

Title page

**Intentional gestures predict complex sociality in wild chimpanzee**

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1 **Abstract**

2 A key challenge for primates is coordinating behavior with conspecifics in large, complex  
3 social groups. Gestures play a key role in this process and chimpanzees show considerable  
4 flexibility communicating through single gestures, sequences of gestures interspersed with  
5 periods of response waiting (persistence) and rapid sequences where gestures are made in quick  
6 succession, too rapid for the response waiting to have occurred. Previous studies examined  
7 behavioral reactions to single gestures and sequences, but whether this complexity is associated  
8 with more complex sociality at the level of the dyad partner and the group as a whole is not  
9 well understood. We used social network analysis to examine how the production of single  
10 gestures and sequences of gestures was related to the duration of time spent in proximity and  
11 individual differences in proximity in wild East African chimpanzees (*Pan troglodytes*  
12 *schweinfurthii*). Pairs of chimpanzees that spent a longer duration of time in proximity had  
13 higher rates of persistence, but not a higher rate of single gesture or rapid sequences. Central  
14 individuals in the social network received higher rates of persistence, but not rapid sequence  
15 or single gesture. Intentional gestural communication plays an important role in regulating  
16 social interactions in complex primate societies.

17 Key words: Chimpanzees, gestural communication, proximity, grooming, cooperation, joint  
18 activity, social bonds, social networks, elaboration, repetition, response, evolutionary trade-  
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## 25 **Introduction**

26 Primate social life has frequently been described as particularly complex in its nature  
27 and when compared with other vertebrates, primates have unusually large brains for their body  
28 size (Dunbar 1993; Dunbar 1998). Primate sociality is based on bonded social relationships  
29 where individuals repeatedly interact with the same group members in many different contexts  
30 (Freeberg et al. 2012). It has been proposed that the sociality of primates is cognitively  
31 demanding, leading to evolution of large brains in both primates and hominins (Dunbar and  
32 Shultz 2007a). In particular, there is a strong positive correlation between group size and brain  
33 size in primates, and particularly neocortex size in relation to the rest of the brain (Dunbar  
34 1993). Thus, primates living in larger groups have larger neocortex ratios (Dunbar and Shultz  
35 2007a). The relationship between brain size and group size may be influenced by the demands  
36 arising from maintaining social relationships in primates. Primates use grooming behavior to  
37 maintain stable, long lasting, and differentiated social relationships with both related and  
38 unrelated individuals (Dunbar 2010). The time and cognitive demands arising from  
39 maintaining social relationships through grooming result in a multilevel group structure, with  
40 hierarchically nested layers of social bonds, delineated by decreasing amounts of time spent in  
41 grooming behaviour (Hill et al. 2008).

42 In addition, gestural communication, defined as voluntary movements of the arms,  
43 head, body postures and locomotory gaits (Bard 1992; Hewes 1973; Roberts et al. 2014a;  
44 Tomasello et al. 1984) is important in maintaining social relationships of primates (Bard 1992;  
45 Bard et al. 2014; Forrester 2008; Fröhlich et al. 2016; Genty et al. 2009; Gillespie-Lynch et al.  
46 2013; Halina et al. 2013; Hewes 1973; Hobaiter and Byrne 2011a; Leavens et al. 2005; Liebal  
47 et al. 2004; Maestriperieri 2005; McCarthy et al. 2012; Pika et al. 2005; Pollick and de Waal  
48 2007; Roberts et al. 2014a; Roberts et al. 2012b; Schneider et al. 2012; Scott 2013; Taglialatela  
49 et al. 2015; Tomasello et al. 1984; Tomasello et al. 1985). Gestural communication is

50 particularly relevant for studies of social cognition because gestures can influence social  
51 bonding through intentional behaviour or emotional expression and this may have important  
52 implications for the complexity of cognitive skills involved in managing of social relationship.  
53 In intentional gesturing, signallers have a goal and influence the recipient flexibly based on an  
54 understanding that recipients have goal states different from their own and these states can  
55 affect their behaviour (Tomasello and Zuberbühler 2002). In addition, gestures can coordinate  
56 social bonding behaviour by fulfilling social bonding function in itself and simply expressing  
57 the signaller's affect. These emotional gestures may not be contingent upon the signaller's goal  
58 but are diffuse expressions of signaller's internal emotional state that can release social bonding  
59 neurohormones in the recipients (Dunbar 2010). For instance, greeting gestures when  
60 encountering each other after a period of separation can influence social bonding with the  
61 recipient and hence influence duration of time spent in close proximity. Thus, emotional  
62 communication has an adaptive function and can coordinate social behaviour because it  
63 influences emotional states of the recipients (Spoor and Kelly 2004).

64 In particular, primate gestures that occur singly or in sequences can reveal the link  
65 between gestural communication and social bonding (Cartmill and Byrne 2007a; Genty and  
66 Byrne 2009; Hobaiter and Byrne 2011b; Leavens et al. 2005; Liebal et al. 2004; McCarthy et  
67 al. 2012; Roberts et al. 2014a; Roberts et al. 2012a; Roberts et al. 2013; Roberts et al. 2014b;  
68 Tanner 2004; Tanner and Perlman 2016; Tempelmann and Liebal 2012; Tomasello et al. 1984)  
69 Series of gestures made in anticipation of a response, as shown by persistence (Gómez 1996;  
70 Moore 2016; Scott-Phillips 2015a; Scott-Phillips 2015b) may be important in social bonding  
71 in primates because they are made intentionally (Cartmill and Byrne 2007a; Leavens et al.  
72 2005; Roberts et al. 2013; Roberts et al. 2014b). In gestural communication that is characterized  
73 by persistence, the signaller makes a gesture, pauses for one to five seconds to wait for a  
74 response, and then if the response is not forthcoming, the signaller makes another gesture

75 (Hobaiter and Byrne 2011b). Moreover, great apes can also make a ‘rapid sequence’ whereby  
76 several gestures are made in quick succession, too rapid for the response waiting to have taken  
77 place (Hobaiter and Byrne 2011b).

