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Title page

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

Short running title: Chimpanzee gesture repertoire and sociality

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1 **Abstract**

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

24 **Keywords:** gesture, repertoire size, proximity, social network, chimpanzee, fission-fusion
25 social system

26 **Introduction**

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

44 Gestures in primates are defined as voluntary movements of the arms, head, body
45 postures and locomotory gaits [Hewes, 1992; Liebal et al., 2004a; Nishida et al., 2010; Plooij,
46 1978; Tomasello et al., 1985]. Gestures occur in different modalities according to the means
47 by which the gesture can be perceived by the recipient [Liebal et al., 2006; Pika et al., 2003;
48 Pika et al., 2005b]. ‘Visual gestures’ are silent and therefore visual contact between the
49 signaller and receiver is necessary for these gestures to be perceived by the recipient. In
50 contrast ‘tactile gestures’ involve contact with recipient’s body and can be perceived through

51 tactile sensation, whether or not the audience is visually attentive. ‘Auditory gestures’
52 produce an audible sound that may differ in amplitude, therefore making these gestures
53 detectable from a short distance (short-range auditory gestures) or from further away (long-
54 range auditory gestures) without visual contact between the signaller and the receiver [Byrne
55 et al., 2017]. This flexibility and diversity in gestural communication may be important for
56 primates in groups to successfully maintain a large set of differentiated social relationships,
57 as it may allow signallers to coordinate behaviour with the recipient more effectively, thereby
58 enabling individuals to respond adaptively in social situations [Roberts and Roberts, 2016b].

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

70 Some studies suggest that in nonhuman primates the gestural repertoire size is
71 strongly influenced by kinship [Hobaiter and Byrne, 2011a; Pika et al., 2005a; Tomasello et
72 al., 1985]. However, social influences, such as audience effects [Bourjade et al., 2018;
73 Roberts and Roberts, 2015], intentionality [Bullinger et al., 2011; Cartmill and Byrne, 2007;
74 Fröhlich et al., 2016a; Leavens et al., 2005; Liebal et al., 2006; Moore, 2016; Pika et al.,
75 2005a; Pika et al., 2005b; Roberts and Roberts, 2018a; Roberts et al., 2013; Roberts et al.,

76 2014b] and learning [Halina et al., 2013; Roberts and Roberts, 2017] shape the diversity of
77 gestures across animals. Examining how variation in the size of the gestural repertoire among
78 nonhuman primates relates to social bonding and the structuring of social interactions
79 therefore provides key information relating to the role of repertoire of gestural
80 communication in primate sociality.

81 The overall repertoire of gestural communication in primates is differentiated by
82 modality and this may have an influence on both the repertoire size and on flexibility in the
83 production of gestures. Some modalities may be better suited to social bonding and social
84 coordination than others, in terms of influencing the behaviour of the recipient [Roberts and
85 Roberts, 2016a]. Social relationships based on close proximity tend to occur between
86 individuals who are close in rank and the lack of prior consensus about the direction of
87 potential aggression reduces individual certainty in social relationships [Ay et al., 2007; Flack
88 et al., 2006]. Visual gestures may be better suited to managing these relationships in regular
89 one on one interactions, because these gestures might appear less forceful and therefore might
90 create a positive perception of fitness rewarding intent of the signaller [Roberts and Roberts,
91 2016a]. However, the lack of forcefulness in visual gestures implies that when managing
92 social interactions, a larger repertoire of visual gestures could contribute to a reduction in the
93 uncertainty following the gesture, and more efficient coordination with the recipient. In
94 contrast, long-range auditory gestures might be more forceful and therefore straightforward
95 for the recipient to respond to, but might sometimes carry the implication of a negative fitness
96 outcome for the recipient as they can be used in agonistic contexts [Roberts and Roberts,
97 2016a]. Thus a large repertoire of such auditory long-range gestures would not necessarily
98 contribute to a reduction in uncertainty in the recipient [Roberts and Roberts, 2016a].

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

101 Semple, 2005], or the size of gestural repertoire according to the characteristics of the species
102 [Maestriperi, 2005]. However, much of this research has been carried out in the vocal
103 domain [Arlet et al., 2015; Fedurek et al., 2013; Mitani et al., 1999; Mitani and Gros-Louis,
104 1998; Schel et al., 2013] and there is a lack of knowledge of how the repertoire size of
105 gestural communication relates to the characteristics of the social network– the number and
106 strength of social bonds maintained between conspecifics.

