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Reciprocal Signaling During Approaches Relates to Close Relationships Within and Between Two Primate Species

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Abstract – Signaling can facilitate coordination and cooperation, aiding relationship formation and maintenance across social animals. Reciprocal signaling may reflect equitable social motivation, thereby supporting coordination and bonding, especially in social systems that face increased social coordination challenges. To examine the link between signaling reciprocity and social bonding across social systems with different levels of coordination challenges, we studied two Western chimpanzee (*Pan troglodytes verus*) and two sooty mangabey (*Cercocebus atys atys*) groups sharing the same environment. We evaluated how reciprocity of non-agonistic signaling - equitable signaling initiation during approaches – differed depending on variation in social bond strength and grooming relationship differentiation within and between groups. Whilst both species formed well-differentiated grooming relationships, mangabeys generally allocated grooming effort to fewer group members than chimpanzees. Reciprocal signaling was positively associated with grooming frequency in both species (but more clearly in chimpanzees) and with equitable grooming effort in chimpanzees only. A strong reliance on matriline members in social bonding in mangabeys may lower coordination challenges, and thus communication needs, limiting the number of grooming and signaling partners compared with chimpanzees. In contrast, in chimpanzees, cooperation needs with non-kin may increase the number of cooperative and signaling partners. Strong fission-fusion dynamics may increase challenges related to coordination and relationship maintenance, promoting signaling production and reciprocity. Both within and between species findings provide support for the hypothesis that social bonding patterns and social complexity influence the propensity to signal reciprocally, potentially influencing aspects of signaling evolution.

Keywords – Social bonding, Dyadic signaling reciprocity, Fission-fusion dynamics, Complex social systems

Within animal groups, cooperative interactions between partners, such as allo-grooming and coalitionary support, are underpinned by various mechanisms and are key components of individual fitness (Borgeaud & Bshary, 2015; Fraser & Bugnyar, 2012; Fruteau, Lemoine, et al., 2011; Fruteau, van de Waal, et al., 2011; Godman, 2013; Kalbitz et al., 2016; Kerth, 2010; Silk, 2007; Silk et al., 2010). Biological market theory describes how cooperative interactions may be exchanged as 'commodities', sometimes reciprocally (Borgeaud & Bshary, 2015; Fraser & Bugnyar, 2012; Fruteau, Lemoine, et al., 2011; Fruteau, van de Waal, et al., 2011; Hammerstein & Noë, 2016; Kaburu & Newton-Fisher, 2015; Kalbitz et al., 2016). Alternatively, concepts of kin selection and collective action define cases in which cooperative behaviors provide indirect fitness benefits and public goods, respectively (Melis & Raihani, 2023). Commodities may also not be reciprocated immediately but rather over a long-term basis (Fraser & Bugnyar, 2012; Gomes et al., 2008; Schino et al., 2007), and lead to the formation of long-lasting relationships (Fruteau, Lemoine, et al., 2011; Samuni et al., 2021). Such relationships that are strong, stable, and equitable, are referred to as social bonds (Cheney, 1992). These resemble human 'friendships' (Massen et al., 2010), providing social support and possible fitness benefits (Kern & Radford, 2016; Silk, 2007; Silk et al., 2010; Wittig et al., 2016). Given time constraints and competitive costs, individuals living in large groups tend to form differentiated relationships, and cooperate preferentially with a limited number of partners. Challenges associated with the formation and maintenance of close relationships in increasingly complex societies may represent drivers of cognitive and communicative skills across species, as posited in the social complexity hypothesis (Aureli et al., 2008; Bergman & Beehner, 2015; Dunbar & Shultz, 2017; Freeberg et al., 2012; McComb & Semple, 2005).

Communication plays a major role in the patterning of social relationships within a group. Empirical studies demonstrated that across a wide range of species, signal production may reflect high social motivation (Bründl et al., 2022; Manser, 2010), facilitate dyadic and group-level coordination and cooperation (Fedurek et al., 2015; King et al., 2019, 2021; Mine et al., 2022), and help to form, maintain and advertise close relationships (Chereskin et al., 2022; Gustison et al., 2019; Lynch Alfaro, 2008; Smith et al., 2011). The social bonding hypothesis posits that vocal communication may serve as an alternative to grooming to maintain coordination between bonded partners, especially in large or complex societies (e.g., societies with strong fission-fusion dynamics), such as those of humans, social primates, and bottlenose dolphins (*Tursiops* spp.) (Chereskin et al., 2022; Dunbar, 1993; McComb & Semple, 2005; Ramos-Fernández, 2005). As with reciprocity in grooming investment (Kalbitz et al., 2016), signaling reciprocity may reflect high relationship strength within societies (Arlet et al., 2015; Fernandez et al., 2017; Kulahci et al., 2015; Levréro et al., 2019; Luef & Pika, 2017; Pougnault et al., 2022; Scheumann et al., 2017). Previous behavioral studies that examined reciprocity in cooperative behaviors, for instance grooming, investigated reciprocity both within and across grooming bouts (Fraser & Bugnyar, 2012; Fruteau, Lemoine, et al., 2011; Fruteau, van de Waal, et al., 2011; Gomes et al., 2008; Kalbitz et al., 2016; Newton-Fisher & Lee, 2011). In contrast, studies on the link between communication reciprocity and relationship strength have primarily examined immediate signal exchanges or responses to signals, particularly with the aim to understand the origin of human conversation rules. Specifically, these studies examined vocal duetting and turn-taking episodes (Fedurek et al., 2013; Fernandez et al., 2017; Levréro et al., 2019; Meunier et al., 2023; Pougnault et al., 2022; Scheumann et al., 2017), and behavioral and vocal responses to vocalizations (Arlet et al., 2015; Kulahci et al., 2015; Luef & Pika, 2017; Ramos-Fernández, 2005).

Here, we test the hypothesis that signaling production can support social coordination and bonding by conducting a comparative study on signaling reciprocity during close-range communication (i.e., social approaches within 2 m) in two primate species. Signaling during social approaches plays a major role in the negotiation of tolerance, coordination, and cooperation across social animals (Reddon et al., 2021; Smith et al., 2011), including in primates (Dal Pesco & Fischer, 2020; De Waal, 1986; Luef & Pika, 2019; Range & Fischer, 2004; Silk et al., 2016). We examined the production of visual and auditory signals as both species employ these communication modalities during approaches (Grampp et al., 2023). We considered signaling initiation through several social approaches, which may reflect equitable coordination effort and social motivation between partners over time. We examined the link between dyadic signaling reciprocity (or bidirectionality) and relationship strength in four sympatric groups of sooty mangabeys

(*Cercocebus atys atys*) and Western chimpanzees (*Pan troglodytes verus*) (two groups per species), from the Taï forest, Ivory Coast. Both species are largely terrestrial, share the same habitat and live in large multimale-multifemale groups with moderately steep dominance hierarchies (Mielke et al., 2017).

Within each species, reciprocal dyadic signaling may reflect equitable social motivation and therefore increase with relationship strength (Arlet et al., 2015; Fedurek et al., 2013; Fernandez et al., 2017; Kulahci et al., 2015; Levréro et al., 2019; Luef & Pika, 2017). Mangabeys form matrilineal societies, with females staying in their natal group and cooperating preferentially with kin (Range, 2006; Range & Noë, 2002). In contrast, in the male-philopatric society of chimpanzees, individuals cooperate extensively with both kin and non-kin group members (Langergraber et al., 2007; Samuni et al., 2021). Further, chimpanzees generally cooperate in a wider range of contexts compared with mangabeys, particularly with regard to collective cooperation (e.g., hunting and border patrolling) (Boesch et al., 2006; Samuni et al., 2021). Therefore, we hypothesized that mangabeys, especially females, may have fewer cooperative partners (i.e., highly restricted to kin), and allocate grooming investment on fewer partners, which may increase the level of differentiation in grooming relationship strength between dyads, compared with chimpanzees. In contrast, a relatively lower level of differentiation in chimpanzees may allow a high degree of collective cooperation in this species (Moscovice et al., 2020; Surbeck et al., 2017). In both species, individuals adjust decision-making in grooming initiation depending on the audience composition (Mielke et al., 2018). Nonetheless, given stronger fission-fusion dynamics, the audience composition may have more influence on decision-making and social outcomes in chimpanzees than in mangabeys (Mielke et al., 2018, 2020). These challenges may increase uncertainty of social relationships in chimpanzees compared with mangabeys (Wittig et al., 2020). Therefore, we expected that higher differentiation and stability of close relationships may be reflected in a stronger link between signaling reciprocity and relationship strength in mangabeys in comparison with chimpanzees.

Alternatively, signaling reciprocity may be particularly adaptive in complex societies, such as those with large group sizes or strong fission-fusion dynamics, acting as an alternative to time-consuming grooming interactions to maintain coordination with many partners (Dunbar, 1993, 2003; Ramos-Fernández, 2005). Indeed, in societies with strong fission-fusion dynamics, signaling plays a determinant role in sustaining group cohesion and cooperation over time and distance (Briseño-Jaramillo et al., 2022; Fedurek et al., 2014, 2021; King et al., 2019; Leighty et al., 2008; Schamberg et al., 2016, 2017; Smith et al., 2011), and fostering close relationships (Bouchard & Zuberbühler, 2022; Chereskin et al., 2022; Luef & Pika, 2017, 2019; Lynch Alfaro, 2008; Smith et al., 2011). Therefore, our alternative hypothesis was that chimpanzees may rely more on signaling reciprocity within close relationships, considering challenges to maintain relationships with numerous partners in a fission-fusion society, and thus show a stronger link between signaling reciprocity and relationship strength than mangabeys.

Methods

Ethics Statement

The data collection protocol was observational and non-invasive, approved by the 'Ethikrat der Max-Planck-Gesellschaft', allowed by the Ministère de l'Enseignement supérieur et de la Recherche scientifique; des Eaux et Forêts en Côte d'Ivoire and the Office Ivoirien des Parcs et Réserves.

Data Collection

M.G. conducted this study in the Taï National Park (5°52′N, 7°20′E, Ivory Coast) (Wittig, 2022), carrying out focal observations (Altmann, 1974) on two individuals per day for 6 hr each, from dawn to midday and then from midday to dusk. Focal subjects were all male and female adult and sub-adult individuals in two wild groups per species of mangabeys and chimpanzees, all habituated to human presence (chimpanzees > 9 years old = 38 individuals, and mangabeys > 2 years old = 50 individuals). Four sympatric groups were studied: two neighboring groups of chimpanzees ('East' and 'South') at the Taï

Chimpanzee Project, and two groups of mangabeys, one at the Taï Chimpanzee Project ('TCP'), which ranges approximately 4 km away from the one at the Taï Monkey Project ('TMP') (Range & Noë, 2002; Wittig, 2022). The order of focal follows was chosen pseudo-randomly (chimpanzees: mean ± SD = 42 ± 8 hr per individual, mangabeys: 23 ± 10 hr per individual, Table S1), with a priority given to less observed individuals to balance observation hours between individuals. M.G. collected data using observational methods with the Cybertracker software (https://cybertracker.org/) on a smartphone device. During a focal follow, when non-focal individuals approached (within 2 m, a distance allowing for full visual and auditory contact between partners) the focal individual, or *vice versa*, M.G. collected data on the identity of these individuals and the signals directed to/from the focal individual (within a maximum of 10 s after the approach in cases when there was initially no change of behavior, i.e., when two rows in the dataset represented the same approach event). We considered signals from the first signaler only, but both cases when a focal individual was the first signaler or the signal receiver. The directionality of signals was estimated depending on the head orientation and the direction of movement during the approach (i.e., signals with unclear recipients were not considered in the analyses).

We defined 'signals' as communicative acts that have been previously described in each species, and are thought to transmit information to others, whether intentionally or unintentionally (Aychet et al., 2021; Bortolato et al., 2023; Hobaiter et al., 2017; Range & Fischer, 2004). We included two communicative acts in both species that may be considered as social cues rather than signals according to the definition of social cues in Maynard-Smith and Harper (2003), i.e., informative traits but that may have not evolved for facilitating transmission of this information. These communicative acts were "withdrawing" in both species and "peering" in mangabeys. These behaviors were considered as communicative acts in other studies (Hobaiter & Byrne, 2011; Range & Marshall-Pescini, 2022). We decided to keep them as candidate signals since distinguishing social cues from signals may not always be straightforward as social cues may also be used by receivers and result in a certain outcome (Fröhlich et al., 2021; Higham & Hebets, 2013). We only considered visual and/or auditory signals emitted whilst engaged in the act of approaching and did not consider tactile signals (Dal Pesco & Fischer, 2018), which were considered as the outcome of an approach. Approaches leading to socio-positive outcomes (affiliative behaviors and/or grooming from either partner) represented 24% in mangabeys and 33% in chimpanzees. Signal categories included visual signals: in chimpanzees: arm raise; and in both species: head movements, standstill displays, withdrawing, bowing/crouching, peering, present body and genitals, extend limb and throw arm (Aychet et al., 2021; Hobaiter & Byrne, 2011; Parr et al., 2007); auditory signals: vocalizations, in chimpanzees: bark, hoo, pant-grunts, pants, pant-hoots, whimper, pant-screams or barks (Bortolato et al., 2023; Fedurek et al., 2021); mangabeys: twitter, growl, copulation call (Range & Fischer, 2004); in both species: grunt and scream; in chimpanzees only: non-vocal sounds (lip-smacking, raspberry blowing, teeth-clacking) (Taglialatela et al., 2012) and multisensory signals (body and arm gestures using body parts, objects, or ground to make sound, e.g., shaking a branch, Table S2). We considered that systematically collecting facial expressions during all approaches was difficult using observational methods, despite representing an important modality of signaling in both species (Aychet et al., 2021; Parr et al., 2007).

To ensure the reliability of the data collected by M.G., we conducted interobserver and inter-method tests with three other experienced observers. The reliability of behavioral data during focal follows between M.G. and another rater was > 90% (including for data on approaches and social interactions). To further ensure the reliability of signaling data during approaches, we calculated Cohen's Kappa coefficients (κ) that also consider the possibility of the agreement occurring by chance (Bakeman & Quera, 2011). We estimated the reliability of data on signaling probability during approaches from videos between M.G. and another rater ($\kappa > 0.9$, in mangabeys: $n_{\text{no/signaling}} = 44/49$; in chimpanzees: $n_{\text{no/signaling}} = 31/44$). We estimated the reliability of data on socio-positive signaling probability during approaches from videos between M.G. and another rater ($\kappa > 0.9$, in mangabeys: $n_{\text{yes/no}} = 16/77$, in chimpanzees: $n_{\text{yes/no}} = 32/44$). Finally, we estimated the reliability of data on signaling probability during approaches collected *in situ* versus from videos: $\kappa > 0.9$, as only 2% of approaches could be filmed, in mangabeys: $n_{\text{no/signaling}} = 28/35$, in chimpanzees: $n_{\text{no/signaling}} = 10/31$).

M.G. also collected focal grooming interactions. We compiled per dyad during the whole study period, (1) the total grooming initiations and duration (including mutual-grooming events), and (2) signaling events during all approaches. We excluded approaches with clear agonistic behaviors by a signaler (i.e., arm wave, screams, barks, chase, charge, bite, hold, grab), as conflicts may reduce cohesion and break coordination between social partners (Smith et al., 2008), and thus weaken social bonds. Then, we considered a filtered dataset, containing approaches only with 'socio-positive' signals: chimpanzees: hoos (Bouchard & Zuberbühler, 2022; Gruber & Zuberbühler, 2013), grunts (Schel et al., 2013), pants, loud scratches (Goodall, 1986); mangabeys: twitters and grunts (Range & Fischer, 2004); both species: peering, extending the arm or presenting a body part (Aychet et al., 2021; Nishida et al., 1999).

Estimation of Social Relationship Parameters

The dyadic grooming index (DGI) was calculated in a similar fashion to the CSI, i.e., Composite Sociality Index (Silk et al., 2006), considering aggregated behaviors that are correlated within dyads. One index was calculated per dyad and for the whole study period, by dividing per two the sum of dyadic rates of grooming duration and initiations divided by the group-level mean of dyadic rates (here considering two types of data: grooming duration and frequency), with more details provided in Grampp et al. (2023). Dyadic grooming rates were calculated as the duration a given dyad groomed divided by the sum of their focal observation times.

We estimated the dominance rank relationships during the study period based on dominance rank hierarchies, calculated with a modification of the Elo-rating method (Neumann et al., 2011), developed by Foerster et al. (2016), with more details provided in Mielke, Crockford, Wittig, et al. (2019) and Mielke et al. (2017). We used long-term data on supplants in mangabeys and pant-grunts in chimpanzees (mangabeys: TCP group: 2013-2018, TMP group: 2018-2020, chimpanzees: East group: 2008-2020, South group: 1999-2020). Both relationship indices were scaled per group within a range from 0 to 1, as in Raulo et al. (2021).

