



Social hair plucking is a grooming convention in a group of captive bonobos (*Pan paniscus*)

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Abstract

Hair plucking is observed in many captive primate species and is often characterized as an abnormal behavior. However, this behavior may be both self-directed and social and may have different etiologies. Early research in captive macaques (*Macaca mulatta*) described the aggressive nature of social hair plucking while more recent observations did not find an association with aggression or grooming, but the behavior was initiated most frequently by individuals with more secure dominance rank. Here, we investigate patterns of social hair plucking in a group of captive bonobos at the Columbus Zoo. We tested the hypothesis that social plucking reflects the dominance hierarchy by examining the association between social plucking and grooming, dominance, and kinship. We collected 128 h of grooming data on 16 captive bonobos using all-occurrence sampling. We ran three Mantel tests between a directed grooming matrix and (1) a plucking matrix, (2) a matrix reflecting dominance, and (3) matrix of relatedness. Grooming and hair plucking were significantly correlated ($r=0.25$, $p<0.01$), however, there was no association between plucking and dominance ($r=-0.04$, $p=0.67$), or plucking and relatedness ($r=0.07$, $p=0.24$). These results support the hypothesis that social plucking in bonobos is a grooming convention and is unrelated to dominance.

Keywords Bonobo · *Pan paniscus* · Hair plucking · Grooming · Abnormal behavior · Social transmission

Introduction

Hair plucking is observed in many captive primate species and may be self-directed or social (Hosey and Skyner 2007; Reinhardt 2005). When self-directed, the behavior is often characterized as abnormal (Lutz et al. 2013, Reinhardt 2005). Early research in captive rhesus macaques (*Macaca mulatta*) described the aggressive nature of social hair plucking, referred to as *social hair pulling* in Reinhardt et al.'s 1986 publication. These interactions were frequently directed down the dominance hierarchy and resulted in fear

responses from the recipients, thus suggesting that the function of the behavior was related to dominance. However, a more recent study on the same species at a different institution did not find an association between social hair pulling and aggression, yet this behavioral pattern was more frequently initiated by individuals with a more stable dominance rank (higher average dominance probability, ADP) (Heagerty et al. 2017). The same authors also noted that the behavior was distinct from grooming (Heagerty et al. 2017). These studies highlight a behavioral continuum for social hair plucking in this species. Overall, this pattern is related to dominance (albeit more complexly in Heagerty et al. 2017) in rhesus macaques and appears to be independent of grooming.

In addition to rhesus macaques, this behavior has also been well characterized in captive bonobos (Brand and Marchant 2015, 2018; Brand et al. 2016). This behavioral pattern was noted to occur predominately during grooming bouts (Brand and Marchant 2015). Recipients of social hair plucking in captive bonobos were described as lacking a fear response; they did not crouch or flinch and the

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behavior appeared to be unrelated to aggression (Brand and Marchant 2015).

The purpose of this study was to test predictions of the “dominance hypothesis” as a functional explanation for social hair plucking. First, we sought to assess whether or not social hair plucking was independent of grooming in captive bonobos, similar to the results of Heagerty et al. (2017). Even if hair plucking rarely occurs outside of grooming bouts, a different, distinct pattern of plucking may occur within grooming. We predicted that patterns of social hair plucking would mirror those found in rhesus macaques and would be directed down the dominance hierarchy, whereas grooming would be directed up the dominance hierarchy. Therefore, a negative relationship between these behaviors would support the “dominance hypothesis.” Second, we also investigated the relationship between social hair plucking and both dominance and kinship. While no overt aggression has been observed with this behavior in bonobos (Brand and Marchant 2015), it is still possible that the behavior is related to dominance, as in both rhesus macaque studies (Heagerty et al. 2017; Reinhardt et al. 1986), and associated with relatedness, as predicted by kin selection theory (Hamilton 1964; Kurland 1980). Thus, we expected an association between social hair plucking and both dominance and kinship such that social hair plucking would be directed toward subordinates and non-kin.

Methods

We collected 128 h of grooming data on 16 captive bonobos (Table 1) at the Columbus Zoo and Aquarium, Columbus, OH, between May and August 2012 using all-occurrence sampling (Altmann 1974). Data were collected using all-occurrence sampling in 15-min samples between 9:00 and 19:00. Hair plucking was recorded during grooming bouts using one-zero sampling (Altmann 1974). 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 at least 30 s of inactivity (Franz 1999). Social grooming bouts were recorded as unidirectional states such that if individual B started grooming individual A while A was grooming B a new bout was recorded. As hair plucking that occurred outside of grooming was so rare, these instances were recorded ad libitum (Franz 1999). We constructed directed dyadic matrices for (1) the rate of grooming bouts and (2) the rate of grooming bouts that involved hair plucking. These rates were weighted by the amount of time (hours) each dyad was observed to be in the same party. This group of bonobos is managed using fission–fusion to emulate their natural social structure (Boose et al. 2013), thus resulting in slight differences in individual/dyad observation time. Two to three parties are created and usually last 2–3 days before new parties are formed (Boose et al. 2013). Parties can consist of possible combinations of individuals, except for one male–male

