

## INFLUENCE OF PARTY SIZE ON SOCIAL BONDING AND GESTURAL PERSISTENCE IN WILD CHIMPANZEES

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**Abstract.** The understanding of the relationship between gestural communication and sociality is important for understanding the co-evolution of social and cognitive complexity. Chimpanzees use gestural communication such as gestures produced singly or in sequences interspersed with response waiting (persistence) as well as sequences made in quick succession (rapid). However, it is unclear if this variation in the use of gestures is associated with sociality at the level of the dyad or a party. The aim of the study was to examine whether use of gestures in wild chimpanzees was associated with the duration of time spent in social bonding behaviour, party size and demography. Chimpanzees were more likely to use persistence than single gesture or rapid sequence when size of the party was larger, when the dyad partners were unrelated, and when they engaged in unidirectional and mutual grooming for longer. These results suggest that in socially complex species such as chimpanzees, individuals can maintain bonded relationships with unrelated individuals through cognitively complex communication more effectively than through less cognitively complex communication. The brain evolution of primates and hominins is hypothesized to have occurred due to increased demands of managing more complex social relationships in larger social groups. The complex cognitive skills underpinning gestural communication enable primates to meet challenges of complex social relationships in larger social groups and thus are likely to have promoted the brain size evolution in primates and humans.

**Keywords:** *Chimpanzees, gestural communication, proximity, grooming, cooperation, joint activity, social bonds, social networks, elaboration, repetition, response, evolutionary trade-off.*

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### 1. Introduction

Understanding language evolution has been stimulating the imagination of biologists, psychologists and anthropologists for centuries who are keen to address a central question of interest to all – what makes us human (Fitch, 2005)? Gestural communication defined as voluntary movements of the hands, head, bodily postures or locomotory gaits has attracted considerable attention because of the emerging evidence that the common ancestor shared these behaviours with primates and humans (Pollick & de Waal, 2007; Roberts *et al.*, 2012a). The similarity between humans' and primates' gestural communication suggests that there was a relatively recent switch towards use of gestures in our hominid ancestors. One key characteristic of this shift is understanding of intentionality, whereby one can appreciate that another has different thoughts that can affect their behaviour. In humans, this ability underpins communication with others, and is key to making social relationships complex. One of the important questions is whether only humans comprehend intentionality, or if monkeys and apes also have this ability. From an evolutionary point of view,

chimpanzees are our closest living relatives and are an obvious starting point to look for this ability.

Studies of captive chimpanzees have shown that they have some understanding of intentionality as evidenced by a signaller's repetition or elaboration of signals until their goal is obtained, or failure is indicated (Leavens *et al.*, 2005). For example, chimpanzees understand if an experimenter knows, or does not know about the location of a hidden food and persist in gesturing until experimenter finds the food (Roberts *et al.*, 2014b). Some studies have proposed that human contact is necessary for chimpanzees to have flexible, intentional gestural communication (Call & Tomasello, 1996). This is because humans interact with chimpanzees in different ways than chimpanzees do amongst themselves, for instance, by attempting to direct their attention towards self or other objects or events. When humans display these behaviours toward captive chimpanzees, the apes may acquire different abilities to those of wild chimpanzees, that is, the enculturated apes may have specifically adapted to contact with humans (Tomasello & Call, 2004). However, recent research into intentionality underlying gestures in wild chimpanzees shows that intentional gestures are more ubiquitous than previously thought (Roberts *et al.*, 2013).

Chimpanzees show complex use of gestures further demonstrated by how they make *sequences* of gestures, i.e. gestures produced consecutively, in response to another's behaviour (Roberts *et al.*, 2012a). Chimpanzees show an awareness of whether or not the recipient of the gesture understands the message the sender is trying to get across. If the recipient only partly understands the message, then the sender repeats the same gesture, while if the recipient does not at all understand the message, then the sender uses new gesture. These findings are important because they show that gestures are not simply a result of emotional states felt by a chimpanzee but are choices designed to influence others, in order to achieve desired goal. Intentional gesture is not acquired in captivity, but is a trait shared with humans and other apes (Call & Tomasello, 1996).

The intentionality in gestural communication, as shown by chimpanzee gestural interchange may enable them to maintain more complex social relationships. Thus, to understand the key evolutionary pressures acting on social complexity in humans, it is important to investigate how the social relationships and gestural communication of chimpanzees are inter-related. Such analyses can increase our understanding of how chimpanzees use communication and other behaviours to maintain their social networks of kin and 'friends'.

Unidirectional grooming, whereby only one individual grooms another at a time, has long been claimed to be important behaviour for building social bonds in chimpanzees. As a consequence of unidirectional grooming chimpanzees develop emotional attachment to the partner and this bond promotes their willingness to engage in coordinated behaviour such as mutual grooming, co-feeding, joint resting and travel. Chimpanzees can build social bonds with related individuals, however, these relationships may be less complex because there are fitness benefits of socially bonding with kin. In contrast, forming social bonds with unrelated individuals may be more demanding because there are no obvious fitness benefits of socially bonding with unrelated individuals. Thus, this form of sociality may require more complex forms of communication that may enable large bonded social groups to emerge during evolution. However, the forms of communication that can facilitate this more complex sociality are currently unclear.

Chimpanzees are an interesting species to address this question because they have complex social system where they cooperate with both kin and non kin through number of social behaviours such as grooming, feeding, resting and they have a communication of high diversity and complexity. For instance, chimpanzees communicate through rapid sequence, persistence sequence and single gesture. This communicative complexity can reveal the link between complexity of cognitive skills underpinning gestural communication and social complexity (Cartmill & Byrne, 2007; Genty & Byrne 2009; Hobaiter & Byrne 2011; Leavens *et al.* 2005; Liebal *et al.* 2004; McCarthy *et al.*, 2012; Roberts *et al.*, 2014a; Roberts *et al.* 2012a; Roberts *et al.*, 2013; Roberts *et al.* 2014b; Tanner 2004; Tanner & Perlman 2016; Tempelmann & Liebal 2012; Tomasello *et al.* 1994). Series of gestures made in anticipation of a response, as shown by persistence are made intentionally and therefore they may be more cognitively complex than other forms of signalling because they are less bound to emotions (Roberts & Roberts, 2018). In gestural communication that is characterized by persistence, the signaller makes a gesture, pauses for 1 to 5 seconds to wait for a response, and then if the response is not forthcoming, the signaller makes another gesture (Hobaiter & Byrne 2011). Moreover, great apes can also make 'rapid sequence' whereby several gestures are made in quick succession, too rapid for the response waiting to have taken place (Hobaiter & Byrne 2011). The aim of this study is to explore how the complexity underlying gesture use is associated with social complexity of wild chimpanzees (*Pan troglodytes schweinfurthii*) living in Budongo Forest, Uganda. Specifically, the aim is to examine how use of persistence, rapid and single gesturing is associated with sociality.

In this study it is hypothesized that in socially complex species such as chimpanzees, individuals can maintain bonded relationships with unrelated individuals through cognitively complex communication more effectively than through less cognitively complex communication. Specifically, it is hypothesized that communicative persistence will enable chimpanzees to build social relationships with unrelated individuals through grooming behaviour more effectively than single gesture or rapid sequence.