Estimation of the Differentiation of Grooming Relationships at the Individual Level: Coefficient of Variation of Dyadic Grooming Index (DGI)

Previous studies typically examined the level of differentiation in social relationships on the group level and for a given period, by using the coefficient of variation (CoV) (Heathcote et al., 2017; Kalbitzer & Chapman, 2021). In this study, we opted for a measure on the individual scale, to consider possible variation in sociality across individuals (Bründl et al., 2022; Tkaczynski et al., 2020). Thus, we estimated the level of differentiation in grooming relationship strength as the coefficient of variation of the DGI per individual per sex combination (four levels on an individual scale: female-female, female-male, male-female, male-male). The coefficient of variation was obtained by dividing the standard deviation by the mean of DGI on an individual level. We distinguished four levels for the sex combination to account for directionality and sex-homophily, as we know from previous studies that cooperative interactions may be more frequent among members from the philopatric sex (generally males in chimpanzees and females in mangabeys) than the dispersing sex in both species (Mielke et al., 2017; Surbeck et al., 2017; Wittig et al., 2020). We considered only individuals who had grooming relationships in each sex combination; thus, we kept only the datapoints of individuals that displayed a mean DGI value above 0 in each sex combination.

Calculation of Reciprocity Indices in Grooming and Signaling Effort Across Dyads: Ri

We considered that a dyad showed high reciprocity in signaling or grooming effort, when both partners contributed equally to initiate signaling during approaches or to grooming duration and initiations, respectively. We did not consider dyads in which neither partner made grooming or signaling effort as we argue that reciprocity cannot be measured unless at least one individual within a dyad is performing our behavior of interest. We did not consider a partner investment relative to its investment in other social relationships, outside the dyad, as in Wang et al. (2013). In these cases, non-reciprocity may result from the variation in the number of social partners (i.e., network centrality of each partner). We calculated reciprocity indices using the formula as in Kalbitz et al. (2016) and Newton-Fisher and Lee (2011):

$$(1)\ RI_{AB} = 1 - \left| (X_{A\text{-}B} - X_{B\text{-}A}) / (X_{A\text{-}B} + X_{B\text{-}A}) \right|$$

In equation (1), RI was calculated per dyad, 'A-B' defining cases when A was the actor and B was the receiver of a social behavior (i.e., grooming or signaling) and vice versa. Therefore, we considered dyads with X strictly above zero, thus which displayed at least one signaling or grooming event. We calculated an index for grooming interactions (dRI: grooming duration), where X was the amount of grooming duration. Then, we calculated two reciprocity indices for signaling interactions (sRI), where X was either the number of all non-agonistic signaling production events during approaches or only socio-positive signaling production, respectively.

Analytical Procedure

We ran several mixed models (Bayesian estimation), to determine within and between species, (1) variation in the level of differentiation of grooming relationships and in grooming reciprocity across sex combinations, and (2) how dyadic signaling reciprocity was associated to variation in relationship strength. Specifically, we examined how signaling reciprocity varied between dyads depending on variation in grooming behavior: duration and frequency, reflected in the DGI, and reciprocity, as a proxy for social bond strength similarly as in other studies (Kalbitz et al., 2016), including these species (Wittig et al., 2020). We examined how signaling reciprocity varied between sex combinations, as variation in the philopatric sex may also shape species differences in cooperation and signaling patterns (Bründl et al., 2022; Fedurek et al., 2019). We evaluated variation between groups to detect traits shared at the species level, while considering possible group differences in social and signaling patterns (Schamberg et al., 2023).

Model 1: Differentiation of Grooming Relationships at the Individual Level

In model 1, we compared the level of differentiation of grooming relationships at the individual level, across sex combinations and groups. Each datapoint represented a CoV of DGI at the individual level (individuals in chimpanzees/mangabeys: n = 38/50). In the test predictors, we implemented the group identity in interaction with sex combination. We also accounted for individual identity as random effects, because of multiple measurements of the same individuals (one index per sex combination) and given variation in focal observation hours (Figure S1). We fitted the model using a Weibull error structure (Figure S2).

Model 2: Grooming Reciprocity

In model 2, we examined whether chimpanzees and mangabeys show different levels of grooming reciprocity between sex combinations. We considered that dyads had a grooming relationship when they groomed at least once in the dataset. Thus, each of these dyads constituted a datapoint (dyads in chimpanzees/mangabeys: n = 214/187). We tested as a fixed effect the group identity in interaction with sex combination (considering 3 levels on a dyadic scale: female-female, mixed, and male-male). We accounted for individual identity as random effects with a multi-membership approach (Raulo et al., 2021), to control for non-independence of the dataset considering repeated measurements of the same individuals within dyadic values. Running the model with a zero-one-inflated beta error structure provided a good fit with the response distribution (Figure S4b).

Models 3-6: Signaling Reciprocity and Social Bond Strength

In these models, we examined whether signaling reciprocity varied depending on relationship strength, using indices for grooming relationship strength and reciprocity, and sex combination as fixed effects. We considered only dyads that had a minimum of two approaches. Signaling was measured during approaches which varied in number between dyads (East group chimpanzees: mean ± SD: 13 ± 8 approaches per dyad; South group chimpanzees: 11 ± 9, TCP group mangabeys: 18 ± 12, TMP group mangabeys: 8 ± 6). A simulation-based analysis demonstrated that a simulated number of approaches did not necessarily increase or decrease associated reciprocity indices. However, this simulation did show that more approaches yielded more accurate measurements of reciprocity, with reduced deviation between observed and expected values (Figure S3).

We tested the influence of relationship strength on signaling reciprocity, considering all non-agonistic signals (models 3 and 5). Because some signals may be produced during approaches in relation to dominance relationships, thus be highly unidirectional (de Waal & Luttrell, 1989; Fedurek et al., 2021; Gust & Gordon, 1993), we also considered a subset of only socio-positive signals (models 4 and 6), where we expected a stronger link between signaling reciprocity and relationship strength. Following the same rationale, we implemented in models 3-6, dominance rank distance as a fixed effect, because dominance signals may be more frequent among dyads with steep and large dominance rank distances, than more shallow dominance relationships. Further, maternal kin may have similar dominance ranks and show high tolerance, association, and cooperation probability in mangabeys (Fruteau, Lemoine, et al., 2011; Mielke et al., 2020; Range, 2006), which may correlate with high signaling flexibility (Fröhlich & van Schaik, 2022), and reciprocity (Meunier et al., 2023). However, because of a lack of data, we could not directly test the effect of kinship on signaling reciprocity.

In these models, each dyad constituted a datapoint (dyads in chimpanzees/mangabeys: model 3: n = 298/490; dyads in model 4: n = 259/186; in model 5: n = 214/185; in model 6: n = 186/117). In models 3 and 4, we tested as fixed effects group identity as two-way interactions with the dyadic grooming index (DGI), and with sex combination (considering 3 levels on a dyadic scale: female-female, mixed, male-male). In models 5 and 6, we tested as fixed effects group identity as a two-way interaction with the grooming reciprocity index (dRI). In models 5 and 6, we also accounted for variation in the other dyadic factors, by also implementing the DGI, sex combination and absolute dominance rank distance as fixed effects.

We ran models 3-6 with a zero-one-inflated beta error structure, showing a good fit with the response distributions (Figure S4c-f). For the same rational as in model 2, we accounted for individual identity as random effects with a multi-membership approach (Raulo et al., 2021).

General Analytic Procedure

Data preparation and analyses were conducted in R 4.3.1 (R Core Team, 2021) using the RStudio Interface (RStudio Team, 2020), and "brms" package (Bürkner, 2017) (more details in supplementary material, Model parametrization and validation). In all models, we included a maximal random slope structure, when enough datapoints allowed for accurate estimation of slopes (DGI and dominance rank distance in models 2-6, dRI in model 5). In female mangabeys, low dominance rank distance, kinship, and high relationship strength may greatly overlap (Range, 2006; Range & Noë, 2002), yet no multicollinearity issues were detected in our models. The maximum variance inflation factor was 2 (sex combination in model 6), indicating no issues with collinearity (function *vif* of 'car' package) (Fox & Weisberg, 2019). Trace plots and model diagnostics (Rhat <1) indicated model convergence and appropriate mixing of chains. We used posterior predictive checks to validate our models (*pp_check* function of "brms", Figure S4).

For the models 2-6, with a zero-one-inflated beta error structure, we considered the effects found on the scale of the whole distribution, thus including beta, zero and one components (i.e., using the formula: (zoi * coi) + μ * (1- zoi), converted to the original scale, by using the inverse: "plogis()") (Bürkner, 2020).

For all models, we considered that there was strong or weak evidence of an effect when the 95% or 89% credible intervals (CI) of the posterior distribution of the models excluded 0, respectively. We also conducted tests on the predictive performance of the models including fixed effects compared with models including only random terms, which indicated clear predictive accuracy of the model 1, more uncertain predictive accuracy of the models 2, 3, 4 and 6, and low predictive accuracy of the model 5 (see details in supplementary material, Model efficiency).

Results

Between-Group Variation in Social Structure

Model 1: Differentiation of Grooming Relationships at the Individual Level

We examined the differentiation of grooming relationships at the individual level (CoV of DGI) across groups and sex combinations (Table S3). Within species, we found that in both chimpanzee groups, males had the least differentiated grooming relationships with other males compared with other sex combinations (Figure S5). In mangabeys, there was no consistent variation in the level of differentiation across sex combinations.

Between groups and within chimpanzees, there was no clear variation in the level of differentiation between East and South groups. Female-female relationships and the relationships of males with females were more differentiated in the TMP than TCP group mangabeys (estimate: 0.38, 95% CI [0.17, 0.59]; 0.31, 89% CI [0.01, 0.61]).

Between species, we found that mangabeys generally had more differentiated grooming relationships than chimpanzees, especially for mixed-sex dyads (Figure 1, Table 1, see Table S3 for all comparisons).

Model 2: Grooming Reciprocity

We examined variation in grooming reciprocity across sex combinations and groups (Table 1, Table S4). Within species, in the two groups of mangabeys, grooming relationships were more reciprocal among female-female than mixed-sex dyads.

Between groups and within species, male-male grooming interactions were more reciprocal in the South group than in East group chimpanzees (South versus East: 0.29, 95% CI [0.06, 0.49], Figure 1b).

There was no consistent variation between species. But between groups, we found some evidence that female-female grooming relationships in the TCP group mangabeys were more reciprocal than in the East group chimpanzees (TCP versus East: 0.14, 89% CI [0.02, 0.25]), and more reciprocal than in the TMP group mangabeys (TMP versus TCP: -0.16, 95% CI [-0.31, -0.001]). We also found some support that among mixed-sex dyads, grooming effort was less reciprocal in the TMP group mangabeys compared with the East group chimpanzees (TMP versus East: -0.15, 89% CI [-0.26, -0.03]) and TCP group mangabeys (TMP versus TCP: -0.14, 89% CI [-0.28, -0.01]).

The Link Between Signaling Reciprocity and Relationship Strength

Models 3 and 5: All Non-Agonistic Signals

For all groups, there was no evidence of a link between signaling reciprocity and grooming relationship strength (Figure 2a, Table S5). Further, among dyads that groomed each other at least once, there was no evidence of a link between signaling reciprocity and grooming reciprocity (Figure 2c, Table S7).

Within female-female dyads, we found no consistent evidence of differences in signaling reciprocity between the two chimpanzee groups. However, we found strong support for the differences between female-female dyads when comparing South group to the mangabey groups, with South group female-female reciprocity 34% and 68% higher than in the TCP and TMP groups (Figure 1c; TCP versus South: -0.14, 95% CI [-0.26, -0.02]; TMP versus South: -0.19, 95% CI [-0.31, -0.05]).

Within mixed-sex dyads, we found no consistent evidence of differences in signaling reciprocity between the two chimpanzee groups. However, we found support when comparing both chimpanzee groups to the mangabey groups, dyads being 53% and 45 % more reciprocal in the East group chimpanzees than TCP and TMP group mangabeys respectively (Figure 1c; TCP versus East: -0.13, 95% CI [-0.26, -0.001]; TCP versus South: -0.15, 95% CI [-0.29, -0.01]; TMP versus East: -0.12, 89% CI [-0.25, -0.02]); TMP versus South: -0.14, 95% CI [-0.28, -0.001]).

We found support for a link between high signaling reciprocity and dominance rank similarity across groups (-0.3, 95% CI [-0.4, -0.2]), without clear group differences (Figure 2e). Specifically, considering three classes of dominance rank distance (low: 1st and 2nd quartiles, intermediate: 3rd quartile and high: 4th quartile), signaling was 133% more reciprocal in dyads with low compared with high dominance rank distance.

Models 4 and 6: Subset of 'Socio-Positive' Signals Only

In line with our predictions, we found a link between socio-positive signaling reciprocity and grooming relationship strength, but only clearly within South group chimpanzees (Figure 2b, Table S6; 0.26, 89% CI [0.02, 0.5]). Signaling was 30% more reciprocal in dyads with high compared with low grooming relationship strength in the South group chimpanzees (considering three classes of DGI similarly as for dominance rank distance above). Similar results were obtained when we analyzed only dyads that groomed each other at least once, with a link between signaling reciprocity and grooming reciprocity in the South group chimpanzees (Figure 2d, Table S8; 0.24, 89% CI [0.03, 0.43]). Similarly, signaling was 25% more reciprocal in dyads with high compared with low level of grooming reciprocity in the South group chimpanzees. Finally, the link between signaling reciprocity and grooming reciprocity was markedly stronger in the South and East group chimpanzees compared with TCP group mangabeys (TCP versus East: -0.19, 89% CI [-0.36, -0.01]; TCP versus South: -0.29, 95% CI [-0.53, -0.02]).

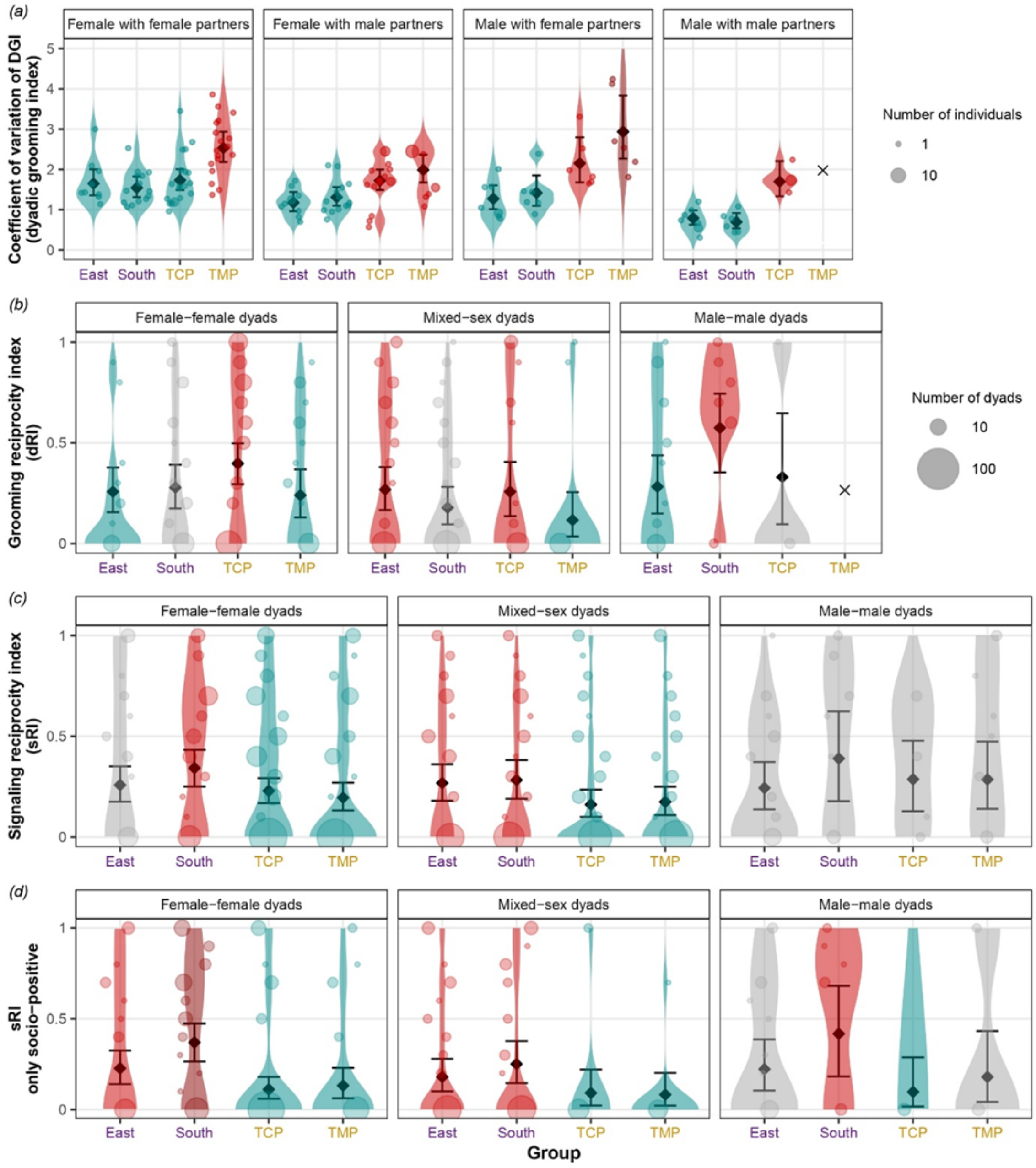
Among female-female dyads, within chimpanzees, signaling reciprocity was higher in the South group than in East group (South versus East: 0.15, 95% CI [0.01, 0.29]). We found support when comparing both chimpanzee groups to the mangabey groups, dyads being 66% and 75% more reciprocal in the East group chimpanzees than TCP and TMP group mangabeys respectively (Figure 1d, Table S6; TCP versus East: -0.14, 95% CI [-0.25, -0.03]; TCP versus South: -0.29, 95% CI [-0.42, -0.16]; TMP versus East: -0.12, 89% CI [-0.22, -0.02]; TMP versus South: -0.27, 95% CI [-0.41, -0.12]).

