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Social bonding, gestural complexity and displacement behaviour of wild chimpanzee

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Abstract

Kinship and demography affect social affiliation in many different contexts such as co-feeding, resting, travel, grooming, visual attention and proximity. Chimpanzees may coordinate these social interactions by using gestural communication to make signaller's goal transparent to the recipient and also by increasing commitment of the recipient through including rewarding property in communication. The rewards of gesturing can be measured through the rates of displacement behaviour made in response to these gestures by the recipient. We tested hypothesis that gestural communication affects social affiliation after controlling for kinship and demography in wild, adult chimpanzees living in Budongo Forest, Uganda. We found that affiliative but not antagonistic gestures positively predicted social affiliation. Contexts differed in their association with gestures according to complexity and association with displacement behaviour. More complex, less intense gestures predicted mutual grooming, travel, visual attention whereas less complex, more intense gestures predicted unidirectional grooming. Mirroring these patterns, reduced displacement activity occurred in response to gestures associated with unidirectional grooming but not other contexts. We highlight that these tactical decisions that wild chimpanzees make in their use of gestural communication may be driven by complexity of social environment that influences effectiveness with which signalers can influence the recipient.

Keywords: social network, gestural communication, chimpanzee, joint action, resting, travel, grooming, co-feeding, proximity, visual attention, complexity, function

Introduction

Social bonds of animals, whereby particular dyads within the group preferentially associate and affiliate with each other have fitness benefits by regulating within-group competition in contexts such as feeding and mating. Such relationships have been found in numerous animal species which include for instance, bottlenose dolphins (Tursiops aduncus) (Möller, Beheregaray, Harcourt, & Krützen, 2001), Bechstein's bats (*Myotis bechsteinii*) (Kerth, Perony, & Schweitzer, 2011), and sperm whales (*Physeter macrocephalus*) (Ortega-Ortiz, Engelhaupt, Winsor, Mate, & Rus Hoelzel, 2012). By far however, the most dynamic and stable societies are those of primate species, and particularly great apes such as chimpanzees whereby conspecifics regularly form social bonds manifest in many different contexts (F. B. M. De Waal, 1982; Goodall, 1986). Unsurprisingly perhaps, considerable research effort has been directed at explaining the emergence and persistence of social bonds in primates (K. Langergraber, Mitani, & Vigilant, 2009; John C Mitani, Watts, Pepper, & Merriwether, 2002; J. B. Silk, Seyfarth, & Cheney, 2018). At first, inclusive fitness behind social bonding with kin was ubiquitously claimed to drive patterns of social bond formation (Hamilton, 1964). Although primates can and do socially bond with kin (Wrangham, 1980), the principal role of kinship in driving primate sociality has been discounted on the basis that in many socially complex primate species such as gorillas, chimpanzees and the bonobos social bonding within dyads is not determined by kinship (F. B. de Waal, 1986; John C Mitani et al., 2002; Watts, 1992). One another explanation that has been provided for existence of social bonds in primates, is that demographic constraints such as membership of the same age cohort can foster social bonding due to potency of peer influence on one's behaviour and familiarity inherent in growing up in the same social context (Goldberg & Wrangham, 1997; Van Schaik & Van Hooff, 1994). For those reasons, primates of same reproductive status or sex, may also be found to have affiliative contact with each other at a higher rate than among primates of different reproductive status or sex. For instance, male chimpanzees are more likely to groom with other males than the females (John C Mitani et al., 2002). Thus, formation of social bonds in primates, often demands that some similarity between interactants exists (Massen & Koski, 2014). However, primate social groups are complex and large, and primates often come into contact with conspecifics who are dissimilar and/or unrelated. For these complex social groups of unrelated individuals to form and persist over time, the social cohesion mechanism has to evolve that facilitates these social interactions. We propose that gestural communication defined as voluntary movements of the hands, legs, head, bodily postures or locomotory gaits (Hewes, 1973; Liebal, Call, & Tomasello, 2004) is one important mechanisms that facilitates formation of social bonds between individuals regardless of similarity.

The gestural communication is highly variable across species but within species, there is also a considerable variation that may facilitate choice of a social partner on the basis of several gesture features. For instance, gestural communication can be multimodal and co-occur with facial expressions or vocalisations, or it can be unimodal. Primates may incorporate objects such as branch of a tree in signalling or the gesture may not contain use of objects. Gestures can be combined with other gestural signals in a single utterance, or gesture may be produced singly (A. I. Roberts, Vick, Roberts, Buchanan-Smith, & Zuberbühler, 2012). The variation in gestural communication may be associated with the degree of social bonding, because gestures vary in the efficiency with which signaller can influence behaviour of the recipient (A. I. Roberts, Vick, Roberts, & Menzel, 2014). Signals of greater complexity that deviate from the population mean, may be more effective at influencing the recipient, than the average signals (Dawkins & Guilford, 1997; Zahavi & Zahavi, 1997). There are however many different pathways to achieving a greater efficiency in gestural communication. Studies in humans, showed that during perception of facial expression accompanied by direct gaze and pointing, the amygdala processes emotional content of communication. However, there is a concurrent integration of the directional communication (pointing, gaze) in the premotor cortex that facilitates re-evaluation of prior expectations regarding perceived signaller's immediate intent from emotional expression alone (Conty, Dezecache, Hugueville, & Grèzes, 2012). Thus, pointing gestures with facial expressions have a greater signal value than facial expressions alone and they can elicit a more accurate response from the recipient. Recently studies documented similar behavioural strategies in primates (S. Roberts & A. I. Roberts, 2018). Chimpanzee females, for example, lower back to make infant climb on it for travel as well as combining this bodily gesture with a manual sweep backwards in direction of the infant, potentially using manual directional gesture to draw the attention of the infant to the bodily gesture even though the infant is only a meter away and can respond to bodily gesture alone. When initiating grooming, male chimpanzee may present the bodily part that he wants to be groomed by the recipient, as well as making almost imperceptible sound to an observer standing only a short distance away, but clearly of fundamental importance to the recipient.

The social relationships of primates, however, may not always be guided by selection for effectiveness of communication (Dawkins & Guilford, 1997). If both interactants have mutual interest in signalling and responding then the recipient may become sensitive to the signaller, whereas signaller may make communication less complex. These scenarios are evolutionarily stable because the communication is effective at achieving its desired goal, whilst reducing the costs of potential harassment by third party or predators in circumstances when the signal is conspicuous and large. An example would be left handed gesture seen in a common goal contexts signifying stronger social bonding (e.g. mutual grooming, joint travel, mutual visual monitoring) versus right handed gestures seen in contexts whereby interactants do not have a common goal signifying weaker social bonding (e.g. unidirectional grooming, lack of mutual visual monitoring) (Noë, 2006). Studies have recently emphasized how low intensity of communication is important for fitness by reducing stress inherent in social interaction (Nakayama, Goto, Kuraoka, & Nakamura, 2005; A. I. Roberts & S. G. B. Roberts, 2016). When individuals who are less strongly bonded interact, there may be a greater conflict of interest and therefore low intensity communication may be ineffective at influencing behavioural change in the recipient (Dawkins & Guilford, 1997). There is a wealth of studies that describe the phenomena whereby recipients respond more strongly to visual communication that is complex than to visual communication that is non-complex. Possibly, the most well-known are the elaborations and repetitions of visual signals seen in mating contexts. For instance, male frogs incorporating a higher rate of action repetition in visual display are more likely to attract female for mating than the males incorporating lower rate of action repetition in the visual display (PAYNE & PAGEL, 1997).

Complex visual signals as effective means of signalling, however, may reach a limit at which further increasing of complexity will not have any bearing on effectiveness of interaction with the recipient. Another way, in which signallers can influence efficiency of their signalling is by stimulating the reward system of the recipient. By making a gesture rewarding, signaller enhances recipient's commitment to the interaction, thereby making these social relationships possible. Such circumstances, for instance, may be present in complex social settings, whereby presence of other conspecifics in vicinity, provides competitive background against which signaller competes for attention of the recipient. By increasing their rewarding value, signals become more pleasurous to the receivers and to that extent become more capable of evoking a response from the recipient. During grooming, chimpanzees sometimes direct visual gestures to make the recipient present body for grooming, but when recipient is unresponsive they switch to gentle, but more intense tactile gestures to achieve their goal (A. I. Roberts, Vick, & Buchanan-Smith, 2013). Higher intensity signals are more perceivable by the receivers and by virtue of being more intense can exert greater influence on the recipient (Zahavi & Zahavi, 1997). Subordinate male chimpanzees for instance, use visual gestures designed to attract female for mating in absence of visual attention from the dominant male, but these gestures become intense and loud when the female is unresponsive because the dominant male is watching the interaction (A. I. Roberts & Roberts, 2015). High intensity however, can reduce or even reverse the preference for signals that are based on complexity of structure hence high intensity signals can become less complex (Gerhardt & Doherty, 1988). For instance, chimpanzee visual gestures are often accompanied by high complexity such as use of mutual attention, low intensity call or synchronized call in contrast to tactile and auditory gestures that are less often accompanied by these characteristics (S. Roberts & A. I. Roberts, 2018).

Final issue of importance for establishing which communication characteristics can influence preference for social affiliation is the positive versus negative communication style. Maestripieri and colleagues (1999, 2005) were amongst the first to recognize that affiliative as opposed to antagonistic gestural communication was of profound importance to the likelihood of social affiliation. Comparing three species of macaques with different social styles, they were able to show that more tolerant macaque species where the influence of kinship on social relationships was reduced displayed a larger repertoire of affiliative communication when compared to less tolerant macaque species where the influence of kinship was stronger. In more tolerant macaque species social interactions can easily disintegrate in response to exposure to aggression demanding higher investment in repair through affiliative communication. More recently, a study of a wild chimpanzee group showed that higher rates of affiliative gestural communication relative to antagonistic gestural communication predict a longer duration of time spent in proximity (S. G. B. Roberts & A. I. Roberts, 2016).

Chimpanzees, *Pan troglodytes*, are particularly good model species to illustrate how gestural communication affects primate social affiliation. Chimpanzees, live in large, fission-fusion social groups of up to 120 individuals, associating and affiliating in subgroups of varying duration and composition (Goodall, 1986). Due to fission-fusion nature of social system, mother and maternal kin are often unavailable as social partners demanding that chimpanzees form social bonds with unrelated group members (Goldberg & Wrangham, 1997; John C Mitani et al., 2002). The chimpanzees derive fitness benefits of social affiliation with unrelated group members in many different contexts such as grooming, coalitions, sharing meat, and hunting (Boesch, 1996; Foerster et al., 2015; Goldberg & Wrangham, 1997; K. E. Langergraber, Mitani, & Vigilant, 2007). Recent research has generated proofs that gestural communication of chimpanzees can influence preference for social affiliation. For example, recent studies have demonstrated the link between proximity measures (an index of sociality) and a number of different indices of communicative complexity such as intentionality (A. I. Roberts, 2018; A. I. Roberts & S. G. B. Roberts, 2018), repertoire size (A. I. Roberts, Chakrabarti, & Roberts, 2019) and multimodality (S. Roberts & A. I. Roberts, 2018). Whereas the role of gestures in maintaining proximity has been made clear, the role of gestural communication has received only limited research attention with regard to its influence on any other aspect of social affiliation in primates. However, in order to develop a deeper understanding of the factors driving social relationships, several measures of the social complexity are needed. As well as proximity, primates use visual attention to monitor conspecifics and also preferentially associate with others during grooming, feeding, resting and travel (Nishida, Zamma, Matsusaka, Inaba, & McGrew, 2010). All these different modes of interaction contribute to forming social relationships (Hinde, 1976). Studies which only focus on one behavioural aspect may therefore miss important features of social relationships.

Here we provide first systematic test of the hypothesis that gestural communication can influence preference of the recipient to form social relationships with the signaller. First, to test this hypothesis we use social network analysis to determine the link between communication and social bonding behaviours. Social network analysis represents individuals as nodes (e.g. individual A or B) and the social relationships (e.g. duration of time spent travelling, per hour spent within 10 m between AB dyad) as the edge or a 'tie'. Social network analysis examines how increase in the value of one variable produced by a dyad is associated with the increase or decrease in the value of another variable by a dyad (Croft, James, & Krause, 2010). For instance, if individual A directs tactile gestures and grooming at the individual B, then social network analysis can determine whether the rate of tactile gestures directed by individual A at the individual B is associated with increase or decrease in the duration of time individual A spends grooming individual B.

It has long been established that animal signals evolve to function effectively in a particular social environment. The variation in the conflict of interest between signaler and the recipient is reflected in how effectively different types of gesturing can influence social bonding. When social bonds are weaker, and the conflict of interest between signaler and the recipient is high, chimpanzees use more effective, and intense gestures (e.g. tactile, auditory). In contrast, when the social bonds are stronger and the conflict of interest is low, chimpanzees use less effective and less intense gestures (e.g. visual). However, intensity of gestures affects the specificity with which signaller can convey their goal of the interaction. Low intensity, visual gestures are less specific to context than more intense tactile or auditory gestures. Lack of specificity may affect the recipient's ability to effectively decode signal meaning and thus respond adaptively. One would therefore predict that communicative complexity would more likely co-occur with less intense gestures (e.g. visual) than with more intense gestures to enable the signaller to increase specificity of the gestures so that the recipient can decode signal meaning. Thus, one may predict that low intensity, complex signals will co-occur with indices of stronger social bonding (e.g. mutual grooming, joint travel), whereas higher intensity, non-complex signals will co-occur with indices of weaker social bonding (e.g. unidirectional grooming). In addition, it seems reasonable to assume that style of the gestural communication will affect the efficiency with which individuals can form social relationships. For instance, more bonded partners may exhibit a higher rate of gestures used in affiliation contexts as compared with antagonistic contexts because signaller gestures affiliatively to increase duration of social bonding. However, to date, this association between social relationships and complexity of gestural communication has not been examined systematically.

Second, we determine whether displacement behaviours such as self-scratching that help primates cope with anxiety (Aureli & Schaik, 1991; Baker & Aureli, 1997; Castles & Whiten, 1998; Diezinger & Anderson, 1986; Schino, Perretta, Taglioni, Monaco, & Troisi, 1996) are associated with gestural communication that facilitates social bonding. Studies of long-tailed macaques (Aureli & Schaik, 1991), olive baboons (Castles & Whiten, 1998) and chimpanzees (Baker & Aureli, 1997) have all used scratching to reliably estimate primate's level of anxiety. Chimpanzees may experience increased anxiety in situations of social uncertainty linked to presence of unpredictable social partners with whom social interactions are infrequent or dominance relationships have been unresolved (Aureli, 1997; Schino, Scucchi, Maestripieri, & Turillazzi, 1988). In this case, one may predict that communication aimed at these social partners may be associated with higher rate of signaller's displacement activity. Furthermore, chimpanzees may experience reduced anxiety in response to communication that has a rewarding property. For instance, vocal communication can prompt a surge in the production of social neurohormones in the recipient, such as a surge of oxytocin that relieves anxiety (Feldman, Gordon, & Zagoory-Sharon, 2011). In this case, it would be predicted that communication associated with weaker social bonds would be associated with reduced rate of displacement activity in the recipient.

Methods

Twelve adult East African chimpanzees (*Pan troglodytes schweinfurthii*) (6 males and 6 females) were observed for a mean (SD) duration of 751.5 (250.9) min per each focal individual (Table 1). The sample included almost all of the uninjured adult males in the community and to match the sample size of the males, a similar number of uninjured females was chosen as focal individuals. The subjects were chosen on the basis that they were lacking physical injury, because the injuries such as deformation of the hand by the snare can influence the type of communication used. Moreover, the sample of males and females was matched as closely as possible in terms of rank categories, including three low ranking and three high ranking males and females).

The chimpanzees lived in the tropical forest, Sonso community at the Budongo Conservation Field Station in Uganda, East Africa. The data was collected during 18 minute focal animal follows, consisting of 9 scans at 2 minute intervals, recording the activity of the focal individual (grooming, travel, resting, feeding), the visual attention, activity and proximity of the nearest neighbor and the identity of all individuals present within 10 m (see Table 2 for definitions). Chimpanzees in the wild, especially when present in large parties, can change behavior and activity frequently. Thus, in order to reduce variability within samples, a focal follow of 18 minute duration was chosen. Gestures were recorded continuously using a digital video camera, verbally recording directly onto the footage the identity and the behavior of the signaler and recipient, along with the goal directedness in the behavior and the functional context.

Using the video footage, the inventory identified gestures as acts of non-verbal behavior that were expressive movements of the limbs, head or the body posture that were intentional, communicative and mechanically ineffective. The detailed description of intentionality coding, along with the video clips of each gesture type, has been described previously (A. I. Roberts, Roberts, & Vick, 2014; A. I. Roberts, Vick, & Buchanan-Smith, 2012; A.I. Roberts et al., 2012). Validation of the coding procedure was established by a second coder and reliability (Kappa coefficient, K) was good for function (K = 0.70), modality of gesturing (K = 0.946) and intentionality (K = 0.74) (S. G. B. Roberts & A. I. Roberts, 2016). The behavioural measures (e.g. joint feeding, mutual grooming) were calculated as the duration of time pairs of chimpanzees engaged in these behaviors, per hour they spent within 10 m. The definitions as well as mean ± SD for all variables entered into the models can be found in Tables 2 and 3. Dyads were classified according to maternal kinship, sex, age class and reproductive state. All communication measures were calculated as a rate per hour chimpanzees spent within 10 m (see Supplementary Table 1 for definitions).

The rates of communication and durations of behavior were used to construct weighted, directed networks. The data was transformed and analyzed using UCINET 6 for Windows (Borgatti, Everett, & Johnson, 2013). The data used in social network matrices is dependent and therefore analysis using randomization (or permutation) have been developed, where the observed value is compared against a distribution of values generated by a large number of random permutations of the networks. The *p* value is calculated by calculating the proportion of random permutations in which a value as large (or as small) as the one observed is present. The relationships between networks were analyzed using Multiple Regression Quadratic Assignment Procedure (MRQAP) (Borgatti et al., 2013). This regression technique resembles a standard regression model as it enables us to examine the association between a number of predictor variables (e.g. rates of gestural communication between dyads, control variables relating to sex and age differences of dyads) and a single dependent variable (e.g. duration of proximity between dyads). We used Double Dekker Semi Partialling MRQAP regression as it is more robust against the effects of network autocorrelation and skewness in the dataset than other forms of network regression (Dekker, Krackhardt, & Snijders, 2007). For this analysis, 2,000 permutations were used following the settings of UCINET.

Running large numbers of models risks inflating significance levels (Field, 2013). To address this issue, following the methods used by Pearce et al. (2017), we examined whether the overall distribution of significant results varied across the different domains of sociality (joint activity, grooming, visual attention, proximity and scratch) and behavioural categories. These data are not subject to potential problems arising from multiple comparisons effects because the p value is used to categorise the results in each category as statistically significant or not, and one chi-square test is then carried out on the overall distribution of results (Pearce et al., 2017). Thus, we used a Chi-square test to examine the overall pattern of association between the behavioral indices and gestural communication. Following the same method as Pearce et al. (2017), this allowed us to examine whether the significant associations between gestural communication and behavior showed a distinct pattern, with certain types of gestural communication associated with specific behavioral indices more commonly than would be expected, as compared to a random distribution. This method is used as an alternative to Bonferroni correction when the multiple comparisons prevent the Bonferroni correction being used (M. J. Silk, Jackson, Croft, Colhoun, & Bearhop, 2015). We created contingency table whereby we included percentage of significant associations ($p < 0.05$) with each variable within each domain of social complexity (Supplementary Table 2). The results showed that the distribution of significant associations was non-random ($\chi 2 = 364.90$, df =60, $p < 0.001$). This demonstrated that the significant results were not randomly distributed across the different domains of sociality, suggesting that different types of gestural communication are differentially associated with the types of sociality. In all tests, two-tailed probabilities were used, with p set at < 0.05. Supplementary Information 2 gives a summary of these findings, with the full models provided in Supplementary Information 1 (Tables S3 – S19).

Results

Based on our 12 focal subjects, we studied directed patterns of social behaviour in pairs of chimpanzees, giving 132 unique dyadic relationships (e.g. the duration of grooming given by BB to HW, and the duration of grooming given by HW to BB). There was a great deal of variation in the rate of social behaviours amongst the dyads and across the different behaviours, as indicated by the fact that for all of the behaviours the standard deviation was larger than the mean (Table 2). Per hour spent within 10 m, the mean ± SD number of minutes dyads spent in social behaviours ranged between 0.44 ±1.58 spent in joint travel and 6.16 ± 10.05 spent in close proximity (within 2 m). Dyads scratched at a mean rate ± SD of 0.64 ± 1.68 instances of scratching, per hour spent within 10 m. Similarly for the communication indices, there was a large amount of variation between dyads, with lowest mean ± SD rate of behaviour for gestures accompanied by facial expression (0.09 ± 0.52) and the highest mean ± SD rate of events (3.18 ± 7.82) – Supplementary Table 2.

Association between the duration of social behaviour and gestural communication categorized according to structure

In the next set of analyses, we used MRQAP network regression analyses to examine how the duration of social behaviours (the dependent variable in all the models) was associated with the rate of different types of gestural communication and demography (see Figures 1 and 2 for visual representation of the networks).

Joint feeding

Same sex dyads ($\beta = 0.31$, $p = 0.001$) , kin ($\beta = 0.29$, $p = 0.010$) and same reproductive status ($\beta = 0.22$, $p = 0.040$) dyads spent a significantly longer amount of time engaged in joint feeding, as compared to different sex dyads, unrelated dyads or different reproductive status dyads. Dyads who spent a longer amount of time jointly feeding had a significantly higher rate of auditory short-range gestures ($\beta = 0.21$, $p = 0.040$) and significantly lower rate of tactile gestural communication ($\beta =- 0.22$, $p = 0.004$).

Joint resting

Same age dyads, as compared to different age dyads, spent a significantly longer amount of time engaged in joint resting ($\beta = 0.29$, $p = 0.003$). There was a positive association between the duration of time spent in joint resting and the rate of auditory short-range ($\beta = 0.13$, $p = 0.040$) and close proximity ($\beta = 0.12$, $p = 0.046$) gestures.

Joint travel

Same-age dyads, as compared to different-age dyads, spent a significantly longer amount of time jointly travelling (β = 0.28, p = 0.010). Further, the duration of joint travel was positively associated with a higher rate of gestural communication without objects (β = 0.47, p = 0.005), visual (β = 0.62, p = 0.010), unimodal (β = 0.22, p = 0.020) and multimodal with facial expression (β = 0.30, p = 0.020), combined (β = 0.41, p = 0.004), accompanied by mutual attention present (β = 0.37, p = 0.010), bodily (β = 0.50, p = 0.003), manual indicative (β = 0.42, p = 0.011), close (β = 0.27, p = 0.015) and far (β = 0.22, p = 0.013), non-repetitive (β = 0.55, p = 0.006), homogeneous (β = 0.43, p = 0.010), single (no sequence) (β = 0.22, p = 0.026), rapid (β = 0.20, p = 0.020) and persistence sequence (β = 0.14, p = 0.045), and accompanied by piloerection (β = 0.38, p = 0.006) , The repertoire size of gesture types (β = 0.34, p = 0.010) and number of events exchanged by each dyad (β = 0.39, p = 0.003) was positively associated with the duration of joint travel. In contrast, a higher rate of auditory long-range gestures was associated with shorter durations of time spent in joint travel (β = -0.28, p = 0.010).

Grooming given

Same-age dyads spent significantly longer engaged in giving grooming (β = 0.21, p = 0.020). The duration of time spent giving grooming was positively associated with a higher rate of production of following categories of gestural communication: no object (β = 0.64, p = 0.001), auditory short-range (β = 0.73, p = 0.001), auditory long-range (β = 0.19, p = 0.010), tactile (β = 0.41, p = 0.001), unimodal (β = 0.75, p = 0.001), dyadic repertoire size (β = 0.26, p = 0.020), single (non-combined) (β = 0.64, p = 0.001), mutual attention absent (β = 0.78, p = 0.001), bodily (β = 0.22, p = 0.023), manual (β = 0.29, p = 0.016), events (β = 0.46, p = 0.002), manual indicative (β = 0.17, p = 0.036), manual non-indicative (β = 0.35, p = 0.014), close (β = 0.76, p = 0.001), repetitive (β = 0.60, p = 0.001), homogenous (β = 0.52, p = 0.004) and single (no sequence) (β = 0.66, p = 0.001). In contrast, the dyads who spent a shorter duration of time giving grooming communicated at a higher rate through the use of objects (β = -0.20, p = 0.010), visual gesture (β =- 0.26, p = 0.010), multimodal (facial expression) (β = -0.23, p = 0.010), combined (β = -0.19, p = 0.020), mutual attention present (β = -0.11, p = 0.040) and far (β = -0.11, p = 0.012).

Grooming mutual

Same age dyad partners spent a longer duration of time mutually grooming (β = 0.20, p = 0.049). A longer duration of time spent mutually grooming was also associated with a higher rate of the following gesture types: no object (β = 0.64, p < 0.001), visual (β = 0.88, p < 0.001), unimodal (β = 0.27, p = 0.020), multimodal (facial expression) (β = 0.44, p = 0.002), dyadic repertoire size (β = 0.45, p = 0.003), combined (β = 0.40, p = 0.003), mutual attention present (β = 0.63, p = 0.001), bodily (β = 0.58, p = 0.001), events (β = 0.45, p = 0.003), manual indicative (β = 0.56, p = 0.001), non-repetitive (β = 0.72, p = 0.001), homogeneous (β = 0.60, p < 0.001), close (β = 0.38, p = 0.004), far (β = 0.22, p = 0.018), single (no sequence) (β = 0.33, p = 0.012), rapid (β = 0.16, p = 0.041) and persistence sequence (β = 0.16, p = 0.030) and piloerection (β = 0.42, p = 0.004).. In contrast, a higher rate of gestures object (β = -0.15, p = 0.020), auditory long range (β = -0.51, p < 0.001), repetitive (β = -0.18, p = 0.004) and heterogeneous (β =- 0.15, p = 0.016) predicted a shorter duration of time spent mutually grooming.

Grooming received

Same-sex dyads, compared to different-sex dyads, spent a significantly longer amount of time receiving grooming (β = 0.20, p = 0.030). Individuals who received a longer duration of grooming from the dyad partners produced gestures with no object (β = 0.22, p = 0.040), visual (β = 0.50, p = 0.020), unimodal (β = 0.25, p = 0.040), bodily (β = 0.25, p = 0.036), manual indicative (β = 0.17, p = 0.046), non-repetitive (β = 0.20, p = 0.035) and homogeneous (β = 0.17, p = 0.048) at a higher rate. However, individuals who received a shorter duration of grooming from the dyad partner directed auditory long range (β = -0.27, p = 0.020) and tactile (β = -0.20, p < 0.001) gestures at them at a higher rate.

Attention present

Presence of mutual attention occurred between dyads of same-sex (β = 0.30, p = 0.010) and same reproductive status (β = 0.28, p = 0.040) at a higher rate. Individuals who spent longer duration of time mutually attending with the dyad partner displayed a significantly higher rate of gestures with no object (β = 0.69, p < 0.001), visual (β = 0.75, p < 0.001), auditory short-range (β = 0.24, p = 0.010), unimodal (β = 0.44, p < 0.001), multimodal (facial expression) (β = 0.31, p = 0.003), dyadic repertoire size (β = 0.42, p = 0.002), single (non-combined) (β = 0.29, p = 0.004), combined (β = 0.30, p = 0.002), mutual attention present (β = 0.56, p < 0.001), bodily (β = 0.54, p = 0.001), events (β = 0.47, p = 0.001), manual indicative (β = 0.54, p = 0.001), close (β = 0.50, p = 0.001), far (β = 0.13, p = 0.045), non-repetitive (β = 0.56, p = 0.004), homogeneous (β = 0.60, p = 0.001), single (no sequence) (β = 0.47, p = 0.001) and piloerection (β = 0.35, p = 0.005). In contrast, individuals who spent a shorter duration of time mutually attending with the dyad partner displayed a significantly higher rate of gestures with object (β = -0.18, p = 0.003), auditory long-range (β = -0.44, p < 0.001), multimodal (vocal) (β = -0.09, p < 0.049) and heterogeneous (β =- 0.09, p = 0.046).

