

RESEARCH ARTICLE

Grooming site preferences in black capuchin monkeys: Hygienic vs. social functions revisited

Romina Pfoh^{1,2}  | Barbara Tiddi^{3,4}  | Mario S. Di Bitetti^{1,2,5}  | Ilaria Agostini^{1,2,6} 

¹Instituto de Biología Subtropical (IBS), Universidad Nacional de Misiones (UNaM), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Puerto Iguazú (Misiones), Argentina

²Asociación Civil Centro de Investigaciones del Bosque Atlántico (CelBA), Puerto Iguazú, Argentina

³Department of Field Conservation and Science, Bristol Zoological Society, Bristol, UK

⁴Division of Human and Social Sciences, School of Anthropology and Conservation, University of Kent, Canterbury, UK

⁵Facultad de Ciencias Forestales, UNaM, Eldorado, Misiones, Argentina

⁶Parque Nacional Nahuel Huapi (CENAC-APN), CONICET, San Carlos de Bariloche, Argentina

Correspondence

Ilaria Agostini, Instituto de Biología Subtropical (IBS), Universidad Nacional de Misiones (UNaM), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Bertoni 85, CP 3370, Puerto Iguazú (Misiones), Argentina.
Email: agostini.ilaria@gmail.com

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Abstract

When primates groom each other, they tend to concentrate on those parts of the body they cannot efficiently self-groom (i.e., not visually accessible), and prefer to intensify grooming in areas with high hair density, thus suggesting a hygienic function. However, preferences for some body sites over others during social grooming may also result from different degrees of social bonding and relative dominance. To assess the relative importance of physical (hygienic) and social factors, we examined grooming interactions in two groups of wild black capuchin monkeys (*Sapajus nigritus*) during 15 nonconsecutive months. We evaluated the distribution of social grooming across body sites according to their accessibility by self-grooming and hair density. At the same time, we assessed whether the degree of dyadic social bonding affects the relative body orientation between groomer and groomee and the access to vulnerable body sites (e.g., face, throat, groin) during grooming. As expected, capuchins preferentially groomed inaccessible body sites (e.g., back and head), with a disproportionate effort directed to the tufts of their partners. We found that dyadic social bond strength, together with rank distance, significantly affected the proportion of grooming in ventro-ventral body relative orientation only in dominant-subordinate groomer-groomee dyads. This may indicate that, when two individuals differ in rank but are strongly bonded, the level of uncertainty related to the social context is already resolved and thus grooming per se is no longer perceived by the subordinate as an uncertain/risky situation. We found no effect of social bonding on grooming vulnerable body sites for any type of dyad. Our findings suggest that grooming site preferences in black capuchin monkeys simultaneously reflect hygienic and social functions.

KEYWORDS

compensation, *Sapajus nigritus*, social bonding, social grooming

1 | INTRODUCTION

Increased parasite infection risk is one of the main disadvantages of sociality, and to reduce its costs behaviors such as social grooming (or allogrooming) had evolved (Kappeler et al., 2015). In group-living primates, individuals devote a large proportion of their social time to this behavior, which is heterogeneously distributed not only among the

members of a social group, but also among different parts of an individual's body. While grooming distribution among group members has been intensely investigated in primatology (e.g., Cheney, 1992; Di Bitetti, 2000; Dunbar, 2010; Henzi & Barrett 1999; Seyfarth, 1980), the study of factors that determine the preferential selection of some body sites over others during social grooming has received overall little attention (Allanic et al., 2020a, 2020b; Boccia, 1983; Freeland, 1981). Initial findings

suggest that physical factors, such as self-accessibility, hair density, and parasite density may influence the selection of groomed body sites (Boccia, 1983; Zamma, 2002a). According to the compensation hypothesis (Pérez & Veà Baró 1999), derived from the hygienic hypothesis (Freeland, 1976, 1981), if the primary function of grooming is maintaining fur and skin clean, social grooming and self-grooming should be distributed in a complementary way. This means that grooming actors (groomers) should focus their cleaning activity on those body sites that are not visually or manually accessible to receivers (groomees), and likely host higher load of ectoparasites (Zamma, 2002a). Ectoparasites tend to concentrate in areas that provide shelter from defensive strategies by the host, such as self-grooming and self-scratching (Murray, 1987a). Besides, hair density and length create gradients of temperature and luminosity which lead to a heterogeneous distribution of ectoparasites across the host body (Akinyi et al., 2013; Murray, 1987b; Zamma, 2002a). Thus, social grooming should be directed to body sites that are otherwise inaccessible and/or invisible to groomees and/or with high hair density, consequently removing ectoparasites, dirt and body debris more effectively (Boccia, 1983; Pérez & Veà Baró 1999).

