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Variable use of polyadic grooming and its effect on access to social partners in wild chimpanzees and bonobos

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In mammals, allogrooming is prominent in forming and maintaining social and cooperative relationships. Yet an animal's social time is constrained, which may limit its access to a large number of partners. Dunbar (1993, *Behavioral and Brain Sciences*, 16 (4), 681–694) proposed that human polyadic conversations, which allow access to several social partners simultaneously, evolved as a form of social grooming to circumvent this time constraint. In nonhuman primates, polyadic grooming (PG), in contrast to dyadic grooming, may similarly be a time-efficient way to maintain weak social relationships with many partners which can be important for group level cooperation. It remains unknown whether PG is used to fulfil specific cooperative needs by accessing numerous weakly bonded partners and increasing the number of partners accessed per unit of time. We compared the use and effect of PG between chimpanzees, *Pan troglodytes*, which are highly territorial and collaborative (especially males), and bonobos, *Pan paniscus*, which are less territorial and collaborative and in which females are the main co-operators. We carried out focal grooming observations in one bonobo and two chimpanzee communities in the wild. As predicted, chimpanzees engaged in more PG than bonobos. Surprisingly, males engaged in PG more than females in both species. While chimpanzees accessed more partners per minute of grooming than bonobos via dyadic grooming, PG increased the number of partners accessed per minute only in bonobos. Finally, chimpanzees primarily used PG with individuals who were close in rank and frequent grooming partners, whereas bonobos used PG with individuals who were distant in rank, close party associates and frequent grooming partners. We suggest that bonobo males use PG to enhance conspecific social tolerance and mate choice. The overall higher rate of PG in chimpanzees suggests that between-group competition may promote polyadic affiliation, which possibly reinforces group cohesion and coordination.

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In group-living animals, individuals frequently maintain social and cooperative relationships with conspecifics by engaging in affiliative exchange with social partners (e.g. allogrooming (hereafter 'grooming') in mammals, Crockford et al., 2013; reviewed in

Seyfarth & Cheney, 2012; allopreening in birds, Fraser & Bugnyar, 2010). More specifically, the exchange of grooming between two individuals can promote cooperation between them either via the formation of strong social relationships (Berghaenel, Ostner, Schroeder, & Schülke, 2011; Samuni, Preis, Mielke, et al., 2018; Schülke, Bhagavatula, Vigilant, & Ostner, 2010) or via the contingent exchange of grooming for other services such as social support in conflicts (reviewed in Schino, 2007) or the exchange of food (de Waal, 1997; Jaeggi, De Groot, Stevens, & Van Schaik, 2013). Beyond dyadic cooperation, strong intergroup competition is linked to additional cooperative requirements, such as collective action during the defence of the territory. As a result, intergroup

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competition can affect the pattern of grooming or allopreening exchange in the group. In cooperatively breeding birds, the rate of allopreening between group members increases when they enter areas where conflicts with other groups are more likely (Radford, 2011). In primates, an early study could not find a clear relationship between the diversity of grooming partners and the participation of females in intergroup encounters (Cheney, 1992). Yet, a recent study, conducted across 15 monkey species, shows that females in groups facing higher rates of, and more violent, intergroup encounters tend to form denser grooming networks with each other (i.e. they have more grooming partners in the group and devote more grooming time to each of them; Majolo, de Bortoli Vizoli, & Lehmann, 2016). Therefore, at least in some mammalian and bird species, access to grooming partners seems important to fulfil individual social and cooperative requirements in within- and between-group contexts.

In larger groups, individuals are thought to need to maintain social relationships with a larger number of individuals and therefore devote more time to grooming than in small groups (Dunbar, 1991), explaining the positive relationship between grooming time and group size (Lehmann, Korstjens, & Dunbar, 2007). Owing to the high level of sociality and cooperation in most human societies, most humans need to maintain social relationships with a large number of partners and Dunbar (1993) proposed that human language evolved as a more efficient substitute for social grooming allowing individuals to interact and maintain social relationships with several partners simultaneously. Here, polyadic conversational exchanges are seen as a more efficient way to access a large number of social partners per unit of time. Likewise, polyadic grooming, which has been observed in several nonhuman primate species (reviewed in Nakamura, 2000) may facilitate more efficient social interactions between one individual and several others. Notably, in chimpanzees, *Pan troglodytes*, the number of partners accessed simultaneously in polyadic grooming clusters is equivalent to those in human classic polyadic conversation (Nakamura, 2000). To our knowledge, the extent to which non-primate species engage in polyadic grooming or polyadic forms of similar affiliative interactions has not been quantitatively reported but is present in certain species. One study on grooming in meerkats, *Suricata suricatta*, mentioned the occurrence of polyadic grooming in this species (Kutsukake & Clutton-Brock, 2006) and polyadic grooming may constitute a significant portion of meerkats' grooming time (Elise Huchard, personal communication 14 April 2020). Hyaenas, *Crocuta crocuta*, sometimes engage in polyadic greetings (Eve Davidian, personal communication 22 April 2020), one of the main forms of affiliative behaviour in this species (Smith et al., 2011). Both meerkats (Bateman, Lewis, Gall, Manser, & Clutton-Brock, 2015) and hyaenas (Watts & Holekamp, 2007) are

highly territorial. In these species, polyadic forms of affiliation may not only allow individuals to access more partners more efficiently but also reinforce group cohesion and promote cooperative territorial defence at a group level. For instance, in chimpanzees, group cohesion increases before and during intergroup conflicts and border patrols (Samuni, Mielke, Preis, Crockford, & Wittig, 2019), and both territorial activities are often preceded by large and sometimes extended polyadic grooming sessions (Samuni et al., 2017). Whether polyadic social interactions are more frequent in highly territorial species is unclear. Furthermore, whether the form of social interaction, and especially polyadic grooming, allows an individual to interact with a larger number of social partners during the same amount of time than sequential dyadic interactions remains to be empirically tested.

In this study, we investigated the pattern of polyadic grooming and its consequences for the efficiency of accessing social partners in our two closest living relatives, the chimpanzees and the bonobos, *Pan paniscus*. As described above, the choice of grooming partners can be tightly linked to the formation of social relationships and access to future cooperation partners. We thus used the contrasting cooperation patterns of the two species (Boesch, Hohmann, & Marchant, 2002; Stumpf, 2011) to test the general hypothesis that the pattern of polyadic grooming exchange reflects the need for individuals to access social and cooperation partners. Here, we built our hypotheses under the assumption that polyadic grooming serves to maintain lower quality relationships with a large number of individuals (described in humans as 'lightweight social grooming', Takano, 2018), whereas dyadic grooming is potentially a more qualitative form of social bonding used to build and maintain strong social ties with a few individuals (see, for humans, Miritello et al., 2013). In turn, strong social ties may facilitate dyadic in-group cooperation, while weak social ties may support polyadic group level cooperation against a single in-group member (e.g. via the formation of large coalitions) or against other groups (see Table 1 for a summary of the predictions).

Chimpanzees and bonobos share similar social organization (multimale multifemale communities with a high degree of fission–fusion dynamics and female dispersal); yet they also exhibit striking differences in the degree of between-group competition they face, in the frequency of group level coordinated actions (e.g. hunting) and in the dominance relationship between the sexes (Pisor & Surbeck, 2019; Stumpf, 2011). Chimpanzees are highly territorial and engage in structured territorial border patrols, as well as hostile and sometimes lethal intergroup encounters (Samuni et al., 2017; Wilson et al., 2014). In chimpanzees, territoriality also has fitness consequences, whereby increased levels of neighbour pressure are associated with lower reproductive success in females (Lemoine et al., 2020). Therefore,

Table 1
Summary of the study predictions and results

Prediction	Statistical model	Supported by the study?	Note
1a. Chimpanzees engage in polyadic grooming more than bonobos	Model 1	Yes	
1b. Male chimpanzees and female bonobos engage in polyadic grooming more than the other sex		Partially	Male chimpanzees engaged in polyadic grooming more than females but male bonobos as well
2a. Polyadic grooming increases the number of grooming partners accessed per unit of time	Model 2	Partially	The increase in grooming partner access was only present in bonobos
2b. The effect of 2a is stronger in chimpanzees		No	
3a. Polyadic grooming is more frequent between partners who rarely associate with one another in parties	Model 3	No	
3b. Polyadic grooming is more frequent between partners who rarely groom each other		No	We found the opposite effect
3c. Polyadic grooming is more frequent between partners who are distant in dominance rank		Partially	This effect was found in bonobos but was reversed in chimpanzees

the fitness gains from becoming a dominating group may have shaped social behaviour to facilitate gaining the competitive edge against neighbouring groups. Specifically, this may have selected for group level cooperation in territorial defence, such as border patrols and coordinated attacks. In contrast, bonobos are not territorial and intergroup encounters are usually less hostile and can even be peaceful (Itani, 1990; Lucchesi et al., 2020; Sakamaki, Ryu, Toda, Tokuyama, & Furuichi, 2018). In chimpanzees, group level cooperation is not limited to intergroup conflicts since most chimpanzee populations hunt monkeys in groups, which increases the hunting success (Boesch, 1994; Samuni, Preis, Deschner, Crockford, & Wittig, 2018; Watts & Mitani, 2002), and some (e.g. in our study population in Taï) also routinely engage in collaborative coordinated hunting (Boesch, 2002). Bonobos at LuiKotale (our study population) also hunt monkeys (Surbeck & Hohmann, 2008) and monkey hunting may involve multiple group members (Hohmann & Fruth, n.d.) but hunting frequency is lower than in Taï chimpanzees (Girard-Buttoz, n.d.) and whether hunting is a coordinated action is still unclear. Finally, while all males are dominant over all females in chimpanzees (Wittig & Boesch, 2003), bonobos have a mixed-sex hierarchy with most females dominating most males but no consistent domination of one sex (Surbeck & Hohmann, 2013). Both species thus differ in their general level of group level cooperation which may affect the need to maintain weak social ties via affiliation (i.e. grooming) with a large number of individuals. In addition, their difference in intersexual dominance relationships may influence the social needs of males and females in each species. For instance, bonobo females may have an incentive to maintain weak social ties with several other individuals as they frequently form opportunistic coalitions with several other females, including both strongly and weakly bonded partners (i.e. the one they groom only rarely, Moscovice et al., 2017; Tokuyama & Furuichi, 2016). In our chimpanzee study communities in Taï, both males and females frequently engage in territorial defence so that the overall need of individual chimpanzees to form any social ties with a large number of individuals is high for both males and females. In contrast, in bonobos, this need might be limited to females and serve mostly for within-group competition.

We used the contrasting territoriality and cooperation pattern of chimpanzees and bonobos to assess whether these differences were reflected in the pattern of access to social partners in the group. We assessed the effect of species and sex on the use of polyadic grooming and the effect of polyadic grooming on the efficiency of access to social partners by comparing grooming dynamics between western chimpanzees in Taï and bonobos in LuiKotale. The pattern of dyadic grooming has been explored in both study populations. In Taï, males initiate more grooming bouts than females but both sexes preferentially groom individuals close in rank and direct grooming up the hierarchy (Mielke et al., 2018). Males and females use grooming to form stable long-lasting social relationships with a subset of group members (Gomes, Mundry, & Boesch, 2009) with whom they preferentially engage in cooperative activities such as food sharing (Samuni, Preis, Mielke, et al., 2018). In contrast, while both male and female bonobos have preferred grooming partners with whom they also associate preferentially in subgroups or parties (Moscovice et al., 2017; Surbeck & Hohmann, 2017), the grooming pattern is not reflected in the dyadic cooperation pattern, such as the formation of coalitions (Moscovice et al., 2017).

