Body Site and Body Orientation Preferences during Social Grooming: A Comparison between Wild and Captive Chimpanzees and Bonobos

Morgane Allanic^a Misato Hayashi^{a, b} Takeshi Furuichi^a Tetsuro Matsuzawa^c

^aPrimate Research Institute, Kyoto University, Inuyama, Japan; ^bJapan Monkey Centre, Inuyama, Japan;

^cKyoto University Institute for Advanced Study, Kyoto, Japan

Keywords

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Abstract

Grooming site preferences have been relatively well studied in monkey species in order to investigate the function of social grooming. They are not only influenced by the amount of ectoparasites, but also by different social variables such as the dominance rank between individuals or their levels of affiliation. However, studies on this topic mainly come from monkey species, with almost no report on great apes. This study aimed to explore whether body site and body orientation preferences during social grooming show species-specific differences (bonobos vs. chimpanzees) and environment-specific differences (captivity vs. wild). Results showed that bonobos groomed the head, the front and faced each other more often than chimpanzees, while chimpanzees groomed the back, anogenitals and more frequently in face-to-back positions. Moreover, captive individuals were found to groom facing one another more often than wild ones, whereas wild individuals groomed the back and in face-to-back positions more. While future studies should expand their scope to include more populations per condition, our

preliminary 2 by 2 comparison study highlights the influence of (i) species-specific social differences such as social tolerance, social attention and facial communication, and (ii) socioenvironmental constraints such as risk of predation, spatial crowding and levels of hygiene, that might be the two important factors determining the grooming patterns in two *Pan* species.

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Introduction

Social grooming is the most prominent social behavior, occupying up to 20% of the daily time budget, in nonhuman primates [Dunbar, 1991; Lehmann et al., 2007]. It is suggested to have both hygienic and social bonding functions [Russell, 2018]. While it has a functional role in skin care and ectoparasite removal [Tanaka and Takefushi, 1993; Zamma, 2002; Akinyi et al., 2013], it also promotes group cohesion [Cheney, 1992; Borries et al., 1994], maintains and strengthens affiliative relationships [Seyfarth, 1980; Seyfarth and Cheney, 1984] and reduces tension and aggression between individuals [Terry, 1970; Schino et al., 1988; Russell and Phelps, 2013]. Moreover, grooming with bond partners produc-

es a greater increase in oxytocin levels – which is a social bonding hormone – compared to nonbond partners or after no grooming [Crockford et al., 2013].

Body site preferences have been relatively well studied in monkey species in order to investigate the function of social grooming. Studies have found that the distributions of body sites for social grooming and self-grooming differ and are complementary in several nonhuman primate species: animals direct more social grooming to body sites that are inaccessible to self-grooming [Hutchins and Barash, 1976; Barton, 1985; Borries, 1992; Reichard and Sommer, 1994; Franz, 1999]. Body site preferences were found to be correlated with the distribution of louse eggs in Japanese macaques (*Macaca fuscata*), with individuals receiving more grooming on body sites where the louse eggs were the most abundant [Zamma, 2002]. Interestingly, in wild baboons and langurs, solitary males were found to be heavily infested with ectoparasites compared to their socially living conspecifics [Washburn and DeVore, 1961; Curtin, 1975], and in these solitary males the highest concentration of ectoparasites was found on body sites that were inaccessible to self-grooming [Curtin, 1975].

Grooming site preference is not only influenced by the amount of ectoparasites, but also by different social variables such as the dominance rank between individuals or their levels of affiliation and social tolerance. For example, in monkey species, low-ranking groomees tend to expose body sites which are relatively less vulnerable [e.g., back and tail, Boccia et al., 1982; Borries, 1992], while frequent grooming partners (e.g., individuals with strong social bonds) prefer to groom the more vulnerable face [Moser et al., 1991]. Moreover, when grooming occurs following a tense situation, such as an attack or when there were signs of tension, individuals performed more face-to-back grooming [McKenna, 1978; Barton, 1983]. Finally, comparisons between closely related species showed that the more despotic pigtail macaques (*M. nemestrina*) groomed the back areas more, while more tolerant bonnet macaques (*M. radiata*) groomed in face-to-face positions [Boccia, 1989]. It is generally suggested that groomees expose relatively invulnerable sites of their body (e.g., back and tail) in order to protect the more vulnerable parts (e.g., face and front) and to avoid eye contact with potentially risky partners, thus reducing the chance of receiving harmful aggression [Boccia et al., 1982; Moser et al., 1991; Borries, 1992].

