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Gestural repertoire size is associated with social proximity measures in wild chimpanzees

Short running title: Chimpanzee gesture repertoire and sociality

Authors: Anna Ilona Roberts[1*], Anwesha Chakrabarti[2], Sam George Bradley Roberts[3]

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Affiliations:

[1]Department of Psychology, University of Chester, Chester; Parkgate Road, Chester CH1 4BJ, UK

[2]Department of Psychology, University Colleges of Science, Technology and Agriculture, University of Calcutta, 92, Acharya Prafulla Chandra Road, Kolkata- 700009, West Bengal, India.

[3]School of Natural Sciences and Psychology, Liverpool John Moores University, Byrom Street, Liverpool, L3 3AF

*Correspondence to: anna.roberts@chester.ac.uk

Abstract

Studying the communication systems of primates can provide insights into the evolutionary origins of human language. Some theories propose that language evolved to help meet the demands of managing complex social relationships. Examining the associations between sociality and communication in the great apes can help to identify the specific selection pressures that may have been important for language evolution. In particular, gestural communication is believed to be important because it is a relatively recent trait seen only in primates and particularly in the great apes. However, the extent to which more complex gestural communication plays a role in managing social relationships, as compared to less complex gestural communication, is not well understood. Using social network analysis, we examined the association between complex gesturing (indexed as repertoire size) and complexity of social relationships indexed as proximity (the duration of time spent within 10 m, per hour spent in same party) in wild chimpanzees (*Pan troglodytes schweinfurthii*). Repertoire size (the total number of gesture types a focal subject produced towards other individuals) and dyadic repertoire size (the number of gesture types produced towards the dyad partner, per hour spent within 10 meters) were positively associated with proximity at the level of the group (centrality in the proximity network) and the dyad (proximity duration between dyads) respectively. Further, the repertoire size of visual and auditory short-range gestures was positively associated with proximity, whilst the repertoire size of tactile gesture was negatively associated with proximity. Overall these results suggest that gestural repertoire size has important implications for maintaining social relationships in wild chimpanzees and more broadly that gestural communication may have played an important role in language evolution.

Keywords: gesture, repertoire size, proximity, social network, chimpanzee, fission-fussion social system

Introduction

The evolutionary origins of language, and whether precursors to language can be found in primate communication systems, has long been one of the key unresolved questions regarding human evolution [Bickerton, 1987; Dunbar, 1993; King, 1994]. Language can be defined as a system of communication, cognition and emotion and some theories propose that language evolved to allow for an improved ability to manage and regulate a differentiated set of social relationships in social groups [Aiello and Dunbar, 1993]. Complex social systems have been defined as those in which individuals interact in many different contexts with many different individuals [Freeberg et al., 2012]. In large and complex social groups, as compared to smaller and less complex groups, there are more relationships to track and a greater range of different types of social relationships [Dunbar and Shultz, 2010]. This means that individuals in large groups spend a higher amount of their time forming and maintaining social relationships with others, as compared to individuals in smaller groups. Complex communication systems, defined as those which contain a larger number of structurally and functionally distinct elements (e.g. a larger repertoire size) [Freeberg et al., 2012; Shannon et al., 1951], may help primates meet the demands arising from creating and maintaining social bonds with conspecifics, thereby permitting emergence of larger and more complex social groups [Roberts, 2018].

Gestures in primates are defined as voluntary movements of the arms, head, body postures and locomotory gaits [Hewes, 1992; Liebal et al., 2004a; Nishida et al., 2010; Plooij, 1978; Tomasello et al., 1985]. Gestures occur in different modalities according to the means by which the gesture can be perceived by the recipient [Liebal et al., 2006; Pika et al., 2003; Pika et al., 2005b]. 'Visual gestures' are silent and therefore visual contact between the signaller and receiver is necessary for these gestures to be perceived by the recipient. In contrast 'tactile gestures' involve contact with recipient's body and can be perceived through tactile sensation, whether or not the audience is visually attentive. ‘Auditory gestures’ produce an audible sound that may differ in amplitude, therefore making these gestures detectable from a short distance (short-range auditory gestures) or from further away (long-range auditory gestures) without visual contact between the signaller and the receiver [Byrne et al., 2017]. This flexibility and diversity in gestural communication may be important for primates in groups to successfully maintain a large set of differentiated social relationships, as it may allow signallers to coordinate behaviour with the recipient more effectively, thereby enabling individuals to respond adaptively in social situations [Roberts and Roberts, 2016b].

One measure of the complexity of a communication system is the reduction in uncertainty following the signal [Berger and Calabrese, 1975; Shannon et al., 1951] and predictability in social relationships is a major modulator of stress in primate groups [Seyfarth and Cheney, 2013]. A more complex and diverse gestural repertoire may give the recipient a greater degree of certainty in predicting the signallers future behaviour, reducing the stresses inherent in group living and allowing proximity to be maintained between the signaller and recipient for a longer duration of time. In humans such increases in certainty about future behaviour can facilitate the development of close social bonds and the coordination of activities [Spoor and Kelly, 2004]. This suggests that the size of the repertoire of signals may be an important factor enabling the maintenance of the differentiated social relationships characteristic of complex societies [Cantor et al., 2015].

Some studies suggest that in nonhuman primates the gestural repertoire size is strongly influenced by kinship [Hobaiter and Byrne, 2011a; Pika et al., 2005a; Tomasello et al., 1985]. However, social influences, such as audience effects [Bourjade et al., 2018; Roberts and Roberts, 2015], intentionality [Bullinger et al., 2011; Cartmill and Byrne, 2007; Fröhlich et al., 2016a; Leavens et al., 2005; Liebal et al., 2006; Moore, 2016; Pika et al., 2005a; Pika et al., 2005b; Roberts and Roberts, 2018a; Roberts et al., 2013; Roberts et al., 2014b] and learning [Halina et al., 2013; Roberts and Roberts, 2017] shape the diversity of gestures across animals. Examining how variation in the size of the gestural repertoire among nonhuman primates relates to social bonding and the structuring of social interactions therefore provides key information relating to the role of repertoire of gestural communication in primate sociality.

The overall repertoire of gestural communication in primates is differentiated by modality and this may have an influence on both the repertoire size and on flexibility in the production of gestures. Some modalities may be better suited to social bonding and social coordination than others, in terms of influencing the behaviour of the recipient [Roberts and Roberts, 2016a]. Social relationships based on close proximity tend to occur between individuals who are close in rank and the lack of prior consensus about the direction of potential aggression reduces individual certainty in social relationships [Ay et al., 2007; Flack et al., 2006]. Visual gestures may be better suited to managing these relationships in regular one on one interactions, because these gestures might appear less forceful and therefore might create a positive perception of fitness rewarding intent of the signaller [Roberts and Roberts, 2016a]. However, the lack of forcefulness in visual gestures implies that when managing social interactions, a larger repertoire of visual gestures could contribute to a reduction in the uncertainty following the gesture, and more efficient coordination with the recipient. In contrast, long-range auditory gestures might be more forceful and therefore straightforward for the recipient to respond to, but might sometimes carry the implication of a negative fitness outcome for the recipient as they can be used in agonistic contexts [Roberts and Roberts, 2016a]. Thus a large repertoire of such auditory long-range gestures would not necessarily contribute to a reduction in uncertainty in the recipient [Roberts and Roberts, 2016a].