Among mixed-sex dyads, we found no consistent evidence of differences in signaling reciprocity between the two chimpanzee groups. But signaling reciprocity was 131% higher in East group chimpanzees compared with TMP group mangabeys (TMP versus East: -0.12, 89% CI [-0.23, -0.01]). Further, among mixed-sex dyads, signaling reciprocity was 132% and 180% higher in South group chimpanzees than in TCP and TMP group mangabeys respectively (TCP versus South: -0.17, 89% CI [-0.31, -0.02]); TMP versus South: -0.2, 95% CI [-0.36, -0.02]).

We found evidence of a general link between reciprocal signaling and dominance rank similarity (Figure 2f, Table S6; -0.2, 95% CI [-0.32, -0.08]). When considering three classes of dominance rank distance (see above), signaling was 70% more reciprocal in dyads with low compared with high rank distance. There was no evidence of group differences in this association.

Figure 1

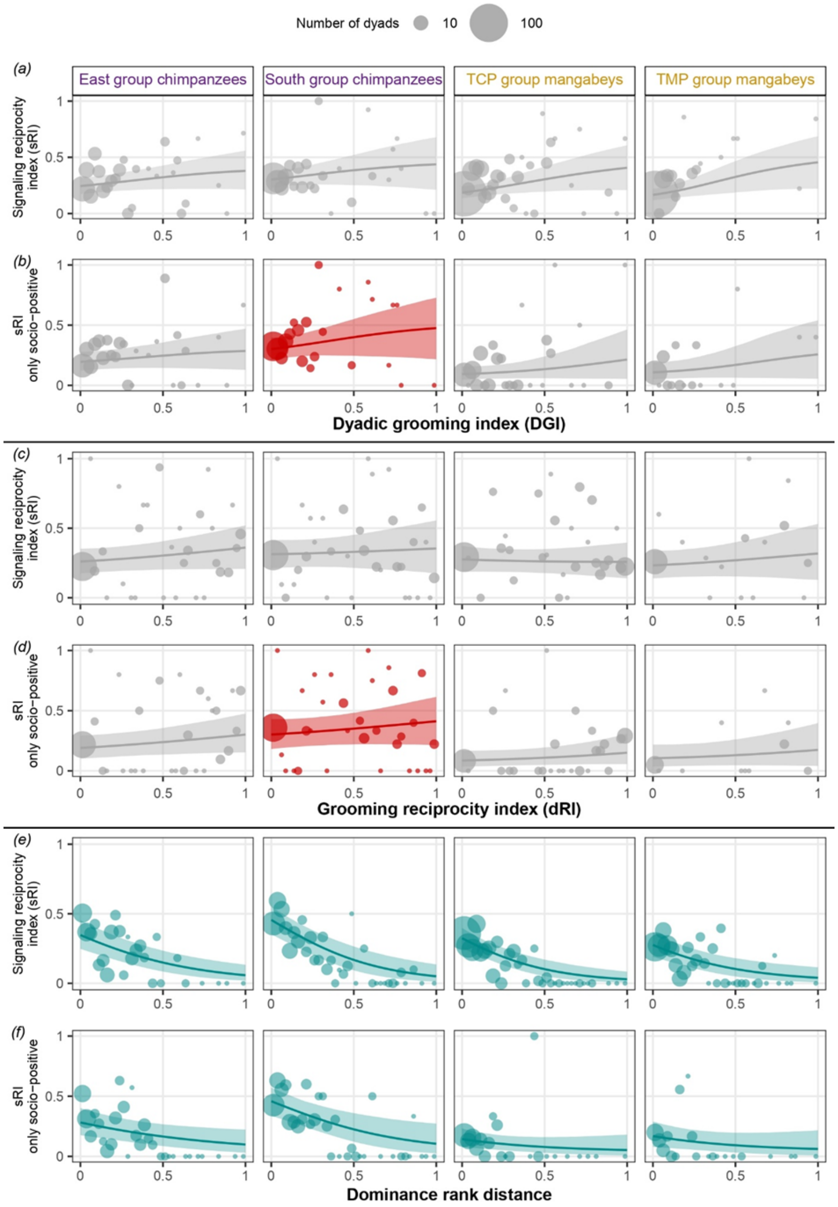
Chimpanzees Generally Showed Less Differentiated Grooming Relationships and More Dyads With Reciprocal Signaling Compared With Mangabeys



Note. Dots and violin plots represent aggregated raw values calculated, (a) per individual and sex combination, (b-d) per dyad. Diamonds represent the mean and 95% CI extracted from the posterior distribution of the models (a: model 1, b: model 2, c: model 3, d: model 4). Red categories had a higher level of differentiation or reciprocity than blue categories. Grey colors depict no consistent variation in the level of reciprocity. Purple and yellow group labels indicate the chimpanzee and mangabey groups, respectively. Cross: no grooming interaction was observed. (a) illustrates that chimpanzees generally had a lower level of differentiation in grooming relationship strength (CoV of DGI) compared with mangabeys. (b) grooming reciprocity was higher among female-female dyads in the TCP group mangabeys compared with TMP group mangabeys and East group chimpanzees. Among mixed-sex dyads, grooming reciprocity was higher in the East and TCP groups compared with the TMP group mangabeys. Among male-male dyads, grooming reciprocity was higher in the South group chimpanzees compared with East group chimpanzees. (c & d) illustrate that signaling reciprocity was generally higher in chimpanzee than in mangabey dyads, especially among female-female and mixed-sex dyads.

Figure 2

Dominance Rank Relationship Affected Signaling Reciprocity in All Groups, Whilst Grooming Relationship Strength and Reciprocity Affected Signaling Reciprocity Only Clearly in the South Group Chimpanzees and Considering Only Socio-Positive Signals



Note. Dots represent aggregated raw dyadic reciprocity indices per relationship index value (forty levels). Lines represent the mean and 95% CI extracted from the posterior distribution of models (a & e: model 3, b & f: model 4, c: model 5, d: model 6). Blue and red colors depict detected decrease or increase of the level of signaling reciprocity, respectively. Grey colors depict no consistent variation in the level of reciprocity. Purple and yellow group labels indicate the chimpanzee and mangabey groups, respectively. (a) There was no evidence of a link between signaling reciprocity with all non-agonistic signals and grooming relationship strength (DGI), (b) within South group chimpanzees, there was some evidence that signaling reciprocity with only socio-positive signals increased with grooming relationship strength (DGI). Although, no group differences in the direction or strength of this association were found; (c) There was no evidence of a link between signaling reciprocity with all non-agonistic signals and grooming reciprocity (dRI), (d) within South group chimpanzees, there was some evidence that signaling reciprocity with only socio-positive signals increased with grooming reciprocity (dRI). There was some evidence that this relation was more positive in South group chimpanzees compared with TCP group mangabeys, and in East group chimpanzees compared with TCP group mangabeys; (e) and (f) illustrate that individuals close in dominance rank were more likely to show reciprocal signaling, considering all and only socio-positive signals, across all groups.

Table 1

Between-Group Variation of the Levels of Differentiation in Grooming Relationship Strength, Dyadic Grooming Reciprocity, and Signaling Reciprocity During Repeated Approaches

<table>
<tr><th>Species</th><th colspan="12">Chimpanzees</th><th colspan="12">Mangabeys</th></tr>
<tr><th>Group</th><th colspan="6">East</th><th colspan="6">South</th><th colspan="6">TCP</th><th colspan="6">TMP</th></tr>
<tr><td>No. of focal subjects (female: ♀/male: ♂)</td><td colspan="6">10/8</td><td colspan="6">14/6</td><td colspan="6">20/6</td><td colspan="6">18/6</td></tr>
<tr><td colspan="25">Grooming behavior</td></tr>
<tr><td>Sex</td><td colspan="3">♀</td><td colspan="3">♂</td><td colspan="3">♀</td><td colspan="3">♂</td><td colspan="3">♀</td><td colspan="3">♂</td><td colspan="3">♀</td><td colspan="3">♂</td></tr>
<tr><td>Average number of grooming partners across individuals (mean ± SD)</td><td colspan="3">10 ± 2</td><td colspan="3">14 ± 2</td><td colspan="3">11 ± 2</td><td colspan="3">15 ± 2</td><td colspan="3">12 ± 4</td><td colspan="3">8 ± 3</td><td colspan="3">6 ± 2</td><td colspan="3">4 ± 2</td></tr>
<tr><td>Sex combination</td><td colspan="2">♀♀</td><td colspan="2">mixed</td><td colspan="2">♂♂</td><td colspan="2">♀♀</td><td colspan="2">mixed</td><td colspan="2">♂♂</td><td colspan="2">♀♀</td><td colspan="2">mixed</td><td colspan="2">♂♂</td><td colspan="2">♀♀</td><td colspan="2">mixed</td><td colspan="2">♂♂</td></tr>
<tr><td>Average number of grooming partners across individuals per sex combination (mean ± SD)</td><td colspan="2">4 ± 2</td><td colspan="2">7 ± 2</td><td colspan="2">7 ± 1</td><td colspan="2">7 ± 2</td><td colspan="2">6 ± 3</td><td colspan="2">5 ± 0</td><td colspan="2">10 ± 3</td><td colspan="2">4 ± 3</td><td colspan="2">1 ± 1</td><td colspan="2">5 ± 2</td><td colspan="2">3 ± 2</td><td colspan="2">-</td></tr>
<tr><td>Dyads that groomed with reciprocal grooming*/total dyads that groomed (model 2)</td><td colspan="2">11%</td><td colspan="2">36%</td><td colspan="2">30%</td><td colspan="2">27%</td><td colspan="2">18%</td><td colspan="2">86%</td><td colspan="2">50%</td><td colspan="2">28%</td><td colspan="2">25%</td><td colspan="2">32%</td><td colspan="2">9%</td><td colspan="2">-</td></tr>
<tr><td colspan="25">Signaling behavior</td></tr>
<tr><td>Dyads with reciprocal signaling effort across approaches*/total dyads that signaled (model 3)</td><td colspan="2">31%</td><td colspan="2">23%</td><td colspan="2">21%</td><td colspan="2">39%</td><td colspan="2">22%</td><td colspan="2">50%</td><td colspan="2">23%</td><td colspan="2">12%</td><td colspan="2">38%</td><td colspan="2">20%</td><td colspan="2">14%</td><td colspan="2">39%</td></tr>
<tr><td>Dyads with reciprocal socio-positive signaling effort*/total dyads that emitted socio-positive signaling (model 4)</td><td colspan="2">29%</td><td colspan="2">18%</td><td colspan="2">32%</td><td colspan="2">44%</td><td colspan="2">22%</td><td colspan="2">64%</td><td colspan="2">16%</td><td colspan="2">9%</td><td colspan="2">0%</td><td colspan="2">15%</td><td colspan="2">6%</td><td colspan="2">29%</td></tr>
</table>

Note. In bold: increased level of differentiation or reciprocity compared with other groups. In TMP mangabeys, no grooming was observed between males.*reciprocal: RI > 0.5 (Newton-Fisher & Lee, 2011).

Discussion

Signaling may help partners to coordinate cohesion in time and space (Leighty et al., 2008; Schamberg et al., 2016; Schel et al., 2013), particularly facilitating joint actions, such as mutual-grooming (Fedurek et al., 2015), coalition formation (Fedurek et al., 2013; Mitani & Nishida, 1993; Moore et al., 2020; Smith et al., 2011; Young et al., 2014), mobbing behavior (Kern & Radford, 2016) and cooperative hunting (Mine et al., 2022). As a result, within groups or social units, dyadic signaling reciprocity could serve as a proxy for the level of social bonding between partners (Arlet et al., 2015; Fernandez et al., 2017; Kulahci et al., 2015; Levréro et al., 2019; Luef & Pika, 2017; Scheumann et al., 2017). Alternatively, previous studies posited that signaling may be a more flexible and low-cost behavior to mediate social relationships than grooming (Fedurek et al., 2013), and thus signaling reciprocity may facilitate short-term coordination with unfamiliar or less bonded group members than frequent grooming partners, such as during vocal exchanges between coalition partners in chimpanzees (Fedurek et al., 2013), and nearest neighbors in red-capped mangabeys (*Cercocebus torquatus*) (Meunier et al., 2023).

Between-Group Variation in the Link Between Signaling Reciprocity and Relationship Strength

In the present study, we examined signaling reciprocity in two sympatric species, mangabeys and chimpanzees that form close and enduring relationships with specific partners (Wittig et al., 2020). First, we found that in both species, individuals formed well-differentiated grooming relationships (i.e., considering high CoV values above one, with a standard deviation higher than the mean). However, chimpanzees, especially males, generally had a larger number of grooming partners, and a lower level of differentiation in grooming relationship strength compared with mangabeys (Figure 1, Table 1). Second, we distinguished between dyads that engaged in high rates of grooming (grooming relationship strength) and dyads that displayed equitable grooming duration (grooming reciprocity). We found some evidence of a positive relation between reciprocal signaling and high grooming relationship strength, but only clearly in the South group chimpanzees and considering only socio-positive signals (Figure 2b). Although, there was no clear evidence of a difference in the direction or strength of the association between grooming relationship strength and reciprocal signaling across the groups of mangabeys and chimpanzees. Further, within South group chimpanzees, there was some support for a positive link between grooming reciprocity and socio-positive signaling reciprocity (Figure 2d). Grooming reciprocity was more positively related to signaling reciprocity with socio-positive signals in the two groups of chimpanzees than in the TCP group mangabeys.

Within species, these findings provide support for the social bonding hypothesis for the evolution of communication (Chereskin et al., 2022; Dunbar, 1993, 2003; Lynch Alfaro, 2008; Smith et al., 2011), but more clearly in chimpanzees than mangabeys. Therefore, between species, our results may be in line with our alternative hypothesis, positing that signaling may play a more determinant role in chimpanzees than mangabeys, possibly to manage close relationships with numerous partners in a fission-fusion system (Ramos-Fernández, 2005). In addition, in mangabeys, a strong reliance on kin-related matriline members in relationship formation (Range, 2006; Range & Noë, 2002), may lower the need to signal to mediate tolerance, coordination, and cooperation between bonded partners, particularly among philopatric females. Previous studies that established a link between high signaling reciprocity and relationship strength focused on responses to vocalizations and vocal duetting (Arlet et al., 2015; Fernandez et al., 2017; Kulahci et al., 2015; Luef & Pika, 2017; McComb et al., 2000; Pougnault et al., 2022; Ramos-Fernández, 2005). Our study extended beyond previous research by demonstrating that the propensity to emit both auditory and visual signals during close-range dyadic communication may increase with the relationship strength with a partner, and thus may help to maintain, reinforce, or advertise social bonds (Luef & Pika, 2017; Lynch Alfaro, 2008; Smith et al., 2011). Further, our results suggested that species may show varying strength of the link between signaling reciprocity and relationship strength, potentially in relation to variation in social systems, and associated level of social complexity. Specifically, we propose that a high number of strong grooming relationships, a low influence of kinship in relationship formation and maintenance, and high challenges of relationship maintenance in a fission-fusion system may promote the level of signaling reciprocity between bonded partners in chimpanzees compared with mangabeys.

For future research, exploring these patterns over a longer time frame and across additional groups within each species than possible in the present study may help us to understand whether the group differences detected here reflect consistent species differences. Further, long-term studies may also allow to capture variation in the stability of close relationships, an important aspect of 'social bonds' (Kalbitz et al., 2016; Wittig et al., 2020), which could not be measured here. Studying other potentially reciprocal social exchanges, such as coalitionary support or infant handling, is also needed to examine further the link between exchanges of 'commodities' and signaling reciprocity (Borgeaud & Bshary, 2015; Fraser & Bugnyar, 2012; Fruteau, van de Waal, et al., 2011), particularly in mangabeys. In this study, male-male grooming interactions in mangabeys occurred only in one group, and within subadult-adult pairs. It is thus possible that alliances among males in mangabeys may be better estimated by the rates of exchange in coalitionary support rather than grooming interactions, as it may be more determinant in species with weak male-male social bonds (Dal Pesco & Fischer, 2020).

Signaling Reciprocity and Dominance Rank Similarity

We found robust evidence across groups and species of a link between reciprocal signaling and low dominance rank distance between partners. Reciprocal signaling production between individuals of similar rank may indicate unclear dominance relationships, reflecting equal probabilities to signal to mediate social tolerance while approaching each other. Further, dyads with shallower dominance relationships may exhibit higher social tolerance than dyads with a large dominance rank distance, which may increase signaling flexibility (Fröhlich & van Schaik, 2022) and reciprocity. For instance, it is possible that socio-positive signals such as 'peering' in chimpanzees may have been reciprocally emitted between partners engaging in relatively low rates of grooming but with close dominance ranks (Figures S6-8). In mangabeys, individuals with close dominance ranks are likely to be maternal kin (Range, 2006), and thus may exhibit high spatial proximity and social tolerance (Mielke et al., 2020). Previous results in the TCP group mangabeys demonstrated a positive link between dyadic association and maternal kinship (Mielke et al., 2020). In comparison, individuals with large dominance rank distance may have clearer dominance relationships and may rather be characterized by unidirectional signaling during approaches, with a frequent emission of submissive signals from lower towards higher-ranking individuals in both species (de Waal & Luttrell, 1989; East et al., 1993; Fedurek et al., 2021; Laporte & Zuberbühler, 2010; Reddon et al., 2021). Although, female mangabeys may also direct benign intent vocalizations towards lower-ranking females prior to affiliative contacts, and in the presence of infants (Fedurek et al., 2019; Range & Fischer, 2004). By examining the contexts of signaling initiation specifically during approaches we could identify systematically a signal receiver during independent signaling events. However, close-range communication may often underpin conflict prevention strategies (Fedurek et al., 2021; Silk et al., 2016), explaining the strong effect of dominance rank distance in our models.