In addition to its hygienic function, a vast body of work has shown that social grooming also serves numerous social functions, including close access to dominant individuals (Seyfarth, 1980), social bonding (Silk, 2002), tension reduction (Aureli et al., 1999; Schino et al., 1988; Terry, 1970) and reconciliation (Koyama, 2001; Palagi et al., 2008). As such, it is plausible to hypothesize that social characteristics may also play a role in influencing grooming site selection (Allanic et al., 2020a; Boccia et al., 1982). It has been found, for example, that following a tense situation individuals performed more face-to-back grooming (Barton, 1983; McKenna, 1978), and comparisons between closely related species showed that the more despotic species groomed the back areas more, while more tolerant ones groomed in face-to-face positions (Allanic et al., 2021; Boccia, 1989).

Dyadic social characteristics, such as sex, kinship, relative dominance rank, rank distance, and grooming frequency (as a proxy for social bonding) have been shown to influence the selection of body sites groomed. For example, in rhesus monkeys (*Macaca mulatta*), females tend to be groomed more on the back and tail than males, and in both sexes high-ranking partners receive more grooming on the rump and tail than low-ranking ones (Boccia et al., 1982). In langurs (*Presbytis entellus*), close-kin female partners direct grooming more frequently at inaccessible body sites than nonkin females (Borries, 1992). Bonobo (*Pan paniscus*) and long-tailed macaque (*Macaca fascicularis*) females and high-ranking individuals tend to preferentially groom areas around faces, whereas males tend to avoid faces and prefer to groom the receiver's back and tail (Franz, 1999; Moser et al., 1991). Low ranking groomees tend to avoid the groomer's glance and to adopt a dorso-ventral (groomer-groomee) relative orientation, probably as a strategy to avoid eye contact and prevent potential aggression (Boccia et al., 1982; Borries, 1992). In addition, social bond strength has been suggested to influence the selection of specific body sites for grooming, with strongly affiliated dyads showing higher rates of facial grooming in a ventro-ventral orientation compared to dyads with a lower social bond strength (Franz, 1999).

Black capuchin monkeys (*Sapajus nigritus*) are diurnal and arboreal primates that live in relatively stable multifemale-multimale groups that range from 7 to 30 independent individuals (Janson et al., 2012). As in other capuchin species, black capuchin monkeys exhibit female philopatry and male dispersal (Fragaszy et al., 2004). In this species, the alpha male plays a central role within the group social network by despotically controlling access to food resources (Janson, 1985) and receiving most of the grooming given by adult females (Di Bitetti, 1997; Tiddi et al., 2011b). Female philopatry, and social dominance are the main factors that influence the patterns of grooming in capuchins, that tend to be concentrated among dominant individuals. Females have stronger grooming relationships and tend to reciprocate more within sessions than males. The reproductive conditions of females, particularly if they have newborn infants, affect their attraction as social partners for other group members (Di Bitetti, 1997). In Iguazú, capuchins exchange grooming up the hierarchy in return of immediate benefits, such as increased tolerance during feeding (Tiddi et al., 2012), and females compete for the opportunity to groom dominant females (Tiddi et al., 2011b). Besides, social factors, such as kinship, dyadic relative rank and affiliation, are known to influence partner selection (Di Bitetti, 1997). So far, the few studies evaluating the factors affecting social grooming distribution on body sites and its possible social function have concentrated in Old World primate species (e.g., Allanic et al., 2020a; Boccia et al., 1982; Borries, 1992). Thus, this study represents the first attempt to investigate grooming site preferences in New World primates.