78 In intentional communication the signaler modifies the production of the signals  
79 flexibly (Bates et al. 1979; Leavens et al. 2005; Tomasello et al. 1984). In support of this role  
80 of gestures, observational and experimental research in experimental tasks, and in conspecific  
81 social interactions, showed that signalers can adjust their gestural communication in relation to  
82 the changes in the behaviour of the recipient (Cartmill and Byrne 2007a; Genty and Byrne  
83 2009; Hobaiter and Byrne 2011b; Leavens et al. 2005; Liebal et al. 2004; McCarthy et al. 2012;  
84 Roberts et al. 2014a; Roberts et al. 2012a; Roberts et al. 2013; Roberts et al. 2014b; Tanner  
85 2004; Tanner and Perlman 2016; Tempelmann and Liebal 2012; Tomasello et al. 1984). In  
86 experimental studies that manipulated the response consequences of ‘unsuccessful’  
87 communication against a baseline of ‘successful’ communication, it was clearly demonstrated  
88 that apes can respond to the different behavioural states of the experimenter (Cartmill and  
89 Byrne 2007b; Leavens et al. 2005). For instance, individuals discontinued communicative  
90 attempts when the desired response was obtained and continued communicating when faced  
91 with an absence of a response (Cartmill and Byrne 2007a; Cartmill and Byrne 2010; Leavens  
92 et al. 2005; Roberts et al. 2012a; Roberts et al. 2013; Roberts et al. 2014b). Moreover, in a food  
93 finding task that required language-trained chimpanzees to guide a naïve human experimenter  
94 to a hidden food item, the chimpanzees coordinated their behavior with the experimenter in a  
95 flexible way, based on the experimenter’s responses to the chimpanzees’ communication. The  
96 chimpanzees used non-indicative gestures such as bobbing when the experimenter accurately  
97 pointed to the food location and indicative gestures such as pointing when the experimenter  
98 pointed to a location where the food was not hidden (Roberts et al. 2014b). However, whilst  
99 the role of persistence in influencing the recipient’s behaviour has been shown in previous

100 studies, the role of persistence in social bonding is currently unclear. In addition, very little is  
101 known about the role of single gestures and rapid sequences in social bonding. Thus, the issue  
102 of whether great apes can use gestural communication flexibly to coordinate social behaviour  
103 with different types of social partners, and how this use relates to variations in social network  
104 size, remains unresolved.

105 Chimpanzees are an ideal species to examine the relationship between sociality and the  
106 production of single gestures, persistence and rapid sequences in primates. Chimpanzees live  
107 in complex fission-fusion groups, where association dynamics are fluid and chimpanzees form  
108 temporary subgroups ('parties') that vary in size, composition and duration (Goodall 1986).  
109 Due to this fission-fusion structure, patterns of interaction between pairs of chimpanzees can  
110 vary on daily basis. In this study we examine the relationship between social interactions and  
111 the production of single gestures, persistence and rapid sequences in wild East African  
112 chimpanzees (*Pan troglodytes schweinfurthii*) in Budongo Forest, Uganda using Social  
113 Network Analysis (SNA). We examine how different types of communication (single gesture,  
114 rapid and persistence sequence) are related to sociality. In this study, consistent with previous  
115 research in this area (Lehmann et al. 2016; Sapolsky et al. 1997; Silk et al. 2013; Silk et al.  
116 2010b), we used proximity to measure differences in sociality between pairs of chimpanzees.  
117 We examined how these differences in sociality relate to patterns of communication between  
118 pairs of chimpanzees.

119 Through emotional communication signaler induces compatible affect in the recipient  
120 and through synchronized affect, the emotional communication facilitates attentional and  
121 behavioral convergence of the dyad partners (Owren and Rendall 2001). In contrast, intentional  
122 communication influences behavior of the recipient by influencing their movement and  
123 attention to achieve a goal such as travel to the same location. It has been argued that intentional  
124 communication has evolved as a means to enable social bonding with dyad partners as it can

125 influence behavior of the recipient more flexibly than emotional gesture and this may have  
126 been accompanied by increase in brain size during the course of hominin evolution. In this  
127 study we explored the associations between proximity and different types of gestural  
128 communication. We hypothesize that proximity will be differentially associated with the rates  
129 of different types of gestural communication – single gestures, rapid sequences and persistent  
130 sequences. Specifically we predict that that intentional communication (e.g. single gesture,  
131 persistence sequence) will be associated with a longer duration of time spent in proximity  
132 relative to emotional gestures (e.g. rapid sequence) (Hypothesis 1).

133         However, it is unclear whether single gestures, rapid and persistence sequences differ  
134 in response types made to the gestures and this would indicate the degree to which these  
135 communication types are intentional. Recipients can respond in a goal directed way by  
136 adjusting behaviour to the goal conveyed in the gesture, but can also respond communicatively.  
137 Thus, we hypothesize that goal directed and communicative responses will be differentially  
138 associated with the type of communication (Hypothesis 2). We predict that intentional gestures  
139 (single gesture, persistence) will be associated with goal directed response (by activity change)  
140 whereas emotional gestures (rapid sequence) will be associated with response by  
141 communication (visual, tactile gesture or vocalisation).

142         Furthermore, it is currently unclear whether the response to the gesture may be  
143 associated with the degree of sociality. Presence and type of response (e.g. goal directed or  
144 communicative) can indicate the willingness of the recipient to coordinate behaviour with the  
145 signaller and thus reflect the level of social bonding (Schneider et al. 2017; Wilke et al. 2017).  
146 Following on from Hypothesis 1, we hypothesize that the presence (Hypothesis 3) and type  
147 (Hypothesis 4) of response will be associated with sociality. Specifically, we predict that if  
148 intentional gestures facilitate social bonding then we would expect longer duration of time  
149 spent in proximity to be associated with higher rate of response present and response by activity

150 change. In contrast shorter duration of time spent in proximity would be associated with higher  
151 rate of response absence and response by communication.

152 Finally, individuals have different positions in the group, with central individuals  
153 having more social bonds relative to peripheral individuals who have fewer social bonds  
154 (Roberts and Roberts 2016a; Roberts and Roberts 2016b). Previous research has suggested that  
155 more central individuals have different overall patterns of communication to peripheral  
156 individuals (Roberts and Roberts 2016a; Roberts and Roberts 2016b). We therefore predict that  
157 the centrality of individual chimpanzees will be associated with the rate of single, rapid and  
158 persistent gestural communication they produce and they receive (Hypothesis 5).