Group size is one common measure of social complexity, however it may not fully reflect the complexity of social relationships because primates can disperse and avoid undesired individuals thus reducing the need to form social bonds with all group members. This is particularly the case in fission-fusion social system whereby individuals form temporary subgroups or 'parties' of varying composition and duration as a function of stresses incurred by group living. Thus, in fission-fusion social groups, the number of individuals in the audience or a party is a more reliable measure of social complexity than group size. Party size shows the number of the individuals with whom primates have to directly build social relationships in order to maintain social cohesion. When parties are small, primates can maintain social bonds with all group members through grooming behaviour. In this context, social bonds between group members may be evident in higher frequency of rapid sequence or single gesture. In contrast, when parties are larger, the chimpanzees cannot maintain social bonds with all group members and thus the bonds become weaker. This would imply that the likelihood of single gestures and rapid sequences would decline in larger parties. Group size is positively associated with grooming duration, whereby primates invest longer duration of grooming when they are in larger social groups. In large social groups, the grooming interactions are less effective in social bonding and the primates invest more time in

grooming that is less likely to be reciprocated. Thus, it can be hypothesized that if persistence facilitates grooming in the contexts whereby the social bond with the recipient is weaker, then there will be a positive correlation between party size and persistence.

Persistence, rapid and single gestures are hypothesized to fulfil different roles in social bonding and therefore it could be predicted that these forms of signalling would be differentiated in the nature of morphological components contributing to the make-up of the communication. Gestures within the sequence can occur on their own or they can be accompanied by use of facial expressions, visual orientation, vocalizations or objects. Gestures can be homogenous, overlapping with the repertoire of gestures used by the recipient, or nonoverlapping and heterogeneous. Understanding the complexity underlying use of gestures is important in increasing understanding of the nature of their influence on the recipient (Levinson & Holler, 2014). For instance, the type of the morphological components used in the sequence is likely to influence the social bonding by influencing the propensity of the gesture to evoke response from the recipient. This is exemplified by use of heterogeneous gestures by the chimpanzees towards the recipient who is unlikely to respond to the gesture, relative to the recipient who is likely to respond to the gesture (Roberts & Roberts, 2017). Here it is hypothesized that rapid, persistence and single gesturing will be differentiated by the type of morphological components contributing to the make-up of communication indicating differentiated role of communication in maintaining social relationships of the chimpanzees.

## **2. Methods**

### ***Study site and subjects***

The behaviour of East African chimpanzees (*Pan troglodytes schweinfurthii*) of the Sonso community at the Budongo Conservation Field Station, Budongo Forest Reserve in Uganda (latitude 1° 37'-2° 00'N; longitude: 31° 22'-31°46'E) was observed in relation to communication and social relationships between March and June 2008, following subjects between 07:00 and 16:00 at least 5 days a week. The distance to the focal chimpanzee and the limb injuries of the chimpanzee can influence the frequency and type of gestural communication. From the total population of approximately 74 individuals including 21 adult females and 10 adult males, the sample group of 12 adult focal subjects (6 adult males and 6 adult females) was chosen to ensure lack of any limb injuries and in accordance with the level of habituation, simultaneously ensuring that age and rank classes were equally represented in the sample. The study was non-invasive and the study methods were approved by the Ethics Committee. Full details of the study site, subjects, data collection, video analysis and classification of gestures has been described previously (Reynolds, 2005b), so only the key information is provided here.

### ***Data collection protocol***

The inventory of the patterns of social relationships and communication for each of the focal individuals was established during quantitative focal animal follows. Focal individuals were selected systematically, as far as possible sampling each focal subject equally at different times of the day and throughout the study period, at least once every week. The chimpanzee behavior was recorded during a standardized observation period of 18 minutes, avoiding dependency in the data set by taking consecutive samples of the

same focal subject at least 20 minutes apart. The behavior of the focal and non-focal chimpanzees was recorded if they were present in the same party, i.e. group of individuals within a spread of around 35m. Two types of behavioral information were recorded for this study. First, 18 minute focal follows consisted of 9 scans recorded at 2 minute intervals of the association and activity patterns (i.e. identity of individuals present within 10 m and more than 10 m away from the focal individual, identity, visual attention, distance and activity of the nearest neighbour). Second, gestural communication to accompany the 18 minute instantaneous sampling of association and behaviour patterns in the chimpanzees was recorded continuously using a digital video camera recorder, with the camera centered on the focal animal but also taking a wider view to include interactants within the visible presence of the focal individual. For each gesture event recorded the identity of the signaller and the recipient, the presence/absence of goal directedness, the response and the functional context of signal production was simultaneously spoken onto the camera. The data collection of association patterns was conducted by an experienced field assistant, who has worked for the project for over 20 years and was unaware of the aims of the study. All field assistants working for the project undergo an annual inter-observer reliability test, in order to maintain the consistency of scoring of the group composition and proximity across field assistants. The results of these tests are consistently above 0.85 Spearman's rank correlation coefficient,  $r_s$ . The video recording of the gestures was carried out by first author to ensure that the data on association patterns and the gestural data were collected independently of each other and only considered together during the data processing and analysis.

#### ***Video analyses of gestural communication***

In order to derive the inventory of gesture types from the video recordings the footage was viewed on a television and coded. The cases of nonverbal behaviour were grouped qualitatively into behaviour types based on the objective judgment of similarity in morphology (i.e. presence/absence and type of head, trunk, arm movement; posture, social orientation). All cases of nonverbal behaviour were recorded and identified as an act of gestural communication if they met following criteria for communication and intentional behaviour: 1) the non-verbal behaviour was an expressive movement of the limbs or head and body posture that was mechanically ineffective, 2) the behaviour was communicative (i.e. consistently produced a change in the behaviour of recipient or facilitated maintenance of activity, e.g. grooming by non-mechanical means), 3) the behaviour was intentional, following the criteria used in previous research (Genty *et al.*, 2009; Hewes, 1973; Leavens *et al.*, 2005; Liebal *et al.*, 2004; Pika & Tomasello, 2002; Tomasello *et al.*, 1994) such as that a) the signaller was visually oriented in the direction of the recipient when producing a gesture towards a recipient and observed the recipient's response during and after the gesture, b) the recipient was visually oriented in the direction of the signaller when the gesture was made with possible exception of tactile or auditory gestures, c) the signaller persisted in gesture production when the recipient failed to respond and stopped gesturing when recipient responded to the gesture, d) the gesture was produced in presence of the immediate audience (within 10 meters). These criteria were evaluated for each gesture type separately, using pooled data across subjects. If 60% of the cases of a particular nonverbal behaviour type displayed at least one of the intentionality criterion listed, I considered that nonverbal behaviour type to be an intentional gesture.

Gestures occur singly or in sequences, defined as one or more than one gesture made consecutively by one individual, towards the same recipient, the same goal, within the same context, within a maximum of 30 s interval. For each single gesture or sequence I recorded: the identity of the signaler (the individual performing a gesture); the identity of the recipient (individual at whom the gesture was visually directed, as determined from the orientation of head and body of the signaler during and immediately after performing a gesture, i.e. the signaler had the recipient within its field of view); the presence and type of change in recipient's behaviour after production of the first gesture (response); the signaler's behaviour and communication prior to and after production of the gesture. The second coder scored a random sample of 45 gesture sequences for modality revealing that the reliability was excellent ( $K = 0.95$ ). Another 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 ( $K = 0.74$ ) (Bakeman & Gottman, 1997).