The two main functions of social grooming described above (hygienic vs. social function) are not mutually exclusive. However, it is important to assess the relative importance of social grooming either as a behavior aimed at reducing ectoparasites or as a behavior that maintains social relationships. One way to test this is by contrasting the observed patterns of social grooming to those predicted by each hypothesis in relation to certain physical and/or social features. According to the compensation hypothesis (Pérez & Veà Baró 1999), if grooming site preferences are mainly determined by a hygienic function, we expect that social grooming: (1) will be concentrated on body sites not accessible to self-grooming, and (2) will be directed towards those sites that may harbor higher ectoparasite density (i.e., sites with higher hair density; see Zamma, 2002a). Moreover, if grooming site preferences reflect high levels of social bonding (Silk et al., 2006) experienced by the grooming partners, we predict that social grooming will be performed in vulnerable body orientation (i.e., ventro-ventral posture) or directed to vulnerable body sites more frequently in dyads that have strong social bonds compared to those with weak social bonds.

2 | MATERIALS AND METHODS

2.1 | Study site

We conducted this study at Iguazú National Park, Argentina (25°40' S 54°30' W, 67,000 ha), located in the Alto Paraná Atlantic Forest

ecoregion (Di Bitetti et al., 2003). This semi-deciduous forest has a humid and subtropical climate, with marked seasonality in day length and temperature, and with rainfall of approximately 2000 mm per year without a distinct dry season (Silva et al., 2014). Food availability exhibits a strong seasonal pattern, with maximum abundance of ripe fruits and arthropods (the items mostly consumed by black capuchin monkeys) between October and December (Di Bitetti & Janson, 2001; Placci et al., 1994).

2.2 | Study subjects

We carried out this study on adult and subadult individuals (i.e., >4 years for females, and >5 years for males) of two groups of black capuchin monkeys: the Macuco group, with 11–15 adults and 1–4 subadults, and the Spot group, counting 7–9 adults and 0–3 subadults. Juveniles and infants were excluded to minimize age-related effects on grooming patterning (e.g., Liao et al., 2018). Changes in group compositions during the study period were due to natural demographic events, such as migrations and deaths (Table S1). Individuals were easily identified using fur color patterns and facial features. Due to the long-term study being carried out on these capuchin groups, maternal kinship was known (Janson et al., 2012).

2.3 | Data collection

RP and 2–3 field assistants at a time collected behavioral data during 15 nonconsecutive months (May–August 2013; December 2013–January 2014; June–November 2014 and late December 2015–early March 2016). Data collection was split across different periods because this study was part of a wider research program in which data collection took place intermittently across different times of the year. The focal groups were followed every day from approximately 7:00–18:00 h during the 2013 and 2014 study periods, and from approximately 6:00–19:00 h 6 days per week during the 2015–2016 summer.

Interobserver reliability was monitored before the beginning of the data collection during initial training periods supervised by RP. Assistants were allowed to start their independent data collection only after expressing an agreement with the data collected by RP of $\geq 95\%$. Data were recorded using 10-min focal animal samples combining instantaneous and continuous recording. Focal samples were randomized across subjects using a permutation schedule with at least 1 h between consecutive samples of a given individual. In addition, ad libitum sampling (Altmann, 1974) was used to record grooming and aggressions opportunistically. We recorded grooming bouts (i.e., a continuous sequence of acts of hair manipulation from one individual to another, which we considered finished if interrupted for more than 10 s) during focal and ad libitum sampling. To minimize the chances of missing some bouts, at least two observers collected data simultaneously during ad libitum sampling (Tiddi et al., 2011a). For each grooming bout we recorded: start time, end time, identities of the groomer and the groomee and body sites groomed. Within each bout,

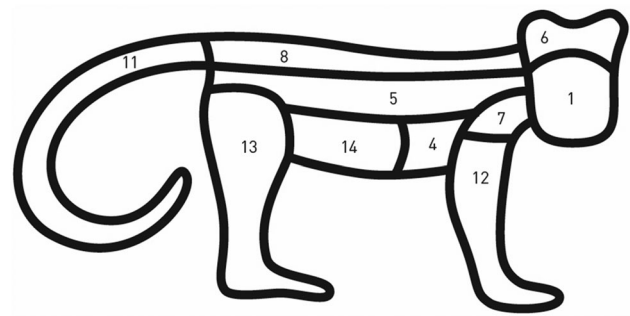


FIGURE 1 Hypothetic black capuchin monkey's body organized into different parts in lateral and frontal (only head) view. Due to perspective, some body sites (e.g., armpits, groin) are not evident in this graph and are presented in Figure S1. References of numbers are given in Table 1

grooming could be directed to different body sites. We identified 15 body sites and categorized them (Figure 1 and Figure S1) according to four parameters: accessibility to self-grooming, hair density, relative body orientation, and vulnerability (Table 1).