The specific aim of this study was to build on these findings by assessing how often polyadic grooming is used by males and females of each species and how this form of grooming compares to dyadic grooming in terms of the efficiency of access to partners and the characteristics of the social partner. Given the species differences in territoriality, we predicted that chimpanzees overall would

engage more in polyadic grooming than bonobos due to the higher incentive in this species to access a large number of partners (prediction 1a). Studies using comparative data and the same behavioural data protocol across species, specifically on Wamba bonobos and Mahale chimpanzees, have already found that the frequency of polyadic grooming is much higher in chimpanzees than in bonobos: 16% and 3.5% of the total grooming time, respectively (Nakamura, 2003; Sakamaki, 2013). We investigated whether this finding can be replicated in other populations. Given the species differences in sex-specific social bonds, dominance and cooperation structure we also expected sex differences with polyadic grooming rates being higher in the more cooperative sex, that is the sex that engages more frequently in within-group coalitions: males in chimpanzees (Boesch & Boesch-Achermann, 2000; Gilby et al., 2013; Langergraber, Mitani, & Vigilant, 2007; Surbeck et al., 2017) and females in bonobos (Moscovice et al., 2017; Surbeck et al., 2017) (prediction 1b). Further, we investigated whether polyadic grooming is used by individuals to access more partners per unit of time, as argued for polyadic conversational exchange by Dunbar (1993). We predicted that individuals who engage the most in polyadic grooming on a given day would have a higher number of partners accessed per minute of grooming (prediction 2a). We also predicted this effect to be stronger in chimpanzees than in bonobos since they might have evolved a polyadic grooming behaviour allowing them to access more partners per unit of time (e.g. by forming larger grooming clusters or switching partners more often) to respond to their social need to access more grooming partners, thereby promoting cooperative territorial defence (prediction 2b). Third, we tested and expanded the hypothesis proposed by Nakamura (2000) that apes living in societies with a high level of fission–fusion dynamics, such as chimpanzees and bonobos, may use polyadic grooming to temporarily access individuals with whom they rarely groom or associate in parties. While grooming is often given up the hierarchy in primates (e.g. Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Tiddi, Aureli, & Schino, 2012), low-ranking individuals usually access higher-ranking individuals close in rank since there might be some tolerance constraints for the lowest-ranking individuals to access individuals at the top of the hierarchy. In turn, both bonobos and chimpanzees may use polyadic grooming to alleviate these tolerance constraints, by enabling access to individuals with a large dominance rank distance to them. We thus assessed how the degree of spatial association and grooming frequency and the difference in social status (i.e. the difference in dominance score) affected the frequency at which individuals accessed each other via polyadic grooming. We predicted that polyadic grooming would be more frequent between partners who rarely associate with one another in parties (prediction 3a), who rarely groom each other (predicted 3b), and with whom there is a large dominance rank difference (prediction 3c). In our study, we focused on grooming exchanges between mature adult and subadult individuals since the cooperative need and motivation of infants and juveniles can be driven by different factors.

METHODS

Study Communities

We conducted the study within the Taï Chimpanzee and the LuiKotale bonobo projects between February 2015 and December 2017 on three fully habituated wild ape communities: two chimpanzee communities (Taï East and Taï South) at the Taï National Park, Côte d'Ivoire (Wittig, 2018) and one bonobo community (LuiKotale Bompusa) at the LuiKotale bonobo research site, Republic Democratic of Congo (Fruth & Hohmann, 2018). For this

study, we focused on adult and subadult individuals (i.e. all individuals 10 or more years of age, hereafter 'adults'). The Taï East chimpanzee community comprised 13 adults (five males and eight females), the Taï South chimpanzee communities comprised 21 adults (seven males and 14 females). One female in Taï East was very shy towards the observers and therefore could not be observed. One male in Taï South died during the study. Finally, the LuiKotale Bompusa community comprised 20 adults (seven males and 13 females).

Ethical Note

The 'Ethikrat' of the Max Planck Society gave ethical approval for the study.

Behavioural Observations

We conducted behavioural observations during two field periods for each of the three communities using identical protocols: February–September 2016 and February–May 2017 for the two chimpanzee communities and February 2015–May 2016 and August–December 2017 for the bonobo community. C.G.B. and six field assistants collected the behavioural data. M.S. initially trained C.G.B. and a field assistant in data collection on bonobos and subsequently, C.G.B. trained three other field assistants who collected data on the bonobos. L.S. trained C.G.B. and the two field assistants collecting data on chimpanzees and we conducted interobserver tests between C.G.B., L.S. and each of the assistants to ensure consistency in data collection (interobserver reliability test, Cohen Kappa >0.9 across all data collectors). The two chimpanzee communities were followed from dawn to dusk (i.e. from when they come out of their night nest in the morning to when they build the nest in the evening). The bonobos were usually followed for half a day either from dawn to noon or from noon to dusk. We conducted focal behavioural observations (Altmann, 1974) on 53 adults (33 chimpanzees and 20 bonobos). We followed the same individual during an entire half-day either in the morning or in the afternoon (ca. 6 h focal follows). When the community was followed for the entire day the observer changed the focal individual around noon (1200 for bonobos and 1230 for chimpanzees since sunrise is later in Taï than in LuiKotale i.e. 0615–0645 versus 0515–0545). We balanced focal follows between morning and afternoon follows for each individual and we chose the order in which the individuals were followed pseudorandomly since this had to be adjusted depending on the individuals present in the party at the beginning of the focal follow. We followed the focal individual until the end of the half-day focal period regardless of changes in the party composition and even when the individual ended up alone so as not to bias data collection towards larger parties with potentially more social interactions occurring than average. During the focal follow, we continuously recorded the activity of the focal individual, the time it spent out of sight as well as any social interaction with other individuals in the party using CyberTracker software (CyberTracker, Cape Town, South Africa) and a Caterpillar smartphone (Catphone Mobile Ltd, Wackersdorf, Germany). In addition, we recorded ad libitum (Altmann, 1974) all the dyadic aggression occurring between adult members of the community and, for chimpanzees, the exchange of pant-grunts, a unidirectional vocalization uttered from subordinate to dominant individuals (Wittig & Boesch, 2003).

Grooming Data Collection

When the focal individual engaged in allogrooming as groomer (actor), groomee (recipient) or both, we recorded the identities of

the individual grooming the focal individual, the individual being groomed by the focal individual and all the individuals present in the grooming cluster but not directly interacting with the focal individual. We defined the grooming cluster from the focal individual's perspective as all the individuals that were grooming directly with the focal individual, with the grooming partners of the focal individual and with their partners (e.g. if A is the focal individual and A grooms B but B grooms C, then the cluster comprises A, B and C and if C is groomed by D then the cluster comprises A, B, C and D). All changes in the identity of the individual grooming or being groomed by the focal individual, as well as changes in the grooming cluster composition, were recorded continuously to the second. A grooming session was defined as a continuous grooming interaction between the focal individual and one or more individuals with less than 5 min interruption in grooming activity. To assess which renewed grooming activity after a pause should be considered as a new grooming session, we examined the temporal distribution of the duration of grooming interruption between grooming sessions, i.e. the latency between the end of grooming between the focal individual and a given partner(s) and the resumption of grooming between the focal individual and the same partner(s). Although we could not detect a clear threshold in the distribution at which this latency was clearly less likely to occur, over 90% of grooming interruptions lasted less than 5 min. Furthermore, a 5 min pause is a criterion commonly used in the study of bonobo and chimpanzee grooming to identify a new grooming session (Mielke et al., 2018; Nakamura, 2000; Sakamaki, 2013; Surbeck & Hohmann, 2015). Therefore, we applied the same criterion to make our study comparable. A new session started whenever the identity of any adult partner in the grooming cluster changed (see above for definition of a grooming cluster) or when the focal individual was not engaged in allogrooming (either as groomer or groomee) for more than 5 min. We defined the sessions as such to capture whether each session was dyadic or polyadic. A dyadic interaction can become polyadic if an individual joins the cluster. In this case, a new session started when the third individual entered the grooming cluster and the first part of the interaction (dyadic) and the second part (polyadic) were treated as two separate sessions. Conversely, a polyadic session interaction can become dyadic if an individual leaves the cluster. In this case, this interaction was treated as one polyadic session followed by a dyadic session and entered as two separate data points in our analysis. Overall, we defined a polyadic grooming session as a session during which two or more individuals other than the focal individual were part of the focal individual's grooming cluster. Accordingly, we assigned to each session whether they were polyadic 'yes' or 'no', and each session provided a data point for our two statistical binomial models 1 and 3 (see below). Note that the focal individual could participate in a polyadic grooming cluster even if it exchanged grooming with only one partner, if this partner was grooming someone else (e.g. focal individual A is in a polyadic grooming cluster if A grooms B and B grooms C).

Assessment of the Dominance Hierarchy

We calculated the dominance hierarchy in each of the study communities using a modified version of the Elo-rating method (Neumann et al., 2011) developed by Foerster et al. (2016) (see Appendix). For the two chimpanzee communities, we used unidirectional submissive pant-grunt vocalizations (given by the lowest ranking of the two individuals towards the highest ranking, Bygott, 1979). We used all the long-term data available from the Taï chimpanzee project, which includes consistently collected ad libitum data from field assistants, students and researchers since 1999 in Taï South and since 2007 in Taï East. For the bonobos long-term

data on both sexes were not available so we used only the data we collected from February 2015 onwards. We used dyadic dominance interactions with a clear winner and a clear loser (i.e. displacements or charges and chases followed by a fleeing or avoidance behaviour of the recipient). Details on how the Elo-ratings were compiled are provided in the Appendix. All Elo-rating scores were standardized between 0 and 1 with 1 being the highest-ranking individual and 0 the lowest ranking daily. We then extracted the Elo-rating score of each individual on the day when each grooming bout occurred.

Assessment of the Association and Grooming Index

To investigate our hypothesis that polyadic grooming allows chimpanzees and bonobos to groom individuals with whom they rarely associate in parties (prediction 3a) and/or which are rare grooming partners (prediction 3b), we constructed two dyadic social indices (similar to the dynamic sociality index DDSI, Kulik, 2015): the dynamic dyadic association index (DDAI) and the dynamic dyadic grooming index (DDGI, see Samuni, Preis, Mielke, et al., 2018). Both indices are considered dynamic since, much like the Elo-rating, they track temporal fluctuations in dyadic associations and grooming patterns. The DDAI value of a dyad increases after each 30 min party in which they have been observed together. Likewise, the DDGI represents a dyadic value that increases after each grooming interaction with the magnitude of the increase proportional to the duration of the grooming event. When the DDAI and DDGI values of a dyad increase, the respective indices of all other dyads comprising one of the two individuals in the dyad proportionally decrease so that the average of both indices remains 0.5 across all dyads in the community. We wanted to assess the DDAI and DDGI independently from the grooming interactions or association patterns occurring on a given observation day. Accordingly, we extracted the DDAI and DDGI values for each dyad the day before each specific grooming bout occurred. Both values were standardized between 0 and 1 within groups and observation days to ensure comparability of the data.