### ***Behavioral measures***

I tested similarity in association patterns between scans and samples to ensure that the sampling protocol did not bias the results. The results demonstrated that the adjacent scans taken at 2 and 4 minutes of the 18 minute sampling period yielded similar findings, as thus these were treated as continuous data. However, the scans first (2 min) and final (18 min) samples differed both for 10 m associations and partly level associations and were therefore independent, as well as the sample proceeding and succeeding the focal follow.

The behavioural measures were then calculated as shown in the following example:

#### The dyadic grooming measure

The dyadic grooming measure (GA) is the duration of time focal subject A groomed with non-focal subject B when B was in close proximity (within 10m) to focal subject A, per hour spent within 10 m of the non-focal subject B, or:

$$GA_{AB} = [(GR_{AB} * 2) * 60] / P10_{AB} * 2$$

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

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

2 = duration of instantaneous subsample interval in minutes

60 = the number of minutes in an hour

#### Attribute measures

First, I used genetic relationships identified in previous studies to classify pairs (dyads) of chimpanzees as maternal kin or non-kin (Reynolds, 2005a). Only maternal kin relations were present among the focal subjects. Wild chimpanzees reach physical and social maturity between ages 15 – 16 years old (Goodall, 1986). The Sonso community is a long running study site and therefore the age of most adult chimpanzees in the community is known. I 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 (Mitani et al., 2002). I also classified chimpanzee dyads according to reproductive similarity. The reproductive status of the female was scored on the basis of the female sexual swelling, which is the enlarged area of the perineal skin which varies in size over the course of the menstrual cycle. I recorded the reproductive status of the female as oestrous if during the observation period the female exhibited maximum tumescence and was observed mating with the males. All the focal males were observed to mate

with females and were therefore all assumed to be reproductively active. I also classified the sex similarity of dyads of chimpanzees, based on observable morphological characteristics. The full details of the categorization of attribute data are provided in Table 1.

**Table 1.** Variables included in generalized linear mixed models

Predictor variable	Definition	Frequencies or mean $\pm$ SD/ 95% CI (duration/frequency per hour spent within 10 meters)
Persistence or rapid sequence	Sequence is either 0 = persistence or 1 = rapid sequence	0 = 53, 1 = 107
Persistence sequence or single gesture	Sequence is either 0 = single gesture or 1 = persistence sequence	0 = 385, 1 = 53
Rapid sequence or single gesture	Sequence is either 0 = single gesture or 1 = rapid sequence	0 = 385, 1 = 107
Sex difference	Sex difference between focal subject and the recipient (0 = opposite sex, 1 = same sex)	0 = 227, 1 = 318
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)	0 = 378, 1 = 167
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)	0 = 78, 1 = 435
Maternal kinship	Maternal kinship presence between focal subject and the recipient (0 = absent, 1 = present)	0 = 530, 1 = 14
Joint feeding	Duration of jointly feeding with the dyad partner when within 2 meters and nearest neighbours per hour spent within 10 meters	2.08 $\pm$ 2.8, [1.84, 2.31]
Joint resting	Duration of jointly resting with the dyad partner when within 2 meters and nearest neighbours per hour spent within 10 meters	3.57 $\pm$ 4.24, [3.21; 3.93]
Grooming given	Duration of grooming given to the dyad partner per hour spent within 10 meters	4.39 $\pm$ 5.87, [3.90, 4.89]
Grooming received	Duration of grooming received from the dyad partner per hour spent within 10 meters	1.54 $\pm$ 2.94, [1.29, 1.79]
Grooming mutual	Duration of mutually grooming with the dyad partner per hour spent within 10 meters	2.31 $\pm$ 4.78, [1.90, 2.71]
Party size	Total number of individuals in the party (adult, subadult, juvenile and infant) during production of the gesture	7.51 $\pm$ 0.23, [7.05, 7.97]
Response absence or presence	Presence of any change in the behaviour of the recipient following production of the gesture (0 = absent, 1 = present)	0 = 208, 1 = 258
Goal directed response or emotional display	Change of behaviour by means of goal directed response, whereby recipient performs some action that conforms to the goal of the signaller (e.g. starts to groom) or emotional display, which may include tactile, visual or vocal behaviour produced by the recipient after the gesture which is not followed by goal directed action that conforms to the goal of the signaller (e.g. embrace during travel, whereby signallers travel immediately before and after the embrace. If both goal directed action and emotional display co-occurred (e.g. vocalise and starts to groom) this was categorized as goal directed action (0 = activity, 1 = emotional display)	0 = 166, 1 = 92
Response by vocal display	Change of behaviour by means of vocal display, which involves production of sound via vocal tract by the recipient, which is not followed by goal directed action towards signaller (e.g. pantgrunt during travel, whereby signallers travel before and after the pantgrunt (0 = absent, 1 = present)	0 = 400, 1 = 66
Response by non-vocal display	Change of behaviour by means of non-vocal display, such as tactile or visual behaviour which excludes production of sound by the recipient via vocal tract. This behaviour is not followed by goal directed action towards signaller (e.g. embrace during travel, whereby signallers travel before and after the embrace (0 = absent, 1 = present)	0 = 440, 1 = 26
Objects	Object is held by the signaller in either detached or attached form (e.g. a branch detached from or attached to a tree) and formed an integral part of signalling behaviour (e.g. shaking of a branch to make a sound) (0 = absent, 1 = present)	0 = 415, 1 = 130