2.4 | Data organization

2.4.1 | Accessibility to self-grooming

To test the compensation hypothesis, body sites were organized based on how accessible to both tactile and visual inspection via self-grooming a certain body part was for the individual. Primates can reach, and scratch, any part of the body with their hands, but the same is not valid for visual reach, which acts as a limitation on the possibility of effectively searching while grooming small parasites and particles. Modifying Boccia's definition (1983), we classified as inaccessible to self-grooming those body sites to which an individual does not have visual access, even if they were easily accessible by hand (e.g., the face or tufts). Because body sites accessible and inaccessible to self-grooming are not equally represented on an individual body, it was necessary to include a correction factor based on the surface area occupied by each category (Barton, 1985; Boccia, 1983; Pérez & Veà Baró 1999). Similarly to Barton (1985) and Pérez and Veà Baró (1999), we assigned to each body site a certain proportion of the total body surface based on our own arrangement of capuchin body sites (Table S2). According to our arrangement, areas inaccessible to self-grooming represent 34.7% of the body surface, while 65.3% of the body surface is accessible to self-grooming.

2.4.2 | Hair density

We categorized hair density as high or low, simply considering whether the skin surface is largely visible without parting the fur. Low hair density body sites, whereby the skin was visible without moving away the fur (see Figure S2 for examples), occupy only 9.7%,

Accessibility	Hair density	Body site	Area (%)	Relative orientation	Vulnerability
Inaccessible	Low	1. Face	1.9	VV	V
		2. Armpits	1.0		NV
	High	3. Throat	0.7		V
		4. Chest	4.5		V
		5. Flank	10.0	Va	NV
		6. Tufts	0.6		V
		7. Shoulders	1.5		NV
		8. Back	10.0	DV	NV
		9. Neck	1.5		NV
		10. Head	3.0	Va	NV
Accessible	High	11. Tail	8.0		NV
		12. Arms	21.0		NV
		13. Legs	29.5		NV
	Low	14. Belly	5.5	VV	V
		15. Groin	1.3		V

TABLE 1 Percent area occupied and classification of body sites by accessibility to self-grooming (accessible: hand and visual reach; inaccessible: without hand and/or visual reach), hair density (high: dense coverage that prevents the skin from being seen without manipulating the hair fibres; low: surface stripped of hair or with low coverage, so skin can be seen), relative orientation (dorso-ventral—DV, ventro-ventral—VV, and variable posture—Va), and vulnerability (vulnerable—V and not vulnerable—NV)

while high hair density sites represented the rest of body surface (Table 1).

2.4.3 | Relative body orientation

Groomer-groomee relative body orientation (hereafter, relative orientation) was divided into three categories: ventro-ventral (i.e., groomer-groomee ventral surfaces faced each other and may have been parallel or within a 90°–180° angle), dorso-ventral (i.e., the groomer ventral surface faced the groomee dorsal surface and was located parallel or within a 90°–180° angle), and variable (i.e., posture that manifests itself indistinctly as ventral, dorsal or with the ventral surface of the groomer facing the side of the body of the groomee; i.e., the groomer can reach these body sites from front, backside or laterally). The classification of relative orientation on the basis of the groomed body site can be unreliable for some primate species, such as chimpanzees or some Old World monkeys species, in which simultaneous mutual (or bidirectional) grooming is relatively common (Allanic et al., 2020b). Here, an individual can groom dorsal parts of another individual, who in turn grooms back on ventral parts of the first individual, both from a relative ventro-ventral orientation. However, this is not the case in black capuchin monkeys, where simultaneous mutual grooming has not been reported. Besides, the body sites according to which we classified strictly ventro-ventral or dorsal-ventral relative orientations were selected with a conservative approach on the basis of our own observations of grooming behavior in this species, leaving body sites that can be groomed indistinctly from dorsal, ventral or lateral orientation in the “variable” category.

2.4.4 | Vulnerability

We categorized body sites according to their vulnerability on the basis of the relative ease of access to vital organs. Vulnerable sites included face, throat, tufts, chest, belly, and groin, while the rest of body sites were classified as not vulnerable (see Boccia et al., 1982; Borries, 1992; Moser et al., 1991). The 15 body sites and their categorization are summarized in Table 1.

