

## Title page

# Visual attention, indicative gestures and calls accompanying gestural communication are associated with sociality in wild chimpanzees

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1 **Abstract**

2 The challenges of life in complex social groups may select for complex communication in order  
3 to regulate interactions among conspecifics. Whereas the association between social living and  
4 vocalizations has been explored in nonhuman primates, great apes also have a rich repertoire  
5 of gestures and how the complexity of gestural communication relates to sociality is still  
6 unclear. We used social network analysis to examine the relationship between the duration of  
7 time pairs of chimpanzees spent in close proximity (within 10 m) and the rates of gestural  
8 communication accompanied by visual orientation of the signaller, one-to-one calls, indicative  
9 gestures (collectively self-relevance cues) and synchronized pant-hoot calls. Pairs of  
10 chimpanzees that spent a longer duration of time in close proximity had a higher rate of visual  
11 gestures accompanied by these behaviours. Further, individual chimpanzees that had a greater  
12 number of close proximity bonds had a larger social network maintained through gestures  
13 accompanied by synchronized pant-hoot calls. In contrast, the network size maintained through  
14 gestures unaccompanied by these behaviours was not positively associated with either close  
15 proximity bonds in pairs of chimpanzees, or individual differences in sociality. These results  
16 suggest that self-relevance cues and synchronized pant-hoot calls accompanying gestures may  
17 increase the efficiency of gestural communication in social bonding and that multimodal  
18 communication may have played a key role in language evolution.

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20 **Key words: chimpanzees, gestural communication, self-relevance cue, visual**  
21 **attention, social network, synchronized call**

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25           **Significance statement**

26           Like humans, nonhuman primates use gestures to communicate with others, but how  
27 combinations of gestures with visual orientation of the signaller, indicative gestures, one-to-  
28 one calls and synchronized calls are related to social relationships is poorly understood. We  
29 demonstrate that use of these behaviours accompanying visual gestures in pairs of wild  
30 chimpanzees was related to the amount of time pairs of chimpanzees spent in close proximity.  
31 Central individuals in the community had a larger network of relationships maintained through  
32 gestures accompanied by synchronized pant-hoot calls. Thus, these behaviours may increase  
33 the efficiency of gestural communication in social bonding. More broadly, these results  
34 illustrate the importance of different types of communication in managing different types of  
35 social relationships in nonhuman primates and other species.

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## 47 **Introduction**

48           The association between sociality and communication has long been of interest both in  
49 understanding complex sociality in nonhuman animals and also in developing theories of how  
50 language evolved in humans (Arbib, Liebal, & Pika, 2008; M. Corballis, 2009; R. Dunbar,  
51 2012; Freeberg, Dunbar, & Ord, 2012; Pollick & de Waal, 2007). Individuals maintaining  
52 complex social relationships may require more complex communication to regulate  
53 interactions with group members (Freeberg et al., 2012). Complex social relationships have  
54 been defined as '*those in which individuals frequently interact in many different contexts, and*  
55 *often repeatedly interact over time*' whilst complex communicative systems have been defined  
56 as '*those that contain a large number of structurally and functionally distinct elements (e.g.*  
57 *large display repertoire sizes) or possess a high amount of bits of information*' (Freeberg et al.,  
58 2012; K. Langergraber, Mitani, & Vigilant, 2009; Mitani, 2009; Silk, 2007; Silk et al., 2010b).  
59 Although in primates individuals can maintain social relationships and communicate with  
60 partners who do not reciprocate their investment into the social relationship, reciprocated social  
61 relationships are a key feature of complex sociality (Foerster et al., 2015; Mitani, 2009).  
62 Language does not leave a direct fossil trace, and therefore studies of communication and  
63 sociality in nonhuman primates can provide insights into factors that have shaped the evolution  
64 of language in humans (Byrne et al., 2017; W. T. Fitch, 2010; Pollick & de Waal, 2007; Sam  
65 G. B. Roberts & Anna I. Roberts, 2016; Robert M Seyfarth & Cheney, 2014). In this study we  
66 explore the association between the complexity of sociality, defined as the presence or absence  
67 of reciprocated close proximity ties, and gestural communication of wild chimpanzees to  
68 provide insight into the origins of language.

69           Many theories of language evolution propose that nonhuman primate vocalisations  
70 provided the starting point for the development of more complex vocal communication seen in  
71 humans (Crockford, Wittig, Mundry, & Zuberbuehler, 2012; Enard et al., 2002; Engh,

72 Hoffmeier, Cheney, & Seyfarth, 2006; W. T. Fitch, 2010; W. T. Fitch, de Boer, Mathur, &  
73 Ghazanfar, 2016; Anne Marijke Schel, Townsend, Machanda, Zuberbühler, & Slocombe,  
74 2013; Robert M Seyfarth & Cheney, 2014; R. M. Seyfarth et al., 2010). Studies of nonhuman  
75 primate vocalisations have focused on examining the association between specific  
76 vocalisations such as alarm calls and external entities (A. M. Schel & Zuberbuhler, 2009; R.  
77 Seyfarth, Cheney, & Marler, 1980) and exploring the overlap between the properties of  
78 nonhuman primate vocalisations and human language (T. Fitch, 2005; Robert M Seyfarth &  
79 Cheney, 2014). More recent studies have examined whether there is a relationship between  
80 vocalisations and sociality (Arlet, Jubin, Masataka, & Lemasson, 2015; McComb & Semple,  
81 2005). Grooming is one key behaviour nonhuman primates use to maintain relationships, but  
82 vocalisations are more efficient in reaching more recipients at a greater distance, and thus some  
83 researchers have proposed that vocalisations can act as a form of ‘grooming at a distance’,  
84 helping nonhuman primates meet the challenges of living in a complex social group (Arlet et  
85 al., 2015; Fedurek, Machanda, Schel, & Slocombe, 2013). For example, there is an association  
86 between pant-hoot chorusing and social bonds in wild chimpanzees (Fedurek et al., 2013).

87         However, nonhuman primates – especially the great apes - also have a rich repertoire  
88 of gestures which they use in a flexible and intentional way to communicate with conspecifics  
89 (Byrne et al., 2017; K. Hobaiter & Byrne, 2011; Roberts, Vick, & Buchanan-Smith, 2012;  
90 Tomasello, Call, Nagell, Olguin, & Carpenter, 1984). Whilst recent findings have shown that  
91 vocalisations in nonhuman primates are produced more flexibly than initially thought  
92 (Crockford et al., 2012; Anne Marijke Schel et al., 2013), nonhuman primates show greater  
93 flexibility in their use of gestural communication, in that the association between the gesture  
94 type and behavioural context is much weaker (Byrne et al., 2017; Catherine Hobaiter & Byrne,  
95 2014; Roberts, Roberts, & Vick, 2014). Nonhuman primates use gestures intentionally - they  
96 communicate with the recipient and adjust their communication in a flexible and dynamic way

97 (Byrne et al., 2017; D. A. Leavens, Russell, & Hopkins, 2005; Roberts, Roberts, et al., 2014).  
98 Because of this greater flexibility of gestural communication as compared to vocal  
99 communication, many researchers propose that gestural communication may have played a key  
100 role in language evolution (Arbib et al., 2008; Call & Tomasello, 1994; M. Corballis, 2009;  
101 Gillespie-Lynch, Greenfield, Lyn, & Savage-Rumbaugh, 2014; Pollick & de Waal, 2007;  
102 Tomasello et al., 1984). For instance, flexible gestural communication has only been recorded  
103 in great apes who are our closest living relatives, whereas vocalisations are present in many  
104 different taxa (Pollick & de Waal, 2007). The flexible use of gestures may have facilitated  
105 language evolution since the gesture areas but not vocal areas correspond to language areas in  
106 the human brain and primates may flexibly modify their behaviour to increase the efficiency  
107 of social bonding (M. C. Corballis, 2003; Freeberg et al., 2012; McComb & Semple, 2005).  
108 Thus, if communication systems play a key role in helping animals navigate the complexities  
109 of social life, there should be an association between gestural communication and sociality  
110 (Pollick & de Waal, 2007; Sam G. B. Roberts & Anna I. Roberts, 2016).

111         As one of the closest living nonhuman primate species to humans, chimpanzees are an  
112 ideal species to examine the association between sociality and gestural communication (Byrne  
113 et al., 2017; T. Fitch, 2005; McGrew, 2010). Chimpanzees have a fission-fusion social system  
114 where the broader community fissions into smaller sub-groups on a daily basis (Aureli et al.,  
115 2008; Eckhardt, Polansky, & Boesch, 2015; Goodall, 1986). Thus chimpanzees frequently  
116 interact with a broad range of social partners across a number of different behavioural contexts  
117 and the patterns of interaction between pairs of chimpanzees changes with the fissioning of the  
118 broader community into sub-groups. Chimpanzees use a complex system of vocalisations and  
119 some studies have demonstrated a link between these vocalisations and different aspects of  
120 sociality (Fedurek et al., 2013; Fedurek & Slocombe, 2013; Mitani & Gros-Louis, 1998).  
121 Chimpanzees also have a complex system of gestural communication and thus far research has

122 been focused on establishing the repertoire, examining flexibility in use and assessing evidence  
123 of intentionality (Byrne et al., 2017; Catherine Hobaiter & Byrne, 2014; C. Hobaiter, Byrne, &  
124 Zuberbühler, 2017; D. A. Leavens & Hopkins, 1998; Pika, Liebal, Call, & Tomasello, 2005;  
125 Roberts, Vick, & Buchanan-Smith, 2013; Roberts, Vick, Roberts, Buchanan-Smith, &  
126 Zuberbühler, 2012; Roberts, Vick, Roberts, & Menzel, 2014).