Table 1 Study subjects

Sex	Age (years)	ID	Rank ^a	Relatives ^b
Female	30	LA	7	JT (d)
Female	30	SU	5	DO (so), JE (gs), LO (d), MR (d), WI (gs)
Female	20	AN	2	BI (so), GI (d), WI (so)
Female	19	UN	1	GA (so), JE (so)
Female	10	JT	4	LA (m)
Female	8	LO		DO (hb), JE (hn), MR (hs), SU (m), TO (f), WI (hn)
Female	6	GI		AN (m), BI (b), WI (hb)
Female	2	MR		DO (b), JE (ha), JI (f), LO (hs), SU (m), WI (ha)
Male	33	JI	9	DO (so), JE (gs), MR (d), WI (gs)
Male	33	TO	10	LO (d)
Male	28	MA	8	
Male	19	DO	3	JE (so), JI (f), LO (hs), MR (si), SU (m), WI (so)
Male	11	BI	6	AN (m), GI (si), WI (hb)
Male	9	GA		UN (m), JE (b)
Male	4	JE		DO (f), GA (b), JI (gf), LO (ha), MR (a), SU (gm), UN (m), WI (hb)
Male	1	WI		AN (m), BI (hb), DO (f), GI (hs), JE (hb), LO (ha), MR (ha), SU (gm)

^aDerived from decided dominance interactions

^bRelative codes: *a* aunt, *b* brother, *d* daughter, *f* father, *gf* grandfather, *gm* grandmother, *gs* grandson, *ha* half-aunt, *hb* half-brother, *hn* half-nephew, *hs* half-sister, *m* mother, *si* sister, *so* son

dyad that is not grouped together because of previous conflict (Boose et al. 2013).

We ran a series of Mantel tests, using the Spearman method and 999 iterations, to examine the association between our predictors. We correlated our plucking matrix with (1) the grooming matrix, (2) a matrix of expected relatedness coefficients for each dyad, and (3) a 0/1 matrix reflecting whether or not an individual was dominant to the other. These matrices are provided in Supplement 1. We were provided with relatedness data, including paternity, which is determined in all infants by genetic analysis (A. Meinelt, pers. comm.). Dominance rank was determined for all adults (age > 10 years) using decided agonistic interactions collected during the same observation period reported in this manuscript. Data analyses were conducted in R (R Core Team 2015) using the package *vegan* (Oksanen et al. 2019) and social networks were visualized with *igraph* (Csardi and Nepusz 2006).

Results

We recorded four hair plucking events outside of grooming bouts on two separate dates: three of which were self-directed and one was social. Grooming and hair plucking distributions were significantly correlated ($r=0.25$, $p < 0.01$) (Fig. 1); however, there was no association between plucking and dominance ($r = -0.04$, $p = 0.67$) or plucking and relatedness ($r=0.07$, $p = 0.24$). We also visually checked for an interaction between dominance and relatedness, as aggression is likely to be directed toward subordinate non-kin and found no such no pattern (Fig. 2).

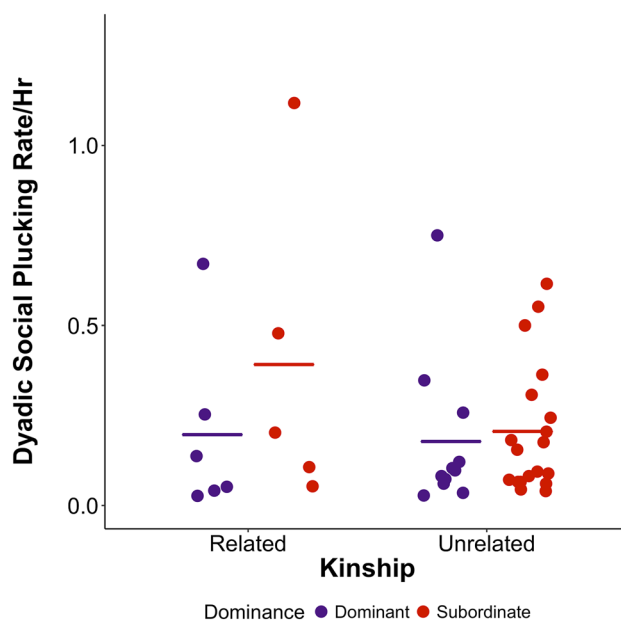
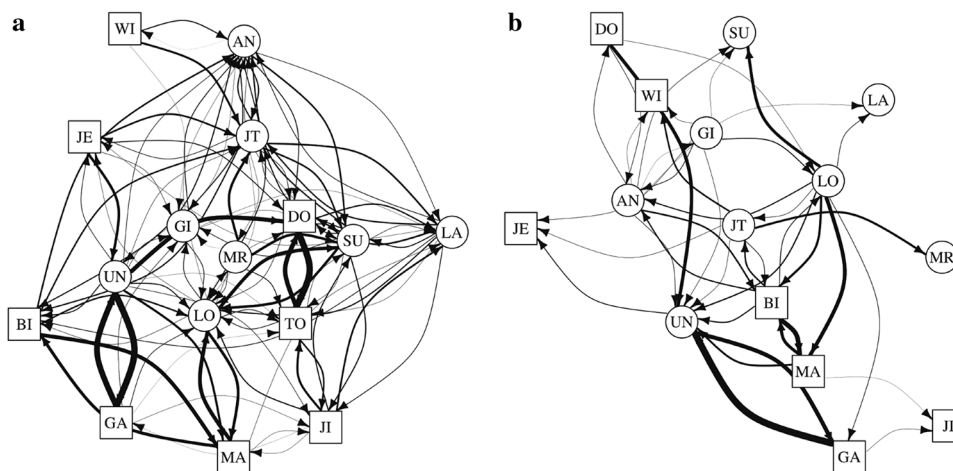


