed plucking behavior, 54% and 57%, respectively. This is the first study to document the significance of plucking in bonobo grooming behavior and contributes to discussions of visitors’ perception of ape well being.

© 2015 Elsevier B.V. All rights reserved.

1. Introduction

Grooming has been well studied in both wild and captive primates. Early observations of the behavior revealed that primates groom themselves and others more frequently than would be required to maintain hygiene (McKenna, 1978). Social grooming serves an important role and may reveal kinship, dominance, and social networks. In captive settings, primates have been observed to overgroom themselves and others. The term “overgrooming” is used to describe high frequencies of grooming that result in the denuding of an individual (Bernstein and Didier, 2009). Overgrooming has been variously described in the primate literature using the terms hair plucking (Tustin et al., 1996), hair pulling (Reinhardt et al., 1986), and fur pulling (Goodwin, 1997). Additionally, some researchers describe hair loss on the head or body that may occur as a result of overgrooming with the term alopecia (Honest et al., 2005). Kroeker et al. (2014) caution that hair plucking does not always explain alopecia and that individuals who hair pluck may not always exhibit hair loss.

Hair plucking is characterized by a distinct motor pattern. A single hair or multiple hairs are plucked with a rapid jerking away of the mouth or hands and may be accompanied by inspection and consumption of the hair shaft and follicle. Hair plucking may be self-directed or directed toward another individual (Reinhardt, 2005). While the behavior often occurs during grooming, hair plucking may also occur at random outside of grooming bouts.

In humans, hair plucking is known as trichotillomania and is diagnosed as an impulse-control disorder and is also associated with the obsessive-compulsive spectrum (American Psychiatric Association, 2013; Christenson and Mansueto, 1999). Individuals typically pluck hair from the scalp, eyebrows, eyelashes, and sometimes, pubic region resulting in alopecia (Christenson and Mansueto, 1999). This hair is often consumed (trichophagia), which may result in the development of trichobezoars (hair balls), which pose potential health risks (Buxbaum, 1960; Galski, 1983). Trichotillomania, while largely self-directed, is occasionally partner-directed. This “social” plucking in humans is largely aggressive in nature (Buxbaum, 1960). Social plucking is more frequent in women than in men; its etiology has been attributed to anxiety and depression (Duke et al., 2010). Trichotillomania is notoriously difficult to treat both pharmacologically and behaviorally (Christenson and Mansueto, 1999).

* Corresponding author. Tel.: +1 541 346 5109.

E-mail address: cbrand2@uoregon.edu (C.M. Brand).

Hair plucking is also observed in other taxa including non-human primates, mice, guinea pig, rabbit, sheep, musk oxen, cat and dog (for review, see Reinhardt, 2005). Hair plucking has been observed in many captive non-human primate species and all captive great apes: orangutan (Edwards and Snowdon, 1980; Zucker et al., 1978), gorilla (Hill, 2004; Less et al., 2013; Pizzutto, 2007), chimpanzee (Ferdowsian et al., 2012; Nash et al., 1999) and bonobo (Miller and Tobey, 2012). To date, the behavior has not been reported in wild ape populations.

Reinhardt et al. (1986) described hair pulling in two groups of rhesus macaques (*Macaca mulatta*). Hair pulling elicited a negative response from the recipient including fear and avoidance behaviors. Hair pulling was largely socially directed with 97% of hair pulling occurring in a dyad. Rank strongly influenced social hair pulling; in 95% of bouts the dominant individual pulled hair from a subordinate. Hair pulling also was influenced by age class and sex; younger individuals pulled hair more frequently than older individuals while females pulled hair more frequently than males, although not significantly. Four females were also observed to hair pull more frequently during pregnancy, than after giving birth. The authors speculate that while nutritional or toxicological factors may promote hair pulling, the lack of abnormal clinical symptoms suggests that the behavior may be the result of psychological maladjustment.