Between-Group Variation in Signaling Reciprocity and Social Structure

Between species, we found that there were more dyads with reciprocal signaling in chimpanzees than in mangabeys, especially when considering socio-positive signaling only and within female-female and mixed-sex dyads. This may again reflect the aforementioned kin-based cooperation seen in mangabeys. Signaling may thus mediate social interactions, and relationships, with a larger number of partners, which may boost the number of dyads with reciprocal signaling in chimpanzees compared with mangabeys. The larger numbers of grooming and signaling partners in chimpanzees compared with mangabeys may also relate to frequent group-level cooperation in this species (Moscovice et al., 2020; Samuni et al., 2018, 2021).

Within chimpanzees, male-male dyads, which are usually the most cooperative ones and with a low differentiation in association patterns (Surbeck et al., 2017), had the least differentiated grooming relationships in our study (Figure S5). Further, among male-male dyads, the levels of reciprocity in grooming exchanges and socio-positive signaling production were higher in the South group than East group. Prior to the current study, dominance rank changes between males were more frequent in the South compared with the East group (Preis et al., 2019). Future research could investigate whether this particularly high level of reciprocity in grooming duration among males in the South group was transitory and corresponded to a period of high social instability, and increased risks of partner defection in a fission-fusion system. High social instability among males in the South group could also promote socio-positive signaling reciprocity in comparison with East group males.

Conclusion

Previous studies suggested that examining signaling patterns within a group may provide information about its social structure (Pougnault et al., 2022; Reddon et al., 2021; Snijders & Naguib, 2017), particularly relating to the strength of relationships within that structure (Fedurek et al., 2013; Levréro et al., 2019). Here, we found some evidence that relationship strength related positively to reciprocal signaling, but more clearly when considering only socio-positive signals and in chimpanzees rather than mangabeys. Overall, individuals had more differentiated grooming relationships and there were fewer dyads with reciprocal signaling in the groups of mangabeys compared with chimpanzees. We propose that in chimpanzees, the need to maintain close relationships with many partners, particularly considering more frequent group-level cooperation (Samuni et al., 2018, 2021), may boost signaling production and reciprocity, as signals during approaches may mediate tolerance, coordination and cooperation with others, and ultimately facilitate relationship management (Fedurek et al., 2013, 2015; Mitani & Nishida, 1993; Reddon et al., 2021; Schel et al., 2013). A greater reliance on kin-related matriline members in relationship formation may limit the number of cooperative partners and result in a lower number of dyads with reciprocal signaling production in mangabeys compared with chimpanzees.

The larger numbers of grooming and reciprocal signaling partners found here in chimpanzees, possibly related to more flexible close relationships (Wittig et al., 2020), may also underlie higher cognitive challenges compared with mangabeys (Melis & Raihani, 2023). Chimpanzees exhibit slower life history traits than mangabeys, which may favor the emergence of cognitive adaptations to the physical and social environments (Schaik & Deaner, 2003). In accordance with this idea, chimpanzees, unlike mangabeys, produce alarm calls depending on the state of knowledge of the audience (Girard-Buttoz, Surbeck, Samuni, Tkaczynski, et al., 2020; Mielke, Crockford, & Wittig, 2019). That said, chimpanzees may have more grooming partners and show more frequent group-level cooperation than bonobos, despite sharing similar socio-cognitive skills (Girard-Buttoz, Surbeck, Samuni, Boesch, et al., 2020; Girard-Buttoz, Surbeck, Samuni, Tkaczynski, et al., 2020). Therefore, whether species differences among mangabeys and chimpanzees in grooming or signaling patterns are underpinned by cognitive differences requires further investigation.

Both within and between-group findings offer some support for a link between signaling reciprocity and high relationship strength, and thus the social bonding hypothesis for the evolution of signaling (Chereskin et al., 2022; Dunbar, 1993, 2003; Lynch Alfaro, 2008; Smith et al., 2011). Our findings suggest that signaling reciprocity may increase with the number of strong relationships and increasing challenges to maintain coordination and relationships in societies with strong fission-fusion dynamics. Further comparative studies are needed to examine how different social complexity factors may promote reciprocal dyadic signaling across a wider range of groups and species, such as the number of strong grooming relationships, the role of kinship in relationship formation, and the levels of fission-fusion dynamics and dominance rank instability.

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Conflict of Interest: We declare we have no competing interests.

Data accessibility: Data (https://doi.org/10.6084/m9.figshare.27220797) and Rcode (https://doi.org/10.6084/m9.figshare.27220806) are provided on Figshare.

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Supplementary Material

Data Collection

Table S1

Sample Sizes per Group

Species	Chimpanzees		Mangabeys	
Group ID	East	South	TCP	TMP
Period of observation	12/2018 - 05/2019 – 10/2019 - 04/2020 (2 field seasons)	01/2019 - 05/2019 – 11/2019 - 07/2020 (2 field seasons)	04/2019 - 05/2019 – 01/2020 - 08/2020 (2 field seasons)	01/2020 – 06/2020
No. of grooming initiations observed	(1 field season)			
Observation hours of directed grooming	253	241	232	81
No. of signaling events during approaches	31	34	21	8
Socio-positive signaling only	786	898	1759	844
Observation hours (h)	1577		1126	

Table S2

Compiled Signal Types Observed During Approaches in Chimpanzees And Mangabeys, from the Three Sensory Modalities: Auditory, Visual, and Multisensory

Sensory Modality	Chimpanzees	Mangabeys	Comments
auditory	Grunt	Grunt	(videos 1 & 4)
auditory	Bark	Twitter	
auditory	Hoo	Growl	
auditory	Scream	Scream	
auditory	Pant-grunts	Copulation call	(video 1)
auditory	Non-vocal sounds		Teeth-clacking, raspberry blowing, lip-smacking
auditory	Pants/Laughter		(video 1)
auditory	Pant-hoots		(video 1)
auditory	Whimper		
auditory	Pant-grunts + screams/barks		Combination of pant-grunts with pant-barks and/or pant-screams (considered as a combination of auditory types).
visual	Head movement	Head movement	Including head/thorax bobbing, shaking: repeated movements of the head, back and forth or on the sides.
visual	Standstill display	Standstill display	Including move back and forth, bounce, swagger, rock (swing whole body or shoulders on the sides or forwards, while bipedal, quadrupedal, or seated) or bipedal stance (videos 1 & 2).
visual	Withdrawing	Withdrawing	Signaler moves or jumps aside from its original spot, enters a tree in reaction to the partner’s approach but stays in proximity to the partner.
multisensory	Movement display	Movement display	Including speed up/run towards, jump forwards, shuffle, stiff walk, gallop, bipedal swagger while moving towards the receiver during the approach (video 1).
visual	Peering	Peering	Signaler is stationary giving a prolonged stare (> 1 second) at close proximity (< 2 meters) at the action conducted by one

			individual (e.g., self-grooming, foraging, inspecting, feeding, or allogrooming)(Nishida et al., 2010).
visual	Present body part	Present body part	Direct a body part towards the receiver (grooming solicitation) (video 1).
visual	Bow; Crouch	Bow; Crouch	Bend (front/hind) limbs, approaching its body to the substrate, hunch.
visual	Present sexual	Present sexual	Direct genital parts towards the receiver or raise the tail to make genital parts visible (video 3).
visual	Extend arm/limb	Extend arm/limb	Extend part of the arm towards the receiver (finger, wrist, hand), beckon, and hold it stationary for a moment.
visual	Throw arm	Throw arm	Upward movement of one/two arms towards the receiver.
visual	Arm raise	Not observed	Extend the arm vertically above the head, eventually grabbing a branch (video 1).
multisensory	Loud scratch	Not observed	Exaggerated (entire arm) loud scratches with response waiting (e.g., looking at the receiver and not immediately leading to self-grooming) (video 1).
multisensory	Contact object	Contact object	Drag, shake, throw, swing, or hold, break a branch (chimpanzees, N=36) (video 1). Throw sand to the receiver (chimpanzees, N=1). Drum tree (chimpanzees, N = 1).
multisensory	Contact ground	Contact ground	Slap, hit ground with hand or stomp feet on the ground (chimpanzees, N=9, mangabeys, N=38).
Unknown: Approaches removed from dataset	N=159	N=129	Signaler's behavior(s) not clearly identified because of poor visibility or inaudibility during the whole or part of the behavioral sequence.
Other: Approaches removed from dataset	N=4	N=13	Clear visibility/listening of the signaler's behavior but unclassified based on ethogram; e.g., mangabeys: touch own's genital parts while looking at partner in visual signals.

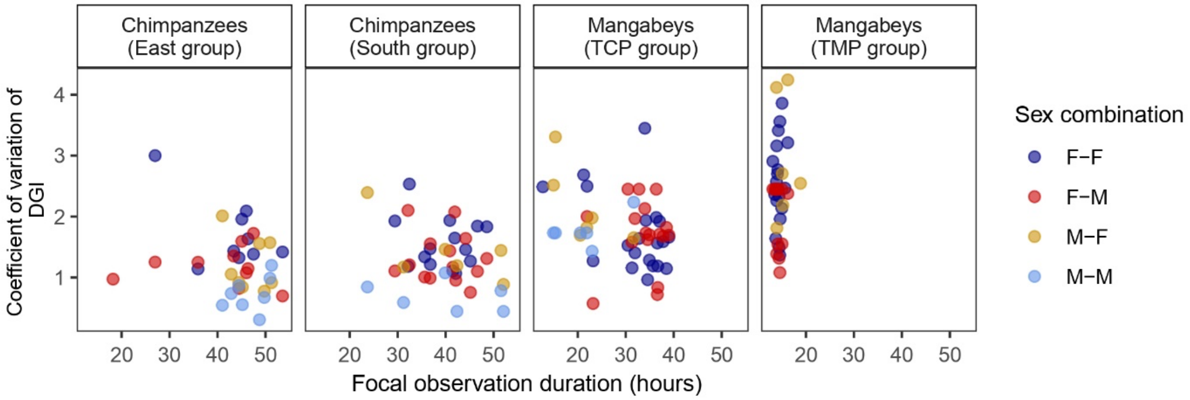
Note. Types are based on the repertoires of signals established in (Aychet et al., 2021), (Range & Fischer, 2004) in mangabeys, and (Bortolato et al., 2023) and (Hobaiter & Byrne, 2011) in chimpanzees. Illustrative videos are published online: video 1 (https://doi.org/10.6084/m9.figshare.21995813.v1), video 2 (https://doi.org/10.6084/m9.figshare.21995930.v1), video 3 (https://doi.org/10.6084/m9.figshare.21995933.v1), video 4 (https://doi.org/10.6084/m9.figshare.21995966.v1).

Statistical Analyses

Model 1: Differentiation of Grooming Relationships at the Individual Level

Figure S1

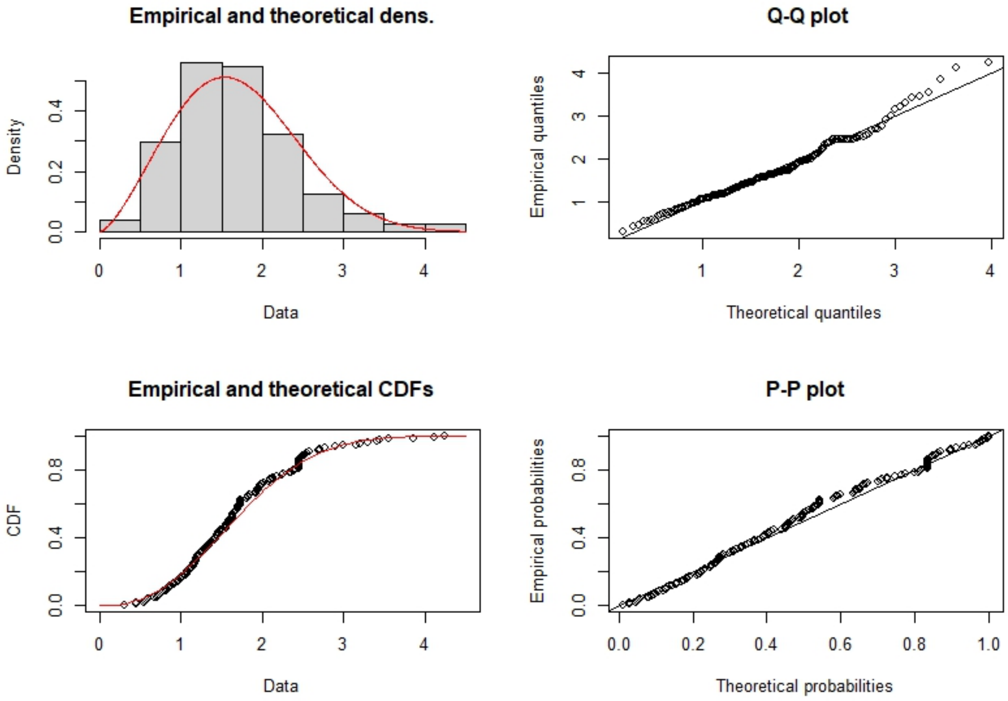
Coefficient of Variation (CoV) of the Dyadic Grooming Index (DGI) on an Individual Level Depending on Total Focal Observation Time in Hours, in the Four Groups and Sex Combinations



Note. The coefficient of variation of DGI served as a proxy for the level of differentiation of grooming relationships at the individual level (estimated per individual and sex combination: female-female, female with male partners, male with female partners, male-male).

Figure S2

Distribution of the Data for the Model 1 Compared with the Theoretical Distribution with a Weibull Error Structure

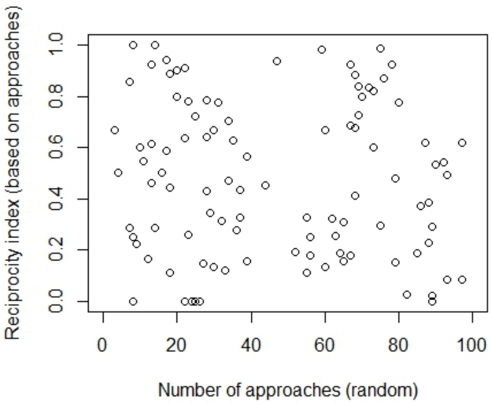


Note. We used the package ‘fitdistrplus’ to compare distributions of the observed data with theoretical distributions with a Weibull structure (Delignette-Muller & Dutang, 2015), which indicated a good fit for the response distribution.

Models 3-6: Signaling Reciprocity and Relationship Strength

Figure S3

Simulation of the Calculation of Reciprocity Indices Based on Randomly Assigned Number of Approaches (From 2 to 100)



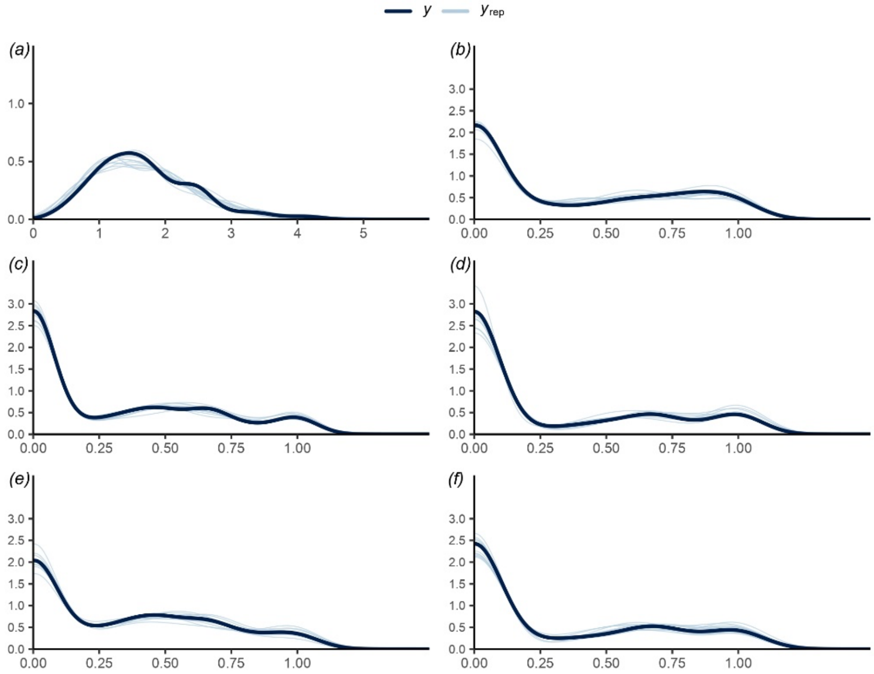
Note. We created a dataset of 100 dyads with a randomly assigned total number of approaches with signaling per dyad (from 2 to 100 approaches). We assigned to these dyads random values of reciprocity indices (RI) in the range (0, 1). Because reciprocity indices are based on the formula: $RI_{AB} = 1 - |(X_{A\text{-}B} - X_{B\text{-}A}) / (X_{A\text{-}B} + X_{B\text{-}A})$, we considered the probability of approach for one individual $P_{(A)}$, with $RI = 1 - | P_{(A)} - (1 - P_{(A)}) |$, and thus as $P_{(A)} = RI/2$. Considering this probability $P_{(A)}$, we created 1000 simulated datasets with one row for one approach per dyad from the initial dataset with a randomly assigned total number of approaches per dyad. Then, we calculated the reciprocity indices from these simulated datasets. There was no clear relation between randomly assigned number of approaches and associated reciprocity indices (Figure S3), as estimated by a mean of 0.04, 95% CI [-0.07, 0.16], with a deviation from ground truth estimated at 0.1, 95% CI [-0.13, 0.32]. Although, deviation from ground truth was negatively correlated with the number of approaches: -0.42, 95% CI [-0.53, -0.29] (average coefficients obtained from 1000 simulated datasets).