Previous studies on primates have used cross-species comparisons to examine the relationship between the repertoire size of vocal communication and sociality [McComb and

Semple, 2005], or the size of gestural repertoire according to the characteristics of the species [Maestripieri, 2005]. However, much of this research has been carried out in the vocal domain [Arlet et al., 2015; Fedurek et al., 2013; Mitani et al., 1999; Mitani and Gros-Louis, 1998; Schel et al., 2013] and there is a lack of knowledge of how the repertoire size of gestural communication relates to the characteristics of the social network– the number and strength of social bonds maintained between conspecifics.

East African chimpanzees are a particularly valuable species to assess this question. Chimpanzees live in fission-fusion communities within which they associate temporarily in subgroups (‘parties’) that vary in size, composition and duration [Goodall, 1986]. Individuals in the community are often spatially and temporarily separated but nonetheless recognise each other and maintain long-term relationships [Foerster et al., 2015; Langergraber et al., 2009; Mitani, 2009; Mitani et al., 2002; Roberts and Roberts, 2016b]. Maintaining the differentiated set of social relationships that arises from this fission-fusion structure is hypothesised to be a key driver of communicative complexity [Freeberg et al., 2012; Roberts and Roberts, 2016b]. Chimpanzees use grooming and communication to establish and maintain social relationships [Babiszewska et al., 2015; Bard et al., 2014; Bard et al., 2017; Fedurek et al., 2013; Fedurek and Slocombe, 2013; Fedurek et al., 2015; Mitani et al., 1999; Mitani and Brandt, 1994; Mitani and Gros-Louis, 1998; Watts, 2006]. In particular, proximity and grooming co-vary with the aspects of the communicative repertoire of vocalisations (e.g. panthoot and food-calls) [Fedurek et al., 2013; Fedurek and Slocombe, 2013; Mitani and Brandt, 1994; Mitani and Gros-Louis, 1998; Mitani and Nishida, 1993; Schel et al., 2013]. However, the unique character of chimpanzee gestural communication is that it encompasses flexible actions at a distance, where all parts of the chimpanzee body are employed as a medium of social communication [Blute, 2006; Sterelny, 1998]. Hence, it could be predicted that gestural communication would be useful in effectively managing social relationships with conspecifics, as reflected in the relationship between gesture repertoire size and patterns of social bonding.

Thus far research on gesture repertoires in wild chimpanzees has focused on establishing the number and type of gestures used across primate species [Hobaiter and Byrne, 2011a; Liebal et al., 2004a; Pollick and de Waal, 2007; Roberts et al., 2014a; Roberts et al., 2012b; van Hooff, 1971], and wild adult chimpanzees have a mean repertoire size of 49 gesture types [Roberts et al., 2014a; Roberts et al., 2012b]. However, the role that the size of the repertoire of gestural communication plays in social relationships is not well understood for either captive or wild chimpanzees. Here we examine how the size of the individual repertoire (the total number of gesture types that one individual has in their repertoire) and how the repertoire size of gestural communication directed at the partner (per hour spent in close proximity) is associated with differing levels of close proximity in wild chimpanzees. By examining the influence of repertoire size on the duration of time spent in close proximity, the role that gestural behaviour plays in social bonds and social organisation can be assessed.

Methods

Study site and subjects

Six adult males and six adult females from the Sonso community of East African chimpanzees (*Pan troglodytes schweinfurthii*) at the Budongo Conservation Field Station, Budongo Forest Reserve in Uganda, East Africa (1°35' and 1° 55'N and 31° 08'and 31°42' E, www.budongo.org) were subject of this study. The Budongo Forest reserve is one of the largest national reserves in Uganda, occupying an area of approximately 793 km^2 at a mean attitude of 1,050 m and includes 482 km^2 of continuous medium-altitude semi-deciduous forest. The study site has previously been used for logging with the forest now in the form of secondary growth, restricting visibility [Reynolds, 2005]. We observed focal subjects in September 2006, between April and July 2007 and between March and June 2008. The individual repertoire size was computed from the data collected during all three study periods. The dyadic repertoire size and social proximity measures were collected during the last study period (March - June 2008). At the beginning of the socio-ecological data collection in March 2008, the Sonso community of chimpanzees consisted of approximately 75 named individuals, 10 adult males and 22 adult females. Only chimpanzees well habituated to observation and who had no limb or other injuries that could potentially affect gestural communication were chosen as focal subjects. All details of the focal subjects, their age, sex, and observation duration are given in Table 1.

Data collection protocol

We used quantitative focal animal follows and chose focal subjects systematically by choosing to follow each of the subjects at least once a week when they were present in the party. We recorded the focal subject's social behaviour and communication during a standardized observation period of 18 minutes, leaving at least a 20 minute interval between consecutive samples of the same focal subjects. As much as possible we aimed to avoid sampling the same focal subject consecutively. Only the behavior of the focal subject and the individuals present in the same party was recorded. A party was defined as a group of individuals within a spread of 35 m. Two types of behavioral data were recorded during the 18 minute focal follows. First, 9 scans each at 2 minutes interval (nine 2-minute intervals) recorded the individuals present within 10 m of the focal subject and the individuals more than 10 m away that were in the same party). Second, concurrently with collecting 9 scans of proximity, we used a video camera to record chimpanzee gestures continuously throughout the 18 minute focal follow. As we observed gestures occurring, we verbally recorded into the camera the behavior of the signaler and recipient, along with the context of the signal production. Although collected concurrently, the data collection of gestures was performed by a different researcher from the data collection of proximity and thus the collection of data on proximity and gestures were performed independently. The concurrent data collection was synchronized between two researchers by using a pager. Thus for each 18 minute focal follow, one researcher was video recording the gestural communication whilst the other researcher was recording the proximity of individuals to the focal chimpanzee at 2 minute intervals. The sampling of association pattern was done with the help of an experienced field assistant who was unaware regarding the aims of the study. An inter-observer reliability test of the chimpanzee identities and proximities is conducted annually to maintain the consistency of the scoring of the group composition and proximity across the field assistants. The Spearman's rank correlation coefficient for this test is at least or above 0.85. This data collection protocol provided a detailed and accurate picture of the patterns of behavioral interactions (proximity, gestures) in the focal chimpanzees.