A survey of British and Irish zoos revealed hair pulling occurred in at least one individual for a diverse array of primate species including white faced saki monkey (*Pithecia pithecia*), diana monkey (*Cercopithecus diana*), mandrill (*Mandrillus sphinx*), hamadryas baboon (*Papio hamadryas*), celebes crested macaque (*Macaca nigra*), western lowland gorilla (*Gorilla gorilla gorilla*), and chimpanzee (*Pan troglodytes*) (Hosey and Skyner, 2007). Despite the occurrence of hair plucking in these taxa, the behavior was relatively infrequent; hair pulling was reported in a total of 10 out of 540 individuals (<2%).

In a survey of hair plucking in Western lowland gorillas in North American zoos, 62% reported housing at least one gorilla who hair plucked (Less et al., 2013). Overall, 15% (35 of 240) of gorillas in the survey were reported to hair pluck. The behavior was primarily self-directed and manual, rather than oral, or a combination of both. Sex, age, group size, origin, rearing type, and group composition were reported to not influence the prevalence and distribution of the behavior but solitarily housed individuals tended to pluck themselves more frequently. Early familiarity appeared to play a role in acquiring the behavior, with individuals who observed the behavior during the first few years of life more likely to develop the behavior (Less et al., 2013).

Hair plucking is often classified as an abnormal or undesirable behavior in captive primates (Birkett and Newton-Fisher, 2011). There is considerable debate over what constitutes “abnormal behavior” in captive animals (Bayne, 1996; Erwin and Deni, 1979). Most definitions characterize a behavior as abnormal if the behavior does not occur in the wild or occurs in higher frequencies in captivity (Erwin and Deni, 1979). The presence of these behaviors in an individual’s behavioral repertoire is often used to assess the psychological well being of captive primates (Novak and Suomi, 1988). Atypical behaviors, such as hair plucking, may indicate an individual is currently stressed or the undesirable behavior may persist as a “scar” of past periods of stress (Mason, 2006).

Earlier work on hair plucking in zoo housed primates relied on survey research. For this study we chose to empirically investigate hair plucking in captive bonobos (*Pan paniscus*). This approach yielded both qualitative and quantitative insights into this behavioral pattern. Given the presence of the behavior in all captive great apes, we anticipated hair plucking would be present. The objective of this study was to assess the prevalence and distribution of the behavior in this group of captive bonobos. We sought to

investigate how individual variables such as age, sex, and dominance rank influenced the occurrence of hair plucking. We also considered party size and composition, habitat (indoor vs outdoor), and zoo visitor density in our analyses.

2. Methods

2.1. Study approval

This study was conducted with approval of the Columbus Zoo and Aquarium, Columbus, OH, USA. The Columbus Zoo and Aquarium is accredited by the Association of Zoos and Aquariums (AZA) and complies with all husbandry and welfare standards set forth by the AZA. The research reported here complied with protocols approved by the Columbus Zoo and Aquarium Institutional Animal Care and Use Committee (IACUC).

2.2. Subjects and housing

Subjects were bonobos housed at the Columbus Zoo and Aquarium (CZA). Seventeen individuals were present in the colony including one infant (El) who was born during the study period. At the time of study, this colony represented approximately 19% of the North American population of bonobos and roughly 10% of bonobos housed in zoological and research facilities outside of Africa.

Using Kano’s (1992) age class definitions (infant: 0–1, juvenile: 2–6, adolescent: 7–14, adult: ≥15) the study subjects included four adult males, four adult females, two adolescent males, two adolescent females, one juvenile male, two juvenile females, one infant male, and one infant female; four of the subjects were wild-born (see Table 1). Wild-born individual’s names and subject codes are bolded.