To describe the distribution of grooming, for each bout, we recorded the groomed body sites. If two or more sites were groomed in a single bout, we considered them as different records, one from each site. For each dyad (according to the role of actor and receiver of each member) in which we observed grooming, we counted the number of bouts each body site was groomed. Then, for each dyad we calculated the proportion of grooming bouts directed to each body site. Since ad libitum samples ($N = 894$ grooming bouts) and focal samples ($N = 279$) did not show any significant difference in the proportion of grooming bouts recorded for most body sites (Table S3), we decided to combine these two sources of grooming data for the two study groups. We used the relative area of each body site to estimate the expected frequencies of grooming directed to each of them (Table 1).

All research reported in this article complied with the guidelines approved by the Ethics Committee of the Argentine Society for the Study of Mammals (SAREM) and adhered to the legal requirements of Argentina. All research protocols were reviewed and approved by the National Parks Administration of Argentina. Finally, our research adhered to the American Society of Primatologists Ethical Principles for the Treatment of Non-Human Primates.

2.5 | Data analysis

To determine the relative rank of grooming partners, we first established a dominance hierarchy based on the direction of dyadic aggressive (i.e., threats, supplants, chases and physical assaults) and displacement (approach-avoidance) interactions using the Elo-rating package (Neumann & Lars, 2014). Those individuals for which we recorded little or no interactions, were not included (Table S1). We built the hierarchy across the study periods on the basis of a total of 234 interactions for Macuco group and 67 interactions for Spot. Based on the hierarchy, we computed the rank distance, calculated as the absolute value of the difference in rank between groomer and groomee. We then established two different types of dyads as dominant-subordinate (DS) and subordinate-dominant (SD) grooming partners, depending on the relative rank of groomer and groomee, respectively, within a dyad. Furthermore, to characterize dyadic sex, we used all combinations of groomer-groomee sex, thus defining four levels: male-male, male-female, female-male, female-female. Dyadic kinship between groomer and groomee within a grooming dyad was expressed using the relatedness coefficient “*r*”, which is a measure of the approximate genetic relationship between two individuals calculated on the basis of maternal lineage (0.50 for mother-offspring, 0.25 for half-siblings, 0.125 for cousins, 0.00 for not related individuals). Finally, to characterize the strength of dyadic social bonds between grooming partners, we used a dyadic Composite Sociality Index (CSI) (Silk et al., 2006) based on grooming, proximity and co-feeding rates calculated from focal animal data. This index measures the extent to which each dyad deviates from other dyads. The mean of CSI is defined as 1, but values can range from 0 to infinity, with high values representing dyads with stronger social bonds than the average dyad in the group, and low values representing dyads with weaker social bonds (Silk et al., 2006). To test the effect of social bond strength on the grooming relative orientation or the selection of body sites according to vulnerability, for each dyad we calculated the proportion of bouts in which ventro-ventral, dorso-ventral or variable orientation was recorded, and the proportion of bouts in which vulnerable or nonvulnerable body sites were recorded, respectively. When a dyad performed grooming in more than one relative orientation within a single bout, that bout counted as one for each of the categories of orientation recorded. Similarly, when a grooming was directed to both vulnerable and nonvulnerable body sites within a single bout, we counted it for each category of body site selection.

2.6 | Statistical analyses

To evaluate how social grooming was distributed according to accessibility and hair density, we carried out chi-square tests of independence with an alpha level of 0.05. Expected frequencies in these tests were estimated based on the area occupied by the different body sites (Table 1).

To evaluate the effect of social bonding on body relative orientation and site selection according to vulnerability, we fit