Attention absent

Same-aged dyad partners spent a longer duration of time mutually non-attending towards one another as compared to different age partners (β = 0.36, p = 0.001). The duration of time dyad partners spent mutually non-attending was positively associated with the rates of gestures with no object (β = 0.24, p = 0.028), auditory short-range (β = 0.29, p = 0.011), unimodal (β = 0.27, p = 0.024), single (non-combined) (β = 0.18, p = 0.045), mutual attention absent (β = 0.28, p = 0.015), events (β = 0.15, p = 0.049), close (β = 0.28, p = 0.021), single (no sequence) (β = 0.23, p = 0.026) and homogeneous (β = 0.17, p = 0.043).

Proximity

In comparison with different-age dyad partners, same-age dyad partners (β = 0.32, p < 0.001) spent a significantly longer duration of time in close proximity (within 2 m). There was a significant positive association between the duration of time spent in close proximity and a higher rate of a wide range of communication: no object (β = 0.56, p < 0.001), visual (β = 0.45, p = 0.010), auditory short-range (β = 0.34, p = 0.010), unimodal (β = 0.44, p = 0.001), multimodal (facial expression) (β = 0.14, p = 0.049), dyadic repertoire size (β = 0.28, p = 0.010), combined (β = 0.29, p = 0.010), mutual attention absent (β = 0.26, p = 0.010), mutual attention present (β = 0.30, p = 0.010), bodily (β = 0.40, p = 0.003), events (β = 0.37, p = 0.003), manual indicative (β = 0.37, p = 0.007), close (β = 0.48, p = 0.001), non-repetitive (β = 0.33, p = 0.012), homogeneous (β = 0.45, p < 0.001), single (no sequence) (β = 0.42, p < 0.001) and piloerection (β = 0.21, p = 0.027). In contrast, there was a significant negative association between the duration of time spent in close proximity and the rate of gestures using object (β = 0.17, p = 0.003), auditory long-range (β = -0.27, p = 0.010) and multimodal (vocal) (β = -0.11, p = 0.040).

Scratch produced

We further examined how the rate of scratch produced was related to the rates of communication using MRQAP (Fig. 1). Same-sex dyad partners had a higher rate of scratch produced than different-sex dyad partners (β = 0.20, p = 0.039). A higher rates of scratch produced were positively associated with higher rates of the following types of gestures: no object (β = 0.40, p = 0.004), visual (β = 0.48, p = 0.008), unimodal (β = 0.18, p = 0.049), multimodal (facial expression) (β = 0.18, p = 0.042), dyadic repertoire size (β = 0.35, p = 0.002), single (non-combined) (β = 0.25, p = 0.016), mutual attention present (β = 0.52, p = 0.001), bodily (β = 0.54, p < 0.001), events (β = 0.36, p = 0.003), manual indicative (β = 0.40, p = 0.003), close (β = 0.21, p = 0.023), far (β = 0.24, p = 0.001), non-repetitive (β = 0.41, p = 0.004), homogeneous (β = 0.37, p = 0.002), persistence (β = 0.57, p < 0.001) and piloerection (β = 0.23, p = 0.022). There was a significant negative association between rates of scratch produced and the rates of auditory long-range (β = -0.16, p = 0.046) and manual (β = -0.18, p = 0.011) gestures.

Scratch received

Same-sex dyad partners had a higher rate of scratch received than different-sex dyad partners (β = 0.20, p = 0.043). There was a significant negative association between rate of scratch received and the rate of auditory short-range gestures (β = -0.010, p = 0.049), gestures accompanied by mutual attention absent (β = -0.13, p = 0.049), close proximity (β = - 0.11, p = 0.048), repetitive (β = -0.44, p = 0.044) and single (no sequence) (β = -0.14, p = 0.044) gestures.

Association between the duration of social behaviour and gestural communication categorized according to function

We examined whether the duration of social behaviours (the dependent variable in all the models) was associated with the rate of different types of gestural communication categorized according to function. Chimpanzee dyads that produced higher rates of gesture threat to dominate spent a shorter duration of time jointly feeding (β = -0.50, p = 0.045), mutually grooming (β = -0.65, p = 0.006) and visually attending to each other (β = -0.64, p = 0.004). Gestures to give groom predicted a longer duration of time spent in jointly feeding (β = 0.17, p = 0.039), giving grooming (β = 0.69, p < 0.001), attention present (β = 0.25, p = 0.011) and absent (β = 0.24, p = 0.019), proximity (β = 0.30, p = 0.007). Further gestures to give groom elicited significantly lower rates of scratch received (β = -0.15, p = 0.020). Chimpanzee dyads that had higher rates of gestures in the context of mutual grooming spent a longer duration of time in mutual grooming (β = 1.14, p = 0.010) and visually attending to each other (β = 0.79, p = 0.025). Gestures to receive grooming were positively associated with the duration of time spent jointly feeding (β = 0.47, p = 0.012), giving grooming (β = 0.20, p = 0.036), mutual grooming (β = 0.53, p = 0.008), receiving grooming (β = 0.90, p = 0.001), attention present (β = 0.51, p = 0.001) and absent (β = 0.38, p = 0.022) and proximity (β = 0.55, p = 0.006). Higher rate of other threat gestures was negatively associated with a longer duration of time spent giving grooming (β = -0.06, p = 0.029) and were positively associated with a higher rate of scratch produced (β = 0.48, p = 0.002). Synchronized high-intensity panthoot was negatively associated with attention absent (β = -0.09, p = 0.049), proximity (β = -0.10, p = 0.012) and scratch received (β = -0.13, p = 0.019). Synchronized low-intensity panthoot was positively associated with joint feeding (β = 0.14, p = 0.043), travel (β = 0.26, p = 0.012), attention present (β = 0.10, p = 0.048) and absent (β = 0.13, p = 0.035) and proximity (β = 0.14, p = 0.023). A higher rates of play gestures were positively associated with the duration of give grooming (β = 0.10, p = 0.010) and negatively associated with the duration of time spent jointly feeding (β = =0.19, p = 0.004), mutual (β = -0.10, p = 0.012) and received grooming (β = -0.20, p = 0.002), attention present (β = -0.09, p = 0.017) and proximity (β = -0.08, p = 0.046). Higher rates of greeting gestures were associated with a longer duration of time spent giving grooming (β = 0.11, p = 0.025) and a shorter duration of time spent receiving grooming (β = -0.08, p = 0.041). Finally, higher rates of travel gestures were positively associated with a longer duration of time spent giving grooming (β = 0.10, p = 0.034) and travel (β = 0.10, p = 0.048).

Discussion

Most studies of chimpanzee social relationships in the wild or in captivity focus on one aspect of relationships, such as proximity (A. I. Roberts & S. G. B. Roberts, 2016; A. I. Roberts & Roberts, 2017; S. G. B. Roberts & A. I. Roberts, 2016). Here we provide first systematic evidence that chimpanzees form social relationships across many different contexts more effectively with those individuals with whom they communicate through gestural communication.

Previous research on male chimpanzees suggested that maternal kinship did not play a critical role in social relationships. Thus, chimpanzees who shared the same mother did not affiliate or cooperate more often than expected by chance (Goldberg & Wrangham, 1997; John

C Mitani et al., 2002). Although these relationships with maternal brothers appear to be important in infancy, demographic constraints on general availability of maternal brothers as potential coalition partners is believed to limit chimpanzee affiliation with maternal brothers (Goldberg & Wrangham, 1997; John C Mitani et al., 2002). On the basis of findings on affiliation and kinship among chimpanzee brothers we expected to find a weak affiliative relationships within mother and the adult offspring dyads. Against our expectation we found that mother offspring dyads maintained close proximity more often than unrelated dyads in co-feeding context but not other contexts. Although adult chimpanzees and mothers appear not to affiliate, they nonetheless remain in proximity in competitive contexts. This raises an important question as to why adult offspring chimpanzees co-feed with mothers if they do not affiliate with them. Research across chimpanzee populations in Africa shows that both adult male and female chimpanzees experience high levels of competition for plant food suggesting that these costs may be reduced by co-feeding with kin (Muller, 2002). Females who are unable to monopolize feeding site alone may engage in co-feeding with adult sons or daughters, thus enhancing their feeding success. In humans, unrelated individuals cooperate contingent upon strength of a social bond (friendship) and potential for reciprocity, whereas kinship has a direct effect on level of cooperation that is independent of social bond strength or reciprocity - the phenomenon termed 'kinship premium' (Curry, Roberts, & Dunbar, 2013). Kinship is more resilient to decay overtime, whereas friendships require more investment into social contact to maintain them at a level of strong social bonding (S. G. Roberts & Dunbar, 2011). The current finding in the chimpanzees that co-feeding with kin occurs in absence of affiliation, suggests that one might expect a similar effect of 'kinship premium' in the chimpanzees. The observations that unrelated sex and reproductive cohort dyads maintain proximity during feeding in presence of affiliation supports this suggestion.

Comparably important to kinship are relationships with partners from the same age cohort (Altmann, 1979). These relationships develop in infancy through association between mothers (Murray et al., 2014). Mirroring previous findings across Africa, the results show that these dyads are associated with high rates of affiliation in many different contexts (K. Langergraber et al., 2009; K. E. Langergraber et al., 2007; J.C. Mitani, Watts, & Muller, 2002). By expectation, the positive association between co-feeding and kinship should therefore also have emerged in the same age cohorts. However, these dyads differed in the patterns of co-feeding from other dyads. Chimpanzees from the same age cohort did not spend more time co-feeding in proximity than chimpanzees from different age cohort. Although these dyads share important interactions and behaviours, these relationships appear competitive and costly, possibly due to the fact that same age partners occupy similar niche and this might create greater competition. For instance, studies of mountain gorillas showed that when there is a high degree of co-feeding, individuals deal with competition by using different parts from the same food source (Watts, 1992). In contrast, same age cohort chimpanzees compete for the same food, dominance status, and position in the network. Same age partners share similar rank, but this equitability may create social relationships prone to decay because there is no prior consensus about the direction of potential aggression (F. B. de Waal, 1986; Flack, De Waal, & Waal, 2004). Indeed, partners of the same age class in rhesus macaques have been found to display high rates of both aggression and affiliation (Widdig, Nurnberg, Krawczak, Streich, & Bercovitch, 2002). To uncover the extent to which this lack of co-feeding in same age cohorts is generalizable to other sites it is first important to examine these relationships in small and large parties of chimpanzees, as these differ in the degree of feeding competition. In large parties when the feeding competition is greater, chimpanzees may associate with kin to diffuse competition, but in smaller parties they may well co-feed with same age partners.

Chimpanzees distribute their affiliative and competitive behaviour according to kinship and demography. However, can gestural communication play a role if influence of these factors has been discounted? In other words, are chimpanzees more affiliative than would be expected by chance, if affiliation was dependent on gestural communication alone? Here our findings contribute to prior research by showing that gestural communication exerts important influence on patterns of social affiliation among chimpanzee dyads. After controlling for kinship and demography, the data shows that chimpanzees spend longer duration of time affiliating with the individuals with whom they communicate through gestures. Thus, as there is an increase in the duration of time A spends in social behaviour with B, there is a corresponding increase or decrease in the rate of gestural communication emitted by A to B. These findings support earlier research from vocal modality which showed that sociality is associated with use of vocal communication (McComb & Semple, 2005). Affilitive gestures such as gestures to initiate grooming or play appear to have an especially important influence on affiliation. Affiliative gestural communication positively influenced the duration of time spent in social behaviour, whereas antagonistic gestural communication negatively influenced duration of time spent in social behaviour. For instance, the higher rate of gestures to initiate giving grooming predicts longer grooming, whereas higher rate of gestures to threaten predict shorter grooming. Thus, affiliative gestures are important in maintaining social relationships and function to coordinate these interactions. For instance, affiliative gestural communication is more common in socially complex egalitarian pigtail macaques, than in less socially complex and despotic rhesus macaques (Maestripieri, 1999).

However, affiliation contexts are not uniformly associated with different degrees of gestural complexity but there is a vast variation in how these measures of complexity are distributed across contexts. In contexts signifying stronger social bonding (e.g. mutual grooming, joint travel, mutual visual monitoring) gestures are primarily of low intensity (visual or auditory short range), ranging from 16 to 17 different forms, that are more complex (e.g. use of facial expressions, gestures were combined with other gesture types). In contrast, in contexts signifying weaker social bonding (e.g. unidirectional grooming) (Noë, 2006) gestures are of higher intensity (tactile, auditory), take 13 different forms that tend to be simpler (e.g. unimodal gesture, non-combined with other gesture types). Gestures given in strong social bonding contexts may therefore be qualitatively different from gestures given when social bonds are weaker.

Why is there such a variation in gesture complexity across contexts? Is this variation attributed to the efficiency with which communication can influence the recipient? The most parsimonious explanation of these data is that chimpanzees in the wild are making decisions on how to communicate, by choosing the gestures that can best influence the recipient in the given context. Our data supports previous research suggesting that there are two key pathways to achieving a greater efficiency in gestural communication. Studies in chimpanzees, showed how intensity of communication can influence efficiency of social bonding in relation to its effectiveness of conveying signaller's goal specifically (A. I. Roberts & S. G. B. Roberts, 2016). For instance, visual bodily gestures accompanied by direct gaze and pointing, have a greater success in coordinating proximity with the recipient than when using visual bodily gestures alone (Conty et al., 2012; S. Roberts & A. I. Roberts, 2018). Thus by making low intensity, inspecific gestures more complex, signallers can increase specificity of their gestures and elicit more accurate response from the recipient. Another way to increase specificity of the gesture is by increasing their intensity and therefore greater complexity of the gesture is not required (A. I. Roberts & S. G. B. Roberts, 2016). This link between intensity of communication and specificity of the response has been shown in studies of nonverbal communication in humans (Zajonc & Sales, 1966). As the intensity of the signal increases, the mapping between structure of the signal and the accompanying context becomes tighter enabling recipient to more accurately make the association between the signal and the signaller's goal. Finally, adding rewarding property to the signal may increase signal's effectiveness in conducting successful interaction (A. I. Roberts & S. G. B. Roberts, 2018). These rewarding properties promote greater commitment to the interaction so that the recipient is more likely to respond to the gesture.

The relationships based on behaviours such as mutual grooming or travel appear to be more mutually appealing as shown by a longer duration of time invested in these behaviours between partners who spend more time in proximity. These relationships are more common between same age cohort partners – growing up together provides context whereby dyads share many similarities and are highly familiar with each other. However, a whole range of signals responsible for maintaining these interactions, for example visual gestures, persistence, repertoire, facial expression were associated with higher rate of self-scratch, indicating higher anxiety experienced by the signallers towards recipients of these gestures. One type of answer that can be given to the question of why chimpanzees experienced higher anxiety in response to communicating with social partners with whom they displayed a higher rate of affiliative behaviour is that social relationships with these social partners have been uncertain due to unresolved dominance relationships. What has long puzzled anthropologists is that dominance hierarchy can sometimes lead to greater social cohesion because it enables signaller to more effectively predict outcome of the interaction before they engage in the interaction with the recipient (Flack, Girvan, De Waal, & Krakauer, 2006). Classical ethologists have shown very clearly how lack of linear dominance hierarchy can make animal societies less predictable and more aggressive (Flack, de Waal, & Krakauer, 2005) demanding complex but low intensity communication to resolve ambiguity in social relationships (A. I. Roberts et al., 2019). This communication can increase trust of the recipient, as it may appear more positive, therefore creating a perception of a fitness rewarding intent of the signaler (Roberts & Roberts, 2016a). In social relationships with dominant chimpanzees, the risks of interaction and direction of potential aggression is known in advance and therefore dominance relationships increase certainty by having predictable outcomes (Ay, Flack, & Krakauer, 2007; Flack et al., 2006). In contrast, equitable ranks are less predictable in that both interactants are equally likely to win if engaged in a fight resulting in high levels of uncertainty. The mutual appeal that draws chimpanzees together in these social interactions, has been insufficient and the power of gestural communication has been exploited to facilitate social interactions between these partners. Low intensity signals designed to effectively convey the intentions of a signaller in a way that leads to a reduction in uncertainty of the recipient about the signaller's goal encompass all common signals seen in these contexts.

In contrast, the relationships based on behaviours such as unidirectional grooming are often directed towards chimpanzees who display higher rank. Gestures made in unidirectional grooming context were associated with reduced rate of self-scratching by the recipient, suggesting that recipients experience reduced anxiety when receiving these gestures. This reveals a possible lack of mutual appeal in these interactions as the signaller actively influences recipient's positive affect to enhance its willingness to associate. As the anxiety is reduced, the signaller increases recipient's commitment to the social interaction forging stronger social bonding. Thus, in these contexts, in addition to conveying goals effectively through more intense gestures, use of signals that increase rewards are important to succeed in engaging the recipient who may otherwise not be particularly interested in the interaction.

The differentiated communication strategies of the chimpanzees may have evolved in response to the demands imposed by competition in complex social settings. Both male and female chimpanzees often compete for food and individual's ability to gain access to food can influence their reproductive success (Muller, 2002). Evidence from chimpanzees indicates that social variables such as party size can affect individual's relative competitive success in feeding contexts. Chimpanzees in larger parties derive benefits from lower predation pressure but may face a higher feeding competition than the chimpanzees in smaller parties. Competition for food may therefore promote evolution of the strategies the individuals use to diffuse this competition. Influential strategy includes grooming to reduce likelihood of potential aggression during co-feeding. In small social groups, chimpanzees face lower social competition and thus can invest in grooming with the social partners that are insecure but appealing. However, when the size of the group increases, the safety of secure relationships promotes feeding efficiency and therefore grooming interactions focus on these social partners. Tactile gestures that have a rewarding property can compete for recipient's attention in larger groups more effectively than visual gestures by being more capable of redirecting recipient's attention from the wider audience onto the signaller. Furthermore, rewarding gestures may have a better coordination value by being able to influence recipient's behaviour more directly through more intense and specific gestures (A. I. Roberts & S. G. B. Roberts, 2016). Studies showed that when larger audience is present, both rewarding and coordination properties of gestural communication facilitate longer grooming and this in turn is associated with longer co-feeding in proximity (A. I. Roberts, 2018). Given the time budgeting constraints on grooming (Dunbar, 1992), there may be a limit for use of grooming as a tool for diffusing social competition in feeding contexts. Our data reveals that chimpanzees incorporated use of objects and vocalisations when gesturing towards conspecifics with whom they spent short periods of time in proximity. Similarly, use of objects such as a trunk of a tree to make sounds accompanied by use of rhythmic vocalisations ('synchronized high-intensity pant hoot') may potentially fulfil such a function as this communication is used most often when joining feeding sites or during travel (Clark & Wrangham, 1994; S. G. B. Roberts & A. I. Roberts, 2016). Supporting these suggestions, our evidence shows that synchronized high-intensity pant hoots were associated with reduced displacement behaviours in the recipient. When social parties become large, the ability to groom with conspecifics may decline and 'synchronized high-intensity pant hoot' may facilitate social cohesion by reducing anxiety of the recipients (S. G. B. Roberts & A. I. Roberts, 2016). This property may draw attention of the recipients from the wider audience onto the signaller facilitating longer interactions such as travel or co-feeding. This finding supports research on humans (Jackson et al., 2018) showing that joint, high intensity behaviours have a role in social cohesion by being intensely rewarding to the dyad partners, regardless of the history of prior interaction.

The complexity of a social system depends on the complexity of individual relationships between animals, as the individual-level social interactions scale to the emergent properties found in the social system (Krause, Croft, & James, 2007). In this study we highlight the tactical decisions that wild chimpanzees make in their use of gestural communication to develop and maintain complexity of their social system. The selective pressures arising from maintaining this social complexity is proposed to have played a key role both in the evolution of communicative complexity and in the evolution of larger brains both in primates and in hominins. However, detailed behavioural evidence of an association between communicative complexity and these differentiated social relationships is lacking. Here we address this issue by examining how different types of social behaviour relate to patterns of gestural communication. Overall, our results suggest that differentiated patterns of gestural communication can help chimpanzees maintain a network of differentiated social relationships, and that this may allow individual primates to successfully navigate a complex social world. Future studies exploring the relationship between the complexity of communication skills, sociality and brain size across a range of primate species would allow for a deeper understanding of the association between complex social systems and complex communication.

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Table 1: Focal ID, sex, year of birth, kinship and reproductive status of the 12 focal subjects included in the study.

Focal subject ID	**Sex**	**Age**	**Female reproductive status**	**Kinship**	**Total observation duration (minutes)**
KU	Female	29	Pregnant	KT (son)	910
KW	Female	27	Nursing		510
ML	Female	33	Cycling		1118
NB[b]	Female	46	Cycling	MS (son)	500
RH	Female	43	Nursing	NK (son)	1038
ZM	Female	40	Cycling		710
BB	Male	21	-		516
HW	Male	15	-		1030
KT	Male	15	-	KU (mother)	1026

MS	Male	17	-	NB (mother)	524
NK[a]	Male	26	-	RH (mother)	582
SQ	Male	17	-		554

Notes. [a] Alpha male, [b] Alpha female.

Table 2. Definitions, means and standard deviations (SD) for social behaviours, based on 132 chimpanzee dyads. All social behaviours measured as durations (mins), per hour dyad spent within 10 m. For joint behaviours (e.g. feeding, resting, travelling) both dyad partners were engaged in the same behaviour. The behaviors are described in depth in (Nishida et al., 2010).

Behaviour[1]	Definition	Mean±SD
Joint feeding	Focal and non-focal subject consume food simultaneously	1.25±2.53
Joint resting	Focal and non-focal subject are in resting position not involved in any activity	1.56±5.73
Joint travel	Focal and non-focal subjects simultaneously relocate from one location in the habitat to another	0.44±1.58
Grooming given	Focal subject grooms non-focal subject by picking dirt and parasite from their hair.	0.69±2.33
Grooming received	Focal subject receives grooming from non-focal subject who is picking dirt and parasites from their hair.	0.67±2.55
Grooming mutual	Both focal and non-focal subject simultaneously pick dirt and parasites from hair of one another.	0.53±2.13
Attention present	Both focal and non-focal subjects are bodily oriented towards one another (one has another within field of view up to 45	3.04±5.68

	degrees body turn)	
Attention absent	Both focal and non-focal subjects are bodily oriented away from one another (one has another away from field of view up to 45 degrees body turn)	1.84±5.68
Proximity	Focal and non-focal subjects are within 2 meters of one another	6.16±10.05
Scratch produced	Focal subject rakes with the fingers through their own hair repeatedly or singly – all chimpanzee scratch (social and non-social) was included	0.64±1.68
Scratch received	Focal subject is recipient of the scratch whereby the non-focal subject rakes their own hair with the fingers through the hair repeatedly or singly (all types of scratch were included)	0.64±1.68

[1] see Roberts and Roberts (2017) for contribution of each dyad to the dataset

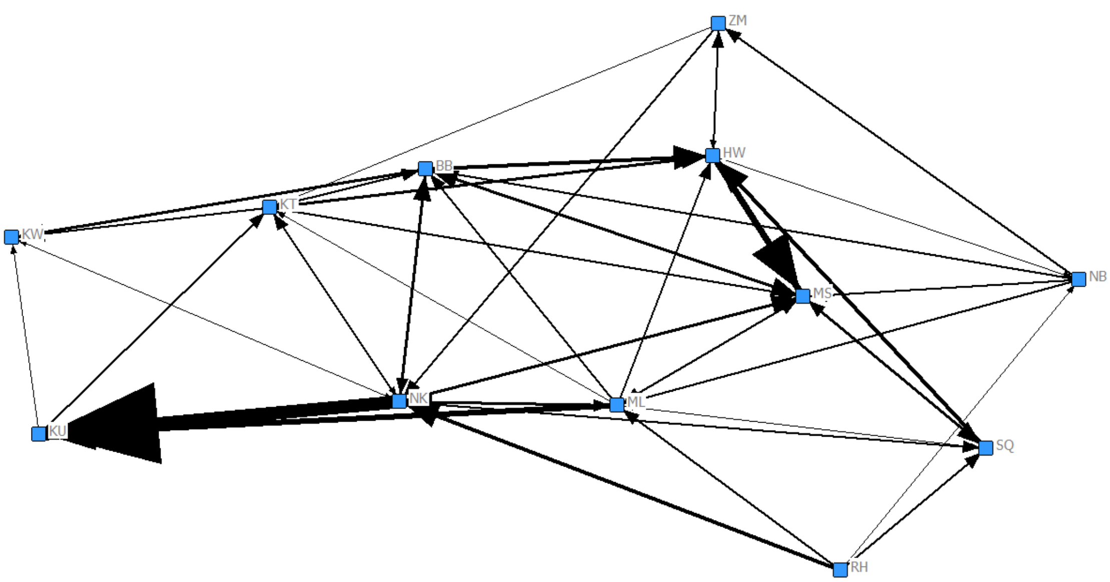
Table 3. Attributes used to classify dyads

Attribute of dyad	**Description**
Sex difference	Sex difference between focal subject and the recipient (0 = opposite sex, 1 = same sex)
Age difference	Age difference between focal subject and the recipient: 0 = different age (more than 5 years age difference with the dyad partner), 1 = same age (up to 5 years age difference)
Reproductive state difference	Reproductive state difference between focal subject and the recipient (0 = different reproductive state: unoestrous female-oestrous female, unoestrous female-male dyad; 1 = same reproductive state: male-male, male-oestrous female, oestrous female

	– male, unoestrous female – unoestrous female, oestrous female-oestrous female dyad, etc.)
Maternal kinship	Maternal kinship (mother-offspring or offspring-mother) presence between focal subject and the recipient (0 = absent, 1 = present)

Figure 1. Social networks: a) attention absent, b) attention present, c) proximity, d) joint feeding, e) grooming given, f) grooming mutual, g) grooming received, h) joint resting, i) joint travel, j) scratch produced, k) scratch received

a)



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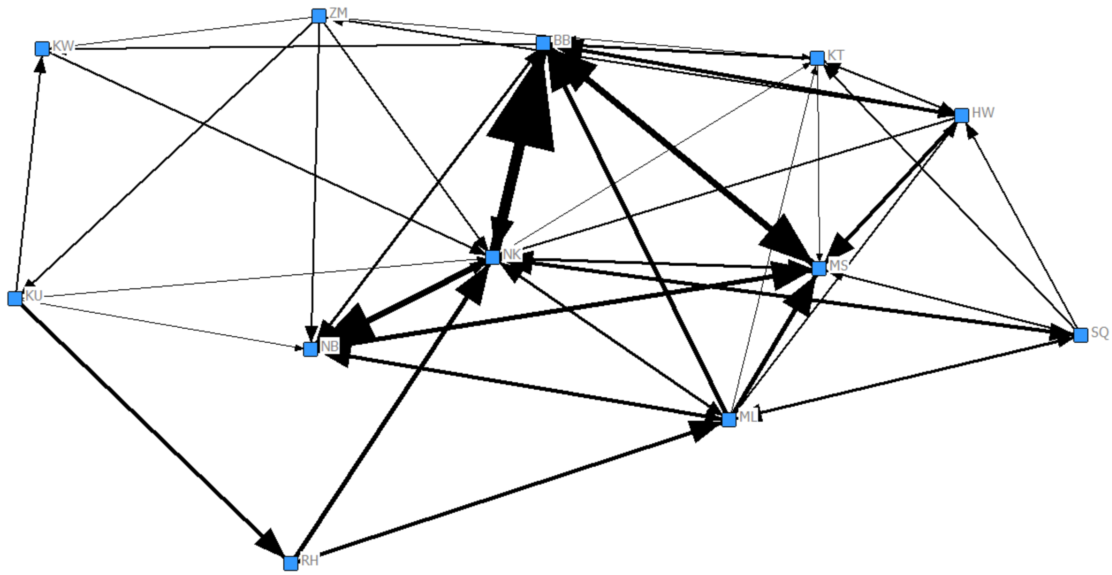