The bonobos are displayed in two indoor habitats and one outdoor enclosure; the zoo also has three off-exhibit outdoor enclosures and four off-exhibit indoor enclosures (for exhibit descriptions and dimensions see Boose et al., 2013). The bonobos at CZA are managed to mimic their species-typical fission-fusion social pattern. Bonobos are given access to each other in the morning and parties (a temporary social group) are formed primarily on individual bonobo preferences rather than keeper decisions. All party combinations are possible except two adult male combinations (Jl and DO, MK and DO) who cannot be housed together due to previous conflicts. Typically, three parties were formed ranging in

Table 1
Study subjects.

Name ^a	Subject code ^b	Age ^c (in years)	Offspring
Ana Neema	An	20	Bila Isia, Gilda, Wilbur
Bila Isia	BI	11	
Donnie	DO	19	Elema, Jerry, Wilbur
Elema	EL	0	
Gander	GA	9	
Gilda	Gi	6	
Jerry	JE	4	
Jimmy	Jl	33	Donnie
JoT	Jo	10	
Lady	La	30	JoT
Lola	Lo	8	
Maiko	MK	28	
Mary Rose	Ma	2	
Susie	Su	30	Donnie, Lola, Mary Rose
Toby	TO	33	Lola
Unga	Un	19	Gander, Jerry, Elema
Wilbur	WI	1	

^a Individuals with **bolded** names wild born.

^b Double upper-case codes are males (e.g., BI); single upper-case and lower-case codes are females (e.g., An).

^c Age (in years) as of August 2012; estimated for wild born individuals.

size from two to nine individuals. These parties lasted two to three days without compositional changes. Each of the three parties was displayed in either the outdoor enclosure or one of the two indoor habitats.

2.3. Data collection

Grooming data were collected on 49 days between May and August 2012 between 9:00 and 19:00 h, using a group focal, all-occurrence sampling in 15 min samples (Altmann, 1974). The active groomer, recipient of the grooming, duration (seconds), site of grooming, and the occurrence of plucking were recorded for each self-directed and social grooming bout. Plucking was recorded using one-zero sampling per grooming bout: a one was scored if plucking was observed during the grooming bout and zero if plucking was not observed (Altmann, 1974). One-zero sampling was employed for hair plucking due to the high frequency of concurrent grooming bouts; the duration of plucking or the exact number of plucks could not be recorded for simultaneous grooming bouts. These plucking scores are therefore a minimum estimate of the incidence of the behavior in this colony. Plucking was noted if the behavior occurred during a grooming bout. A grooming bout was defined as a period of investigation of the hair using hand, mouth, or both (Franz, 1999). A bout was considered complete following a pause of 30+ seconds of inactivity. Instances of hair plucking were also recorded *ad libitum* outside of grooming bouts but occurred at very low frequency.

In addition to group focal for grooming behavior, group scan sampling (Altmann, 1974) was accomplished with a standard ethogram for activity budget in 5 min intervals during the 15 min sample. Undesirable behaviors (e.g., coprophagy, urophagy) were recorded using *ad libitum* sampling during the sample.

To assess the impact of zoo visitors on the behavior of the animals, visitor traffic through the area surrounding both the indoor and outdoor bonobo habitats was designated as either low, medium, or heavily trafficked for each day of observation. Low traffic described 25 visitors or less, on average, per hour, medium traffic described 100 visitors or less, and heavy traffic more than 100 visitors. Data were not collected during the daily keeper talk, which resulted in increased numbers of zoo visitors and may have influenced the behavior of the bonobos.

2.4. Data analyses

Plucking scores were calculated per individual per day by dividing the number of grooming bouts involving hair plucking by the total number of grooming bouts. Thus, daily plucking scores were the unit of analysis. Infants and two dependent juveniles were excluded from all data analyses. The presence of an infant in a party was not accounted for when calculating party size, as infants were never in a party different to that of their mother. ANOVAs were used to test for significant differences in hair plucking among individuals for all variables, except for age and sex. A priori orthogonal planned comparisons were used to test for significant differences between both sexes and age classes (Sokal and Rohlf, 2012). All statistical analyses were performed using SAS[®], Version 9.4. (SAS Institute, Cary NC).