159 The relationship between communication and social behaviour could arise simply as a  
160 relation between a behaviour that requires proximity with a metric of proximity. To avoid this  
161 possibility, in all analyses we control for the duration of time spent in close proximity (all  
162 communication indices are calculated per duration of time spent within 10 m). Furthermore, in  
163 addition to the sequence type, biological factors such as reproductive status, age similarity, sex  
164 similarity and kinship have been shown to influence patterns of social bonding between pairs  
165 of chimpanzees (Langergraber et al. 2009; Mitani 2009; Roberts and Roberts 2016b). Thus we  
166 control for these biological factors in all models.

## 167 **Methods**

### 168 Study site and subjects

169 The behaviour of East African chimpanzees (*Pan troglodytes schweinfurthii*) of the Sonso  
170 community at the Budongo Conservation Field Station, Budongo Forest Reserve in Uganda  
171 (latitude 1° 37'-2° 00'N; longitude: 31° 22'-31°46'E) was observed in relation to communication  
172 and social relationships between March and June 2008, following subjects between 07:00 and  
173 16:00 at least 5 days a week. The distance to the focal chimpanzee and the limb injuries of the  
174 chimpanzee can influence the frequency and type of gestural communication. Thus from the



175 community of approximately 74 individuals including 21 adult females and 10 adult males, a  
176 sample group of 12 adult focal subjects (6 adult males and 6 adult females) was chosen to  
177 ensure lack of any limb injuries and in accordance with the level of habituation, simultaneously  
178 ensuring that age and rank classes were equally represented in the sample – see Table 1  
179 (Roberts and Roberts 2016b) for demographic and sampling details of the focal chimpanzees.  
180 The study was non-invasive and the study methods were approved by the University of Stirling  
181 Ethics Committee. Full details of the study site, subjects, data collection, video analysis and  
182 classification of gestures have been described previously (Roberts et al. 2014a), so only the  
183 key information is provided here.

#### 184 Data collection protocol

185 During 18-minute focal follows consisting of 9 scans (nine 2-minute intervals), two types of  
186 social information were recorded. First, the association and activity patterns were recorded.  
187 These included the identity of individuals present within 10 m and more than 10 m away from  
188 the focal individual, and the identity, visual attention, distance and activity of the nearest  
189 neighbour to the focal individual. Second, gestural communication to accompany the 18-  
190 minute instantaneous sampling of association and behaviour patterns in the chimpanzees was  
191 recorded continuously using a digital video camera recorder.

192 Visual attention between the focal individual and the nearest neighbour was recorded using  
193 categories presented in Supplementary Information 2. We tested the similarity in association  
194 patterns between the scans taken at 2 minute intervals, to examine the extent to which  
195 association patterns changed during the 18 minute focal follows, and between one focal follow  
196 and the next. For full details of this analysis, see (Roberts and Roberts 2016a; Roberts and  
197 Roberts 2016b). Briefly, the results demonstrated that the adjacent scans taken at 2 and 4  
198 minutes of the 18-minute sampling period yielded similar findings, and thus adjacent 2 minute

199 scans within a focal follow were treated as continuous data. However, the first scan (2 min)  
200 and final scan (18 min) during the focal follow differed both for 10 m associations and party  
201 level associations. Thus the association patterns change significantly over the course of an 18-  
202 minute focal follow, meaning each 18-minute focal follow can be considered an independent  
203 sample of association patterns.

#### 204 Behavioural measures

205 First, we used the genetic relationships identified in previous studies to classify pairs (dyads)  
206 of chimpanzees as kin or non-kin (Reynolds 2005), taking into account maternal kin relations  
207 only (relatedness 0.5). We classified dyads of chimpanzees as belonging to the same (5 years  
208 or less age difference) or a different (above 5 years age difference) age class (Mitani et al.  
209 2002) and also according to reproductive and sex similarity. The details of the categorization  
210 of attribute data are provided in Table 2.

211 Second, to establish the rates of gestures between dyads, the video footage was viewed on a  
212 television and the cases of nonverbal behaviour that were identified were coded as an act of  
213 gestural communication if they met following criteria: 1) the non-verbal behaviour was an  
214 expressive movement of the limbs or head and body posture that was mechanically ineffective,  
215 2) the behaviour was communicative by non-mechanical means (i.e. consistently produced a  
216 change in the behaviour of recipient or facilitated maintenance of activity, e.g. grooming).  
217 Whilst the criterion of ‘non-mechanical means’ did not exclude cases of physical bodily  
218 movement by the signaller of a social partner, it was important that such cases had a  
219 communicative purpose, i.e. rather than just move the body part of the social partner physically,  
220 these cases also displayed communicative purpose, For example during grooming, the light  
221 touch of the body and subsequent slight displacement of the body part also meant the desire  
222 for the social partner to move the body part. Next, behaviour had to be goal directed to be

223 considered intentional (Bard 1992; Bates et al. 1979). The intentionality of gestures was coded  
224 sensu Tomasello et al. (Tomasello et al. 1985) who gave following example to explain  
225 intentionality of gestures: ‘a child might be struggling to open a cabinet, crying and whining  
226 as s/he struggles. Seeing this, the mother might come to the rescue and open the cabinet. This  
227 is a perlocutionary act because, while communication may be said to have occurred, the  
228 "sender" (the child) did not intentionally direct any behavior towards the mother. If, on the  
229 other hand, the child has turned its attention from the cabinet to the mother and whined at her,  
230 the whining now becomes a social-communicatory act with the intention of obtaining adult  
231 aid’. Operationally, thus, one clear evidence for intentionality of gestures comes from the  
232 presence of an audience and visual attention between signaller and the recipient during  
233 production of the gesture. In this dataset, all cases of gesturing included the presence of an  
234 audience in close proximity (Supplementary Information 1 and 2), so the intentionality of the  
235 gestures in this dataset was not differentiated by the presence of the audience. In addition, the  
236 presence and absence of bodily orientation before and during the gesture were coded to  
237 establish intentionality of gestures (see Supplementary Information 2 for details for each  
238 gesture type). The presence and absence of communicative persistence was also coded in this  
239 paper following communicative persistence sensu Hobaiter and Byrne (Hobaiter and Byrne  
240 2011a; Townsend et al. 2016). In order to establish communicative persistence, gesture events  
241 were scored in accordance to whether they occurred singly or in sequences, defined as one or  
242 more than one gesture made consecutively by one individual, towards the same recipient, with  
243 the same goal, within the same context, and made within a maximum of 30 seconds interval to  
244 ensure independence. According to the classification by Hobaiter and Byrne (Hobaiter and  
245 Byrne 2011b), persistence of gesturing is when the chimpanzee produces one gesture or a  
246 gesture sequence, then after a period of response waiting (1-5s) they produce another gesture -  
247 here such instances are termed a ‘persistence sequence’. However, when a chimpanzee