127 More recently, using the same dataset as used in the present study, Roberts and Roberts  
128 (A. I. Roberts & S. G. B. Roberts, 2016; Roberts & Roberts, 2017; Sam G. B. Roberts & Anna  
129 I. Roberts, 2016) explored how different aspects of communication in wild chimpanzees are  
130 related to sociality. Overall, rates of both gestures and vocalisations were positively related to  
131 the duration of time pairs of wild chimpanzees spent in close proximity (Sam G. B. Roberts &  
132 Anna I. Roberts, 2016). Further, there were important differences between the different  
133 modalities of gestures, such as visual (e.g. arm raise), tactile (e.g. embrace), auditory short-  
134 range (can be heard within 10m e.g. tap object) and auditory long-range (can be heard more  
135 than 10m away e.g. drum) (A. I. Roberts & S. G. B. Roberts, 2016). Auditory gestures are  
136 classified as such because the gesture itself makes a sound. These auditory gestures may or  
137 may not be accompanied by a vocalization. Higher rates of visual gestures (as compared to  
138 tactile or auditory gestures) were associated with time spent in close proximity (A. I. Roberts  
139 & S. G. B. Roberts, 2016). Overlap in the gestural repertoire was also related to duration of  
140 time pairs of chimpanzees spent in social behavior (Roberts & Roberts, 2017). However these  
141 studies, or any other studies of nonhuman primate gestural communication, have not examined  
142 the association between sociality and one key aspect of gestural communication - the extent to  
143 which gestures are accompanied by cues that direct recipient's attention and facilitate  
144 responding to signaller's gestures ('self-relevance cues'). In this framework, the integration of  
145 self-relevance cues and gestural communication increases the degree of self-relevance of the  
146 perceived gestural communication (Sander, Grafman, & Zalla, 2003). For instance, when there

147 are several individuals in close proximity, accompanying the gesture with a self-relevance cue  
148 may enable the recipient to perceive that the gesture is directed at them and respond to it more  
149 effectively than if a self-relevance cue accompanying the gesture is absent. Thus one aim of  
150 this study is to examine the association between the rate of gestures accompanied by these self-  
151 relevance cues and the duration of time pairs of chimpanzees spend in close proximity.

152         A key challenge for group living animals is detecting whether communication is  
153 directed at them, or at another conspecific and to respond to communication effectively (Engel  
154 et al., 2006; Grèzes & Dezcaché, 2014). This is especially true for chimpanzees detecting  
155 gestural communication in a dense forest habitat. Chimpanzees often accompany their gestures  
156 with a set of cues that may help receivers better coordinate behaviour with the signaller (K.  
157 Hobaiter & Byrne, 2011; Roberts, Roberts, et al., 2014). In line with previous literature in this  
158 area, we term these set of cues ‘self-relevance cues’, as they are all cues which enhance the  
159 relevance of the signaller’s communication to the recipient – the target of the communication  
160 (Grèzes, Adenis, Pougas, & Armony, 2013; Grèzes, Philip, et al., 2013; N’diaye, Sander, &  
161 Vuilleumier, 2009; Sander et al., 2003; Soussignan et al., 2013). For example, previous  
162 research on human communication has demonstrated the processing of emotional expression  
163 is influenced by whether or not the signaller’s gaze is directed at the recipient. Thus gaze  
164 direction acts as a self-relevance cue, indicating that the emotional expression is directed at the  
165 recipient (N’diaye et al., 2009; Soussignan et al., 2013). In this study we examine how the rate  
166 of gestural communication accompanied by three different self-relevance cues is associated  
167 with sociality. *Visual orientation of the signaller* has long been used as an indicator of the  
168 target of communication, both in research on nonhuman primate gestural communication and  
169 in human communication (D. A. Leavens, Hostetter, Wesley, & Hopkins, 2004; D. A. Leavens  
170 et al., 2005; N’diaye et al., 2009; Roberts, Roberts, et al., 2014). Gestures in which the signaller  
171 is oriented towards the recipient act as a cue to the recipient that the gesture is directed at them.



172 Further, gestures accompanied by vocalisations draw the intended recipient's attention  
173 towards the signaller – so-called 'attention getters' (Gillespie-Lynch et al., 2014; Hopkins,  
174 Taglialatela, & Leavens, 2007; D. A. Leavens et al., 2004; Taglialatela et al., 2015). These  
175 vocalisations are given by the signaller alone at another single recipient (*one-to-one call*) (Sam  
176 G. B. Roberts & Anna I. Roberts, 2016). Finally, *indicative gestures* refer to movements of the  
177 hand or arm towards the recipient without physical touch (e.g. arm beckon) (Catherine Hobaiter  
178 & Byrne, 2014; Roberts, Vick, et al., 2014). Again, there is evidence in both humans (Grèzes  
179 & Dezechache, 2014) and nonhuman primates (Catherine Hobaiter & Byrne, 2014; Roberts,  
180 Roberts, et al., 2014) that indicative gestures act as a cue to the recipient that the gesture is  
181 directed at them and facilitate processing of the gesture. Because of their manual nature, all  
182 indicative gestures are visual gestures. In addition to these self-relevance cues, chimpanzees  
183 can also accompany their gestures with synchronized pant-hoot calls that can function to  
184 socially bond and coordinate behaviour with several individuals simultaneously (*synchronized*  
185 *call*). These calls are produced jointly by several individuals at the same time. The  
186 simultaneous and rhythmically matched production of the sound and the gesture can act as an  
187 alternative mechanism to the gestures accompanied by self-relevance cues as it may not require  
188 mutual attention and one-to-one coordination to regulate social bonding. In this paper, we refer  
189 collectively to gestures with all types of cues (Mutual attention, One-to-one call, Indicative  
190 gesture, Synchronized call) as gesture with a cue. All of the gestures that did not include a use  
191 of self-relevance or synchronized cue were classified as gesture *no cue*.

192 One important feature of gestural communication is the conspicuousness of the signal.  
193 Primate gestures vary from loud vigorous sounds made by slapping or drumming their hands  
194 against objects, tactile behaviours such as strokes on another individual's body part, to more  
195 subtle visual behaviours such as waving a hand from a distance (Liebal, Call, & Tomasello,  
196 2004). For recipients, detecting and responding appropriately to more subtle visual gestures

197 could be a more difficult task than detecting and responding to more vigorous auditory gestures.  
198 Use of the cues, however, can facilitate maintenance of social relationships through more subtle  
199 gestures. In humans, simultaneous presentation of the gesture and multimodal cues (e.g.  
200 vocalizations) improves the detection and recognition of more subtle gestures (Van den Stock,  
201 Grèzes, & de Gelder, 2008). It is therefore reasonable to assume that the cues will be more  
202 important in managing social relationships through visual gestures than managing social  
203 relationships through tactile or auditory gestures. However, the relationship between the use  
204 of cues across modalities of gestures and duration of social behavior has not been examined.

205 In addition, the effectiveness of gestural communication in maintaining social relationships  
206 may vary as a function of the type of social cues. For instance, in humans the efficiency of  
207 social bonding increased when partners were positioned in sight of each other (i.e. Skype  
208 conversation) rather than out of sight (i.e. telephone conversation) (Vlahovic, Roberts, &  
209 Dunbar, 2012). In chimpanzees, the use of pant-hoot call accompanying visual gestures was  
210 associated with longer duration of time spent in social bonding behavior than the use of gestures  
211 for mutual grooming and travel (Sam George Bradley Roberts & Anna Ilona Roberts, 2016).  
212 However, it is currently unclear whether there is a relationship between the type of the cue and  
213 the efficiency of gestures in managing social relationships despite its importance in furthering  
214 our understanding of how communicative complexity is linked to social complexity in both  
215 primates and humans.

216 In this study we examined the effect of self-relevance cues whilst the recipient was  
217 visually attending to the signaller to take into account influence of visual attention on duration  
218 of time spent in proximity. Thus for *visual orientation of the signaller, one-to-one calls and*  
219 *indicative gestures*, there had to be mutual visual contact between the signaller and the recipient  
220 for the gesture to be classified as being accompanied by a self-relevance cue. For *synchronized*  
221 *call*, we included all the individuals within 10m as involved in the call, as pant-hoots can

222 influence social bonding with many individuals simultaneously when compared with one-to-  
223 one calls such as pant-grunts (Fedurek et al., 2013).

224 In line with the definition of communicative complexity given above, all of these  
225 gestures accompanied by cues can be considered as more complex than gestures  
226 unaccompanied by these cues (Freeberg et al., 2012). Gestures accompanied by self-relevance  
227 cues contain both the gesture itself, and also the self-relevance cue making it clearer to the  
228 intended recipient the gesture is directed at them and facilitating responding to the gestures. In  
229 contrast, gestures accompanied by synchronized cues enable individuals to bond on a larger  
230 scale without the need for dyadic coordination in behaviour. Thus if there is a link between  
231 social complexity and communicative complexity, more complex communication in the form  
232 of gestures accompanied by cues may be expected to be associated with pairs of chimpanzees  
233 spending a longer duration of time in proximity, per hour spent in the same party. As the  
234 different cues have different acoustic and physical properties, the different cues may be  
235 differentially associated with sociality (A. I. Roberts & S. G. B. Roberts, 2016). However, the  
236 underlying similarity between all these cues is that they enhance the efficiency of the  
237 communication in social bonding (Grèzes, Adenis, et al., 2013; Grèzes, Philip, et al., 2013;  
238 Soussignan et al., 2013). We therefore examine both the overall use of gestures without the  
239 cues and then how gestures with the cue improve association of the gestures with sociality. As  
240 previous research has shown patterns of sociality are differentially related to the different  
241 modalities of gestural communication (A. I. Roberts & S. G. B. Roberts, 2016), we examined  
242 how different cues accompanied by different modalities of communication were associated  
243 with proximity. For consistency with previous research using the same database and population  
244 of chimpanzees as the current study, we categorized gestural communication into visual, tactile,  
245 auditory short-range and auditory long range modalities (A. I. Roberts & S. G. B. Roberts,

246 2016). Full definitions of the cues, gesture modalities and gestures included in each category  
247 are provided in Table 1.

248         Based on the above definitions of the cues, we used social network analyses to explore  
249 the association between rates of cues accompanying gestural communication and sociality in  
250 wild East African chimpanzees (*Pan troglodytes schweinfurthii*). Network analysis allows for  
251 examination of the association between communication and sociality both at the level of the  
252 social network as a whole, and of individual variation in sociality and communication  
253 (Lehmann & Dunbar, 2009; McCowan, Anderson, Heagarty, & Cameron, 2008; Sueur, Jacobs,  
254 Amblard, Petit, & King, 2011; Wey, Blumstein, Shen, & Jordan, 2008). In the first set of  
255 analyses, we explored how the rate of gestures accompanied by cues was associated with the  
256 duration of time pairs of chimpanzees in the same party spent in close proximity. In this  
257 analysis, using a social network approach allows us to have the dyad as the unit of analysis  
258 (Sueur et al., 2011), rather than analyzing each gestural event separately using a generalized  
259 linear mixed modelling approach (Prieur, Barbu, Blois-Heulin, & Pika, 2017). Thus we  
260 examined how the duration of proximity between pairs of chimpanzees was associated with  
261 characteristics of the communication between those pairs of chimpanzees. As previous findings  
262 have shown that the rate of visual gestures is most strongly associated with the duration of  
263 proximity (A. I. Roberts & S. G. B. Roberts, 2016), we predicted that pairs of chimpanzees that  
264 spend a longer duration of time in close proximity will have a higher rate of visual gestures  
265 accompanied by the cues.