General Analytical Procedure

Model Parameterization and Validation. We used the Hamiltonian Monte Carlo methods, with the “RStan” package (Stan Development Team, 2022) and the “brms” package (Bürkner, 2017). For the fixed effects, we used weakly regularizing priors (β~Normal (0,1)) and for the random effects the default priors provided by the *get_prior* function of “brms”, i.e., a weakly regularizing half student-t prior (3, 0, 2.5) for the random intercepts, and a uniform LKJ Cholesky prior (η=1) for covariance of the random slopes and intercepts. We defined the number of chains and iterations to get bulk effective sample sizes for each parameter above 100 times the number of chains (e.g., three chains of 10,000 iterations).

Figure S4

Posterior Predictive Checks of The Models 1: a To 6: f



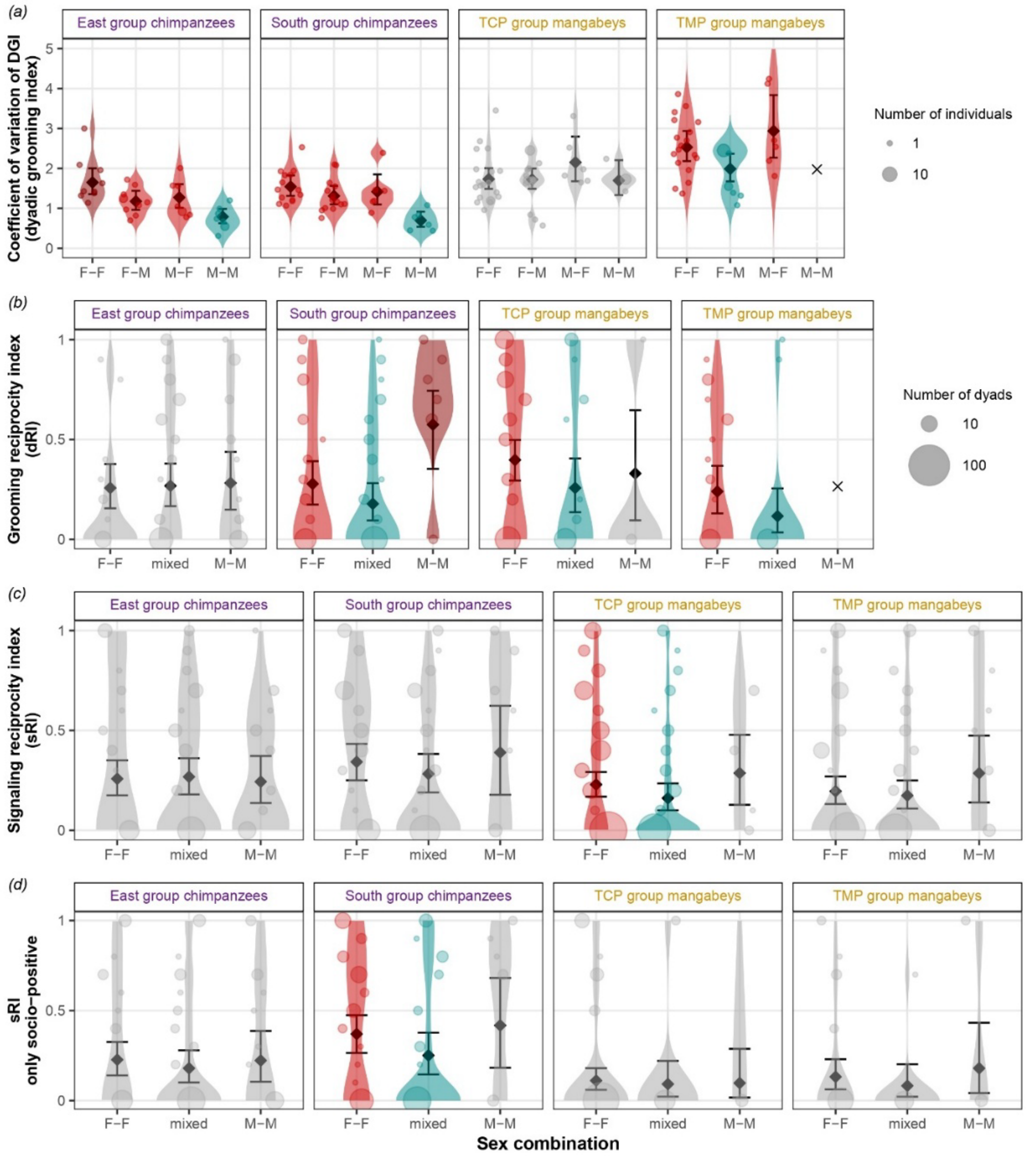
Note. The graph compares 'y' the observed outcome variable to simulated datasets 'y_{rep}' from the posterior predictive distribution.

Model Efficiency. To evaluate model efficiency (or predictive performance) of the model 1, we estimated the R^2 (representing the variance of modelled predicted means divided by the total variance of the response, ranging from 0 to 1 (Gelman et al., 2019)), conditional (considering all predictors) = 0.60, 95% CI [0.48, 0.70], and marginal (only with fixed effects) = 0.50, 95% CI [0.40, 0.58]. We also ran a loo comparison between each model, and the same model excluding tested fixed effects. For models 2-6, we ran only loo comparisons, considering the zero-one-inflated beta error structure of these models. We considered absolute 'elpd difference' values above 4 as indicating clear difference in predictive performance, also considering the range, with twice the error value: ± 2*SE (Vehtari et al., 2023). For model 1, model efficiency was high (for the model without fixed effects: model 1: elpd difference = -31.1 ± (2*8=16)). For models 2, 3, 4 and 6, predictive performance was more uncertain, as the range of 'elpd difference' values did not include 0, but included values below 4 (for models without fixed effects: model 2: elpd difference = -13.5 ± 12.8; model 3: elpd difference = -17.3 ± 14.6; model 4: elpd difference = -13.8 ± 11.6; model 6: elpd difference = -11.4 ± 9.4). For model 5, predictive performance was low, as the range of 'elpd difference' included 0 (for the model without fixed effects: model 5: elpd difference = -7.1 ± 10.4).

Results

Figure S5

Within-Group Variation of the Levels of Differentiation of Grooming Relationships, Grooming Reciprocity and Signaling Reciprocity



Note. Within chimpanzee groups, male-male dyads generally showed lower differentiation in grooming relationship strength compared with other sex combinations. Within mangabey groups, female-female dyads showed higher grooming reciprocity than mixed sex dyads. No within-group variation was consistently found within species in terms of signaling reciprocity. Dots and violin plots represent aggregated raw values calculated, (a) per individual and sex combination, (b-d) per dyad. Diamonds represent the mean and 95% CI extracted from the posterior distribution of the models (a: model 1, b: model 2, c: model 3, d: model 4). Red categories had a higher level of differentiation or reciprocity than blue categories. Grey colours depict no consistent variation in the level of reciprocity. Purple and yellow group labels indicate the chimpanzee and mangabey groups, respectively. Cross: no grooming interaction was observed. (a) illustrates that among chimpanzees, male-male dyads generally had a lower level of differentiation in grooming relationship strength (CoV of DGI) compared with other sex combinations. (b) illustrates that among mangabeys, grooming reciprocity was higher in female-female than mixed-sex dyads. (c) Considering all non-agonistic signals, there was some support for a higher level of signaling reciprocity in female-female compared with mixed-sex dyads in TCP group mangabeys. (d) Considering only socio-positive signals, there was some support for a higher level of signaling reciprocity in female-female compared with mixed-sex dyads in South group chimpanzees.

Table S3

Results from the Model 1 Depicting the Variation in CoV of the Grooming Relationship Strength (DGI) on an Individual Level, Between Sex Combinations and Groups

(a)

Hypotheses for model 1	**Estimate**	**Error**	**95% CI**	
			lower	**upper**
Within groups				
East group chimpanzees				
Female-male versus female-female	**-0.34**	**0.13**	**-0.58**	**-0.09**
Male-female versus female-female	-0.26	0.15	-0.55	0.03
Male-male versus female-female	**-0.74**	**0.15**	**-1.03**	**-0.44**
Male-female versus female-male	0.08	0.16	-0.23	0.39
Male-male versus female-male	**-0.4**	**0.15**	**-0.7**	**-0.1**
Male-male versus male-female	**-0.48**	**0.15**	**-0.77**	**-0.18**
South group chimpanzees				
Female-male versus female-female	-0.16	0.11	-0.37	0.05
Male-female versus female-female	-0.09	0.15	-0.39	0.22
Male-male versus female-female	**-0.8**	**0.16**	**-1.09**	**-0.47**
Male-female versus female-male	0.07	0.16	-0.22	0.39
Male-male versus female-male	**-0.64**	**0.16**	**-0.94**	**-0.31**
Male-male versus male-female	**-0.71**	**0.16**	**-1.03**	**-0.39**
TCP group mangabeys				
Female-male versus female-female	-0.01	0.1	-0.2	0.18
Male-female versus female-female	0.21	0.15	-0.07	0.52
Male-male versus female-female	-0.03	0.15	-0.31	0.28
Male-female versus female-male	0.22	0.15	-0.07	0.53
Male-male versus female-male	-0.02	0.15	-0.3	0.28
Male-male versus male-female	-0.24	0.16	-0.56	0.09
TMP group mangabeys				
Female-male versus female-female	**-0.24**	**0.1**	**-0.44**	**-0.04**
Male-female versus female-female	0.14	0.15	-0.15	0.45
Male-male versus female-female	-	-	-	-
Male-female versus female-male	**0.38**	**0.16**	**0.07**	**0.71**
Male-male versus female-male	-	-	-	-
Male-male versus male-female	-	-	-	-
Between groups				
Sex combination female-female				
South versus East group chimpanzees	-0.06	0.13	-0.32	0.19
TCP mangabeys versus East chimpanzees	0.05	0.12	-0.19	0.29
TMP mangabeys versus East chimpanzees	**0.43**	**0.12**	**0.19**	**0.68**
TCP mangabeys versus South chimpanzees	0.12	0.11	-0.11	0.34
TMP mangabeys versus South chimpanzees	**0.49**	**0.11**	**0.27**	**0.71**
TMP versus TCP group mangabeys	**0.38**	**0.11**	**0.17**	**0.59**
Sex combination female-male				
South versus East group chimpanzees	0.11	0.13	-0.15	0.37
TCP mangabeys versus East chimpanzees	**0.38**	**0.13**	**0.13**	**0.63**
TMP mangabeys versus East chimpanzees	**0.53**	**0.13**	**0.26**	**0.79**
TCP mangabeys versus South chimpanzees	**0.27**	**0.12**	**0.04**	**0.51**
TMP mangabeys versus South chimpanzees	**0.42**	**0.12**	**0.17**	**0.66**
TMP versus TCP group mangabeys	0.14	0.12	-0.08	0.37
Sex combination male-female				
South versus East group chimpanzees	0.11	0.17	-0.23	0.45
TCP mangabeys versus East chimpanzees	**0.52**	**0.17**	**0.18**	**0.87**
TMP mangabeys versus East chimpanzees	**0.83**	**0.18**	**0.49**	**1.18**
TCP mangabeys versus South chimpanzees	**0.42**	**0.19**	**0.05**	**0.79**
TMP mangabeys versus South chimpanzees	**0.42**	**0.12**	**0.17**	**0.66**
TMP versus TCP group mangabeys	0.31	0.19	-0.06	0.68
Sex combination male-male				
South versus East group chimpanzees	-0.13	0.18	-0.47	0.22
TCP mangabeys versus East chimpanzees	**0.76**	**0.17**	**0.43**	**1.1**
TMP mangabeys versus East chimpanzees	-	-	-	-
TCP mangabeys versus South chimpanzees	**0.89**	**0.19**	**0.52**	**1.25**
TMP mangabeys versus South chimpanzees	-	-	-	-
TMP versus TCP group mangabeys	-	-	-	-

(b)

Summary from model 1 Response: CoV of DGI			**95% CI**			
	Estimate	Error	**lower**	**upper**	Bulk ESS	Tail ESS
Intercept	0.5	0.1	0.3	0.7	3281.34	4184.88
Group (East) South	-0.06	0.13	-0.32	0.19	3710.95	5366.25
TCP mangabeys	0.05	0.12	-0.19	0.29	3324.93	5291.88
TMP mangabeys	**0.43**	**0.12**	**0.19**	**0.68**	**3788.8**	**5093.33**
Sex combination (F-F) F-M	**-0.34**	**0.13**	**-0.58**	**-0.09**	**3798.77**	**5346.38**
South*F-M	0.17	0.16	-0.14	0.5	4197.81	5632.79
TCP mangabeys*F-M	**0.33**	**0.15**	**0.02**	**0.63**	**4014.73**	**6066.65**
TMP mangabeys *F-M	0.1	0.16	-0.22	0.41	4280.84	6094.27
Sex combination (F-F) M-F	-0.26	0.15	-0.55	0.03	2856.38	4346.02
South*M-F	**0.17**	**0.21**	**-0.24**	**0.6**	**3996.06**	**5394.5**
TCP mangabeys*M-F	**0.47**	**0.21**	**0.07**	**0.89**	**3419.27**	**4959.62**
TMP mangabeys *M-F	0.4	0.21	-0.01	0.82	4026.8	5237.77
Sex combination (F-F) M-M	-0.74	0.15	-1.03	-0.44	3724.94	5626.73
South*M-M	-0.06	0.22	-0.49	0.37	4346.66	5619.22
TCP mangabeys*M-M	**0.71**	**0.21**	**0.31**	**1.11**	**4274.77**	**6145.94**
*TMP mangabeys *M-M*	-	-	-	-	-	-

Note. Blue/bold and green cells indicate estimates whose directions are supported by the 95% and 89% CI of the posterior distribution. In brackets: the reference level. Results from the model 1: (a) comparisons between groups and sex combinations, (b) summary table of results. In italics: no grooming event observed.