248 produces a sequence and there is no intermittent pause between gestures, then the chimpanzee  
249 has not persisted – here such instances are here termed a ‘rapid sequence’. Supplementary  
250 Information 2 contains detailed information for the percentages of each gesture type occurring  
251 within each sequence type. Moreover, Supplementary Information 1 (Table 2) provides the  
252 number of cases of single gestures, persistence and rapid sequences per each focal subject  
253 separately. The panthoot behaviour is broadcast at a wider audience and within social network  
254 analysis we counted all individuals present within 10 meters as recipients of any gestures  
255 accompanied by pant hoots produced by the focal subject. The identity of the recipients of the  
256 panthoot was taken from the scan sample recorded every 2 minutes.

257 A random sample of 50 sequences of gestures was coded by a second coder for intentionality  
258 (response waiting and persistence) and the Cohen’s Kappa coefficient showed good reliability  
259 ( $K = 0.74$ ) (Bakeman and Gottman 1997). In this sample of reliability coding of persistence,  
260 one requirement for categorizing the event as persistence was the presence of mutual bodily  
261 orientation between the signaller and the recipient. Thus in this sample, response waiting and  
262 persistence co-occurred in all cases of gesturing.

263 Having established the independence of the data collection protocol, the behavioural measures  
264 for each dyad of the signaller and the recipient were calculated in the following manner:

265 The dyadic communication measure

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

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

270 where  $C_{AB}$  = the number of times A communicated with B when in close proximity (within  
271 10m) to B

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

273 2 = duration of instantaneous subsample interval in minutes

274 60 = the number of minutes in an hour

275 Social Network Analysis (SNA)

276 The behavioral measures were entered into a network matrix consisting of 12 rows and 12  
277 columns, with each row and column designating a different focal chimpanzee. In this analysis  
278 only data on 132 focal and non-focal subject dyads was included in the analysis, excluding any  
279 data where the recipient was not a focal subject in this study. The number of entries for each  
280 behavioural measure are provided in Table 2. The values in each cell of the matrix represented  
281 the value for communication or proximity for a specific pair of chimpanzees (e.g. the rate of  
282 persistence sequence between Bwoba and Hawa, per hour spent within 10m). These networks  
283 were weighted – i.e. each cell consisted of a continuous value representing that behaviour,  
284 rather than a 1 or a 0 indicating the presence or absence of a tie. Further, the networks were  
285 directed in that the rate of gestures by Bwoba that were directed to Hawa may be different from  
286 the rate of gestures by Hawa that were directed to Bwoba.

287 The observations that make up network data are not independent of each other and thus in  
288 general standard inferential statistics cannot be used on network data. Instead, a set of analyses  
289 using randomisation (or permutation) tests have been developed where the observed value is  
290 compared against a distribution of values generated by a large number of random permutations  
291 of the data. The proportion of random permutations in which a value as large (or as small) as  
292 the one observed is then calculated, and this provides the *p* value of the test (Borgatti et al.  
293 2013). We used Multiple Regression Quadratic Assignment Procedure (MRQAP) to examine  
294 the relationships between the networks (Borgatti et al. 2013). MRQAP regression is similar to  
295 standard regression in that it allows for the examination of the effect of a number of  
296 independent variables (e.g. gestural communication network) on an outcome variable (e.g.  
297 proximity network). Several different types of MRQAP regression are available and we used

298 Double Dekker Semi-Partialling MRQAP regression, which is more robust against the effects  
299 of network autocorrelation and skewness in the data (Dekker et al. 2007). The number of  
300 permutations used in this analysis was 2,000. All data transformations and analyses were  
301 carried out using UCINET 6 for Windows (Borgatti et al. 2014).

## 302 **Results**

### 303 **Type of sequence**

304 We examined a total of 545 sequences (1044 instances of gestures) performed by 12 focal adult  
305 individuals towards other focal and non-focal adult individuals to examine the extent to which  
306 the gestures presented in this dataset were intentional. The percentage of association between  
307 each gesture type separately and indices of intentionality is given in Supplementary  
308 Information 1, Table 1. Moreover, frequencies of gesture events within these categories are  
309 provided in Supplementary Information 2. In this sample (consisting of adult to adult gestures  
310 only) the mean percentage  $\pm$  SD [95% CI] of cases of all gesture types associated with the  
311 presence of bodily orientation by the signaller towards the recipient during production of the  
312 gesture was  $91.5 \pm 18.5\%$ , [87, 95]. The mean percentage  $\pm$  SD [95% CI] of cases of all gesture  
313 types associated with the presence of recipients' bodily orientation towards signaller, when the  
314 signaller's bodily orientation towards the recipient was absent, was  $6.9 \pm 15.4\%$  [3, 10].  
315 Finally, the mean percentage  $\pm$  SD [95% CI] of cases of all gesture types where neither signaller  
316 nor the recipient were bodily oriented towards one another during production of the gesture  
317 was  $1.5 \pm 11\%$  [0, 3]. This shows that the gestures in our dataset were communicative and  
318 intentional according to the previously established criteria for defining intentionality in  
319 preverbal humans and primates (Bard 1992; Bates et al. 1979). In this paper, sequences were  
320 categorized as either single gestures, persistence sequences or rapid sequences following  
321 Hobaiter and Byrne (Hobaiter and Byrne 2011b), taking into account both manual and bodily  
322 gestures (Roberts et al. 2014a; Roberts et al. 2012b). Per focal individual, the mean number  $\pm$

323 SD [95% CI] of single gestures was  $32.0 \pm 32$ , [11.69, 52.47], for persistence sequences was  
324  $4.41 \pm 5.85$ , [0.69, 8.13] and for rapid sequences was  $8.9 \pm 9.09$ , [3.14, 14.69] – see also  
325 Supplementary Information 1, Table 2 for frequency of single gestures, persistence and rapid  
326 sequences for each focal subject separately. In this study we used two main sets of analyses:  
327 Multiple Regression Quadratic Assignment Procedures (MRQAP) and node-level regression.  
328 The description of all the variables included in these models are provided in Table 2. In all  
329 analyses, the age, sex, reproductive status, kinship were included in the models, including the  
330 recipient of the gesture entered as a dyad partner in all models. Only statistically significant  
331 findings are presented in this block of results. Full details of the models including all variables  
332 are provided in Tables 3 - 9.