Video analysis and classification of gestural communication

First, we derived an inventory of gesture types from the video recordings [Roberts et al., 2012b]. The cases of any nonverbal behavior that may act as a gesture were noted and behavior classified as a gesture if it met following criteria: 1) the non-verbal behavior was an expressive movement of the limbs or head and body posture that was mechanically ineffective, 2) the behavior was communicative by non-mechanical means (i.e. consistently produced a change in the behavior of recipient or facilitated maintenance of activity, e.g. grooming). Next, behavior had to be goal directed to be considered intentional [Bard, 1992; Bates et al., 1979]. We used audience presence and visual attention to score the behavior as intentional, following the example described by Tomasello et al. [1985]: 'a child might be struggling to open a cabinet, crying and whining as s/he struggles. Seeing this, the mother might come to the rescue and open the cabinet. This is a perlocutionary act because, while communication may be said to have occurred, the "sender" (the child) did not intentionally direct any behavior towards the mother. If, on the other hand, the child has turned its attention from the cabinet to the mother and whined at her, the whining now becomes a social-communicatory act with the intention of obtaining adult aid'.

In this dataset, all cases of gesturing included the presence of an audience within 10 meters. In addition, another criterion for defining intentionality (directing visual attention at the recipient by the signaler) was fulfilled by the gestures. The mean percentage ± SD [95% CI] of cases of all gesture types associated with the presence of bodily orientation by the signaller towards the recipient during the production of the gesture was 91.5 ± 18.5%, [87, 95]. Finally, the criterion of communicative persistence was coded to identify intentional gestures. Following the classification by Hobaiter and Byrne [2011b], persistence of gesturing was scored when the chimpanzee produced one gesture or a gesture sequence, then after a period of response waiting (1-5s) they produced another gesture. The details of intentionality criteria scoring by each gesture type and each criterion separately can be found in [Roberts and Roberts, 2018a]. Validation of the coding procedure was established by a second coder who scored a random sample of 45 of the sequences of gestures for concordance in function and modality. The Cohen's Kappa coefficient showed that reliability was good for function (K = 0.70) and modality of gesturing (K = 0.946) [Bakeman and Gottman, 1997]. A different sample of 50 sequences of gestures was coded by a second coder for intentionality (response waiting and persistence) and the Cohen's Kappa coefficient showed good reliability (K = 0.74).

Behavioral Data

Gesture events were scored in accordance to whether they occurred singly or in sequences, defined as one or more than one gesture made consecutively by one individual, towards the same recipient, with the same goal, within the same context, and made within a maximum of 30 seconds interval to ensure independence. Single gestures and sequences can be categorized as uni-modal gestures which are gestures from a single modality (e.g. only visual gestures) or multi-modal gestures, which are gestures from more than one modality (e.g. both visual and auditory gestures). For instance, a single gesture can be multimodal if the signaller produces two gesture types of different modality simultaneously, e.g. arm waving and stomping. A sequence of the gestures can be multimodal if the signaller produces two gesture types of different modality consecutively, e.g. arm waving and then stomping. Here we did not refer to gestures as multimodal if one behavior could be classified as having two different modalities simultaneously (e.g. a single tactile gesture can be both felt and seen). In these instances, the gesture was classified as belonging to the modality with the higher intensity – so tactile or auditory gestures over visual gestures (e.g. a single tactile gesture would be classified as tactile rather than visual). It was important to identify unimodal and multimodal single gesture and sequences because if the sequence was multimodal and we identified the repertoire of each modality type from these sequences, the data may be dependent as the repertoire size could overlap across modalities, meaning some events would be counted twice (e.g. arm wave and stomping). Thus, to reduce the dependency in the dataset, in all analyses, repertoire size was calculated using uni-modal single gestures and sequences only. This was so the patterns of association between gestures of different modalities and proximity could be examined.

For instance, if the unimodal communication produced by chimpanzee A towards chimpanzee B (AB dyad) was one sequence consisting of three gestures and which contained three different gesture types, and a single gesture containing one different gesture type, then four gesture types would be recorded as directed from A to B. Then the rate of gestures, per hour the AB dyad spent within 10 m, would be calculated to give the dyadic repertoire size for A to B, i.e. the number of gesture types A produced towards B, per hour spent within 10 m of B. If a single gesture event was a combination of two gesture types of the same modality type (e.g. two visual gestures), this would have been recorded as two gesture types. Given the wide variety of multi-modal gestural sequences (sequences that contain some combination of the four gestural modalities), also examining how different types of multi-modal gesture sequences are associated with proximity was beyond the scope of this paper.

Moreover, in this work we only took into account those instances of gestural communication when the intended recipient of the gestural communication was within 10 m of the signaller. Previous research in a mating context has shown that primates approach the recipient before communicating gesturally [Liebal et al., 2004b] at a mean distance of 6.4 m [Roberts and Roberts, 2015], when all distances between signalers and the recipients while communicating were taken into account in mating contexts (i.e. when the recipient was both within and above 10 m away from the signaller). The distance of 10 m was chosen in order to avoid bias in results towards the communication patterns that are limited to very close proximity (e.g. gestures made during grooming) and to avoid excluding those communication patterns that may be important for social bonding but are often used at a longer distance (e.g. to initiate or maintain travelling), whilst taking into account the ability of the recipient to perceive the signal [Roberts and Roberts, 2016b].

Next, to ensure that the sampling procedure did not bias our results, we examined whether there was a similarity in association patterns between scans taken at 2 (scan 1), 4 (scan 2) and 18 minutes (scan 9) interval of the focal sample including both sexes. These analyses showed that there was no significant difference in the number of times focal and non-focal subjects were in close proximity within the samples but there was a difference between the samples [Roberts and Roberts, 2016b]. The behavioural measures were then derived and the method can be summarized by the following equations:

The dyadic association measure

The dyadic association measure (DA) is the duration of time focal subject A spent in close proximity (within 10 meters) to non-focal subject B per hour spent in the same party, or:

$DA_{AB} = [(P10_{AB}*2)* 60)] /PSP_{AB}*2$

where $P10_{AB}$ = the number of times A was in close proximity (within 10 m) to B

PSP_{AB} = the number of times A was in the same party as B

2 = duration of instantaneous subsample interval in minutes

60 = the number of minutes in an hour

Note that the multiplication by 60 enabled meaningful comparisons between indices (see below).