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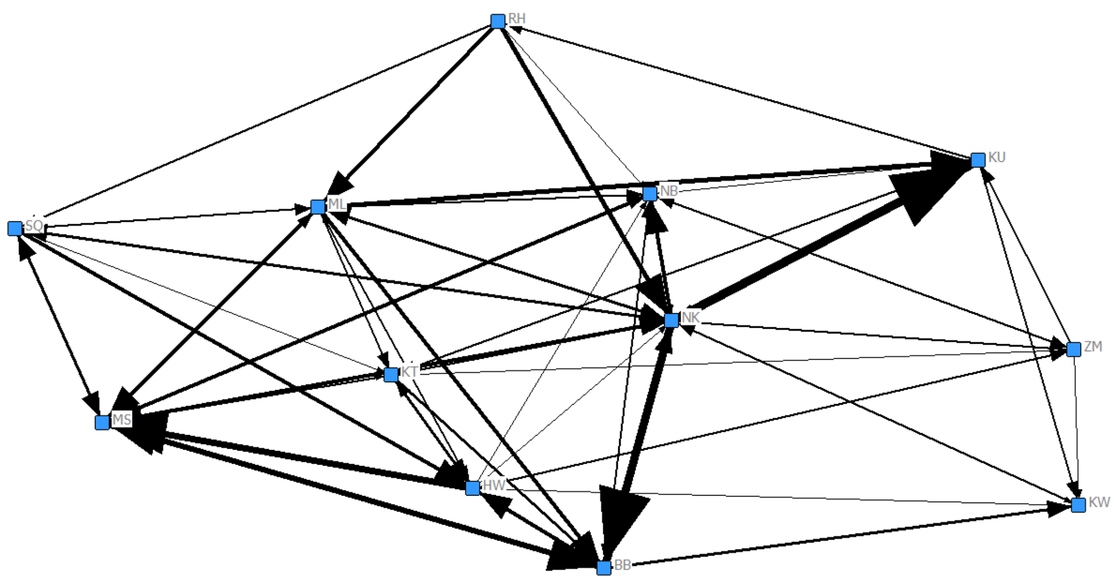

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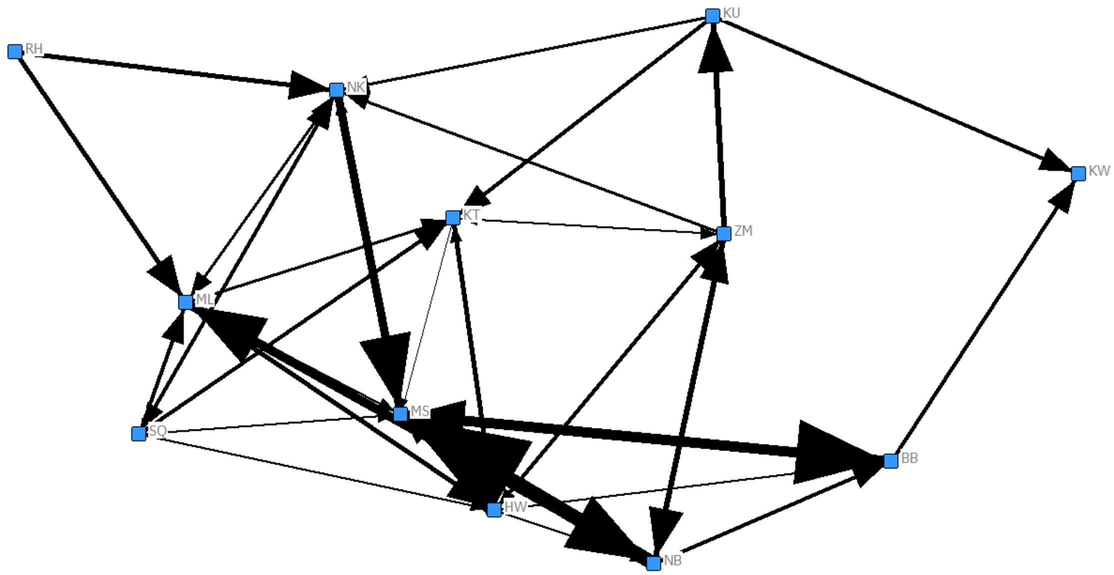

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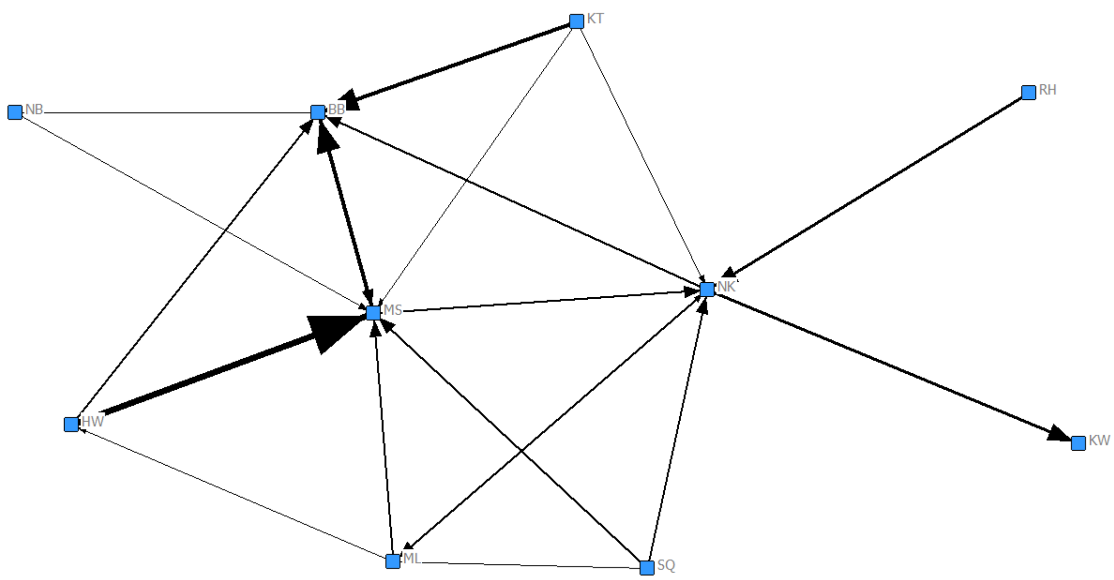

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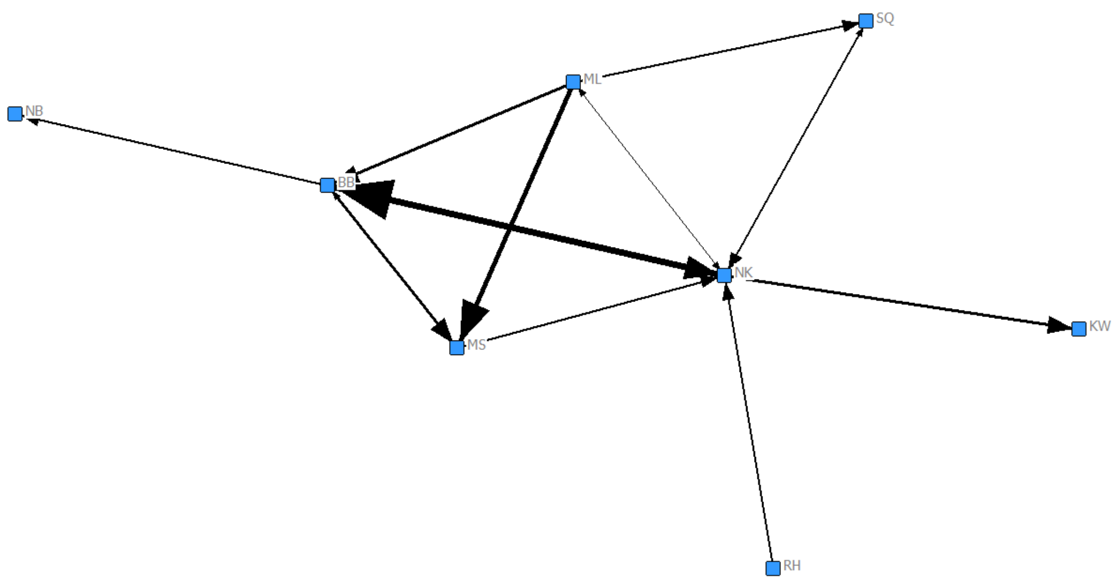

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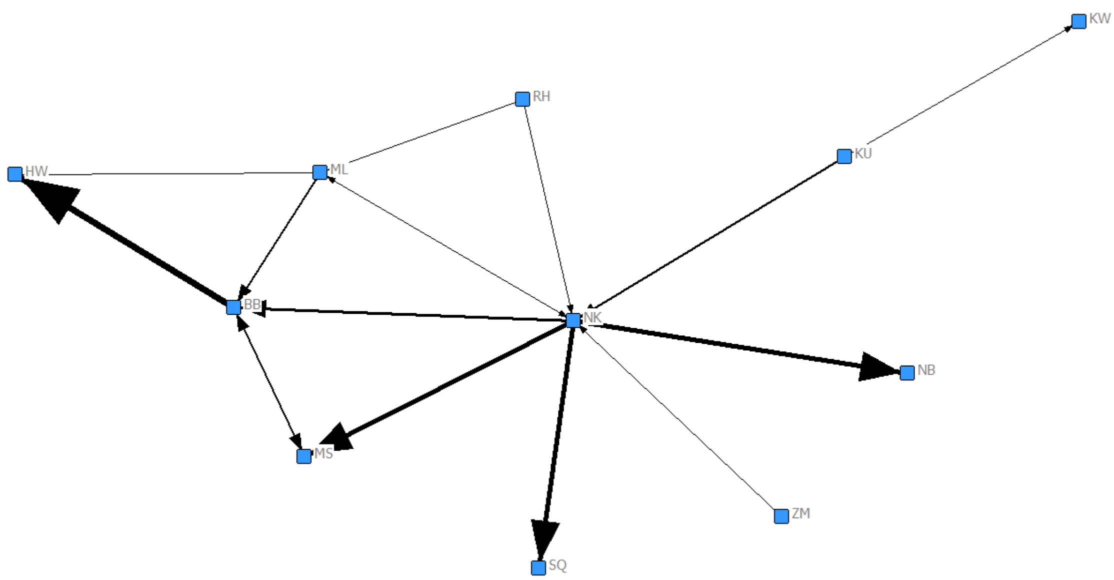

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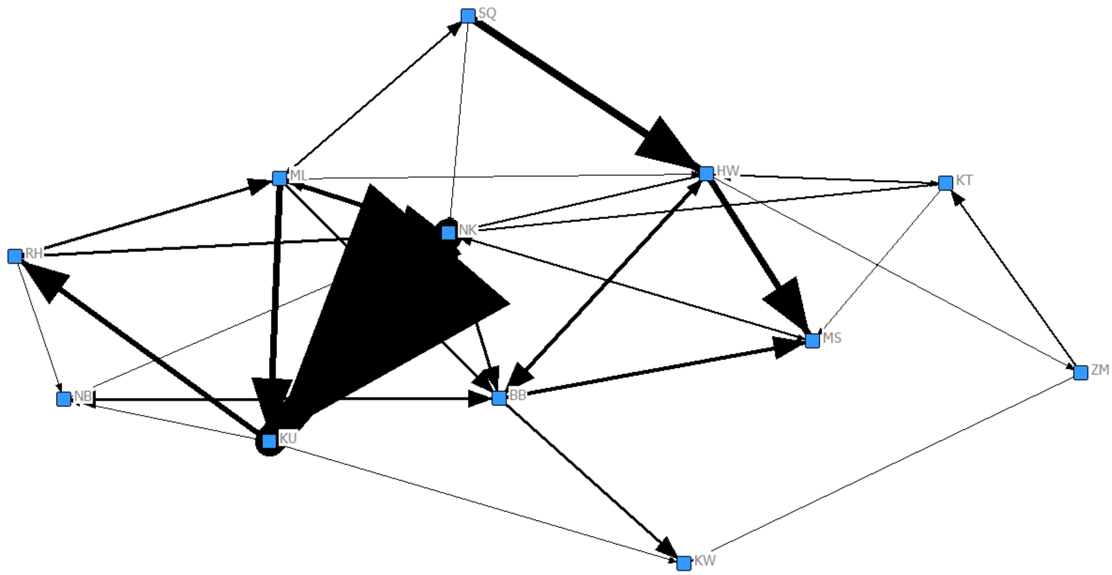
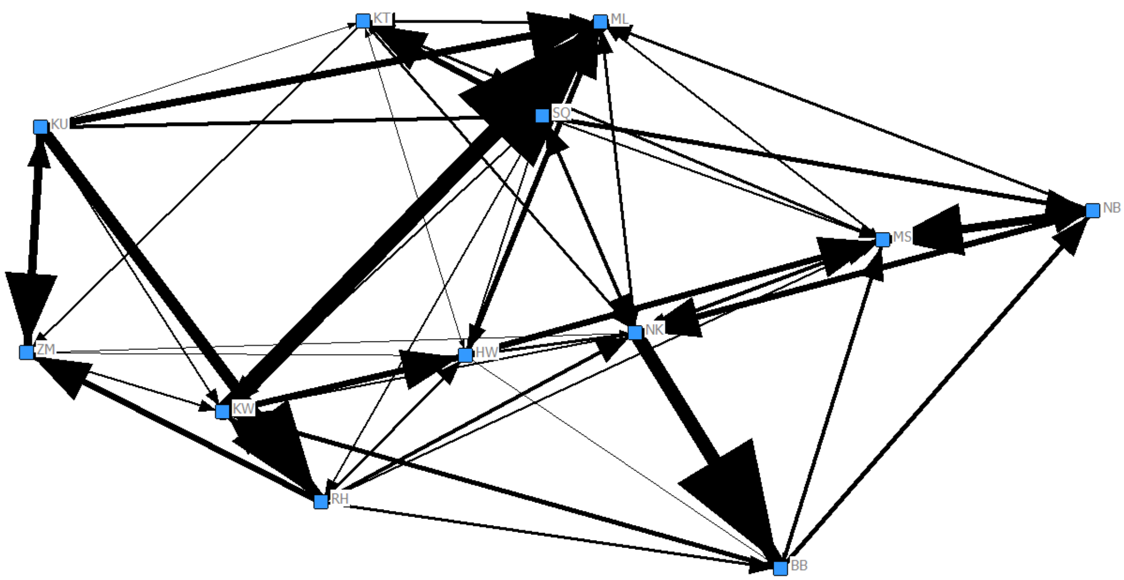


i)

j)



k)

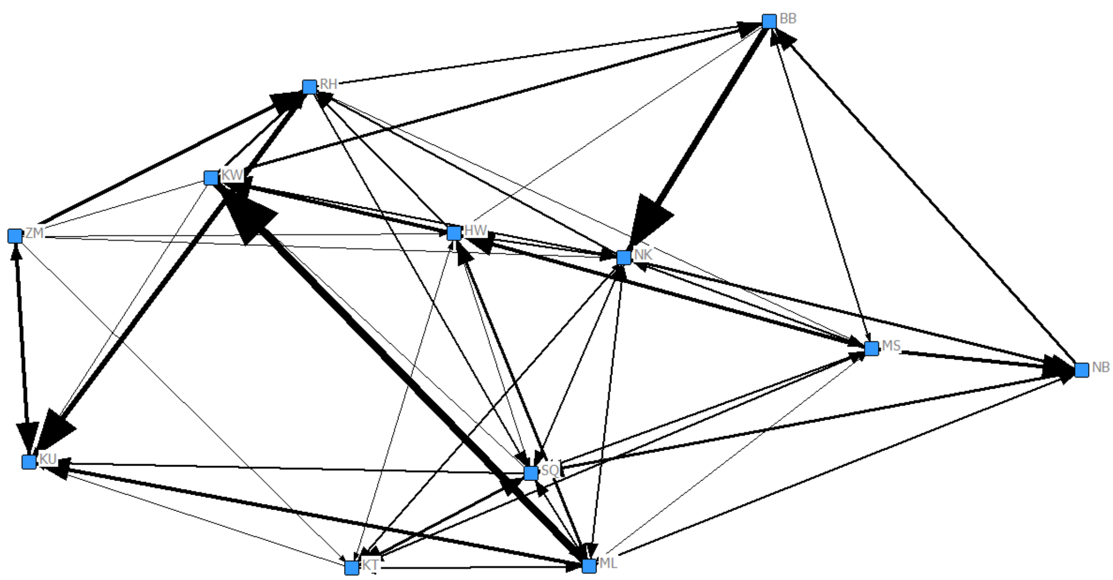
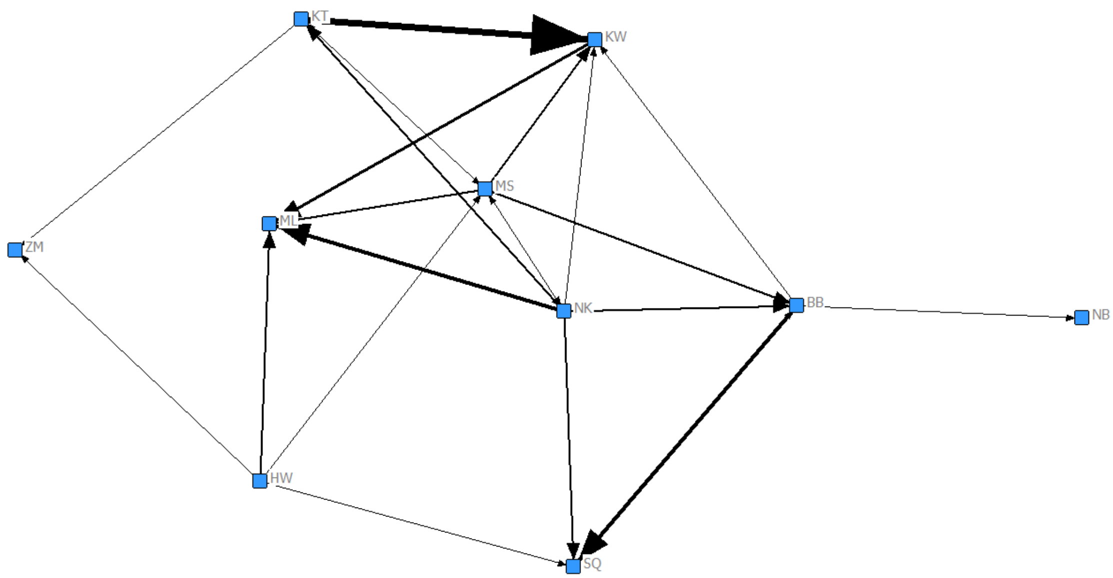


Figure 2. Social networks of gestures categorised according to Modality: a) auditory long range, b) auditory short range, c) tactile, d) visual; e) Repertoire size; Object use: f) objects, g) no objects; Combined gestures: h) combined, i) single (non-combined); Indicative: j) manual indicative, k) manual non-indicative; Bodily and manual: l) bodily, m) manual; Attention: n)

mutual attention present, o) mutual attention absent; Multimodal: p) multimodal (facial expression), q) multimodal (vocal), r) unimodal; Homogeneity: s) homogenous, t) heterogeneous

a)



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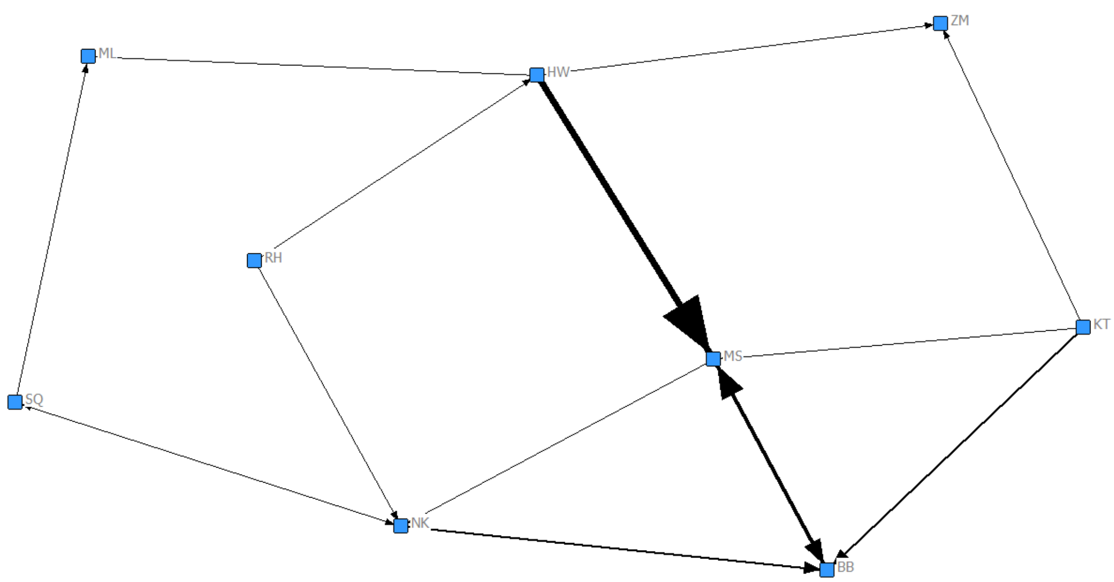

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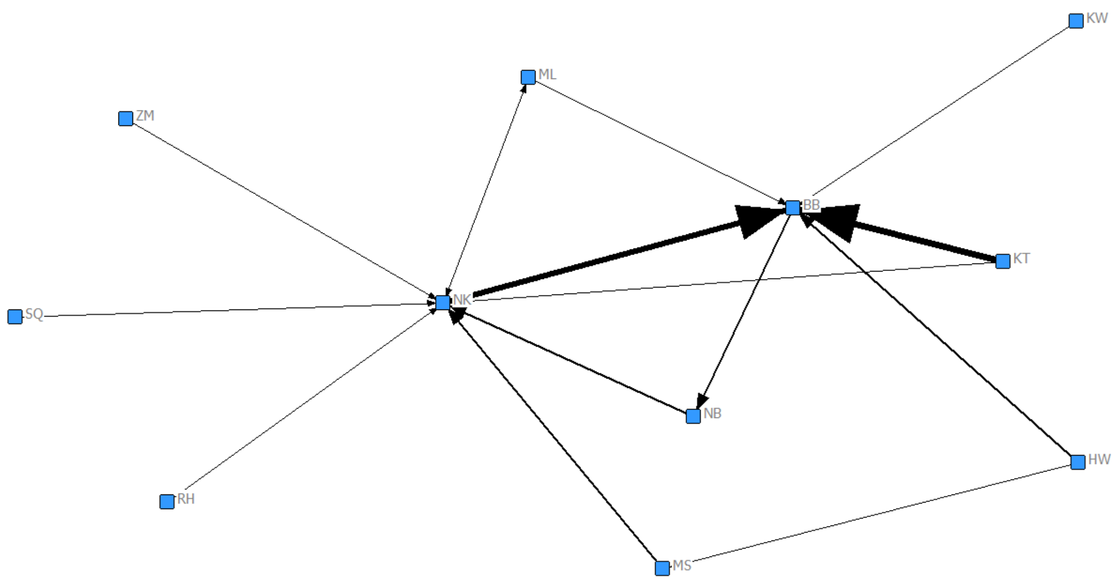

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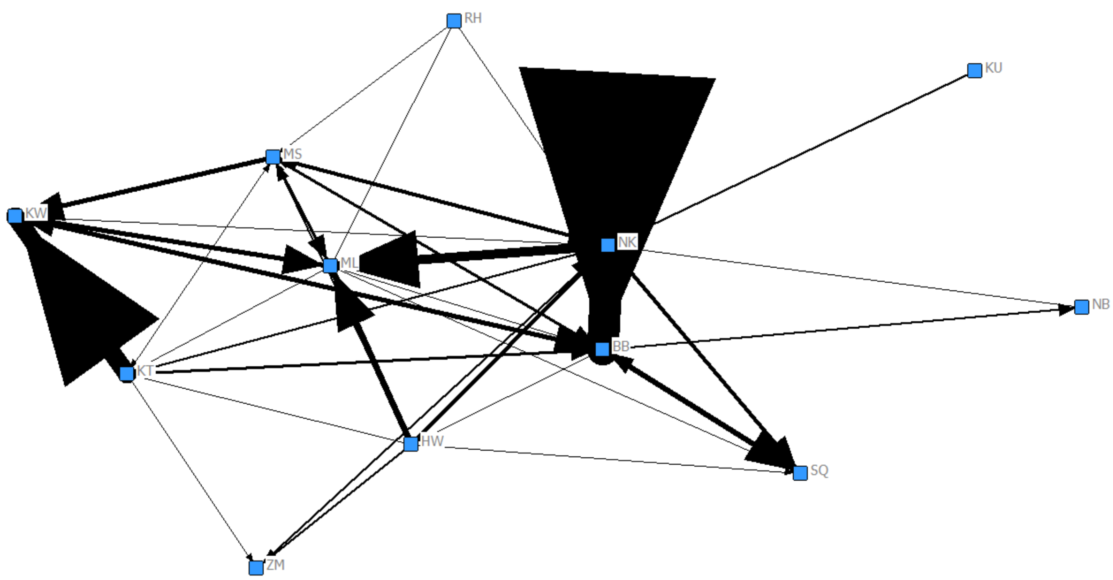

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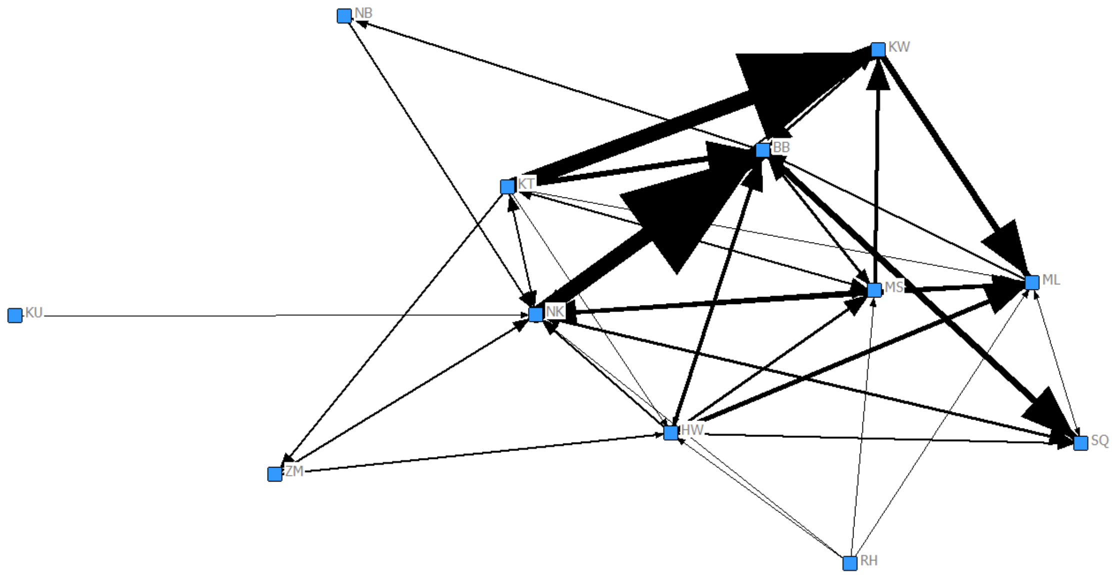

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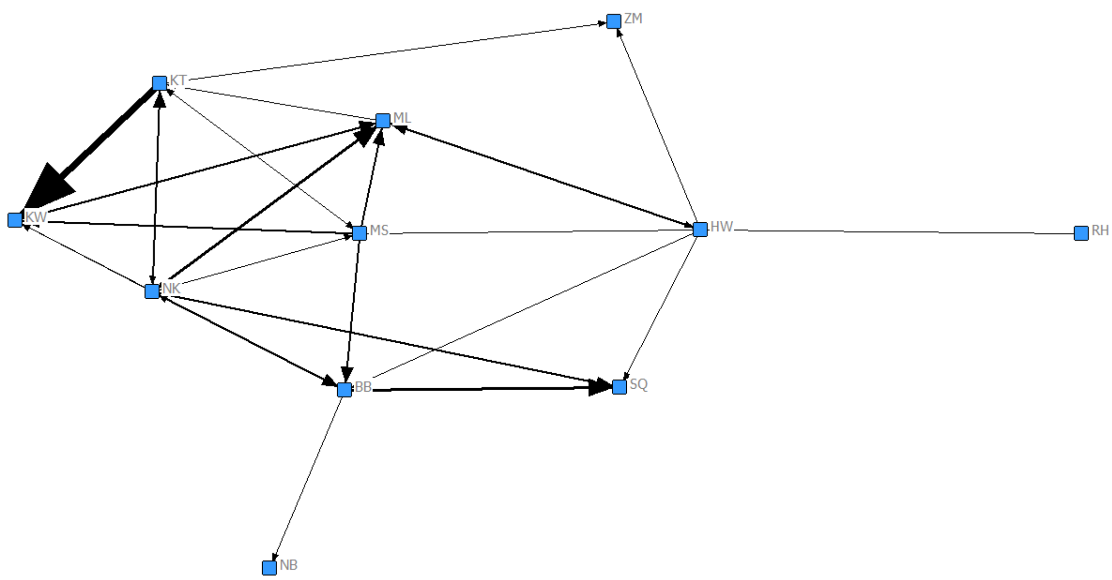