Facial expression	Gesture is accompanied by simultaneous production of facial expression (0 = absent, 1 = present)	0 = 530, 1 = 15
Unimodal	Gestures that are not accompanied by simultaneous production of facial expressions or vocalisations (0 = absent, 1 = present)	0 = 120, 1 = 425
Manual indicative	Movement of the arm and hand towards the recipient, without physical touch such as arm beckon, arm flap, arm raise, forceful extend, hand bend, limp extend, linear sweep, stiff extend, stretched extend, unilateral swing, vertical extend (0 = absent, 1 = present)	0 = 488, 1 = 57
Rhythmic repetition	A repetition of visual movement in regular and cyclical fashion that indicates that the movement forms one gesture e.g. repeated movement of the fingers of the hand forward and away (0 = absent, 1 = present)	0 = 501, 1 = 44
Mutual attention	Gesture is accompanied by simultaneous presence of mutual visual contact between signaller and the recipient. Mutual visual contact is defined as such category of bodily orientation whereby signaller's and recipient's body are within each other's field of view (up to 45 degrees body turn) (0 = absent, 1 = present)	0 = 153, 1 = 297
Broadcast call	Production of gesture is accompanied by simultaneous production of panthoot vocalisation (0 = absent, 1 = present)	0 = 505, 1 = 40
One to one call	Gesture is accompanied by simultaneous production of vocalisation other than panthoot call (0 = absent, 1 = present)	0 = 413, 1 = 129
Elaboration	Sequence of gestures whereby more than one gesture type is present (0 = absent, 1 = present)	0 = 398, 1 = 147
Repetition	Sequence of gestures composed whereby only one gesture type is present (0 = absent, 1 = present)	0 = 532, 1 = 13
Homogenous gesture	Gesture type is absent in the recipient's repertoire (0 = heterogeneous) or is present in both signaller's and recipient's repertoire of gestures (1 = homogenous)	0 = 76, 1 = 274
Visual gesture	Gestures that can only be received by looking at the signaller. Frequency of both overlapping and non-overlapping events across modalities were taken into account	1.00±0.06, [0.87, 1.13]
Tactile gesture	Gesture received by physical contact between signaller and the recipient. Frequency of both overlapping and non-overlapping events across modalities were taken into account	0.17±0.02, [0.12, 0.21]
Auditory short-range gesture	Gesture can be received by hearing from a short distance without direct visual contact. Frequency of both overlapping and non-overlapping events across modalities were taken into account	0.32±0.02, [0.27, 0.38]
Auditory long-range gesture	Gesture can be received by hearing from a long distance without direct visual contact. Frequency of both overlapping and non-overlapping events across modalities were taken into account	0.41±0.06, [0.27, 0.54]
Bodily	Signaller uses head, legs, torso but not hands to gesture	1.39±0.09, [1.22, 1.57]
Manual	A gesture is made exclusively with the hand	0.50±0.04, [0.42, 0.59]
Combined	Gesture is made simultaneously with another gesture	0.33±0.05, [0.22, 0.43]
Non-combined	Gesture is not made simultaneously with another gesture	1.23±0.03, [1.16, 1.30]
Penile erection	Gesture is made simultaneously with penis erection of the penis	0 = 488, 1 = 57
Piloerection	Gesture is made simultaneously with involuntary erection of hairs	0 = 464, 1 = 81
Laterality	Gesture is made with left hand (0) or right hand (1)	0 = 72, 1 = 76
Gesture events	Number of consecutive gesture events in the sequence. One gesture event can contain gestures combined or not combined with other gestures or modalities of signalling (e.g. calls)	1.56±1.61, [1.42, 1.65]
Overall repertoire size	Total number of gesture types produced by the signaller which are present in the sequence.	1.58±1.084, [1.45, 1.66]
Repertoire size homogenous gesture	Total number of gesture types which are present in both signaller's and recipient's repertoire of gestures present in the sequence	1.07±0.82, [0.99, 1.15]
Repertoire size non-homogenous gesture	Total number of gesture types produced by a signaller towards the recipient which are not present in recipient's repertoire of gestures	0.48±0.94, [0.39, 0.57]

Due to missing data, the total number of cases differs between variables.

### ***Generalized Linear Mixed Models (GLMM)***

For each gesture sequence, the presence or absence of a response, the type of signalling (single gesture, persistence sequence, and rapid sequence) and other communication characteristics (Table 1) were scored. I used Generalized Linear Mixed Models (GLMM) to examine the factors influencing these response variables. The descriptive statistics regarding variables included in the GLMMs are provided in Table 1. In these GLMMs, the data was hierarchically structured with two levels - Level 1 was the focal individual, Level 2 was the recipient of the gesture. These models represent a



form of a regression where the data has a hierarchical clustering structure. The response variables in all the GLMMs were binary: the presence or absence of a response, single gesture or rapid sequence, single gesture or persistence sequence, rapid or persistence sequence. The data analysis was carried out in this way because I was interested in differences in characteristics of the sequences and single gestures rather than identifying features of each sequence type or single gesture per se. The models were fitted using a binomial error structure with logit link. The random effects included were the focal individual identity and the focal individual identity by recipient identity –for these effects random intercepts were used. In all of the analyses the demographic relationships (e.g. age similarity) were controlled for. Further, I used a Chi-square test to test the overall pattern of association between the behavioural indices and gestural communication. Following the same method as Pearce et al. (2017), this allowed me to examine whether the significant associations between gestural communication and behavior showed a distinct pattern, with certain types of gestural communication associated with specific behavioural indices more commonly than would be expected, as compared to a random distribution. All analyses were carried out using IBM SPSS Statistics 22.

### 3. Results

In this study I used Generalized Linear Mixed Models (GLMM) to examine association between gesture use and sociality. The description of all the variables included in these models is provided in Table 1. In all analyses, the age, sex, reproductive status, kinship were accounted for, including the recipient of the gesture entered as a dyad partner in all models. Only relevant significant findings to the hypothesis being tested are presented.

#### *Association between party size and social behaviour*

Using GLMM models, I examined the association of party size with the independent variables relating to the degree of social bonding (duration of grooming given, received and mutual; joint feeding, resting per hour spent within 10 meters), demography (maternal kinship, reproductive similarity, age similarity and sex similarity) and response (absent or present) – see SI Table 1. The results show that increasing size of the party, was associated with a higher likelihood of a chimpanzee directing a gesture at kin ( $\beta = -4.221, p < 0.001$ ), shorter duration of time spent mutually grooming ( $\beta = -0.160, p = 0.006$ ). Chimpanzees were more likely to respond to the gesture in parties of increasing size ( $\beta = -2.185, p < 0.001$ ).

#### *Social behavior and demography predicting type of sequence*

Using GLMM models, the target of the analyses in this section was to determine how the independent variables relating to the degree of social bonding (duration of grooming given, received and mutual; joint feeding, resting per hour spent within 10 meters), demography (maternal kinship, reproductive similarity, age similarity and sex similarity) and party size related to production of gesture sequences (SI Tables 2 – 4).

**Table 2.** Summary of results on communicative complexity and sequence type

Independent variables:	Dependent variables:		
	Persistence (0) or rapid sequence (1)	Single (0) or rapid sequence (1)	Single (0) or persistence sequence (1)
Objects absent (0) or present (1)	-	-	-
Unimodal absent (0) or present (1)	+	+	+
Facial expression absent (0) or present (1)		-	-
Broadcast call absent (0) or present (1)	-	-	+
One to one call absent (0) or present (1)	-	-	-
Manual indicative absent (0) or present (1)		-	-
Rhythmic repetition absent (0) or present (1)		-	-
Mutual attention absent (0) or present (1)	+		-
Homogeneity absent (0) or present (1)		-	
Laterality left-hand (0) or right-hand (1)	+		-
Penile erection absent (0) or present (1)	+		-
Piloerection absent (0) or present (1)	-	-	-
Elaboration absent (0) or present (1)	-	N/A	N/A
Repetition absent (0) or present (1)	+	N/A	N/A
Bodily frequency	+	N/A	N/A
Manual frequency		N/A	N/A
Combined frequency	+	N/A	N/A
Non-combined frequency		N/A	N/A
Visual gesture frequency	+	N/A	N/A
Tactile gesture frequency		N/A	N/A
Auditory short-range gesture frequency	-	N/A	N/A
Auditory long range gesture frequency	+	N/A	N/A
Gesture repertoire size	+	N/A	N/A
Frequency events	+	N/A	N/A
Homogenous gesture repertoire size	+	N/A	N/A
Non-homogenous gesture repertoire size		N/A	N/A
Response absent (0) or present (1)	-	-	
Response goal directed (0) or emotional (1)	-	-	-
Non-vocal response absent (0) or present (1)			-
Vocal response absent (0) or present (1)	-	-	-

n/a - not applicable, blank cell – association not significant, + or – beta coefficient sign indicating the direction of significant association between variables.