The dyadic communication measure

The dyadic communication measure (CA) which represents the rate focal subject A communicated to non-focal subject B when B was in close proximity (within 10 m) to focal subject A per hour spent within 10 m of the non-focal subject B, or:

$CA_{AB} = (C_{AB}* 60) / P10_{AB} *2$

where C_{AB} = the number of times A communicated with B when in close proximity (within 10 m) to B

$P10_{AB}$ = the number of times A was in close proximity (within 10 m) to B

2 = duration of instantaneous subsample interval in minutes

60 = the number of minutes in an hour

Attribute measures

Proximity between pairs of chimpanzees can be associated with biological factors such as the reproductive status of the dyad, age, sex and kinship [Langergraber et al., 2009; Mitani et al., 2002; Roberts and Roberts, 2016a; Roberts and Roberts, 2017; Roberts and Roberts, 2018a;

Roberts and Roberts, 2018b; Roberts and Roberts, 2016b]. The genetic relationships of this community of chimpanzees have been previously determined and we used this information to classify the dyads as maternally related or not [Reynolds, 2005]. Moreover, the age of most of the subjects in the community is known from long term project records. Wild chimpanzees reach physical and social maturity between ages 15 – 16 years old [Goodall, 1986]. We classified dyads of chimpanzees as belonging to the same (5 years or less age difference) or a different (above 5 years age difference) age class following previous studies [Mitani et al., 2002]. The reproductive status was scored on the basis of the presence of the female sexual swelling. Females who displayed swelling and were seen mating with the males were scored as reproductively active – see ESM Table 1 for further explanation of the attribute variables used in this study. In all analyses we controlled for these biological attributes.

Social network analysis:

The details of social network analysis have been previously described [Roberts and Roberts, 2016a]. We entered weighted behavioral data into 12 rows and 12 columns representing 12 focal chimpanzees. However, the weighted network matrices cannot distinguish between ‘reciprocated’ and ‘one-sided’ relationships and therefore in order to distinguish between different types of social relationships based on patterns of association, three binary proximity networks were created with ‘1’, indicating a presence of a bond and ‘0’ indicating absence of a bond. First, we created a binary proximity network, where dyads of individuals who had values of proximity association equal or above the mean plus half SD (who spent 30.3 or more minutes in close proximity, per hour spent in the same party), were scored as 1 if the proximity was reciprocated (i.e. both A to B and B to A displayed values of close proximity association equal or above 30.3 minutes duration - ‘preferred reciprocated close proximity bonds’), whereas other dyads were scored as 0. Second, a binary network was created, where dyads of individuals who had values of proximity association equal or greater than the mean plus half SD, were scored as 1 when the proximity was non-reciprocated (i.e. only A to B but not B to A had duration of proximity association equal or above the 30.3 minutes - ‘preferred, non-reciprocated close proximity bonds’), whereas other dyads were scored as 0. Third, the binary proximity network was created, where dyads of individuals who had values of proximity association equal or below the mean minus half SD (who spent 16.23 or less minutes in close proximity to each other per hour spent in same party), were scored as 1 (‘non-preferred close proximity bonds’), whereas other dyads were scored as 0.

Moreover, from the network matrix the normalized degree centrality was calculated [Croft et al., 2010]. This normalized degree centrality is the average value of a specific behavior for each focal individual. As the communication networks are directed, indegree and outdegree were calculated separately. Outdegree is the behavior of the focal individual towards the conspecifics. (e.g. gestures produced by the focal chimpanzee) whilst indegree refers to the behaviors of conspecifics toward the focal individual (e.g. gestures received by the focal chimpanzee). Degree centrality was used rather than other measures of centrality which take into account indirect ties, such as eigenvector centrality or beta centrality [Borgatti et al., 2013]. These measures of centrality are based not just on the direct ties between chimpanzees A and its conspecifics, but also the ties present between conspecifics. Degree centrality provides a clearer indication of the direct ties of focal chimpanzees have with their conspecifics in the network and thus the likely costs of maintaining these relationships, since it incorporates frequency and number of interactions that the focal individual is directly involved with. Further, recent simulation analysis shows that when only part of a network is sampled, degree centrality is a more reliable measure than more complex measures of centrality (such as betweenness or eigenvector centrality), which are more reliant on accurately measuring the complete network structure [Silk et al., 2015].

For data transformation and analysis we used UCINET 6 for Windows [Borgatti et al., 2014]. Social network matrices cannot be analysed by normal inferential statistical techniques, as the observations that make up network data are not independent of each other. Instead, a set of 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 [Borgatti et al., 2013]. For analysis of relationships between different behavioural networks, we used the Multiple Regression Quadratic Assignment Procedure (MRQAP) [Borgatti et al., 2013]. This is similar to a standard regression model because it enables the association between a number of predictor variables (gestural communication networks of different modalities, control variables relating to sex and age) and a single outcome variable (proximity network) to be examined. Among the different types of MRQAP regression, we used the Double Dekker Semi Partialling MRQAP regression, as it is more robust against the effects of network autocorrelation and skewness in the dataset [Dekker et al., 2007]. For this analysis, 2,000 permutations were used. For the node level regressions we used a similar procedure, using 10,000 random permutations to assess the effect of several predictor variables (such as the outdegree of gestures and sex of focal chimpanzee) on the outcome variable (the proximity outdegree). We used node-level regressions to examine the predictors of proximity in degree by the dyadic repertoire in and outdegree. In these analyses the average value of the proximity network matrix was taken to calculate the normalised degree centrality for each individual chimpanzee (N = 12) [Croft et al., 2010]. The rate of the behaviour directed by conspecifics towards the focal chimpanzee determines indegree of given behavior, whilst outdegree indicates the rate of the behaviour directed by the focal chimpanzee towards the conspecifics. In addition, the node-level regression was used to examine the predictors of proximity indegree by individual repertoire size. In these analyses the average value of the strong proximity bond network matrix, where dyads of individuals who had values of proximity association equal or above the mean plus half SD, were scored as 1 (‘strong bonds’) and taken to calculate the normalized degree centrality for each individual chimpanzee (N = 12) [Croft et al., 2010]. Finally, we used Geary’s C statistics to examine the autocorrelation between attribute data (the total duration of observation) and network data (gestural networks). This statistic has a value of 1 for no association, with values of less than 1 indicating a positive association and values of more than 1 indicating a negative association.

Sampling effort:

In this study, a mean of 12.52 (range 8.33 – 18.63) hours of independent focal data per individual subject was used to compute the dyadic repertoire size and sociality indices. This mean value pertains only to the duration of 18-minute focal follows during which scan samples were collected at 2 minute intervals during March and June 2008. This length of observation of gestural communication of each focal subject in relation to social factors is much greater than previously reported in studies that examined gestural communication (e.g. 3 – 5 hours of focal observation duration) [Hobaiter et al., 2017; Wilke et al., 2017]. Geary’s C statistic was used to examine the autocorrelations between the total duration of observation for each focal chimpanzee and gesture networks. There was not a statistically significant relationship between the total duration of observation and the networks for the repertoire size of gestures overall (C = 1.054, p = 0.402) or any of the gesture modalities separately - auditory long range gestures (C = 0.412, p = 0.118), auditory short range gestures (C = 0.758, p = 0.290), visual gestures (C = 0.756, p = 0.161) and tactile gestures (C = 1.029, p = 0.445). This suggests that the sampling duration for each dyad was not systematically related to the gestural repertoire size observed in communication between that dyad, and that the sampling duration was therefore sufficient.