3. Results

3.1. Prevalence of hair plucking

A total of 1450 self-directed and social grooming bouts were recorded during 128 h of observation. Hair plucking was observed at least once in 20.6% of all grooming bouts and did not significantly differ over the course of the study period ($F(47, 324) = 1.37$,

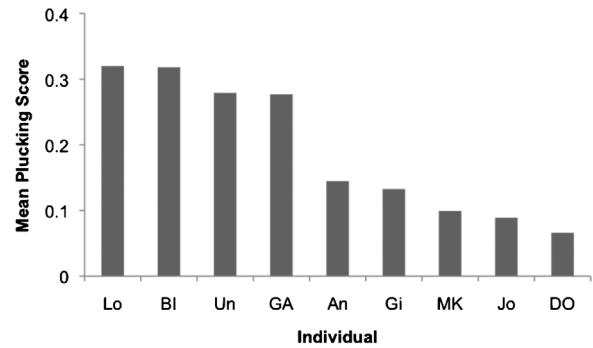


Fig. 1. Daily mean plucking score for the nine individuals who hair plucked. Listed in descending order.

$P = 0.0710$). For bouts that involved plucking, 64.2% were social grooming bouts and 35.8% were self-directed. Hair plucking was never observed to elicit a fear or pain response from the recipient of the behavior, such as fleeing or crouching. The behavior was never observed to be self-injurious among the study individuals.

Eight individuals were never observed to pluck themselves or another individual. These individuals include all four wild-born adults (JI, La, Su, TO), both infants (El and WI), and a juvenile male and female (JE and Mr, respectively). Hair plucking was significantly different among individuals who did hair pluck ($F(8, 324) = 5.09$, $P < 0.0001$). Daily mean plucking scores per individual are illustrated in Fig. 1.

3.2. Age, sex, and dominance rank

There was no significant difference in plucking between males or females ($F(1, 371) = 0.01$, $P = 0.9275$). Hair plucking also did not differ significantly between adolescent and adult females ($F(1, 371) = 0.57$, $P = 0.4494$). Adult females mean plucking score was 0.21 (SE = 0.03), while adolescent females mean score was 0.18 (SE = 0.03). However, plucking scores were significantly different in adolescent and adults males; adolescents plucked more often than adults ($F(1, 371) = 20.56$, $P < 0.0001$). Adult males mean plucking score was 0.08 (SE = 0.02) and adolescent males mean score was 0.30 (SE = 0.04). Social plucking was not influenced by dominance rank, however, the two individuals with the highest percentage of grooming bouts that involved self-directed plucking were the dominant male, BI (54%), and dominant female, Un (57%).

3.3. Habitat

Overall, mean grooming scores per individual per hour were significantly different between the indoor and outdoor habitats ($F(1, 12) = 31.09$, $P < 0.0001$). Bonobos groomed more often when housed indoors. Plucking was also observed to occur more frequently when bonobos were housed indoors ($F(1, 8) = 6.64$, $P = 0.0328$). The mean plucking score when housed indoors was 0.31 (SE = 0.05) and 0.20 (SE = 0.06) when housed outdoors.

While the number of zoo visitors present at the bonobo habitats did fluctuate throughout the day (peaking around the afternoon), each day of observation could be generalized as low, medium, or heavily trafficked. The amount of zoo visitors present did not impact plucking scores ($F(2, 344) = 0.40$, $P = 0.6703$).