Fig. 2 Rates of social grooming bouts with hair plucking per observation hour by dominance and kinship. Horizontal bars represent means

Discussion

Contrary to our predictions from social hair plucking in rhesus macaques, we found that this behavior in a group of captive bonobos was significantly correlated with grooming and unrelated to dominance or kinship. These data suggest a different patterning of social hair plucking in bonobos compared to rhesus macaques. Unlike the rhesus macaques in Heagerty et al. (2017), bonobo social hair plucking is embedded in grooming. Further, the dominance component from both rhesus macaque studies, measured by absolute rank (Reinhardt et al. 1986) and ADP (Heagerty et al. 2017), is absent in this group of bonobos. We note that grooming

Fig. 1 Directed social networks for grooming (a) and hair plucking (b). Nodes are labeled with individual IDs and shape indicates sex (female = circle, male = square). Edge weight represents the rate of grooming bouts per observation hour or the rate of grooming bouts that involved hair plucking per observation hour



was not correlated with dominance; however, this is consistent with reports of other captive bonobos groups (Franz 1999, but see Vervaecke et al. 2000).

These results do not support the “dominance hypothesis” as an explanation for the function of this behavior in this group of bonobos. Further, Brand et al. (2016) found that social hair plucking in this group was unrelated to urinary cortisol, indicating that stress is also an unlikely explanation. Our finding from the present study that social hair plucking is a grooming convention in this taxon lends support to another hypothesis: the social transmission hypothesis (e.g., Hopper et al. 2016; Nash et al. 1999). The literature on grooming conventions in both captive and wild chimpanzees is linked to chimpanzee cultural patterns, e.g., the grooming hand clasp (McGrew and Tutin 1978; McGrew et al. 2001; Nakamura 2002; de Waal and Seres 1997) and social scratch (Nakamura et al. 2000). The social transmission hypothesis posits that particular behavioral patterns have multiple etiologies and that the occurrence of the behavior in some individuals is the result of observation of a conspecific. We speculate that this hypothesis may explain the occurrence of social hair plucking in many captive bonobos. This idea is further buttressed by the observation that the occurrence of other abnormal behaviors is not a good predictor of bonobo social hair plucking (Brand and Marchant 2018). However, given the rarity of these events, clear support for this hypothesis usually draws from single reports either in nature or captive conditions [e.g., social transmission of ant fishing in chimpanzees (O’Malley et al. 2012)]. In this report, we suggest the source of this behavior pattern is traceable to a single bonobo. The individual, an adult female, was known to hair pluck before being transferred to this zoo. Following her integration into the bonobo group, zoo personnel observed social hair plucking in other individuals lending further support for this hypothesis (A. Meinelt, pers. comm.). Social transmission is also believed to have resulted in the propagation of regurgitation and reingestion (R&R) among captive bonobos at a zoo in Belgium (Stevens and Wind 2011).

The social transmission hypothesis calls into question the reliability or usefulness of certain behavioral patterns, including hair plucking, as a defining or diagnostic measure of individual welfare (Hopper et al. 2016). Nonetheless, we acknowledge that this interpretation does not completely rule out welfare concerns. For example, the amount of *self*-directed plucking was positively related to cortisol levels in female bonobos (Brand et al. 2016). The prospect that certain behaviors are the result of social transmission prompts the question of how these patterns can be mitigated as this is often the goal from an animal management perspective. Attempts to reduce hair plucking in captive apes have yielded inconsistent results (reviewed in Brand and Marchant 2015; Brand et al. 2016). It is possible that socially transmitted patterns may be more difficult to mitigate or

eliminate; however, the question has yet to be thoroughly explored. When resources allow, we strongly encourage zoos and other facilities that house captive primates, especially apes, to collect systematic behavioral data in the weeks before an individual (or individuals) is (are) introduced to a social group and in the weeks following the completion of this introduction process. These data will provide valuable empirical insight into the social transmission of behavioral patterns in primates.

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