**Table 3.** Summary of results on communicative complexity and response type

Independent variables:	Response absent (0), present (1)	Goal directed response (0), emotional display (1)	Response by vocal display absent (0), present (1)
Objects absent (0) or present (1)	-	-	-
Facial expression absent (0) or present (1)			
Unimodal absent (0) or present (1)		+	+
Manual indicative absent (0) or present (1)			
Rhythmic repetition absent (0) or present (1)	+	-	-
Mutual attention absent (0) or present (1)	+		+
Broadcast call absent (0) or present (1)	-	-	-
One to one call absent (0) or present (1)			+
Elaboration absent (0) or present (1)		-	-
Repetition absent (0) or present (1)	-		+
Homogeneity absent (0) or present (1)		-	
Penile erection absent (0) or present (1)			
Piloerection absent (0) or present (1)		-	-
Bodily frequency			
Manual frequency			+
Combined frequency			
Non-combined frequency	+		+
Visual gesture frequency	+		
Tactile gesture frequency		-	-
Auditory short-range gesture frequency	-		-
Auditory long range gesture frequency			
Gesture repertoire size		+	+
Homogenous gesture repertoire size	+	+	+
Non-homogenous gesture repertoire size			
Frequency events			

n/a - not applicable, blank cell – association not significant, + or – beta coefficient sign indicating the direction of significant association between variables. Laterality results are reported elsewhere (Roberts, Murray, & Roberts, under review).

As compared with single gestures, the rapid sequences were more likely with partners of same sex ( $\beta = -1.014$ ,  $p = 0.015$ ) and the different reproductive state ( $\beta = 1.486$ ,  $p = 0.001$ ). Moreover, the duration of joint resting ( $\beta = 0.134$ ,  $p = 0.039$ ) was longer when chimpanzees produced rapid sequences as compared with single gestures. In contrast, the duration of joint feeding ( $\beta = -0.235$ ,  $p = 0.006$ ) and grooming given ( $\beta = -0.083$ ,  $p = 0.003$ ) was longer when chimpanzees produced single gestures, as compared to rapid sequence. Chimpanzees were more likely to respond to the gesture, when the signaler produced rapid sequence than single gesture ( $\beta = -1.340$ ,  $p = 0.030$ ). When comparing single gestures and persistence sequences, the persistence was more likely with partners of different age class ( $\beta = 3.815$ ,  $p < 0.001$ ), opposite sex ( $\beta = 0.882$ ,  $p = 0.004$ ) and in non-kin dyad partners ( $\beta = 14.311$ ,  $p < 0.001$ ). In addition, the duration of joint resting ( $\beta = 0.305$ ,  $p < 0.001$ ) and grooming mutual ( $\beta = 0.151$ ,  $p < 0.001$ ) were

longer when using persistence sequences when compared with single gestures. In contrast, the duration of grooming received was shorter when using persistence sequences when compared with single gestures ( $\beta = -0.212$ ,  $p = 0.001$ ). Chimpanzees were more likely to use persistence than single gesture when there was a larger party size ( $\beta = 0.045$ ,  $p = 0.020$ ).

Persistence was more likely with non-kin ( $\beta = -14.357$ ,  $p < 0.001$ ) and with chimpanzees from different age class ( $\beta = -5.407$ ,  $p < 0.001$ ) and opposite sex ( $\beta = -1.024$ ,  $p = 0.043$ ) than the rapid sequence. Further, the comparison of rapid and persistence sequences shows that persistence was associated with longer durations of joint feeding ( $\beta = -0.307$ ,  $p < 0.001$ ), grooming given ( $\beta = -0.306$ ,  $p < 0.001$ ) and grooming mutual ( $\beta = -0.209$ ,  $p < 0.001$ ) than rapid sequence. Chimpanzees were more likely to use persistence than rapid sequence when there was a larger party size ( $\beta = -0.082$ ,  $p = 0.045$ ). Chimpanzees were more likely to use persistence than rapid sequence when the response to the gesture was absent ( $\beta = -0.955$ ,  $p = 0.001$ ).

### ***Communicative complexity predicting type of sequence***

I used GLMMs to examine how independent variables relating to communication complexity (presence or absence of objects, facial expressions, unimodal gestures, manual indicative gestures, rhythmic repetition, mutual attention, broadcast call, one to one call, elaboration, repetition, homogeneity, repertoire size overall, repertoire size of homogenous and non-homogenous gestures, frequency of gesture events, frequency of visual, tactile, auditory short-range and auditory long range gestures in the sequence, frequency of bodily, manual, combined and non-combined gestures in the sequence, presence or absence of penile and piloerection accompanying gestures, left or right handed) were associated with the dependent variable of the sequence type (single gesture, persistence sequence or rapid sequence) entering each variable for communicative complexity separately in each model and whilst controlling for demography.

Comparing single gesture and rapid sequence, the presence of objects ( $\beta = -2.579$ ,  $p < 0.001$ ), facial expressions ( $\beta = -2.100$ ,  $p = 0.007$ ), rhythmic repetition ( $\beta = -4.974$ ,  $p < 0.001$ ), manual indicative gestures ( $\beta = -1.086$ ,  $p = 0.002$ ), broadcast call ( $\beta = -2.781$ ,  $p < 0.001$ ), one to one call ( $\beta = -1.578$ ,  $p < 0.001$ ), homogeneity ( $\beta = -1.714$ ,  $p = 0.002$ ), piloerection ( $\beta = -3.075$ ,  $p < 0.001$ ) were more likely when chimpanzees produced rapid sequences than single gesture. In contrast, the presence of unimodal gestures ( $\beta = 1.815$ ,  $p < 0.001$ ) was more likely when chimpanzees produced single gestures.

When comparing single gestures and persistence sequences, the presence of objects ( $\beta = -1.182$ ,  $p < 0.001$ ), facial expressions ( $\beta = -2.900$ ,  $p = 0.001$ ), rhythmic repetition ( $\beta = -4.717$ ,  $p < 0.001$ ), manual indicative gestures ( $\beta = -1.628$ ,  $p < 0.001$ ), mutual attention ( $\beta = -1.673$ ,  $p < 0.001$ ), one to one call ( $\beta = -1.724$ ,  $p < 0.001$ ), piloerection ( $\beta = -1.606$ ,  $p = 0.009$ ), penile erection ( $\beta = -1.379$ ,  $p = 0.007$ ) was more likely when chimpanzees produced persistence sequences. In contrast, the presence of unimodal gestures ( $\beta = 1.564$ ,  $p < 0.001$ ), and broadcast call ( $\beta = 12.609$ ,  $p < 0.001$ ) was more likely when chimpanzees produced single gestures, as compared with persistence sequences. Persistence was more likely right-handed than left-handed single gesture ( $\beta = -1.509$ ,  $p < 0.001$ ).

Finally, when comparing rapid and persistence sequences, the presence of objects ( $\beta = -1.109$ ,  $p < 0.001$ ), broadcast call ( $\beta = -14.788$ ,  $p < 0.001$ ), one to one call

( $\beta = -0.376, p = 0.041$ ), elaboration ( $\beta = -2.895, p < 0.001$ ), piloerection ( $\beta = -2.139, p < 0.001$ ) was more likely when the chimpanzees produced rapid sequences than persistence sequence. Moreover, a larger repertoire size of gestures overall ( $\beta = 0.690, p < 0.001$ ), a larger repertoire size of homogenous gestures ( $\beta = 0.929, p < 0.001$ ) and a higher frequency of gesture events ( $\beta = 0.229, p = 0.006$ ), visual gestures ( $\beta = 0.219, p < 0.001$ ), auditory long range gestures ( $\beta = 0.685, p = 0.003$ ), bodily gestures ( $\beta = 0.356, p = 0.005$ ), combined gestures ( $\beta = 0.382, p = 0.004$ ) were positively associated with rapid sequences, as compared with the persistence sequences. In contrast, the presence of mutual attention ( $\beta = 1.875, p < 0.001$ ), repetition ( $\beta = 2.895, p < 0.001$ ), unimodal ( $\beta = 0.612, p = 0.017$ ) and penile erection ( $\beta = 1.676, p = 0.015$ ) was positively associated with persistence sequences, as compared to rapid sequences of gestures. Persistence sequences contained higher frequency of auditory short-range gestures than rapid sequences ( $\beta = -0.299, p < 0.001$ ). Persistence was more likely right-handed than rapid sequence, which was more likely left-handed ( $\beta = 1.508, p = 0.013$ ).