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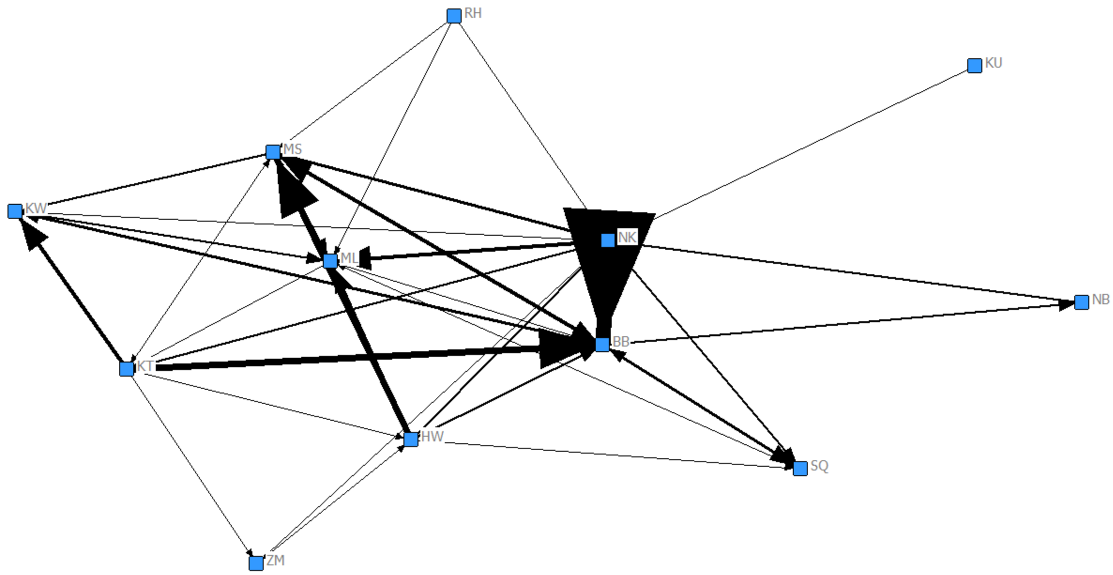
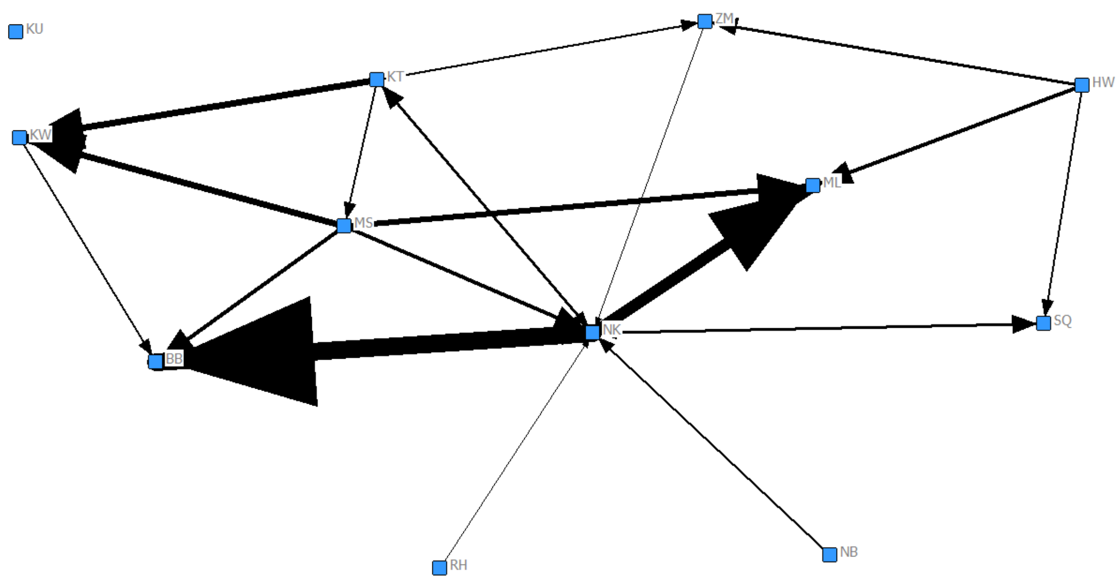


h)



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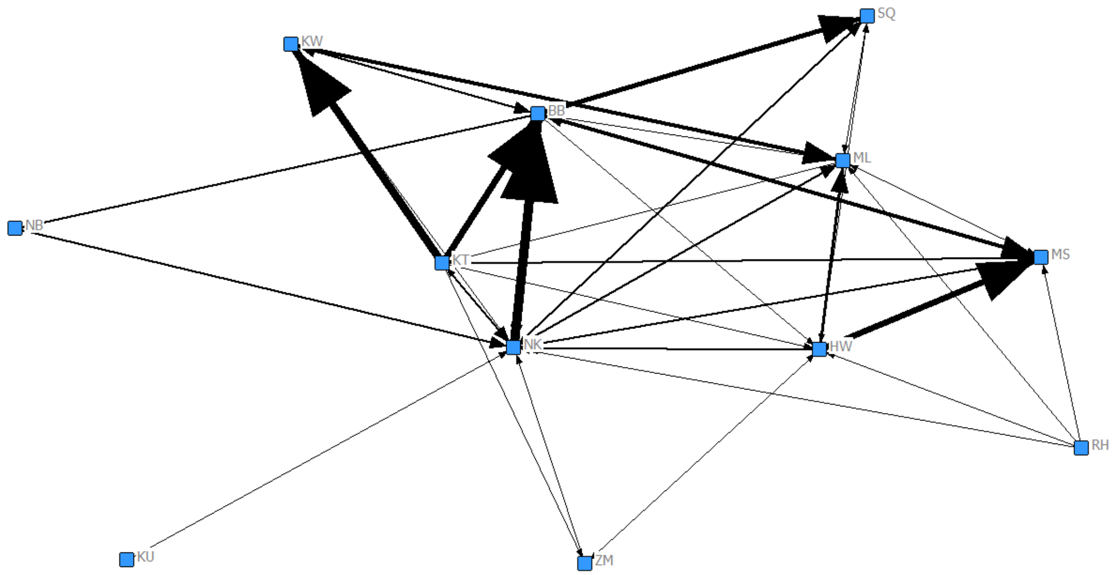

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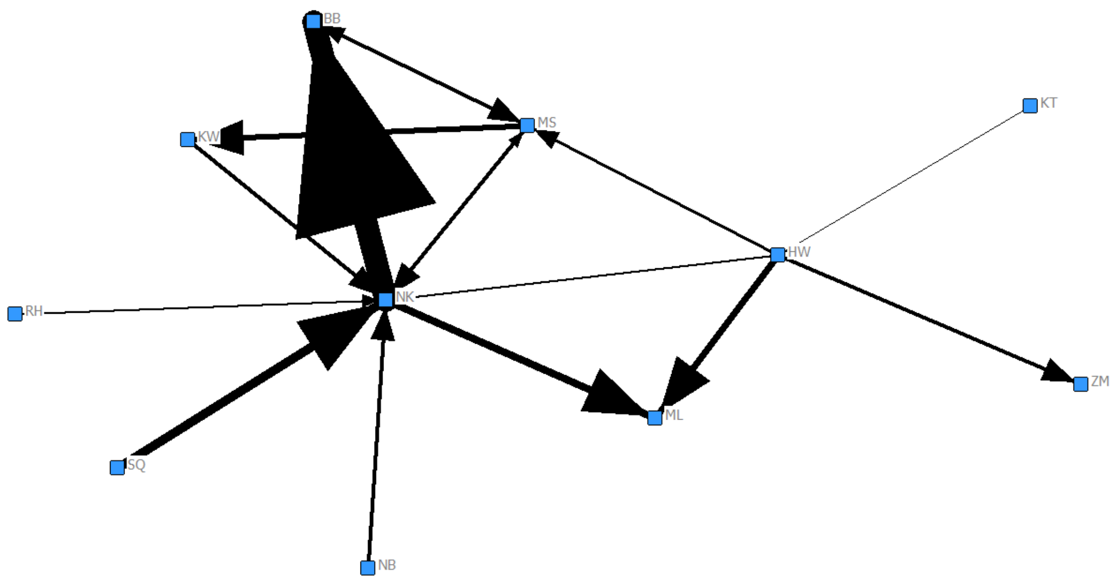

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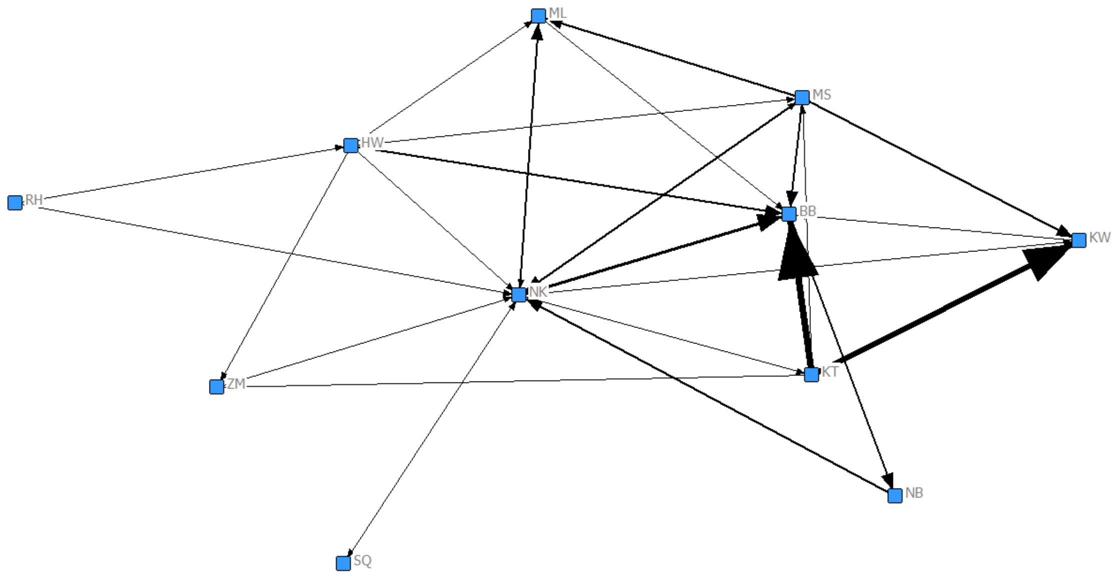

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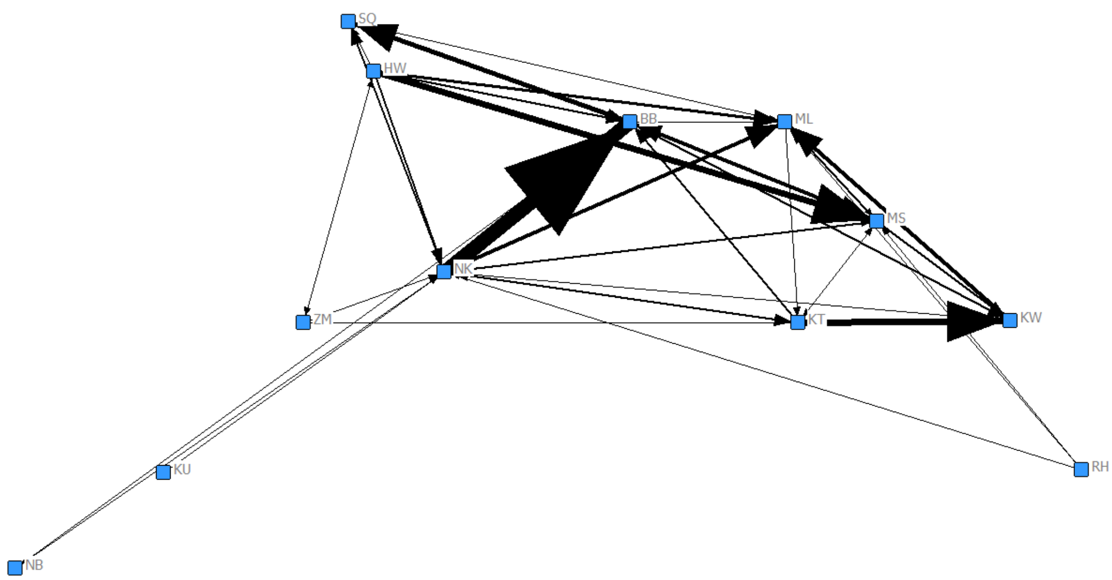

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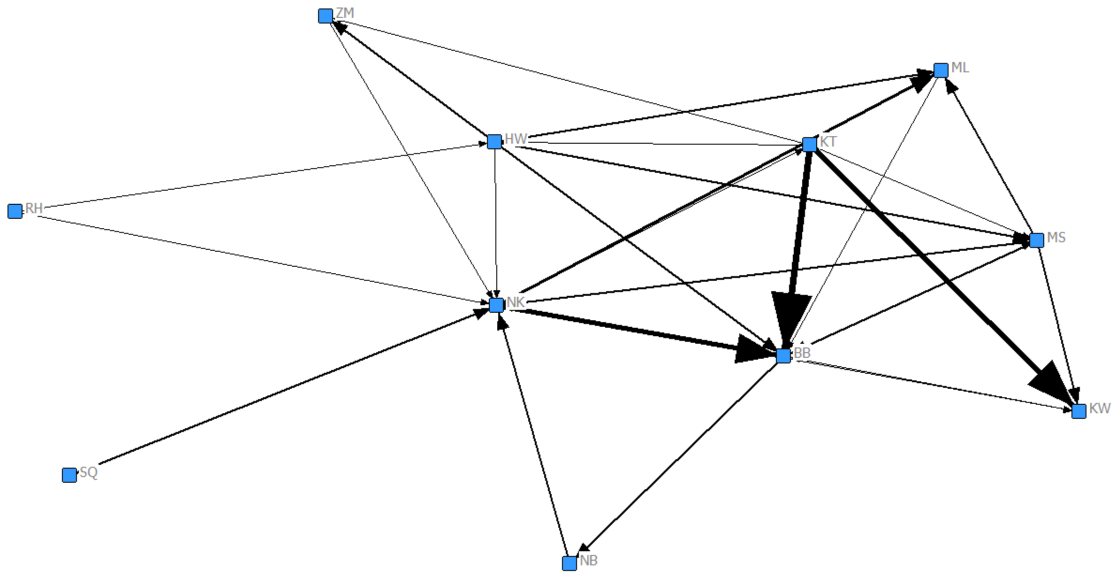

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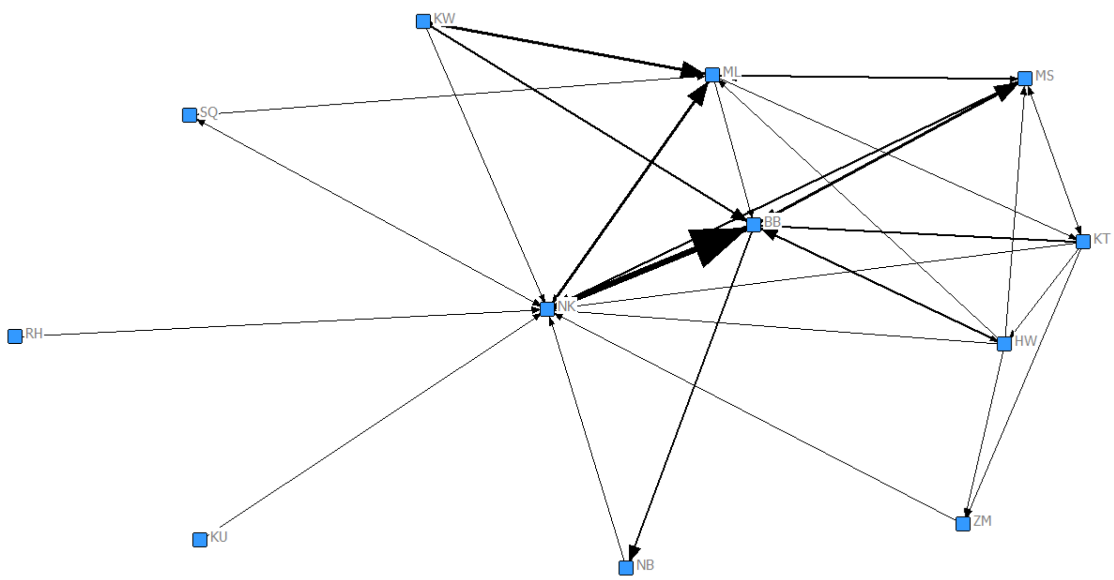
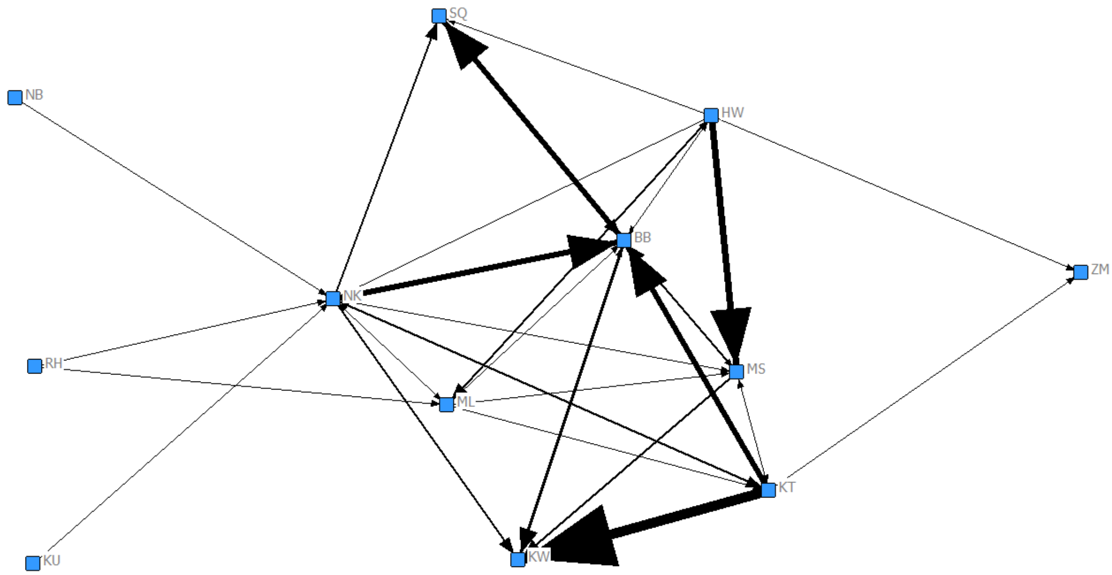
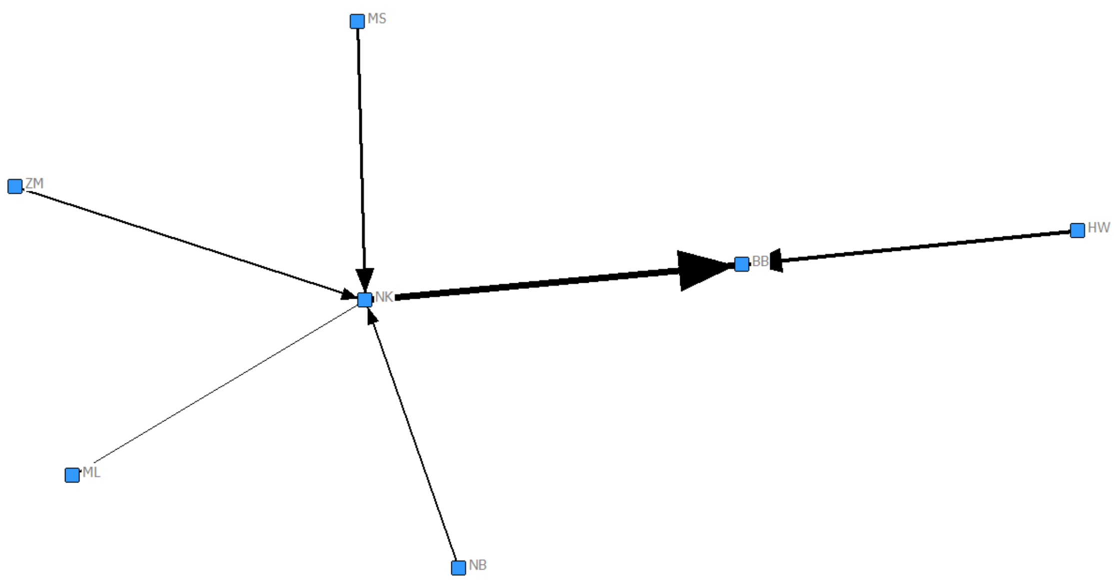


o)



p)



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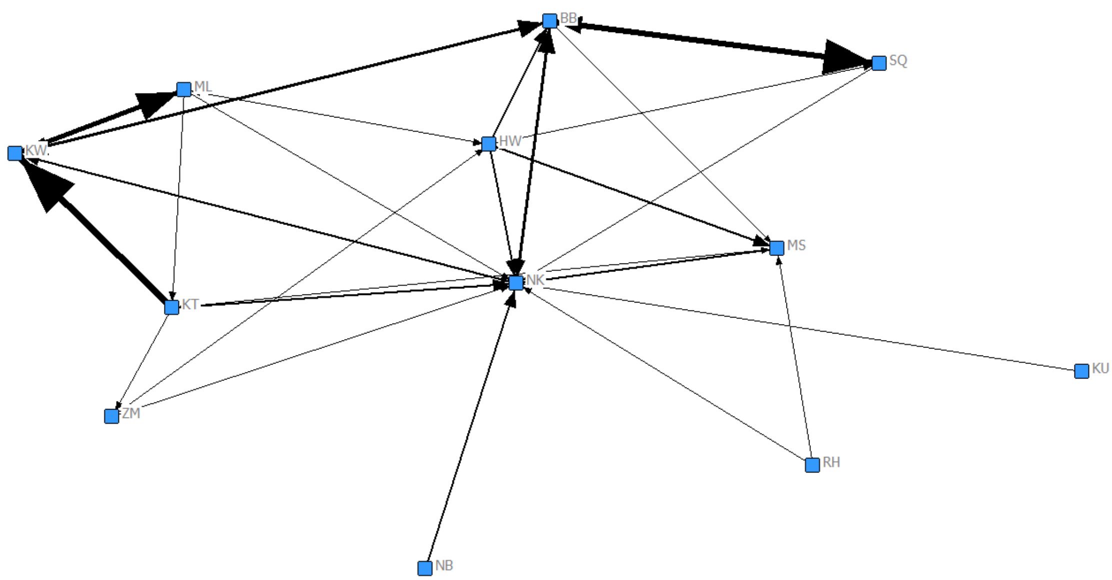

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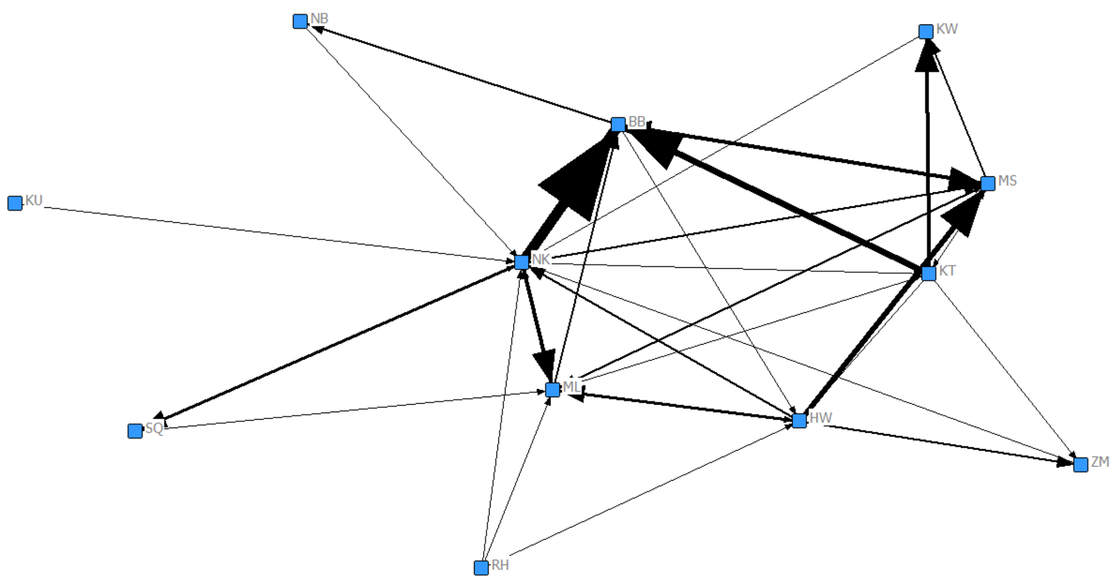
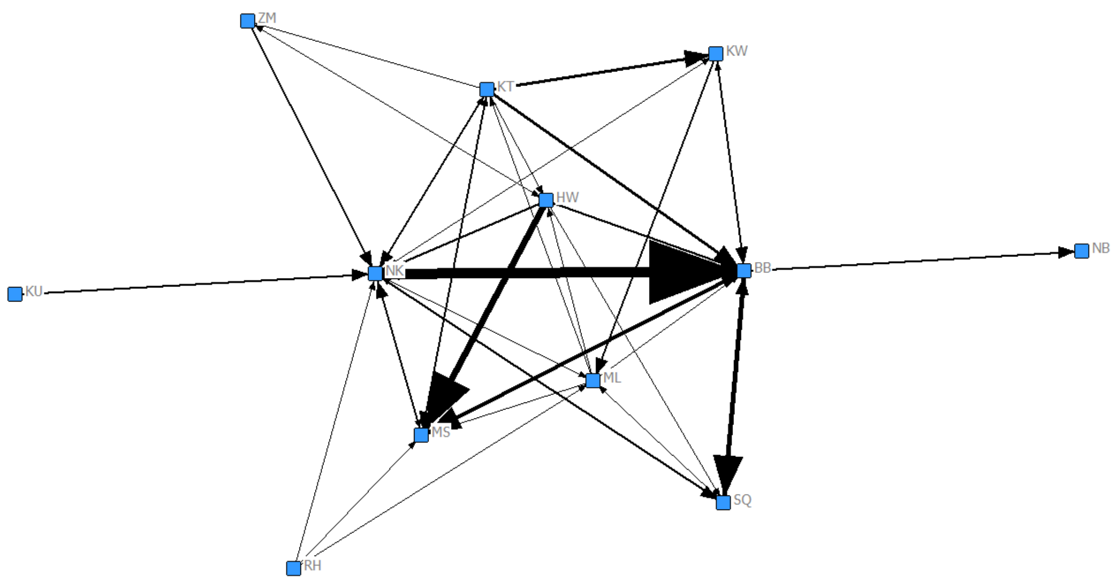
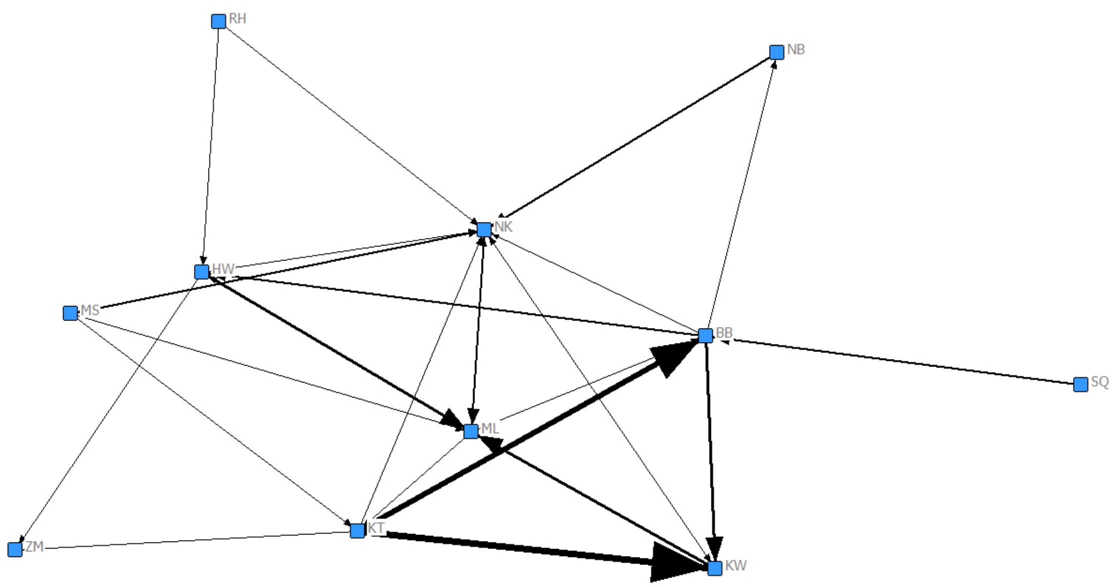


s)



t)



Supplementary Information 1

Social bonding, gestural complexity and displacement behaviour of wild chimpanzee

Table S1. Definitions, means and standard deviations (SD) for different types of gestural communication. Data based on gestural communication between 132 chimpanzee dyads. All gestural communication measured as the rate per hour dyad spent within 10 m. For detailed description of all gesture types and accompanying video footage see [Roberts et al. , 2014].