Results

Asymptote of repertoire size

To ensure that the repertoire in our study approached or reached an asymptote, we examined the relationship between the cumulative frequency of gesture types produced by focal subjects across the entire study period. This included 3,237 gesture events, spanning 8 months of observation in the field and 107 days in which gestures were observed. Previous studies focusing on gestures in wild chimpanzees suggested that repertoire asymptote of all focal subjects combined can be achieved after approximately 150 days of field observation time (focusing on subadult subjects in all contexts) [Hobaiter and Byrne, 2011a], or 20 days of field observation time (focusing on mother-infant interactions in joint travel contexts) [Fröhlich et al., 2016b]. In our study of adult chimpanzee gestures and across all contexts, the focal subject's repertoire approached or reached an asymptote after 90 days of field observation time (Fig. 1).

How is dyadic repertoire size of gestures related to context?

The definitions of gesture functions are given in ESM Table 2. Full details of all models reported in this study can be found in ESM Tables 3 – 11. First, we examined the relationship between the dyadic repertoire size of each modality of gestures and their function. The details of gesture categorization according to modality and function can be found in Table 2. Significant associations indicate that for pairs of chimpanzees, larger gestural repertoire sizes were observed in specific contexts. The significant predictors of repertoire size of long-range auditory gestures were gesture to receive groom (r^2=0.504, β=0.278, p = 0.028), reassurance (r^2=0.504, β=0.602, p = 0.049), travel (r^2=0.504, β=0.131, p = 0.013), copulation (r^2=0.504, β=0.178, p = 0.011) and high intensity panthoots (r^2=0.504,

β=0.612, *p* = 0.010). The significant predictors of repertoire size of short-range auditory gestures were gestures to mutually groom (r^2=0. 926, β=0.795, *p* = 0.001), gestures to receive groom (r^2=0.926, β=0.308, *p* = 0.001), gestures to give groom (r^2=0. 926, β=0.222, *p* = 0.001) and gestures to play (r^2=0. 926, β=0.412, *p* = 0.001). Moreover, the significant predictors of repertoire size of tactile gestures were reassurance (r^2=0.911, β=0.444, *p* = 0.018), gestures to play (r^2=0.911, β=0.753, *p* = 0.001) and greeting (r^2=0.911, β=0.179, *p* = 0.002). Finally, the significant predictors of repertoire size of visual gestures were other threat (r^2=0.918, β=0.074, *p* = 0.037), travel (r^2=0.918, β=0.130, *p* = 0.001), copulation (r^2=0.911, β=0.173, *p* = 0.001), reassurance (r^2=0.911, β=0.589, *p* = 0.012), greeting (r^2=0.911, β=0.426, *p* = 0.001), gestures to receive groom (r^2=0.911, β=0.204, *p* = 0.002), play (r^2=0.911, β=0.175, *p* = 0.001) and low intensity panthoot (r^2=0.911, β=0.148, *p* = 0.001).

How is dyadic repertoire size of gestures related to time spent in proximity?

Across the 132 dyads, each chimpanzee dyad produced a mean 2.05 (overall range 0 – 40) gesture types for each hour spent in close proximity. For each modality of gestures separately, mean rate (overall range) of gesture type production was: auditory long range (0.08; 0 - 5), auditory short range (0.07; 0 – 2.5), visual (0.57; 0 – 12.50) and tactile (0.15; 0 – 7.06). We used MRQAP to examine whether the gestural repertoire size for each dyad predicted preferred reciprocated close proximity bonds, whilst controlling for sex, age, kinship and reproductive similarity of the dyad. Including gestures of all modalities, overall a larger gestural repertoire size significantly predicted the presence of a preferred reciprocated close proximity bond (r^2=0.087, β=0.196, p = 0.036). We then examined whether the repertoire size of each modality separately predicted preferred reciprocated close proximity bonds (Fig. 2). A larger repertoire size of auditory short range gestures (r^2=0.237, β=0.283, *p* = 0.049) and visual gestures (r^2=0.237, β=0.433, *p* = 0.004) predicted the presence of preferred reciprocated close proximity bonds. In contrast, chimpanzee dyads that were less likely to associate with each other through close proximity had a significantly larger repertoire of tactile gestures (r^2=0.237, β= - 0.380, *p* = 0.006). Next, we examined whether the gestural repertoire size for each dyad per each modality of gestures predicted presence of preferred non-reciprocated close proximity bonds. There were no significant associations between the repertoire size of any of the gestural modalities and the presence of this type of bond. Finally, we examined whether the gestural repertoire size for each dyad per each modality of gestures predicted presence of non-preferred close proximity bonds. A larger repertoire size of tactile gestures (r^2=0.131, β=0.263, *p* = 0.047) predicted the presence of non-preferred close proximity bonds, whereas visual gestures were negatively correlated with this type of bond (r^2=0.131, β= - 0.404, *p* = 0.002).

How is dyadic repertoire size of gestures related to position in proximity network?

We used node-level regressions to examine the predictors of proximity in degree by the repertoire size of gestures overall and by the repertoire size of auditory long range, auditory short range, visual and tactile gestures in and out degree. Here we controlled for the duration of time spent in proximity to oestrus females, time spent in proximity to kin, and the age and sex of the focal chimpanzee. When the overall gestural repertoire size was considered, in degree proximity was significantly associated with the out-degree repertoire size - that is the size of the gestural repertoire produced by the focal individual (r^2=0.791, β=0.763, *p* = 0.049). When the repertoire size for each modality was considered in one model, chimpanzees with a high proximity in degree had a high visual repertoire size outdegree (r^2=1, β=2.730, *p* = 0.041). Thus focal chimpanzees that produced a greater variety of visual gestures had higher rates of proximity to a greater number of conspecifics.

How is individual repertoire size of gestures related to time spent in proximity?

At the individual level, each chimpanzee produced a mean (overall range) of 48.75 (34 – 59) gesture types. The mean (overall range) of repertoire size for each modality of gesturing was:

auditory long range (7.75; 3 - 14), auditory short range (2.16; 0 - 4), visual (25.41; 19 – 30) and tactile (13.41; 7 - 19). The details of individual repertoire size of all gestures combined and by modality is presented in ESM Table 12. Geary's C statistic was used to examine the autocorrelations between individual repertoire size of each focal chimpanzee (all gestures combined and per modality type) and the proximity networks ('preferred reciprocated close proximity bonds', 'non-preferred close proximity bonds'). Overall, chimpanzees who had a similar repertoire size of all gestures combined were more likely to have a preferred reciprocated close proximity bonds with conspecifics (Geary's autocorrelation, $C = 0.481$, $p = 0.044$). Chimpanzees who had dissimilar repertoire size of all gestures combined were more likely to have a non-preferred close proximity bonds ($C = 1.346$, $p = 0.009$). However, there were no significant relationships between the repertoire size of each modality of gestures considered separately and proximity networks (ESM Table 13).

How is individual repertoire size of gestures related to position in proximity network?