Statistical Analysis

We used a series of generalized linear mixed models (GLMMs) to test our predictions regarding species and sex differences on the general rate of polyadic grooming, the effect of polyadic grooming on the number of partners accessed and the social characteristics of the partners accessed via polyadic grooming (Table 1). For all statistical models, we used community as a predictor variable rather than species because community could not be incorporated as a random factor due to its lack of level (only three study groups). This inclusion also provides the advantage of detecting whether the pattern found is consistent across the two chimpanzee communities, which allows for assessing whether the effect is more likely to be population or community specific.

Species and sex differences in polyadic grooming model

In the first model (polyadic grooming occurrence model, Model 1) we addressed the hypothesis that polyadic grooming is related to the general need to maintain access to potential cooperation partners. Specifically, we tested prediction 1a that the species engaging the most frequently in group level coordinated activities (i.e. the chimpanzees) also engages most in polyadic grooming, possibly as a means to maintain social relationships with a wider range of partners. We also tested prediction 1b that the most 'cooperative' sex in each species (i.e. males in chimpanzees and females in bonobos) would engage more in polyadic grooming for the same reason. In Model 1, we used each grooming session as one data point and defined whether the session was dyadic or polyadic. We then built a

GLMM with 'was the session polyadic yes/no' as the response variable and focal sex, study community and the interaction between the two variables as test predictors. We included the interaction here since the sex effect on polyadic grooming rate is expected to be different between chimpanzees and bonobos and, therefore, community specific. In Model 1, we also added the number of adult individuals present in the party during the grooming session, to control for partner availability. To avoid pseudoreplication, we incorporated focal individual identity as a random factor. Dyadic sessions that turned into polyadic sessions or vice versa produced two data points which were not fully independent. Since only about 20% of the grooming sessions in chimpanzees and about 10% of the grooming sessions in bonobos were polyadic, a vast majority of sessions were independent of each other. Creating a random factor of 'event number' and assigning a similar number to two consecutive non-independent sessions would not provide an accurate estimate of the variance of this random factor, since around 85% of levels would have only one data point in the data set. We therefore did not include this random factor in our analyses. However, to ensure that the problem of nonindependence did not alter our results, we ran a set of additional permutation analyses by randomly selecting only one data point for each level of the factor 'grooming bout event number' and rerunning Model 1 on this subset of data 100 times. We then averaged the estimates and *P* values from these 100 models (see details in Appendix).

Polyadic grooming and partner access model

In the second model (grooming partner access model, Model 2) we addressed the hypothesis that polyadic grooming enhances the efficiency of access to a large number of partners per unit of time. We tested the prediction 2a that the rate of polyadic grooming per focal follow (half-days) positively influences the number of partners accessed per minute of grooming. In Model 2, each half-day focal follow constituted a data point and we only considered focal follows during which the focal individual groomed with conspecifics for at least 5 min in total (i.e. regardless of the duration of the single grooming session so that even very short grooming interactions were considered since the aim was to assess the total number of partners accessed that half-day). We applied this criterion since days with less than 5 min of grooming created some instability in our statistical model due to highly variable and unreliable estimation of the number of partners accessed per minute based on very short grooming times. Through this process, we removed 140 days during which the focal individual groomed for less than 5 min in total (out of 437 days, i.e. 32%). In each community, at least some males and females groomed less than 5 min on at least 1 day so that the days removed were not concentrated on a single community or sex (see Appendix Table A1 for details). In this model, we used the number of adult partners groomed that half-day as the response variable and the percentage of grooming time with adults that was polyadic, the study community and the interaction between these two variables as test predictors. Here we included the interaction between community and polyadic grooming time to test prediction 2b that the effect of polyadic grooming on partner access efficiency is stronger in chimpanzees than in bonobos. To control for sex differences in grooming partner access we also added focal sex as a control factor as well as its interaction with community since chimpanzee males are expected to have access to more grooming partners than females whereas the reverse is expected in bonobos. For the same reason, we also incorporated the rank (Elo-ratings) of the focal individual that day since higher-ranking individuals potentially have access to more grooming partners due to the reduced social constraints on partner choice. We also incorporated the number of potential adult partners available during the focal follow as a control factor and the log

of the total grooming time (s) as an offset term (to assess the number of partners accessed per unit of grooming time). Finally, we added focal identity as a random factor to avoid pseudoreplication.

In addition to Model 2, we wanted to assess how the use of dyadic and polyadic grooming was distributed across the dyads and whether it differed across the different sex combinations in Tai chimpanzees and LuiKotale bonobos. In particular, we investigated whether certain dyads access each other only via dyadic or only via polyadic grooming to better understand whether polyadic grooming serves not only to access more partners more rapidly but also to access certain partners who are never accessed via dyadic grooming.

Polyadic grooming and access to rare social partner model

In the third model (Model 3) we tested the hypothesis that polyadic grooming is used to access rare social partners to maximize the efficiency of social interactions over limited opportunities. We tested the predictions that both species engage in polyadic grooming more with individuals with whom they rarely associate in parties (prediction 3a) and/or with individuals who are rare grooming partners in general (prediction 3b). We also tested the prediction that individuals engage in polyadic grooming more with conspecifics with whom they are distant in dominance rank since the polyadic grooming set-up may alleviate some tolerance constraints pertaining to dyadic grooming (prediction 3c). For Model 3, we used the same grooming sessions as in Model 1, but we broke the polyadic sessions down into several dyadic sessions (with one line for each social partner); each resulting dyadic data point was used in the model in addition to all the original dyadic sessions. Note that the dyadic data points derived from polyadic grooming sessions relate to each of the partners that a given focal individual was grooming and/or being groomed by in a given polyadic grooming cluster. Partners who were present in the polyadic grooming cluster but did not directly groom or were groomed by the focal individual were not included in these dyads. As in Model 1, the response variable was whether the bout was polyadic (yes/no) but the approach we applied here allowed us to investigate the influence of the characteristics of the dyad on the likelihood of the bout being polyadic. We used DDAI, DDGI and dominance rank difference (absolute difference in Elo-rating score between the two individuals of the dyad) as predictor variables, all in interaction with community. We also incorporated the sex combinations between the two individuals (three levels: male–male, male–female and female–female) in interaction with species to account for the fact that different sex combinations groom each other at different rates in the two species, which may in turn influence the likelihood of polyadic grooming. We also included whether individuals were kin or not as a control variable and the number of individuals in the party at the time of the grooming session to account for partner availability. Finally, we added focal identity, the partner identity and the dyad identity as random factors to avoid pseudoreplication. As in Model 1, polyadic sessions that became dyadic and vice versa were also not independent. We ran similar permutations as for Model 1 to ensure that this nonindependence did not affect our results (see details in the [Appendix](#)).

All analyses were conducted in R 3.5.1 (R Core Team, 2018) using the function `glmer` from the package ‘lme4’ (Bates, Mächler, Bolker, & Walker, 2015). For all models, we included the maximal random slope structure between each fixed predictor (test and control) and each random effect (Baayen, Davidson, & Bates, 2008; Barr, Levy, Scheepers, & Tily, 2013). In each model, we tested for the overall significance of the test predictors by comparing the full model to a null model comprising all control predictors, all the random effects and random slopes, but without the test predictors. We tested each full model against its corresponding null model using a likelihood ratio test (LRT, Dobson, 2002). We then assessed the significance of each predictor variable using an LRT between the full model and a reduced model comprising all the variables except the one to evaluate. This process was repeated across all variables using the `drop1` function. If the LRT revealed that one interaction had a P value > 0.1 (the threshold for a trend) we reran the model without this interaction and reassessed the significance of all the predictors.

For each model we tested for collinearity issues between our predictor variables using the function `vif` from the package ‘car’ (Fox & Weisberg, 2011). Collinearity was not an issue (all $vif < 1.5$). We also assessed model stability removing one level of each random effect at a time and recalculating the estimates of the different predictors which revealed no stability issues. Finally, we tested for overdispersion in Model 2 (Poisson error structure), which showed no overdispersion (dispersion parameter = 1.24).

RESULTS

We collected a total of 3413 focal hours of data (Table 2). During these focal hours, we recorded 140.8 h of grooming between the focal and adult grooming partners (Table 2) over 1468 different sessions (534 sessions in Tai East, 573 sessions in Tai South and 361 sessions in LuiKotale Bompusa). The time allocated to grooming was higher in bonobos (Table 3). A total of 248 adult–adult dyads groomed each other during the focal observation (56/66 (85%) in Tai East, 123/190 (65%) in Tai South and 69/190 (36%) in LuiKotale Bompusa; Table 4). Maternal kin (i.e. mother–son, mother–daughter and maternal siblings) accounted for five of these dyads in bonobos (out of eight maternal kin dyads) and one (out of three maternal kin dyads) in chimpanzees. Four of the five bonobo adult–adult kin dyads were mother–son dyads (i.e. all possible mother–son dyads since the three other males in the community had lost their mother before the study period). In contrast, the only kin dyad that groomed during the observation hours in chimpanzees was a sister–brother dyad. Table 1 summarizes the main findings of our study in relation to the original predictions.

Species and Sex Differences in Polyadic Grooming

The predictor variables community ID and sex significantly influenced the rate of polyadic grooming (full–null model comparison in the polyadic grooming occurrence model, Model 1, LRT: $\chi^2_5 = 28.53$, $P < 0.001$). The interaction between community and sex was not significant (LRT: $\chi^2_2 = 0.58$, $P = 0.749$). A reduced

Table 2

Summary for the three study communities of the number of individuals studied, overall observation and grooming time, and number of grooming days

	LuiKotale Bompusa	Tai East	Tai South
No. of adult focal individuals	20	12	21
No. of focal adult males	7	5	7
No. of focal adult females	13	7	14
Total focal observation time (h)	1228	983	1202
Total focal grooming time (h)	67.5	35.6	37.7
No. of half-days with total grooming time >5 min	88	98	111

Table 3

Detailed summary of observation time and grooming time per individual per community, grooming session durations, polyadic grooming time and the number of grooming partners accessed

	LuiKotale Bompusa				Taï East				Taï South			
	Mean	SE	Min	Max	Mean	SE	Min	Max	Mean	SE	Min	Max
Observation time per individual (h)	61.4	0.9	54.5	68.1	81.9	4.3	45.0	98.3	57.3	4.8	8.7	85.6
Grooming time with adult partners per individual (min)	202.6	31.3	3.0	504.4	177.9	30.4	18.7	326.2	107.7	27.2	5.8	527.2
% Observation time spent grooming adults	5.6	0.9	0.1	13.1	3.5	0.5	0.5	5.6	3.2	0.7	0.1	13.8
Dyadic session duration (min)	12.3	3.6	1.0	109.8	4.4	1.5	1.0	42.6	4.3	1.0	1.0	32.0
Polyadic session duration (min)	3.2	0.4	1.0	9.7	2.6	0.5	1.0	10.2	2.8	0.5	1.0	20.7
% Daily grooming time with adults that was polyadic	7.4	3.6	0.0	68.3	15.4	4.4	0.0	58.4	15.1	2.4	0.0	48.8
No. of grooming partners accessed per half-day	1.5	0.1	1.0	4.0	3.0	0.3	1.0	9.0	3.1	0.2	1.0	10.0

Table 4

Summary of the number and percentage of dyads that groomed within dyadic and polyadic sessions in the three study communities

Sex combination	Lui Kotale bonobos			Taï East chimpanzees			Taï South chimpanzees		
	FF	MM	FM	FF	MM	FM	FF	MM	FM
No. of dyads	78	21	91	21	10	35	91	15	84
No. of dyads that groomed	31	6	32	14	10	32	47	13	63
% Dyads that groomed	39.7	28.6	35.2	66.7	100.0	91.4	51.6	86.7	75.0
No. of dyads that groomed only in dyadic sessions	21	4	19	4	0	14	26	5	29
% Grooming dyads that groomed only in dyadic sessions	67.7	66.7	59.4	28.6	0.0	43.8	55.3	38.5	46.0
No. of dyads that groomed in dyadic and polyadic sessions	9	2	12	10	10	17	15	8	28
% Grooming dyads that groomed in dyadic and polyadic sessions	29.0	33.3	37.5	71.4	100.0	53.1	31.9	61.5	44.4
No. of dyads that groomed only in polyadic sessions	1	0	1	0	0	1	6	0	6
% Grooming dyads that groomed only in polyadic sessions	3.2	0.0	3.1	0.0	0.0	3.1	12.8	0.0	9.5

F: female; M: male.