### 333 **Type of sequence and proximity (Hypothesis 1)**

334 We used MRQAP to examine the relationship between duration of time spent in proximity  
335 (within 10 meters per hour spent in same party) and the rate of production of gestures  
336 (frequency per hour spent within 10 m) and demography (Table 3). The proximity was  
337 significantly positively associated with a higher rate of persistence sequence between dyads ( $\beta$   
338 = 0.164,  $p = 0.034$ ). In contrast, the rate of rapid sequences or persistence sequences was not  
339 significantly associated with the proximity (Fig. 1).

### 340 **Type of sequence and type of response (Hypothesis 2)**

341 We then examined how the rate of response type to the gestures (response by visual or tactile,  
342 gesture, response by vocalization, response by activity change) was associated with the type of  
343 sequence (rapid sequence, persistence sequence, single gesture) (Tables 4 - 6). There was a  
344 positive association between response by vocalization and rapid sequence ( $\beta = 0.857$ ,  $p =$   
345 0.001). Moreover, there was a positive association between a single gesture and response type  
346 by activity change ( $\beta = 0.488$ ,  $p = 0.001$ ) and positive association between a single gesture and

347 response by visual or tactile gesture ( $\beta = 0.392$ ,  $p = 0.001$ ). Finally, there was a positive  
348 association between response by activity change and persistence ( $\beta = 1.132$ ,  $p = 0.001$ ) but  
349 negative association between response by tactile or visual gesture and persistence ( $\beta = -0.754$ ,  
350  $p = 0.001$ ).

### 351 **Presence and absence of response and proximity (Hypothesis 3)**

352 We next examined how the rate of response type to the gestures (response presence and  
353 absence) was associated with the proximity (Table 7) There was a significant positive  
354 association between proximity and response presence ( $\beta = 0.178$ ,  $p = 0.026$ ).

### 355 **Type of response and proximity (Hypothesis 4)**

356 We next examined how the rate of response type to the gestures (response by visual or tactile,  
357 gesture, response by vocalization, response by activity change) was associated with the  
358 proximity (Table 8). There was a significant negative association between proximity and  
359 response by visual or tactile gesture ( $\beta = -0.391$ ,  $p = 0.012$ ). In contrast, there was a significant  
360 positive association between the proximity and response by activity change ( $\beta = 0.603$ ,  $p =$   
361  $0.002$ ).

### 362 **Sequence network size and centrality in proximity network (Hypothesis 5)**

363 Finally, we used node-level regressions to examine the association between gesture sequences  
364 (rapid and persistence), single gestures and individual position in the proximity network  
365 (centrality outdegree). Out degree refers to behaviours directed by the focal chimpanzee to  
366 conspecifics, whilst in degree refers to behaviours directed by conspecifics towards the focal  
367 chimpanzee. The network can vary between dyad A to B and B to A (e.g. proximity of Bwoba  
368 to Hawa can be different from proximity of Hawa to Bwoba), therefore in degree and out degree  
369 are calculated separately. All analyses controlled for the duration of time spent in proximity  
370 to oestrus females, time spent in proximity to kin, and the age and sex of the focal chimpanzee.



371 We found that there was a positive association between the proximity outdegree and a  
372 persistence sequence indegree ( $\beta = 1.858$ ,  $p = 0.015$ , Table 9). Thus individual chimpanzees  
373 with a higher rate of social behaviours directed at them also received a higher rate of persistence  
374 sequence directed at them.

## 375 **Discussion**

376 An important aspect in understanding the evolution of complex sociality in humans is  
377 to understand the role of primate sequences of gestures in social bonding at the level of the  
378 dyad and the group. Primates produce single gestures (produced singly rather than in series),  
379 persistence sequences (series of gestures interspersed with periods of response waiting) and  
380 rapid sequences (series of gestures made in quick succession without periods of response  
381 waiting) (Hobaiter and Byrne 2011b). Recent theoretical accounts emphasize the role of  
382 gestures not purely as a means of information transfer (Seyfarth et al. 2010), but as a time-  
383 efficient mechanism of social bonding (Dunbar 2012). However, studies to date have examined  
384 the characteristics of gesture in isolation from the social system (Bard 2017; Bard et al. 2017;  
385 Byrne et al. 2017; Leavens et al. 2017). Thus, the mechanisms through which gesture sequences  
386 can be associated with more complex social systems remain unresolved. In this study, we used  
387 a sample of twelve wild chimpanzees to examine how the production of gesture sequences is  
388 related to patterns of sociality at both the individual and group levels. This extends previous  
389 research which has focused on the associated between type of gesture sequence and the  
390 response of the recipient. Overall the results demonstrate a significant association between  
391 patterns of proximity between pairs of chimpanzees and rates of different types of gestural  
392 communication.

393 Longer durations of proximity, per hour they spent within 10m, were associated with a  
394 higher rate of persistence sequence, but not a higher rate of single gesture or rapid sequences,

395 supporting Hypothesis 1. Further, higher rates of intentional gestures (persistence, single  
396 gesture) were associated with response by activity change, whereas higher rate of emotional  
397 gestures (rapid sequence) were associated with response by vocalisation supporting Hypothesis  
398 2. Finally, longer durations of proximity were associated with a higher rates of response present  
399 and response by means of activity change, supporting Hypotheses 3 and 4. These results  
400 suggest that one possible function of communication between individuals who spent a longer  
401 duration of time in social behaviors is to enable behavioral synchrony by influencing the  
402 behaviour of the recipient in goal directed and intentional way. Thus, one important dimension  
403 of complex social interactions is the degree of successful inter-individual adjustment between  
404 interactants, enabling them to coordinate joint activities such as travel or mutual grooming  
405 through intentional gesturing. Recent studies have provided evidence that gestural  
406 communication responded to by the recipient appears to be related to stronger social bonds  
407 than communication which has not been responded to (Schneider et al. 2017). Therefore one  
408 reason why individuals who spent longer durations of time in proximity use intentional gestures  
409 is because they can influence recipient flexibly to facilitate social interaction and achieve the  
410 communication goal (Roberts et al. 2014a).