266         In the second set of analyses, we examined how individual differences between rates at  
267 which the 12 focal chimpanzees accompanied their gestures with the cues were associated with  
268 individual differences in centrality in the social network (i.e. the number of proximity bonds  
269 the focal chimpanzees had with conspecifics). As previous findings have shown that  
270 synchronized communication plays a role in maintaining social bonds across larger numbers

271 of individuals both in humans (Tarr, Launay, Cohen, & Dunbar, 2015; Tarr, Launay, & Dunbar,  
272 2016; Weinstein, Launay, Pearce, Dunbar, & Stewart, 2016a, 2016b) and in nonhuman  
273 primates (Fedurek et al., 2013; Mitani & Gros-Louis, 1998), we predicted that individual  
274 chimpanzees with a higher rate of gestures accompanied by synchronized vocalizations will  
275 have a higher degree of centrality. In addition to specific types of gestural communication,  
276 demographic factors also play an important role in nonhuman primate sociality, with rates of  
277 proximity higher between kin, between similar age chimpanzees, between chimpanzees of the  
278 same sex and between reproductively active individuals (K. Langergraber et al., 2009; K. E.  
279 Langergraber, Mitani, & Vigilant, 2007; Mitani, 2009). We therefore controlled for these  
280 demographic factors in all our models.

## 281 **Methods**

### 282 Study site and subjects

283 The Sonso community of East African chimpanzees (*Pan troglodytes schweinfurthii*)  
284 at the Budongo Conservation Field Station, Budongo Forest Reserve in Uganda  
285 ([www.budongo.org](http://www.budongo.org)) was studied in September 2006, between April and July 2007 and March  
286 and June 2008. Instances of communication and social relationships of the 12 focal subjects (6  
287 adult males and 6 adult females) who did not have any limb injuries and were well-habituated  
288 for detailed data collection. Full details of the study site, subjects and data collection protocol  
289 have been described previously, so only essential information is provided here (Roberts &  
290 Roberts, 2015; Roberts, Roberts, et al., 2014; A.I. Roberts et al., 2012). The study was approved  
291 by the University of Stirling Ethics committee. The data collection and methods for this study  
292 were approved by the Budongo Conservation Field Station research committee (Prof. Klaus  
293 Zuberbuehler). The research was non-invasive and all methods were performed in accordance  
294 with the Association for the Study of Animal Behaviour guidelines.

295 Data collection protocol

296 Quantitative focal animal follows were conducted to examine the patterns of social  
297 relationships and communication for each of the focal individuals. The focal animals were  
298 chosen systematically and the behaviour of the focal subjects was recorded during a  
299 standardised observation period. We aimed to sample each individual equally at different times  
300 of the day and study period, and at least once every week. Consecutive samples of the same  
301 focal subject were taken at least 20 minutes apart in order to avoid dependency in the data set.  
302 The behaviour of the focal and non-focal individuals was recorded for the individuals who were  
303 present in the same party. Individuals belonged to the same party if they were a part of the  
304 group of individuals who were found within a spread of about 35 m. Behavioural data collected  
305 in this study came from the following sources: First, 18 minute focal follows, which consisted  
306 of 9 scans at 2 minute intervals of focal association patterns. These recorded the identity of  
307 individuals present within 10 m and more than 10 m from the focal individual, the bodily  
308 orientation between the focal subject and the nearest neighbour, the bodily orientation between  
309 the focal subject and the dominant individual in the party, the proximity between the focal  
310 subject and the nearest neighbour, and the proximity between the focal subject and the  
311 dominant individual in the party). Individuals within 10m of the focal were classified as being  
312 in close proximity. Secondly, the instantaneous sampling of associations was accompanied by  
313 data collection of gestures. A digital video camera recorder was used to record the gestures  
314 continuously, with the camera centred on the focal animal but also taking a wider view to  
315 include interactants within the visible presence of the focal individual. Communication was  
316 recorded in real time and for each gesture instance, the identity of the signaller and the recipient,  
317 the description of the response and the functional context of signal production was spoken onto  
318 the camera. The proximity and gestural data were collected at the same time by two different  
319 observers. The recording of association patterns was conducted by the experienced field

320 assistant, who did not know the aims of the study. The field assistant is subject to inter-observer  
321 reliability test annually, with results consistently above 0.85 Spearman's rank correlation  
322 coefficient,  $r_s$ . The video recording of the gestures was carried out by AR.

### 323 Video analyses of gestural communication

324 Instances of social behaviour which appeared communicative were first viewed on a  
325 television and coded. A full description of the coding scheme used for this dataset and a detailed  
326 discussion of intentionality in gestural communication can be found in Roberts et al. (Roberts,  
327 Roberts, et al., 2014; A. I. Roberts et al., 2012). Briefly, from full initial catalogue of social  
328 behaviour, specific instances of social behaviour were recorded as an act of gestural  
329 communication if it was an expressive movement of the limbs or head and body posture that  
330 met the following three criteria. First, the behaviour was mechanically ineffective – a gesture  
331 always elicited a change in the recipient's behaviour by non-mechanical means, rather than by  
332 for example physically manipulating a limb of the recipient into a desired position. Second,  
333 gestures were communicative – at the level of the gesture type, communication was  
334 consistently associated with a change in the behaviour of the recipient after the signal. Thus  
335 gestures always occurred in social circumstances – a chimpanzee turning its back simply to  
336 change position would not be considered a gesture, whereas a chimpanzee turning its back to  
337 initiate being groomed would be considered a gesture. Third, instances of behaviour had to be  
338 intentional to be classified as a gesture. Noting the criteria used in previous studies (Bates,  
339 Benigni, Bretherton, Camaioni, & Volterra, 1979; Byrne et al., 2017; D. A. Leavens et al.,  
340 2005), intentionality was scored for each gesture type separately, using pooled data across all  
341 subjects. Gestures above the threshold of 60% of cases were classified as intentional (Roberts,  
342 Roberts, et al., 2014). This criterion enabled us to eliminate the behaviours where there was no  
343 consistent association between the behaviour type and intentional use when considering the  
344 following criteria:

345 i) The presence of an audience; ii) Response waiting (the signaller directs a gesture at a  
346 recipient and observes the recipient's response during and after the gesture)

347         These two criteria for intentionality of gestures were coded following the schema  
348 suggested by Tomasello et al. (1985) who gave following example to explain the intentionality  
349 of gestures: 'a child might be struggling to open a cabinet, crying and whining as s/he struggles.  
350 Seeing this, the mother might come to the rescue and open the cabinet. This is a perlocutionary  
351 act because, while communication may be said to have occurred, the "sender" (the child) did  
352 not intentionally direct any behavior towards the mother. If, on the other hand, the child has  
353 turned its attention from the cabinet to the mother and whined at her, the whining now becomes  
354 a social-communicatory act with the intention of obtaining adult aid'. Following this  
355 description of intentional communication, we used the presence of an audience as one clear  
356 criterion for intentionality. In this dataset, all cases of gesturing included the presence of an  
357 audience within 10 meters. Secondly, response waiting was shown by the presence of bodily  
358 orientation by the signaller towards the recipient during the gesture as described by Tomasello  
359 et al. (1985) citation above. Visual attention between the signaller and the recipient was first  
360 recorded using 6 categories of bodily orientation: (1) the recipient is in signaller's view of  
361 vision and recipient's bodily orientation relative to signaller's is either: (a) recipient is facing  
362 the signaller with the side of the body (b) recipient is facing the signaller with the chest or (c)  
363 recipient is facing the signaller with the back (2) the recipient is out of signallers view of vision  
364 and the recipients bodily orientation relative to signaller's is one of the three: a) recipient is  
365 facing the signaller with the side of the body (b) recipient is facing the signaller with the chest  
366 or (c) recipient is facing the signaller with the back. In the sample of 545 sequences of gestures  
367 (consisting of adult to adult gestures only) the mean percentage  $\pm$  SD [95% CI] of cases of all  
368 gesture types when recipient was in view of the signaller during production of the gesture was  
369  $91.5 \pm 18.5\%$ , [87, 95]. Of the remaining gesture cases (when the recipient was not in view of



370 the signaller) the mean percentage  $\pm$  SD [95% CI] of cases of all gesture types associated with  
371 the presence of recipients' bodily orientation towards signaller (recipient facing signaller with  
372 the chest or the side of the body) was  $6.9 \pm 15.4\%$  [3, 10]. Finally, the mean percentage  $\pm$  SD  
373 [95% CI] of cases of all gesture types where neither signaller nor the recipient were in view of  
374 one another during production of the gesture was  $1.5 \pm 11\%$  [0, 3]. This shows that the gestures  
375 in our dataset were intentional according to the previously established criteria for defining  
376 intentionality in preverbal humans by Tomasello et al. (1985).

377 iii) The signaller persists in gesture production when the recipient fails to respond

378 Gesture events were scored in accordance to whether they occurred singly or in sequences,  
379 defined as one or more than one gesture made consecutively by one individual, towards the  
380 same recipient, with the same goal, within the same context, and made within a maximum of  
381 30 seconds interval to ensure independence. Following Hobaiter and Byrne (2011; see also  
382 Townsend et al., 2016) persistent sequence is when the chimpanzee produces a gesture then  
383 after a pause (1-5s) it produces another gesture. Chimpanzee produces a rapid sequence when  
384 there is no pause between gestures. Of a total of 545 sequences per focal individual, the mean  
385 number  $\pm$  SD [95% CI] of single gestures was  $32.0 \pm 32$ , [11.69, 52.47], for persistence  
386 sequences, the same variables were  $4.41 \pm 5.85$ , [0.69, 8.13] and rapid sequences  $8.9 \pm 9.09$ ,  
387 [3.14, 14.69].

388 We grouped gestures qualitatively based on characteristics of the morphology (i.e. the  
389 presence/absence and type of bodily movement, bodily posture, head movement, leg  
390 movement, locomotory gait, manual movement). A complete description of the gestural  
391 repertoire, with video clips for each gesture type can be found in Roberts et al. 2012 and 2014  
392 (Roberts, Roberts, et al., 2014; A. I. Roberts et al., 2012). This procedure has been widely used  
393 to identify distinct gesture types both in chimpanzees (K. Hobaiter & Byrne, 2011; Liebal et

394 al., 2004; Pollick & de Waal, 2007; Tomasello et al., 1984) and in other nonhuman primates  
395 (Byrne et al., 2017; Genty, Breuer, Hobaiter, & Byrne, 2009). The broad morphological  
396 categories (e.g. head, leg and manual) were used to distinguish between single gestures and  
397 their combinations (where more than one gesture was made simultaneously by the signaller,  
398 e.g. ‘bite’ and ‘embrace’). Consistent with previous research (A. I. Roberts & S. G. B. Roberts,  
399 2016), gestures were classified according to the sensory modality (visual, tactile, short-range  
400 auditory, long-range auditory, Table 1). Additionally, gestures were classified as to whether  
401 they were accompanied by simultaneous production of vocalisations. For each instance of a  
402 gesture, the following data were recorded: identity of the signaller (the individual performing  
403 a gesture) and the identity of the recipient (individual at whom the gesture was most clearly  
404 directed, as determined from the orientation of the body of the signaller during or immediately  
405 after performing a gesture, i.e. the signaller had the recipient within its field of view).