With the exception of one study in captive bonobos [Franz, 1999] and one in wild bonobos [Allanic et al., 2020a], there has been no study examining body site pref-

erences in great apes. The recent study showed that, in wild bonobos, the strength of social bond, measured through grooming frequency and composition of the dyad (intragroup dyads vs. intergroup dyads), did not influence body site preferences, contrasting with monkey species [Allanic et al., 2020a]. The generally nonaggressive nature of wild bonobos might explain why dyads with low levels of affiliation do not need to be cautious by presenting relatively invulnerable sites of their body. However, the relationship between levels of social tolerance and the selection of body sites and body orientation still need to be determined. In captivity, bonobos were found to focus their grooming on the face of their partner [25% with head: Jordan, 1977; 29% without head: Franz, 1999]. Moreover, de Waal [1988] mentioned that captive bonobos seem to be grooming the face more than chimpanzees but direct comparisons are however lacking.

Bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) can be good comparative models to study. Even though they are sister species, they show distinct differences in their levels of social tolerance, facial communication and social attention. Bonobos are often considered to be more socially tolerant than chimpanzees due to their high rates of adult play [Palagi, 2006], less distinct territorial ranges [Hashimoto et al., 1998; Furuichi, 2011; Sakamaki et al., 2018] and the fact that lethal aggression and infanticide have never been reported [Wilson et al., 2014]. Moreover, unlike chimpanzees, bonobos frequently engage in face-to-face sexual interactions between all age-sex combinations [de Waal, 1988; Kano, 1992]. Finally, eye-tracking experiments have revealed differences in social attention within the *Pan* genus: bonobos make more eye contact and focus more on the eyes and face, while chimpanzees focus more on the anogenital region and target objects [Kano et al., 2015]. It is therefore reasonable to presume that these differences could be reflected in their patterns of social grooming.

In addition to species comparisons, it is also important to consider comparisons with and between different environments, as the latter has been found to influence social grooming. For example, a higher frequency is generally found in captive individuals compared to those in the wild, which is suggested to serve as a coping mechanism to reduce tensions created by crowding [Nieuwenhuijsen and de Waal, 1982; de Waal, 1989; Bercovitch and Lebrón, 1991; Novak et al., 1992; Dyck et al., 2003]. Moreover, captive and wild environments differ in their levels of constraints. For example, in contrast to captivity, risks of predation are present in the wild, which may lead wild individuals to spend more time being vigilant than cap-

tive ones. Competition for resources (food and mates) is also expected to be higher for wild individuals, while captive individuals benefit from frequent food provisioning and are often limited in their mate choice and mating strategies due to group composition and physical constraints. Levels of hygiene might also differ between captive and wild conditions as captive environments are regularly kept clean and dry by humans. Furthermore, in the wild, both *Pan* species frequently engage in intergroup encounters and group hunting [Goodall, 1986; Wrangham, 1999; Watts and Mitani, 2002; Surbeck and Hohmann, 2008; Sakamaki et al., 2018]. All these activities are collaborative and play an important role in the maintenance of social bonds between individuals of the same group but cannot be performed in captive settings. Comparisons between captive and wild environments can thus shed light onto how individuals reinforce and maintain their social bonds through social grooming when facing different socioenvironmental constraints.

Direct comparisons of social grooming between *Pan* species are scarce. Here, we present the first direct comparison of social grooming between chimpanzees and bonobos living in both captive and wild conditions. Specifically, this study was designed to examine whether their body site and body orientation preferences during social grooming show species-specific and environment-specific differences. Our hypotheses are twofold: one is the species difference hypothesis in which bonobos should socially groom in face-to-face position and groom the face and frontal areas more than chimpanzees due to their difference in social attention (i.e., bonobos make more eye contact than chimpanzees); another is the environmental constraints hypothesis in which wild ones should have the preference to the backside for removing external parasites in the face-to-back position. Our aim is that this preliminary study with a 2 by 2 comparison may shed light onto the social grooming of the two *Pan* species.

Materials and Methods

Study Sites

We observed captive bonobos and chimpanzees at Kumamoto Sanctuary of the Kyoto University Wildlife Research Center [Uki, Japan; Morimura et al., 2011; Matsuzawa, 2020]. Captive bonobos were housed in two outdoor enclosures (93 m² – 4 m high and 95 m² – 4 m high) covered by iron mesh fences (wall and roof) and connected to a total of 6 indoor rooms (125 m² in total – 4 m high) where individuals spent their nights. Captive chimpanzees were housed in an outdoor open enclosure area (270 m²) from 09:00 to 17:00, connected to 7 indoor rooms (67 m² in total – 4 m high) where individuals spent their nights. All enclosures provided an

enriched environment with many wooden platforms, climbing structures, food devices and hammocks. Additionally, a 13-m-high climbing frame, numerous trees and grass-covered terrain enriched the chimpanzee outdoor enclosure. Subjects were fed 3 times a day with industrial pellets and fresh seasonal fruits and vegetables, on top of which they received dietary enrichment throughout the day. Water was available ad libitum. We observed wild bonobos in Wamba, Luo Scientific Reserve, Democratic Republic of Congo, whose habitat was composed of primary forest, old and young secondary forests, swamp forests, cultivated lands and small residential areas used by local people [Hashimoto et al., 1998; Terada et al., 2015; Furuichi, 2019]. We observed wild chimpanzees in Bossou, Nimba Mountains Biosphere Reserve, Republic of Guinea, whose habitat was composed of a mosaic of primary and secondary rain forest as well as cultivated and abandoned fields [Matsuzawa et al., 2011].