Gesture	**Definition**	**Mean**	**SD**
Gesture with no object	Gesture is produced not using object	2.56	7.14
Gesture with object	Gesture is produced using object (e.g. shake branch) [Nishida et al. , 2010]	0.88	3.12
Visual gesture	Perception of gesture is only possible by looking at the signaller	1.97	5.54
Auditory short-range gesture	Sounds produced by the gesture can be heard within 10 m of the signaller	0.41	2.33
Auditory long-range gesture	Sounds produced by the gesture can be heard over 10 m from the signaller	0.67	2.30
Tactile gesture	Perception of the gesture is possible via physical contact	0.44	2.43
Unimodal gesture	Gesture does not include accompanying facial expression or vocalization	1.79	5.81
Multimodal	Gesture accompanied by simultaneous production of	0.09	0.52

gesture (facial expression)	facial expression		
Mulitmodal gesture (vocalization)	A vocalization is produced whilst the signaller is gesturing	1.15	3.44
Dyadic repertoire size	The number of gesture types produced towards the dyad partner, per hour spent within 10 m	1.97	5.11
Single gesture	A single gesture is produced by the signaller	2.47	6.60
Combined gesture	Two or more of different gesture types are produced simultaneously by the signaller (e.g. embrace full and thrust) [Nishida et al. , 2010]	0.46	1.70
Gesture with mutual attention absent	Gesture is not accompanied by simultaneous presence of mutual bodily orientation between signaller and the recipient. Mutual bodily orientation is when signaller's and recipient's body are within each other's field of view (up to 45 degrees body turn)	0.78	3.39
Gesture with mutual attention present	Gesture is accompanied by simultaneous presence of mutual bodily orientation between signaller and the recipient.	1.23	4.15
Bodily	A gesture is produced by the signaller with the part of the body (e.g. head, legs, torso) that does not involve	2.52	6.80

	use of hands		
Manual	A gesture is made exclusively with the hand	0.93	3.19
Events	Number of consecutive gesture events in the sequence whereby gestures are made in quick succession with or without pauses for response waiting. One gesture event can contain gestures combined or not combined with other gestures (e.g. embrace full and thrust co-occurring would be counted as one event) [Nishida et al. , 2010]	3.18	7.82
Manual indicative	Movement of the arm and hand towards the recipient, without physical touch or contact with substrate	0.14	0.54
Manual non-indicative	Movement of the arm and hand that involves physical touch or contact with the substrate or visual but does not involve movement of the hand towards the recipient	0.80	3.01
Close	Signaler produced a gesture within 1 meter from the recipient	1.09	4.40
Far	Signaler produced a gesture from above 1 meter away from the recipient	1.64	5.03
Non-repetitive	A gesture that does not involve repetition of movement in regular and cyclical fashion such as static presentation of a torso for grooming	1.82	5.72
Repetitive	A gesture involves repetition of movement in regular and cyclical fashion in predictable manner that indicates	1.69	4.80

	that the movement forms part of one gesture		
Heterogeneous	Gesture type occurs only in signaller's repertoire of gestures	0.72	2.64
Homogeneous	Gesture type is present in both signaller's and recipient's repertoire of gestures	1.76	5.49
Single no sequence	A single gesture that is not made in series and where there is at least 30 seconds to the next consecutive gesture [Hobaiter and Byrne, 2011]	1.27	4.07
Rapid sequence	A series of gestures without pauses between consecutive gestures [Hobaiter and Byrne, 2011]	0.45	1.30
Persistence sequence	A series of gestures whereby there are pauses of up to 5 seconds between consecutive gestures [Hobaiter and Byrne, 2011]	0.11	0.45
Penile erection	Production of a gesture is accompanied by simultaneous erection of the penis by the signaller	0.19	0.99
Piloerection	Production of a gesture is accompanied by simultaneous involuntary erection of hairs	1.21	5.11
Threat to dominate	Aggressive context with or without physical contact, where there is no tangible reason for conflict of interest but the recipient reacts with fear (e.g. screams)	0.07	0.66
Food sharing	Context where food is in recipient's possession and in view of the signaller who makes successful or	0.002	0.031

	unsuccessful gestures in anticipation of receiving food item, e.g. beg with hand [Nishida et al. , 2010]		
Other threat	Communication motivated by clear conflict of interest, whereby there is aggression over the resource such as food or behavior such as attempt at mating.	0.07	0.36
Travel	Gestures made prior or during travel, which are followed by the recipient relocating together with the signaller, from one location in the habitat to the next.	0.03	0.33
Copulation	Gestures produced by a male or a tumescent female in order to initiate the approach for copulation.	0.14	0.79
Reassurance	Gestures produced in reaction to recipient’s distress, fright or hurt by the signallers own behaviour or third party threat.	0.08	0.87
Greeting	Gestures made in any of the following contexts: approaching, being approached or leaving approach with the individual who is non-threatening or when the recipient or third party distressed, frightened or hurt the signaller.	0.27	0.74
Mutual groom	Gestures made to initiate simultaneous grooming between signaller and the recipient.	0.07	0.66
Receive groom	Gestures made to solicit grooming of the signaller by the recipient.	0.19	0.80

Give groom	Gestures made to initiate grooming of the recipient by the signaller.	0.37	1.94
Play	Gestures which initiate bouts of wrestling, chasing, tickling in non-agonistic relaxed manner accompanied by play-face.	0.17	1.99
Synchronized low-intensity panthoot	Pant-hoot call produced jointly with other group members and accompanied by simultaneous production of visual gestures, which can be perceived only by looking at signaller.	0.05	0.36
Solo high-intensity panthoot	Pant-hoot call produced solo (without joining in by other group members) and accompanied by simultaneous production of auditory gestures, which produce sounds audible at a distance of at least 10 meters independently of the acoustic properties of the pant-hoot call. If both visual and auditory gestures simultaneously accompanied the pant-hoot call within the same sequence it was scored as high-intensity.	0.08	0.47
Synchronized high-intensity panthoot	Pant-hoot call plus simultaneous production of auditory gestures such as drumming. Vocalisation is produced jointly with other group members.	0.20	1.0

Table S2. Percentage of indicators for each behavioural categories that is significantly associated with behavioural indices of 5 domains of sociality (joint activity, grooming, visual attention, proximity and scratch).

Behaviour	Number of categories of complexity	Joint activity	Groom	Attention	Proximity	Scratch
Demography	4	41.67	25.00	37.50	25.00	25.00
Object use	2	16.67	83.33	75.00	100.00	50.00
Modality	4	41.67	75.00	50.00	75.00	50.00
Multimodal	3	22.22	55.56	66.67	100.00	66.67
Repertoire size	1	33.33	66.67	50.00	100.00	100.0p0
Combined gestures	2	16.67	50.00	75.00	50.00	50.00
Attention	2	16.67	50.00	50.00	100.00	50.00
Bodily and manual	2	16.67	66.67	25.00	50.00	100.00
Events	1	33.33	66.67	100.00	100.00	100.00
Indicative	2	16.67	66.67	25.00	50.00	50.00
Proximity	2	50.00	66.67	75.00	50.00	100.00
Repetitive	2	16.67	66.67	25.00	50.00	50.00

Homogeneity	2	16.67	66.67	75.00	50.00	50.00
Sequences	3	33.33	44.44	33.33	33.33	33.33
Penile erection	1	0.00	0.00	0.00	0.00	0.00
Piloerection	1	33.33	33.33	50.00	100.00	100.00
Function	14	16.67	33.33	39.29	35.71	10.71

Association between the duration of social behavior and gestural communication categorized according to structure

Demographic Factors

Supplementary Table S3. MRQAP regression models predicting durations of social behavior, per hour dyad spent within 10m. Predictors were demographic variables. Dyads were classified as same age or different age (within 5 years), same sex or different sex, related by maternal kinship and as the same or different reproductive status (reproductively active, not reproductively active). Based on 132 dyadic relationships of the chimpanzees. Significant *p* values are indicated in bold. R squared (r^2) denotes amount of variance in the dependent variable explained by the regression model.

Table S3.1 Duration of joint feeding behaviour (r^2 = 0.119)

	Standardized coefficient	Standard error	*p*
Age	-0.01	0.65	0.49
Sex	0.31	0.69	**0.001**

Kinship	0.29	1.28	**0.01**
Reproductive status	0.22	0.72	**0.04**

Table S3.2 Duration of joint resting behaviour (r^2 = 0.070)

	Standardized coefficient	Standard error	*p*
Age	0.29	1.37	**0.003**
Sex	-0.14	1.31	0.13
Kinship	-0.02	2.25	0.47
Reproductive status	-0.04	1.46	0.36

Table S3.3 Duration of joint travelling behaviour (r^2 = 0.09)

	Standardized coefficient	Standard error	*p*
Age	0.28	0.42	**0.01**
Sex	0.05	0.39	0.68
Kinship	0.01	0.72	0.86
Reproductive status	0.01	0.43	0.93

Table S3.4 Duration of giving grooming (r^2 = 0.07)

	Standardized	Standard error	*p*

	coefficient		
Age	0.21	0.54	**0.02**
Sex	0.11	0.53	0.18
Kinship	0.10	0.96	0.12
Reproductive status	0.03	0.66	0.42

Table S3.5 Duration of mutual grooming ($r^2 = 0.04$)

	Standardized coefficient	Standard error	*p*
Age	0.20	0.70	**0.050**
Sex	0.02	0.72	0.49
Kinship	0.02	1.29	0.29
Reproductive status	0.14	0.87	0.18

Table S3.6 Duration of receiving grooming ($r^2 = 0.03$)

	Standardized coefficient	Standard error	*p*
Age	-0.09	0.48	0.18
Sex	0.20	0.51	**0.03**
Kinship	-0.01	0.88	0.62
Reproductive status	0.08	0.63	0.28

Table S3.7 Duration of visual attention towards dyad partner (r^2 = 0.11)

	Standardized coefficient	Standard error	*p*
Age	0.12	1.47	0.13
Sex	0.30	1.55	**0.01**
Kinship	0.18	2.62	0.06
Reproductive status	0.28	2.12	**0.04**

Table S3.8 Duration of visual attention away dyad partner (r^2 = 0.12)

	Standardized coefficient	Standard error	*p*
Age	0.367	1.730	**0.001**
Sex	-0.064	1.277	0.251
Kinship	0.071	2.783	0.145
Reproductive status	0.041	1.395	0.370

Table S3.9 Duration of time in close proximity – within 2 m (r^2 = 0.11)

	Standardized coefficient	Standard error	*p*
Age	0.32	2.50	**0.0005**
Sex	0.12	2.49	0.15
Kinship	0.15	4.39	0.06

Reproductive status	0.14	3.55	0.19

Table S3.10 Rate of scratch produced (r^2 = 0.046)

	Standardized coefficient	Standard error	*p*
Age	0.016	0.606	0.41829
Sex	0.201	0.560	**0.03948**
Kinship	0.079	1.143	0.18341
Reproductive status	0.030	0.423	0.38131

Table S3.11 Rate of scratch received (r^2 = 0.046)

	Standardized coefficient	Standard error	*p*
Age	0.02	0.61	0.42779
Sex	0.20	0.56	**0.04348**
Kinship	0.08	1.14	0.18991
Reproductive status	0.03	0.44	0.37481

Object use in gestural communication

Supplementary Table S4. MRQAP regression models predicting durations of social behavior, per hour dyad spent within 10m. Predictor variables were rates of gestural communication (without objects and with objects) and demographic variables. Based on 132 chimpanzee dyads. Significant *p* values are indicated in bold. R squared (r^2) denotes amount of variance in the dependent variable explained by the regression model.

Table S4.1 Duration of joint feeding behaviour (r^2 = 0.12)

	Standardized coefficient	Standard error	*p*
Age	-0.01	0.68	0.47
Sex	0.31	0.70	**0.003**
Kinship	0.29	1.35	**0.009**
Reproductive status	0.22	0.76	**0.047**
Object use	-0.01	0.08	0.56
No object use	0.03	0.04	0.30

Table S4.2 Duration of joint resting behaviour (r^2 = 0.08)

	Standardized coefficient	Standard error	*p*
Age	0.28	1.45	**0.01**
Sex	-0.16	1.37	0.10
Kinship	-0.02	2.41	0.42
Reproductive status	-0.05	1.45	0.35
Object use	-0.08	0.18	0.07

No object use	0.10	0.08	0.07

Table S4.3 Duration of joint travelling behaviour (r^2 = 0.29)

	Standardized coefficient	Standard error	*p*
Age	0.21	0.35	**0.01**
Sex	-0.01	0.32	0.44
Kinship	0.02	0.58	0.25
Reproductive status	-0.01	0.32	0.46
Object use	-0.04	0.04	0.24
No object use	0.47	0.02	**0.005**

Table S4.4 Duration of giving grooming (r^2 = 0.39)

	Standardized coefficient	Standard error	*p*
Age	0.12	0.45	0.08
Sex	0.02	0.44	0.41
Kinship	0.10	0.85	0.08
Reproductive status	0.00	0.46	0.47
Object use	-0.20	0.06	**0.01**
No object use	0.64	0.04	**0.001**

Table S4.5 Duration of mutual grooming (r^2 = 0.38)

	Standardized coefficient	Standard error	*p*
Age	0.11	0.55	0.10
Sex	-0.07	0.53	0.24
Kinship	0.02	1.00	0.26
Reproductive status	0.10	0.58	0.12
Object use	-0.15	0.07	**0.02**
No object use	0.64	0.04	**0.0005**

Table S4.6 Duration of receiving grooming (r^2 = 0.07)

	Standardized coefficient	Standard error	*p*
Age	-0.12	0.49	0.09
Sex	0.17	0.49	0.05
Kinship	0.00	0.91	0.66
Reproductive status	0.07	0.56	0.27
Object use	-0.04	0.06	0.34
No object use	0.22	0.03	**0.04**

Table S4.7 Duration of visual attention towards dyad partner (r^2 = 0.49)

	Standardized coefficient	Standard error	*p*

Age	0.02	1.10	0.39
Sex	0.20	1.12	**0.01**
Kinship	0.19	2.11	**0.01**
Reproductive status	0.24	1.42	**0.01**
Object use	-0.18	0.14	**0.003**
No object use	0.69	0.10	**0.0005**

Table S4.8 Duration of visual attention away from dyad partner ($r^2 = 0.16$)

	Standardized coefficient	Standard error	*p*
Age	0.335	1.671	**0.002**
Sex	-0.083	1.277	0.180
Kinship	0.069	2.892	0.138
Reproductive status	0.003	1.271	0.517
Object use	-0.098	0.202	0.070
No object use	0.240	0.097	**0.028**

Table S4.9 Duration of time in close proximity – within 2 m ($r^2 = 0.37$)

	Standardized coefficient	Standard error	*p*
Age	0.24	2.05	**0.001**

Sex	0.04	2.05	0.32
Kinship	0.15	3.60	**0.03**
Reproductive status	0.11	2.54	0.17
Object use	-0.17	0.26	**0.003**
No object use	0.56	0.15	**0.0005**

Table S4.10 Rate of scratch produced (r^2 = 0.190)

	Standardized coefficient	Standard error	*p*
Age	-0.043	0.591	0.35782
Sex	0.175	0.525	0.05097
Kinship	0.085	1.162	0.17541
Reproductive status	-0.031	0.438	0.33633
Object use	-0.016	0.072	0.49375
No object use	0.400	0.034	**0.0045**

Table S4.11 Rate of scratch received (r^2 = 0.050)

	Standardized coefficient	Standard error	*p*
Age	0.03	0.63	0.38331

Sex	0.20	0.57	**0.03998**
Kinship	0.08	1.12	0.17841
Reproductive status	0.04	0.45	0.30585
Object use	-0.01	0.08	0.56822
No object use	-0.06	0.03	0.26087

Modality of gestural communication

Supplementary Table S5. MRQAP regression models predicting durations of social behavior, per hour dyad spent within 10m. Predictor variables were rates of gestural communication of different modalities (visual, tactile, auditory short-range, auditory long-range) and demographic variables. Based on 132 chimpanzee dyads. Significant *p* values are indicated in bold. R squared (r^2) denotes amount of variance in the dependent variable explained by the regression model.

Table S5.1 Duration of joint feeding behaviour (r^2 = 0.17)

	Standardized coefficient	Standard error	*p*
Age	-0.07	0.68	0.27
Sex	0.33	0.70	**0.002**
Kinship	0.29	1.30	**0.01**
Reproductive status	0.21	0.71	**0.03**
Visual gestures	0.15	0.07	0.12

Auditory long-range gestures	-0.08	0.13	0.21
Auditory short-range gestures	0.21	0.11	**0.04**
Tactile gestures	-0.22	0.13	**0.004**

Table S5.2 Duration of joint resting behaviour (r^2 = 0.09)

	Standardized coefficient	Standard error	*p*
Age	0.26	1.43	**0.01**
Sex	-0.16	1.38	0.10
Kinship	-0.03	2.43	0.39
Reproductive status	-0.05	1.51	0.33
Visual gestures	0.02	0.15	0.36
Auditory long-range gestures	-0.06	0.34	0.21
Auditory short-range gestures	0.13	0.24	**0.04**
Tactile gestures	0.004	0.29	0.36

Table S5.3 Duration of joint travelling behaviour (r^2 = 0.32)

	Standardized coefficient	Standard error	*p*

Age	0.21	0.33	**0.01**
Sex	0.04	0.30	0.36
Kinship	0.02	0.58	0.25
Reproductive status	0.00	0.30	0.50
Visual gestures	0.62	0.04	**0.01**
Auditory long-range gestures	-0.28	0.08	**0.01**
Auditory short-range gestures	0.04	0.05	0.11
Tactile gestures	-0.02	0.07	0.43

Table S5.4 Duration of giving grooming (r^2 = 0.74)

	Standardized coefficient	Standard error	*p*
Age	0.06	0.27	0.11
Sex	-0.02	0.27	0.38
Kinship	0.09	0.47	**0.03**
Reproductive status	0.00	0.33	0.46
Visual gestures	-0.26	0.04	**0.01**
Auditory long-range gestures	0.19	0.08	**0.01**
Auditory short-	0.73	0.09	**0.0005**

range gestures			
Tactile gestures	0.41	0.08	**0.0005**

Table S5.5 Duration of mutual grooming ($r^2 = 0.48$)

	Standardized coefficient	Standard error	*p*
Age	0.12	0.49	0.07
Sex	-0.01	0.49	0.47
Kinship	0.03	0.87	0.27
Reproductive status	0.12	0.53	0.08
Visual gestures	0.88	0.07	**0.0005**
Auditory long-range gestures	-0.51	0.12	**0.0005**
Auditory short-range gestures	0.01	0.08	0.25
Tactile gestures	-0.03	0.10	0.37

Table S5.6 Duration of receiving grooming ($r^2 = 0.11$)

	Standardized coefficient	Standard error	*p*
Age	-0.15	0.50	**0.04**
Sex	0.21	0.49	**0.02**
Kinship	0.00	0.91	0.32

Reproductive status	0.07	0.56	0.24
Visual gestures	0.50	0.06	**0.02**
Auditory long-range gestures	-0.27	0.13	**0.02**
Auditory short-range gestures	0.04	0.08	0.11
Tactile gestures	-0.20	0.12	**0.0005**

Table S5.7 Duration of visual attention towards dyad partner (r^2 = 0.21)

	Standardized coefficient	Standard error	*p*
Age	-0.01	1.06	0.47
Sex	0.25	1.13	**0.004**
Kinship	0.19	1.97	**0.007**
Reproductive status	0.26	1.40	**0.007**
Visual gestures	0.75	0.15	**0.0005**
Auditory long-range gestures	-0.44	0.25	**0.0005**
Auditory short-range gestures	0.24	0.19	**0.01**
Tactile gestures	-0.02	0.22	0.50

Table S5.8 Duration of visual attention away from dyad partner (r^2 = 0.20)

	Standardized coefficient	Standard error	*p*
Age	0.296	1.683	**0.004**
Sex	-0.083	1.347	0.178
Kinship	0.064	2.799	0.129
Reproductive status	0.001	1.338	0.496
Auditory long-range gestures	-0.032	0.368	0.412
Auditory short-range gestures	0.290	0.285	**0.011**
Tactile gestures	0.031	0.366	0.247
Visual gestures	0.033	0.179	0.327

Table S5.9 Duration of time in close proximity – within 2 m (r^2 = 0.40)

	Standardized coefficient	Standard error	*p*
Age	0.20	2.05	**0.01**
Sex	0.07	2.05	0.22
Kinship	0.15	3.65	**0.03**
Reproductive status	0.12	2.59	0.15
Visual gestures	0.45	0.28	**0.01**

Auditory long-range gestures	-0.27	0.48	**0.01**
Auditory short-range gestures	0.34	0.39	**0.01**
Tactile gestures	0.01	0.42	0.33

Table S5.10 Rate of scratch produced (r^2 = 0.201)

	Standardized coefficient	Standard error	*p*
Age	-0.064	0.601	0.27286
Sex	0.208	0.529	**0.02699**
Kinship	0.090	1.128	0.14893
Reproductive status	-0.019	0.430	0.41979
Visual gestures	0.484	0.071	**0.0085**
Auditory long-range gestures	-0.163	0.126	**0.04698**
Auditory short-range gestures	0.127	0.100	0.07496
Tactile gestures	-0.072	0.120	0.2014

Table S5.11 Rate of scratch received (r^2 = 0.060)

	Standardized coefficient	Standard error	*p*
Age	0.03	0.65	0.34983
Sex	0.21	0.60	**0.03448**
Kinship	0.08	1.23	0.18041
Reproductive status	0.04	0.45	0.29135
Visual gestures	0.08	0.07	0.22539
Auditory long-range gestures	-0.08	0.14	0.23138
Auditory short-range gestures	-0.10	0.10	**0.04948**
Tactile gestures	-0.07	0.13	0.27186

Unimodal and multimodal gestural communication

Supplementary Table S6. MRQAP regression models predicting durations of social behavior, per hour dyad spent within 10m. Predictor variables were rates of unimodal and multi-modal gestural communication and demographic variables. Based on 132 chimpanzee dyads. Significant *p* values are indicated in bold. R squared (r^2) denotes amount of variance in the dependent variable explained by the regression model.

Table S6.1 Duration of joint feeding behaviour (r^2 = 0.14)

	Standardized coefficient	Standard error	*p*
Age	-0.01	0.69	0.47
Sex	0.31	0.68	**0.002**
Kinship	0.28	1.29	**0.01**
Reproductive status	0.20	0.73	**0.04**
Unimodal gestures	0.16	0.05	0.07
Multimodal (facial expressions)	-0.13	0.53	0.09
Multimodal (vocalisations)	-0.07	0.07	0.23

Table S6.2 Duration of joint resting behaviour (r^2 = 0.08)

	Standardized coefficient	Standard error	*p*
Age	0.28	1.45	**0.004**
Sex	-0.16	1.36	0.10
Kinship	-0.02	2.41	0.41
Reproductive status	-0.06	1.48	0.36
Unimodal gestures	0.06	0.11	0.19
Multimodal (facial	0.06	1.12	0.15

expressions)			
Multimodal (vocalisations)	-0.06	0.16	0.20

Table S6.3 Duration of joint travelling behaviour (r^2 = 0.31)

	Standardized coefficient	Standard error	*p*
Age	0.24	0.34	**0.01**
Sex	-0.01	0.31	0.41
Kinship	0.02	0.62	0.25
Reproductive status	-0.02	0.32	0.43
Unimodal gestures	0.22	0.03	**0.02**
Multimodal (facial expressions)	0.30	0.31	**0.02**
Multimodal (vocalisations)	0.01	0.04	0.30

Table S6.4 Duration of giving grooming (r^2 = 0.46)

	Standardized coefficient	Standard error	*p*
Age	0.13	0.38	**0.03**
Sex	0.05	0.38	0.24

Kinship	0.11	0.72	0.05
Reproductive status	-0.02	0.42	0.39
Unimodal gestures	0.75	0.04	**0.0005**
Multimodal (facial expressions)	-0.23	0.40	**0.01**
Multimodal (vocalisations)	-0.07	0.05	0.09

Table S6.5 Duration of mutual grooming ($r^2 = 0.42$)

	Standardized coefficient	Standard error	*p*
Age	0.15	0.54	**0.04**
Sex	-0.07	0.52	0.21
Kinship	0.02	0.94	0.29
Reproductive status	0.09	0.57	0.16
Unimodal gestures	0.27	0.04	**0.02**
Multimodal (facial expressions)	0.44	0.47	**0.002**
Multimodal	-0.03	0.06	0.33

(vocalisations)			

Table S6.6 Duration of receiving grooming ($r^2 = 0.08$)

	Standardized coefficient	Standard error	*p*
Age	-0.11	0.52	0.12
Sex	0.17	0.52	0.06
Kinship	0.00	0.93	0.65
Reproductive status	0.04	0.61	0.36
Unimodal gestures	0.25	0.04	**0.04**
Multimodal (facial expressions)	0.001	0.44	0.43
Multimodal (vocalisations)	-0.09	0.05	0.06

Table S6.7 Duration of visual attention towards dyad partner ($r^2 = 0.50$)

	Standardized coefficient	Standard error	*p*
Age	0.06	1.06	0.21
Sex	0.20	1.11	**0.01**
Kinship	0.19	1.98	**0.01**

Reproductive status	0.22	1.46	**0.02**
Unimodal gestures	0.44	0.09	**0.0005**
Multimodal (facial expressions)	0.31	0.93	**0.003**
Multimodal (vocalisations)	-0.09	0.12	**0.05**

Table S6.8 Duration of visual attention away from dyad partner (r^2 = 0.17)

	Standardized coefficient	Standard error	*p*
Age	0.344	1.712	**0.001**
Sex	-0.065	1.286	0.254
Kinship	0.071	2.929	0.142
Reproductive status	-0.003	1.331	0.471
Multimodal (facial expressions)	-0.043	1.405	0.295
Multimodal (vocalisations)	-0.076	0.195	0.123

Unimodal gestures	0.270	0.132	**0.024**

Table S6.9 Duration of time in close proximity – within 2 m (r^2 = 0.37)

	Standardized coefficient	Standard error	*p*
Age	0.27	2.07	**0.002**
Sex	0.05	2.01	0.31
Kinship	0.15	3.55	**0.03**
Reproductive status	0.09	2.54	0.22
Unimodal gestures	0.44	0.17	**0.001**
Multimodal (facial expressions)	0.14	1.69	**0.05**
Multimodal (vocalisations)	-0.11	0.23	**0.04**

Table S6.10 Rate of scratch produced (r^2 = 0.191)

	Standardized coefficient	Standard error	*p*
Age	-0.029	0.593	0.37781
Sex	0.171	0.536	0.05847

Kinship	0.089	1.098	0.14393
Reproductive status	-0.018	0.448	0.43278
Unimodal gestures	0.180	0.045	**0.04948**
Multimodal (facial expressions)	0.184	0.489	**0.04298**
Multimodal (vocalisations)	0.138	0.065	0.06597

Table S6.11 Rate of scratch received (r^2 = 0.056)

	Standardized coefficient	Standard error	*p*
Age	0.03	0.65	0.38331
Sex	0.20	0.56	**0.03448**
Kinship	0.08	1.18	0.2004
Reproductive status	0.04	0.47	0.29685
Unimodal gestures	-0.12	0.05	0.11894
Multimodal (facial	0.06	0.52	0.26737

expressions)			
Multimodal (vocalisations)	0.00	0.07	0.45377

Dyadic repertoire size

Supplementary Table S7. MRQAP regression models predicting durations of social behavior, per hour dyad spent within 10m. Predictor variables were dyadic repertoire size, per hour dyad spent within 10m and demographic variables. Based on 132 chimpanzee dyads. Significant *p* values are indicated in bold. R squared (r^2) denotes amount of variance in the dependent variable explained by the regression model.