3.4. Party size and composition

Party size may influence hair plucking. Parties ranged between two and seven individuals (excluding dependent infants) over the course of the study period. The analysis for individuals and party size yielded a statistically significant interaction term ($F(4$,

308) = 1.67, $P=0.0189$). This indicates that party size does not affect plucking behavior in all individual bonobos, only some. The overall mean plucking scores, with respect to party size, exhibit a slight bimodal distribution; scores were approximately 5% higher in party sizes of 2, 3, 6, and 7 across all individuals. Social composition appears to effect hair plucking. When the dominant male was present in a party, plucking occurred significantly more frequently in two adolescents, GA and Lo, and one adult female, Un ($F(6, 100) = 3.36, P=0.0047$). Gander's mean score increased by 0.15 and the scores of both females increased by approximately 0.05. The presence of the dominant female also significantly increased the mean plucking score by approximately 0.05 in several individuals: An, BI, GA, Lo, and MK ($F(7, 103) = 3.02, P=0.0063$).

3.5. Undesirable behavior

Of the undesirable behaviors listed by Birkett and Newton-Fisher (2011), only eight were present in this colony: display to human, drink urine, eat feces, eat feces of another, pluck hair, pluck hair of other, spit, and twirl. When hair plucking is excluded, the remaining undesirable behaviors were exhibited rarely; fewer than 30 total behaviors across all individuals were recorded during 128 h of observation. The majority of these behaviors (approximately 80%) were coprophagy and urophagy.

4. Discussion

We found that hair plucking was present in this colony and was not uniformly distributed. The behavior is prevalent, occurring during approximately 21% of all grooming bouts. In the large sample of gorillas, $N=240$, reported by Less et al. (2013) only 35 individuals, or 15%, were rated as hair pluckers and this was principally self-directed. In our much smaller sample of bonobos, $N=17$, nine of the subjects, or 53%, engaged in plucking. It occurred in bouts of both social and self-grooming; for social grooming it occurred in excess of 50% of all bouts for one individual (BI) and at almost 9% for the individual who did the least social plucking (DO). We need comparative data from other zoos that house bonobos to better ascertain the prevalence of this behavior in the captive population.

Wild-born individuals (JI, La, Su, TO) were never observed to hair pluck and were rarely the recipients of plucking behavior. These wild-born individuals are housed with other bonobos who frequently hair pluck and thus have observed the behavior. This result supports the suggestion that early exposure and observation of hair plucking, or the lack thereof, influences the development of the behavior. Less et al. (2013) found that early familiarity with the behavior correlated significantly with hair plucking as an adult while relatedness did not. They suggest the behavior is learned rather than inherited. In humans, Azrin and Nunn (1973) also hypothesized that trichotillomania is largely a learned behavior. However, Duke et al.'s (2010) review paper suggests there may be a genetically based susceptibility to learning the behavior. The absence of observed plucking in wild-born individuals in this colony suggests that early exposure to this behavior pattern strongly influences the incidence of hair plucking in captive primates. Although no hair plucking was observed in any wild-born individual during the course of this study, one of the wild-born adult males, TO, is reported by zoo staff to have plucked his own hair in the past (A. Meinelt, personal communication).

While hair plucking was not significantly different between sexes, adolescent males plucked more frequently than adult males. Our findings are similar to those of Reinhardt et al. (1986); adolescent rhesus macaques plucked significantly more frequently than adults. Reinhardt et al. (1986) speculate that the decreased frequency of the behavior in adult animals is explained by adjusting

to a stressful environment. They argue that as adolescents, animals exposed to a stressful environment will hair pluck; as adults they have adjusted to the environment and thus exhibit decreased frequencies of plucking. While this may explain the difference in subadult and adult males, it does not explain the lack of difference in plucking scores exhibited by subadult and adult females.