Study Subjects

Captive bonobos included 6 individuals (2 males and 4 females) living in two social groups whose composition was regularly changed to mimic their wild fission-fusion society [Kano, 1982]. Captive chimpanzees included 7 individuals (1 male and 6 females) living in one social group. Captive chimpanzees did not experience fission-fusion dynamics but had the choice to isolate themselves in the indoor rooms during the day. Wild bonobo subjects included 15 individuals (5 males and 10 females) of the PE group in Wamba. At the time of the study, the PE group consisted of 27 individuals: 15 mature (study subjects) and 12 immature individuals. Wild chimpanzee subjects included 7 individuals (2 males and 5 females) in the Bossou community. At the time of the study, the Bossou group consisted of 8 individuals: 7 mature (study subjects) and 1 immature individuals. All subjects were either adolescent or adult individuals (≥ 8 years old). We did not include younger individuals in this research to assure consistency in the comparison between populations. See Table 1 for detailed information on each subject. Captive individuals were already habituated to human presence in proximity to their enclosure, and wild individuals were fully habituated to human presence due to the maintenance of long-term research projects at each field site: habituation started in 1986 for wild bonobos at Wamba [Kano, 1982; Furuichi, 2019] and in 1976 for wild chimpanzees at Bossou [Sugiyama and Koman, 1979]. Group composition was mainly biased toward adults and females, thus we could not examine the influence of variables such as sex or age that may also impact grooming patterns. However, the use of a single observer (M.A.) and methodological protocol consistently in all four conditions enhances the comparative value of this study.

Data Collection

The raw data were collected by the single researcher, M.A., to keep the standard and constant way of comparing 2 by 2 conditions. In the captive condition, M.A. observed captive bonobos for a total of 211.71 h over 61 days from September 2015 to February 2016, and captive chimpanzees for 119.30 h over 43 days from September to December 2015 and May to June 2016. M.A. collected data in the outdoor enclosures from 09:00 to 11:30 and from 13:30 to 16:00, observing each captive group for either 2.5 h (morning or afternoon) or 5 h (morning and afternoon) per day. In the field conditions, M.A. observed wild bonobos for 558.92 h over 88 days from March to August 2017. M.A. followed the group from their

Table 1. Detailed information on the subjects at the time of the study

Species	Environment	Place	Name	Sex	Age, years	Age category
Bonobo	Captive	KS	Louise	F	43	Adult
	Captive	KS	Connie-Lenore	F	34	Adult
	Captive	KS	Lolita	F	26	Adult
	Captive	KS	Ikela	F	24	Adult
	Captive	KS	Junior	M	21	Adult
	Captive	KS	Vijay	M	12	Adolescent
	Wild	Wamba	Gai	M	44*	Adult
	Wild	Wamba	Malusu	M	35*	Adult
	Wild	Wamba	Snare	M	26*	Adult
	Wild	Wamba	Turkey	M	25*	Adult
	Wild	Wamba	Bokuta	F	54*	Adult
	Wild	Wamba	Kabo	F	45*	Adult
	Wild	Wamba	Hide	F	42*	Adult
	Wild	Wamba	Maluta	F	32*	Adult
	Wild	Wamba	Ichi	F	28*	Adult
	Wild	Wamba	Pao	F	28*	Adult
	Wild	Wamba	Saku	F	22*	Adult
	Wild	Wamba	Marie	F	16*	Adult
	Wild	Wamba	Nara	F	16*	Adult
	Wild	Wamba	Ikura	M	13*	Adolescent
	Wild	Wamba	Lucie	F	9*	Adolescent
Chimpanzee	Captive	KS	Black	M	44	Adult
	Captive	KS	Oumu	F	39	Adult
	Captive	KS	Haruna	F	37	Adult
	Captive	KS	Candy	F	33	Adult
	Captive	KS	Chiko	F	26	Adult
	Captive	KS	Yoshie	F	26	Adult
	Captive	KS	Sakura	F	24	Adult
	Wild	Bossou	Foaf	M	36	Adult
	Wild	Bossou	Jeje	M	19	Adult
	Wild	Bossou	Yo	F	50+*	Adult
	Wild	Bossou	Velu	F	50+*	Adult
	Wild	Bossou	Fana	F	40+*	Adult
	Wild	Bossou	Jire	F	40+*	Adult
	Wild	Bossou	Fanle	F	19	Adult

KS, Kumamoto Sanctuary. Estimated ages are marked with an asterisk.

morning nests to midday (up to 13:30). We did not follow the group until their night nest since their usual long-duration grooming sessions occurred before or during midday. However, field assistants followed the subjects until they made their nest site and could confirm the rarity of grooming events occurring in the late afternoon. Wild chimpanzee observations totaled 394.88 h over 58 days from September to December 2016. We left the field station at 06:00 in the morning to find the chimpanzees and followed them until they made their night nest. Since *Pan* species show fission-fusion dynamics, in the case of a group split M.A. followed the largest party throughout the observation period in both Wamba and Bossou groups.