411 In line with previous research in this area (Lehmann et al. 2016; Sapolsky et al. 1997;  
412 Silk et al. 2013; Silk et al. 2010b) we used proximity to measure the level of sociality of pairs  
413 of chimpanzees. This allowed for the association between sociality and rates of different types  
414 of gestural communication to be explored. However, different types of social behaviors may  
415 play a different roles in social cohesion in primates. For instance, the role of grooming in  
416 primate social relationships is well established (Dunbar 2010), but the role of other joint  
417 behaviours such as joint travel or joint feeding is less clear (Gruber and Zuberbühler 2013;  
418 King et al. 2011). Similarly, in humans cooperative contexts whereby actors co-regulate  
419 behaviour with one another to achieve common goal (e.g. joint travel) reflect stronger social

420 bonding than other contexts (Pollet et al. 2013; Wolf et al. 2016). However, whether these  
421 different dimensions of sociality are differentially linked to gestural communication within  
422 dyads is unclear from this study and future work could examine specific instances of behaviour  
423 (e.g. grooming interactions, travel initiation) to explore the role of different types of gestural  
424 communication in coordinating this behaviour (Fedurek et al. 2015).

425         This interpersonal adjustment in social relationships may be particularly cognitively  
426 demanding and this this is especially the case in species where individuals have to manage a  
427 larger number of differentiated social relationships (Dunbar 2012; Freeberg et al. 2012). In  
428 particular, fission- fusion societies, and species of primates that live in large social groups,  
429 face cognitive challenges in maintaining a differentiated social network consisting of both  
430 stronger and weaker social ties (Silk et al. 2010a). Maintaining these different types of social  
431 bonds is necessary to preserve group cohesion (Henzi et al. 1997). In this study, we found that  
432 individual differences in sociality (centrality in the network) was associated with different  
433 patterns of gestural communication, supporting Hypothesis 5. Specifically centrality was  
434 positively associated with the rate of persistence sequence directed at the central individual,  
435 but not the rate of single gesture or rapid sequences directed at the central individual. This  
436 suggests that flexible use of persistence sequences is valuable to ensure the goal of  
437 communication is met (Roberts et al. 2014a) and intentional gestures play an important role in  
438 chimpanzee sociality.

439         The conclusions drawn in this study could be influenced by the uneven representation  
440 of different gestures within dataset. Previous studies which employed continuous observation  
441 of gestures have ranged between three (Hobaiter et al. 2017) to five hours (Wilke et al. 2017)  
442 of observation of each focal individual during study period. In the current study, we observed  
443 12 focal subjects from a single study group for a mean duration of 12 hours per each focal  
444 chimpanzee, ranging between 8.3 hours to 18.63 hours (taking into account the video data

445 collected in parallel with the socio-ecological samples during the last data collection season).  
446 However, the sampling of focal individuals was uneven and single gestures and sequences vary  
447 in their occurrence rates. For instance, in this study, there were 160 sequences of different types  
448 whereas there were 385 single gestures. Similarly, gesture types were not distributed evenly  
449 across categories, as a majority of gesture types were confined to most common occurrence  
450 categories. Thus whilst the results are broadly in line linking gestural communication with  
451 sociality and coordination of behavior in primates (Byrne et al. 2017; Leavens et al. 2005;  
452 Roberts et al. 2014b), further research is needed to explore how gestural communication is  
453 associated with sociality in other chimpanzee communities and other primate species. This  
454 further research could focus on compiling a dataset whereby gesture sequences and gesture  
455 types would be represented more equally. Further, whilst we explored associations between  
456 sociality and gestural communication, we could not demonstrate a causal relationship between  
457 gestural communication and a longer durations of proximity between pairs of chimpanzees.  
458 Research examining how specific types of gestural communication are associated with the  
459 durations of specific instances of social behavior would be needed to establish such a causal  
460 relationship. Many gestures are produced in the context of grooming (Byrne et al. 2017;  
461 Roberts et al. 2012a) and one promising area for future research would be to examine whether  
462 specific types of gestures given in grooming contexts are associated with longer grooming  
463 bouts or reduced probability of defecting to an alternative grooming partner (Fedurek et al.  
464 2015; Kaburu and Newton-Fisher 2016)

465         The predictability of conspecifics' behaviour is a major modulator of stress in group  
466 living animals (Seyfarth and Cheney 2013) and greater use of intentional gestures may reduce  
467 this stress by increasing the likelihood of the recipient responding appropriately to the gesture.  
468 This is especially important as gestural communication can be used in both affiliative and  
469 agonistic contexts in close proximity and thus intentional gestures may lead to greater

470 coordination between the pair of chimpanzees. Previous research has focused on how  
471 intentionality in gestural communication is related to the recipients' response and  
472 comprehension of signaling, both in relation to human and conspecific recipients. Whilst this  
473 research has detailed the extent to which chimpanzees can flexibility adjust their  
474 communication, and explored how sensitive these adjustments are to different aspects of the  
475 recipients response, it has not demonstrated how this flexibility in communication helps  
476 chimpanzees meet the key adaptive challenges faced by group living animals – maintaining a  
477 differentiated set of stable, long-term social relationships and responding appropriately to  
478 others (Dunbar and Shultz 2007a). If the key driving force of brain evolution in both primates  
479 and hominins has been evolution of complex social relationships rather than ecological factors  
480 (Dunbar and Shultz 2007b), the cognitive skills underpinning flexibility in communication  
481 should enable primates to meet these social challenges. The current results suggest that  
482 intentional gestural communication may enable greater levels of behavioural coordination  
483 when interacting at close proximity and thus longer durations of proximity and affiliative  
484 activities such as grooming.