Table 5

Results of the three GLMMs

Model	Response	Predictor	Estimate	SE	CI _{low}	CI _{high}	χ^2	<i>P</i>
1	Was the grooming session polyadic? (Y/N)	Intercept	-2.36	0.19	-2.80	-2.00		
		Community (Taï East)	0.85	0.21	0.47	1.30	17.36	<0.001
		Community (Taï South)	0.74	0.21	0.36	1.18		
		Sex (male)	0.56	0.14	0.30	0.84	11.56	0.001
		No. of adults in the party ^a	0.20	0.09	0.01	0.38	3.88	0.049
2	No. of adult grooming partners accessed	Intercept	-7.29	0.12	-7.56	-7.07		
		% Grooming time that was polyadic	0.43	0.13	0.08	0.63		
		Community (Taï East)	1.06	0.19	0.72	1.44		
		Community (Taï South)	1.44	0.17	1.11	1.78		
		Sex (male) ^a	-0.11	0.19	-0.47	0.25		
		Dominance rank i.e. Elo score ^a	-0.10	0.07	-0.25	0.05	1.94	0.163
		No. of potential adult grooming partners ^a	0.24	0.05	0.15	0.34	17.37	<0.001
		% Polyadic*Community (Taï East)	-0.44	0.14	-0.68	-0.10	7.90	0.019
		% Polyadic*Community (Taï South)	-0.34	0.14	-0.58	0.00		
		Sex (male)*Community (Taï East)	0.41	0.29	-0.20	0.94	8.04	0.018
		Sex (male)*Community (Taï South)	-0.22	0.28	-0.79	0.33		
3	Was the grooming session polyadic? (Y/N) (dyadic analysis)	Intercept	-2.57	0.32	-3.31	-1.99		
		Community (Taï East)	1.62	0.35	1.01	2.36		
		Community (Taï South)	1.41	0.32	0.84	2.14		
		DDAI	0.57	0.26	0.08	1.19		
		Dominance rank difference i.e. Elo score difference	0.62	0.27	0.07	1.17		
		Sex combination (F-M)	0.09	0.27	-0.43	0.67	3.33	0.189
		Sex combination (M-M)	0.53	0.29	-0.05	1.08		
		DDGI	0.26	0.11	0.05	0.47	5.53	0.019
		Kin (Y/N) ^a	-0.51	0.49	-1.62	0.43	1.09	0.296
		No. of adults in the party ^a	0.35	0.10	0.15	0.55	9.79	0.002
		Community (Taï East)*DDAI	-0.77	0.33	-1.51	-0.15	5.20	0.074
		Community (Taï* South)*DDAI	-0.52	0.30	-1.17	0.04		
		Community (Taï East)*rank difference	-1.16	0.35	-1.86	-0.49	12.23	0.002
		Community (Taï South)*rank difference	-0.74	0.33	-1.39	-0.11		

Y: yes; N: no; F: female; M: male; DDAI: dynamic dyadic association index; DDGI: dynamic dyadic grooming index. Model 1 investigated species and sex differences in the rate of polyadic grooming. Model 2 investigated the effect of polyadic grooming on partner access and Model 3 investigated the social characteristics of the grooming partner accessed via polyadic grooming. In each model, the reference levels are 'LuiKotale Bompusa' for community, 'female' for sex, and 'FF' for the sex combination. SE indicates the standard error of the estimate for each predictor. The coded level for each categorical predictor is indicated in parentheses. Significant *P* values (<0.05) are indicated in bold. Trends (*P* < 0.1) are indicated in italics. CI_{low} and CI_{high} indicate the lower and upper limits of the 95% confidence interval for the estimates of each predictor.

^a Control predictors.

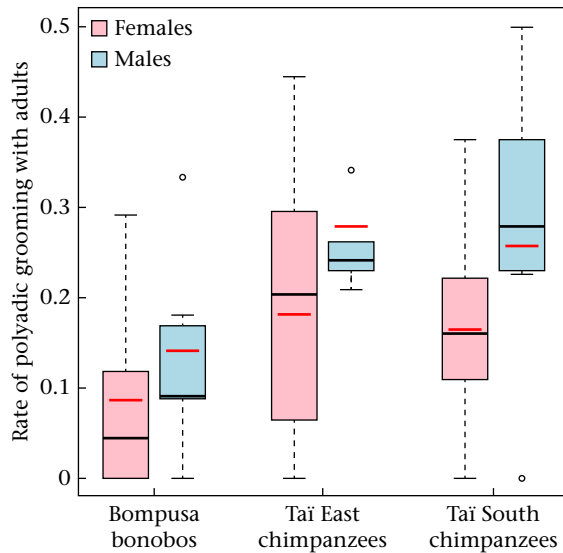


Figure 1. Rate of polyadic grooming for males and females in the three study communities. The box plot indicates the median (thick black line) and 25% and 75% quartiles. Dashed horizontal lines indicate the 10% and 90% deciles. Open dots indicate the data points that did not fall within the 10–90% deciles. The red horizontal line indicates the model prediction (Model 1).

model without this interaction revealed that in all three communities, males engaged significantly (1.5 times) more often in polyadic grooming than females (Table 5; mean \pm SE percentage of polyadic grooming sessions: males = $22.1 \pm 3.1\%$, females = $14.1 \pm 2.1\%$, $P = 0.001$; Fig. 1). Independent of the sex of the focal individual, chimpanzees in both communities engaged significantly more (over twice as much) in polyadic grooming than bonobos (mean \pm SE percentage of polyadic grooming sessions per individual: Tai East = $22.1 \pm 3.7\%$, Tai South = $21.1 \pm 2.8\%$ and LuiKotale Bompusa = $9.5 \pm 2.28\%$, $P = 0.001$; Fig. 1). The results based on permutations controlling for the nonindependence of consecutive dyadic and polyadic sessions with the same partners were similar to those of Model 1 (i.e. both predictors sex and community were also significant in the permutations; Appendix Table A2).

Polyadic Grooming and Access to a Wide Range of Partners

When engaging only in dyadic grooming, bonobos accessed on average almost five times fewer partners than chimpanzees in both study communities (as shown in Fig. 2 on half-days with 0% polyadic grooming; Tai East: 0.14 partners per minute of grooming; Tai South 0.14; LuiKotale Bompusa: 0.03). Only when bonobos invested between 70 and 90% of their grooming time in polyadic grooming (which happened very rarely; Fig. 2) did they access a similar number of grooming partners per minute of grooming as chimpanzees (Fig. 2). That is because polyadic grooming had a strong influence on the number of adult grooming partners accessed (full-null model comparison in the efficiency of access to grooming partner model, Model 2, LRT: $\chi^2_5 = 16.93$, $P = 0.005$) but only in bonobos (interaction percentage of polyadic grooming*community, LRT: $\chi^2_2 = 7.90$, $P = 0.019$; Table 5). More specifically, the model predicted the number of partners accessed per minute of grooming to be over eight times higher on days with only polyadic grooming than on days with only dyadic grooming (0.03 partners per min on fully dyadic days versus 0.26 partners per min on fully polyadic days, Fig. 2). In contrast, polyadic grooming did not increase the number of partners accessed per minute of grooming in Tai East and had only a weak effect in Tai South chimpanzees (Fig. 2). However, as bonobos rarely engaged in polyadic grooming, the

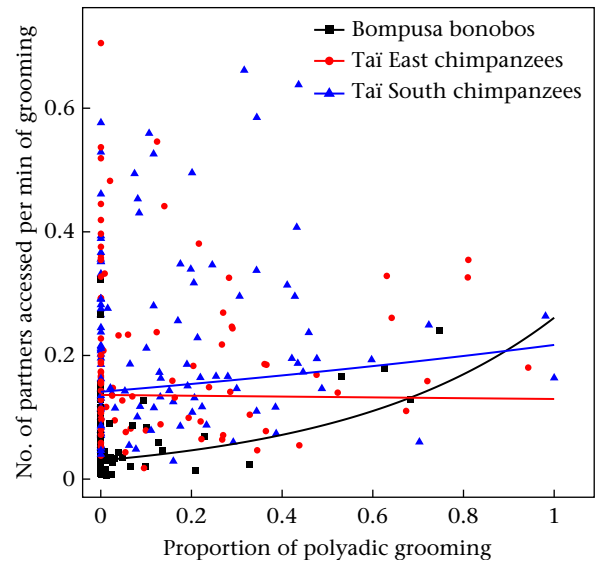


Figure 2. Influence of polyadic grooming on the number of partners accessed per minute of grooming. Each half-day focal follow is depicted by one symbol. The lines indicate the predictions of Model 2 for the three communities.

average number of grooming partners accessed per half-day was lower in bonobos than in chimpanzees (Table 3) and this difference was reflected in the number of dyads that groomed each other during the study period (Table 4).

In the access to grooming partner model (Model 2), the sex of the focal individual also had an effect on the number of grooming partners accessed per min but this effect was different across the three communities, as revealed by the significant interaction between community and sex (Table 5). The sex effect was not consistent across the two chimpanzee communities with Tai East males accessing more partners per minute of grooming than females and females accessing more partners than males in Tai South (Fig. A1). The sex effect in bonobos was weak (Fig. A1). Finally, the number of potential partners present in the party during the half-day focal follow had a significant positive effect on the number of grooming partners accessed per min (Table 5); however, the dominance rank of the focal subject did not (Table 5).

Distribution of Dyadic and Polyadic Grooming Across Dyads

Across all sex combinations, the percentage of all possible dyads in each community that were observed grooming at some point during the study was lower in bonobos than in the two chimpanzee communities (Table 4). Among the dyads that groomed each other, only around one-third of bonobo dyads across all sex combinations groomed each other using polyadic grooming and most dyads only engaged in dyadic grooming (Table 4). In contrast, in chimpanzees, across all sex combinations except female–female in Tai South, most of the dyads (and in particular male–male dyads) groomed each other within both dyadic and polyadic sessions (Table 4). Finally, the percentage of dyads that groomed each other only in polyadic sessions was 3% or less across all sex combinations in bonobos and Tai East chimpanzees as well as for male–male dyads in Tai South chimpanzees (Table 4). A small portion of female–female and female–male dyads groomed each other only in polyadic grooming sessions in Tai South chimpanzees (Table 4).