Definition of Grooming

We defined grooming as an individual touching the hair of another individual using its hands and/or mouth (Fig. 1). We defined the following terms:

Grooming bout refers to the period one individual (A) groomed another individual (B). When a change in direction (B groomed A or A and B mutually groomed each other at the same time) occurred, we scored a new grooming bout.

Grooming session refers to the total of all grooming bouts exchanged. A grooming session was deemed to have ended when the two individuals did not groom for more than 5 min or when they changed their behavior (e.g., moving, feeding, playing and copulating).

Video Data Collection

We used video recordings of grooming in all four study locations to maximize comparability between locations as much as possible. The fully video-recorded data in all 2 by 2 conditions allowed us to repeatedly seeing and examining the grooming behavior to ascertain the reliability of the further data analysis. We recorded captive individuals continuously using two video cameras

Fig. 1. Grooming performed by the four study groups: captive bonobos in Kumamoto Sanctuary (Japan), wild bonobos in Wamba (Democratic Republic of Congo), captive chimpanzees in Kumamoto Sanctuary (Japan) and wild chimpanzees in Bossou (Guinea).

(Panasonic HC-W570M) placed at different parts of the enclosures to provide maximum coverage. Wild individuals were recorded using one video camera (Panasonic HC-W570M), and we recorded continuously during their resting activities and during periods when they were likely to groom so as not to miss the start of a grooming session. During video recording of all captive and wild subjects, we filmed the maximum number of individuals possible. Often, not all individuals were visible on camera simultaneously, thus we focused on individuals that were actively grooming when arriving on site or on those deemed most likely to groom (e.g., resting in close proximity). When a grooming session started, we focused the camera on it and zoomed in to obtain a more detailed capture. If several sessions occurred at the same time but at different places, we followed this hierarchical order for priorities: (i) sessions where the start could be recorded, (ii) sessions between not more than two individuals, and (iii) sessions between adult and/or adolescent dyads. We only included grooming sessions with the following criteria in the analyses: (i) fully recorded grooming sessions where the start and end were visible on camera to avoid missing any important data, (ii) dyadic grooming sessions to avoid a limitation in the access and selection of body sites and orientations, and (iii) grooming sessions which lasted longer than 1 min to avoid a bias towards short durations.

Video Coding

We used ELAN 5.9 software [Brugman et al., 2004; Sloetjes and Wittenburg, 2008; ELAN, 2020] to code the grooming sessions recorded on videos. M.A. recorded continuously the role of each individual: (i) “groomer” where the individual was the only one actively grooming but did not receive any, (ii) “groomee” where the individual was receiving grooming but did not give any, and (iii) “mutual” where both individuals were actively grooming each other. Although a previous study [Allanic et al., 2020b] reported the details of mutual grooming occurrence in captive *Pan* species, the present study simply treated mutual grooming to code both individuals as “groomer.” M.A. manually selected the beginning and end of each grooming bout and then assigned the role of each individual (i.e., groomer, groomee or mutual). When the role of an

Fig. 2. Illustration of the five categories of body site: “head” in blue, “front” in yellow, “anogenitals” in pink, “back” in orange and “limbs” in black.

individual was either “groomer” or “mutual,” M.A. continuously and manually recorded the body sites groomed. We coded five categories of body sites (Fig. 2): (i) “head” (including face and ears), (ii) “front” (including chest, abdomen, neck and collarbone areas), (iii) “back” (including back and shoulder blades), (iv) “anogenitals” (relatively “hairless” areas of the anal and genital regions) and (v) “limbs” (including left/right arms/hands, left/right legs/feet, underarms, and top of shoulders). M.A. also recorded body orientation continuously. We coded three categories of orientation (Fig. 3): (i) “face-to-face” where the two individuals were facing each other with shoulders parallel (from 0- to approx. 20-degree angles), (ii) “intermediate” where the two individuals did not have shoulders parallel, and (iii) “face-to-back” where the groomer was facing the back of the groomee with shoulders parallel (from 0- to approx. 20-degree angles). We extracted all duration data as a time in seconds. Then, for each grooming session, we calculated:

Proportion of time each body site was groomed by individual A corresponding to the duration one body site was groomed by

Fig. 3. Illustration of the three categories of body orientation.