Table S7.1 Duration of joint feeding behaviour (r^2 = 0.12)

	Standardized coefficient	Standard error	*p*
Age	-0.01	0.65	0.49
Sex	0.31	0.68	**0.0005**
Kinship	0.28	1.32	**0.01**
Reproductive status	0.22	0.75	**0.04**
Dyadic repertoire size	-0.02	0.04	0.45

Table S7.2 Duration of joint resting behaviour (r^2 = 0.07)

	Standardized coefficient	Standard error	*p*
Age	0.29	1.43	**0.003**

Sex	-0.14	1.30	0.13
Kinship	-0.02	2.58	0.43
Reproductive status	-0.04	1.45	0.36
Dyadic repertoire size	0.001	0.10	0.38

Table S7.3 Duration of joint travelling behaviour (r^2 = 0.21)

	Standardized coefficient	Standard error	*p*
Age	0.25	0.38	**0.01**
Sex	0.05	0.34	0.36
Kinship	0.03	0.66	0.24
Reproductive status	0.02	0.36	0.41
Dyadic repertoire size	0.34	0.03	**0.01**

Table S7.4 Duration of giving grooming (r^2 = 0.13)

	Standardized coefficient	Standard error	*p*
Age	0.18	0.53	**0.02**
Sex	0.10	0.52	0.17
Kinship	0.11	0.97	0.11

Reproductive status	0.04	0.60	0.37
Dyadic repertoire size	0.26	0.04	**0.02**

Table S7.5 Duration of mutual grooming (r^2 = 0.24)

	Standardized coefficient	Standard error	*p*
Age	0.16	0.60	**0.05**
Sex	0.01	0.59	0.51
Kinship	0.04	1.11	0.22
Reproductive status	0.15	0.68	0.11
Dyadic repertoire size	0.45	0.05	**0.003**

Table S7.6 Duration of receiving grooming (r^2 = 0.04)

	Standardized coefficient	Standard error	*p*
Age	-0.10	0.49	0.13
Sex	0.20	0.50	**0.03**
Kinship	0.00	0.87	0.33
Reproductive status	0.08	0.60	0.24

Dyadic repertoire size	0.14	0.04	0.08

Table S7.7 Duration of visual attention towards dyad partner (r^2 = 0.28)

	Standardized coefficient	Standard error	*p*
Age	0.08	1.24	0.16
Sex	0.29	1.38	**0.002**
Kinship	0.21	2.50	**0.02**
Reproductive status	0.29	1.87	**0.02**
Dyadic repertoire size	0.42	0.11	**0.002**

Table S7.8 Duration of visual attention away from dyad partner (r^2 = 0.12)

	Standardized coefficient	Standard error	*p*
Age	0.361	1.687	**0.001**
Sex	-0.065	1.276	0.255
Kinship	0.074	2.826	0.129
Reproductive status	0.036	1.371	0.370
Dyadic repertoire size	0.063	0.119	0.164

Table S7.9 Duration of time in close proximity – within 2 m (r^2 = 0.21)

	Standardized coefficient	Standard error	*p*
Age	0.29	2.38	**0.001**
Sex	0.11	2.27	0.15
Kinship	0.16	4.12	**0.03**
Reproductive status	0.15	3.25	0.14
Dyadic repertoire size	0.28	0.20	**0.01**

Table S7.10 Rate of scratch produced (r^2 = 0.167)

	Standardized coefficient	Standard error	*p*
Age	-0.016	0.583	0.43878
Sex	0.193	0.529	**0.03398**
Kinship	0.096	1.076	0.13343
Reproductive status	0.008	0.417	0.45527
Dyadic repertoire size	0.352	0.042	**0.002**

Table S7.11 Rate of scratch received (r^2 = 0.048)

	Standardized coefficient	Standard error	*p*
Age	0.02	0.62	0.42829
Sex	0.20	0.55	**0.03698**
Kinship	0.08	1.21	0.21039
Reproductive status	0.03	0.44	0.38131
Dyadic repertoire size	-0.04	0.04	0.33483

Single and combined gestures

Supplementary Table S8. MRQAP regression models predicting durations of social behavior, per hour dyad spent within 10m. Predictor variables were rates of single and combined gestures, per hour dyad spent within 10m and demographic variables. Based on 132 chimpanzee dyads. Significant *p* values are indicated in bold. R squared (r^2) denotes amount of variance in the dependent variable explained by the regression model.

Table S8.1 Duration of joint feeding behaviour (r^2 = 0.12)

	Standardized coefficient	Standard error	*p*
Age	-0.01	0.71	0.47
Sex	0.31	0.68	**0.001**
Kinship	0.29	1.34	**0.01**
Reproductive status	0.22	0.77	**0.048**
Combined gesture	0.01	0.16	0.43

Single gesture	0.02	0.04	0.42

Table S8.2 Duration of joint resting behaviour (r^2 = 0.07)

	Standardized coefficient	Standard error	*p*
Age	0.28	1.38	**0.002**
Sex	-0.15	1.32	0.11
Kinship	-0.02	2.50	0.46
Reproductive status	-0.04	1.47	0.37
Combined gesture	-0.03	0.34	0.37
Single gesture	0.06	0.10	0.17

Table S8.3 Duration of joint travelling behaviour (r^2 = 0.31)

	Standardized coefficient	Standard error	*p*
Age	0.23	0.35	**0.01**
Sex	0.05	0.32	0.31
Kinship	0.03	0.64	0.24
Reproductive status	-0.01	0.32	0.44
Combined gesture	0.41	0.09	**0.004**

Single gesture	0.09	0.02	0.12

Table S8.4 Duration of giving grooming ($r^2 = 0.35$)

	Standardized coefficient	Standard error	*p*
Age	0.13	0.47	0.06
Sex	0.06	0.46	0.25
Kinship	0.11	0.84	0.07
Reproductive status	0.06	0.51	0.30
Combined gesture	-0.19	0.12	**0.02**
Single gesture	0.64	0.04	**0.001**

Table S8.5 Duration of mutual grooming ($r^2 = 0.32$)

	Standardized coefficient	Standard error	*p*
Age	0.14	0.57	0.07
Sex	0.00	0.53	0.52
Kinship	0.04	1.04	0.23
Reproductive status	0.11	0.61	0.13
Combined gesture	0.40	0.16	**0.003**
Single gesture	0.19	0.04	0.05

Table S8.6 Duration of receiving grooming (r^2 = 0.06)

	Standardized coefficient	Standard error	*p*
Age	-0.11	0.49	0.11
Sex	0.19	0.49	**0.02**
Kinship	0.00	0.85	0.29
Reproductive status	0.07	0.58	0.28
Combined gesture	0.13	0.15	0.11
Single gesture	0.08	0.04	0.18

Table S8.7 Duration of visual attention towards dyad partner (r^2 = 0.38)

	Standardized coefficient	Standard error	*p*
Age	0.05	1.19	0.28
Sex	0.28	1.26	**0.002**
Kinship	0.21	2.23	**0.01**
Reproductive status	0.27	1.65	**0.01**
Combined gesture	0.30	0.30	**0.002**
Single gesture	0.29	0.09	**0.004**

Table S8.8 Duration of visual attention away from dyad partner (r^2 = 0.14)

	Standardized coefficient	Standard error	*p*
Age	0.341	1.724	**0.001**
Sex	-0.076	1.319	0.215
Kinship	0.075	2.879	0.123
Reproductive status	0.026	1.379	0.419
Combined gesture	-0.029	0.422	0.385
Single gesture	0.183	0.112	**0.045**

Table S8.9 Duration of time in close proximity – within 2 m (r^2 = 0.28)

	Standardized coefficient	Standard error	*p*
Age	0.26	2.24	**0.003**
Sex	0.10	2.33	0.38
Kinship	0.17	4.09	**0.05**
Reproductive status	0.14	2.96	0.29
Combined gesture	0.29	0.16	**0.01**
Single gesture	0.15	0.58	0.10

Table S8.10 Rate of scratch produced (r^2 = 0.179)

	Standardized coefficient	Standard error	*p*
Age	-0.037	0.596	0.33833
Sex	0.194	0.530	**0.03348**
Kinship	0.093	1.110	0.14993
Reproductive status	-0.014	0.420	0.45027
Combined gesture	0.155	0.154	0.06747
Single gesture	0.259	0.039	**0.01649**

Table S8.11 Rate of scratch received (r^2 = 0.051)

	Standardized coefficient	Standard error	*p*
Age	0.03	0.64	0.38431
Sex	0.21	0.58	**0.03248**
Kinship	0.08	1.19	0.18541
Reproductive status	0.03	0.44	0.33133
Combined gesture	0.09	0.16	0.18041
Single gesture	-0.14	0.04	0.05497

Mutual attention accompanying gestures

Supplementary Table S9. MRQAP regression models predicting durations of social behavior, per hour dyad spent within 10m. Predictor variables were rates of gestures with and without mutual attention between the recipient and the signaller, per hour dyad spent within 10m and demographic variables. Based on 132 chimpanzee dyads. Significant *p* values are indicated in bold. R squared (r^2) denotes amount of variance in the dependent variable explained by the regression model.

Table S9.1 Duration of joint feeding behaviour (r^2 = 0.12)

	Standardized coefficient	Standard error	*p*
Age	-0.01	0.68	0.48
Sex	0.31	0.69	**0.002**
Kinship	0.29	1.31	**0.01**
Reproductive status	0.21	0.76	0.05
Gesture with mutual attention	0.05	0.06	0.26
Gesture without mutual attention	-0.04	0.08	0.38

Table S9.2 Duration of joint resting behaviour (r^2 = 0.08)

	Standardized coefficient	Standard error	*p*
Age	0.28	1.41	**0.01**
Sex	-0.16	1.32	0.10
Kinship	-0.02	2.41	0.44

Reproductive status	-0.05	1.50	0.35
Gesture with mutual attention	0.004	0.16	0.37
Gesture without mutual attention	0.10	0.19	0.08

Table S9.3 Duration of joint travelling behaviour (r^2 = 0.28)

	Standardized coefficient	Standard error	*p*
Age	0.23	0.36	**0.01**
Sex	-0.02	0.32	0.40
Kinship	0.02	0.60	0.29
Reproductive status	-0.03	0.31	0.39
Gesture with mutual attention	0.37	0.04	**0.01**
Gesture without mutual attention	0.12	0.04	0.07

Table S9.4 Duration of giving grooming (r^2 = 0.57)

	Standardized coefficient	Standard error	*p*
Age	0.16	0.39	**0.01**

Sex	-0.01	0.39	0.45
Kinship	0.10	0.72	0.07
Reproductive status	0.01	0.43	0.45
Gesture with mutual attention	-0.11	0.04	**0.04**
Gesture without mutual attention	0.78	0.07	**0.0005**

Table S9.5 Duration of mutual grooming (r^2 = 0.42)

	Standardized coefficient	Standard error	*p*
Age	0.14	0.49	0.06
Sex	-0.07	0.49	0.41
Kinship	0.03	0.94	0.68
Reproductive status	0.08	0.49	0.32
Gesture with mutual attention	0.63	0.07	**0.001**
Gesture without mutual attention	-0.01	0.06	0.78

Table S9.6 Duration of receiving grooming (r^2 = 0.07)

	Standardized	Standard error	*p*

	coefficient		
Age	-0.11	0.49	0.10
Sex	0.17	0.48	0.051
Kinship	0.00	0.86	0.67
Reproductive status	0.06	0.55	0.30
Gesture with mutual attention	0.21	0.06	0.054
Gesture without mutual attention	0.02	0.06	0.24

Table S9.7 Duration of visual attention towards dyad partner ($r^2 = 0.49$)

	Standardized coefficient	Standard error	*p*
Age	0.06	1.03	0.23
Sex	0.20	1.07	**0.01**
Kinship	0.19	1.99	**0.01**
Reproductive status	0.22	1.33	**0.02**
Gesture with mutual attention	0.56	0.14	**0.0005**
Gesture without mutual attention	0.12	0.13	0.07

Table S9.8 Duration of visual attention away from dyad partner ($r^2 = 0.19$)

	Standardized coefficient	Standard error	*p*
Age	0.348	1.662	**0.001**
Sex	-0.094	1.299	0.142
Kinship	0.068	2.725	0.130
Reproductive status	0.003	1.329	0.494
Gesture with mutual attention	-0.032	0.167	0.384
Gesture without mutual attention	0.288	0.201	**0.015**

Table S9.9 Duration of time in close proximity – within 2 m (r^2 = 0.36)

	Standardized coefficient	Standard error	*p*
Age	0.27	2.10	**0.002**
Sex	0.03	2.06	0.75
Kinship	0.15	3.73	**0.04**
Reproductive status	0.10	2.57	0.36
Gesture with mutual attention	0.30	0.24	**0.01**
Gesture without mutual attention	0.26	0.26	**0.01**

Table S9.10 Rate of scratch produced (r^2 = 0.299)

	Standardized coefficient	Standard error	*p*
Age	-0.031	0.540	0.36832
Sex	0.165	0.488	0.05097
Kinship	0.086	1.004	0.15242
Reproductive status	-0.033	0.402	0.33983
Gesture with mutual attention	0.527	0.061	**0.001**
Gesture without mutual attention	-0.026	0.068	0.43028

Table S9.11 Rate of scratch received (r^2 = 0.058)

	Standardized coefficient	Standard error	*p*
Age	0.02	0.64	0.4018
Sex	0.21	0.56	**0.03298**
Kinship	0.08	1.15	0.17841
Reproductive status	0.04	0.44	0.32184

Gesture with mutual attention	0.05	0.06	0.24138
Gesture without mutual attention	-0.13	0.08	**0.04948**

Bodily and manual gestures

Supplementary Table S10. MRQAP regression models predicting durations of social behavior, per hour dyad spent within 10m. Predictor variables were rates of bodily and manual gestures between the recipient and the signaller, per hour dyad spent within 10m and demographic variables. Based on 132 chimpanzee dyads. Significant *p* values are indicated in bold. R squared (r^2) denotes amount of variance in the dependent variable explained by the regression model.

Table S10.1 Duration of joint feeding behaviour (r^2 = 0.156)

	Standardized coefficient	Standard error	*p*
Age	-0.043	0.674	0.365
Sex	0.150	0.581	0.083
Kinship	0.285	1.291	**0.010**
Reproductive status	0.259	0.538	**0.001**
Bodily	0.066	0.041	0.237
Manual	-0.082	0.088	0.201

Table S10.2 Duration of joint resting behaviour (r^2 = 0.072)

	Standardized coefficient	Standard error	*p*
Age	0.280	1.405	**0.004**
Sex	-0.116	1.102	0.081
Kinship	-0.018	2.383	0.463
Reproductive status	-0.027	1.113	0.405
Bodily	0.060	0.091	0.169
Manual	-0.014	0.192	0.486

Table S10.3 Duration of joint travelling behaviour (r^2 = 0.294)

	Standardized coefficient	Standard error	*p*
Age	0.177	0.345	**0.027**
Sex	0.034	0.279	0.345
Kinship	0.021	0.619	0.286
Reproductive status	-0.066	0.252	0.191
Bodily	0.503	0.026	**0.003**
Manual	-0.062	0.049	0.194

Table S10.4 Duration of giving grooming (r^2 = 0.291)

	Standardized coefficient	Standard error	*p*
Age	0.171	0.498	**0.025**
Sex	0.045	0.410	0.290
Kinship	0.124	0.919	0.078
Reproductive status	0.092	0.405	0.124
Bodily	0.220	0.034	**0.024**
Manual	0.293	0.072	**0.016**

Table S10.5 Duration of mutual grooming (r^2 = 0.327)

	Standardized coefficient	Standard error	*p*
Age	0.073	0.589	0.219
Sex	-0.102	0.494	0.132
Kinship	0.031	1.081	0.270
Reproductive status	0.097	0.456	0.115
Bodily	0.585	0.043	**0.001**
Manual	-0.075	0.077	0.149

Table S10.6 Duration of receiving grooming (r^2 = 0.087)

	Standardized coefficient	Standard error	*p*
Age	-0.148	0.516	**0.046**
Sex	0.123	0.426	0.099
Kinship	0.004	0.886	0.350
Reproductive status	0.136	0.423	0.054
Bodily	0.255	0.037	**0.036**
Manual	-0.092	0.080	0.101

Table S10.7 Duration of visual attention towards dyad partner (r^2 = 0.421)

	Standardized coefficient	Standard error	*p*
Age	-0.013	1.188	0.452
Sex	0.070	0.977	0.202
Kinship	0.198	2.219	**0.011**
Reproductive status	0.261	1.183	**0.005**
Bodily	0.549	0.092	**0.001**
Manual	-0.024	0.153	0.401

Table S10.8 Duration of visual attention away from dyad partner (r^2 = 0.144)

	Standardized coefficient	Standard error	*p*
Age	0.340	1.771	**0.002**
Sex	-0.069	1.294	0.219
Kinship	0.076	2.905	0.126
Reproductive status	0.021	1.307	0.431
Bodily	0.139	0.122	0.083
Manual	0.028	0.226	0.291

Table S10.9 Duration of time in close proximity – within 2 m (r^2 = 0.312)

	Standardized coefficient	Standard error	*p*
Age	0.226	2.251	**0.006**
Sex	-0.008	1.713	0.462
Kinship	0.164	4.044	**0.037**
Reproductive status	0.163	2.074	0.052
Bodily	0.406	0.164	**0.003**
Manual	0.006	0.311	0.421

Table S10.10 Rate of scratch produced (r^2 = 0.241)

	Standardized coefficient	Standard error	*p*
Age	-0.098	0.599	0.14443
Sex	0.189	0.522	**0.03448**
Kinship	0.088	1.063	0.15442
Reproductive status	-0.018	0.394	0.4038
Bodily	0.546	0.041	**0.0005**
Manual	-0.184	0.079	**0.01149**

Table S10.11 Rate of scratch received (r^2 = 0.051)

	Standardized coefficient	Standard error	*p*
Age	0.02	0.65	0.42129
Sex	0.20	0.58	**0.04248**
Kinship	0.08	1.19	0.1994
Reproductive status	0.04	0.45	0.33183
Bodily	-0.02	0.04	0.47776
Manual	-0.06	0.08	0.29685

Gesture events

Supplementary Table S11. MRQAP regression models predicting durations of social behavior, per hour dyad spent within 10m. Predictor variable was rates of gesture events between the recipient and the signaller, per hour dyad spent within 10m and demographic variables. Based on 132 chimpanzee dyads. Significant *p* values are indicated in bold. R squared (r^2) denotes amount of variance in the dependent variable explained by the regression model.

Table S11.1 Duration of joint feeding behaviour (r^2 = 0.151)

	Standardized coefficient	Standard error	*p*
Age	-0.026	0.656	0.417
Sex	0.149	0.567	0.076
Kinship	0.287	1.236	**0.008**
Reproductive status	0.260	0.563	**0.003**
Events	-0.008	0.027	0.509

Table S11.2 Duration of joint resting behaviour (r^2 = 0.071)

	Standardized coefficient	Standard error	*p*
Age	0.287	1.397	**0.005**
Sex	-0.116	1.070	0.066
Kinship	-0.018	2.342	0.451
Reproductive	-0.027	1.122	0.427

status			
Events	0.042	0.069	0.208

Table S11.3 Duration of joint travelling behaviour ($r^2 = 0.240$)

	Standardized coefficient	Standard error	*p*
Age	0.225	0.366	**0.017**
Sex	0.035	0.302	0.348
Kinship	0.026	0.622	0.252
Reproductive status	-0.062	0.268	0.219
Events	0.396	0.018	**0.003**

Table S11.4 Duration of giving grooming ($r^2 = 0.293$)

	Standardized coefficient	Standard error	*p*
Age	0.141	0.484	**0.047**
Sex	0.046	0.414	0.290
Kinship	0.125	0.886	0.064
Reproductive status	0.086	0.389	0.128
Events	0.467	0.027	**0.002**

Table S11.5 Duration of mutual grooming (r^2 = 0.248)

	Standardized coefficient	Standard error	*p*
Age	0.130	0.618	0.105
Sex	-0.101	0.524	0.150
Kinship	0.035	1.110	0.241
Reproductive status	0.103	0.508	0.139
Events	0.451	0.031	**0.003**

Table S11.6 Duration of receiving grooming (r^2 = 0.071)

	Standardized coefficient	Standard error	*p*
Age	-0.117	0.483	0.086
Sex	0.123	0.404	0.092
Kinship	0.007	0.876	0.315
Reproductive status	0.137	0.450	0.056
Events	0.164	0.025	0.065

Table S11.7 Duration of visual attention towards dyad partner (r^2 = 0.369)

	Standardized coefficient	Standard error	*p*
Age	0.032	1.226	0.344
Sex	0.071	0.973	0.197
Kinship	0.202	2.239	**0.009**
Reproductive status	0.265	1.266	**0.003**
Events	0.474	0.067	**0.001**

Table S11.8 Duration of visual attention away from dyad partner (r^2 = 0.143)

	Standardized coefficient	Standard error	*p*
Age	0.346	1.708	**0.002**
Sex	-0.068	1.267	0.232
Kinship	0.077	2.752	0.095
Reproductive status	0.021	1.362	0.430
Events	0.152	0.078	**0.049**

Table S11.9 Duration of time in close proximity – within 2 m (r^2 = 0.288)

	Standardized coefficient	Standard error	*p*

Age	0.256	2.271	**0.005**
Sex	-0.007	1.668	0.472
Kinship	0.168	3.990	**0.027**
Reproductive status	0.165	2.197	0.057
Events	0.373	0.122	**0.003**

Table S11.10 Rate of scratch produced (r^2 = 0.172)

	Standardized coefficient	Standard error	*p*
Age	-0.033	0.585	0.37281
Sex	0.189	0.528	**0.03598**
Kinship	0.094	1.106	0.15692
Reproductive status	-0.016	0.432	0.43478
Events	0.364	0.027	**0.003**

Table S11.11 Rate of scratch received (r^2 = 0.051)

	Standardized coefficient	Standard error	*p*
Age	0.03	0.62	0.38731

Sex	0.20	0.55	**0.03998**
Kinship	0.08	1.14	0.1929
Reproductive status	0.04	0.46	0.33183
Events	-0.07	0.03	0.1909

Non-indicative and indicative gestures

Supplementary Table S12. MRQAP regression models predicting durations of social behavior, per hour dyad spent within 10m. Predictor variables were rates of non-indicative and indicative gestures between the recipient and the signaller, per hour dyad spent within 10m and demographic variables. Based on 132 chimpanzee dyads. Significant *p* values are indicated in bold. R squared (r^2) denotes amount of variance in the dependent variable explained by the regression model.

Table S12.1 Duration of joint feeding behaviour (r^2 = 0.162)

	Standardized coefficient	Standard error	*p*
Age	-0.044	0.652	0.348
Sex	0.153	0.560	0.067
Kinship	0.283	1.263	**0.008**
Reproductive status	0.251	0.554	**0.005**
Manual indicative	0.095	0.406	0.115
Manual non-	-0.081	0.075	0.113

indicative			

Table S12.2 Duration of joint resting behaviour (r^2 = 0.072)

	Standardized coefficient	Standard error	*p*
Age	0.287	1.414	**0.005**
Sex	-0.114	1.123	0.086
Kinship	-0.020	2.471	0.445
Reproductive status	-0.028	1.123	0.427
Manual indicative	0.046	1.028	0.161
Manual non-indicative	0.000	0.182	0.622

Table S12.3 Duration of joint travelling behaviour (r^2 = 0.280)

	Standardized coefficient	Standard error	*p*
Age	0.226	0.356	**0.011**
Sex	0.052	0.279	0.275
Kinship	0.011	0.600	0.287
Reproductive status	-0.076	0.259	0.177

Manual indicative	0.429	0.281	**0.011**
Manual non-indicative	0.041	0.046	0.150

Table S12.4 Duration of giving grooming (r^2 = 0.275)

	Standardized coefficient	Standard error	*p*
Age	0.203	0.496	**0.011**
Sex	0.051	0.405	0.269
Kinship	0.122	0.938	0.080
Reproductive status	0.096	0.405	0.129
Manual indicative	0.173	0.365	**0.036**
Manual non-indicative	0.354	0.066	**0.014**

Table S12.5 Duration of mutual grooming (r^2 = 0.362)

	Standardized coefficient	Standard error	*p*
Age	0.120	0.556	0.094
Sex	-0.079	0.470	0.186

Kinship	0.018	1.031	0.260
Reproductive status	0.079	0.452	0.179
Manual indicative	0.561	0.459	**0.001**
Manual non-indicative	0.016	0.068	0.246

Table S12.6 Duration of receiving grooming (r^2 = 0.071)

	Standardized coefficient	Standard error	*p*
Age	-0.118	0.483	0.089
Sex	0.132	0.414	0.084
Kinship	0.000	0.807	0.685
Reproductive status	0.135	0.436	0.060
Manual indicative	0.170	0.382	**0.046**
Manual non-indicative	-0.019	0.070	0.541

Table S12.7 Duration of visual attention towards dyad partner (r^2 = 0.463)

	Standardized	Standard error	*p*

	coefficient		
Age	0.029	1.052	0.342
Sex	0.092	0.851	0.098
Kinship	0.185	2.029	**0.013**
Reproductive status	0.243	1.134	**0.002**
Manual indicative	0.545	0.946	**0.001**
Manual non-indicative	0.057	0.139	0.171

Table S12.8 Duration of visual attention away from dyad partner (r^2 = 0.137)

	Standardized coefficient	Standard error	*p*
Age	0.359	1.719	**0.001**
Sex	-0.065	1.277	0.249
Kinship	0.074	2.902	0.134
Reproductive status	0.023	1.329	0.405
Manual indicative	0.089	1.115	0.112
Manual non-indicative	0.071	0.213	0.120

Table S12.9 Duration of time in close proximity – within 2 m (r^2 = 0.312)

	Standardized coefficient	Standard error	*p*
Age	0.263	2.228	**0.003**
Sex	0.008	1.660	0.454
Kinship	0.156	3.667	**0.026**
Reproductive status	0.154	1.997	0.062
Manual indicative	0.370	1.763	**0.007**
Manual non-indicative	0.081	0.295	0.144

Table S12.10 Rate of scratch produced (r^2 = 0.193)

	Standardized coefficient	Standard error	*p*
Age	-0.039	0.574	0.34783
Sex	0.208	0.544	**0.03148**
Kinship	0.077	1.105	0.18441
Reproductive status	-0.024	0.392	0.3938

Manual indicative	0.402	0.430	**0.003**
Manual non-indicative	-0.047	0.070	0.32234

Table S12.11 Rate of scratch received (r^2 = 0.051)

	Standardized coefficient	Standard error	*p*
Age	0.01	0.60	0.44328
Sex	0.20	0.55	**0.03998**
Kinship	0.08	1.13	0.17741
Reproductive status	0.03	0.44	0.34133
Manual indicative	0.01	0.41	0.4023
Manual non-indicative	-0.07	0.08	0.17191

Gestures made at close and far proximity

Supplementary Table S13. MRQAP regression models predicting durations of social behavior, per hour dyad spent within 10m. Predictor variables were rates of gestures made at close and far proximity between the recipient and the signaller, per hour dyad spent within 10m and demographic variables. Based on 132 chimpanzee dyads. Significant *p* values are indicated in bold. R squared (r^2) denotes amount of variance in the dependent variable explained by the regression model.