Polyadic Grooming and Access to Rare Social Partners

Dyadic social characteristics (i.e. partner specificity) significantly influenced the likelihood of polyadic grooming (full-null

model comparison in Model 3, $LRT: \chi^2_{13} = 28.51, P = 0.008$). Yet contrary to prediction 3a, in all communities, the likelihood of a given grooming bout within a dyad being polyadic was higher if these two individuals groomed more often in general (i.e. with a high DDGI; Table 5). The dominance rank difference between two partners also significantly influenced the likelihood of polyadic grooming but the effect differed across the three communities (Table 5). While in both chimpanzee communities, individuals engaged more frequently in polyadic grooming with individuals closer in rank (with a stronger effect in Taï East than in Taï South), bonobos more frequently engaged in polyadic grooming with individuals further in rank (Fig. 3). There was a trend towards DDAI influencing the likelihood of polyadic grooming in interaction with community ($LRT: \chi^2_2 = 5.20, P = 0.074$; Table 5). Yet, unlike the other community differences, the different pattern observed here was between the two chimpanzee communities and not between chimpanzees and bonobos (Fig. 4). While both bonobos and Taï South chimpanzees engaged in polyadic grooming more often with individuals they often associated with (i.e. high DDAI), with a much stronger effect for the bonobos ($\beta = 0.57$) than for Taï South chimpanzees ($\beta = 0.05$) (Fig. 4), Taï East chimpanzees engaged in polyadic grooming more often with individuals they least often associated with ($\beta = -0.2$) (Fig. 4). As in Model 1, the number of adult individuals in the party (i.e. the number of potential grooming partners) also had a significant positive effect on the likelihood of polyadic grooming occurring (Table 5) but not kinship or sex combination (Table 5). The results based on permutations controlling for the nonindependence of consecutive dyadic and polyadic sessions with the same partners were similar to those of Model 3 (i.e. the predictors DDGI and community*rank difference were also significant in the permutations and the predictor community*DDAI was significant in the permutations and only a trend in Model 3; Table A2).

DISCUSSION

In this study, we tested a set of hypotheses linking the function of polyadic grooming to cooperative and social needs in

chimpanzees and bonobos (Nakamura, 2000; see also Table 1). As we predicted, both males and females of the more territorial species, the chimpanzees, engaged more in polyadic grooming than individuals of both sexes of its less territorial sister species, the bonobo. In addition, we found evidence, in bonobos only, for the suggested function of polyadic social interactions in general (Dunbar, 1993), and of polyadic grooming in particular (Nakamura, 2000), to groom more partners within the same time period. This highlights that polyadic grooming may be used to fulfil different needs in the two species (discussed below). In turn, the fact that polyadic grooming does not increase the efficiency of access to grooming partners in chimpanzees challenges Dunbar (1993) view of polyadic conversations having evolved from humans' need to save time allocated to social interactions. Our study shows that polyadic social interactions do not consistently result in increased partner access per unit of social time across our two closest relatives. In both species, males engaged more in polyadic grooming than females. This result does not support our predictions of species-specific sex differences in rates of cooperation, with only chimpanzees following our predicted pattern (Table 1). Furthermore, in both species, and contrary to our prediction (based on Nakamura, 2000), polyadic grooming did not appear to consistently serve the function of accessing rare grooming partners or rare associates. In fact, polyadic grooming was more often used with frequent grooming partners, and the effect of association in parties on polyadic grooming patterns was inconsistent across the two chimpanzee communities. This was also reflected in the fact that, except for female–female and female–male dyads in Taï South chimpanzees, virtually all other dyads in Taï chimpanzees and LuiKotale bonobos who groomed each other within polyadic grooming clusters also groomed each other dyadically. Moreover, when examining the characteristics of dyads, we found that chimpanzees tended to be more likely to participate in polyadic grooming with conspecifics closer in dominance rank (which are usually the preferred grooming and food-sharing partners in the Taï population; Mielke et al., 2018; Samuni, Preis, Mielke, et al., 2018), while LuiKotale bonobos engaged in polyadic grooming more often with individuals further away in dominance rank. Finally, our study reveals some general differences in the diversity of adult grooming partners between Taï chimpanzees and LuiKotale bonobos. Less

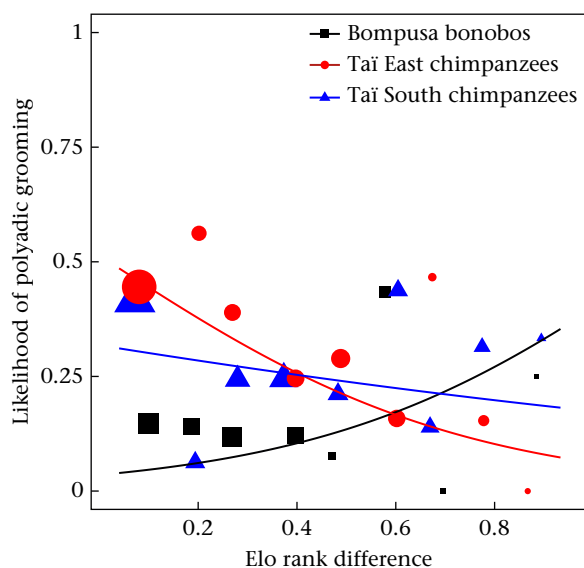


Figure 3. Influence of dominance rank difference on the dyadic occurrence of polyadic grooming. Each grooming bout is depicted by one symbol. The lines indicate the predictions of Model 3 for the three communities. The size of each symbol is proportional to the number of data points.

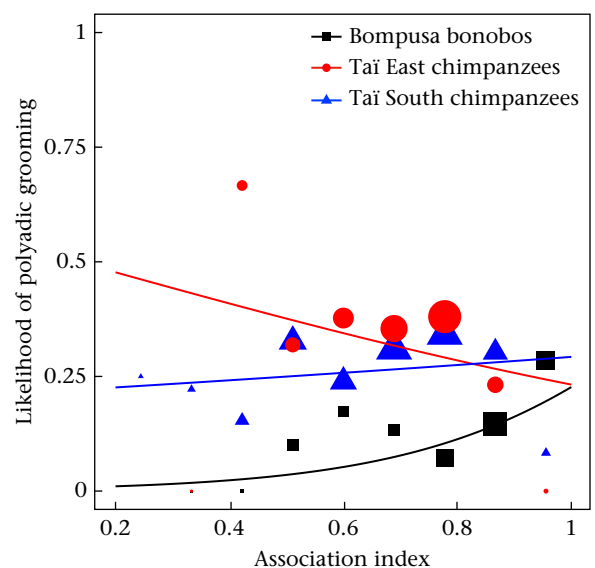


Figure 4. Influence of the dynamic dyadic association index (DDAI) on the dyadic occurrence of polyadic grooming. Each grooming bout is depicted by one symbol. The lines indicate the predictions of Model 3 for the three communities. The size of each symbol is proportional to the number of data points.

than 50% of all possible adult–adult dyads in each sex combination groomed each other in bonobos whereas in chimpanzees over 50% of possible adult–adult dyads groomed and this number reached 100% for male–male dyads in Tai East chimpanzees (Table 4). Our study also showed that, on average, the Tai chimpanzees accessed more partners per minute of grooming. This result indicates that they change partners more often than LuiKotale bonobos and, therefore, devote, on average, less time to each partner. Our study has some limitations since it reports data on two communities from one population of chimpanzees and one community in one population of bonobos and we are aware that the pattern described here might not apply to the two species as a whole.

The difference in grooming partner selectivity and in the use and effect of polyadic grooming between Tai chimpanzees and LuiKotale bonobos highlights different potential strategies in the two populations of the two species in terms of grooming partner choice in response to different social needs. Tai chimpanzees appear to use dyadic grooming in a fluid way to access a large number of grooming partners by changing grooming partners more often than LuiKotale bonobos. In Tai chimpanzees, polyadic grooming, on the other hand, might serve to strengthen further social bonds with preferred affiliative partners in a different social constellation, as it was mostly used with strongly bonded partners and only rarely with partners who never groomed dyadically (Table 4). In contrast, LuiKotale bonobos did not appear to need to access a large number of grooming partners on a regular basis and their grooming was highly selective and targeted to a narrow number of partners since less than 50% of all possible dyads in each sex combination groomed each other in LuiKotale bonobos (Table 4). LuiKotale bonobos also contrasted with Tai chimpanzees in that they appeared to use polyadic grooming to access more grooming partners in a shorter time, but this ‘social strategy’ was relatively rare. Yet LuiKotale bonobos as well did not use polyadic grooming to expand their overall grooming network since the partners that they groomed within polyadic grooming sessions were the same partners that they groomed dyadically (Table 4).

In chimpanzees, maintaining a broad social network, via access to a large number of grooming partners, might be crucial to ensure cohesive group territory defence. Both male and female chimpanzees build specific relationships with a subset of individuals, some of which are labelled social bonds (Crockford et al., 2013; Lehmann & Boesch, 2009; Mitani, 2009). Yet they need to maintain some level of social relationship with all in-group conspecifics because every one of them may be needed for territorial defence (Samuni et al., 2017). In turn, outnumbering opponents might be a key determinant to winning intergroup encounters (Wrangham, 1999) and social cohesion can contribute to shifting the imbalance of power in one’s own favour since it allows parties (subgroups) to be larger if individuals stay together as a social unit (Samuni et al., 2019; Wrangham & Glowacki, 2012). It is therefore not surprising that, via dyadic grooming, Tai chimpanzees accessed five times more partners per minute of grooming than LuiKotale bonobos. What is more surprising, and against our expectation, is that polyadic grooming did not increase the efficiency of access to partners compared to dyadic grooming. This contradicts Dunbar (1993) general idea, and Nakamura (2003) specific argument on chimpanzees, that polyadic social interactions serve as more efficient strategies to access a larger number of social partners when social time is limited. Note, however, that a different effect could be found in other chimpanzee communities with a larger number of individuals (e.g. up to 140 individuals in Ngogo, Wood, Watts, Mitani, & Langergraber, 2017) where different grooming strategies might have evolved to maximize access to other group members.

If polyadic grooming does not serve to improve time investment efficiency, what is its function in Tai chimpanzees? Chimpanzees

participated in polyadic grooming more with the individuals they already groomed with the most and with individuals closer in dominance rank. This suggests that polyadic grooming in Tai chimpanzees serves to strengthen already existing social relationships, possibly via a different social configuration, rather than to expand social networks or establish new relationships. In chimpanzees, engaging in polyadic social activities, such as grooming, might, therefore, be important to reinforce social ties between several close cooperation partners simultaneously, specifically individuals who gain by engaging often in successful coordinated group level cooperative actions such as hunting and territorial defence (Boesch, 1994; Lemoine et al., 2020; Samuni, Preis, Deschner, et al., 2018; Samuni et al., 2017). Here again, coordination and cohesion are key aspects of success (Samuni et al., 2019) and polyadic grooming activity, which often occurs before and during territorial activities (Samuni et al., 2017), might act to reinforce this cohesion and coordination by engaging in a larger-scale affiliative activity than dyadic grooming. Yet whether polyadic grooming itself affects group cohesion and whether this potential effect is the same when polyadic grooming occurs around, compared to outside, territorial contexts remains to be investigated.