Table 2. Mean $\pm$ SE percentages (converted from the data in proportions) of each body site groomed and each body orientation performed in the four conditions: wild bonobos, captive bonobos, wild chimpanzees and captive chimpanzees

	Wild bonobos	Captive bonobos	Wild chimpanzees	Captive chimpanzees
Body sites				
Head	18.8 $\pm$ 2.9	36.0 $\pm$ 4.1	8.3 $\pm$ 4.4	6.0 $\pm$ 2.1
Front	9.7 $\pm$ 1.3	8.8 $\pm$ 2.5	5.6 $\pm$ 1.7	3.7 $\pm$ 1.3
Back	26.0 $\pm$ 2.8	8.3 $\pm$ 3.6	33.3 $\pm$ 6.7	13.6 $\pm$ 4.7
Anogenitals	2.5 $\pm$ 0.4	1.0 $\pm$ 0.5	8.4 $\pm$ 3.8	22.8 $\pm$ 13.1
Limbs	42.9 $\pm$ 3.1	45.9 $\pm$ 2.8	44.4 $\pm$ 12.7	53.9 $\pm$ 9.8
Body orientations				
Face-to-face	31.0 $\pm$ 2.2	49.9 $\pm$ 7.2	15.0 $\pm$ 4.5	23.7 $\pm$ 6.1
Face-to-back	35.6 $\pm$ 2.8	27.4 $\pm$ 6.4	71.0 $\pm$ 5.4	43.7 $\pm$ 8.8
Intermediate	33.4 $\pm$ 2.6	22.7 $\pm$ 2.4	14.1 $\pm$ 4.2	32.6 $\pm$ 9.5

Data are calculated from the mean of each individual for body sites and from the mean of each dyad for body orientations.

individual A divided by the total duration individual A groomed in the session (total of A $\rightarrow$ B bouts including mutual grooming). In addition, if both individuals actively groomed in the session, we also calculated the proportion of time each body site was groomed by individual B corresponding to the duration one body site was groomed by individual B divided by the total duration individual B groomed in the session (total of B $\rightarrow$ A bouts including mutual grooming). For example, in a 2-min session (120 s) where individual A groomed the head of B for 100 s and individual B groomed the limbs of A for 20 s, we recorded a proportion of 1 for head (100/100) and 0 for the four other body sites (0/100) for groomer A, and a proportion of 1 for the limbs (20/20) and 0 for the four other body sites (0/20) for groomer B.

Proportion of time each body orientation was performed corresponding to the duration one body orientation was performed divided by the total duration the grooming session lasted (total of all grooming bouts). For example, in a 2-min session (120 s) consisting wholly of face-to-face grooming, we recorded a proportion of 1 for face-to-face (120/120), 0 for face-to-back (0/120) and 0 for intermediate orientation (0/120).

Video Coding Reliability

For reliability purposes, 20% of the video data were assigned to a novel observer, which resulted in a total of 90 videos out of 454. The novel observer coded the body sites groomed and the body orientation performed. As data were quantitative, we analyzed the intraclass correlation coefficient for interrater reliability of these variables giving 0.96 [excellent] and 0.91 [excellent], respectively.

Statistics

We constructed two generalized linear mixed-effect models to analyze whether species and environment affected the (i) body sites selected and (ii) body orientations used during social grooming. For the model on body sites (model 1), we used the proportion of time a body site was groomed as a response variable weighted by the total duration of that grooming session. We used body sites (5 levels: head, front, anogenitals, back, limbs), species (2 levels: bonobos, chimpanzees) and environment (2 levels: captivity, wild) as predictor variables with a nested structure: site/(species + environment). We used this nested structure because in a multilevel factor model it allows to directly compare the proportion of time

Fig. 4. Mean $\pm$ SE proportion of time each body site was groomed depending on the species. These data are calculated from the mean of each individual. ** $p < 0.01$, *** $p < 0.001$.

each body site was groomed between species (bonobos vs. chimpanzees) and environments (captivity vs. wild). We used groomer and groomee identities as random effects. For the model on body orientation (model 2), we used the proportion of time a body orientation was performed as a response variable weighted by the total duration of that grooming session. We used orientation (3 levels: face-to-face, face-to-back, intermediate), species and environment as predictor variables with a nested structure: orientation/(species + environment). Similarly as the previous model, the nested structure allowed to directly compare the proportion of time each body orientation was used between species and between environments. In this model, we used dyad identities as random effects. We could not include the interaction between species and environment in both models because of the complexity of the model which does not allow the models to run (i.e., too many interactions). We constructed both models with a binomial error structure as the response variables were proportional data. We ensured that all relevant model assumptions were met by visually inspecting histograms of the residuals and plots of the residuals against fitted values. We found strong overdispersion in both models due to the high number of zeros. Thus, to adjust for overdispersion, we corrected the Z and p values by adjusting the coefficient table (i.e., we multiplied the standard error by the square root of the dispersion factor, see <http://bbolker.github.io/mixed-models-misc/glmmFAQ.html>). We also checked for correlations between our predictor variables to avoid potential confounding effects of multicollinearity by calculating variance inflation factors (values less than 2 acceptable). In addition, as body site groomed is not independent of body orientation (e.g., limited access to the

back areas from a face-to-face position), we constructed the same first model (model 1) while holding body orientation constant. This was to assure that the variation in body site choice is not a feature of the variation in grooming orientation choice. We performed all tests with R 3.5.3 software [R Core Team, 2019] with level of significance set at 0.05.