Furthermore, I used GLMMs to examine how the variables describing communication complexity (single gesture, persistence or rapid sequence type) were associated with the variables relating to response types to the gestures (see Table 2 for summary of these results). First, I examined the relationship between communication type and the probability of the gesture being responded to by the recipient. In these models, the presence or absence of the response or response type was the independent variable. Overall, rapid sequences were more likely to elicit a response, as compared to persistence sequences ( $\beta = -0.972, p < 0.001$ ) or single gesture ( $\beta = -1.473, p = 0.009$ ). Second, I examined the association between communication type and the probability that the gestures elicited goal directed response or response by emotional display. Persistence ( $\beta = -1.046, p = 0.003$ ) and single gesture ( $\beta = -1.999, p < 0.001$ ) in comparison with rapid sequence were more likely to elicit goal directed response than emotional display. Single gesture in comparison with persistence was more likely to elicit goal directed response than emotional display ( $\beta = -0.817, p = 0.030$ ). The pattern of results by vocal response absent or present was similar. Rapid sequence in comparison with persistence ( $\beta = -1.759, p = 0.001$ ) and single gesture ( $\beta = -2.415, p < 0.001$ ) was more likely to elicit vocal response. Persistence in comparison with single gesture was more likely to elicit vocal response ( $\beta = -0.788, p = 0.006$ ). Finally, persistence in comparison with single gesture was more likely to elicit non-vocal response ( $\beta = -1.174, p = 0.034$ ).

### ***Communicative complexity predicting response to the gesture***

In the final set of GLMM tests, I examined how the variables describing communication complexity (presence or absence of objects, facial expressions, unimodal gestures, manual indicative gestures, rhythmic repetition, mutual attention, broadcast call, one to one call, elaboration, repetition, homogeneity, repertoire size overall, repertoire size of homogenous and non-homogenous gestures, frequency of gesture events, frequency of visual, tactile, auditory short-range and auditory long range gestures, frequency of bodily, manual, combined and non-combined gestures, presence or absence of penile and piloerection) were associated with the variables relating to response types to the gestures (see Table 3 for summary of these results). First, I examined the relationship between communication type and the probability of the gesture being responded to by the recipient. In these models, the presence or absence of the response was the dependent variable. The gesture sequences more likely to elicit a

response were those which contained larger repertoire size of homogenous gestures ( $\beta = 0.471, p = 0.022$ ), the presence of objects ( $\beta = -1.161, p < 0.001$ ), broadcast call ( $\beta = -3.706, p < 0.001$ ), repetition ( $\beta = -1.060, p = 0.029$ ), higher frequency of non-combined gestures ( $\beta = 0.438, p = 0.008$ ) and visual gestures ( $\beta = 0.454, p = 0.022$ ). In contrast, gestures less likely to elicit a response from the recipient were associated with presence of rhythmic repetition ( $\beta = 1.059, p = 0.018$ ), mutual visual attention ( $\beta = 0.690, p = 0.041$ ) and a higher frequency of auditory short-range gestures ( $\beta = -2.196, p = 0.002$ ).

Second, I examined whether a goal directed response, or a response by means of emotional display (see Table 1 for definition), can predict the types of communication produced by chimpanzees. In these analyses, a goal directed response or response by emotional display was used as the dependent variable predicted by communicative complexity. The gesture sequences were more likely to elicit a response by emotional display when they contained presence of objects ( $\beta = -2.248, p < 0.001$ ), rhythmic repetition ( $\beta = -1.595, p < 0.001$ ), broadcast call ( $\beta = -3.248, p = 0.001$ ), elaboration ( $\beta = -1.859, p < 0.001$ ), piloerection ( $\beta = -3.213, p < 0.001$ ) and homogeneity ( $\beta = -0.926, p = 0.003$ ). In addition, the presence of response by emotional display predicted a larger number of gesture types overall ( $\beta = 0.589, p < 0.001$ ) and a larger number of homogenous gesture types ( $\beta = 0.741, p < 0.001$ ). In contrast, the presence of a goal directed response was predicted by the presence of unimodal gestures ( $\beta = 0.947, p = 0.022$ ) and a higher frequency of tactile gestures in the sequence ( $\beta = -0.301, p = 0.006$ ).

Next I examined the correlations between communication type and a response to the sequence being by vocal display (presence or absence), using response as a dependent variable in these models. The gesture sequences more likely to elicit a response by vocal display were those which contained the presence of objects ( $\beta = -3.211, p < 0.001$ ), rhythmic repetition ( $\beta = -1.447, p = 0.006$ ), broadcast call ( $\beta = -5.089, p < 0.001$ ), elaboration ( $\beta = -2.241, p < 0.001$ ), piloerection ( $\beta = -3.676, p < 0.001$ ) and had a larger number of gesture types overall ( $\beta = 0.635, p < 0.001$ ), larger number of homogenous gesture types ( $\beta = 0.708, p < 0.001$ ), higher rate of manual gestures ( $\beta = 0.393, p = 0.021$ ), higher rate of non-combined gestures ( $\beta = 0.556, p = 0.025$ ). In contrast, the gesture sequences less likely to elicit a response by vocal display were associated with presence of mutual attention ( $\beta = 1.143, p = 0.008$ ), one to one call ( $\beta = 0.932, p = 0.026$ ), repetition ( $\beta = 10.196, p < 0.001$ ), unimodal ( $\beta = 1.547, p = 0.002$ ) and a higher frequency of tactile ( $\beta = -0.756, p = 0.021$ ) and auditory short range gestures ( $\beta = -3.656, p = 0.001$ ).

### ***Overall distribution***

Running large numbers of models risks inflating significance levels. Thus it is important to test the overall pattern of significant results across the models, to examine whether these overall patterns were significantly different from what would be expected from a random pattern of association. A contingency table was created where the percentage of significant associations ( $p < 0.05$ ) with each variable within each gesture comparison was included. The distribution of significant associations across different comparisons of gestures (response absent or present, goal directed or emotional response, vocal response absent or present) and indices of communicative complexity was non-random ( $\chi^2 = 7.29, df = 2, p < 0.001$ ; Supplementary Table 7).

#### 4. Discussion

Whilst previous studies on gestural communication of wild chimpanzees have focused on examining variation in gestural communication in relation to the responses of the recipient (Cartmill & Byrne, 2007; Leavens *et al.*, 2005), this study is the previously undocumented demonstration that gestural communication varies in relation to the extent of the social bonding and size of the party.