Bonobos, which are not territorial, may not have the same need as chimpanzees to maintain social ties with most of their group members. This is reflected in their much narrower diversity of grooming partners (Table 4) and suggests that LuiKotale bonobos may form strong social ties with a small number of targeted individuals. This is in line with a previous study on the same bonobo community showing that females have stable preferred female grooming partners (Moscovice et al., 2017). Yet there is no evidence that special grooming relationships favour social support in conflicts in bonobos (Moscovice et al., 2017; Tokuyama & Furuichi, 2016), and the social benefit female bonobos derive from selective grooming relationships remains to be explored. For male bonobos, females are valuable social partners. Even though males rarely engage in coalitions, when they do so, they most often choose females as coalitionary partners (Surbeck et al., 2017). Grooming exchange with several females may facilitate this form of cooperation. In fact, male–female bonobo dyads, but not male–male dyads, groom each other on average more than expected by chance (Boesch & Boesch-Achermann, 2000), indicating that males invest more in their grooming relationship with females than with males. Male bonobos who have their mothers present in the community usually establish strong social ties with their mothers and receive strong social support from them (Surbeck, Mundry, & Hohmann, 2011), which increases the mating success of these males (Surbeck et al., 2011). This might explain, at least partially, the narrow diversity of grooming partners in male bonobos. As in chimpanzees, male bonobos engaged more in polyadic grooming than females. Yet, unlike in chimpanzees, polyadic grooming greatly increased access to a large number of grooming partners. This suggests that male bonobos have more incentives or needs to use polyadic grooming to access a large number of social partners than females.

Female bonobos have an extended sexual receptive period compared to chimpanzees (Douglas, Hohmann, Murtagh, Thiessen-Bock, & Deschner, 2016) which may allow them, in combination with their high social status (Surbeck & Hohmann, 2013), to exert strong female choice towards male mating partners. In this context, it may be beneficial for male bonobos to use polyadic grooming to maintain some form of social relationship with a wider range of female partners to enhance mate choice in their favour. In addition, grooming access to a large number of individuals may enhance the social tolerance of conspecifics towards males and hence their social integration. This might be particularly important for low-

ranking males and/or males without mothers who are often excluded from access to feeding trees (C. Girard-Buttoz, personal observation).

Our comparative study also allows us to elaborate on the mechanisms linking between-group competition and within-group affiliation dynamics. Theoretical and mathematical models (e.g. Alexander & Borgia, 1978; Reeve & Hölldobler, 2007) and empirical and experimental studies on birds (Radford, 2011), fish (Bruintjes, Lynton-Jenkins, Jones, & Radford, 2015) and certain nonhuman primate species (Cords, 2002; Payne, Lawes, & Henzi, 2003) have focused on linking intergroup pressure to increased time devoted to within-group affiliations. Yet the time devoted to affiliations per se might not be the most important parameter in this context, as shown by our study where chimpanzees devoted less time to grooming adults than bonobos despite being the more territorial species. This is also reflected in a meta-analysis that failed to find a significant positive relationship between total grooming time and intergroup encounter rates across primates (Grueter, 2013). However, the diversity of partners accessed as well as the rate of polyadic affiliation (grooming in our study) might be more important social parameters to be influenced by intergroup competition pressure as shown by the results of our study. In fact, across several monkey species, females were found to have more grooming partners (i.e. a denser social network, Majolo et al., 2016) in groups facing high rates of violent intergroup encounters. Diversity of affiliative partners rather than the time devoted to sociality might thus be more important to ensure successful cooperation during intergroup conflicts. We propose that polyadic grooming (and possibly polyadic affiliation in general) might also be an important feature in this respect.

The extent to which polyadic grooming or preening occurs in nonprimate mammals or in birds remains largely unexplored and has, to our knowledge, been mentioned only in the highly territorial and cooperative meerkats (Kutsukake & Clutton-Brock, 2006). Yet the pattern of other forms of polyadic affiliations such as polyadic greetings in hyaenas (see above) or huddling could be considered in the same framework. The formation of polyadic huddling clusters is a common phenomenon in a broad range of mammals and birds (reviewed in Gilbert et al., 2010). While huddling has a primary function of thermoregulation (Gilbert et al., 2010), it can also be an affiliative behaviour through which animals form social relationships (e.g. prairie voles, *Microtus ochrogaster*, Amadei et al., 2017; Norway rats, *Rattus norvegicus*, Schweinfurth et al., 2017; meerkats, Palagi, Marchi, Cavicchio, & Bandoli, 2019) and huddling relationships are predicted by grooming relationships in macaques (Campbell, Tkaczynski, Lehmann, Mouna, & Majolo, 2018; Ogawa & Takahashi, 2003). Therefore, polyadic interactions, such as huddling, may require investigating to understand the link between polyadic affiliation and cooperation during territoriality in social mammals.

In conclusion, our study provides some nuances to general theories linking dyadic affiliation pattern to between-group competition intensity (Alexander & Borgia, 1978; Reeve & Hölldobler, 2007) by showing that between-group conflicts may promote diversity of social partners and polyadic affiliative exchanges rather than simply increasing the time devoted to affiliative behaviours. We found that the highly territorial chimpanzees, and especially the males (i.e. the philopatric sex and the most active in territorial activities and in-group coalition formations) engaged more frequently in polyadic grooming, possibly to reinforce group cohesion and coordination. In bonobos, polyadic grooming allowed individuals to access more grooming partners per unit of time. Males, compared with female bonobos, engaged more in polyadic grooming possibly because they need this form of social interaction to enhance social tolerance from conspecifics and thereby their

social integration in the community and to favour female mate choice. Our results challenge Dunbar (1993) idea that polyadic social interactions are universally more efficient in maximizing an individual's social time by accessing more partners while allocating the same time to social interactions. Future studies should consider social grooming and other affiliative exchanges not as a whole but in their various forms (polyadic and dyadic). In fact, polyadic social interactions and the diversity of social ties appear to be fundamental in linking within-group sociality, territorial defence that requires group level cooperation, and general individual social and cooperative needs.

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References

- Alexander, R. D., & Borgia, G. (1978). Group selection, altruism, and the levels of organization of life. *Annual Review of Ecology and Systematics*, 9, 449–474. Retrieved from JSTOR.
- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49(3–4), 227–267. <https://doi.org/10.1163/156853974X00534>
- Amadei, E. A., Johnson, Z. V., Kwon, Y. J., Shpiner, A. C., Saravanan, V., Mays, W. D., et al. (2017). Dynamic corticostriatal activity biases social bonding in monogamous female prairie voles. *Nature*, 546(7657), 297–301. <https://doi.org/10.1038/nature22381>
- Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language*, 59(4), 390–412. <https://doi.org/10.1016/j.jml.2007.12.005>
- Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E., & Hill, R. A. (1999). Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society B: Biological Sciences*, 266, 665–670.
- Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, 68(3), 255–278. <https://doi.org/10.1016/j.jml.2012.11.001>
- Bateman, A. W., Lewis, M. A., Gall, G., Manser, M. B., & Clutton-Brock, T. H. (2015). Territoriality and home-range dynamics in meerkats, *Suricata suricatta*: A mechanistic modelling approach. *Journal of Animal Ecology*, 84(1), 260–271. <https://doi.org/10.1111/1365-2656.12267>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Berghaenel, A., Ostner, J., Schroeder, U., & Schülke, O. (2011). Social bonds predict future cooperation in male Barbary macaques, *Macaca sylvanus*. *Animal Behaviour*, 81(6), 1109–1116. <https://doi.org/10.1016/j.anbehav.2011.02.009>
- Boesch, C. (1994). Cooperative hunting in wild chimpanzees. *Animal Behaviour*, 48(3), 653–667.
- Boesch, C. (2002). Cooperative hunting roles among Taï chimpanzees. *Human Nature—an Interdisciplinary Biosocial Perspective*, 13(1), 27–46. <https://doi.org/10.1007/s12110-002-1013-6>

- Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Tai forest: Behavioural ecology and evolution*. Oxford University Press.
- Boesch, C., Hohmann, G., & Marchant, L. F. (2002). *Behavioural diversity in chimpanzees and bonobos*. Cambridge University Press.
- Bruintjes, R., Lynton-Jenkins, J., Jones, J. W., & Radford, A. N. (2015). Out-group threat promotes within-group affiliation in a cooperative fish. *The American Naturalist*, 187(2), 274–282. <https://doi.org/10.1086/684411>
- Bygott, J. (1979). Agonistic behaviour, dominance, and social structure in wild chimpanzees of the Gombe National Park. *The Great Apes*, 405–428.
- Campbell, L. A. D., Tkaczynski, P. J., Lehmann, J., Mouna, M., & Majolo, B. (2018). Social thermoregulation as a potential mechanism linking sociality and fitness: Barbary macaques with more social partners form larger huddles. *Scientific Reports*, 8(1), 1–8. <https://doi.org/10.1038/s41598-018-24373-4>
- Cheney, D. L. (1992). Intragroup cohesion and intergroup hostility: The relation between grooming distributions and intergroup competition among female primates. *Behavioral Ecology*, 3(4), 334–345. <https://doi.org/10.1093/beheco/3.4.334>
- Cords, M. (2002). Friendship among adult female blue monkeys (*Cercopithecus mitis*). *Behaviour*, 139, 291–314. <https://doi.org/10.1163/156853902760102681>
- Crockford, C., Wittig, R. M., Langergraber, K., Ziegler, T. E., Zuberbuehler, K., & Deschner, T. (2013). Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, 280(1755), 20122765. <https://doi.org/10.1098/rspb.2012.2765>
- Dobson, A. J. (2002). *An introduction to the generalized linear models* (2nd ed.). Chapman and Hall/CRC Press.
- Douglas, P. H., Hohmann, G., Murtagh, R., Thiessen-Bock, R., & Deschner, T. (2016). Mixed messages: Wild female bonobos show high variability in the timing of ovulation in relation to sexual swelling patterns. *BMC Evolutionary Biology*, 16(1). <https://doi.org/10.1186/s12862-016-0691-3>, 140–140.
- Dunbar, R. I. M. (1991). Functional significance of social grooming in primates. *Folia Primatologica*, 57(3), 121–131. <https://doi.org/10.1159/000156574>
- Dunbar, R. I. M. (1993). Coevolution of neocortical size, group size and language in humans. *Behavioral and Brain Sciences*, 16(4), 681–694. <https://doi.org/10.1017/S0140525X00032325>
- Foerster, S., Franz, M., Murray, C. M., Gilby, I. C., Feldblum, J. T., Walker, K. K., et al. (2016). Chimpanzee females queue but males compete for social status. *Scientific Reports*, 6, 35404. <https://doi.org/10.1038/srep35404>
- Fox, J., & Weisberg, S. (2011). *An R Companion to Applied Regression* (2nd ed.). Sage Publications. Retrieved from: <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>.
- Fraser, O. N., & Bugnyar, T. (2010). The quality of social relationships in ravens. *Animal Behaviour*, 79(4), 927–933. <https://doi.org/10.1016/j.anbehav.2010.01.008>
- Fruth, B., & Hohmann, G. (2018). Food sharing across borders. *Human Nature*, 29(2), 91–103. <https://doi.org/10.1007/s12110-018-9311-9>
- Gilbert, C., McCafferty, D., Maho, Y. L., Martrette, J.-M., Giroud, S., Blanc, S., et al. (2010). One for all and all for one: The energetic benefits of huddling in endotherms. *Biological Reviews*, 85(3), 545–569. <https://doi.org/10.1111/j.1469-185X.2009.00115.x>
- Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J., et al. (2013). Fitness benefits of coalitional aggression in male chimpanzees. *Behavioral Ecology and Sociobiology*, 67(3), 373–381. <https://doi.org/10.1007/s00265-012-1457-6>
- Girard-Buttoz, C. (n.d.). *Comparative dataset on hunting frequency in wild bonobos at LuiKotale and wild chimpanzees at Tai*. Unpublished raw data.
- Gomes, C. M., Mundry, R., & Boesch, C. (2009). Long-term reciprocation of grooming in wild West African chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, 276(1657), 699–706. <https://doi.org/10.1098/rspb.2008.1324>
- Grueter, C. C. (2013). No effect of inter-group conflict on within-group harmony in non-human primates. *Communicative & Integrative Biology*, 6(6), Article e26801. <https://doi.org/10.4161/cib.26801>
- Hohmann, G., & Fruth, B. (n.d.). *Dataset on hunting behavior in wild bonobos at LuiKotale*. Unpublished raw data.
- Itani, G. (1990). Relations between unit-groups of bonobos at Wamba, Zaire: Encounters and temporary fusions. *African Study Monographs*, 11(3), 153–186. <https://doi.org/10.14989/68066>
- Jaeggi, A. V., De Groot, E., Stevens, J. M. G., & Van Schaik, C. P. (2013). Mechanisms of reciprocity in primates: Testing for short-term contingency of grooming and food sharing in bonobos and chimpanzees. *Evolution and Human Behavior*, 34(2), 69–77. <https://doi.org/10.1016/j.evolhumbehav.2012.09.005>
- Kulik, L. (2015). *Development and consequences of social behavior in rhesus macaques (Macaca mulatta)*. Ph.D. thesis. University of Leipzig. Retrieved from: https://pure.mpg.de/pubman/faces/ViewItemOverviewPage.jsp?itemId=item_2271212.
- Kutsukake, N., & Clutton-Brock, T. H. (2006). Social functions of allogrooming in cooperatively breeding meerkats. *Animal Behaviour*, 72(5), 1059–1068. <https://doi.org/10.1016/j.anbehav.2006.02.016>
- Langergraber, K. E., Mitani, J. C., & Vigilant, L. (2007). The limited impact of kinship on cooperation in wild chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America*, 104(19), 7786–7790. <https://doi.org/10.1073/pnas.0611449104>
- Lehmann, J., & Boesch, C. (2009). Sociality of the dispersing sex: The nature of social bonds in West African female chimpanzees, *Pan troglodytes*. *Animal Behaviour*, 77(2), 377–387. <https://doi.org/10.1016/j.anbehav.2008.09.038>
- Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007). Group size, grooming and social cohesion in primates. *Animal Behaviour*, 74(6), 1617–1629. <https://doi.org/10.1016/j.anbehav.2006.10.025>
- Lemoine, S., Preis, A., Samuni, L., Boesch, C., Crockford, C., & Wittig, R. M. (2020). Between-group competition impacts reproductive success in wild chimpanzees. *Current Biology*, 30(2), 312–318. <https://doi.org/10.1016/j.cub.2019.11.039.e3>
- Lucchesi, S., Cheng, L., Janmaat, K., Mundry, R., Pisor, A., & Surbeck, M. (2020). Beyond the group: How food, mates, and group size influence intergroup encounters in wild bonobos. *Behavioral Ecology*, 31(2), 519–532. <https://doi.org/10.1093/beheco/anz214>
- Majolo, B., de Bortoli Vizioli, A., & Lehmann, J. (2016). The effect of intergroup competition on intragroup affiliation in primates. *Animal Behaviour*, 114, 13–19. <https://doi.org/10.1016/j.anbehav.2016.01.009>
- Mielke, A., Preis, A., Samuni, L., Gogarten, J. F., Wittig, R. M., & Crockford, C. (2018). Flexible decision-making in grooming partner choice in sooty mangabeys and chimpanzees. *Royal Society Open Science*, 5(7), 172143. <https://doi.org/10.1098/rsos.172143>
- Miritello, G., Moro, E., Lara, R., Martínez-López, R., Belchamber, J., Roberts, S. G. B., et al. (2013). Time as a limited resource: Communication strategy in mobile phone networks. *Social Networks*, 35(1), 89–95. <https://doi.org/10.1016/j.socnet.2013.01.003>
- Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, 77(3), 633–640. <https://doi.org/10.1016/j.anbehav.2008.11.021>
- Moscovice, L. R., Douglas, P. H., Martínez-Iñigo, L., Surbeck, M., Vigilant, L., & Hohmann, G. (2017). Stable and fluctuating social preferences and implications for cooperation among female bonobos at LuiKotale, Salonga National Park, DRC. *American Journal of Physical Anthropology*, 163(1), 158–172. <https://doi.org/10.1002/ajpa.23197>
- Nakamura, M. (2000). Is human conversation more efficient than chimpanzee grooming? *Human Nature*, 11(3), 281–297. <https://doi.org/10.1007/s12110-000-1014-2>
- Nakamura, M. (2003). 'Gatherings' of social grooming among wild chimpanzees: Implications for evolution of sociality. *Journal of Human Evolution*, 44(1), 59–71. [https://doi.org/10.1016/S0047-2484\(02\)00194-X](https://doi.org/10.1016/S0047-2484(02)00194-X)
- Neumann, C., Dubocq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., et al. (2011). Assessing dominance hierarchies: Validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour*, 82(4), 911–921. <https://doi.org/10.1016/j.anbehav.2011.07.016>
- Ogawa, H., & Takahashi, H. (2003). Triadic positions of Tibetan macaques huddling at a sleeping site. *International Journal of Primatology*, 24(3), 591–606. <https://doi.org/10.1023/A:1023792431064>
- Palagi, E., Marchi, E., Cavicchio, P., & Bandoli, F. (2019). Sharing playful mood: Rapid facial mimicry in *Suricata suricatta*. *Animal Cognition*, 22(5), 719–732. <https://doi.org/10.1007/s10071-019-01269-y>
- Payne, H., Lawes, M., & Henzi, S. P. (2003). Competition and the exchange of grooming among female samango monkeys (*Cercopithecus mitis erythrarchus*). *Behaviour*, 140(4), 453–471. <https://doi.org/10.1163/156853903322127931>
- Pisor, A. C., & Surbeck, M. (2019). The evolution of intergroup tolerance in nonhuman primates and humans. *Evolutionary Anthropology: Issues, News, and Reviews*, 28(4), 210–223. <https://doi.org/10.1002/evan.21793>
- R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from: <https://www.R-project.org/>.
- Radford, A. N. (2011). Preparing for battle? Potential intergroup conflict promotes current intragroup affiliation. *Biology Letters*, 7(1), 26–29. <https://doi.org/10.1098/rsbl.2010.0507>
- Reeve, H. K., & Hölldobler, B. (2007). The emergence of a superorganism through intergroup competition. *Proceedings of the National Academy of Sciences*, 104(23), 9736–9740. <https://doi.org/10.1073/pnas.0703466104>
- Sakamaki, T. (2013). Social grooming among wild bonobos (*Pan paniscus*) at Wamba in the Luo Scientific Reserve, DR Congo, with special reference to the formation of grooming gatherings. *Primates*, 54(4), 349–359. <https://doi.org/10.1007/s10329-013-0354-6>
- Sakamaki, T., Ryu, H., Toda, K., Tokuyama, N., & Furuichi, T. (2018). Increased frequency of intergroup encounters in wild bonobos (*Pan paniscus*) around the yearly peak in fruit abundance at Wamba. *International Journal of Primatology*, 39(4), 685–704. <https://doi.org/10.1007/s10764-018-0058-2>
- Samuni, L., Mielke, A., Preis, A., Crockford, C., & Wittig, R. M. (2019). Intergroup competition enhances chimpanzee (*Pan troglodytes verus*) in-group cohesion. *International Journal of Primatology*, 1–21. <https://doi.org/10.1007/s10764-019-00112-y>
- Samuni, L., Preis, A., Deschner, T., Crockford, C., & Wittig, R. M. (2018). Reward of labor coordination and hunting success in wild chimpanzees. *Communications Biology*, 1(1), 1–9. <https://doi.org/10.1038/s42003-018-0142-3>
- Samuni, L., Preis, A., Mielke, A., Deschner, T., Wittig, R. M., & Crockford, C. (2018). Social bonds facilitate cooperative resource sharing in wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, 285(1888), 20181643. <https://doi.org/10.1098/rspb.2018.1643>
- Samuni, L., Preis, A., Mundry, R., Deschner, T., Crockford, C., & Wittig, R. M. (2017). Oxytocin reactivity during intergroup conflict in wild chimpanzees. *Proceedings of the National Academy of Sciences*, 114(2), 268–273. <https://doi.org/10.1073/pnas.1616812114>

- Schino, G. (2007). Grooming and agonistic support: A meta-analysis of primate reciprocal altruism. *Behavioral Ecology*, 18(1), 115–120. <https://doi.org/10.1093/beheco/arl045>
- Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. *Current Biology*, 20(24), 2207–2210. <https://doi.org/10.1016/j.cub.2010.10.058>
- Schweinfurth, M. K., Neuenschwander, J., Engqvist, L., Schneeberger, K., Rentsch, A. K., Gygas, M., et al. (2017). Do female Norway rats form social bonds? *Behavioral Ecology and Sociobiology*, 71(6), 98. <https://doi.org/10.1007/s00265-017-2324-2>
- Seyfarth, R. M., & Cheney, D. L. (2012). The evolutionary origins of friendship. *Annual Review of Psychology*, 63, 153–177.
- Smith, J. E., Powning, K. S., Dawes, S. E., Estrada, J. R., Hopper, A. L., Piotrowski, S. L., et al. (2011). Greetings promote cooperation and reinforce social bonds among spotted hyaenas. *Animal Behaviour*, 81(2), 401–415. <https://doi.org/10.1016/j.anbehav.2010.11.007>
- Stumpf, R. M. (2011). Chimpanzees and bonobos: Inter- and intraspecies diversity. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, & S. K. Bearder (Eds.), *Primates in perspective*. Oxford University Press.
- Surbeck, M., Boesch, C., Girard-Buttoz, C., Crookford, C., Hohmann, G., & Wittig, R. M. (2017). Comparison of male conflict behavior in chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), with specific regard to coalition and post-conflict behavior. *American Journal of Primatology*, 79(6), Article e22641. <https://doi.org/10.1002/ajp.22641>
- Surbeck, M., & Hohmann, G. (2008). Primate hunting by bonobos at LuiKotale, Salonga National Park. *Current Biology*, 18(19), R906–R907. <https://doi.org/10.1016/j.cub.2008.08.040>
- Surbeck, M., & Hohmann, G. (2013). Intersexual dominance relationships and the influence of leverage on the outcome of conflicts in wild bonobos (*Pan paniscus*). *Behavioral Ecology and Sociobiology*, 67(11), 1767–1780. <https://doi.org/10.1007/s00265-013-1584-8>
- Surbeck, M., & Hohmann, G. (2015). Social preferences influence the short-term exchange of social grooming among male bonobos. *Animal Cognition*, 18, 573–579. <https://doi.org/10.1007/s10071-014-0826-0>
- Surbeck, M., & Hohmann, G. (2017). Affiliations, aggressions and an adoption: Male-male relationships in wild bonobos. In B. Hare, & S. Yamamoto (Eds.), *Bonobos: Unique in mind, brain, and behavior* (pp. 35–46). Oxford University Press.
- Surbeck, M., Mundry, R., & Hohmann, G. (2011). Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). *Proceedings of the Royal Society B: Biological Sciences*, 278(1705), 590–598. <https://doi.org/10.1098/rspb.2010.1572>
- Takano, M. (2018). Two types of social grooming methods depending on the trade-off between the number and strength of social relationships. *Royal Society Open Science*, 5(8), 180148. <https://doi.org/10.1098/rsos.180148>
- Tiddi, B., Aureli, F., & Schino, G. (2012). Grooming up the hierarchy: The exchange of grooming and rank-related benefits in a new world primate. *PLoS One*, 7(5), Article e36641. <https://doi.org/10.1371/journal.pone.0036641>
- Tokuyama, N., & Furuichi, T. (2016). Do friends help each other? Patterns of female coalition formation in wild bonobos at Wamba. *Animal Behaviour*, 119, 27–35. <https://doi.org/10.1016/j.anbehav.2016.06.021>
- de Waal, F. B. M. (1997). The chimpanzee's service economy: Food for grooming. *Evolution and Human Behavior*, 18(6), 375–386. [https://doi.org/10.1016/S1090-5138\(97\)00085-8](https://doi.org/10.1016/S1090-5138(97)00085-8)
- Watts, H. E., & Holekamp, K. E. (2007). Hyena societies. *Current Biology*, 17(16), R657–R660. <https://doi.org/10.1016/j.cub.2007.06.002>
- Watts, D. P., & Mitani, J. C. (2002). Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, 23(1), 1–28. <https://doi.org/10.1023/A:1013270606320>
- Wilson, M. L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I. C., Hashimoto, C., et al. (2014). Lethal aggression in *Pan* is better explained by adaptive strategies than human impacts. *Nature*, 513(7518), 414–417. <https://doi.org/10.1038/nature13727>
- Wittig, R. M. (2018). Tai chimpanzees. In J. Vonk, & T. K. Shackelford (Eds.), *Encyclopedia of animal cognition and behavior*. Springer International.
- Wittig, R. M., & Boesch, C. (2003). Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. *International Journal of Primatology*, 24(4), 847–867. <https://doi.org/10.1023/A:1024632923180>
- Wood, B. M., Watts, D. P., Mitani, J. C., & Langergraber, K. E. (2017). Favorable ecological circumstances promote life expectancy in chimpanzees similar to that of human hunter-gatherers. *Journal of Human Evolution*, 105, 41–56. <https://doi.org/10.1016/j.jhev.2017.01.003>
- Wrangham, R. W. (1999). Evolution of coalitionary killing. *Yearbook of Physical Anthropology*, 42, 1–30.
- Wrangham, R. W., & Glowacki, L. (2012). Intergroup aggression in chimpanzees and war in nomadic hunter-gatherers. *Human Nature*, 23(1), 5–29. <https://doi.org/10.1007/s12110-012-9132-1>