406         The reliability of the coding scheme for communicative function of the gesture (e.g.  
407 gesture type, context and response) has been assessed in our previous studies (A. I. Roberts et  
408 al., 2012; Roberts et al., 2013). Here we examined instances of gesturing recorded between  
409 adult individuals (Bakeman & Gottman, 1997). The subsample for reliability scoring was taken  
410 from a corpus of 545 sequences (1044 instances) of gesturing. A subset of gestures from video  
411 was coded by a second coder in accordance with schema presented in previous studies in the  
412 field (K. Hobaiter & Byrne, 2011). Here the gesture rates were examined in relation to  
413 association patterns (duration of time dyad partners spent within 10 meters per hour spent in  
414 the same party and the number of dyad partners with whom chimpanzees maintained  
415 proximity). The proximity of the partners was not taken from the footage, but was  
416 independently recorded on the check sheet at 2-minute intervals by the field assistant and  
417 therefore the reliability coding could not be influenced by the observation of proximity. The  
418 second coder assigned a random sample of 45 gestures to categories of gesture modality.

419 Cohen's Kappa coefficient showed that reliability was excellent for modality of signaling (K  
420 = 0.95) (Bakeman & Gottman, 1997). A sample of 50 gestures was coded by a second coder  
421 for intentionality (response waiting and persistence) and the Cohen's Kappa coefficient showed  
422 good reliability (K = 0.74) (Bakeman & Gottman, 1997). Finally, a sample of 55 gestures was  
423 second coded for the presence or absence of the cues accompanying gestural communication.  
424 The Cohen's Kappa coefficient again showed good reliability (K = 0.74) (Bakeman &  
425 Gottman, 1997). The reliability for intentionality and the cues is lower than for modality, but  
426 is in line with previous research in this area (K. Hobaiter & Byrne, 2011). Further, given the  
427 analysis is carried out on the overall communication patterns between dyads, any slight  
428 disagreement between observers about the intentionality or presence of the cues for individual  
429 gestural events is unlikely to have a large effect on the overall pattern of results.

#### 430 Behavioural data

431 Previous studies on this population of chimpanzees have shown that the mean distance  
432 between signaller and the recipient before communicating gesturally is 6.4 m (Roberts &  
433 Roberts, 2015). In the current study, instances of gestural communication when the intended  
434 recipient of the gestural communication was within 10 m of the signaller were included in the  
435 analyses. This enables us to avoid excluding those communication patterns that are important  
436 for social bonding but are often used at a larger distance (e.g. to initiate or maintain travelling),  
437 whilst controlling for the ability of the recipient to perceive the signal (Sam George Bradley  
438 Roberts & Anna Ilona Roberts, 2016). There is not a single, agreed measure of bondedness  
439 within or between species (R. I. Dunbar & Shultz, 2010). Our measure of proximity bonds  
440 (duration of time spent in proximity within 10 meters, per hour spent in the same party) has  
441 been validated in previous studies on this population of chimpanzees, which demonstrated that  
442 pairs of chimpanzees who spend the longest duration in proximity within 10 m also have higher  
443 durations of other indices of social bonding such as duration of time spent within 2 meters,

444 resting, travelling, grooming, visual attention, gestures and vocalisations (A. I. Roberts & S.  
445 G. B. Roberts, 2016; Sam George Bradley Roberts & Anna Ilona Roberts, 2016). Thus, this  
446 measure of proximity bonds appears to capture important aspects of variation in social behavior  
447 between conspecifics. Further, the duration of proximity between pairs of chimpanzees has  
448 been used in other studies to measure the nature of their social relationships (Fedurek et al.,  
449 2013; K. E. Langergraber et al., 2007; Mitani, 2009)

450 We analyzed gesture events both accompanied and unaccompanied by the cues. In this  
451 selection, only those events were taken into account which were independent, i.e. they were  
452 solely visual, auditory or tactile (not taking into account the modality of the cue) and  
453 accompanied by one cue only (not taking into account mutual visual attention). Since self-  
454 relevance cues (e.g. indicative gesture) were not counted unless visual orientation was also  
455 present, these self-relevance cues were additional/compounded cues. For synchronized calls  
456 the presence of mutual attention between interactants was not taken into account. The detailed  
457 description of all cues can be found in Table 1. Only those gestures unaccompanied by any of  
458 the cues listed were scored as lacking cues (no cue) and this includes synchronized calls.  
459 Gestures unaccompanied by cues were included in the models to compare the strength of  
460 association of gestures accompanied by and unaccompanied by cues with the presence and  
461 absence of proximity bonds. Thus the models examine whether the rate of gestures  
462 accompanied by cues was significantly associated with proximity, taking into account the rate  
463 of gestures unaccompanied by cues.

464 Next, to ensure that the sampling procedure did not bias our results, we examined  
465 whether there was a similarity in association patterns between scans taken at 2 minutes (scan  
466 1), 4 minutes (scan 2) and 18 minutes (scan 9) of the focal sample (A. I. Roberts & S. G. B.  
467 Roberts, 2016). These analyses showed that there was no significant difference in the number  
468 of times the focal and non-focal subjects were in close proximity between scan 1 (Median = 2,

469 IQ range = 0 - 5) and scan 2 (Median = 2, IQ range = 1 - 5, Wilcoxon signed-ranks test,  $T =$   
470 411.50,  $n = 132$ ,  $p = 0.435$ ). The aim of this analysis was to examine the likelihood that there  
471 was a change in group composition during the 2 minute interval. Since the analysis showed  
472 that there was no change in composition between scans 1 and 2, it did not seem reasonable to  
473 assume that the result would be different if differences in the focal-partner proximity were  
474 examined between scans 2 and 3, 3 and 4, etc. Thus, we did not undertake such additional  
475 analysis. However, there was a significant difference in the number of times the focal and non-  
476 focal subjects were in close proximity between scan 1 and scan 9 (Median = 2, IQ range = 1 -  
477 4; Wilcoxon signed-ranks test,  $T = 2656.50$ ,  $n = 132$ ,  $p = 0.011$ ). Similarly, there was no  
478 significant difference in the number of times the focal and non-focal subjects were in the same  
479 party between scan 1 (median = 5, IQ range: 3 - 10) and scan 2 (median = 5, IQ range: 3 - 10;  
480 Wilcoxon signed-ranks test,  $T = 218.50$ ,  $n = 132$ ,  $p = 0.571$ ), whilst there was a significant  
481 difference in the number of times the focal and non-focal subjects were in the same party  
482 between scan 1 and scan 9 (median = 5, IQ range: 2 - 10; Wilcoxon signed-ranks test,  $T = 1460$ ,  
483  $n = 132$ ,  $p = 0.010$ ). These results demonstrate that the adjacent scans were similar both for 10  
484 m associations and party level associations. These scans were therefore treated as continuous  
485 data sampling and used to calculate durations of proximity between pairs of individuals. If  
486 chimpanzee A and chimpanzee B were recorded as being in 10 m proximity at Scan 2, they  
487 were assumed to have been together for the 2 minutes preceding Scan 2, as 10 m associations  
488 between pairs of chimpanzees do not change significantly between adjacent scans. However,  
489 the first and final sample scans at 1 minute and 18 minute interval differed for both 10m  
490 associations and party level associations. This suggests that these scans were independent, as  
491 were the focal samples preceding and succeeding the 18 minute focal follow. Thus each  
492 separate 20 min focal follow can be considered as an independent sampling of the  
493 chimpanzees' association patterns.

494           Based on these behavioural data, we calculated association measures for proximity  
495 (duration of time pairs of chimpanzees spent within 10 m, per hour spent in same party) and  
496 communication (rate of communication between pairs of chimpanzees, per hour spent within  
497 10 m). These measures have been previously described (Sam George Bradley Roberts & Anna  
498 Ilona Roberts, 2016) so only the detailed calculation for the dyadic association measure is  
499 presented here as an example. The dyadic association measure (DA) is the duration of time the  
500 focal subject A spent in close proximity (within 10m) to the non-focal subject B, per hour spent  
501 in the same party, or:

$$502 \quad DA_{AB} = [(P10_{AB} * 2) * 60] / PSP_{AB} * 2$$

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

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

505   2 = duration of instantaneous subsample interval in minutes

506   60 = the number of minutes in an hour

#### 507   Attribute measures

508           Demographic factors such as age, kinship, sex and reproductive state can influence  
509 chimpanzees' propensity to associate with each other. The genetic relationships in the study  
510 group were established by previous research, enabling us to categorize chimpanzee dyads  
511 according to maternal kinship (mother offspring dyads) presence or absence (Reynolds, 2005).  
512 Moreover, the age of most subjects in the community is known from long term project records.  
513 In the wild, chimpanzees reach physical and social maturity between ages 15 – 16 years old  
514 (Goodall, 1986). We classified dyads of chimpanzees as belonging to the same (5 years or less  
515 age difference) or a different (above 5 years age difference) age class following previous  
516 studies (Mitani, Watts, Pepper, & Merriwether, 2002). Chimpanzee dyads were also  
517 categorized according to similarity of reproductive status. First, the reproductive status of the

518 female was scored on the basis of the size of the sexual swelling, i.e. an enlarged area of the  
519 perineal skin varying in size over the course of the menstrual cycle. The reproductive status of  
520 the female was recorded as oestrous if during the observation period the female exhibited  
521 maximum tumescence and was observed mating with the males. All focal males were observed  
522 to mate with the females and therefore assumed to be reproductively active. Sex similarity was  
523 also scored based on observable morphological characteristics referring to sex, with dyads  
524 classified as composed of same sex or opposite sex pairs. Further details of the categorization  
525 of attribute data can be found in Supplementary Table 1

#### 526 Social Network Analysis

527         The different networks were created using the behaviour categories described above.  
528 Each network matrix was composed of 12 rows and 12 columns, with each row and column  
529 denoting a different focal chimpanzee. Each cell of the matrix represented the value for the  
530 duration or the rate of occurrence of that particular behaviour for a specific pair of chimpanzees  
531 (e.g. the duration of proximity between Bwoba and Kutu, per hour they spent in the same party).  
532 The communication networks used in this study were weighted - that is each cell consisted of  
533 a continuous value representing that behaviour, rather than a 1 or a 0 indicating the presence  
534 or absence of a tie. The networks were also directed, in that they represented the rate of  
535 behaviour made by the focal Bwoba to Kutu, as well as the focal Kutu to Bwoba. For example,  
536 the rate of gestures produced by Bwoba and directed at Kutu may be different than the rate of  
537 the gestures produced by Kutu and directed at Bwoba.