Studies of grooming in captive bonobos have illustrated that dominance rank significantly influences social grooming with lower ranking individuals dedicating more time to grooming higher ranking individuals than vice-versa (Vervaecke et al., 2000). The two lowest ranking adult females (La, Su) were never observed to groom the highest ranking female, Un. The second ranked female, An, groomed Un less frequently than the lower ranking females. This result contrasts with the findings of Reinhardt et al. (1986); in their study rank strongly influenced hair pulling in captive rhesus macaques with 95% of hair pulling directed down the dominance hierarchy. While grooming was not frequent between adult females, this has been observed in other captive bonobo populations (Stevens et al., 2006). While it is possible dominance rank may influence hair plucking, our results do not support a relationship between social hair plucking and dominance. This study highlights a fundamental difference between macaque hair pulling and bonobo hair plucking: hair pulling is an agonistic behavior that is largely directed toward subordinate individuals while hair plucking is not aggressive and is independent of the dominance hierarchy.

Self-directed plucking however, was strongly influenced by dominance. The dominant male and female, BI and Un, respectively, exhibited the highest frequencies of self-directed plucking. As a dominant individual, there is a potential risk of losing the role of alpha male or female. Lower ranking individuals by definition do not experience this pressure although other 'costs' of low rank are a potential source of stress (Sapolsky, 2005). Given our results, social stress associated with high rank may be implicated as a driving force for self-directed hair plucking. High frequencies of plucking in dominant individuals in other bonobo colonies, or other primates, would support this hypothesis.

Both grooming and hair plucking occurred more frequently when individuals were housed inside rather than outside. These increased rates may be explained by proximity; individuals have greater ability to disperse when exhibited outside. The presence of different levels of zoo visitor traffic did not impact the prevalence of hair plucking. While additional data could better explain this phenomenon, it is likely that hair plucking is not a response to stress caused by the presence of zoo visitors. One aspect of this study that warrants further investigation is the possibility of hair plucking as a seasonal behavior. As the study was conducted during the summer, plucking may vary during the rest of the year. Additionally, this warrants investigation in other captive populations of bonobos.

The management style of the Columbus Zoo allows for various parties of different size and composition. While size does not appear to impact plucking, group composition may influence the frequency of the behavior. The presence of either dominant individual resulted in higher plucking frequencies in several individuals, most notably the adolescents.

Hair plucking in captive apes often coincides with other undesirable behaviors (Birkett and Newton-Fisher, 2011; Less et al., 2013). The low frequency of undesirable behaviors in this colony outside of hair plucking is unusual compared to the co-occurrence of other undesirable behaviors that are observed along with hair plucking in other captive ape populations (Birkett and Newton-Fisher, 2011; Less et al., 2013).

Plucking behavior in captive bonobos does not appear to result in any immediate deleterious physiological or health consequences although no studies have directly scrutinized the potential

ill health effects of this behavior. The only notable phenotypic effect is alopecia that results from excessive plucking. However, hair is essential to maintaining homeothermy in mammals, and thus is important for primate health and well being. Ideally captive primates are exhibited with attention to ambient temperature and their health is monitored regularly; however, we suggest the resulting alopecia from hair plucking may pose a challenge to homeothermy. Additionally, alopecia may also pose a risk to newborn infants who use hair as a “grasping substrate.” Skin may prove more difficult to grasp than hair and thus the ability of an infant to hold onto its mother may be compromised by alopecia, thus increasing the risk of injury from falling.

The impact of plucking on an ape’s appearance and the response of zoo visitors is a separate but related issue. Visitors may reach erroneous conclusions about the primate’s health, and this in turn may impact their perception of animal care and ape well being. Qualitative comments from zoo visitors highlight concerns about the health status of several individuals who had significant hair loss from plucking.

Efforts to treat this behavior pharmacologically in gorillas have had varied results (see Less et al., 2013). Hill (2004) and Pizzutto (2007) found that increased foraging opportunities and time spent with keepers appeared to reduce the frequency of hair plucking in captive gorillas. While these studies demonstrate the ability to decrease the frequency of hair plucking in captive apes, it appears that the behavior is extremely difficult to eradicate; no studies to date have documented the elimination of the behavior in any captive primate population. Further studies are needed to ascertain the etiology and health effects of this behavior. The widespread presence of hair plucking not only in captive bonobo populations, but captive primate populations in general, warrants further investigation of the behavior.