Appendix

Assessment of the dominance hierarchy

We calculated the dominance hierarchy in each of the study communities using a modified version of the Elo-rating method

(Neumann et al., 2011) developed by Foerster et al. (2016). Elo-rating allows the researcher to assess dominance power scores between individuals in a dynamic way so that rank changes can be detected. Following each dyadic winner–loser interaction the score of the winner increases and that of the loser decreases by the same magnitude and this increase/decrease is proportional to the initial power difference between the two individuals. The original Elo-rating makes every individual enter the hierarchy at the same fixed value and requires the researcher to make arbitrary decisions on how to set the k parameter which defines how much individuals gain and lose from each interaction. The modification by Foerster et al. (2016) uses maximum-likelihood estimation to optimize the k and allow individuals to start at different values. This approach reduces the likelihood of artefactual rank changes between two individuals occurring because of interactions with a third party, while increasing the detection of true rank changes occurring between individuals who rarely interact. It also limits the need for a burn-in phase (by allowing different starting values for each individual) which was essential in our study since no long-term data were available on the bonobos for both sexes. For the two chimpanzee communities, we used unidirectional submissive pant-grunt vocalizations (given by the lowest ranking of the two individuals towards the highest ranking; Bygott, 1979). We used all the long-term data available from the Tai chimpanzee project, which includes consistently collected ad libitum data from field assistants, students and researchers since 1999 in Tai South and since 2007 in Tai East. For the bonobos long-term data on both sexes were not available so we used only the data we collected from February 2015 onwards. We used dyadic dominance interactions with a clear winner and a clear loser (i.e. displacements or charges and chases followed by fleeing or avoidance behaviour of the recipient). To account for the required burn-in phase of the method before obtaining reliable dominance scores for each individual we assessed the dominance score (i.e. Elo-rating) after 3 months of data collection. For bonobos, we then used the dominance score obtained after 3 months for each individual as its dominance score for each day during the first 3 months of the study. For chimpanzees, this procedure was not necessary since the data used dated back years before the data collection for this study started. The Elo-rating score of all bonobo individuals was highly stable throughout the study period indicating that the 3-month burn-in phase was sufficient. For chimpanzees, we calculated male and female Elo-rating scores separately using only male–male dominance interactions for the male hierarchy and female–female dominance interactions for the female hierarchy. Eventually, we combined male and female hierarchies into a single dominance hierarchy. Since all males are dominant over all females in the Tai chimpanzees (Gomes et al., 2009), we removed a fixed value (here 4000) from the Elo-rating score of each female each day so that all the female Elo-ratings were below the Elo-rating of the lowest-ranking male. In contrast, bonobos are known to have a mixed-sex hierarchy with most females dominating most males but no consistent domination of one sex. Accordingly, we calculated individual Elo-rating scores for males and females combined. The k parameters for the different study communities were 18.83 for females and 682.44 for males in Tai East, 53.85 for females and 1426.25 for males in Tai South and 1.42 for LuiKotale Bompusa bonobos. The number of dominance interactions used for the calculation of the Elo-ratings was 102 for females and 2738 for males in Tai East, 895 for females and 6145 for males in Tai South and 216 for LuiKotale Bompusa bonobos. All Elo-rating scores were standardized between 0 and 1 with 1 being the highest-ranking individual and 0 the lowest-ranking daily. We then extracted the Elo-rating score of each individual on the day when each grooming bout occurred.

Permutation tests for Model 1 and Model 3

In Model 1, dyadic sessions that turned into polyadic sessions when an individual joined the grooming cluster or polyadic sessions that turned into dyadic sessions when an individual left the grooming cluster were treated as separate sessions. These sessions represent a continuous 'event' and, thus, are not fully independent from each other. Therefore, to avoid pseudoreplication, it is necessary to account for potential nonindependence of the same 'grooming events'. For that purpose, we assigned the same 'event number' to consecutive grooming sessions if at least one grooming partner remained the same from one session to the next and when the two sessions were less than 5 min apart. As most grooming sessions in our data were strictly dyadic, we found little variation within the different 'event numbers' (i.e. >80% of event numbers included a single grooming session), meaning that we could not include it as a random effect in our models. Nevertheless, to confirm that the nonindependence of these data points did not affect our results, we conducted model permutations. For each 'event number', we randomly selected a single entry of data, thus creating a data set with a size equivalent to the number of unique 'event numbers'. We then fitted a model with an identical fixed and random effect structure as Model 1 on this subset of data. We carried out this procedure 100 times and averaged the models' estimates and *Z* and *P* values provided by the permutations. For Model 3, we took the same approach but in addition randomly selected only one dyad for each polyadic grooming session irrespective of the number of dyads involved in the session. Permutation results are provided in Table A2.

The permutation procedure for both models revealed slightly different estimates but the overall significance of the test predictors

of sex and community (Model 1) and DDGI and community*rank difference (Model 3) did not change. The only difference revealed by permutations was that the interaction between community and DDAI (Model 3) was significant in the permutations and only a trend in the original model.

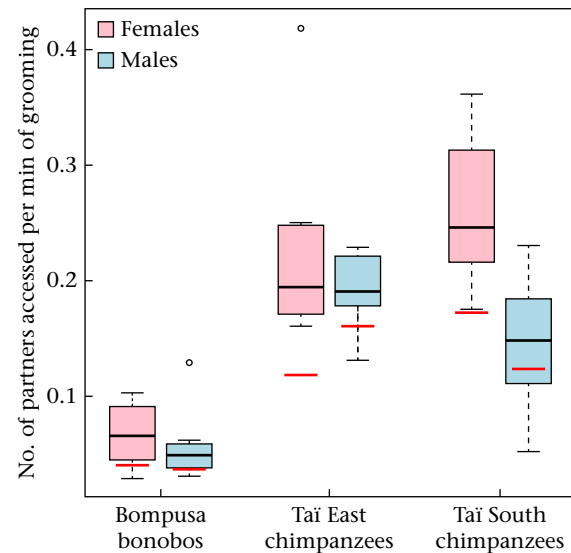


Figure A1. Sex and species differences in the number of partners accessed per minute of grooming. The box plot indicates the median (thick black line) and 25% and 75% quartiles. Dashed horizontal lines indicate the 10% and 90% deciles. Open dots indicate the data points that did not fall within the 10–90% deciles. The red horizontal line indicates the model prediction (Model 2).

Table A1

Distribution of the half-day focal follows with less than 5 min of grooming for males and females of the three study communities

Community	LuiKotale Bompusa bonobos		Tai_East chimpanzees		Tai_South chimpanzees	
	F	M	F	M	F	M
Mean no. of half-days with grooming time <5 min per individual	1.2	1.1	5.0	3.4	3.4	2.4
Minimum no. of half-days with grooming time <5 min per individual	0	0	3	2	0	0
Maximum no. of half-days with grooming time <5 min per individual	3	3	8	6	6	6

F: female; M: male.

Table A2

Results of the permutations run on the data set for Model 1 and Model 3

Model permutation	Response	Predictor	Estimate	SE	Z	P
1	Was the grooming session polyadic? (Y/N)	Intercept	−3.07	0.34		
		Community (Tai East)	1.04	0.37	2.82	0.008
		Community (Tai South)	1.05	0.35	2.93	
		Sex (male)	0.48	0.21	2.29	0.041
		Number of adults in the party ^a	0.19	0.10	1.89	<i>0.084</i>
3	Was the grooming session polyadic? (Y/N) (dyadic analysis)	Intercept	−2.80	0.35		
		Community (Tai East)	1.41	0.36		
		Community (Tai South)	1.27	0.34		
		DDAI	0.47	0.27		
		Dominance rank difference i.e Elo score difference	0.57	0.28		
		Sex combination (F-M)	0.05	0.29	0.16	0.762
		Sex combination (M-M)	0.39	0.31		
		DDGI	0.28	0.11	2.45	0.021
		Kin (Y/N) ^a	−0.45	0.50	−0.90	0.389
		Number of adults in the party ^a	0.35	0.09	3.78	<0.001
		Community (Tai East)*DDAI	−0.67	0.32	−2.1	0.045
		Community (Tai South)*DDAI	−0.48	0.30	−1.60	
Community (Tai East)*rank difference	−0.99	0.37	−2.68	0.009		
Community (Tai South)*rank difference	−0.63	0.35	−1.79			

Y: yes; N: no; F: female; M: male; DDAI: dynamic dyadic association index; DDGI: dynamic dyadic grooming index. In each model, the reference levels are 'LuiKotale Bompusa' for community, 'female' for sex and 'FF' for the sex combination. SE indicates the standard error of the estimate for each predictor. The coded level for each categorical predictor is indicated in parentheses. Significant *P* values (<0.05) are indicated in bold. Trends (*P* < 0.1) are indicated in italics.

^a Control predictors.