two pairs of Generalized Linear Mixed Models with a binomial distribution and logit link function, using the function `glmer` in the `lme4` package (Bates et al., 2015). In the first pair of models run for the two different types of dyads (DS: dominant individuals as groomers and subordinate individuals as groomees; SD: subordinates as groomers and dominants as groomees), we tested whether dyads with stronger social relationships performed more grooming in ventro-ventral relative orientation. The proportion of grooming bouts in which individuals' relative orientation was ventro-ventral (with respect to dorso-ventral position), was the response variable and CSI was the main predictor. We excluded from this analysis the “variable” relative orientation because it did not provide a unique form of access to the body sites, i.e., only ventral, or only dorsal. In the second pair of models run for the two different types of dyads (DS, SD), we tested whether stronger social relationships led to more grooming directed at vulnerable body sites. Here, the proportion of grooming directed to vulnerable body sites was the response variable, and CSI was the main predictor. To control for potential confounding factors, we included dyadic sex, rank distance and kinship as fixed effects. Dyads nested within years were included as random effects. We checked for model assumptions by visually inspecting histograms of the residuals, plots of the residuals against fitted values, and by calculating the parameter of dispersion. We did not find strong overdispersion (dispersion parameter values < 1.2) in any of the models we run. We also checked for correlations between our predictor variables to avoid potential confounding effects of multicollinearity by calculating generalized variance inflation factors (all values < 3). We carried out the selection of models by using a stepwise progression and evaluating the *p* values of successive models based on likelihood ratio tests comparisons. All statistical analyses were performed using R software (v. 3.5.0; R Core Team 2018). The data that support the findings of this study are available from the corresponding author upon request.

3 | RESULTS

3.1 | Grooming distribution according to physical characteristics of body sites

We recorded a total of 1173 grooming bouts performed by a total of 156 dyads. Black capuchins directed a higher-than-expected frequency of social grooming bouts to body sites that are inaccessible to self-grooming ($\chi^2 = 1067.3$, $df = 1$, $p < 0.001$). These body sites represent 34.70% of body surface but concentrated 77.24% of grooming (Figure 2). In contrast, individuals devoted 90.83% of grooming bouts to high density body sites, a proportion similar to that expected based on their representation (91.70%) of the body surface ($\chi^2 = 1.24$, $df = 1$, $p = 0.265$). When considering each body site, we found that capuchins directed a higher-than-expected percentage of grooming records to the tufts (10 times higher; observed = 6.87% vs. expected = 0.60%), head (almost 6 times higher; observed = 17.01% vs. expected = 3.00%), back

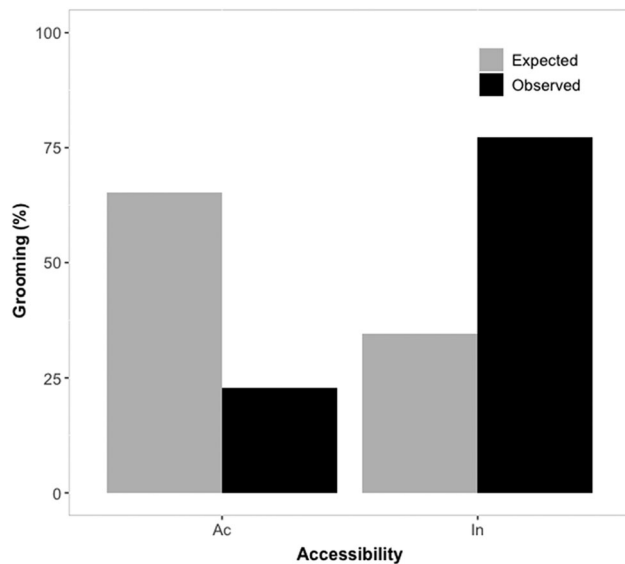


FIGURE 2 Observed and expected percentage of grooming bouts on body sites according to accessibility to self-grooming (Ac: accessible, In: inaccessible).

(almost 4 times higher; observed = 37.51% vs. expected = 10.00%), neck (3 times higher; observed = 5.65% vs. expected = 1.50%), and shoulders (1.79 times higher; observed = 2.68% vs. expected = 1.50%). Sites with lower than expected grooming were the legs (<1/8 of the expected amount; observed = 3.32% vs. expected = 29.50%), arms (1/5 of the expected amount; observed = 4.19% vs. expected = 21.00%), chest (1/3 of what was expected; observed = 1.75% vs. expected = 4.50%), groin (1/3 of what was expected; observed = 0.41% vs. expected = 1.30%), flank (<1/2 of what was expected; observed = 4.48% vs. expected = 10.00%), and belly (2/3 of what was expected; observed = 3.67% vs. expected = 5.50%) ($\chi^2 = 4495.5$, $df = 14$, $p < 0.001$).