Table S4

Results from the Model 2 Depicting Variation in Grooming Reciprocity (dRI) Across Sex Combinations and Groups

(a)

Hypotheses for model 2 Response: grooming reciprocity dRI	Estimate	Error	95% lower	95% upper
Within groups				
East group chimpanzees				
Mixed versus female-female	0.01	0.06	-0.11	0.13
Male-male versus female-female	0.02	0.08	-0.13	0.19
Male-male versus mixed	0.01	0.08	-0.13	0.17
South group chimpanzees				
Mixed versus female-female	-0.1	0.06	-0.22	0.02
Male-male versus female-female	**0.3**	**0.11**	**0.07**	**0.49**
Male-male versus mixed	**0.4**	**0.1**	**0.19**	**0.57**
TCP group mangabeys				
Mixed versus female-female	-0.14	0.08	-0.28	0.02
Male-male versus female-female	-0.07	0.14	-0.31	0.24
Male-male versus mixed	0.07	0.15	-0.19	0.4
TMP group mangabeys				
Mixed versus female-female	-0.12	0.07	-0.26	0.03
Male-male versus female-female				
Male-male versus mixed				
Between groups				
Sex combination female-female				
South versus East group chimpanzees	0.02	0.07	-0.12	0.16
TCP mangabeys versus East chimpanzees	0.14	0.07	-0.01	0.27
TMP mangabeys versus East chimpanzees	-0.02	0.08	-0.16	0.13
TCP mangabeys versus South chimpanzees	0.12	0.07	-0.03	0.26
TMP mangabeys versus South chimpanzees	-0.04	0.08	-0.19	0.12
TMP versus TCP group mangabeys	-0.16	0.08	-0.31	0
Sex combination mixed-sex				
South versus East group chimpanzees	-0.09	0.07	-0.23	0.05
TCP mangabeys versus East chimpanzees	-0.01	0.08	-0.17	0.16
TMP mangabeys versus East chimpanzees	-0.15	0.08	-0.29	0.01
TCP mangabeys versus South chimpanzees	0.08	0.08	-0.07	0.24
TMP mangabeys versus South chimpanzees	-0.06	0.07	-0.19	0.1
TMP versus TCP group mangabeys	-0.14	0.09	-0.31	0.04
Sex combination male-male				
South versus East group chimpanzees	**0.29**	**0.11**	**0.06**	**0.49**
TCP mangabeys versus East chimpanzees	0.05	0.15	-0.21	0.37
TMP mangabeys versus East chimpanzees	-	-	-	-
TCP mangabeys versus South chimpanzees	-0.24	0.17	-0.54	0.12
TMP mangabeys versus South chimpanzees	-	-	-	-
TMP versus TCP group mangabeys	-	-	-	-

(b)

Summary From Model 2			95% CI			
Response: Grooming Reciprocity dRI	Estimate	Error	lower	upper	Bulk ESS	Tail ESS
Intercept	-0.02	0.29	-0.6	0.57	6310.42	6518.35
Group (East) South	-0.04	0.35	-0.72	0.65	6142.08	6596.91
TCP mangabeys	0.51	0.33	-0.12	1.15	5956.16	6699.59
TMP mangabeys	0.35	0.37	-0.38	1.08	6048.93	6633.51
Sex combination (F-F) mixed	0.34	0.33	-0.31	0.97	6121.35	6516.53
South* mixed	-0.3	0.42	-1.12	0.52	5769.46	6742.88
TCP mangabeys* mixed	-0.54	0.51	-1.54	0.47	6193.26	6675.06
TMP mangabeys * mixed	-0.23	0.66	-1.51	1.08	5529.05	6326.47
Sex combination (F-F) M-M	0.41	0.39	-0.36	1.17	5919.86	6612.14
South*M-M	0.78	0.51	-0.23	1.77	5911.79	6704.33
TCP mangabeys*M-M	0.02	1.01	-1.96	1.96	4879.44	4991.39
TMP mangabeys *M-M	0.03	1	-1.92	1.95	4960.71	5424.54
Phi intercept	0.78	0.31	0.17	1.37	5863.6	6642.6
Zoi intercept	0.05	0.38	-0.69	0.8	6995.48	6905.93
Coi intercept	-3.66	0.67	-5.06	-2.4	6011.41	6207.08
Phi group South	-0.2	0.35	-0.88	0.51	5831.88	6490.56
Phi group TCP	0.31	0.35	-0.36	1.01	5922	6900.28
Phi group TMP	0.51	0.43	-0.35	1.33	6389.89	6333.05
Phi sex combination (female-female) mixed-sex	-0.1	0.34	-0.76	0.56	6030.98	6997.01
Phi group South*sex combination mixed-sex	0.75	0.46	-0.16	1.63	5696.33	6808.15
Phi group TCP*sex combination mixed-sex	-0.43	0.5	-1.43	0.56	5694.31	6178.71
Phi group TMP*sex combination mixed-sex	-0.99	0.61	-2.18	0.22	5932.07	6179.35
Phi sex combination male-male	-0.07	0.4	-0.88	0.72	5883.73	6197.56
Phi group South*sex combination male-male	0.75	0.55	-0.36	1.82	6024.07	6645.18
Phi group TCP*sex combination male-male	-0.01	0.98	-1.93	1.94	5205.12	5193.6
Phi group TMP*sex combination male-male	-0.01	1	-1.96	1.92	5296.63	5211.16
Zoi sex combination mixed-sex	0.19	0.38	-0.57	0.94	6744.67	6449.2
Zoi group South*sex combination mixed-sex	0.75	0.52	-0.28	1.78	6574.92	6758.87
Zoi group TCP*sex combination mixed-sex	0.98	0.54	-0.06	2.05	6563.32	6935.08
Zoi group TMP*sex combination mixed-sex	1.01	0.66	-0.2	2.32	5918.36	6112.34
Zoi sex combination male-male	0.17	0.51	-0.84	1.18	6453.93	6274.27
Zoi group South*sex combination male-male	-1.21	0.73	-2.67	0.2	6099	6283.14
Zoi group TCP*sex combination male-male	0.97	0.81	-0.59	2.6	5367.55	6073.97
Zoi group TMP*sex combination male-male	0	1	-1.96	1.96	5306.92	5425.15
Zoi group South	-0.25	0.49	-1.2	0.7	6768.55	6176.67
Zoi group TCP	0.01	0.45	-0.89	0.89	7275.01	6780.07
Zoi group TMP	0.41	0.5	-0.6	1.4	6665.49	6952.53
Coi sex combination mixed-sex	-0.39	0.65	-1.68	0.88	6186.71	6120.77
Coi group south*sex combination mixed-sex	0.2	0.84	-1.47	1.81	5485.74	6420.78
Coi group TCP*sex combination mixed-sex	0.17	0.7	-1.2	1.54	6274.67	6569.4
Coi group TMP*sex combination mixed-sex	-0.25	0.92	-2.1	1.52	5433.75	5510.43
Coi sex combination male-male	-0.23	0.78	-1.79	1.27	5542.46	6053.52
Coi group South*sex combination male-male	-0.07	0.97	-1.97	1.78	5602.63	5509.71
Coi group TCP*sex combination male-male	0.14	0.85	-1.5	1.79	6020.16	6167.37
Coi group TMP*sex combination male-male	0.03	1.01	-1.93	2.01	5140.37	5155.94
Coi group South	-0.28	0.78	-1.84	1.18	5748.49	6028.77
Coi group TCP	2.12	0.65	0.89	3.43	5941.95	5974.97
Coi group TMP	-0.62	0.82	-2.31	0.96	5377.37	5812.11

Note. Blue/bold and green cells indicate estimates whose directions are supported by the 95% and 89% CI of the posterior distribution. In brackets: the reference level. (a) Comparison of model parameters on the original scale across groups. To get the overall mean score of a parameter, depending on Beta, zero and one components, we used the formula : (zoi * coi) + µ * (1- zoi) *(Bürkner, 2020)*, converted to the original scale, by using the inverse: "plogis()", (b) model parameters as shown in the initial summary, on the link scale (logit for all except for "phi" parameters). In italics: no grooming event observed.

Table S5

Results from the Model 3 Depicting the Link Between Signaling Reciprocity and Variation in Grooming Relationship Strength Across Groups

(a)

Hypotheses for model 3 Response: signaling reciprocity index sRI	Estimate	Error	**95% CI**	
			lower	**upper**
Dyadic grooming index				
East group	0.11	0.1	-0.08	0.31
South group	0.13	0.14	-0.14	0.4
TCP group	0.16	0.12	-0.08	0.39
TMP group	0.2	0.14	-0.08	0.45
South versus East group	0.02	0.14	-0.25	0.29
TCP mangabey versus East group	0.05	0.13	-0.2	0.29
TMP mangabey versus East group	0.09	0.14	-0.19	0.35
TCP mangabey versus South group	0.03	0.16	-0.29	0.34
TMP mangabey versus South group	0.07	0.17	-0.26	0.4
TMP mangabey versus TCP group	0.04	0.16	-0.27	0.34
Dominance rank distance				
Whole dataset	**-0.3**	**0.05**	**-0.4**	**-0.2**
Sex combination				
Within groups				
East group chimpanzees				
Mixed versus female-female	0	0.06	-0.11	0.12
Male-male versus female-female	-0.02	0.07	-0.16	0.13
Male-male versus mixed	-0.02	0.08	-0.17	0.14
South group chimpanzees				
Mixed versus female-female	-0.07	0.07	-0.2	0.06
Male-male versus female-female	0.04	0.13	-0.2	0.29
Male-male versus mixed	0.12	0.13	-0.13	0.36
TCP group mangabeys				
Mixed versus female-female	-0.08	0.05	-0.17	0.02
Male-male versus female-female	0.06	0.1	-0.13	0.26
Male-male versus mixed	0.14	0.1	-0.05	0.34
TMP group mangabeys				
Mixed versus female-female	-0.03	0.05	-0.13	0.08
Male-male versus female-female	0.11	0.1	-0.07	0.32
Male-male versus mixed	0.14	0.1	-0.05	0.35
Between groups				
Sex combination female-female				
South versus East group	0.1	0.07	-0.03	0.22
TCP mangabey versus East group	-0.05	0.06	-0.16	0.07
TMP mangabey versus East group	-0.09	0.06	-0.21	0.03
TCP mangabey versus South group	**-0.14**	**0.06**	**-0.26**	**-0.02**
TMP mangabey versus South group	**-0.19**	**0.06**	**-0.31**	**-0.05**
TMP mangabey versus TCP group	-0.04	0.05	-0.15	0.06
Sex combination mixed-sex				
South versus East group	0.02	0.07	-0.13	0.16
TCP mangabey versus East group	**-0.13**	**0.07**	**-0.26**	**-0.001**
TMP mangabey versus East group	-0.12	0.07	-0.25	0.01
TCP mangabey versus South group	**-0.15**	**0.07**	**-0.29**	**-0.01**
TMP mangabey versus South group	**-0.14**	**0.07**	**-0.28**	**-0.001**
TMP mangabey versus TCP group	0.01	0.06	-0.11	0.12
Sex combination male-male				
South versus East group	0.16	0.13	-0.09	0.4
TCP mangabey versus East group	0.03	0.11	-0.18	0.25
TMP mangabey versus East group	0.04	0.11	-0.17	0.26
TCP mangabey versus South group	-0.13	0.15	-0.42	0.17
TMP mangabey versus South group	-0.12	0.15	-0.41	0.19
TMP mangabey versus TCP group	0.01	0.13	-0.25	0.28

(b)

Summary from Model 3			95% CI			
Response: Signaling Reciprocity Index sRI	Estimate	Error	lower	upper	Bulk ESS	Tail ESS
Intercept	0.34	0.22	-0.08	0.76	4950.07	6432.78
Phi intercept	2.29	0.34	1.63	2.97	5645.06	6000.21
Zoi intercept	0.68	0.35	0	1.37	6428.97	6655.57
Coi intercept	-1.35	0.39	-2.15	-0.62	6717.59	6743.69
Group (East) South	0.12	0.25	-0.36	0.61	5070.02	5773.55
TCP mangabeys	-0.32	0.24	-0.77	0.16	5130.84	5824.83
TMP mangabeys	-0.04	0.25	-0.54	0.46	4940.95	6229.87
Sex combination (F-F) mixed	0.25	0.23	-0.19	0.7	5003.61	5643.51
Sex combination (F-F) M-M	-0.3	0.3	-0.87	0.31	5023.87	5673.57
Dyadic grooming index (DGI)	-0.24	0.45	-1.12	0.64	7286.9	6949.89
Dominance rank distance	-1.66	0.36	-2.35	-0.94	6519.97	6666.84
South* mixed	-0.09	0.29	-0.66	0.46	5161.55	6199.53
TCP mangabeys* mixed	-0.37	0.29	-0.94	0.22	5577.46	6064.6
TMP mangabeys * mixed	-0.49	0.3	-1.08	0.1	4962.76	6180.98
South*M-M	1.05	0.52	0.04	2.1	5801.51	6383.9
TCP mangabeys*M-M	0.25	0.48	-0.71	1.17	5834	6577.19
TMP mangabeys *M-M	0.07	0.46	-0.82	0.97	5131.43	6421.34
South*DGI	-0.16	0.66	-1.45	1.14	6560.52	6734.57
TCP mangabeys*DGI	0.44	0.59	-0.72	1.58	6733.44	6916.16
TMP mangabeys *DGI	0.34	0.64	-0.93	1.61	6957.78	6131.95
Phi group South	0.12	0.39	-0.64	0.89	6103.71	6655.46
Phi group TCP	-0.54	0.35	-1.24	0.17	5603.67	6709.49
Phi group TMP	0.16	0.39	-0.63	0.92	6055.05	6770.75
Phi sex combination (female-female) mixed-sex	-0.3	0.35	-1	0.39	5550.32	5822.44
Phi sex combination male-male	-0.37	0.41	-1.17	0.41	6217.26	6605.12
Phi dyadic grooming index	-0.1	0.65	-1.39	1.21	4907.67	6695.4
Phi dominance rank distance	-0.16	0.63	-1.38	1.07	6327.95	6537.86
Phi group South*sex combination mixed-sex	0.22	0.49	-0.73	1.19	6261.16	6593.13
Phi group TCP*sex combination mixed-sex	0.25	0.45	-0.63	1.14	5756.42	6740.92
Phi group TMP*sex combination mixed-sex	-0.13	0.48	-1.09	0.82	5453.3	6670.39
Phi group South*sex combination male-male	0.11	0.69	-1.27	1.41	6036.1	6737.5
Phi group TCP*sex combination male-male	-0.12	0.59	-1.29	1.01	6347.96	6774.41
Phi group TMP*sex combination male-male	-0.25	0.64	-1.52	0.97	5866.27	6575.12
Phi South*DGI	-0.6	0.81	-2.18	1.03	6490.76	6990.04
Phi TCP mangabeys*DGI	0.31	0.74	-1.16	1.75	6807.35	6898.9
Phi TMP mangabeys *DGI	0.2	0.9	-1.53	1.94	5375.56	6455.58
Zoi group South	-0.73	0.43	-1.56	0.11	6873.58	6891.15
Zoi group TCP	-0.31	0.4	-1.09	0.49	6466.77	6208.56
Zoi group TMP	0.49	0.41	-0.28	1.29	6772.6	6569.3
Zoi sex combination mixed-sex	-0.28	0.35	-0.97	0.39	6673.8	6881.51
Zoi sex combination male-male	-0.2	0.49	-1.16	0.74	6110.41	6801.86
Zoi dyadic grooming index	-2.1	0.72	-3.48	-0.64	6258.52	6353.55
Zoi dominance rank distance	2.06	0.5	1.09	3.08	6377.13	5992.09
Zoi group South*sex combination mixed-sex	0.54	0.46	-0.38	1.44	5887.23	6333.47
Zoi group TCP*sex combination mixed-sex	0.78	0.44	-0.1	1.65	5890.25	6494.69
Zoi group TMP*sex combination mixed-sex	0.08	0.46	-0.82	0.98	6494.97	6778.39
Zoi group South*sex combination male-male	0.62	0.74	-0.88	2.01	7038.45	6896.83
Zoi group TCP*sex combination male-male	-0.6	0.75	-2.07	0.85	6174.61	6712.58
Zoi group TMP*sex combination male-male	-0.3	0.68	-1.61	1.03	6329.72	6199.28
Zoi South*DGI	0.13	0.9	-1.61	1.86	6070.55	6497.5
Zoi TCP mangabeys*DGI	-0.41	0.83	-2.03	1.2	6686.09	6593.72
Zoi TMP mangabeys *DGI	-1.48	0.92	-3.29	0.34	5933.62	5815.85
Coi group South	0.2	0.5	-0.78	1.18	6922.27	6970.06
Coi group TCP	-0.48	0.46	-1.37	0.41	7083.7	7055.43
Coi group TMP	-0.48	0.46	-1.37	0.45	6466.16	6513.61
Coi sex combination mixed-sex	-0.57	0.46	-1.49	0.33	6647.25	6675.32

Coi sex combination male-male	-0.14	0.58	-1.27	0.98	6659.67	6360.45
Coi dominance rank distance	-0.21	0.8	-1.82	1.37	6072.73	6404.29
Coi dyadic grooming index	-2.43	0.73	-3.88	-1.03	6212.53	5957.51
Coi group south*sex combination mixed-sex	-0.37	0.66	-1.68	0.88	6802.21	6758.45
Coi group TCP*sex combination mixed-sex	0.05	0.62	-1.18	1.26	5770.54	6575.44
Coi group TMP*sex combination mixed-sex	0.15	0.6	-1.05	1.33	6563.92	6423.74
Coi group South*sex combination male-male	0.18	0.81	-1.42	1.72	6433.77	6403.26
Coi group TCP*sex combination male-male	-0.24	0.93	-2.11	1.59	6260.21	6322.38
Coi group TMP*sex combination male-male	0.87	0.74	-0.6	2.3	6293.25	6744.19
Coi South*DGI	-0.18	0.94	-2.02	1.67	6185.6	6481.73
Coi TCP mangabeys*DGI	0.13	0.9	-1.65	1.91	6154.11	6541.72
Coi TMP mangabeys *DGI	0	0.98	-1.95	1.92	6005.09	6181.9

Note. Blue/bold and green cells indicate estimates whose directions are supported by the 95% and 89% CI of the posterior distribution. In brackets: the reference level. (a) Comparison of model parameters on the original scale across groups. To get the overall mean score of a parameter, depending on Beta, zero and one components, we used the formula : (zoi * coi) + μ * (1- zoi) *(Bürkner, 2020)*, converted to the original scale, by using the inverse: “plogis()”, (b) Model parameters as shown in the initial summary, on the link scale (logit for all except for “phi” parameters).