Conflict of interest statement

The authors declare that there are no conflicts of interest.

Acknowledgements

We thank the Columbus Zoo and Aquarium Congo Expedition staff, especially Assistant Curator Audra Meinelt, for their insight and support of this project. We extend deep gratitude to Frances White for help with the statistical analyses of the data. We would also like to thank the journal editors, two anonymous reviewers, and Alexander Weiss who provided many helpful comments and insightful suggestions that greatly improved this manuscript. Funding for this study was provided by the Rebecca Jeanne Andrew Memorial Award and the College of Arts and Science Dean’s Scholar Award, Miami University.

References

- Altmann, J., 1974. Observational study of behavior: sampling methods. *Behavior* 49, 227–267.
- American Psychiatric Association, 2013. *Diagnostic and Statistical Manual of Mental Disorders*, fifth ed. American Psychiatric Association, Washington, DC, USA.
- Azrin, N., Nunn, R., 1973. Habit reversal: a method of eliminating nervous habits and tics. *Behav. Res. Ther.* 11, 619–628.
- Bayne, K., 1996. Normal and abnormal behaviors of laboratory animals: what do they mean? *Lab Anim.* 25, 21–24.
- Bernstein, J.A., Didier, P.J., 2009. Nonhuman primate dermatology: a literature review. *Vet Dermatol.* 20, 145–156.
- Birkett, L.P., Newton-Fisher, N.E., 2011. How abnormal is the behaviour of captive, zoo-living chimpanzees? *PLoS ONE* 6 (6), e20101, <http://dx.doi.org/10.1371/journal.pone.0020101>
- Boose, K.J., White, F.J., Meinelt, A., 2013. Sex differences in tool use acquisition in bonobos (*Pan paniscus*). *Am. J. Primatol.* 75, 917–926.
- Buxbaum, E., 1960. Hair pulling and fetishism. *Psychoanal. Study Child* 15, 243–260.
- Christenson, G.A., Mansueto, C.S., 1999. Trichotillomania: descriptive characteristics and phenomenology. In: Stein, D.J., Christenson, G.A., Hollander, E. (Eds.), *Trichotillomania*. American Psychiatric Press, Washington, DC, pp. 1–41.
- Duke, D.C., Keeley, M.L., Geffken, G.R., Storch, E.A., 2010. Trichotillomania: a current review. *Clin. Psychol. Rev.* 30, 181–193.
- Edwards, S.D., Snowdon, C.T., 1980. Social behavior of captive, group-living orangutans. *Int. J. Primatol.* 1, 39–62.
- Erwin, J., Deni, R., 1979. Strangers in a strange land: abnormal behaviors or abnormal environments? In: Erwin, J., Maple, T.L., Mitchell, G. (Eds.), *Captivity and Behavior*. Van Nostrand Reinhold Co, New York, NY, USA, pp. 1–28.
- Ferdowsian, H.R., Durham, D.L., Johnson, C.M., Brüne, M., Kimwele, C., Kranendonk, G., Otali, E., Akugizibwe, T., Mulcahy, J.B., Ajarova, L., 2012. Signs of generalized anxiety and compulsive disorders in chimpanzees. *J. Vet. Behav.* 7, 353–361.
- Franz, C., 1999. Allogrooming behavior and site grooming preferences in captive bonobos (*Pan paniscus*): association with female dominance. *Int. J. Primatol.* 20, 525–546.
- Galski, T., 1983. Hair pulling (trichotillomania). *Psychoanal. Rev.* 70, 331–346.
- Goodwin, J., 1997. The application, use, and effects of training and enrichment variables with Japanese snow macaques (*Macaca fuscata*) at the Central Park Wildlife Center. In: American Zoo and Aquarium Association (AZA) Regional Conference Proceedings, pp. 510–515.