In larger parties bonds weaken and this is evident in the shorter duration of time spent in mutual grooming behaviour when the size of the party increases. Thus, the mechanisms are required that can facilitate social bonding when the number of conspecifics in close proximity increases if these complex social structures are to emerge during evolution. Persistence was more likely to occur in larger parties relative to single gesture or rapid sequence. The data of this study shows that when size of the party increased, persistence acted as a social bonding mechanism in itself and this propensity had an important positive influence on duration of mutual grooming behaviour in larger parties relative to rapid sequence and single gesture. Moreover, in larger parties persistence acted as a tool for social coordination of grooming behaviour as shown by longer duration of unidirectional grooming relative to rapid sequence. Thus it appears that persistence evolved specifically to facilitate social bonding when number of conspecifics in the party increased. In these larger parties, communicative persistence appears to fulfil a dual function of coordinating grooming bouts and social bonding. This finding is in agreement with recent research which shows that individuals maintain larger social networks of proximity through persistence relative to single gesture or rapid sequence (Roberts & Roberts, 2018). One key question in science is the role of cognitive complexity underpinning communication in social structure and coordinated behaviour. These results are the first empirical demonstration that more complex social structure can emerge through cognitively complex behaviour.

In contrast, in smaller parties the bonds are stronger as shown by longer duration of mutual grooming in smaller parties relative to larger parties. Here chimpanzees can engage in grooming with all group members and thus the bonds are stronger. This is reflected in the higher likelihood of single gestures and rapid sequences in smaller parties relative to larger parties. Thus, this shows that there is a cognitive and time constraint on grooming behaviour and this constraint can influence the differentiation of communication in relation to the size of the party.

In sum, these results appear to suggest that chimpanzees use more complex communication in larger parties and less complex communication in smaller parties. Thus, the association between group size and brain size may have emerged due to complexity of cognitive skills underpinning gestural communication (Roberts & Roberts, 2018). However, understanding cognitive complexity underpinning gestural communication is challenging because it is difficult to disentangle whether chimpanzees use gestures to influence others' intentional states (i.e. what the other knows or comprehends) or emotions (i.e. make the other feel something without influencing his knowledge). For instance, repetition of the original gestures in the sequence is suggested to occur when the communication reflects an internal state of the signaller that depends on the changes in the availability of the goal itself. In contrast, elaboration of the original gestures is suggested to occur when the signaller is aware of the impact that the gesture has on the recipient, and communicates flexibly in relation to the changes in recipient's behaviour relative to the goal (Golinkoff, 1986, 1993). In this

study it was not differentiated between repetition and elaboration of the gestures within sequences. Moreover, persistence was more likely a repetition than rapid sequence which was mostly an elaboration. Thus, it is conceivable that in larger parties, chimpanzees use persistence by repetition to prolong the ongoing grooming behaviour and increase social bonding rather than influence comprehension states about the intention of the signaller. Studies in captivity and in the wild have nevertheless shown that chimpanzees can intentionally and flexibly use their gestures to influence others to attain their goals. Gestures are not so constrained by specific emotions but display degree of voluntary control (Leavens *et al.*, 2004; Pollick & de Waal, 2007). Future studies should investigate the nature of communicative persistence in more detail in terms of whether primates vary use of repetition and elaboration in relation to the size of the party.

Previous studies have emphasized the role of gestural communication in flexibly influencing behavior of the recipient (Cartmill & Byrne, 2007; Genty & Byrne, 2009; Hobaiter & Byrne, 2011; Leavens *et al.*, 2005; Liebal *et al.*, 2004; McCarthy *et al.*, 2012; Roberts *et al.*, 2014a; Roberts *et al.*, 2012b; Roberts *et al.*, 2013; Roberts *et al.*, 2014b; Tanner, 2004; Tanner & Perlman, 2016; Tempelmann & Liebal, 2012; Tomasello *et al.*, 1994). Here these findings were extended by demonstrating that this flexibility helps chimpanzees meet the key adaptive challenges faced by group living animals – coordinating social behavior with a differentiated set of social partners in presence of large number of conspecifics (Dunbar & Shultz, 2007a; Dunbar & Barrett, 2007). It is hypothesized that the brain evolution of primates and hominins has occurred due to increased demands behind managing more complex social system (Dunbar & Shultz, 2007b) and the evolution of cognitive skills underpinning communication should enable primates to meet these challenges. The results of this study suggest that it is specifically, cognitive demands behind establishing and maintaining social ties with the partners in large social groups that has promoted evolution of more complex communication strategies in primates. Use of communicative persistence enables chimpanzees to improve the efficiency of social bonding through grooming behavior thereby enabling larger groups to emerge during evolution (Roberts & Roberts, 2016). This type of communication is complex because it requires a set of cognitive skills such as controlling arousal underpinning use of persistence. Social environments represent maps of potential social opportunities and this study provides evidence that chimpanzees monitor their social environments in a dynamic way by using communicative persistence to establish social bonds in large social parties more effectively. Thus, chimpanzees can flexibly adjust their gestures according to the social situation and this ability is likely to have driven the growth of larger social groups and brain size in human evolution.

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### Supplementary Information 1

Supplementary Table 1. Influence of audience size on strength of social bonds between individuals

**Fixed Coefficients**

Target:group\_size

Model Term	Coefficient ▼	Std.Error	t	Sig.	95% Confidence Interval	
					Lower	Upper
Intercept	14.290	2.311	6.183	.000	9.748	18.833
Sex_difference=0	0.944	0.910	1.038	.300	-0.844	2.733
Sex_difference=1	0 <sup>a</sup>					
Age_difference=0	-0.559	1.118	-0.499	.618	-2.757	1.640
Age_difference=1	0 <sup>a</sup>					
Reproductive_state_difference=0	-0.687	1.166	-0.590	.556	-2.979	1.604
Reproductive_state_difference=1	0 <sup>a</sup>					
Maternal_kinship=0	-4.221	1.277	-3.306	.001	-6.730	-1.711
Maternal_kinship=1	0 <sup>a</sup>					
Joint_feeding	-0.142	0.167	-0.849	.397	-0.470	0.187
Joint_resting	-0.025	0.185	-0.137	.891	-0.389	0.338
Grooming_given	-0.006	0.080	-0.071	.944	-0.162	0.151
Grooming_received	-0.079	0.306	-0.259	.796	-0.681	0.522
Grooming_mutual	-0.160	0.058	-2.754	.006	-0.274	-0.046
Response_reverse=0	-2.185	0.539	-4.052	.000	-3.244	-1.125
Response_reverse=1	0 <sup>a</sup>					

Probability distribution:Normal  
Link function:Identity

<sup>a</sup>This coefficient is set to zero because it is redundant.

Supplementary Table 2. Comparison of persistence and rapid sequence

**Fixed Coefficients**

Target:Persistence Rapid\_sequence  
Reference Category:Slow sequence

Model Term	Coefficient ▼	Std.Error	t	Sig.	95% Confidence Interval	
					Lower	Upper
Intercept	22.458	2.781	8.075	.000	16.948	27.967
Sex_difference=0	-1.024	0.500	-2.046	.043	-2.015	-0.032
Sex_difference=1	0 <sup>a</sup>					
Age_difference=0	-5.407	1.312	-4.121	.000	-8.006	-2.807
Age_difference=1	0 <sup>a</sup>					
Reproductive_state_difference=0	1.303	0.907	1.436	.154	-0.495	3.101
Reproductive_state_difference=1	0 <sup>a</sup>					
Maternal_kinship=0	-14.357	1.131	-12.690	.000	-16.598	-12.116
Maternal_kinship=1	0 <sup>a</sup>					
Joint_feeding	-0.307	0.080	-3.847	.000	-0.465	-0.149
Joint_resting	0.051	0.042	1.212	.228	-0.032	0.134
Grooming_given	-0.306	0.080	-3.819	.000	-0.465	-0.147
Grooming_received	-0.017	0.039	-0.424	.672	-0.094	0.061
Grooming_mutual	-0.209	0.052	-4.025	.000	-0.312	-0.106
Response_reverse=0	-0.955	0.276	-3.465	.001	-1.501	-0.409
Response_reverse=1	0 <sup>a</sup>					
group_size	-0.082	0.041	-2.025	.045	-0.163	-0.002

Probability distribution:Multinomial  
Link function:Generalized logit

<sup>a</sup>This coefficient is set to zero because it is redundant.