As usual for nonexperimental studies, we did not collect the same number of grooming sessions per individual and per dyad. We used the raw data to run the generalized linear mixed-effect models, as the latter controlled for this matter. However, for illustration purposes and standardization, the data presented in Table 2 and Figures 4–7 were calculated from the mean of each individual for body sites and from the mean of each dyad for body orientation (individual/dyad means were calculated from the grooming sessions).

Results

We recorded a total of 138 sessions from captive bonobos (range of session duration = 1–58.7 min, mean $\pm$ SE of session duration = 14.8 ± 1.0 min), 63 from captive chimpanzees (range = 1–25.3 min, mean $\pm$ SE = 6.7 ± 0.7 min), 152 from wild bonobos (range = 1–118.2 min, mean $\pm$ SE = 17.8 ± 1.5 min) and 101 from wild chimpanzees (range = 1–50.9 min, mean $\pm$ SE = 9.3 ± 1.1 min).

Fig. 5. Mean $\pm$ SE proportion of time the body site “back” was groomed depending on the environment in which individuals live. These data are calculated from the mean of each individual. *** $p < 0.001$.

Body Sites

Captive and wild bonobos dedicated 36.0 and 18.8% of their grooming time to the head, 8.8 and 9.7% to the front, 8.3 and 26.0% to the back, 1.0 and 2.5% to the anogenitals, and 45.9 and 42.9% to the limbs, respectively. Captive and wild chimpanzees dedicated 6.0 and 8.3% of their grooming time to the head, 3.7 and 5.6% to the front, 13.6 and 33.3% to the back, 22.8 and 8.4% to the anogenitals, and 53.9 and 44.4% to the limbs, respectively (Table 2).

Bonobos directed significantly more grooming to the head ($\beta \pm SE = -1.53 \pm 0.26$, $Z = -5.95$, $p < 0.001$) and front ($\beta \pm SE = -0.85 \pm 0.28$, $Z = -3.06$, $p < 0.01$) than chimpanzees. Chimpanzees directed more grooming to the back ($\beta \pm SE = 0.71 \pm 0.23$, $Z = 3.16$, $p < 0.01$) and anogenitals ($\beta \pm SE = 1.46 \pm 0.28$, $Z = 5.14$, $p < 0.001$) than bonobos, but they did not differ significantly in their grooming of the limbs ($\beta \pm SE = -0.30 \pm 0.22$, $Z = -1.38$, $p = 0.17$, Fig. 4). Even when body orientation was held constant in face-to-face grooming, bonobos groomed the head ($\beta \pm SE = -1.60 \pm 0.23$, $Z = -7.01$, $p < 0.001$) and front ($\beta \pm SE = -1.53 \pm 0.26$, $Z = -5.95$, $p < 0.01$) significantly more often than chimpanzees, while chimpanzees directed

Fig. 6. Mean $\pm$ SE proportion of time when face-to-face and face-to-back groomings were performed depending on the species. These data are calculated from the mean of each dyad. * $p < 0.05$, *** $p < 0.001$.

more grooming to the limbs ($\beta \pm SE = 1.43 \pm 0.21$, $Z = 6.96$, $p < 0.001$) and back (e.g., during face-to-face mutual grooming while the partner grooms the inner thighs or genital region, $\beta \pm SE = 2.70 \pm 0.50$, $Z = 5.41$, $p < 0.001$) than bonobos. They did not differ significantly in their grooming of anogenitals when face-to-face orientation was held constant ($\beta \pm SE = 1.08 \pm 0.59$, $Z = 1.82$, $p = 0.07$).

Wild individuals directed significantly more grooming to the back than those in captivity ($\beta \pm SE = 0.95 \pm 0.22$, $Z = 4.34$, $p < 0.001$, Fig. 5), but they did not differ significantly in their grooming of the front ($\beta \pm SE = 0.23 \pm 0.23$, $Z = 0.97$, $p = 0.33$), anogenitals ($\beta \pm SE = -0.04 \pm 0.28$, $Z = -0.13$, $p = 0.90$) or limbs ($\beta \pm SE = -0.23 \pm 0.21$, $Z = -1.12$, $p = 0.26$). Captive individuals were found to direct more grooming to the head than wild individuals ($\beta \pm SE = -0.69 \pm 0.22$, $Z = -3.21$, $p < 0.01$); however, this was the case only for bonobos and not chimpanzees.