538         The behavioural network related to the duration in minutes of proximity (within 10 m)  
539 between specific pairs of the focal individuals, per hour that pair were in the same party. Across  
540 the 132 chimpanzee dyads, dyads spent a mean of 21.16 (range 0 - 60) minutes in close  
541 proximity (within 10m) with conspecifics, per hour spent in the same party. In this network,  
542 95.5% of potential connections to group members were present (range 82 – 100%). As with

543 previous studies on this population of chimpanzees (A. I. Roberts & S. G. B. Roberts, 2016;  
544 Sam G. B. Roberts & Anna I. Roberts, 2016) a binary proximity network was created, whereby  
545 dyads who displayed values of proximity association equal or above the mean plus half  
546 standard deviation (equal or above 30.3 minutes spent in close proximity per hour spent in the  
547 same party), were scored as 1 if the proximity was reciprocated (i.e. both A to B and B to A  
548 dyads displayed values of proximity association equal or above the mean plus half standard  
549 deviation). These dyads were termed ‘preferred reciprocated close proximity bonds’. Dyads  
550 who had values below 30.3 minutes of proximity, or where the proximity was not reciprocated,  
551 were scored as 0. In this network of preferred reciprocated close proximity bonds, only 15.1%  
552 of potential connections were present (range 0 – 46%). The communication networks consisted  
553 of the rate of different type of communication between pairs of the focal individuals, per hour  
554 that pair of chimpanzees spent within 10m. For example, the rate of visual gestures  
555 accompanied by one-to-one calls between Bwoba and Kutu was used as the weighted, directed  
556 value of communication for this dyad in the ‘visual gestures with one-to-one call’ network.

557         The centrality measures were calculated from these network matrices, using normalized  
558 degree centrality (Croft, James, & Krause, 2010). We calculated the normalized degree  
559 centrality for each individual chimpanzee, i.e. the average value of each row or column of the  
560 strong proximity bond network matrix, where dyads of individuals who had values of proximity  
561 association equal or above the mean plus half standard deviation, were scored as 1 (‘close  
562 proximity bonds’). The networks used in this study are directed and therefore in-degree and  
563 out-degree were calculated separately for each behaviour. Out-degree is a measure that denotes  
564 behaviours directed by the focal chimpanzee to conspecifics. In contrast, in-degree denotes  
565 behaviours directed by conspecifics towards the focal chimpanzee. In these analyses, the  
566 proximity network was directed because some strong proximity bonds were not reciprocated  
567 and therefore in-degree was used in all models.



568 All data transformations and analyses were carried out using UCINET 6 for Windows  
569 (Borgatti, Everett, & Freeman, 2014). In order to examine the normalised mean degree across  
570 proximity and communication networks, networks were dichotomized and symmetrized.  
571 Normalised mean degree is the mean proportion of all possible ties which are present. In order  
572 to dichotomize the network, all values larger than zero are scored as 1 (tie present) and all  
573 values of zero were categorised as absent. In symmetrisation, a tie is scored as present if there  
574 is a 1 in either of the two cells corresponding to each pair of individuals (cell  $i, j$  or cell  $j, i$ ).

575 The observations that were used to create the network are not independent of each other  
576 and thus general standard inferential statistics cannot be used. Instead, analyses using  
577 randomisation tests are used, where the observed value is compared against the distribution of  
578 values generated by a large number of random permutations of the data. The proportion of  
579 random permutations in which a value as large (or as small) as the one observed is then  
580 calculated, and this provides the  $p$  value of the test (Borgatti, Everett, & Johnson, 2013). The  
581 type of randomised test used to examine the relationship between different behavioural and  
582 communication networks was MRQAP regression (Multiple Regression Quadratic Assignment  
583 Procedure) (Borgatti et al., 2013). MRQAP regression resembles standard regression as it  
584 allows for the examination of the relationship between a numbers of different predictor  
585 variables (e.g. different communication networks) on a single outcome variable (proximity  
586 network). In our analysis this outcome variable was a binary one – whether or not a dyad was  
587 classified as having a preferred reciprocated close proximity bonds, scored as a 1 or 0. As with  
588 a standard regression analysis, MRQAP produces standardized coefficients and standard errors  
589 for the predictor variables. With a binary outcome variable, positive coefficients indicate that  
590 a higher value for that predictor variable (e.g. a higher rate of visual gestures accompanied by  
591 self-relevance cues) is associated with the presence of close proximity bonds.

592 As MRQAP is a modified form of regression analysis for network data, we used a  
593 hierarchical approach to building these models, as is common practice in standard forms of  
594 multiple regression (Field, 2013). We first constructed a model containing only the  
595 demographic variables - age difference between dyads, sex difference between dyads, whether  
596 the dyads were kin or not kin and reproductive similarity (Supplementary Table 1). We then  
597 added gestural communication not accompanied by cues, before in the final model adding  
598 gestural communication accompanied by cues. As in standard regression, we used the F statistic  
599 to assess the significance of the change in  $R^2$  between each model. Using this approach allowed  
600 us to examine whether gestures accompanied by cues explained significantly more variance in  
601 proximity bonds than either a model just containing demographic variables, or a model  
602 containing demographic variables and gestures unaccompanied by cues.

603 There are a number of different types of MRQAP regression and we used Double  
604 Dekker Semi-Partialling MRQAP regression as it is more robust against the effects of network  
605 autocorrelation and skewness in the data (Dekker, Krackhardt, & Snijders, 2007). In these  
606 MRQAP analyses, we used 2,000 permutations. In our node-level regressions, similar  
607 procedure was used, whereby 10,000 random permutations were used to determine the  
608 association between number of predictor variables (e.g. the out-degree for visual gestures) on  
609 a single outcome variable (proximity in-degree). Moreover, in order to assess autocorrelation  
610 between attribute data (e.g. the total duration of observation) and network data (e.g. visual  
611 gesture network) we used Geary's C statistic. A value of 1.0 for the Geary statistic indicates  
612 no association between variables, values of less than 1.0 indicate a positive association and  
613 values over 1.0 indicate a negative association.

## 614 **Results**

615 **The rate of gestures with cues predicts the presence of reciprocated close proximity bonds**

616 In this study, a mean of 12.52 (range 8.33 – 18.63) hours of focal footage per individual  
617 subject was examined. The definitions of categories of cues and modalities of gestures are  
618 given in Table 1. The descriptive statistics on the rate of production and mean degrees of  
619 gestures (the percentage of potential connections chimpanzees had with others) accompanied  
620 and unaccompanied by cues are provided in Table 2. The details of sampling effort can be  
621 found in Supplementary Table 2. We used MRQAP regression to examine whether rates of  
622 gestural communication accompanied and unaccompanied by cues were a predictor of the  
623 presence of preferred reciprocated close proximity bonds, building up the models in a  
624 hierarchical method. For full details of all models, including insignificant findings, see Tables  
625 3 – 4.

626 To examine the overall association between cues and the presence of preferred  
627 reciprocated close proximity bonds, initially we pooled all gesture types and examined whether  
628 gestures accompanied and unaccompanied by cues were significantly associated with  
629 proximity bonds (Table 3). In Model 1, none of the demographic variables were significantly  
630 associated with the presence of proximity bonds. Model 2 included the rate of gestures  
631 unaccompanied by cues – again none of the predictor variables were significantly associated  
632 with the presence of proximity bonds and including the rate of gestures unaccompanied by cues  
633 did not significantly improve the amount of variance explained, with the  $R^2$  only increasing  
634 from 0.049 in Model 1 to 0.056 in Model 2,  $F(1, 126) = 0.934, p > 0.05$ . In contrast, when the  
635 rate of gestures accompanied by cues was added in Model 3, there was a significant increase  
636 in the  $R^2$  to 0.135,  $F(1, 125) = 11.416, p < 0.001$ . The rate of gestures accompanied by cues  
637 was significantly associated with the presence of preferred, reciprocated close proximity bonds  
638 between pairs of chimpanzees ( $r^2=0.135, \beta=0.329, p = 0.009$ ). There was no statistically  
639 significant association between the rate of gestures unaccompanied by cues and the presence  
640 of preferred, reciprocated close proximity bonds ( $\beta = -0.074, p = 0.204$ , Table 3, Figure 1).

641           Given that overall rate of gestures accompanied by cues was associated with close  
642 proximity bonds, we then examined which categories of gestures accompanied by cues were  
643 significantly associated with proximity bonds, taking into account all combinations of  
644 modalities and cues (Table 4). We again used a hierarchical model building approach,  
645 comparing a model containing only demographic variables (Model 4), to one including the rate  
646 of gestures of different modalities unaccompanied by cues (Model 5) to a model including the  
647 rate of gestures of different modalities accompanied by self-relevance cues (Model 6) and  
648 finally to a model including the rate of gestures of different modalities accompanied by  
649 synchronized cues (Model 7). In Model 5, the rate of visual gestures unaccompanied by cues  
650 (visual no cue) was significantly higher in dyads with a close proximity bond. However, overall  
651 there was no significant improvement in the  $R^2$  between Model 4 and Model 5,  $F(4, 123) =$   
652  $1.924, p > 0.05$ . In contrast, including the rate of gestures of different modalities accompanied  
653 by self-relevance cues significantly improved the  $R^2$  in Model 6 compared to Model 5,  $F(7,$   
654  $116) = 3.204, p < 0.01$ . In this model, only visual gestures accompanied with self-relevance  
655 cues were significant predictors of preferred, reciprocated close proximity bonds. Pairs of  
656 chimpanzees that had preferred, reciprocated close proximity bonds had higher rates of visual  
657 gestures accompanied by one-to-one call ( $\beta=0.171, p = 0.044$ ) and indicative gestures  
658 ( $\beta=0.352, p = 0.045$ ; Figure 2). In contrast, in Model 6, the rate of visual gestures  
659 unaccompanied by cues (visual no cue) was significantly negatively associated with the  
660 presence of proximity bonds ( $\beta= -0.254, p = 0.043$ ). Further, for tactile gestures, auditory  
661 short-range gestures and auditory long-range gestures, the rate of gestures either accompanied  
662 or unaccompanied by cues was not significantly associated with the presence of preferred,  
663 reciprocated close proximity bonds. Finally, in Model 7 including the rate of gestures of  
664 different modalities accompanied by synchronized cues again significantly improved the  $R^2$  in  
665 Model 7 compared to Model 6,  $F(2,114) = 5.227, p < 0.01$ . In this model the higher rate of

666 visual gestures accompanied by one-to-one call ( $\beta=0.175$ ,  $p = 0.046$ ), indicative gestures  
667 ( $\beta=0.355$ ,  $p = 0.028$ ) and synchronized calls ( $\beta=0.254$ ,  $p = 0.005$ ) positively predicted presence  
668 of preferred, reciprocated close proximity bonds. Dyad partners who had a higher rate of visual  
669 gestures unaccompanied by the cue were less likely to have a preferred, reciprocated close  
670 proximity bond with each other ( $\beta=-0.252$ ,  $p = 0.031$ ; Figure 2).