We next used node-level regressions to examine the predictors of proximity indegree by repertoire size of gestures combined across modalities, and then by the repertoire size of auditory long range, auditory short range, visual and tactile gestures entered in one model. Here we controlled for the duration of time spent in proximity to oestrus females, the time spent in proximity to kin, and the age and sex of the focal chimpanzee. Examining the repertoire size of each chimpanzee as an individual attribute revealed that overall repertoire size was not correlated with strong bonds proximity indegree (ESM Table 14). When combining all modalities of gestures in one model, chimpanzees with a larger repertoire size of tactile gestures had a higher proximity indegree ($r^2 = 0.408$, $\beta = 0.777$, $p = 0.047$, ESM Table 15).

Discussion

We used social network analysis to examine the relationship between the repertoire size of gestural communication and proximity at the individual, dyadic and group levels. We demonstrated that chimpanzees did not associate at the similar rate with all individuals in the group, but displayed a great degree of variation in proximity across dyads. In addition, chimpanzees differed both in the number of gesture types they produced overall and the number of gestures they directed at their social partners. One key finding is that chimpanzees who had a similar size of gesture repertoire (i.e. the total number of gesture types individual produced towards other individuals) were more likely to remain in proximity to each other, whereas chimpanzees who did not have a similar repertoire of gestures were less likely to remain in proximity. The significant association between the similarity in the size of the repertoire produced by each chimpanzee and the level of proximity of that dyad partners shows importance of the communication skills in subgrouping patterns at the level of the chimpanzee community. Thus chimpanzee A may have a large individual repertoire of gestures and maintain high degree of proximity with chimpanzees who also possesses large repertoire size. However, chimpanzee B produces small repertoire of gestures and thus maintains a low degree of proximity with the chimpanzee who has a large repertoire size.

A second key finding is that, individuals who directed a larger repertoire of gestures at the recipient tended to remain in close proximity for longer. Further, different modalities of gestures were differentially associated with proximity. Previous research described repertoire of gestures and examined variation in overlap in gesture types in relation to characteristics of social system [Roberts and Roberts, 2017]. However, in line with previous findings in macaques [Maestripieri, 1999] this is the first study to show that repertoire size is also an important dimension of chimpanzee sociality [Maestripieri, 1999]. Strong proximity bonds were associated with a larger repertoire size of visual gestures, and of auditory short range gestures. The analysis was based on the repertoire size per hour dyads spent in close proximity, rather than the overall repertoire size of individuals. The significant association between repertoire size and proximity therefore shows flexibility in the production of the repertoire of gestures when associating with different interaction partners, with a greater variety of gestures produced with strong proximity bonds. In contrast, if chimpanzees showed less flexibility and produced their repertoire of gestures at the same rate with different interaction partners, there would be no significant association between proximity and repertoire size per hour spent with these different interaction partners.

Chimpanzees, in common with other primates, maintain a small number of close social relationships, and it is these frequent interaction partners that are important in buffering primates from the stresses of group living [Foerster et al., 2015; Lehmann and Boesch, 2009; Mitani, 2009; Mitani et al., 2002; Muller and Mitani, 2005; Seyfarth and Cheney, 2013]. A larger repertoire size of visual and auditory short-range gestures may operate in a similar way to short-range, low intensity grunts in baboons, allowing for the regulation of social relationships when in close proximity, using a visual or auditory short-range mode of communication [Palombit et al., 1999]. However, because these gestures are more subtle or less intense, they may be less efficient in coordinating social behaviour with conspecifics and the recipient. Different gestures are associated with different ‘dominant responses’ by recipients [Hobaiter and Byrne, 2014; Roberts et al., 2014a; Roberts et al., 2012a]. A more varied repertoire of visual or auditory short-range gestures (i.e. greater complexity in the gestural repertoire) may lead to a greater reduction in uncertainty in the recipient, as the gesture can more precisely convey the communication goal. Using a greater variety of gestures may make it more likely the recipient will respond appropriately to the gestures, facilitating social interaction and allowing for close proximity to be maintained over longer periods. This interpretation is consistent with previous findings from this population of chimpanzees which showed that elaboration in gestural sequences is used more frequently if the recipients' response to the initial visual gesture is not congruent with the communication goal [Cartmill and Byrne, 2010; Liebal et al., 2004a; Roberts and Roberts, 2018a; Roberts et al., 2013].

An increased repertoire size of visual gestures was associated with communication in both affiliative (e.g. reassurance, greeting, receive groom, copulation) and antagonistic (e.g. other threat) contexts and this wide range of contexts may require a corresponding large repertoire size. Individuals that can use this extensive repertoire flexibly, and elaborate with alternative gestures if the recipient does not respond appropriately [Leavens et al., 2005], may be at selective advantage in eliciting appropriate responses from recipients [Roberts et al., 2014a]. For example, subordinate chimpanzees use gestural communication to elicit matings and flexibly adjust the modality of the gestural communication according to the presence and visual attention of rival males [Roberts and Roberts, 2015]. Subordinate males with a larger repertoire of gestures, and with greater flexibility in the production of those gestures, may be at a selective advantage in soliciting matings.

In contrast to visual gestures, the repertoire size of tactile gestures was negatively associated with the amount of time pairs of chimpanzees spent in close proximity. For these social bonds, the diversity of the gestural repertoire may be less driven by the constraints resulting from modality of gesture use. Instead, a larger repertoire of tactile gestures may allow for more efficient resumption of social relationships after the lengthy periods of separation chimpanzees experience due to the fission-fusion social structure [Dunbar and Shultz, 2010]. When two chimpanzees meet after a period apart, they need to be able to reestablish the social relationship and resolve any uncertainties that may have arisen due to the period of absence – for example relating to changes in alliances, dominance status and third party relationships [Amici et al., 2008]. The reduction in uncertainty associated with greater communicative complexity (a larger repertoire size) in tactile gestures may therefore be related to the nature of social relationship. A larger repertoire of tactile gestures was associated with affiliative contexts (reassurance, gestures to play and greeting) and these contexts are important in reestablishing social relationships with chimpanzees encountered less frequently than the strong proximity bonds [Roberts and Roberts, 2016b]. Thus, large repertoire of tactile gestures appears to be important for these partners were the individuals maintain affiliative relationship but stay in proximity less often.