485         To conclude, the ability to accurately coordinate social behavior through gestural  
486 signals with conspecifics is a key aspect of successful group living (Seyfarth and Cheney 2013).  
487 The findings of this study demonstrated that flexibility in gestural communication is associated  
488 with sociality and may help chimpanzees meet the challenges of group living, with persistence  
489 in particular being associated with longer durations of proximity. Individual variation in the  
490 strength of social bonds in primates is strongly linked to fitness outcomes (Silk 2007) and our  
491 results suggest that flexibility in gestural communication may play an important role in  
492 explaining some of this individual variation in social relationships.

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676

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

678 in the study.

<b>Focal subject ID</b>	<b>Sex</b>	<b>Age</b>	<b>Female reproductive status</b>	<b>Total observation duration (minutes)</b>
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 <sup>c</sup>	Female	46	Cycling	500
NK <sup>a</sup>	Male	26	-	582
RH	Female	43	Nursing	1038
SQ	Male	17	-	554
ZM	Female	40	Cycling	710

679 Notes. <sup>a</sup> Alpha male, <sup>b</sup> Alpha female.

680 Dominance based on unidirectional pant-grunt calls – for full details, see (Roberts and

681 Roberts 2016b)

682 Table 2. Variables included in the models

Independent variable	Definition	Frequencies or mean±SD/ 95% CI (duration/frequency per hour spent within 10 meters)
Persistence sequence	A series of gestures whereby there are pauses of 1 -5 seconds between consecutive gestures	0.11±0.45, [0.03, 0.18]
Single gesture	A single gesture that is not made in series and where there is at least 30 seconds to the next consecutive gesture	1.27±4.07, [0.57, 1.97]

Rapid sequence	A series of gestures without pauses between consecutive gestures	0.45±1.30, [0.23, 0.68]
Sex difference	Sex difference between focal subject and the recipient (0 = different sex: male-female or female-male, 1 = same sex: male-male or female-female)	0 = 60, 1 = 60
Age difference	Age difference between focal subject and the recipient (0 = different age: more than 5 years age difference between individuals in the dyad, 1 = same age: no more than 5 years age difference between individuals in the dyad)	0 = 102, 1 = 30
Oestrous similarity	Reproductive state difference between focal subject and the recipient (0 = reproductively inactive: unoestrous female- unoestrous female, unoestrous female-oestrous female, oestrous female-oestrous female, unoestrous female-male, male-male; 1 = reproductively active: male-oestrous female)	0 = 96, 1 = 36
Maternal kinship	Maternal kinship presence between focal subject and the recipient (0 = unrelated dyad, 1 = mother-son; son-mother)	0 = 126, 1 = 6
Proximity	Duration of time individual spent in proximity within 10 metres per hour spent in the same party	23.26±1.22, [20.84, 25.69]
Response by activity change	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)	0.58±1.80, [0.26, 0.89]
Response by vocalization	Change of behaviour by means of vocalization (production of sound via vocal tract) by the recipient,	0.47±2.02, [0.12, 0.82]

	which is not followed by goal directed action towards signaller (e.g. pantgrunt during travel, whereby signallers travel before and after the pantgrunt)	
Response by visual or tactile gesture	Change of behaviour by means of visual or tactile gesture 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)	0.08±0.40, [0.01, 0.14]

683 Table 3. MRQAP regression models showing predictors of proximity (duration of time spent  
684 within 10 meters per hour spent in same party) by sequence type of gestures between N = 12,  
685 132 dyadic relationships of the chimpanzees. Significant P values are indicated in bold.

Attribute category/ rate of gesture sequence per hour spent in close proximity	Standardized coefficient	Standard error	P
Age similarity	0.162	3.658	0.060
Sex similarity	-0.091	3.760	0.239
Kinship similarity	0.065	6.742	0.258
Oestrous similarity	0.006	4.328	0.487
Rapid sequence	-0.025	1.107	0.389
Single gesture	0.110	0.370	0.138
Persistence sequence	0.164	3.109	<b>0.034</b>

687 Table 4. MRQAP regression models showing predictors of rapid sequence (rate of production  
 688 per hour spent within 10 meters) by rate of response to the gesture between N = 12, 132 dyadic  
 689 relationships of the chimpanzees. Significant P values are indicated in bold.

Attribute category/ rate of gesture sequence per hour spent in close proximity	Standardized coefficient	Standard error	P
Age similarity	0.010	0.160	0.386
Sex similarity	-0.057	0.169	0.176
Kinship similarity	-0.037	0.283	0.142
Oestrous similarity	-0.060	0.193	0.171
Response by visual or tactile gesture	0.006	0.353	0.471
Response by activity change	-0.067	0.084	0.271
Response by vocalisation	0.857	0.065	<b>0.001</b>

690

691 Table 5. MRQAP regression models showing predictors of persistence sequence (rate of  
 692 production per hour spent within 10 meters) by rate of response to the gesture between N = 12,  
 693 132 dyadic relationships of the chimpanzees. Significant P values are indicated in bold.

Attribute category/ rate of gesture sequence per hour spent in close proximity	Standardized coefficient	Standard error	P
Age similarity	-0.029	0.086	0.373

Sex similarity	0.042	0.086	0.327
Kinship similarity	-0.015	0.152	0.437
Oestrous similarity	0.053	0.095	0.275
Response by visual or tactile gesture	-0.754	0.181	<b>0.001</b>
Response by activity change	1.132	0.048	<b>0.001</b>
Response by vocalisation	0.067	0.019	0.134

694

695 Table 6. MRQAP regression models showing predictors of single gesture (rate of production  
 696 per hour spent within 10 meters) by rate of response to the gesture between N = 12, 132 dyadic  
 697 relationships of the chimpanzees. Significant P values are indicated in bold.

Attribute category/ rate of gesture sequence per hour spent in close proximity	Standardized coefficient	Standard error	P
Age similarity	0.103	0.492	<b>0.017</b>
Sex similarity	0.047	0.493	0.195
Kinship similarity	0.002	0.844	0.373
Oestrous similarity	0.037	0.534	0.282
Response by visual or tactile gesture	0.392	0.901	<b>0.001</b>
Response by activity change	0.488	0.247	<b>0.001</b>
Response by vocalisation	0.068	0.100	0.083

698

699 Table 7. MRQAP regression models showing predictors of proximity (duration spent within  
700 10 meters per hour spent in same party) by rate of response present or absent to the gesture  
701 between N = 12, 132 dyadic relationships of the chimpanzees. Significant P values are  
702 indicated in bold.