Body Orientation

Captive and wild bonobos spent 49.9 and 31.0% of their grooming time in face-to-face, 27.4 and 35.6% in face-to-back, and 22.7 and 33.4% in intermediate position, respectively. Captive and wild chimpanzees spent 23.7 and 15.0% of their grooming time in face-to-face,

Fig. 7. Mean $\pm$ SE proportion of time when face-to-face and face-to-back groomings were performed depending on the environment in which individuals live. These data are calculated from the mean of each dyad. *** $p < 0.001$.

43.7 and 71.0% in face-to-back, and 32.6 and 14.1% in intermediate position, respectively (Table 2).

Bonobos groomed in face-to-face ($\beta \pm SE = -0.29 \pm 0.13$, $Z = -2.18$, $p = 0.030$) and intermediate ($\beta \pm SE = -0.60 \pm 0.16$, $Z = -3.68$, $p < 0.001$) orientations significantly more often than chimpanzees, while chimpanzees groomed in the face-to-back position more often than bonobos ($\beta \pm SE = 0.74 \pm 0.13$, $Z = 5.61$, $p < 0.001$, Fig. 6).

Wild individuals groomed in face-to-back orientations more often than those in captivity ($\beta \pm SE = 0.78 \pm 0.12$, $Z = 6.45$, $p < 0.001$), while captive individuals groomed face-to-face more often than those in the wild ($\beta \pm SE = -0.76 \pm 0.11$, $Z = -6.98$, $p = 0.001$, Fig. 7). Subjects in the wild and captivity did not differ significantly in their grooming in intermediate orientations ($\beta \pm SE = 0.12 \pm 0.13$, $Z = 0.97$, $p = 0.33$).

Discussion

This study aimed to explore whether body site and body orientation preferences during social grooming show species-specific differences (bonobos vs. chimpanzees) and environment-specific differences (captivity vs. wild). First, we found that *Pan* species focus their grooming efforts on different body sites and use different body orientations. Bonobos groomed the head, the front and in

face-to-face positions more often than chimpanzees, while chimpanzees groomed the back, anogenitals and in face-to-back positions more often than bonobos. This suggests that each species might use specific sites and orientations to reinforce the social bond between individuals. Bonobos, for example, spent a considerable amount of time grooming the head, the front and in face-to-face positions when compared to chimpanzees. These findings are consistent with other reports about location preferences of bonobo grooming, in particular concerning the facial region [Jordan, 1977; de Waal, 1988; Franz, 1999]. The consistency of such results further supports the suggestion that facial communication is important in bonobo society. Facial communication in bonobos is also frequent outside social grooming contexts. Indeed, they frequently engage in ventroventral sexual behaviors between all age-sex combinations, which is not the case in chimpanzees [de Waal, 1988; Kano, 1992; Hohmann, 2015]. Chimpanzees, on the other hand, were found to groom the anogenital areas more often than bonobos. In chimpanzees, touching and gripping the genitals and rump is used as a reassurance behavior to reduce tension between individuals [van Lawick-Goodall, 1968; Sugiyama, 1969; Goodall, 1986]. Therefore, our findings suggest that chimpanzees might groom this region for appeasement and social bonding. Finally, eye-tracking experiments revealed differences in terms of social attention between the *Pan* species, with bonobos making more eye contact than chimpanzees [Kano et al., 2015]. When presented pictures of conspecifics, bonobos looked at the eyes and face longer than did chimpanzees, while chimpanzees instead looked at the mouth, anogenitals and target objects longer than did bonobos. These results align with our finding that bonobos groomed the head more often than chimpanzees, and chimpanzees groomed the anogenitals more often than bonobos, suggesting that the species-specific differences in social attention might influence the selection of body sites and orientations during social grooming.

An ultimate explanation for the different body site and orientation preferences between the *Pan* species could be the influence of the levels of social tolerance. Indeed, bonobos are often considered to be more socially tolerant than chimpanzees due to their higher rates of adult play [Palagi, 2006] and the fact that lethal aggression and infanticide have never been reported [Wilson et al., 2014]. In macaque species, the more tolerant bonnet macaques (*M. radiata*) were found to face each other and groom the facial region and front to a greater extent than did the more despotic pigtail macaques [*M. nemestrina*; Boccia,

1989]. Notably, grooming the back areas and in face-to-back orientation was more prominent in chimpanzees than in bonobos. It has been suggested from studies in macaques and langurs that this orientation provides protection of the more vulnerable sites of the body (face and front) and precludes eye contact with potentially risky partners, reducing the chance of receiving harmful aggression [Boccia et al., 1982; Moser et al., 1991; Borries, 1992]. Additionally, Fedurek et al. [2015] found that chimpanzee lip-smacks were more likely to be produced when grooming vulnerable body sites or while in face-to-face positions. They suggested that lip-smacks are used to communicate benign intent in such socially risky situations. In contrast, bonobos have not been reported to produce such auditory signals during social grooming. Our results suggest that, similar to monkey species, the level of social tolerance might have an influence on the body site and orientation preferences during social grooming in *Pan* species, but this would need to be directly tested in future studies.