As well as the large amount of variation in levels of proximity between pairs of chimpanzees, there was also a large amount of variation in the number of proximity bonds chimpanzees maintained with others. Individual chimpanzees that had a larger repertoire of visual gestures had a larger number of proximity bonds. Maintaining and communicating with a larger number of social partners places both cognitive and time demands on individuals [Dunbar, 1993; Lehmann and Dunbar, 2009] because of the need to remember and track past and present relationships and use this information to flexibly produce and respond appropriately to gestural communication. This is particularly the case when responding to visual signals when manipulating information about a larger number of social relationships. The efficiency of social coordination may limit the number of relationships that could be maintained with a restricted repertoire of gestures, but a larger repertoire allows for more efficient coordination with the receiver, and thus more efficient communication by signallers [Shannon et al., 1951]. The mean repertoire size for visual gestures (25 gesture types) was greater than all the other modalities combined and using this large repertoire size flexibly to communicate with the recipients may allow individual chimpanzees to maintain a larger number of proximity bonds. Individuals with a larger repertoire of visual gestures may be better equipped to regulate social interactions and manage the tensions of social life, for example when feeding on patchy food sources such as figs where chimpanzees are forced into close proximity for extended periods of time. In contrast, the size of the repertoire of tactile or loud auditory gestures was not significantly related to the size of the proximity network. These gestures might be more intense and therefore the mere frequency of use of the gestures, rather than the size of the repertoire, may be sufficient to maintain the larger number of weaker relationships in the network.

The findings of this study are in line with previous research showing that chimpanzees show considerable flexibility in gestural communication [Gillespie-Lynch et al. 2013; Hopkins and Wesley, 2002; Liebal et al., 2004b; Masur, 1982; Nishida, 1980; Schneider et al., 2012; Schneider et al., 2017; Tomasello et al., 1994], have a large and varied gestural repertoire [Hobaiter and Byrne, 2011a; Liebal et al., 2004a; Roberts et al., 2014a; Roberts et al., 2012b; Tomasello et al., 1985], and that several different features of gestural communication are related to sociality [Roberts and Roberts, 2018a; Roberts and Roberts, 2018b]. However, the study was based on 12 focal individuals and whilst network analysis allows for the analysis of relationships at the level of the dyad rather than the individual [Borgatti et al., 2013], the findings of this study should be replicated on a larger sample. All the great ape species [Byrne et al., 2017] and some monkey species [Maestripieri, 1999] have a varied repertoire of gestural communication and future research on how the size of this gestural repertoire relates to sociality is needed to determine whether the association between repertoire size and proximity is found across different populations of the same species, and across different species.

A second area for future research is to examine the relative importance of similarity of repertoire size of two individuals for maintaining proximity. Whilst this study showed overall similarity in the individual repertoire size of chimpanzees is associated with proximity, it did not examine whether two chimpanzees both with a small repertoire size spent longer in proximity than two chimpanzees both with a large repertoire size. Examining this question will provide further insights into whether it is specifically larger repertoire sizes that allow pair of chimpanzees to maintain proximity for longer durations of time, or whether the overlap in repertoire size between individuals is more important in maintaining proximity.

Overall the results of this study may provide new insights into gestural theories of language evolution, by demonstrating a link between flexibility in use of a larger repertoire of gestures and the maintenance of different types of social bonds. A key challenge in large and complex social groups, both for primates and our hominin ancestors, is managing an increasingly differentiated set of social relationships, consisting of a set of strongly bonded regular interaction partners and also a more numerous set of weakly-bonded individuals with less regular interaction [Dunbar, 2012]. This is a particularly issue in fission-fusion systems that characterize many primate species and are also likely to have been present through much of hominin evolution [Amici et al., 2008; Anderson et al., 2002]. Further, interaction with these social partners occurs across a wide range of both affiliative and agnostic contexts. A larger repertoire of gestural communication, and being able to use this larger repertoire in a flexible way, may help to meet the time and cognitive challenges involved in sociality by increasing efficiency of communication suitable for maintaining close proximity with others. This reduction in uncertainty may allow for individuals to maintain closer proximity over longer periods of time. Human language is characterized by both an extensive repertoire and flexibility in how that repertoire is used [Burling, 1993]. Given the strong association between individual variation in the strength of social bonds and fitness outcomes [Silk et al., 2009] an increasing repertoire of gestural communication, and flexibility in employing that repertoire with varied social partners and across multiple contexts, may have played an important role in the evolution of complex communication in both primates and humans.

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Conflict of interest

Authors have no conflict of interest to declare

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

Focal subject ID	**Sex**	**Age**	**Female reproductive status**	**Total observation duration in minutes**
BB	Male	21	-	516
HW	Male	15	-	1030
KT	Male	15	-	1026
KU	Female	29	Pregnant	910
KW	Female	27	Nursing	510
ML	Female	33	Cycling	1118
MS	Male	17	-	524
NB[a]	Female	46	Cycling	500
NK[b]	Male	26	-	582
RH	Female	43	Nursing	1038
SQ	Male	17	-	554
ZM	Female	40	Cycling	710

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

Dominance based on unidirectional pant-grunt calls

Table 2. Gesture types observed in adult to adult interactions categorised according to modality and function. The data from last study period was included to make this table.

Gesture type	Modality	Function
BODILY MOVEMENT		
Bob	Visual	Other threat, greeting
Bounce	Auditory long-range	Travel, copulation, threat to dominate, pant-hoot
Dangle	Visual	Travel, greeting, threat to dominate, pant-hoot
Drag self	Visual	Greeting
Lunge	Visual	Other threat, greeting, threat to dominate
Push by rump	Tactile	Greeting
Rock	Visual	Greeting, pant-hoot,
Roll over	Visual	Receive groom
Slide	Tactile	Greeting
Sway	Auditory long-range	Travel, copulation, threat to dominate, pant-hoot
Thrust genitals	Tactile	Greeting
BODILY POSTURE		
Bow	Visual	Greeting
Crouch	Visual	Greeting

Present genitals	Visual	Copulation
Present mount	Visual	Copulation
Present rump	Visual	Other threat, copulation, reassurance, greeting, threat to dominate
Present torso	Visual	Greeting, mutually groom, receive groom, give groom
Stand tandem	Tactile	Reassurance, greeting
Stationary stiff	Visual	Other threat, travel, copulation, reassurance, threat to dominate, pant-hoot
Turn back	Visual	Copulation, greeting,
HEAD GESTURES		
Bite	Tactile	Greeting
Clip by mouth	Auditory short-range	Copulation, give groom
Hold object	Visual	Copulation
Kiss	Tactile	Greeting
Lower head	Visual	Receive groom
Nod	Visual	Greeting
Smack lip	Auditory short-	Greeting, mutually groom, receive groom, give

	range	groom,
Sniff	Visual	Reassurance, greeting
Stroke by mouth	Tactile	Greeting, give groom
Tip head	Visual	Other threat
Turn head	Visual	Other threat
LEG GESTURE		
Drum	Auditory long-range	Travel, threat to dominate, pant-hoot, other threat,
Kick	Auditory long-range	Threat to dominate
Present leg	Visual	Receive groom
Stamp quadrupedal	Auditory long-range	Other threat, travel, copulation, threat to dominate, pant-hoot,
Stamp sitting	Auditory long-range	Travel, copulation, threat to dominate,
LOCOMOTORY GAIT		
Crouch run	Visual	Other threat, reassurance, greeting, pant-hoot
Crouch walk	Visual	Other threat, copulation, greeting, pant-hoot
Jump	Visual	Other threat, greeting, threat to dominate, travel,

		copulation
Locomote tandem	Tactile	Reassurance, greeting
Run stiff	Visual	Other threat, reassurance, greeting, threat to dominate, pant-hoot, travel
Shuffle	Auditory long-range	Threat to dominate, pant-hoot
Swagger bipedal	Visual	Other threat, travel, threat to dominate, pant-hoot
Swagger quadrupedal	Visual	Travel, threat to dominate, pant-hoot
Swing	Auditory long-range	Other threat, greeting, pant-hoot, travel, threat to dominate,
Walk stiff	Visual	Other threat, travel, copulation, threat to dominate, pant-hoot
MANUAL		
Arm beckon	Visual	Copulation
Arm flap	Visual	Other threat, threat to dominate, pant-hoot,
Arm raise	Visual	Copulation, mutually groom,
Beat	Auditory long-range	Pant-hoot, travel,