3.2 | Grooming distribution according to dyadic social relationships

Black capuchins performed 9.90% of their grooming in ventro-ventral relative orientation and 46.35% in dorso-ventral orientation. The proportion of grooming in ventro-ventral relative orientation increased according to the strength of dyadic social relationships only when the groomer was dominant and the groomee was subordinate (Table 2, Table S4, Figure 3). In contrast, no effect of this predictor was found for relative orientation in dyads in which the subordinate individual was the groomer (Table 2 and Table S4). As for body site selection according to vulnerability, black capuchins dedicated 16.58% if their grooming to vulnerable body sites, and we found no significant effect of social bonding on the proportion of grooming directed at vulnerable body sites neither for DS nor for SD groomer-groomee dyads (Table 3 and Table S5).

TABLE 2 Results of GLMMs testing the influence of Composite Sociality Index (CSI) on ventro-ventral relative orientation for (a) DS dyads (i.e., dyads in which the groomer is a dominant and the groomee is a subordinate individual, $N = 66$), and (b) SD dyads (i.e., dyads in which the groomer is a subordinate and the groomee is a dominant individual, $N = 73$)

(a)		
Main predictors	Estimate \pm SE	(95% CI)
Intercept	-1.881 \pm 0.376	-2.618 -1.144
CSI	0.127 \pm 0.055	0.020 0.235
Control factors		
Rank distance	0.106 \pm 0.047	0.014 0.198
Kinship	-1.126 \pm 1.313	-3.699 1.447
Sex		
FM	-0.239 \pm 0.715	-1.641 1.162
MF	-1.298 \pm 0.476	-2.232 -0.364
MM	0.294 \pm 0.638	-0.957 1.545
(b)		
Main predictors	Estimate \pm SE	(95% CI)
Intercept	-2.055 \pm 0.561	-3.154 -0.955
CSI	-0.044 \pm 0.076	-0.193 0.105
Control factors		
Rank distance	0.001 \pm 0.047	-0.092 0.093
Kinship	-1.336 \pm 1.671	-4.611 1.939
Sex		
FM	0.941 \pm 0.445	0.068 1.814
MF	0.492 \pm 0.482	-0.454 1.438
MM	0.050 \pm 0.738	-1.397 1.497

Note: Estimates and standard errors (\pm SE) with 95% confidence intervals (CI) are presented. Bold font indicates predictors with a significant effect on the response as indicated by CIs excluding 0. For the control categorical variable sex, levels not included in the intercept are the following: female-male (FM), male-female (MF) and male-male (MM), while the reference level included in the intercept is female-female (FF).

4 | DISCUSSION

In this study, we analyzed the distribution of grooming across body sites in black capuchin monkeys and assessed the relative importance of its hygienic and social functions. Our results suggest that both physical and social factors affect the distribution of grooming on body sites. As predicted by the compensation hypothesis, capuchin monkeys directed social grooming preferentially to body sites that are inaccessible to self-grooming. According to our accessibility-based classification, body sites inaccessible to self-grooming represented 34.7% of the body surface, but the proportion of grooming directed to them was twice as high. This preference for grooming inaccessible hard-to-see body sites, which are potentially more susceptible to ectoparasite

TABLE 3 Results of GLMMs testing the influence of Composite Sociality Index (CSI) on grooming vulnerable body sites for (a) DS dyads (i.e., dyads in which the groomer is a dominant and the groomee is a subordinate individual, $N = 71$), and (b) SD dyads (i.e., dyads in which the groomer is a subordinate and the groomee is a dominant individual, $N = 85$)

(a)		
Main predictors	Estimate \pm SE	(95% CI)
Intercept	-1.671 \pm 0.340	-2.338 -1.005
CSI	0.004 \pm 0.054	-0.101 0.110
Control variables		
Rank distance	0.043 \pm 0.042	-0.039 0.125
Kinship	-0.492 \pm 1.291	-3.023 2.039
Sex		
FM	-0.342 \pm 0.710	-1.734 1.050
MF	-0.558 \pm 0.381	-1.306 0.189
MM	-0.620 \pm 0.809	-2.205 0.965
(b)		
Main predictors	Estimate \pm SE	(95% CI)
Intercept	-1.631 \pm 0.423	-2.460 -0.802
CSI	-0.067 \pm 0.076	-0.216 0.082
Control variables		
Rank distance	-0.026 \pm 0.050	-0.124 0.071
Kinship	1.112 \pm 1.328	-1.491 3.714
Sex		
FM	0.035 \pm 0.438	-0.823 0.893
MF	0.304 \pm 0.459	-0.597 1.204
MM	-0.350 \pm 0.710	-1.742 1.042

Note: Estimates and standard errors (\pm SE) with 95% confidence intervals (CI) are presented. Bold font indicates predictors with a significant effect on the response as indicated by CIs excluding 0. For the control categorical variable Sex, levels not included in the intercept are the following: female-male (FM), male-female (MF) and male-male (MM), while the reference level included in the intercept is female-female (FF). Abbreviation: GLMM, Generalized Linear Mixed Model.

dominant groomers and subordinate groomees may indicate trustfulness in socially bonded dyads.