Table S6

Results from the Model 4 Depicting the Link Between Socio-Positive Signaling Reciprocity and Variation in Grooming Relationship Strength Across Groups

(a)

Hypotheses for model 4 Response: socio-positive signaling reciprocity index	Estimate	Error	**95% CI**	
			lower	**upper**
Dyadic grooming index				
East group	0.09	0.1	-0.1	0.29
South group	0.26	0.15	-0.03	0.53
TCP group	0.01	0.14	-0.23	0.31
TMP group	0.05	0.15	-0.22	0.38
South versus East group	0.18	0.14	-0.1	0.44
TCP mangabey versus East group	-0.08	0.13	-0.32	0.19
TMP mangabey versus East group	-0.03	0.14	-0.29	0.25
TCP mangabey versus South group	-0.26	0.17	-0.58	0.1
TMP mangabey versus South group	-0.21	0.18	-0.54	0.15
TMP mangabey versus TCP group	0.04	0.17	-0.29	0.38
Dominance rank distance				
Whole dataset	**-0.2**	**0.06**	**-0.31**	**-0.08**
Sex combination **Within groups**				
East group chimpanzees				
Mixed versus female-female	-0.05	0.06	-0.17	0.06
Male-male versus female-female	0	0.08	-0.15	0.17
Male-male versus mixed	0.05	0.09	-0.11	0.24
South group chimpanzees				
Mixed versus female-female	-0.13	0.08	-0.28	0.03
Male-male versus female-female	0.05	0.14	-0.22	0.32
Male-male versus mixed	0.18	0.14	-0.09	0.46
TCP group mangabeys				
Mixed versus female-female	-0.02	0.06	-0.13	0.13
Male-male versus female-female	-0.02	0.08	-0.13	0.2
Male-male versus mixed	0	0.1	-0.19	0.24
TMP group mangabeys				
Mixed versus female-female	-0.06	0.06	-0.17	0.07
Male-male versus female-female	0.07	0.12	-0.11	0.34
Male-male versus mixed	0.12	0.12	-0.08	0.41
Between groups				
Sex combination female-female				
South versus East group	**0.15**	**0.07**	**0.01**	**0.29**
TCP mangabey versus East group	**-0.14**	**0.06**	**-0.25**	**-0.03**
TMP mangabey versus East group	-0.12	0.06	-0.24	0.01
TCP mangabey versus South group	**-0.29**	**0.07**	**-0.42**	**-0.16**
TMP mangabey versus South group	**-0.27**	**0.07**	**-0.41**	**-0.12**
TMP mangabey versus TCP group	0.02	0.06	-0.09	0.14
Sex combination mixed-sex				
South versus East group	0.08	0.08	-0.08	0.24
TCP mangabey versus East group	-0.1	0.08	-0.25	0.06
TMP mangabey versus East group	-0.12	0.07	-0.26	0.02
TCP mangabey versus South group	-0.18	0.09	-0.35	0.01
TMP mangabey versus South group	**-0.2**	**0.09**	**-0.36**	**-0.02**
TMP mangabey versus TCP group	-0.02	0.08	-0.2	0.14
Sex combination male-male				
South versus East group	0.2	0.14	-0.07	0.47
TCP mangabey versus East group	-0.15	0.1	-0.35	0.06
TMP mangabey versus East group	-0.05	0.13	-0.27	0.22
TCP mangabey versus South group	**-0.35**	**0.15**	**-0.65**	**-0.05**
TMP mangabey versus South group	-0.25	0.17	-0.57	0.1
TMP mangabey versus TCP group	0.1	0.14	-0.16	0.4

(b)

Summary from Model 4			95% CI			
Response: Socio-Positive Signaling Reciprocity Index	Estimate	Error	lower	upper	Bulk ESS	Tail ESS
Intercept	0.58	0.22	0.15	1.02	6516.28	6768.83
Phi intercept	2.8	0.46	1.93	3.7	5934.19	6443.15
Zoi intercept	1.33	0.39	0.62	2.16	6413.71	6002.97
Coi intercept	-1.66	0.45	-2.59	-0.83	6302.17	6436.9
Group (East) South	0.02	0.25	-0.46	0.53	5902.93	6246.33
TCP mangabeys	0.18	0.3	-0.39	0.76	6702.12	6743.38
TMP mangabeys	0.44	0.35	-0.25	1.14	6208.95	6570.2
Sex combination (F-F) mixed	-0.01	0.26	-0.51	0.5	6583.47	6759.52
Sex combination (F-F) M-M	0.07	0.35	-0.61	0.77	6772.21	6356.09
Dyadic grooming index	-0.68	0.48	-1.62	0.27	6464.45	6196.71
Dominance rank distance	-1.33	0.56	-2.4	-0.24	6356.01	6604.21
South* mixed	0.04	0.36	-0.66	0.75	6315.51	6145.01
TCP mangabeys* mixed	0	1.01	-2.01	1.99	6166.99	5792.75
TMP mangabeys * mixed	0.02	0.58	-1.15	1.2	6837.96	6499.66
South*M-M	0.53	0.5	-0.45	1.54	7188.28	6540.84
TCP mangabeys*M-M	0.01	1	-1.95	1.92	5816.26	5953.8
TMP mangabeys *M-M	0	1	-1.94	1.92	5833.43	5947.73
Group (East) South*DGI	0.55	0.69	-0.8	1.91	6635.51	7064.63
TCP mangabeys*DGI	0.37	0.71	-1.03	1.78	6458.33	6300.36
TMP mangabeys*DGI	-0.2	0.72	-1.59	1.26	6292.95	5542.03
Phi group South	-0.47	0.47	-1.41	0.45	6479.18	6713.12
Phi group TCP	0.69	0.69	-0.67	2.06	6398.73	5900.36
Phi group TMP	0.6	0.8	-0.91	2.23	5981.1	6444.19
Phi sex combination (female-female) mixed-sex	-0.33	0.49	-1.29	0.63	6613.53	6118.74
Phi sex combination male-male	-0.05	0.6	-1.23	1.16	6698.39	6808.69
Phi dyadic grooming index	-0.21	0.79	-1.71	1.38	5045.54	5132.13
Phi dominance rank distance	-0.49	0.84	-2.12	1.18	6439.73	6149.59
Phi group South*sex combination mixed-sex	-0.03	0.62	-1.27	1.14	6494.25	6703.52
Phi group TCP*sex combination mixed-sex	0	0.99	-1.92	1.95	5463.89	5793.08
Phi group TMP*sex combination mixed-sex	0.14	0.95	-1.72	2.02	6459.47	6351.28
Phi group South*sex combination male-male	0.53	0.78	-1.02	2.03	6381.58	6681.78
Phi group TCP*sex combination male-male	0	1	-1.91	2	6137.5	5656.97
Phi group TMP*sex combination male-male	-0.02	0.99	-1.96	1.91	6026.92	5481.15
Phi group South*DGI	-0.36	0.84	-1.98	1.32	6039.37	6418.98
Phi group TCP*DGI	-0.07	0.96	-1.91	1.81	5872.02	6010.17
Phi group TMP*DGI	0.03	0.96	-1.8	1.96	5607.07	6302.43
Zoi group South	-0.93	0.44	-1.81	-0.11	6786.93	6187.24
Zoi group TCP	1.35	0.5	0.35	2.33	6662.01	6674.99
Zoi group TMP	1	0.54	-0.04	2.06	6158.36	6167.2
Zoi sex combination mixed-sex	0.32	0.41	-0.5	1.12	6458.96	6261.93
Zoi sex combination male-male	0.5	0.56	-0.57	1.64	6344.87	6423.22
Zoi dyadic grooming index	-1.63	0.82	-3.13	0.09	5151.75	5957.45
Zoi dominance rank distance	0.97	0.65	-0.3	2.26	6007.75	6345.92
Zoi group South*sex combination mixed-sex	0.54	0.52	-0.48	1.54	6339.82	6698.33
Zoi group TCP*sex combination mixed-sex	0.75	0.81	-0.78	2.41	5989.48	6058.01
Zoi group TMP*sex combination mixed-sex	0.26	0.76	-1.16	1.77	6340.8	6594.74
Zoi group South*sex combination male-male	-0.01	0.76	-1.52	1.44	5886.98	5808.25
Zoi group TCP*sex combination male-male	0.28	0.92	-1.49	2.1	5862.48	5460.18
Zoi group TMP*sex combination male-male	0.39	0.91	-1.33	2.23	6293.42	5952.98
Zoi group South*DGI	-0.28	0.91	-2.05	1.49	5948.87	6065.38
Zoi group TCP*DGI	0.15	0.89	-1.58	1.9	5936.79	6476.08
Zoi group TMP*DGI	-0.63	0.94	-2.47	1.26	5423.55	5666.09
Coi group South	0.62	0.51	-0.38	1.64	6570.33	6690.33
Coi group TCP	-0.7	0.51	-1.71	0.28	6714.14	6946.91
Coi group TMP	-0.77	0.58	-1.93	0.33	6748.38	6768.45
Coi sex combination mixed-sex	-0.35	0.48	-1.32	0.56	6892.86	6739.8

Coi sex combination male-male	0.16	0.57	-1.01	1.27	6604.27	6205.78
Coi dyadic grooming index (DGI)	0.1	0.8	-1.52	1.62	5967.57	6635.89
Coi dominance rank distance	-1.66	0.73	-3.11	-0.24	5868.13	5990.89
Coi group south*sex combination mixed-sex	-0.2	0.61	-1.4	0.98	6138.62	6352.59
Coi group TCP*sex combination mixed-sex	0.23	0.73	-1.23	1.63	6424.04	6241.28
Coi group TMP*sex combination mixed-sex	-0.56	0.83	-2.25	1.04	6170.83	6003.68
Coi group South*sex combination male-male	0.07	0.82	-1.57	1.67	6369.85	6485.64
Coi group TCP*sex combination male-male	-0.51	0.88	-2.3	1.17	6075.54	5975.87
Coi group TMP*sex combination male-male	0.6	0.8	-0.99	2.16	6141.29	6480.28
Coi group South*DGI	-0.17	0.94	-2.01	1.65	5553.17	6184
Coi group TCP*DGI	0.23	0.9	-1.58	1.98	6303.74	6203.67
Coi group TMP*DGI	-0.2	0.97	-2.1	1.68	5408.17	5826.84

Note. Blue/bold and green cells indicate estimates whose directions are supported by the 95% and 89% CI of the posterior distribution. In brackets: the reference level. (a) Comparison of model parameters on the original scale across groups. To get the overall mean score of a parameter, depending on Beta, zero and one components, we used the formula : (zoi * coi) + µ * (1- zoi) (Bürkner, 2020), converted to the original scale, by using the inverse: “plogis()”. (b) Model parameters as shown in the initial summary, on the link scale (logit for all except for “phi” parameters).

Table S7

Results from the model 5 depicting the link between signaling reciprocity and grooming reciprocity (dRI) (a)

			95% CI	
Hypotheses for model 5 Response: signaling reciprocity index sRI	Estimate	Error	lower	upper
Grooming reciprocity index				
East group	0.09	0.08	-0.08	0.24
South group	0.08	0.12	-0.15	0.31
TCP group	-0.02	0.09	-0.19	0.17
TMP group	0.05	0.13	-0.2	0.3
South versus East group	0	0.12	-0.24	0.24
TCP mangabey versus East group	-0.1	0.1	-0.3	0.11
TMP mangabey versus East group	-0.04	0.13	-0.29	0.22
TCP mangabey versus South group	-0.1	0.13	-0.34	0.15
TMP mangabey versus South group	-0.04	0.15	-0.33	0.26
TMP mangabey versus TCP group	-0.06	0.13	-0.32	0.2

(b)

Summary from Model 5			95% CI			
Response: Signaling Reciprocity Index sRI	Estimate	Error	lower	upper	Bulk ESS	Tail ESS
Intercept	0.16	0.24	-0.33	0.62	5420.99	5681.91
Phi intercept	2.17	0.39	1.41	2.95	4629.2	5853.97
Zoi intercept	0.22	0.4	-0.56	1.04	6256.11	7005.87
Coi intercept	-1.64	0.6	-2.92	-0.58	6132.82	6372.74
Group (East) South	0.22	0.27	-0.3	0.76	5360.26	6107.83
TCP mangabeys	-0.27	0.28	-0.8	0.29	5490.87	6112.65
TMP mangabeys	-0.03	0.29	-0.61	0.53	5619.88	5981.65
dRI	0.57	0.3	-0.01	1.17	6003.03	6711.5
Dyadic grooming index	-0.15	0.35	-0.85	0.54	6215.89	6501.59
Sex combination (F-F) mixed	0.09	0.16	-0.23	0.4	5609.67	6988.91
Sex combination (F-F) M-M	-0.08	0.29	-0.64	0.5	5772.53	6376.01
Dominance rank distance	-1.49	0.41	-2.26	-0.65	6364.21	6524.71
Group (East) South* dRI	0.02	0.44	-0.84	0.85	5822.95	5579.84
TCP mangabeys* dRI	-0.25	0.39	-1	0.52	6576.75	6713.68
TMP mangabeys* dRI	-0.26	0.5	-1.23	0.73	6229.59	6188
Phi group South	0.12	0.42	-0.68	0.95	4763.05	6048.64
Phi group TCP	-0.17	0.4	-0.95	0.6	6224.3	6644.85
Phi group TMP	0.24	0.46	-0.67	1.15	6038.37	6324.81
Phi dRI	-0.13	0.48	-1.1	0.8	5974.67	6544.11
Phi DGI	0.08	0.63	-1.1	1.39	4667.7	6119.95
Phi sex combination (female-female) mixed-sex	-0.09	0.31	-0.69	0.5	6557.88	6057.31
Phi sex combination male-male	-0.34	0.45	-1.23	0.56	5643.88	6507.58
Phi dominance rank distance	-0.04	0.7	-1.42	1.35	6067.6	6602.74
Phi group South* dRI	-0.04	0.71	-1.43	1.31	5992.53	6274.05
Phi group TCP* dRI	-0.23	0.57	-1.38	0.87	5907.11	6446.17
Phi group TMP* dRI	0.02	0.77	-1.48	1.56	5773.61	6438.67
Zoi group South	-0.21	0.45	-1.11	0.7	6243.25	6689.17
Zoi group TCP	-0.38	0.46	-1.29	0.53	6255.77	6527.54
Zoi group TMP	0.11	0.48	-0.87	1.05	6850.03	6767.99
Zoi dRI	-0.48	0.49	-1.44	0.49	6340.39	6263.99
Zoi dyadic grooming index	-1.55	0.63	-2.8	-0.34	6305.84	6560.75
Zoi sex combination mixed-sex	0.09	0.3	-0.5	0.68	6343.44	6775.73
Zoi sex combination male-male	0.37	0.5	-0.61	1.35	6231.02	5924.58
Zoi dominance rank distance	1.73	0.58	0.6	2.89	6339.73	6480.52
Zoi group South* dRI	0.44	0.69	-0.91	1.78	5942	5891.76
Zoi group TCP* dRI	0.68	0.63	-0.59	1.88	6391.66	6100.57
Zoi group TMP* dRI	-0.15	0.79	-1.69	1.37	5858.09	5379.79
Coi group South	0.11	0.63	-1.12	1.32	5794.8	6550.04
Coi group TCP	0.31	0.62	-0.95	1.54	6682.05	6587.94
Coi group TMP	-0.39	0.67	-1.71	0.89	6476.11	6987.03
Coi dRI	-0.7	0.71	-2.08	0.69	6307.75	6699.56
Coi dyadic grooming index	0	0.87	-1.72	1.73	6112.34	6417.5
Coi sex combination mixed-sex	-0.59	0.54	-1.67	0.44	5923.11	6573.91
Coi sex combination male-male	-0.19	0.71	-1.59	1.16	6104.08	6547.05
Coi dominance rank distance	-1.74	0.81	-3.37	-0.16	5633.9	6025.97
Coi group South*dRI	-0.12	0.86	-1.82	1.56	5805.94	5756.94
Coi group TCP*dRI	-0.42	0.81	-2.02	1.17	6174.79	6396.25
Coi group TMP*dRI	-0.01	0.95	-1.86	1.84	6050.33	5802.14

Note. Blue/bold and green cells indicate estimates whose directions are supported by the 95% and 89% CI of the posterior distribution. In brackets: the reference level. (a) Comparison of model parameters on the original scale across groups. To get the overall mean score of a parameter, depending on Beta, zero and one components, we used the formula : (zoi * coi) + µ * (1- zoi) *(Bürkner, 2020)*, converted to the original scale, by using the inverse: "plogis()". (b) Model parameters as shown in the initial summary, on the link scale (logit for all except for "phi" parameters).