Table S13.1 Duration of joint feeding behaviour (r^2 = 0.156)

	Standardized coefficient	Standard error	*p*
Age	-0.026	0.641	0.409
Sex	0.142	0.576	0.092
Kinship	0.282	1.250	**0.006**
Reproductive status	0.251	0.557	**0.003**
Close proximity	0.055	0.053	0.223
Far proximity	-0.065	0.044	0.203

Table S13.2 Duration of joint resting behaviour (r^2 = 0.082)

	Standardized coefficient	Standard error	*p*
Age	0.284	1.421	**0.005**
Sex	-0.131	1.125	0.055
Kinship	-0.025	2.482	0.423
Reproductive status	-0.040	1.124	0.365
Close proximity	0.121	0.123	**0.046**
Far proximity	-0.048	0.112	0.235

Table S13.3 Duration of joint travelling behaviour (r^2 = 0.241)

	Standardized coefficient	Standard error	*p*
Age	0.225	0.360	**0.009**
Sex	0.013	0.309	0.445
Kinship	0.016	0.660	0.314
Reproductive status	-0.059	0.275	0.248
Close proximity	0.273	0.030	**0.015**
Far proximity	0.223	0.026	**0.013**

Table S13.4 Duration of giving grooming (r^2 = 0.589)

	Standardized coefficient	Standard error	*p*
Age	0.128	0.346	**0.018**
Sex	-0.042	0.282	0.242
Kinship	0.085	0.625	0.068
Reproductive status	0.022	0.274	0.383
Close proximity	0.765	0.055	**0.001**
Far proximity	-0.112	0.029	**0.012**

Table S13.5 Duration of mutual grooming (r^2 = 0.288)

	Standardized coefficient	Standard error	*p*
Age	0.125	0.604	0.101
Sex	-0.136	0.518	0.073
Kinship	0.022	1.067	0.263
Reproductive status	0.095	0.499	0.157
Close proximity	0.387	0.052	**0.004**
Far proximity	0.223	0.044	**0.018**

Table S13.6 Duration of receiving grooming (r^2 = 0.074)

	Standardized coefficient	Standard error	*p*
Age	-0.117	0.495	0.099
Sex	0.109	0.400	0.128
Kinship	0.001	0.897	0.352
Reproductive status	0.132	0.437	0.069
Close proximity	0.153	0.044	0.083
Far proximity	0.053	0.039	0.167

Table S13.7 Duration of visual attention towards dyad partner (r^2 = 0.439)

	Standardized coefficient	Standard error	*p*
Age	0.026	1.152	0.368
Sex	0.020	0.935	0.386
Kinship	0.181	2.133	**0.009**
Reproductive status	0.242	1.179	**0.010**
Close proximity	0.500	0.119	**0.001**
Far proximity	0.131	0.086	**0.045**

Table S13.8 Duration of visual attention away from dyad partner (r^2 = 0.190)

	Standardized coefficient	Standard error	*p*
Age	0.341	1.683	**0.001**
Sex	-0.102	1.258	0.105
Kinship	0.062	2.737	0.144
Reproductive status	-0.005	1.292	0.481
Close proximity	0.287	0.147	**0.021**
Far proximity	-0.066	0.116	0.158

Table S13.9 Duration of time in close proximity – within 2 m (r^2 = 0.376)

	Standardized coefficient	Standard error	*p*
Age	0.249	2.163	**0.004**
Sex	-0.058	1.643	0.226
Kinship	0.145	3.680	**0.035**
Reproductive status	0.134	2.103	0.094
Close proximity	0.480	0.213	**0.001**
Far proximity	0.029	0.155	0.297

Table S13.10 Rate of scratch produced ($r^2 = 0.174$)

	Standardized coefficient	Standard error	*p*
Age	-0.032	0.582	0.3903
Sex	0.175	0.539	0.05697
Kinship	0.089	1.120	0.15192
Reproductive status	-0.007	0.445	0.47126
Close proximity	0.210	0.051	**0.02399**
Far proximity	0.244	0.045	**0.01299**

Table S13.11 Rate of scratch received ($r^2 = 0.058$)

	Standardized coefficient	Standard error	*p*
Age	0.03	0.66	0.3908
Sex	0.22	0.58	**0.03598**
Kinship	0.08	1.19	0.18691
Reproductive status	0.05	0.45	0.27236
Close proximity	-0.11	0.05	**0.04898**
Far proximity	0.01	0.05	0.38131

Non-repetitive and repetitive gestures

Supplementary Table S14. MRQAP regression models predicting durations of social behavior, per hour dyad spent within 10m. Predictor variables were rates of non-repetitive and repetitive gestures between the recipient and the signaller, per hour dyad spent within 10m and demographic variables. Based on 132 chimpanzee dyads. Significant *p* values are indicated in bold. R squared (r^2) denotes amount of variance in the dependent variable explained by the regression model.

Table S14.1 Duration of joint feeding behaviour (r^2 = 0.158)

	Standardized coefficient	Standard error	*p*
Age	-0.029	0.658	0.410
Sex	0.144	0.562	0.085
Kinship	0.291	1.288	**0.009**

Reproductive status	0.262	0.565	**0.002**
Non-repetitive	-0.071	0.047	0.192
Repetitive	0.090	0.051	0.158

Table S14.2 Duration of joint resting behaviour (r^2 = 0.072)

	Standardized coefficient	Standard error	*p*
Age	0.286	1.419	**0.005**
Sex	-0.116	1.101	0.064
Kinship	-0.019	2.464	0.459
Reproductive status	-0.027	1.120	0.415
Non-repetitive	0.028	0.102	0.245
Repetitive	0.021	0.126	0.259

Table S14.3 Duration of joint travelling behaviour (r^2 = 0.353)

	Standardized coefficient	Standard error	*p*
Age	0.222	0.309	**0.004**
Sex	0.054	0.250	0.234
Kinship	0.002	0.551	0.391

Reproductive status	-0.080	0.215	0.138
Non-repetitive	0.559	0.028	**0.006**
Repetitive	-0.092	0.028	0.065

Table S14.4 Duration of giving grooming (r^2 = 0.409)

	Standardized coefficient	Standard error	*p*
Age	0.138	0.431	**0.030**
Sex	0.028	0.355	0.343
Kinship	0.129	0.770	**0.035**
Reproductive status	0.106	0.358	0.070
Non-repetitive	-0.061	0.035	0.115
Repetitive	0.606	0.047	**0.001**

Table S14.5 Duration of mutual grooming (r^2 = 0.470)

	Standardized coefficient	Standard error	*p*
Age	0.126	0.509	0.059
Sex	-0.074	0.420	0.186
Kinship	0.005	0.917	0.371

Reproductive status	0.077	0.424	0.181
Non-repetitive	0.726	0.052	**0.001**
Repetitive	-0.189	0.045	**0.004**

Table S14.6 Duration of receiving grooming (r^2 = 0.080)

	Standardized coefficient	Standard error	*p*
Age	-0.115	0.503	0.094
Sex	0.131	0.424	0.088
Kinship	-0.002	0.858	0.654
Reproductive status	0.133	0.436	0.065
Non-repetitive	0.207	0.039	**0.035**
Repetitive	-0.040	0.045	0.424

Table S14.7 Duration of visual attention towards dyad partner (r^2 = 0.464)

	Standardized coefficient	Standard error	*p*
Age	0.028	1.143	0.376
Sex	0.088	0.950	0.141
Kinship	0.179	2.173	**0.032**

Reproductive status	0.249	1.127	**0.002**
Non-repetitive	0.567	0.104	**0.004**
Repetitive	-0.003	0.090	0.543

Table S14.8 Duration of visual attention away from dyad partner (r^2 = 0.149)

	Standardized coefficient	Standard error	*p*
Age	0.345	1.731	**0.001**
Sex	0.345	1.731	**0.001**
Kinship	-0.072	1.307	0.219
Reproductive status	0.077	2.732	0.107
Non-repetitive	0.026	1.363	0.414
Repetitive	0.015	0.127	0.352

Table S14.9 Duration of time in close proximity – within 2 m (r^2 = 0.307)

	Standardized coefficient	Standard error	*p*
Age	0.253	2.241	**0.004**
Sex	0.000	1.681	0.483
Kinship	0.154	3.809	**0.033**

Reproductive status	0.159	2.109	0.067
Non-repetitive	0.331	0.177	**0.012**
Repetitive	0.111	0.193	0.118

Table S14.10 Rate of scratch produced (r^2 = 0.215)

	Standardized coefficient	Standard error	*p*
Age	-0.0346	0.5810	0.37881
Sex	0.2024	0.5279	**0.03248**
Kinship	0.0765	1.1127	0.1919
Reproductive status	-0.0259	0.4175	0.38731
Non-repetitive	0.4196	0.0419	**0.0045**
Repetitive	-0.0013	0.0470	0.55822

Table S14.11 Rate of scratch received (r^2 = 0.060)

	Standardized coefficient	Standard error	*p*
Age	0.03	0.63	0.38731
Sex	0.21	0.54	**0.02499**

Kinship	0.07	1.19	0.1959
Reproductive status	0.03	0.45	0.34633
Non-repetitive	0.05	0.05	0.22239
Repetitive	-0.14	0.05	**0.04498**

Heterogeneous and homogeneous gestures

Supplementary Table S15. MRQAP regression models predicting durations of social behavior, per hour dyad spent within 10m. Predictor variables were rates of heterogeneous and homogeneous gestures between the recipient and the signaller, per hour dyad spent within 10m and demographic variables. Based on 132 chimpanzee dyads. Significant *p* values are indicated in bold. R squared (r^2) denotes amount of variance in the dependent variable explained by the regression model.

Table S15.1 Duration of joint feeding behaviour (r^2 = 0.)

	Standardized coefficient	Standard error	*p*
Age	-0.02	0.66	0.41629
Sex	0.15	0.58	0.08346
Kinship	0.29	1.29	**0.01199**
Reproductive status	0.26	0.55	**0.002**
Heterogeneous	0.00	0.08	0.43328
Homogeneous	-0.01	0.04	0.53173

Table S15.2 Duration of joint resting behaviour (r^2 = 0.075)

	Standardized coefficient	Standard error	*p*
Age	0.27	1.44	**0.0085**
Sex	-0.12	1.14	0.08496
Kinship	-0.02	2.40	0.44878
Reproductive status	-0.03	1.12	0.3958
Heterogeneous	-0.02	0.20	0.47076
Homogeneous	0.08	0.11	0.10895

Table S15.3 Duration of joint travelling behaviour (r^2 = 0.251)

	Standardized coefficient	Standard error	*p*
Age	0.17	0.36	**0.04048**
Sex	0.01	0.29	0.44428
Kinship	0.01	0.60	0.33633
Reproductive status	-0.07	0.27	0.2019
Heterogeneous	-0.03	0.05	0.38281
Homogeneous	0.43	0.03	**0.01049**

Table S15.4 Duration of giving grooming (r^2 = 0.364)

	Standardized coefficient	Standard error	*p*
Age	0.09	0.47	0.12944
Sex	0.02	0.39	0.3953
Kinship	0.11	0.84	0.06697
Reproductive status	0.08	0.37	0.14543
Heterogeneous	0.11	0.07	0.06747
Homogeneous	0.52	0.04	**0.004**

Table S15.5 Duration of mutual grooming (r^2 = 0.358)

	Standardized coefficient	Standard error	*p*
Age	0.03	0.56	0.34533
Sex	-0.14	0.49	0.08046
Kinship	0.01	1.05	0.33633
Reproductive status	0.08	0.46	0.16392
Heterogeneous	-0.15	0.08	**0.01649**
Homogeneous	0.60	0.05	**0.0005**

Table S15.6 Duration of receiving grooming (r^2 = 0.072)

	Standardized coefficient	Standard error	*p*
Age	-0.14	0.51	0.05697
Sex	0.11	0.42	0.12544
Kinship	0.00	0.89	0.37831
Reproductive status	0.14	0.44	0.05697
Heterogeneous	-0.01	0.08	0.62919
Homogeneous	0.17	0.04	**0.04898**

Table S15.7 Duration of visual attention towards dyad partner (r^2 = 0.455)

	Standardized coefficient	Standard error	*p*
Age	-0.05	1.19	0.23888
Sex	0.04	0.98	0.31434
Kinship	0.18	2.21	**0.01699**
Reproductive status	0.25	1.16	**0.0035**
Heterogeneous	-0.09	0.15	**0.04698**
Homogeneous	0.60	0.10	**0.001**

Table S15.8 Duration of visual attention away from dyad partner (r^2 = 0.151)

	Standardized coefficient	Standard error	*p*
Age	0.33	1.77	**0.0035**
Sex	-0.08	1.31	0.1924
Kinship	0.07	2.85	0.13793
Reproductive status	0.02	1.32	0.44478
Heterogeneous	0.04	0.23	0.21289
Homogeneous	0.17	0.12	**0.04348**

Table S15.9 Duration of time in close proximity – within 2 m (r^2 = 0.335)

	Standardized coefficient	Standard error	*p*
Age	0.20	2.25	**0.01899**
Sex	-0.03	1.67	0.35082
Kinship	0.15	3.93	**0.03798**
Reproductive status	0.15	2.08	0.06597
Heterogeneous	-0.03	0.30	0.4013
Homogeneous	0.45	0.18	**0.0005**

Table S15.10 Rate of scratch produced (r^2 = 0.186)

	Standardized coefficient	Standard error	*p*
Age	-0.067	0.603	0.25437
Sex	0.169	0.540	0.07046
Kinship	0.083	1.099	0.17341
Reproductive status	-0.019	0.436	0.42579
Heterogeneous	0.053	0.077	0.21939
Homogeneous	0.378	0.042	**0.0025**

Table S15.11 Rate of scratch received (r^2 = 0.054)

	Standardized coefficient	Standard error	*p*
Age	0.03	0.65	0.36182
Sex	0.21	0.57	**0.03748**
Kinship	0.08	1.19	0.17141
Reproductive status	0.04	0.45	0.29985
Heterogeneous	-0.03	0.09	0.4008

Homogeneous	-0.08	0.04	0.16142

Gestures accompanied by penile erection

Supplementary Table S16. MRQAP regression models predicting durations of social behavior, per hour dyad spent within 10m. Predictor variables were rates of gestures between the recipient and the signaller are accompanied by penile erection, per hour dyad spent within 10m and demographic variables. Based on 132 chimpanzee dyads. Significant *p* values are indicated in bold. R squared (r^2) denotes amount of variance in the dependent variable explained by the regression model.

Table S16.1 Duration of joint feeding behaviour (r^2 = 0.153)

	Standardized coefficient	Standard error	*p*
Age	-0.03	0.64	0.42429
Sex	0.16	0.58	0.07646
Kinship	0.29	1.28	**0.007**
Reproductive status	0.26	0.54	**0.0035**
Penile erection	0.04	0.22	0.27036

Table S16.2 Duration of joint resting behaviour (r^2 = 0.070)

	Standardized coefficient	Standard error	*p*
Age	0.29	1.40	**0.002**

Sex	-0.12	1.12	0.08696
Kinship	-0.02	2.49	0.45727
Reproductive status	-0.02	1.10	0.4018
Penile erection	-0.01	0.49	0.5947

Table S16.3 Duration of joint travelling behaviour (r^2 = 0.095)

	Standardized coefficient	Standard error	*p*
Age	0.28	0.43	**0.005**
Sex	0.06	0.34	0.27886
Kinship	0.01	0.74	0.29885
Reproductive status	-0.02	0.33	0.44378
Penile erection	0.07	0.14	0.13443

Table S16.4 Duration of giving grooming (r^2 = 0.086)

	Standardized coefficient	Standard error	*p*
Age	0.21	0.56	**0.01899**
Sex	0.06	0.45	0.26137
Kinship	0.11	0.97	0.11444

Reproductive status	0.14	0.50	0.06997
Penile erection	0.02	0.20	0.27086

Table S16.5 Duration of mutual grooming (r^2 = 0.055)

	Standardized coefficient	Standard error	*p*
Age	0.19	0.74	0.07746
Sex	-0.09	0.61	0.1959
Kinship	0.01	1.22	0.28636
Reproductive status	0.16	0.65	0.10745
Penile erection	-0.04	0.23	0.36432

Table S16.6 Duration of receiving grooming (r^2 = 0.047)

	Standardized coefficient	Standard error	*p*
Age	-0.10	0.49	0.15742
Sex	0.12	0.41	0.10745
Kinship	0.00	0.87	0.63968
Reproductive status	0.16	0.47	**0.03198**

Penile erection	-0.04	0.21	0.30285

Table S16.7 Duration of visual attention towards dyad partner (r^2 = 0.155)

	Standardized coefficient	Standard error	*p*
Age	0.10	1.40	0.16492
Sex	0.08	1.15	0.18241
Kinship	0.18	2.68	0.06297
Reproductive status	0.33	1.66	**0.0045**
Penile erection	-0.01	0.47	0.50825

Table S16.8 Duration of visual attention away from dyad partner (r^2 = 0.121)

	Standardized coefficient	Standard error	*p*
Age	0.37	1.75	**0.0015**
Sex	-0.06	1.29	0.25187
Kinship	0.07	2.83	0.13493
Reproductive status	0.04	1.39	0.36932
Penile erection	-0.01	0.62	0.56722

Table S16.9 Duration of time in close proximity – within 2 m (r^2 = 0.156)

	Standardized coefficient	Standard error	*p*
Age	0.31	2.55	**0.001**
Sex	0.00	1.80	0.45977
Kinship	0.15	4.22	**0.04248**
Reproductive status	0.21	2.68	0.05147
Penile erection	-0.01	0.80	0.52074

Table S16.10 Rate of scratch produced (r^2 = 0.056)

	Standardized coefficient	Standard error	*p*
Age	0.021	0.607	0.41429
Sex	0.218	0.558	**0.02849**
Kinship	0.086	1.124	0.15942
Reproductive status	0.018	0.431	0.42229
Penile erection	0.102	0.222	0.11494

Table S16.11 Rate of scratch received (r^2 = 0.046)

	Standardized	Standard error	*p*

	coefficient		
Age	0.02	0.61	0.44728
Sex	0.20	0.55	**0.04148**
Kinship	0.08	1.13	0.18291
Reproductive status	0.03	0.44	0.36282
Penile erection	0.00	0.23	0.5942

Gestures accompanied by piloerection

Supplementary Table S17. MRQAP regression models predicting durations of social behavior, per hour dyad spent within 10m. Predictor variables were rates of gestures between the recipient and the signaller are accompanied by piloerection, per hour dyad spent within 10m and demographic variables. Based on 132 chimpanzee dyads. Significant *p* values are indicated in bold. R squared (r^2) denotes amount of variance in the dependent variable explained by the regression model.

Table S17.1 Duration of joint feeding behaviour (r^2 = 0.153)

	Standardized coefficient	Standard error	*p*
Age	-0.02	0.64	0.43828
Sex	0.15	0.57	0.08396
Kinship	0.29	1.29	**0.0085**
Reproductive status	0.26	0.57	**0.002**

Piloerection	-0.04	0.04	0.35782

Table S17.2 Duration of joint resting behaviour (r^2 = 0.070)

	Standardized coefficient	Standard error	*p*
Age	0.30	1.38	**0.004**
Sex	-0.12	1.11	0.08496
Kinship	-0.02	2.39	0.43878
Reproductive status	-0.02	1.13	0.43728
Piloerection	-0.02	0.10	0.49525

Table S17.3 Duration of joint travelling behaviour (r^2 = 0.231)

	Standardized coefficient	Standard error	*p*
Age	0.22	0.38	**0.01749**
Sex	0.06	0.30	0.24438
Kinship	0.02	0.65	0.28036
Reproductive status	-0.03	0.28	0.36982
Piloerection	0.38	0.03	**0.006**

Table S17.4 Duration of giving grooming (r^2 = 0.094)

	Standardized coefficient	Standard error	*p*
Age	0.19	0.56	**0.03098**
Sex	0.06	0.44	0.24588
Kinship	0.11	1.00	0.11994
Reproductive status	0.14	0.49	0.06747
Piloerection	0.09	0.04	0.10845

Table S17.5 Duration of mutual grooming (r^2 = 0.229)

	Standardized coefficient	Standard error	*p*
Age	0.13	0.63	0.10495
Sex	-0.07	0.52	0.23188
Kinship	0.03	1.10	0.24588
Reproductive status	0.14	0.54	0.08646
Piloerection	0.42	0.04	**0.004**

Table S17.6 Duration of receiving grooming (r^2 = 0.065)

	Standardized	Standard error	*p*

	coefficient		
Age	-0.12	0.50	0.09045
Sex	0.13	0.42	0.07896
Kinship	0.01	0.88	0.31334
Reproductive status	0.15	0.46	0.05547
Piloerection	0.14	0.04	0.08896

Table S17.7 Duration of visual attention towards dyad partner (r^2 = 0.278)

	Standardized coefficient	Standard error	*p*
Age	0.04	1.32	0.31284
Sex	0.10	1.08	0.14193
Kinship	0.20	2.42	**0.02099**
Reproductive status	0.31	1.46	**0.0015**
Piloerection	0.35	0.10	**0.0055**

Table S17.8 Duration of visual attention away from dyad partner (r^2 = 0.121)

	Standardized coefficient	Standard error	*p*
Age	0.36	1.76	**0.001**

Sex	-0.06	1.32	0.24188
Kinship	0.07	2.87	0.13493
Reproductive status	0.04	1.42	0.35882
Piloerection	0.02	0.13	0.29685

Table S17.9 Duration of time in close proximity – within 2 m (r^2 = 0.200)

	Standardized coefficient	Standard error	*p*
Age	0.27	2.37	**0.002**
Sex	0.01	1.77	0.41279
Kinship	0.16	4.15	**0.03898**
Reproductive status	0.20	2.52	**0.04248**
Piloerection	0.21	0.17	**0.02749**

Table S17.10 Rate of scratch produced (r^2 = 0.101)

	Standardized coefficient	Standard error	*p*
Age	-0.020	0.618	0.43228
Sex	0.210	0.548	**0.02699**
Kinship	0.088	1.150	0.15892

Reproductive status	0.020	0.408	0.3973
Piloerection	0.237	0.043	**0.02249**

Table S17.11 Rate of scratch received (r^2 = 0.048)

	Standardized coefficient	Standard error	*p*
Age	0.02	0.64	0.4058
Sex	0.20	0.56	**0.04598**
Kinship	0.08	1.14	0.18091
Reproductive status	0.03	0.44	0.36332
Piloerection	-0.05	0.04	0.32784

Single gestures, rapid and persistence sequences

Supplementary Table S18. MRQAP regression models predicting durations of social behavior, per hour dyad spent within 10m. Predictor variables were rates of single gestures, rapid and persistence sequences between the signaller and the recipient, per hour dyad spent within 10m and demographic variables. Based on 132 chimpanzee dyads. Significant *p* values are indicated in bold. R squared (r^2) denotes amount of variance in the dependent variable explained by the regression model.

Table S18.1 Duration of joint feeding behaviour (r^2 = 0.157)

	Standardized	Standard error	*p*

	coefficient		
Age	-0.03	0.67	0.3978
Sex	0.14	0.58	0.09445
Kinship	0.28	1.31	**0.008**
Reproductive status	0.25	0.56	**0.0045**
Rapid sequence	-0.06	0.19	0.27286
Single no sequence	0.08	0.06	0.16042
Persistence	-0.03	0.53	0.37131

Table S18.2 Duration of joint resting behaviour (r^2 = 0.077)

	Standardized coefficient	Standard error	*p*
Age	0.29	1.39	**0.0015**
Sex	-0.13	1.12	0.05497
Kinship	-0.02	2.41	0.44328
Reproductive status	-0.04	1.13	0.3993
Rapid sequence	-0.03	0.47	0.35282
Single no sequence	0.08	0.15	0.09995
Persistence	0.03	1.25	0.22889

Table S18.3 Duration of joint travelling behaviour (r^2 = 0.259)

	Standardized coefficient	Standard error	*p*
Age	0.22	0.37	**0.01449**
Sex	0.02	0.31	0.38581
Kinship	0.02	0.65	0.25737
Reproductive status	-0.07	0.28	0.21689
Rapid sequence	0.20	0.11	**0.02049**
Single no sequence	0.22	0.04	**0.02699**
Persistence	0.14	0.29	**0.04548**

Table S18.4 Duration of giving grooming (r^2 = 0.474)

	Standardized coefficient	Standard error	*p*
Age	0.11	0.41	0.07246
Sex	0.01	0.33	0.41979
Kinship	0.10	0.73	0.05447
Reproductive status	0.02	0.34	0.44878

Rapid sequence	0.03	0.13	0.2024
Single no sequence	0.66	0.06	**0.001**
Persistence	-0.05	0.38	0.14243

Table S18.5 Duration of mutual grooming (r^2 = 0.286)

	Standardized coefficient	Standard error	*p*
Age	0.13	0.61	0.08346
Sex	-0.13	0.53	0.09845
Kinship	0.03	1.14	0.26437
Reproductive status	0.08	0.49	0.16942
Rapid sequence	0.16	0.17	**0.04198**
Single no sequence	0.33	0.06	**0.01249**
Persistence	0.16	0.48	**0.03498**

Table S18.6 Duration of receiving grooming (r^2 = 0.077)

	Standardized coefficient	Standard error	*p*
Age	-0.11	0.51	0.12044

Sex	0.11	0.43	0.13293
Kinship	0.00	0.84	0.31384
Reproductive status	0.12	0.46	0.09595
Rapid sequence	0.00	0.16	0.37331
Single no sequence	0.16	0.05	0.05147
Persistence	0.05	0.46	0.14343

Table S18.7 Duration of visual attention towards dyad partner ($r^2 = 0.433$)

	Standardized coefficient	Standard error	*p*
Age	0.02	1.18	0.38431
Sex	0.04	0.97	0.30135
Kinship	0.19	2.19	**0.01049**
Reproductive status	0.23	1.15	**0.02099**
Rapid sequence	0.09	0.36	0.12094
Single no sequence	0.47	0.13	**0.001**
Persistence	0.09	1.04	0.12444

Table S18.8 Duration of visual attention away from dyad partner (r^2 = 0.168)

	Standardized coefficient	Standard error	*p*
Age	0.34	1.74	**0.001**
Sex	-0.09	1.31	0.16492
Kinship	0.07	2.71	0.12994
Reproductive status	0.00	1.33	0.48226
Rapid sequence	-0.01	0.48	0.47926
Single no sequence	0.23	0.17	**0.02649**
Persistence	0.02	1.49	0.33083

Table S18.9 Duration of time in close proximity – within 2 m (r^2 = 0.354)

	Standardized coefficient	Standard error	*p*
Age	0.25	2.19	**0.003**
Sex	-0.04	1.66	0.28636
Kinship	0.15	3.68	**0.02549**
Reproductive status	0.13	2.07	0.09995
Rapid sequence	0.04	0.65	0.27586

Single no sequence	0.42	0.25	**0.0005**
Persistence	0.06	1.86	0.1954

Table S18.10 Rate of scratch produced ($r^2 = 0.397$)

	Standardized coefficient	Standard error	*p*
Age	0.04	0.51	0.29735
Sex	0.12	0.46	0.10395
Kinship	0.09	0.92	0.10645
Reproductive status	-0.02	0.34	0.4053
Rapid sequence	-0.02	0.15	0.44528
Single no sequence	0.08	0.05	0.12244
Persistence	0.57	0.50	**0.0005**

Table S18.11 Rate of scratch received ($r^2 = 0.061$)

	Standardized coefficient	Standard error	*p*
Age	0.04	0.63	0.34783
Sex	0.21	0.55	**0.03298**

Kinship	0.08	1.21	0.18141
Reproductive status	0.05	0.45	0.24938
Rapid sequence	0.01	0.19	0.42379
Single no sequence	-0.14	0.06	**0.04448**
Persistence	0.06	0.51	0.2034

Association between the duration of social behaviour and gestural communication categorized according to function

Gesture functions

Supplementary Table S19. MRQAP regression models predicting durations of social behavior, per hour dyad spent within 10m. Predictors were demographic variables and functions of gestures. Dyads were classified as same age or different age (within 5 years), same sex or different sex, related by maternal kinship and as the same or different reproductive status (reproductively active, not reproductively active). Based on 132 dyadic relationships of the chimpanzees. Significant *p* values are indicated in bold. R squared (r^2) denotes amount of variance in the dependent variable explained by the regression model.