### 671 **Gestures accompanied by self-relevance cues are associated with proximity centrality**

672 We used node-level regressions to examine the predictors of proximity in-degree by the  
673 n degree of gestures accompanied and unaccompanied by cues (the percentage of all potential  
674 connections chimpanzees had with others). The focal chimpanzees with a high proximity in-  
675 degree had a larger number of connections maintained through gestures accompanied by  
676 presence of the cues ( $r^2=0.596$ ,  $\beta= 1.440$ ,  $p = 0.016$ , Supplementary Table 3). In contrast, the  
677 size of the social network maintained through gestures unaccompanied by presence of cues was  
678 not associated with proximity in-degree ( $\beta= -0.635$ ,  $p = 0.166$ ).

679 Finally, for communication networks accompanied by self-relevance cues, we  
680 calculated normalized degree and examined its relationship with proximity in-degree. First, we  
681 combined all gestures accompanied self-relevance cues in one model (indicative gesture, one-  
682 to-one call, mutual attention, Supplementary Table 4). The only positive predictor of proximity  
683 in-degree was the network size of the visual gestures accompanied by mutual attention ( $r^2 =$   
684  $0.675$ ,  $\beta= 2.895$ ,  $p = 0.039$ ). Second, we combined gestures accompanied by self-relevance  
685 cues with gestures accompanied by synchronized cues according to each modality of  
686 synchronized cue entered separately (visual and auditory). In a model combining visual, tactile  
687 and auditory gestures accompanied by self-relevance cues (indicative gesture, one-to-one call,  
688 mutual attention) and visual gestures accompanied by synchronized cue, the positive predictor  
689 of proximity in-degree was the network size of the visual gestures accompanied by  
690 synchronized call ( $r^2 = 1$ ,  $\beta= 2.739$ ,  $p = 0.038$ ). The size of the tactile mutual attention network

691 was negatively correlated with the proximity in-degree ( $\beta = -5.075$ ,  $p = 0.019$ , Supplementary  
692 Table 5). In a similar analysis, using auditory long-range gestures accompanied by  
693 synchronized cue, instead of visual gestures accompanied by synchronized cue, the pattern was  
694 similar. There was a positive correlation between proximity in-degree and the network size of  
695 the auditory long-range gestures accompanied by synchronized cue ( $r^2 = 1$ ,  $\beta = 2.083$ ,  $p =$   
696  $0.045$ ). However, there was a negative correlation between proximity in-degree and the size of  
697 the tactile mutual attention network ( $\beta = -4.324$ ,  $p = 0.022$ ) and the size of the auditory long-  
698 range mutual attention network ( $\beta = -3.297$ ,  $p = 0.011$ , Supplementary Table 6).

## 699 **Discussion**

700 Many nonhuman primates live in social groups and it has been proposed that these  
701 complex groups require complex communication systems (Freeberg et al., 2012). Whilst there  
702 has been much focus on nonhuman primate vocalizations (T. Fitch, 2005; R. Seyfarth &  
703 Cheney, 2010; R. M. Seyfarth et al., 2010), less is known about how nonhuman primate  
704 gestural communication is related to sociality (Byrne et al., 2017; Sam G. B. Roberts & Anna  
705 I. Roberts, 2016). Integration of self-relevance cues such as visual attention, indicative gesture  
706 or one-to-one vocalisation with the gestures can increase the degree of self-relevance of  
707 perceived gestural communication (Sander et al., 2003). It is hypothesized that self-relevance  
708 cues facilitate social bonding because they make it clearer to the recipients that the gesture is  
709 directed at them and facilitate processing of the gesture. In addition, synchronized cues such as  
710 pant-hoot call accompanying use of a gesture are produced jointly with group members, with  
711 simultaneous, rhythmically matched sound production and movement. These features are  
712 predicted to increase efficiency of social bonding in large social networks by removing the  
713 need for one-to-one social coordination. In this study we examined whether the rates of gestures  
714 accompanied by cues as compared to the rates of gestures unaccompanied by cues, both overall  
715 and by modality, were a better predictor of sociality of wild chimpanzees. The complexity of

716 sociality was measured by the presence of reciprocated, proximity bonds (time pairs of  
717 chimpanzees spent within 10 m per hour they spent in the same party) between dyad partners.  
718 There were two key findings. First, pairs of chimpanzees that spent a longer duration of time  
719 in proximity (those that had preferred, reciprocated close proximity bonds) had a higher rate of  
720 gestures accompanied by cues, per hour they spent within 10 m. In particular, a higher rate of  
721 visual gestures accompanied by cues was associated with close proximity bonds. Second,  
722 individual chimpanzees who had a greater number of close proximity bonds produced a higher  
723 rate of gestures accompanied by cues, and specifically a higher rate of gestures accompanied  
724 by synchronized pant-hoot calls.

725         Previous research on this population of chimpanzees has shown that pairs of  
726 chimpanzees that spend more time in close proximity have a higher rate of gestural  
727 communication (A. I. Roberts & S. G. B. Roberts, 2016; Sam G. B. Roberts & Anna I. Roberts,  
728 2016). The current findings extend this research by demonstrating that it is not just the overall  
729 rate of gestural communication that is associated with proximity bonds, but specifically the  
730 rate of gestural communication accompanied by cues. When considering separately from  
731 gestures accompanied by cues, gestures unaccompanied by the cues did not predict the  
732 presence of proximity bonds. Thus in a combined model which included both the rate of  
733 gestures accompanied by cues and the rate of gestures unaccompanied by cues, only the rate  
734 of gestures accompanied by cues was associated with the presence of proximity bonds  
735 between pairs of chimpanzees.

736         Likewise, the results of the current study extend previous research showing an  
737 association between visual gestures and proximity bonds (A. I. Roberts & S. G. B. Roberts,  
738 2016) by demonstrating that the rate of visual gestures accompanied by cues predicts the  
739 presence of proximity bonds. In contrast, the rate of visual gestures unaccompanied by cues

740 was negatively associated with proximity bonds. Visual gestures may be particularly well-  
741 suited to coordinating behaviour between pairs of chimpanzees when interacting at close  
742 proximity – for example when pairs of chimpanzees are forced into close proximity due to the  
743 clumped nature of the food resources such as fig trees (A. I. Roberts & S. G. B. Roberts, 2016).  
744 In contrast to loud auditory gestures, visual gestures are not aversive to recipients when both  
745 signaller and recipient are close together. By producing these visual gestures at a higher rate,  
746 pairs of chimpanzees in close proximity to each other may be able to coordinate their behaviour  
747 more effectively (A. I. Roberts & S. G. B. Roberts, 2016). The predictability of conspecifics’  
748 behaviour is a major modulator of stress in group-living animals (Robert M Seyfarth & Cheney,  
749 2013) and a higher rate of visual gestures may increase this predictability and facilitate social  
750 interaction in chimpanzees (A. I. Roberts & S. G. B. Roberts, 2016). These visual gestures may  
751 operate in a similar way to grunts in Guinea baboons, where a high rate of grunts helps regulate  
752 social behaviour when baboons are interacting in close proximity (Maciej, Ndao,  
753 Hammerschmidt, & Fischer, 2013).

754         However, for visual gestures to be effective in increasing the predictability of  
755 conspecifics’ behaviour, recipients need at a minimum to detect the gesture is directed at them,  
756 rather than another conspecific (Engh et al., 2006). By accompanying their visual gestures with  
757 self-relevance cues such as visual attention, one-to-one call or indicative gesture, signalers can  
758 make it clearer to the recipient that the gesture is directed at them, and thus better coordinate  
759 their behaviour with the recipient. In turn, this has a potential to increase the effectiveness of  
760 communication, resulting in pairs of chimpanzees that spend a greater duration of time  
761 together, per hour in the same party. Previous research across both nonhuman primates (Byrne  
762 et al., 2017; Roberts, Roberts, et al., 2014) and humans (Grèzes & Dezecache, 2014; N'diaye  
763 et al., 2009) has examined how these ‘self-relevance’ cues affect how the signaller detects and  
764 responds to communication, but has not directly examined how use of these cues is associated



765 with sociality in wild nonhuman primates. The current results suggest that it is specifically  
766 visual gestures accompanied by self-relevance cues that may play a key role in coordinating  
767 social behaviour in wild chimpanzees. In contrast, the rate of tactile and auditory gestures  
768 accompanied by self-relevance cues was not positively associated with proximity bonds  
769 between pairs of chimpanzees. One reason for this may be because visual gestures are harder  
770 for signalers to detect than tactile gestures, in which the signaller makes direct physical contact  
771 with the receiver, or auditory gestures in which the noise produced by the gesture can draw the  
772 receivers attention towards the signaler (Gillespie-Lynch et al., 2014; Hopkins et al., 2007).  
773 Whilst this study did not examine the response of the recipient to the gesture, previous research  
774 has shown that not only can self-relevance cues help recipients detect communication is  
775 directed at them, it can also trigger brain activity associated with preparing an appropriate  
776 response to the signal from the large set of potential action opportunities (Grèzes & Dezeache,  
777 2014). Further research in this area could explore whether visual gestures accompanied by self-  
778 relevance cues, as compared to those unaccompanied by such cues, are more efficient in  
779 eliciting appropriate responses from recipients, as has been shown for other complex forms of  
780 gestural communication in chimpanzees such as persistence and elaboration (Byrne et al.,  
781 2017; Roberts, Roberts, et al., 2014; Roberts, Vick, et al., 2014).