Table S8

Results from the Model 6 Depicting the Link Between Socio-Signaling Reciprocity and Grooming Reciprocity (dRI)
(a)

Hypotheses for model 6			**95% CI**	
Response: socio-positive signaling reciprocity index	Estimate	Error	**lower**	**upper**
Grooming reciprocity index				
East group	0.13	0.09	-0.02	0.31
South group	0.24	0.13	-0.01	0.47
TCP group	-0.05	0.1	-0.23	0.16
TMP group	-0.02	0.13	-0.25	0.27
South versus East group	0.1	0.12	-0.14	0.34
TCP mangabey versus East group	-0.19	0.11	-0.4	0.03
TMP mangabey versus East group	-0.15	0.13	-0.4	0.13
TCP mangabey versus South group	**-0.29**	**0.13**	**-0.53**	**-0.02**
TMP mangabey versus South group	-0.26	0.16	-0.54	0.07
TMP mangabey versus TCP group	-0.03	0.13	-0.32	0.21

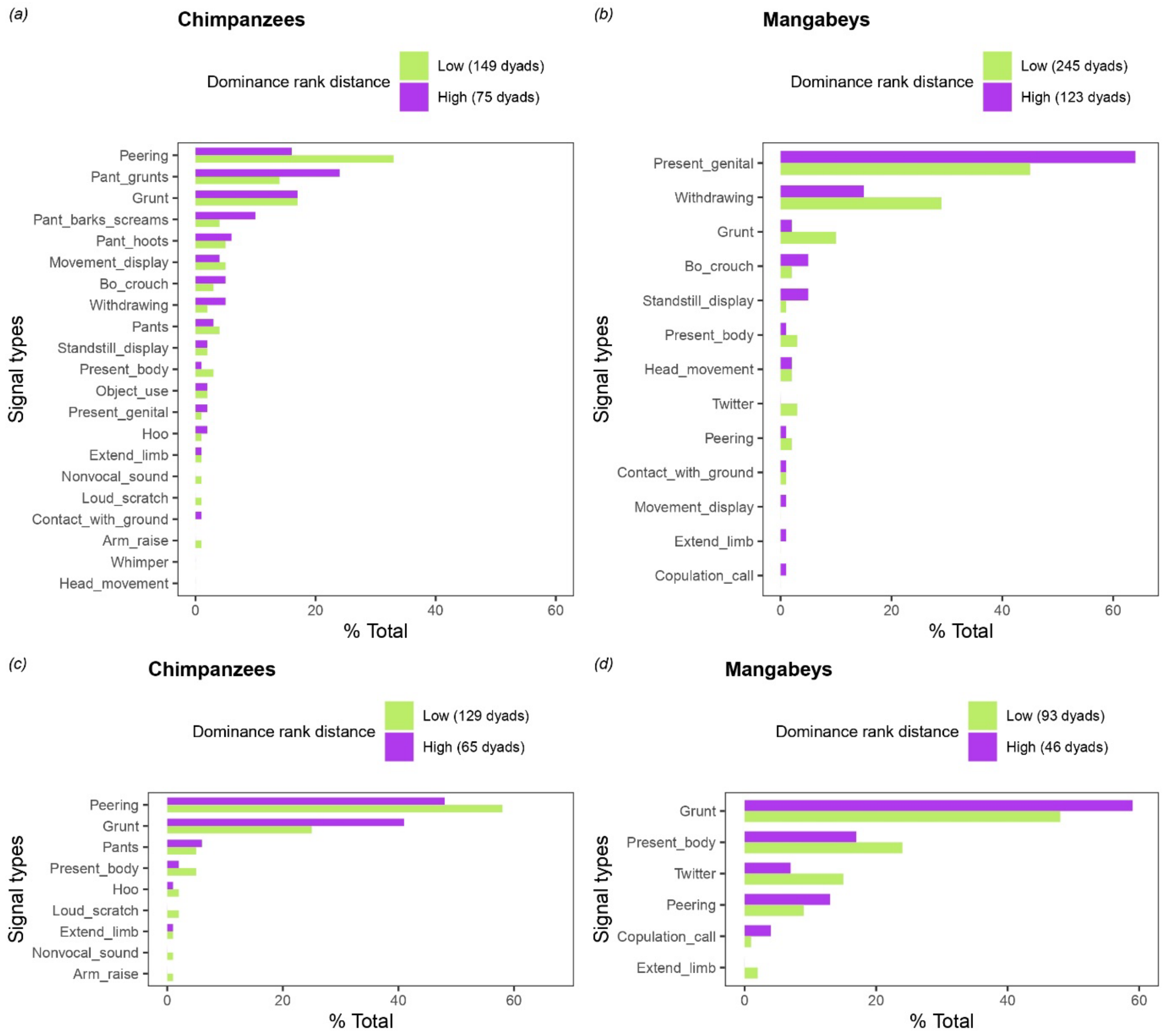
(b)

Summary from Model 6			95% CI			
Response: socio-positive signaling reciprocity index	Estimate	Error	lower	upper	Bulk ESS	Tail ESS
Intercept	0.45	0.26	-0.06	0.97	5182.12	6305.81
Group (East) South	0.2	0.28	-0.34	0.76	4971.2	5213.2
TCP mangabeys	0.4	0.4	-0.42	1.17	4737.15	6091.71
TMP mangabeys	0.64	0.53	-0.45	1.65	5596.02	6254.5
dRI	0.25	0.33	-0.39	0.9	4637.26	5780.32
Group (East) South* dRI	0.47	0.46	-0.42	1.37	5257.49	5756.58
TCP mangabeys* dRI	-0.33	0.55	-1.4	0.77	4395.63	5999.61
TMP mangabeys* dRI	-0.52	0.7	-1.88	0.93	5628.88	6484.82
Dominance rank distance	-1.21	0.64	-2.43	0.08	5903.99	5894.77
Dyadic grooming index	-0.71	0.44	-1.55	0.22	5184.02	5667.71
Sex combination (F-F) mixed	-0.04	0.23	-0.49	0.41	5263.68	5921.18
Sex combination (F-F) M-M	0.26	0.3	-0.31	0.85	5124.91	6171.51
Phi intercept	2.81	0.59	1.71	4.04	3934.6	4963.6
Zoi intercept	1.14	0.52	0.2	2.25	4662.22	5800.39
Coi intercept	-1.98	0.66	-3.39	-0.81	4254.97	5548.61
Phi group South	-0.42	0.53	-1.46	0.61	5267.81	6093.77
Phi group TCP	0.53	0.8	-1.03	2.11	6380.32	6833.65
Phi group TMP	0.28	0.88	-1.43	2.09	5641.66	6737.81
Phi sex combination (female-female) mixed-sex	-0.33	0.46	-1.25	0.58	6035.12	6485.28
Phi sex combination male-male	0.14	0.65	-1.1	1.44	5470.35	6124.21
Phi dominance rank distance	-0.15	0.91	-1.91	1.65	4239.32	6075.21
Phi dRI	0.16	0.63	-1.07	1.42	6454.15	5970.64
Phi DGI	-0.18	0.82	-1.75	1.45	4583.78	4800.95
Phi group South* dRI	-0.03	0.75	-1.52	1.45	6305.33	6986.73
Phi group TCP* dRI	0.02	0.89	-1.7	1.77	5633.69	6495.6
Phi group TMP* dRI	0.33	0.96	-1.54	2.23	6758.86	6473.65
Zoi group South	-0.74	0.52	-1.78	0.25	6223.57	6559.59
Zoi group TCP	1.61	0.61	0.42	2.81	5938.56	6105.09
Zoi group TMP	0.9	0.65	-0.37	2.19	6433.99	6306.19
Zoi dRI	-0.59	0.52	-1.62	0.43	6212.36	6448.57
Zoi dyadic grooming index	-1.29	0.75	-2.7	0.25	4632.07	6127.67
Zoi sex combination mixed-sex	0.65	0.4	-0.12	1.44	5729.97	6296.88
Zoi sex combination male-male	0.44	0.58	-0.71	1.58	5530.41	6538.95
Zoi dominance rank distance	1	0.69	-0.34	2.38	5926.47	6634.14
Zoi group South* dRI	0.33	0.68	-1.01	1.69	6361.18	6319.33
Zoi group TCP* dRI	-0.06	0.73	-1.48	1.38	6430.83	6356.63
Zoi group TMP* dRI	-0.21	0.84	-1.82	1.42	7161.81	7025.47
Coi group South	0.6	0.6	-0.56	1.8	5321.82	6767.05
Coi group TCP	-0.67	0.65	-1.96	0.6	6155.61	6432.17
Coi group TMP	-1.2	0.79	-2.76	0.32	6595.3	6388.28
Coi dRI	0.59	0.61	-0.6	1.79	6544.09	6445.94
Coi dyadic grooming index	0.19	0.83	-1.48	1.78	6746.07	6648.07
Coi sex combination mixed-sex	-0.37	0.5	-1.36	0.59	6559.39	6557.79
Coi sex combination male-male	-0.09	0.66	-1.43	1.21	6258.66	6367.8
Coi dominance rank distance	-1.23	0.79	-2.78	0.32	7065.45	6848.92
Coi group South*dRI	-0.61	0.8	-2.18	0.94	7079.81	6847.56
Coi group TCP*dRI	0.04	0.75	-1.43	1.51	6806.47	6544.42
Coi group TMP*dRI	-0.38	0.94	-2.23	1.42	6933.67	6415.71

Note. Blue/bold and green cells indicate estimates whose directions are supported by the 95% and 89% CI of the posterior distribution. In brackets: the reference level. (a) Comparison of model parameters on the original scale across groups. To get the overall mean score of a parameter, depending on Beta, zero and one components, we used the formula : (zoi * coi) + μ * (1- zoi) *(Bürkner, 2020)*, converted to the original scale, by using the inverse: "plogis()". (b) Model parameters as shown in the initial summary, on the link scale (logit for all except for "phi" parameters).

Figure S6

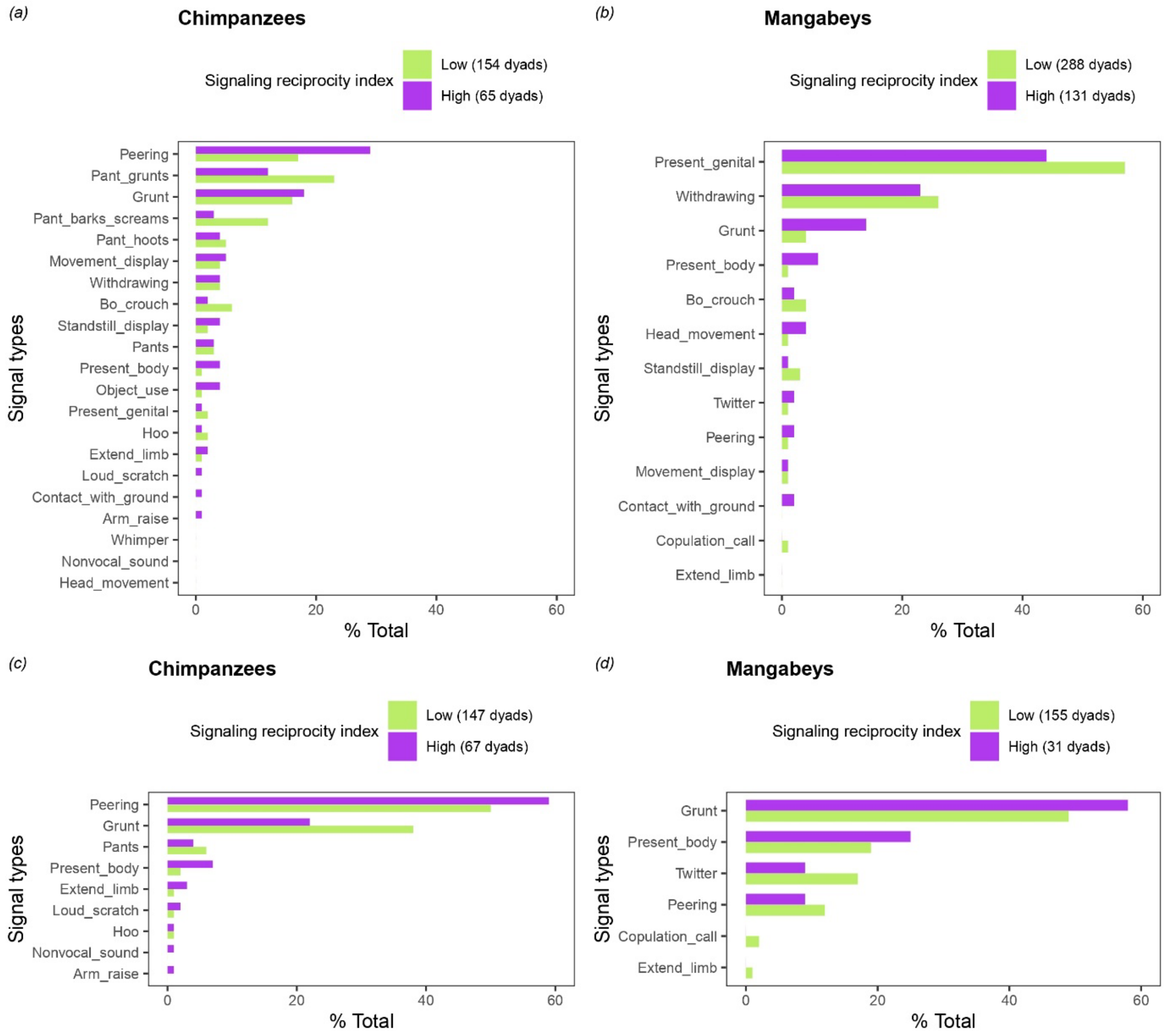
Signal Types Among Dyads Showing the Highest and Lowest Dominance Rank Distance Indices in Chimpanzees and Mangabeys



Note. Within each group, we considered the dyads with low versus high dominance rank distance values (arbitrary cut-off values: low: 1st and 2nd quartiles, high: 4th quartile). Then, percentages were calculated within each category (low and high). (a & c) in chimpanzees, (b & d) in mangabeys, considering the datasets on signaling reciprocity with all non-agonistic signals and socio-positive signals only, respectively.

Figure S7

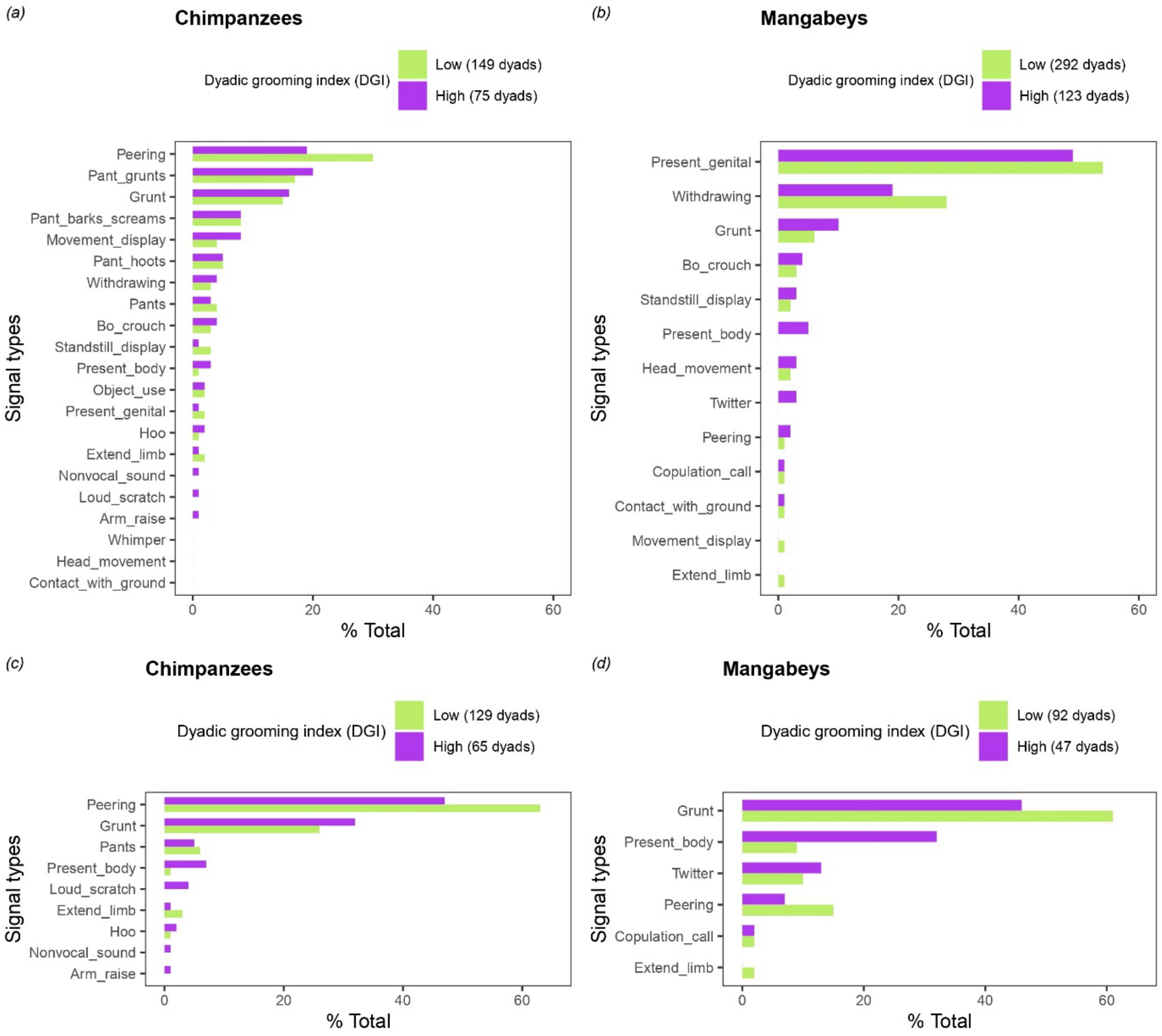
Signal Types Among Dyads Showing the Highest and Lowest Signaling Reciprocity Indices (sRI) in Chimpanzees And Mangabeys



Note. Within each group, we considered the dyads with low versus high signaling reciprocity indices (arbitrary cut-off values: low: 1st and 2nd quartiles, high: 4th quartile). Then, percentages were calculated within each category (low and high). (a & c) in chimpanzees, (b & d) in mangabeys, considering the datasets on signaling reciprocity with all non-agonistic signals and socio-positive signals only, respectively. In (d), because the value of the 3rd quartile was zero in both mangabey groups, for dyads with high signaling reciprocity indices we considered dyads with signaling reciprocity indices above the mean.

Figure S8

Signal Types Among Dyads Showing the Highest and Lowest Relationship Strength Indices (DGI) in Chimpanzees and Mangabeys



Note. Within each group, we considered the dyads with low versus high dyadic grooming indices (arbitrary cut-off values: low: 1st and 2nd quartiles, high: 4th quartile). Then, percentages were calculated within each category (low and high). (a & c) in chimpanzees, (b & d) in mangabeys, considering the datasets on signaling reciprocity with all non-agonistic signals and socio-positive signals only, respectively.