Supplementary Table 3. Comparison of single gesture and rapid sequence

**Fixed Coefficients**  
**Target:Single\_Rapid**  
**Reference Category:SINGLE**

Model Term	Coefficient ▼	Std.Error	t	Sig.	95% Confidence Interval	
					Lower	Upper
Intercept	-0.661	1.124	-0.588	.557	-2.871	1.548
Sex_difference=0	-1.014	0.415	-2.441	.015	-1.831	-0.197
Sex_difference=1	0 <sup>a</sup>					
Age_difference=0	0.262	0.474	0.553	.581	-0.670	1.195
Age_difference=1	0 <sup>a</sup>					
Reproductive_state_difference=0	1.486	0.447	3.327	.001	0.608	2.364
Reproductive_state_difference=1	0 <sup>a</sup>					
Maternal_kinship=0	0.196	0.648	0.303	.762	-1.079	1.471
Maternal_kinship=1	0 <sup>a</sup>					
Joint_feeding	-0.235	0.085	-2.767	.006	-0.401	-0.068
Joint_resting	0.134	0.065	2.068	.039	0.007	0.261
Grooming_given	-0.083	0.028	-2.983	.003	-0.137	-0.028
Grooming_received	-0.159	0.113	-1.402	.162	-0.381	0.064
Grooming_mutual	-0.020	0.027	-0.732	.465	-0.074	0.034
Response_reverse=0	-1.340	0.616	-2.177	.030	-2.551	-0.130
Response_reverse=1	0 <sup>a</sup>					
group_size	-0.014	0.023	-0.579	.563	-0.060	0.033

Probability distribution:Multinomial  
 Link function:Generalized logit

<sup>a</sup>This coefficient is set to zero because it is redundant.

Supplementary Table 4. Comparison of single gesture and persistence sequence

**Fixed Coefficients**  
**Target:Single\_Persistence**  
**Reference Category:SINGLE**

Model Term	Coefficient ▼	Std.Error	t	Sig.	95% Confidence Interval	
					Lower	Upper
Intercept	-21.031	0.824	-25.520	.000	-22.651	-19.410
Sex_difference=0	0.882	0.301	2.933	.004	0.291	1.474
Sex_difference=1	0 <sup>a</sup>					
Age_difference=0	3.815	0.467	8.172	.000	2.897	4.733
Age_difference=1	0 <sup>a</sup>					
Reproductive_state_difference=0	-1.158	0.919	-1.260	.208	-2.965	0.649
Reproductive_state_difference=1	0 <sup>a</sup>					
Maternal_kinship=0	14.311	0.882	16.223	.000	12.575	16.046
Maternal_kinship=1	0 <sup>a</sup>					
Joint_feeding	0.094	0.096	0.974	.331	-0.096	0.283
Joint_resting	0.305	0.058	5.279	.000	0.191	0.418
Grooming_given	-0.013	0.025	-0.533	.594	-0.062	0.035
Grooming_received	-0.212	0.065	-3.284	.001	-0.339	-0.085
Grooming_mutual	0.151	0.030	5.060	.000	0.092	0.209
Response_reverse=0	-0.609	0.529	-1.152	.250	-1.649	0.431
Response_reverse=1	0 <sup>a</sup>					
group_size	0.045	0.019	2.346	.020	0.007	0.082

Probability distribution:Multinomial  
 Link function:Generalized logit

<sup>a</sup>This coefficient is set to zero because it is redundant.

Supplementary Table 5. Example of analysis from the section ‘Communicative complexity predicting type of sequence’

**Fixed Coefficients**  
**Target:Single\_Rapid**  
**Reference Category:SINGLE**

Model Term	Coefficient ▼	Std.Error	t	Sig.	95% Confidence Interval	
					Lower	Upper
Intercept	-10.814	0.613	-17.653	.000	-12.020	-9.608
Sex_difference=0	-0.540	0.548	-0.987	.325	-1.619	0.538
Sex_difference=1	0 <sup>a</sup>					
Age_difference=0	0.319	0.468	0.682	.496	-0.602	1.240
Age_difference=1	0 <sup>a</sup>					
Reproductive_state_difference=0	0.970	0.657	1.476	.141	-0.324	2.264
Reproductive_state_difference=1	0 <sup>a</sup>					
Maternal_kinship=0	9.542	0.361	26.428	.000	8.831	10.253
Maternal_kinship=1	0 <sup>a</sup>					
Response_reverse=0	-0.919	0.635	-1.446	.149	-2.170	0.333
Response_reverse=1	0 <sup>a</sup>					
homogeneity_non_homogeneity=0	-1.714	0.556	-3.084	.002	-2.808	-0.620
homogeneity_non_homogeneity=1	0 <sup>a</sup>					

Probability distribution:Multinomial  
 Link function:Generalized logit

<sup>a</sup>This coefficient is set to zero because it is redundant.

Supplementary Table 6. Example of analysis from the section ‘Communicative complexity predicting response to the gesture’

**Fixed Coefficients**

Target: response by activity versus response by visual, tactile, vocal communication is not followed by activity towards the signaller  
Reference Category: response by activity change

Model Term	Coefficient ▼	Std.Error	t	Sig.	95% Confidence Interval	
					Lower	Upper
Intercept	-9.305	0.343	-27.162	.000	-9.982	-8.628
Sex_difference=0	0.381	0.451	0.844	.400	-0.511	1.272
Sex_difference=1	0 <sup>a</sup>					
Age_difference=0	-0.468	0.187	-2.508	.013	-0.837	-0.099
Age_difference=1	0 <sup>a</sup>					
Reproductive_state_difference=0	-0.090	0.500	-0.180	.857	-1.079	0.898
Reproductive_state_difference=1	0 <sup>a</sup>					
Maternal_kinship=0	8.986	0.353	25.445	.000	8.288	9.684
Maternal_kinship=1	0 <sup>a</sup>					
homogeneity_non_homogeneity=0	-0.926	0.308	-3.009	.003	-1.535	-0.318
homogeneity_non_homogeneity=1	0 <sup>a</sup>					

Probability distribution: Multinomial  
Link function: Generalized logit

<sup>a</sup>This coefficient is set to zero because it is redundant.

Supplementary Table 7. Percentage of indicators for each behavioural categories that is significantly associated with 25 indices of communicative complexity across three comparisons of gestures (response absent or present, goal directed or emotional response, vocal response absent or present)

Behaviour	Response absent or present	Goal directed or emotional response	Vocal response absent or present
<i>Communicative complexity</i>	36	40	60