782         However, visual gestures accompanied by self-relevance cues demand a high degree of  
783 inter-individual coordination through proximity and mutual visual contact. Thus, these  
784 interactions may be less efficient in socially bonding with a larger number of social partners.  
785 When visual gestures accompanied by self-relevance cues were included in one model with  
786 visual gestures accompanied by synchronized calls, the model explained a greater amount of  
787 variation in social relationships. Thus, visual gestures accompanied by synchronized calls may  
788 be more effective in meeting the demands of maintaining social relationships in primates.

789           In addition to variation in the duration of time pairs of chimpanzees spent in close  
790 proximity to each other, there were also important individual differences between the focal  
791 chimpanzees, with some focal individuals maintaining proximity to more numerous  
792 conspecifics, as measured by network centrality. The focal individuals with high network  
793 centrality had a higher rate of gestures accompanied by synchronized pant-hoot calls, per hour  
794 they spent within 10m of conspecifics. This finding builds on previous work showing an  
795 association between pant-hoot chorusing and social bonds in chimpanzees (Fedurek et al.,  
796 2013; Mitani & Gros-Louis, 1998) and suggest that accompanying gestures with synchronized  
797 calls may be particularly important to coordinate behaviour and maintain social relationships  
798 with multiple individuals simultaneously (Fedurek et al., 2013; Sam G. B. Roberts & Anna I.  
799 Roberts, 2016). Research on humans has shown that synchronized vocalizations such as  
800 singing and laughter are associated with the release of endorphins, which in turn helps social  
801 bonding (Manninen et al., 2017; Tarr et al., 2016; Weinstein et al., 2016a, 2016b). In a similar  
802 way, synchronized vocalizations in chimpanzees may provide a time-efficient way to form and  
803 maintain social bond with numerous conspecifics, particularly for individuals with numerous  
804 social partners (Arlet et al., 2015; Fedurek et al., 2013; Sam G. B. Roberts & Anna I. Roberts,  
805 2016). How baseline rate of vocal behavior without a gesture could influence effectiveness of  
806 maintaining chimpanzee social relationships is thus an important avenue of research for future  
807 studies, which could compare how overall gesture and vocalization are associated with the  
808 presence of social bonding.

809           Overall, these findings support the link between communication and social complexity  
810 (Freeberg et al., 2012). Higher rates of more complex communication (gestures accompanied  
811 by cues, as compared to gestures unaccompanied by cues) were associated with greater  
812 sociality in wild chimpanzees. However, the results also suggest that different types of  
813 communicative complexity may be differentially suited to different types of social interaction,

814 enabling nonhuman primates to meet the challenges that come from living in a complex social  
815 group (Gillespie-Lynch et al., 2014; Sam G. B. Roberts & Anna I. Roberts, 2016). Whilst visual  
816 gestures accompanied by self-relevance cues may help chimpanzees coordinate their behaviour  
817 and regulate proximity at a dyadic level, synchronized pant-hoot calls may be more effective  
818 at coordinating behaviour of multiple individuals over larger distances (Sam G. B. Roberts &  
819 Anna I. Roberts, 2016). Further tests of the link between communication and sociality could  
820 focus on how different types of communication are used to maintain and regulate different  
821 types of social relationships, rather than on simply the overall association between social and  
822 communicative complexity (McComb & Semple, 2005). Further, if using complex  
823 communication helps animals meet the challenges of living in social groups (Freeberg et al.,  
824 2012), individual variation in communication patterns could be related to both social  
825 integration in the group and to fitness outcomes (Robert M Seyfarth & Cheney, 2013, 2015;  
826 Silk et al., 2010a).

827         More broadly, these results have important implications for our understanding of the  
828 evolution of language. Nonhuman primates in larger groups spend a greater percentage of their  
829 day grooming, but the amount of time that can be devoted to grooming is limited (R. I. M.  
830 Dunbar, 2010). Thus as group size increased through human evolution, it has been theorised  
831 that synchronized vocalisations (Pearce, Launay, & Dunbar, 2015; Weinstein et al., 2016b) and  
832 language played an important role in maintaining social bonds and group cohesion (R. Dunbar,  
833 2008). Other researchers have argued that gestures or multi-modal communication may have  
834 been important precursors to language (Arbib et al., 2008; M. Corballis, 2009; Gillespie-Lynch,  
835 Greenfield, Feng, Savage-Rumbaugh, & Lyn, 2013; Tagliabata et al., 2015). Our results  
836 suggest that both gestures and synchronized vocalisations may be important in enabling  
837 chimpanzees to meet the time and cognitive challenges of maintaining a large set of  
838 differentiated social relationships. In particular, the use of self-relevance cues may enhance

839 recipients' detection that communication is directed at them and therefore increase the efficiency  
 840 of gestural communication in facilitating social interaction. Through the course of human  
 841 evolution, increased flexibility in the use of different types of multi-modal communication to  
 842 maintain different types of social relationships may have enabled larger groups of hominins to  
 843 maintain social cohesion, acting as an alternative to other mechanisms that require physical  
 844 contact, such as grooming and as a precursor to human language (R. Dunbar, 2012; Freeberg et  
 845 al., 2012).

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853 Table 1. Ethogram of behavioural categories

<b>Category</b>	<b>Definition</b>
Modality	
Visual gesture <sup>a</sup>	Gesture perception is possible only by looking at signaler. Gestures included were: <i>Arm beckon, Arm flap, Arm raise, Bob, Bow, Crouch, Crouch run, Crouch walk, Dangle, Forceful extend, Hand bend, Jump, Limp extend, Linear sweep, Lower head, Lunge, Present genitals, Present leg, Present mount, Present rump, Present torso, Rock, Roll over, Run stiff, Slap self, Sniff, Stationary stiff, Stiff extend,</i>

*Stretched extend*, Swagger bipedal, Swagger quadrupedal, Tip head, Touch self, Turn back, Turn head, *Unilateral swing*, *Vertical extend*, Walk stiff, Wipe

Tactile gesture Gesture perception is possible via physical contact. Gestures included were: Bite, Embrace, Grab, Hold hands, Kiss, Locomote tandem, Pull another, Push by hand, Push by rump, Rub, Shake limb, Slide, Stand tandem, Stroke by mouth, Tap another, Thrust genitals, Tickle, Touch backhand, Touch innerhand, Touch long

Auditory short-range gesture Sounds produced by the gesture can be heard within short distance from the signaller up to 10 meters. Gestures included were: Clip by mouth, Smack lip, Tap object

Auditory long-range gesture Sounds produced by the gesture are audible at a distance of more than 10 meters away from the signaller. Gestures included were: Beat, Bounce, Drum, Knock, Pound, Shake mobile, Shake stationary, Stamp quadrupedal, Stamp sitting, Sway, Swing

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Cue

Visual orientation of the signaller Signaller produces a gesture whilst in visual contact with the recipient, without simultaneous production of indicative gestures or calls. Visual contact was defined as when the signaller had the recipient within its field of view (up to 45 degrees body turn). The recipient also had to be in visual contact with the signaller.

One-to-one call Signaller produces a gesture with simultaneous production of one-to-one call (produced by one signaller at one recipient) and without simultaneous production

of indicative gestures or synchronized calls. The recipient of the gesture was an individual at whom signaller was bodily oriented during production of the call. Vocalisations included were pant-grunt, pant, scream, bark. The recipient also had to be in visual contact with the signaller.

**Synchronized call**      Vocalisation accompanying a gesture is produced simultaneously by a signaller and by other individuals who are present within 10 meters. Here cases of simultaneous production of indicative gestures or one-to-one calls by a focal subject were excluded. Vocalisations included were pant-hoot call.

**Indicative gesture**      Signaller produces a gesture with simultaneous production of indicative gesture (movement of the arm and hand towards the recipient, without physical touch) and without simultaneous production of one-to-one calls or synchronized calls. Indicative gestures included were: arm beckon, arm flap, arm raise, forceful extend, hand bend, limp extend, linear sweep, stiff extend, stretched extend, unilateral swing, vertical extend. All indicative gestures were visual gestures. The recipient also had to be in visual contact with the signaller.

**No cue**      Signaller produces a gesture without simultaneous production of one-to-one calls or synchronized calls or indicative gestures and whilst not in mutual visual contact with the recipient.

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854 *Note:* Description of gesture types, accompanying video clips and criteria used to establish  
855 whether a nonverbal behaviour can be classified as a gesture can be found in (Roberts,  
856 Roberts, et al., 2014; A.I. Roberts et al., 2012). Nonverbal behaviours were only considered  
857 to be a gesture if they were mechanically ineffective, communicative and intentional.

858 <sup>a</sup>Visual gesture types classified as indicative gestures are indicated in italics.

859 Table 2. Rate of gesture production per hour spent in close proximity (within 10 m) and  
 860 normalized degree (the percentage of potential connections chimpanzees had with others)

<b>Modality</b>	<b>Type of cue</b>	<b>Rate</b>	<b>Rate overall range</b>	<b>Normalized degree (%)</b>	<b>Normalized degree overall range (%)</b>
Visual	Mutual attention	0.48	0 - 20	33.3	0 - 73
	One-to-one call	0.10	0 - 3.91	15.1	0 - 64
	Synchronized call	0.05	0 - 4	9	0 - 27
	Indicative gesture	0.09	0 - 5	15.1	0 - 46
	No cue	0.40	0 - 20	31.8	0 - 73
Tactile	Mutual attention	0.17	0 - 10	16.6	0 - 55
	One-to-one call	0.02	0 - 1.82	4	0 - 27
	No cue	0.14	0 - 17.65	6	0 - 27
Auditory short-range	Mutual attention	0.16	0 - 10.43	10.6	0 - 36
	No cue	0.24	0 - 22.50	13.6	0 - 36
Auditory long-range	Mutual attention	0.11	0 - 7.50	12.1	0 - 36
	Synchronized call	0.32	0 - 15	21.2	0 - 46
	No cue	0.01	0 - 0.97	4.55	0 - 18
All gestures combined	Cue	1.53	0 - 40	46.9	9 - 100
	No cue	0.81	0 - 22.94	36.3	0 - 82

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862 **Table 3.** MRQAP regression model showing predictors of proximity between N = 132 dyadic  
863 relationships of the chimpanzees. Significant P values are indicated in bold. Dyads of  
864 individuals who had values of proximity association equal or greater than the mean plus half  
865 SD, were scored as 1 ('strong ties'), if the proximity was reciprocated (i.e. both A to B and B  
866 to A displayed values of proximity association equal or greater than the mean plus half SD)  
867 whereas dyads who had values less than then mean plus half SD were scored as 0 ('weak ties').