Table S19.1 Duration of joint feeding behaviour (r^2 = 0.310)

	Standardized coefficient	Standard error	*p*
Age	-0.04	0.65	0.34233

Sex	0.11	0.55	0.11494
Kinship	0.27	1.20	**0.0055**
Reproductive status	0.22	0.56	**0.006**
Copulation	0.05	0.31	0.16292
Food sharing	0.10	8.36	0.08096
Threat to dominate	-0.50	1.64	**0.04548**
Give groom	0.17	0.13	**0.03998**
Mutually groom	0.66	2.39	0.09795
Receive groom	0.47	0.55	**0.01249**
Reassurance	-0.59	1.87	0.11194
Other threat	-0.02	0.71	0.41279
Synchronized high-intensity panthoot	-0.08	0.29	0.10545
Solo high-intensity panthoot	0.02	0.53	0.30985
Synchronized low-intensity panthoot	0.14	0.69	**0.04398**
Play	-0.19	0.13	**0.0045**
Greeting	-0.11	0.30	0.05347
Travel	0.05	0.81	0.13493

Table S19.2 Duration of joint resting behaviour (r^2 = 0.099)

	Standardized coefficient	Standard error	*p*
Age	0.27	1.63	**0.01499**
Sex	-0.12	1.25	0.08746
Kinship	-0.02	2.70	0.43428
Reproductive status	-0.05	1.28	0.35432
Copulation	0.01	0.84	0.33883
Food sharing	0.01	23.98	0.32234
Threat to dominate	-0.20	3.57	0.17641
Give groom	0.11	0.31	0.06097
Mutually groom	0.10	6.48	0.35732
Receive groom	0.08	1.44	0.16492
Reassurance	0.03	4.55	0.49125
Other threat	-0.03	1.75	0.32534
Synchronized high-intensity panthoot	-0.07	0.66	0.09645
Solo high-intensity panthoot	-0.01	1.34	0.49825
Synchronized low-intensity panthoot	0.05	2.00	0.09045
Play	-0.04	0.27	0.18841
Greeting	0.04	0.75	0.17291

Travel	0.03	1.73	0.13493

Table S19.3 Duration of joint travelling behaviour ($r^2 = 0.420$)

	Standardized coefficient	Standard error	*p*
Age	0.20	0.35	**0.01399**
Sex	0.08	0.29	0.18191
Kinship	0.02	0.58	0.24038
Reproductive status	-0.06	0.26	0.21139
Copulation	0.05	0.18	0.08496
Food sharing	-0.01	5.05	0.44828
Threat to dominate	0.03	1.10	0.34733
Give groom	0.05	0.07	0.16042
Mutually groom	0.03	1.42	0.44578
Receive groom	0.08	0.32	0.17391
Reassurance	0.37	1.02	0.12394
Other threat	-0.05	0.39	0.11044
Synchronized high-intensity panthoot	-0.06	0.14	0.11694
Solo high-intensity panthoot	0.10	0.30	0.05547
Synchronized low-intensity panthoot	0.26	0.45	**0.01249**

Play	-0.03	0.07	0.2099
Greeting	0.01	0.17	0.34783
Travel	0.10	0.44	**0.04898**

Table S19.4 Duration of giving grooming (r^2 = 0.740)

	Standardized coefficient	Standard error	*p*
Age	0.06	0.30	0.11244
Sex	-0.01	0.24	0.3988
Kinship	0.09	0.48	**0.02199**
Reproductive status	0.00	0.23	0.53273
Copulation	-0.01	0.21	0.43878
Food sharing	-0.01	6.39	0.28286
Threat to dominate	-0.20	1.17	0.10745
Give groom	0.69	0.12	**0.0005**
Mutually groom	-0.10	1.45	0.33183
Receive groom	0.20	0.33	**0.03648**
Reassurance	0.20	1.08	0.18991
Other threat	-0.06	0.47	**0.02949**
Synchronized high-intensity panthoot	0.03	0.18	0.12244

Solo high-intensity panthoot	0.00	0.34	0.38831
Synchronized low-intensity panthoot	-0.04	0.44	0.06197
Play	0.19	0.09	**0.01049**
Greeting	0.11	0.19	**0.02549**
Travel	0.10	0.54	**0.03498**

Table S19.5 Duration of mutual grooming (r^2 = 0.586)

	Standardized coefficient	Standard error	*p*
Age	0.12	0.53	0.07246
Sex	-0.16	0.45	**0.007**
Kinship	-0.01	0.90	0.58871
Reproductive status	0.08	0.42	0.11044
Copulation	0.01	0.25	0.27386
Food sharing	-0.02	9.54	0.28936
Threat to dominate	-0.65	1.45	**0.006**
Give groom	0.03	0.11	0.21839
Mutually groom	1.14	1.97	**0.01049**
Receive groom	0.53	0.48	**0.0085**
Reassurance	-0.25	1.47	0.21439

Other threat	-0.03	0.58	0.31184
Synchronized high-intensity panthoot	0.01	0.27	0.5922
Solo high-intensity panthoot	0.01	0.40	0.35582
Synchronized low-intensity panthoot	0.05	0.58	0.08146
Play	-0.10	0.10	**0.01249**
Greeting	-0.05	0.21	0.11144
Travel	0.01	0.73	0.34483

Table S19.6 Duration of receiving grooming (r^2 = 0.338)

	Standardized coefficient	Standard error	*p*
Age	-0.07	0.50	0.24388
Sex	0.03	0.41	0.33033
Kinship	-0.03	0.85	0.30585
Reproductive status	0.10	0.41	0.11844
Copulation	-0.02	0.24	0.43228
Food sharing	-0.01	6.74	0.4038
Threat to dominate	0.04	1.29	0.32384
Give groom	0.01	0.10	0.52524

Mutually groom	-0.52	2.01	0.07346
Receive groom	0.90	0.53	**0.001**
Reassurance	-0.04	1.37	0.37881
Other threat	0.02	0.53	0.1919
Synchronized high-intensity panthoot	-0.02	0.20	0.37381
Solo high-intensity panthoot	-0.01	0.41	0.48626
Synchronized low-intensity panthoot	-0.01	0.60	0.56172
Play	-0.20	0.10	**0.002**
Greeting	-0.08	0.25	**0.04148**
Travel	0.02	0.55	0.13093

Table S19.7 Duration of visual attention towards dyad partner (r^2 = 0.641)

	Standardized coefficient	Standard error	*p*
Age	0.00	1.07	0.47326
Sex	0.01	0.86	0.43478
Kinship	0.16	1.96	**0.01349**
Reproductive status	0.23	1.06	**0.0015**

Copulation	0.02	0.53	0.26837
Food sharing	0.01	16.60	0.28686
Threat to dominate	-0.64	2.91	**0.0045**
Give groom	0.25	0.26	**0.01149**
Mutually groom	0.79	3.97	**0.02549**
Receive groom	0.51	0.96	**0.001**
Reassurance	-0.02	3.10	0.47926
Other threat	-0.01	1.16	0.51474
Synchronized high-intensity panthoot	-0.07	0.48	0.07146
Solo high-intensity panthoot	0.03	0.89	0.24588
Synchronized low-intensity panthoot	0.10	1.25	**0.04848**
Play	-0.09	0.24	**0.01799**
Greeting	-0.02	0.60	0.41529
Travel	0.04	1.33	0.14193

Table S19.8 Duration of visual attention away dyad partner (r^2 = 0.276)

	Standardized coefficient	Standard error	*p*

Age	0.33	1.87	**0.001**
Sex	-0.10	1.41	0.11044
Kinship	0.06	2.76	0.12744
Reproductive status	-0.03	1.35	0.38731
Copulation	0.01	0.84	0.32584
Food sharing	0.09	26.60	0.05147
Threat to dominate	0.10	4.63	0.25037
Give groom	0.24	0.37	**0.01999**
Mutually groom	-0.10	6.45	0.43478
Receive groom	0.38	1.55	**0.02249**
Reassurance	-0.29	5.47	0.2019
Other threat	-0.05	2.13	0.21489
Synchronized high-intensity panthoot	-0.09	0.72	**0.04998**
Solo high-intensity panthoot	0.01	1.47	0.33333
Synchronized low-intensity panthoot	0.13	2.06	**0.03598**
Play	-0.04	0.33	0.2044
Greeting	0.04	0.90	0.23938

Travel	0.06	2.13	0.09545

Table S19.9 Duration of time in close proximity – within 2 m (r^2 = 0.515)

	Standardized coefficient	Standard error	*p*
Age	0.23	2.15	**0.004**
Sex	-0.06	1.62	0.16442
Kinship	0.13	3.59	**0.04448**
Reproductive status	0.11	1.77	0.07546
Copulation	0.02	0.99	0.25287
Food sharing	0.07	29.25	0.10595
Threat to dominate	-0.29	5.50	0.09545
Give groom	0.30	0.47	**0.0075**
Mutually groom	0.38	8.36	0.16192
Receive groom	0.55	1.95	**0.006**
Reassurance	-0.21	6.33	0.27486
Other threat	-0.03	2.35	0.27936
Synchronized high-intensity panthoot	-0.10	0.89	**0.01299**
Solo high-intensity panthoot	0.03	1.70	0.25737

Synchronized low-intensity panthoot	0.14	2.59	**0.02399**
Play	-0.08	0.40	**0.04698**
Greeting	0.01	1.08	0.4013
Travel	0.06	2.56	0.09995

Table S19.10 Rate of scratch produced (r^2 = 0.465)

	Standardized coefficient	Standard error	*p*
Age	-0.05	0.55	0.30035
Sex	0.17	0.49	**0.03348**
Kinship	0.10	0.99	0.09045
Reproductive status	0.01	0.41	0.46977
Copulation	0.12	0.27	0.07396
Food sharing	-0.02	7.31	0.49425
Threat to dominate	0.19	1.42	0.1929
Give groom	0.10	0.11	0.10545
Mutually groom	0.48	2.05	0.15692
Receive groom	-0.12	0.46	0.16542
Reassurance	-0.20	1.54	0.32334

Other threat	0.48	0.65	**0.002**
Synchronized high-intensity panthoot	-0.04	0.23	0.33933
Solo high-intensity panthoot	-0.04	0.45	0.29785
Synchronized low-intensity panthoot	0.11	0.59	0.07496
Play	-0.05	0.11	0.1954
Greeting	0.07	0.25	0.14793
Travel	-0.04	0.60	0.27586

Table S19.11 Rate of scratch received (r^2 = 0.095)

	Standardized coefficient	Standard error	*p*
Age	0.09	0.72	0.1974
Sex	0.21	0.63	**0.03448**
Kinship	0.09	1.34	0.17041
Reproductive status	0.05	0.49	0.28336
Copulation	0.03	0.34	0.27186
Food sharing	-0.07	11.31	0.12894
Threat to dominate	0.01	1.88	0.3978

Give groom	-0.15	0.15	**0.02099**
Mutually groom	0.20	2.67	0.34183
Receive groom	0.10	0.60	0.24288
Reassurance	-0.35	2.01	0.26787
Other threat	0.02	0.71	0.27536
Synchronized high-intensity panthoot	-0.13	0.31	**0.01949**
Solo high-intensity panthoot	0.05	0.52	0.22139
Synchronized low-intensity panthoot	0.09	0.67	0.10795
Play	-0.05	0.14	0.28136
Greeting	0.08	0.35	0.17341
Travel	0.01	0.83	0.35132

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Supplementary Information 2

Social bonding, gestural complexity and displacement behaviour of wild chimpanzee

Table 1. Multiple Regression Quadratic Assignment Procedure (MRQAP) regression models predicting duration of social behaviour and rates of scratch from rates of gestural communication. Summary table provides standardized coefficients (standard errors) and *p* values. In all models, the dependent variable was the duration of behaviour in mins, per hour dyad spent within 10 meters or rates of scratch per hour dyad spent within 10 meters. Shaded lines indicate different MRQAP models for demographic variables and for each type of gestural communication. All models include the control variables relating to the age, sex, kinship and reproductive status of the dyad. Green shading indicates statistically significant positive relationships, red shading indicates statistically significant negative relationships. Full results for all models are provided in Supplementary Tables. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

	Joint activity			Groom			Attention		Proximity	Scratch	
Behaviour	Feed	Rest	Travel	Give	Mutual	Receive	present	absent		Produced	Received
Demography											
Age	-0.01 (0.65)	0.29 (1.37)**	0.28 (0.42)**	0.21 (0.54)*	0.20 (0.70)***	-0.09 (0.48)	0.12 (1.47)	0.37 (1.73)**	0.32 (2.50)***	0.02 (0.61)	0.02 (0.61)
Sex	0.31 (0.69)**	-0.14 (1.31)	0.05 (0.39)	0.11 (0.53)	0.12 (2.49)	0.20 (0.51)*	0.30 (1.55)**	-0.06 (1.28)	0.12 (2.49)	0.20 (0.56)*	0.20 (0.56)*
Kinship	0.28 (1.28)*	-0.02 (2.25)	0.01 (0.72)	0.10 (0.96)	0.15 (4.39)	-0.01 (0.88)	0.18 (2.62)	0.07 (2.78)	0.15 (4.39)	0.08 (1.14)	0.08 (1.14)
Reproductive status	0.22 (0.72)*	0.04 (1.46)	0.01 (0.43)	0.03 (0.42)	0.14 (3.55)	0.08 (0.63)	0.28 (2.12)*	0.04 (1.39)	0.14 (3.55)	0.03 (0.42)	0.03 (0.44)
Modality											
Visual	0.15 (0.07)	0.02 (0.15)	0.62 (0.04)*	-0.26 (0.04)**	0.88 (0.07)***	0.50 (0.06)*	0.75 (0.15)***	0.033 (0.179)	0.45 (0.28)*	0.48 (0.07)*	0.08 (0.07)
ASR	0.21 (0.11)*	0.13 (0.24)*	0.04 (0.05)	0.73 (0.09) ***	0.01 (0.08)	0.04 (0.08)	0.24 (0.19)*	0.290 (0.28)*	0.34 (0.39)*	0.13 (0.10)	-0.10 (0.10)*
ALR	-0.08 (0.13)	-0.06 (0.34)	-0.28 (0.08)**	0.19 (0.08)*	-0.51 (0.12)***	-0.27 (0.13)*	-0.44 (0.25)***	-0.03 (0.37)	-0.27 (0.48)**	-0.16 (0.13)*	-0.08 (0.14)
Tactile	-0.22	0.004	-0.02	0.41	-0.03	-0.20	-0.02	0.03	0.01	-0.07	-0.07

	Joint activity			Groom			Attention		Proximity	Scratch	
Behaviour	Feed	Rest	Travel	Give	Mutual	Receive	present	absent		Produced	Received
	(0.13)**	(0.29)	(0.07)	(0.08) ***	(0.10)	(0.12)***	(0.22)	(0.37)	(0.42)	(0.12)	(0.13)
Object use											
No object	0.03 (0.04)	0.10 (0.08)	0.47 (0.02)**	0.64 (0.04)**	0.64 (0.04)***	0.22 (0.03)*	0.69 (0.10)***	0.24 (0.10)*	0.56 (0.15)***	0.40 (0.03)*	-0.06 (0.03)
Object	-0.01 (0.08)	-0.08 (0.18)	-0.04 (0.04)	-0.20 (0.06)**	-0.15 (0.07)**	-0.04 (0.07)	-0.18 (0.14)**	-0.10 (0.20)	-0.17 (0.26)**	-0.02 (0.07)	-0.01 (0.08)
Multimodal											
Unimodal	0.16 (0.05)	0.06 (0.11)	0.22 (0.03)*	0.75 (0.04) ***	0.27 (0.04)*	0.25 (0.04)*	0.44 (0.09) ***	0.27 (0.13)*	0.44 (0.17)**	0.18 (0.04)*	-0.12 (0.05)
Multimodal (facial expression)	-0.13 (0.53)	0.06 (1.12)	0.30 (0.31)*	-0.23 (0.40)**	0.44 (0.47)*	0.001 (0.44)	0.31 (0.93)**	-0.04 (1.40)	0.14 (1.69)*	0.18 (0.49)*	0.06 (0.52)
Multimodal (vocal)	-0.07 (0.07)	-0.06 (0.16)	0.01 (0.04)	-0.07 (0.05)	-0.03 (0.06)	-0.09 (0.05)	-0.09 (0.12)*	-0.08 (0.19)	-0.11 (0.23)*	0.14 (0.06)	0.01 (0.07)
Repertoire size											
Dyadic repertoire size	-0.02 (0.04)	0.001 (0.10)	0.34 (0.03)**	0.26 (0.04)*	0.45 (0.05)**	0.14 (0.04)	0.42 (0.11)**	0.06 (0.12)	0.28 (0.20)*	0.35 (0.04)*	-0.04 (0.04)
Combined gestures											
Single (non-combined)	0.02 (0.04)	0.06 (0.10)	0.09 (0.02)	0.64 (0.04)	0.19 (0.04)	0.08 (0.04)	0.29 (0.09)**	0.18 (0.11)*	0.29 (0.16)	0.26 (0.04)*	-0.14 (0.04)
Combined	0.01 (0.16)	-0.03 (0.34)	0.41 (0.09)**	-0.19 (0.12)*	0.40 (0.16)**	0.13 (0.15)	0.30 (0.30)**	-0.03 (0.42)	0.15 (0.58) **	0.15 (0.15)	0.09 (0.16)
Attention											
Mutual	-0.04	0.10	0.12	0.78	-0.01	0.02	0.12	0.29	0.30	-0.03	-0.13

	Joint activity			Groom			Attention		Proximity	Scratch	
Behaviour	Feed	Rest	Travel	Give	Mutual	Receive	present	absent		Produced	Received
attention absent	(0.08)	(0.19)	(0.04)	(0.07) ***	(0.06)	(0.06)	(0.13)	(0.20)*	(0.24)**	(0.07)	(0.08)*
Mutual attention present	0.05 (0.06)	0.004 (0.16)	0.37 (0.04)**	-0.11 (0.04)*	0.63(0.07)**	0.21 (0.06)	0.56 (0.14)***	-0.03 (0.17)	0.26 (0.26)*	0.53 (0.06)*	0.05 (0.06)
Bodily and manual											
Bodily	0.067 (0.04)	0.06 (0.09)	0.50 (0.03)*	0.22 (0.03)*	0.58 (0.04)**	0.25 (0.04)*	0.55 (0.09)***	0.14 (0.12)	0.41 (0.16)*	0.55 (0.04)*	-0.02 (0.04)
Manual	-0.08 (0.09)	-0.01 (0.19)	-0.06 (0.05)	0.29 (0.07)*	-0.07 (0.08)	-0.09 (0.08)	-0.02 (0.15)	0.03 (0.23)	0.01 (0.31)	-0.18 (0.08)*	-0.06 (0.08)
Events											
Events	-0.01 (0.03)	0.04 (0.07)	0.40 (0.02)*	0.47 (0.03)*	0.45 (0.03)*	0.16 (0.02)	0.47 (0.07)***	0.15 (0.08)*	0.37 (0.12)*	0.36 (0.03)*	-0.07 (0.03)
Indicative											
Manual indicative	0.09 (0.41)	0.05 (1.03)	0.43 (0.28)*	0.17 (0.36)*	0.56 (0.46)***	0.17 (0.38)*	0.54 (0.95)***	0.09 (1.11)	0.37 (1.76)*	0.40 (0.43)*	0.01 (0.41)
Manual non-indicative	-0.08 (0.07)	0.01 (0.18)	0.04 (0.05)	0.35 (0.06)*	0.02 (0.07)	-0.02 (0.07)	0.06 (0.14)	0.07 (0.21)	0.08 (0.29)	-0.05 (0.07)	-0.07 (0.08)
Proximity											
Close	0.05 (0.05)	0.12 (0.12)*	0.27 (0.03)*	0.76 (0.05)***	0.39 (0.05)*	0.15 (0.04)	0.50 (0.12)*	0.29 (0.15)*	0.48 (0.21)***	0.21 (0.05)*	-0.11 (0.05)*
Far	-0.06 (0.04)	-0.05 (0.11)	0.22 (0.03)*	-0.11 (0.03)*	0.22 (0.04)*	0.05 (0.04)	0.13 (0.09)*	-0.07 (0.12)	0.03 (0.15)	0.24 (0.04)*	0.01 (0.05)
Repetitive											
Non-repetitive	-0.07 (0.05)	0.03 (0.10)	0.56 (0.03)*	-0.06 (0.04)	0.73 (0.05)***	0.21 (0.04)*	0.57 (0.10)*	0.03 (1.36)	0.33 (0.18)*	0.42 (0.042)*	0.05 (0.05)
Repetitive	0.09 (0.05)	0.02 (0.13)	-0.09 (0.03)	0.61 (0.05)***	-0.19 (0.04)*	-0.04 (0.04)	-0.01 (0.09)	0.01 (0.13)	0.11 (0.19)	-0.01 (0.05)	-0.14 (0.05)*

	Joint activity			Groom			Attention		Proximity	Scratch	
Behaviour	Feed	Rest	Travel	Give	Mutual	Receive	present	absent		Produced	Received
Homogeneity											
Heterogeneous	0.01 (0.08)	-0.02 (0.20)	-0.03 (0.05)	0.11 (0.07)	-0.15 (0.08)*	-0.01 (0.08)	-0.09 (0.15)*	0.04 (0.23)	-0.03 (0.30)	0.05 (0.08)	-0.03 (0.09)
Homogeneous	-0.01 (0.04)	0.08 (0.11)	0.43 (0.03)*	0.52 (0.04)*	0.60 (0.05)***	0.17 (0.04)*	0.60 (0.10)**	0.17 (0.12)*	0.45 (0.18)***	0.38 (0.042)*	-0.08 (0.04)
Sequences											
Single (no sequence)	0.08 (0.06)	0.08 (0.15)	0.22 (0.04)*	0.66 (0.06)**	0.33 (0.06)*	0.16 (0.05)	0.47 (0.13)*	0.23 (0.17)*	0.42 (0.25)***	0.08 (0.05)	-0.14 (0.06)*
Rapid sequence	-0.06 (0.19)	-0.03 (0.47)	0.20 (0.11)*	0.03 (0.13)	0.16 (0.17)*	0.01 (0.16)	0.09 (0.36)	-0.01 (0.48)	0.04 (0.65)	-0.02 (0.15)	0.01 (0.19)
Persistence	-0.03 (0.53)	0.03 (1.25)	0.14 (0.29)*	-0.05 (0.38)	0.16 (0.48)*	0.05 (0.46)	0.09 (1.04)	0.02 (1.49)	0.06 (1.86)	0.57 (0.50)***	0.06 (0.51)
Penile erection											
Penile erection	0.04 (0.22)	-0.01 (0.49)	0.07 (0.14)	0.02 (0.20)	-0.04 (0.23)	-0.04 (0.21)	-0.01 (0.47)	-0.01 (0.62)	-0.01 (0.80)	0.10 (0.22)	0.01 (0.23)
Piloerection											
Piloerection	-0.04 (0.04)	-0.02 (0.10)	0.38 (0.03)*	0.09 (0.04)	0.42 (0.04)*	0.14 (0.04)	0.35 (0.10)*	0.02 (0.13)	0.21 (0.17)*	0.24 (0.04)*	-0.05 (0.04)
Gesture function											
Copulation	0.05 (0.31)	0.01 (0.84)	0.05 (0.18)	-0.01 (0.21)	0.01 (0.25)	-0.02 (0.24)	0.02 (0.53)	0.01 (0.84)	0.02 (0.99)	0.12 (0.27)	0.03 (0.34)
Food sharing	0.1 (8.36)	0.01 (23.98)	-0.01 (5.05)	-0.01 (6.39)	-0.02 (9.54)	-0.01 (6.74)	0.01 (16.6)	0.09 (26.6)	0.07 (29.25)	-0.02 (7.31)	-0.07 (11.31)
Threat to dominate	-0.5 (1.64)*	-0.2 (3.57)	0.03 (1.1)	-0.2 (1.17)	-0.65 (1.45)**	0.04 (1.29)	-0.64 (2.91)**	0.1 (4.63)	-0.29 (5.5)	0.19 (1.42)	0.01 (1.88)
Give groom	0.17 (0.13)*	0.11 (0.31)	0.05 (0.07)	0.69 (0.12)***	0.03 (0.11)	0.01 (0.1)	0.25 (0.26)*	0.24 (0.37)*	0.3 (0.47)**	0.1 (0.11)	-0.15 (0.15)*

	Joint activity			Groom			Attention		Proximity	Scratch	
Behaviour	Feed	Rest	Travel	Give	Mutual	Receive	present	absent		Produced	Received
Mutually groom	0.66 (2.39)	0.1 (6.48)	0.03 (1.42)	-0.1 (1.45)	1.14 (1.97)*	-0.52 (2.01)	0.79 (3.97)*	-0.1 (6.45)	0.38 (8.36)	0.48 (2.05)	0.2 (2.67)
Receive groom	0.47 (0.55)*	0.08 (1.44)	0.08 (0.32)	0.2 (0.33)*	0.53 (0.48)**	0.9 (0.53)**	0.51 (0.96)**	0.38 (1.55)*	0.55 (1.95)**	-0.12 (0.46)	0.1 (0.6)
Reassurance	-0.59 (1.87)	0.03 (4.55)	0.37 (1.02)	0.2 (1.08)	-0.25 (1.47)	-0.04 (1.37)	-0.02 (3.1)	-0.29 (5.47)	-0.21 (6.33)	-0.2 (1.54)	-0.35 (2.01)
Other threat	-0.02 (0.71)	-0.03 (1.75)	-0.05 (0.39)	-0.06 (0.47)*	-0.03 (0.58)	0.02 (0.53)	-0.01 (1.16)	-0.05 (2.13)	-0.03 (2.35)	0.48 (0.65)**	0.02 (0.71)
Synchronized high-intensity panthoot	-0.08 (0.29)	-0.07 (0.66)	-0.06 (0.14)	0.03 (0.18)	0.01 (0.27)	-0.02 (0.2)	-0.07 (0.48)	-0.09 (0.72)*	-0.1 (0.89)*	-0.04 (0.23)	-0.13 (0.31)*
Solo high-intensity panthoot	0.02 (0.53)	-0.01 (1.34)	0.1 (0.3)	0 (0.34)	0.01 (0.4)	-0.01 (0.41)	0.03 (0.89)	0.01 (1.47)	0.03 (1.7)	-0.04 (0.45)	0.05 (0.52)
Synchronized low-intensity panthoot	0.14 (0.69)*	0.05 (2)	0.26 (0.45)*	-0.04 (0.44)	0.05 (0.58)	-0.01 (0.6)	0.1 (1.25)*	0.13 (2.06)*	0.14 (2.59)*	0.11 (0.59)	0.09 (0.67)
Play	-0.19 (0.13)**	-0.04 (0.27)	-0.03 (0.07)	0.19 (0.09)*	-0.1 (0.1)*	-0.2 (0.1)**	-0.09 (0.24)*	-0.04 (0.33)	-0.08 (0.4)*	-0.05 (0.11)	-0.05 (0.14)
Greeting	-0.11 (0.3)	0.04 (0.75)	0.01 (0.17)	0.11 (0.19)*	-0.05 (0.21)	-0.08 (0.25)*	-0.02 (0.6)	0.04 (0.9)	0.01 (1.08)	0.07 (0.25)	0.08 (0.35)
Travel	0.05 (0.81)	0.03 (1.73)	0.1 (0.44)*	0.1 (0.54)*	0.01 (0.73)	0.02 (0.55)	0.04 (1.33)	0.06 (2.13)	0.06 (2.56)	-0.04 (0.6)	0.01 (0.83)