Break	Auditory long-range	Threat to dominate
Clip by hand	Auditory short-range	Copulation, give groom,
Drag object	Auditory long-range	Pant-hoot
Embrace	Tactile	Reassurance, greeting
Forceful extend	Visual	Other threat, copulation,
Grab	Tactile	Reassurance, greeting
Hand bend	Visual	Greeting
Hit object	Auditory long-range	Copulation, greeting
Hold hands	Tactile	Greeting
Inspect	Auditory short-range	Give groom
Knock	Auditory long-range	Pant-hoot
Limp extend	Visual	Greeting, mutually groom, give groom
Linear sweep	Visual	Copulation, greeting, pant-hoot

Offer hand	Tactile	Reassurance, play
Poke	Tactile	Reassurance
Pound	Auditory long-range	Pant-hoot
Pull another	Tactile	Copulation, give groom, greeting
Push by hand	Tactile	Give groom
Retrieve	Visual	Other threat
Rub	Tactile	Play, reassurance,
Shake limb	Tactile	Play
Shake mobile	Auditory long-range	Other threat, travel, copulation, threat to dominate, pant-hoot,
Shake stationary	Auditory long-range	Other threat, travel, copulation, threat do dominate, pant-hoot
Slap another	Tactile	Other threat
Slap object	Auditory long-range	Other threat, pant-hoot
Slap self	Visual	Pant-hoot
Stiff extend	Visual	Travel, greeting, threat do dominate,
Stretched extend	Visual	Greeting

Stroke short	Tactile	Other threat
Tap another	Tactile	Reassurance, greeting
Tap object	Auditory short-range	Other threat
Tickle	Tactile	Play
Touch backhand	Tactile	Reassurance, greeting, receive groom, give groom,
Touch innerhand	Tactile	Give groom
Touch long	Tactile	Reassurance, greeting
Touch self	Visual	Copulation
Unilateral swing	Visual	Travel, copulation, threat to dominate, pant-hoot
Wipe	Visual	Copulation
Vertical extend	Visual	Food sharing, other threat, copulation, reassurance, greeting,

Figure titles

Fig. 1. Cumulative record of gestural repertoire of adult chimpanzees at Sonso. The cumulative repertoire was plotted against the number of active gesture days for all focal subjects combined. Asymptote appears to be achieved at approximately 90 days of active gesturing days for all subjects combined.

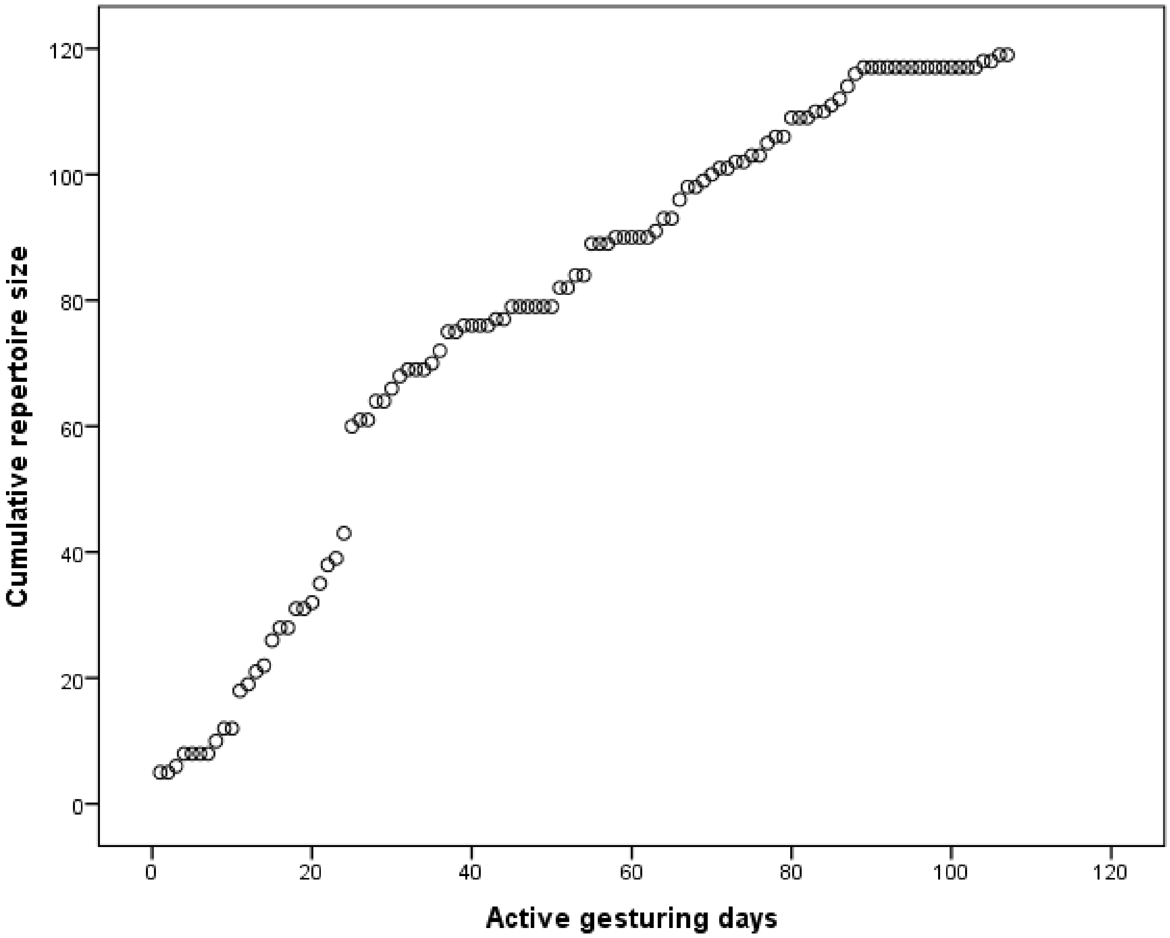

Fig. 2 Mean rate of gesture repertoire production across four modalities, per hour dyad spent in close proximity (within 10m).