Attribute category/ rate of gesture sequence per hour spent in close proximity	Standardized coefficient	Standard error	P
Age similarity	0.149	3.748	0.078
Sex similarity	-0.059	3.704	0.321
Kinship similarity	0.064	6.619	0.252
Oestrous similarity	0.030	4.282	0.397
Response absent	0.006	0.573	0.466
Response present	0.178	0.380	<b>0.026</b>

703

704 Table 8. MRQAP regression models showing predictors of proximity (duration spent within  
705 10 meters per hour spent in same party) by rate of response to the gesture between N = 12, 132  
706 dyadic relationships of the chimpanzees. Significant P values are indicated in bold.

Attribute category/ rate of gesture sequence per hour spent in close proximity	Standardized coefficient	Standard error	P
Age similarity	0.198	3.887	0.026
Sex similarity	-0.127	3.802	0.154

Kinship similarity	0.063	6.539	0.239
Oestrous similarity	-0.004	4.093	0.479
Response by visual or tactile gesture	-0.391	6.567	<b>0.012</b>
Response by activity change	0.603	1.746	<b>0.002</b>
Response by vocalisation	-0.088	0.761	0.198

707

708 Table 9. Node-level regression models predicting proximity out (overall durations of time spent  
709 in proximity within 10 meters per hour dyad spent in same party produced). Out degree refers  
710 to behaviours directed by the focal chimpanzee to conspecifics, whilst in degree refers to  
711 behaviours directed by conspecifics towards the focal chimpanzee. Based on 12 chimpanzees.  
712 Significant *p* values are indicated in bold.

Attribute category/ Agreement in gesture repertoires	Standardized coefficient	<i>P</i>
Reproductive state of female	-1.605	<b>0.025</b>
Kinship	0.359	0.250
Sex/ age	-0.492	0.210
Rapid sequence outdegree	-0.112	0.466
Rapid sequence indegree	-0.046	0.471
Single gesture outdegree	0.255	0.431
Single gesture indegree	-0.691	0.166



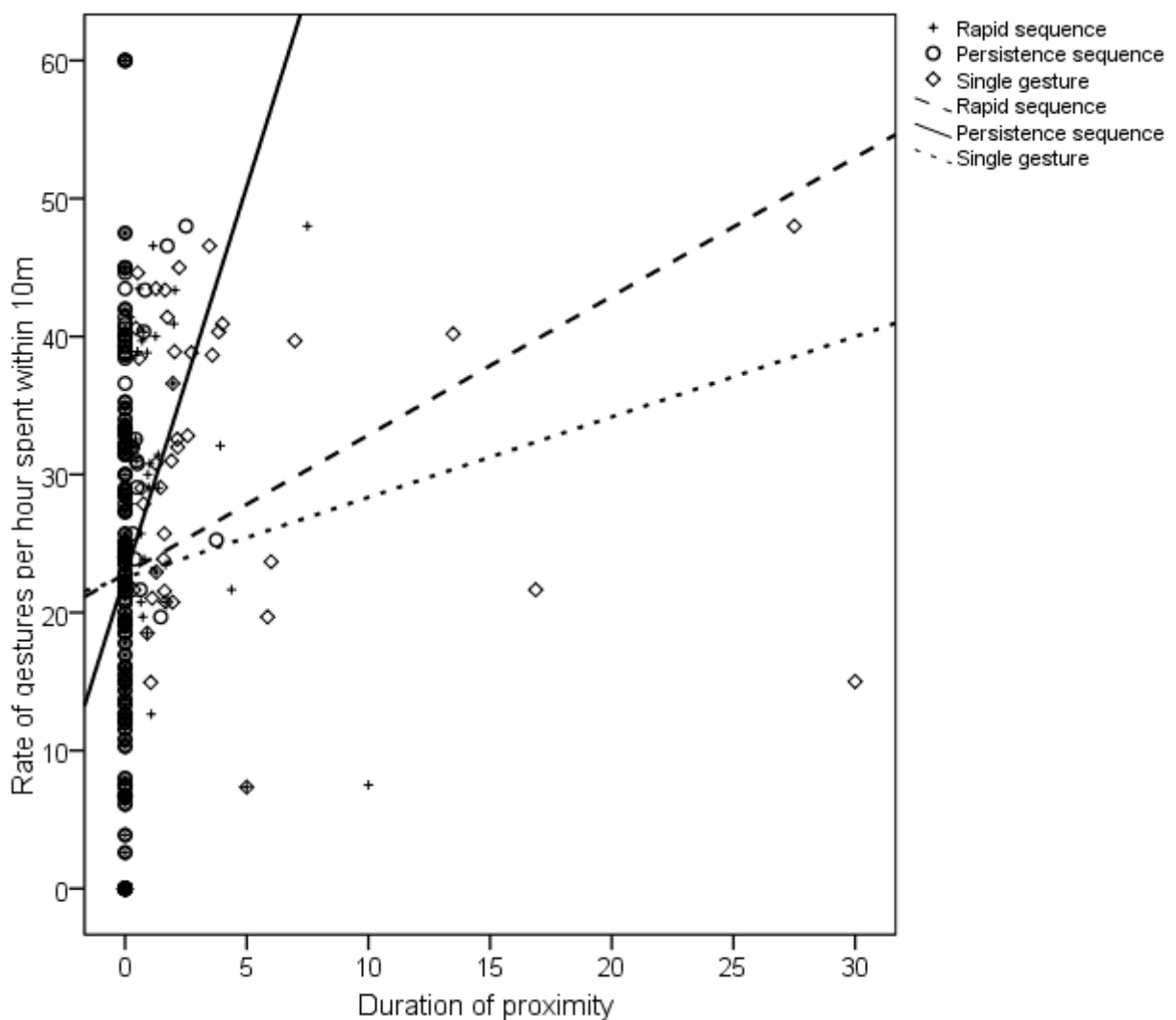
Persistence sequence outdegree	-0.208	0.389
Persistence sequence indegree	1.858	<b>0.015</b>

713

714 Fig 1. Proximity (duration of time spent within 10 meters per hour spent in the same party) and

715 rate of single gestures, rapid sequences and persistence sequences in dyads of chimpanzees (n

716 = 132).



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