- Hill, S.P., 2004. Reduction of abnormal behaviour in two captive western lowland gorillas (*Gorilla gorilla gorilla*). *Zoo Res. News* 5, 2–3.
- Honess, P.E., Gimpel, J.L., Wolfensohn, S.E., Mason, G.J., 2005. Alopecia scoring: the quantitative assessment of hair loss in captive macaques. *Altern. Lab. Anim.* 33, 193–206.
- Hosey, G.R., Skyner, L.J., 2007. Self-injurious behavior in zoo primates. *Int. J. Primatol.* 28, 1431–1437.
- Kano, T., 1992. *The Last Ape: Pygmy Chimpanzee Behavior and Ecology*. Stanford University Press, Stanford, pp. 91–248.
- Kroeker, R., Bellanca, R.U., Lee, G.H., Thom, J.P., Worlein, J.M., 2014. Alopecia in three macaque species housed in a laboratory environment. *Am. J. Primatol.* 76, 325–334.
- Less, E.H., Kuhar, C.W., Lukas, K.E., 2013. Assessing the prevalence and characteristics of hair-plucking behaviour in captive western lowland gorillas (*Gorilla gorilla gorilla*). *Anim. Welf.* 22, 175–183.
- Mason, G., 2006. Stereotypic behaviour in captive animals: fundamentals and implications for welfare and beyond. In: Mason, G., Rushen, J. (Eds.), *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare*. Cromwell Press, Trowbridge, pp. 342–343.
- McKenna, J.J., 1978. Biosocial functions of grooming behavior among the common Indian langur monkey (*Presbytis entellus*). *Am. J. Phys. Anthropol.* 48, 503–509.
- Miller, L.J., Tobey, J.R., 2012. Regurgitation and reingestion in bonobos (*Pan paniscus*): Relationships between abnormal and social behavior. *Appl. Anim. Behav. Sci.* 141, 65–70.
- Nash, L.T., Fritz, J., Alford, P.A., Brent, L., 1999. Variables influencing the origins of diverse abnormal behaviors in a large sample of captive chimpanzees (*Pan troglodytes*). *Am. J. Primatol.* 48, 15–29.
- Novak, M.A., Suomi, S.J., 1988. Psychological well-being of primates in captivity. *Am. Psychol.* 43, 765–773.
- Pizzutto, C., 2007. Reduction of abnormal behavior in a gorilla (*Gorilla gorilla gorilla*) through social interaction with human beings. *Lab. Primate Newsl.* 46, 6–10.
- Reinhardt, V., 2005. Hair pulling: a review. *Lab. Anim.* 39, 361–369.
- Reinhardt, V., Reinhardt, A., Houser, D., 1986. Hair pulling and eating in captive rhesus monkey troops. *Folia Primatol.* 47, 158–164.
- Sapolsky, R.M., 2005. The influence of social hierarchy on primate health. *Science* 308, 648–652.
- Sokal, R.R., Rohlf, F.J., 2012. *Biometry: The Principles and Practice of Statistics in Biological Research*. W.H. Freeman and Co., New York, NY, pp. 937.
- Stevens, J.M.G., Vervaecke, H., De Vries, H., Van Elsacker, L., 2006. Social structures in *Pan paniscus*: testing the female-bonding hypothesis. *Primates* 47, 210–217.
- Tustin, G.W., Williams, L.E., Brady, A.G., 1996. Rotational use of a recreational cage for the environmental enrichment of Japanese macaques (*Macaca fuscata*). *Lab. Primate Newsl.* 35, 5–7.
- Vervaecke, H., De Vries, H., Van Elsacker, L., 2000. The pivotal role of rank in grooming and support behavior in a captive group of bonobos (*Pan paniscus*). *Behaviour* 137, 1463–1485.
- Zucker, E.L., Mitchell, G., Maple, T., 1978. Adult male-offspring interactions within a captive group of orang-utans (*Pongo pygmaeus*). *Primates* 19, 379–384.