

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) 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 ± 32 , [11.69, 52.47], for persistence
386 sequences, the same variables were 4.41 ± 5.85 , [0.69, 8.13] and rapid sequences 8.9 ± 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

Category	Definition
Modality	
Visual gesture ^a	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

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.

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 ^aVisual 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)

Modality	Type of cue	Rate	Rate overall range	Normalized degree (%)	Normalized degree overall range (%)
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>
Model 1 ($R^2 = 0.049$)			
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
Model 2 ($R^2 = 0.056$)			
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
Model 3 ($R^2 = 0.135$)			

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	0.009

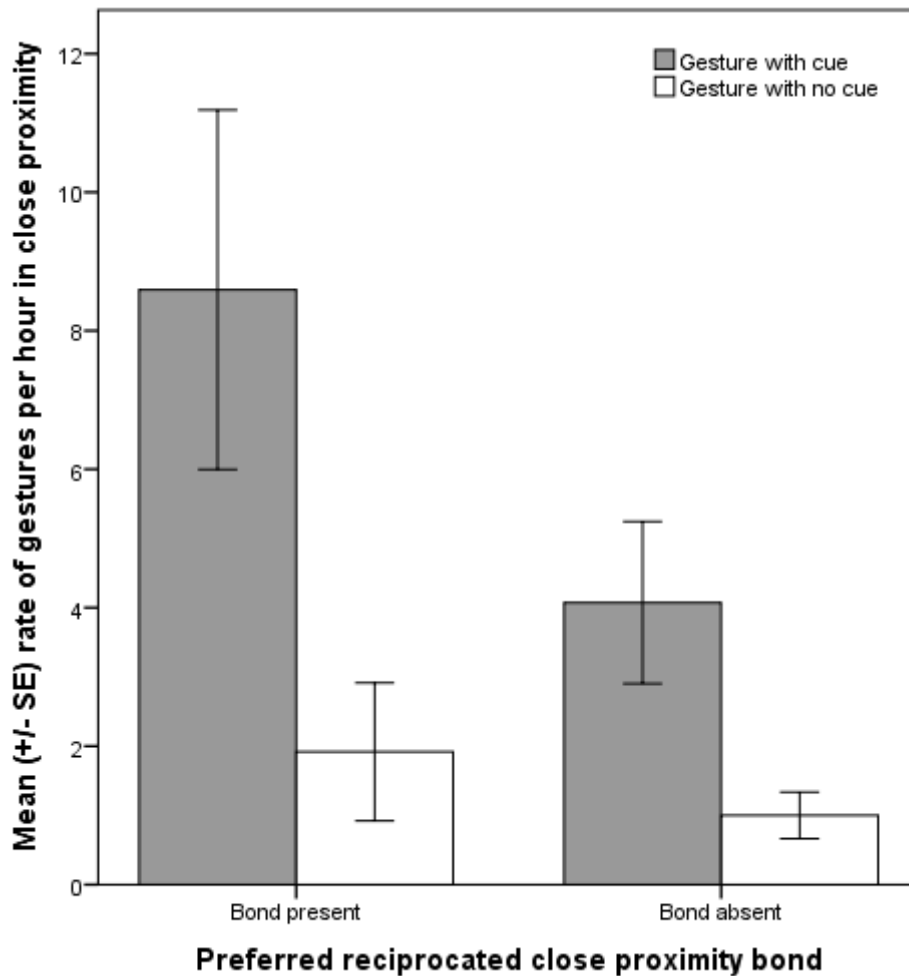
868

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>
Model 4 ($R^2 = 0.049$)			
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

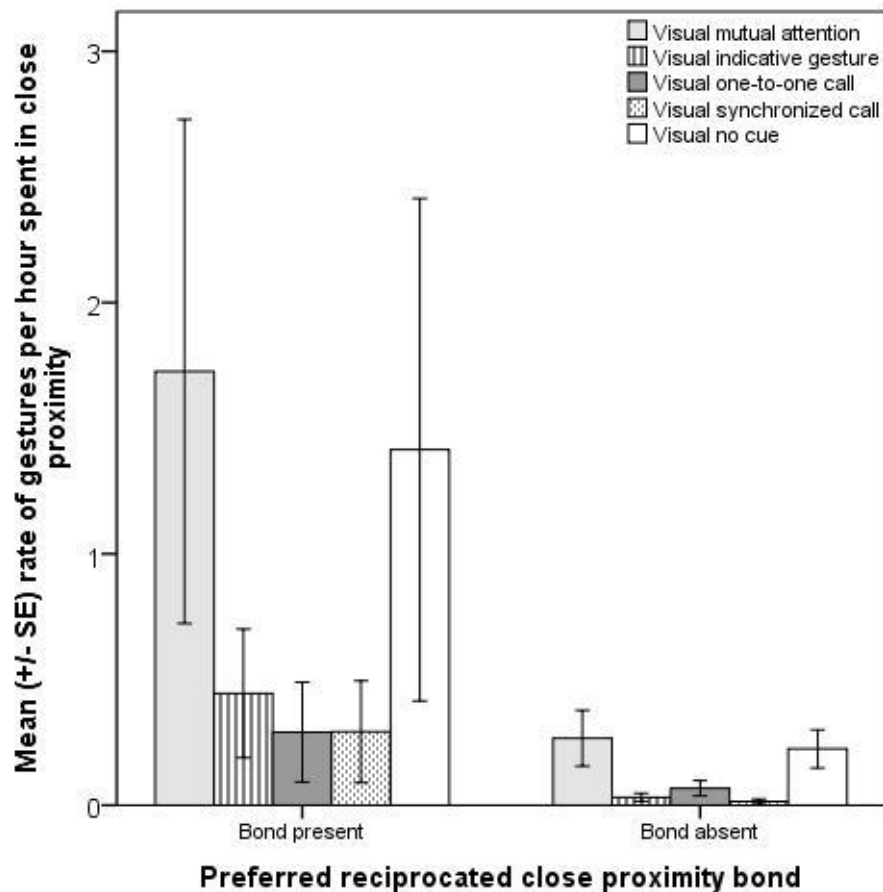
Model 5 ($R^2 = 0.105$)			
Age similarity	0.120	0.123	0.174
Sex similarity	-0.040	0.120	0.388
Kinship similarity	-0.072	0.211	0.363
Oestrous similarity	-0.164	0.149	0.185
Auditory long-range no cue	0.087	0.288	0.214
Auditory short-range no cue	-0.043	0.016	0.303
Tactile no cue	-0.032	0.022	0.434
Visual no cue	0.208	0.018	0.035
Model 6 ($R^2 = 0.250$)			
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	0.043
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	0.045
Visual mutual attention	0.413	0.055	0.067
Visual one-to-one call	0.171	0.079	0.044
Model 7 ($R^2 = 0.313$)			
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	0.031
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	0.028
Visual mutual attention	0.394	0.053	0.062
Visual one-to-one call	0.175	0.078	0.046
Visual synchronized call	0.254	0.105	0.005



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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.
 887

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