Due to limitations in the group composition of the study subjects (e.g., mainly biased towards females), we could not examine the influence of sex on the body site and orientation preferences. It is important to note that the lower levels of grooming on the head, front and in face-to-face positions in chimpanzees compared to bonobos could be explained by the small number of chimpanzee males in the study groups. Indeed, chimpanzee males are highly sociable and show the strongest association of all sex combinations [Goodall, 1986; Boesch and Boesch-Achermann, 2000; Mitani, 2009]. However, with the exception of one male-male dyad which spent 23% of their grooming bouts on the face, Nishida and Hosaka [1996] generally found that male chimpanzees rarely groomed the faces of other males. In the Bossou group, the two males who were the most frequent grooming partners spent only 11% of their grooming on the head including the face. Further studies will have to investigate the influence of sex and other social variables on the body site and orientation preferences in *Pan* species.

This study also revealed differences in body site and body orientation preferences between captive and wild populations. We found that captive individuals faced each other during grooming more often than their wild conspecifics, whereas wild individuals groomed the back and in face-to-back positions more often than those in captivity. Environmental constraints are also known to influence social grooming, and in particular a higher frequency is generally found in captive individuals compared to those in the wild, which is suggested to serve as a coping mech-

anism to reduce tensions created by crowding [Nieuwenhuisen and de Waal, 1982; de Waal, 1989; Bercovitch and Lebrón, 1991; Novak et al., 1992; Dyck et al., 2003]. Indeed, in captivity, individuals are challenged by space limitations and by limited possibilities to hide or run away following the initiation of an aggression, so they must find ways to cope with the increased levels of tension. In our study, we found that captive subjects faced each other more often than did wild subjects while grooming. Face-to-face grooming might enable individuals to develop stronger social bonds and thus might help reduce tensions under confined conditions. On the other hand, the physical features of a captive environment might also help captive individuals pay closer attention to each other during social grooming by facing each other and less attention to the world beyond compared to their conspecifics living in the wild. Indeed, in the corner of a cage, individuals can be sure to be protected on several sides from anyone sneaking up, whether predators or conspecifics. Moreover, we also found that wild individuals groomed the back areas and in face-to-back positions more often than captive individuals, suggesting that the levels of hygiene might play a role in the determination of the sites groomed. Indeed, captive individuals are usually believed to have less ectoparasites than those in the wild, since captive environments have limited vegetation and are kept clean and dry by humans, while bushy and humid environments found in the wild favor the persistence of ectoparasites [Rechav, 1982; Mooring, 1995]. Thus, a higher amount of social grooming should be dedicated to sites that are inaccessible via self-grooming in the wild. The hygienic function of social grooming has always been demonstrated by comparing body site preferences between self- and allogrooming [Hutchins and Barash, 1976; Barton, 1985; Borries, 1992; Reichard and Sommer, 1994; Franz, 1999], but never directly between captive and wild individuals. Therefore, it would be informative to directly test this by counting the number of ectoparasites in both wild and captive individuals, potentially giving a more accurate understanding of how the environments differ in regard to their levels of hygiene. Indeed, parasite infections might spread faster in captive environments due to the close proximity and high density of their hosts.

Future research should expand on this current preliminary study by addressing out two main limitations – (1) number of populations per condition and (2) distribution of age and sex classes. This would allow a more definitive conclusion at the species or environmental levels than in our current first attempt of 2 by 2 comparisons. However, this study carried out the first direct comparison of 4 con-

ditions from a standard and consistent viewpoint and provided new information on specific patterns of *Pan* social grooming. As the two postulated hypotheses predicted, we found the clear influence of (i) species-specific social differences (i.e., levels of social tolerance, social attention and facial communication) and (ii) socioenvironmental constraints (i.e., risk of predation, spatial crowding and levels of hygiene). Further study will illuminate the detailed aspects of social grooming of *Pan* species through quantitative measures in terms of grooming site preferences.

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Statement of Ethics

This study was noninvasive and purely observational.

Conflict of Interest Statement

The authors have no conflicts of interest to declare.

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Author Contributions

All authors made substantial contributions to this paper. M.A. collected the raw data and analyzed them to draft the article as a part of her PhD dissertation. M.H., T.F. and T.M. contributed to make the necessary arrangement of the studies in the field and the captivity. They also provided the framework of the theoretical analysis and revised the paper critically for important intellectual content. All authors gave final approval of the submitted version.

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