Attribute category/ rate of gesture sequence per hour spent in close proximity	Standardized coefficient	Standard error	<i>P</i>
<b>Model 1 (<math>R^2 = 0.049</math>)</b>			
Age similarity	0.133	0.120	0.169
Sex similarity	-0.025	0.118	0.396
Kinship similarity	-0.078	0.214	0.346
Oestrous similarity	-0.132	0.152	0.242
<b>Model 2 (<math>R^2 = 0.056</math>)</b>			
Age similarity	0.125	0.121	0.176
Sex similarity	-0.038	0.122	0.398
Kinship similarity	-0.077	0.213	0.365
Oestrous similarity	-0.138	0.152	0.236
All gestures combined no cue	0.088	0.010	0.165
<b>Model 3 (<math>R^2 = 0.135</math>)</b>			



Age similarity	0.103	0.115	0.209
Sex similarity	-0.051	0.114	0.365
Kinship similarity	-0.068	0.206	0.341
Oestrous similarity	-0.131	0.135	0.207
All gestures combined no cue	-0.074	0.010	0.204
All gestures combined with cue	0.329	0.010	<b>0.009</b>

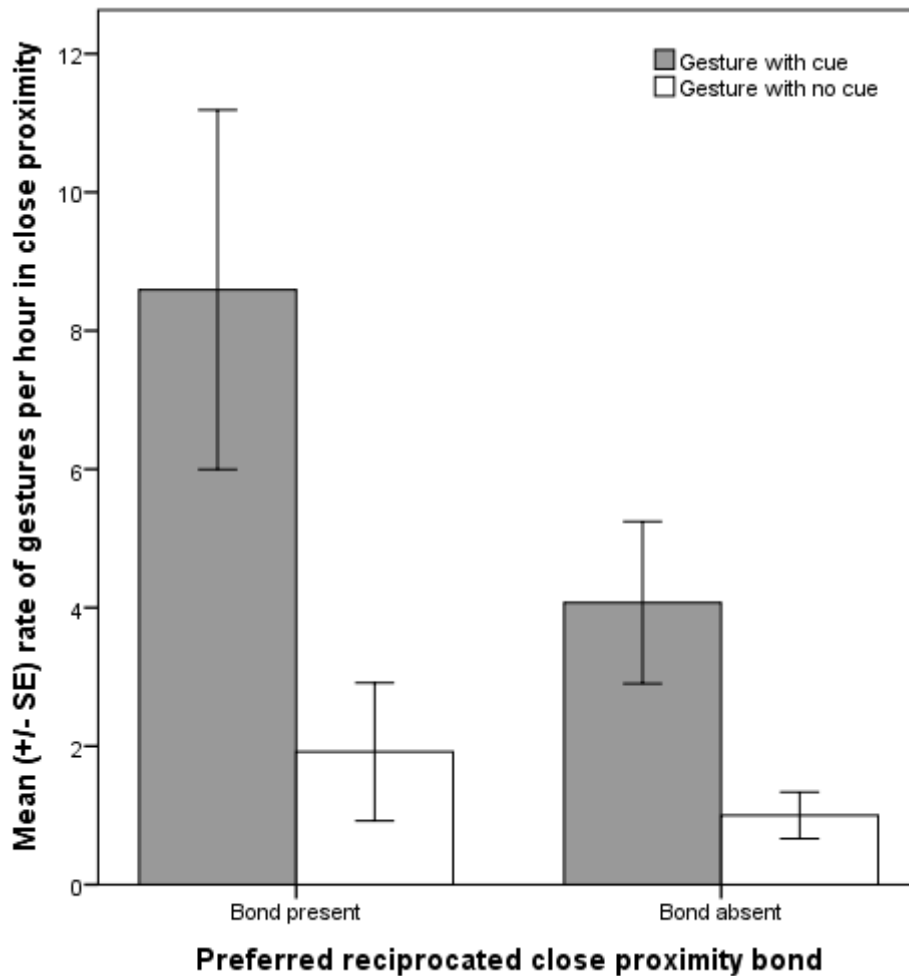
868

869 **Table 4.** MRQAP regression models showing predictors of proximity between N = 132 dyadic  
870 relationships of the chimpanzees. Significant P values are indicated in bold. Dyads of  
871 individuals who had values of proximity association equal or greater than the mean plus half  
872 SD, were scored as 1 ('strong ties'), if the proximity was reciprocated (i.e. both A to B and B  
873 to A displayed values of proximity association equal or greater than the mean plus half SD)  
874 whereas dyads who had values less than then mean plus half SD were scored as 0 ('weak ties').

Attribute category/ rate of gesture sequence per hour spent in close proximity	Standardized coefficient	Standard error	<i>P</i>
<b>Model 4 (<math>R^2 = 0.049</math>)</b>			
Age similarity	0.133	0.120	0.169
Sex similarity	-0.025	0.118	0.396
Kinship similarity	-0.078	0.214	0.346
Oestrous similarity	-0.132	0.152	0.242

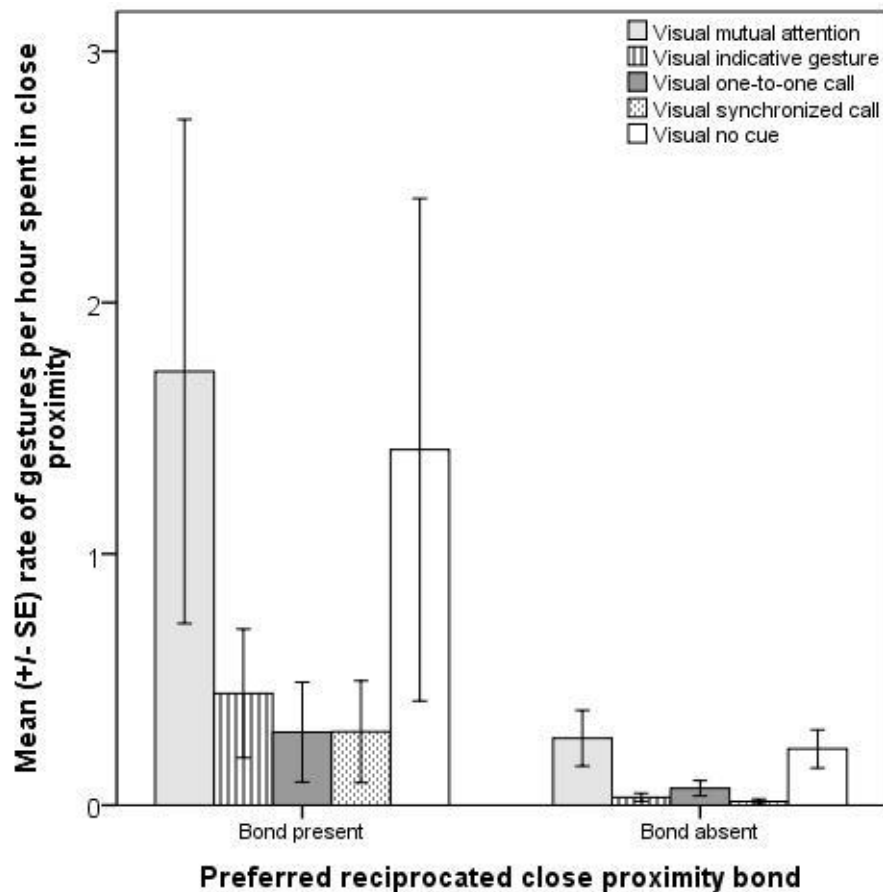
<b>Model 5 (<math>R^2 = 0.105</math>)</b>			
Age similarity	0.120	0.123	0.174
Sex similarity	-0.040	0.120	0.388
Kinship similarity	-0.072	0.211	0.363
Oestrous similarity	-0.164	0.149	0.185
Auditory long-range no cue	0.087	0.288	0.214
Auditory short-range no cue	-0.043	0.016	0.303
Tactile no cue	-0.032	0.022	0.434
Visual no cue	0.208	0.018	<b>0.035</b>
<b>Model 6 (<math>R^2 = 0.250</math>)</b>			
Age similarity	0.086	0.111	0.234
Sex similarity	-0.076	0.113	0.290
Kinship similarity	-0.078	0.205	0.262
Oestrous similarity	-0.149	0.137	0.155
Auditory long-range no cue	0.152	0.318	0.065
Auditory short-range no cue	-0.051	0.018	0.245
Tactile no cue	0.045	0.026	0.223
Visual no cue	-0.254	0.040	<b>0.043</b>
Auditory long-range mutual attention	-0.203	0.086	0.076
Auditory short-range mutual attention	0.216	0.047	0.098

Tactile mutual attention	-0.292	0.098	0.083
Tactile one-to-one call	0.028	0.202	0.232
Visual indicative gesture	0.352	0.149	<b>0.045</b>
Visual mutual attention	0.413	0.055	0.067
Visual one-to-one call	0.171	0.079	<b>0.044</b>
<b>Model 7 (<math>R^2 = 0.313</math>)</b>			
Age similarity	0.094	0.114	0.195
Sex similarity	-0.045	0.112	0.353
Kinship similarity	-0.066	0.200	0.298
Oestrous similarity	-0.138	0.133	0.160
Auditory long-range no cue	0.156	0.316	0.053
Auditory short-range no cue	-0.052	0.018	0.232
Tactile no cue	0.042	0.025	0.226
Visual no cue	-0.252	0.037	<b>0.031</b>
Auditory long-range synchronized call	-0.061	0.022	0.182
Auditory long-range mutual attention	-0.191	0.084	0.075
Auditory short-range mutual attention	0.189	0.044	0.105
Tactile mutual attention	-0.269	0.094	0.096
Tactile one-to-one call	0.005	0.200	0.328
Visual indicative gesture	0.355	0.143	<b>0.028</b>
Visual mutual attention	0.394	0.053	0.062
Visual one-to-one call	0.175	0.078	<b>0.046</b>
Visual synchronized call	0.254	0.105	<b>0.005</b>



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Fig. 1 Mean rate (+/- 1 standard error) of gestures with and without cues in dyads with and without preferred reciprocated proximity bonds. Preferred reciprocated proximity bonds were defined as when dyad A to B and B to A spent 30.3 or more minutes in close proximity, per hour spent in the same party.



883 Fig. 2 Mean ( $\pm$  1 standard error) rate of visual gestures in dyads with and without preferred  
 884 reciprocated proximity bonds. Preferred reciprocated proximity bonds were defined as when  
 885 dyad A to B and B to A spent 30.3 or more minutes in close proximity, per hour spent in the  
 886 same party.  
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