In addition to influencing the relative participation and distribution of grooming among capuchin dyads (Di Bitetti, 1997; Tiddi et al., 2012), our findings suggest that dominance hierarchy also influences the choice of body sites to groom within dyads. In fact, as rank distance increased, frontal relative orientation increased in DS (groomer-groomee) dyads. This finding is in contrast to what has been found in Old World species of macaques and langurs, in which subordinate groomees tend to face away to avoid eye contact with potentially dangerous groomers (Boccia et al., 1982; Borries, 1992; Moser, 1991). This difference could be related to the level of social tolerance experienced within groups in different primate societies, with more

despotic species showing risk avoidance strategies more frequently than more tolerant species (Allanic et al., 2021). Thus, the relative proneness of subordinate individuals to bear the risk of receiving a frontal grooming by a dominant individual when the rank distance is high could be due to a relatively higher social tolerance in black capuchins (Brosnan & de Waal, 2003; de Waal, 1997; but see Amici et al., 2012). This pattern repeats in other Neotropical primates, where grooming in ventro-ventral orientation, embraces and pectoral sniffs in spider monkeys (*Ateles geoffroyi rufiventris*) appear to involve risk, as these behaviours require close proximity and exposure of vulnerable body sites (Schaffner & Aureli 2005). It is likely that affiliative behaviors displayed in such potentially risky situations may serve as a signal of benign disposition to reduce uncertainty and social tension (Tiddi et al., 2010), since they have a relaxing effect on both the groomee (Aureli et al., 1999; Dunbar, 2010) and the groomer (Shutt et al., 2007).

In conclusion, our findings suggest that both hygienic and social functions of grooming are important in black capuchin monkeys. On one hand, the importance of a hygienic function is evidenced by grooming preference for inaccessible over accessible to self-grooming body sites. However, to find full support for the compensation hypothesis, further exploration of both self-grooming distribution patterns, ectoparasite load over different body sites, and the techniques used to remove them, simultaneously with social grooming site preferences, are required. On the other hand, the social importance of grooming is suggested by the higher frequency of frontal relative orientation according to the degree of social affiliation in DS grooming dyads, which reinforces the role of grooming as a behavior aimed at maintaining social bonds. In future studies, it would be useful to investigate whether social affiliation also affects other aspects of grooming not studied here, such as who initiates a grooming bout, the part of the body exposed during grooming solicitation, and the rate of parasite removal. At the same time, relating the grooming bouts to the social context, e.g., stressful events or agonistic interactions, would also help to distinguish the relative weight of the social and hygienic functions, which are not mutually exclusive (Di Bitetti, 1997).

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AUTHOR CONTRIBUTIONS

Romina Pfoh: conceptualization (equal); data curation (lead); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (lead); project administration (lead); writing original draft (lead); writing review and editing (equal). **Barbara Tiddi:** conceptualization (equal); formal

analysis (equal); funding acquisition (supporting); investigation (equal); methodology (equal); project administration (equal); supervision (equal); writing original draft (equal); writing review and editing (equal). **Mario Di Bitetti**: conceptualization (lead); formal analysis (equal); investigation (equal); methodology (equal); supervision (equal); writing original draft (equal); writing review and editing (equal). **Ilaria Agostini**: conceptualization (equal); formal analysis (equal); funding acquisition (supporting); investigation (equal); methodology (equal); project administration (equal); supervision (lead); writing original draft (equal); writing review and editing (lead).

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon request.

ORCID

Romina Pfoh  <https://orcid.org/0000-0002-8792-7145>

Barbara Tiddi  <https://orcid.org/0000-0002-1832-835X>

Mario S. Di Bitetti  <https://orcid.org/0000-0001-9704-8649>

Ilaria Agostini  <https://orcid.org/0000-0002-3136-0872>

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