107 East African chimpanzees are a particularly valuable species to assess this question.
108 Chimpanzees live in fission-fusion communities within which they associate temporarily in
109 subgroups (‘parties’) that vary in size, composition and duration [Goodall, 1986]. Individuals
110 in the community are often spatially and temporarily separated but nonetheless recognise
111 each other and maintain long-term relationships [Foerster et al., 2015; Langergraber et al.,
112 2009; Mitani, 2009; Mitani et al., 2002; Roberts and Roberts, 2016b]. Maintaining the
113 differentiated set of social relationships that arises from this fission-fusion structure is
114 hypothesised to be a key driver of communicative complexity [Freeberg et al., 2012; Roberts
115 and Roberts, 2016b]. Chimpanzees use grooming and communication to establish and
116 maintain social relationships [Babiszewska et al., 2015; Bard et al., 2014; Bard et al., 2017;
117 Fedurek et al., 2013; Fedurek and Slocombe, 2013; Fedurek et al., 2015; Mitani et al., 1999;
118 Mitani and Brandt, 1994; Mitani and Gros-Louis, 1998; Watts, 2006]. In particular, proximity
119 and grooming co-vary with the aspects of the communicative repertoire of vocalisations (e.g.
120 panthoot and food-calls) [Fedurek et al., 2013; Fedurek and Slocombe, 2013; Mitani and
121 Brandt, 1994; Mitani and Gros-Louis, 1998; Mitani and Nishida, 1993; Schel et al., 2013].
122 However, the unique character of chimpanzee gestural communication is that it encompasses
123 flexible actions at a distance, where all parts of the chimpanzee body are employed as a
124 medium of social communication [Blute, 2006; Sterelny, 1998]. Hence, it could be predicted
125 that gestural communication would be useful in effectively managing social relationships

126 with conspecifics, as reflected in the relationship between gesture repertoire size and patterns
127 of social bonding.

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

141 **Methods**

142 Study site and subjects

143 Six adult males and six adult females from the Sonso community of East African
144 chimpanzees (*Pan troglodytes schweinfurthii*) at the Budongo Conservation Field Station,
145 Budongo Forest Reserve in Uganda, East Africa (1°35' and 1° 55'N and 31° 08'and 31°42'
146 E, www.budongo.org) were subject of this study. The Budongo Forest reserve is one of the
147 largest national reserves in Uganda, occupying an area of approximately 793 km² at a mean
148 attitude of 1,050 m and includes 482 km² of continuous medium-altitude semi-deciduous
149 forest. The study site has previously been used for logging with the forest now in the form of

150 secondary growth, restricting visibility [Reynolds, 2005]. We observed focal subjects in
151 September 2006, between April and July 2007 and between March and June 2008. The
152 individual repertoire size was computed from the data collected during all three study
153 periods. The dyadic repertoire size and social proximity measures were collected during the
154 last study period (March - June 2008). At the beginning of the socio-ecological data
155 collection in March 2008, the Sonso community of chimpanzees consisted of approximately
156 75 named individuals, 10 adult males and 22 adult females. Only chimpanzees well
157 habituated to observation and who had no limb or other injuries that could potentially affect
158 gestural communication were chosen as focal subjects. All details of the focal subjects, their
159 age, sex, and observation duration are given in Table 1.

160 Data collection protocol

161 We used quantitative focal animal follows and chose focal subjects systematically by
162 choosing to follow each of the subjects at least once a week when they were present in the
163 party. We recorded the focal subject's social behaviour and communication during a
164 standardized observation period of 18 minutes, leaving at least a 20 minute interval between
165 consecutive samples of the same focal subjects. As much as possible we aimed to avoid
166 sampling the same focal subject consecutively. Only the behavior of the focal subject and the
167 individuals present in the same party was recorded. A party was defined as a group of
168 individuals within a spread of 35 m. Two types of behavioral data were recorded during the
169 18 minute focal follows. First, 9 scans each at 2 minutes interval (nine 2-minute intervals)
170 recorded the individuals present within 10 m of the focal subject and the individuals more
171 than 10 m away that were in the same party). Second, concurrently with collecting 9 scans of
172 proximity, we used a video camera to record chimpanzee gestures continuously throughout
173 the 18 minute focal follow. As we observed gestures occurring, we verbally recorded into the
174 camera the behavior of the signaler and recipient, along with the context of the signal

175 production. Although collected concurrently, the data collection of gestures was performed
176 by a different researcher from the data collection of proximity and thus the collection of data
177 on proximity and gestures were performed independently. The concurrent data collection
178 was synchronized between two researchers by using a pager. Thus for each 18 minute focal
179 follow, one researcher was video recording the gestural communication whilst the other
180 researcher was recording the proximity of individuals to the focal chimpanzee at 2 minute
181 intervals. The sampling of association pattern was done with the help of an experienced field
182 assistant who was unaware regarding the aims of the study. An inter-observer reliability test
183 of the chimpanzee identities and proximities is conducted annually to maintain the
184 consistency of the scoring of the group composition and proximity across the field assistants.
185 The Spearman's rank correlation coefficient for this test is at least or above 0.85. This data
186 collection protocol provided a detailed and accurate picture of the patterns of behavioral
187 interactions (proximity, gestures) in the focal chimpanzees.

188 Video analysis and classification of gestural communication

189 First, we derived an inventory of gesture types from the video recordings [Roberts et al.,
190 2012b]. The cases of any nonverbal behavior that may act as a gesture were noted and
191 behavior classified as a gesture if it met following criteria: 1) the non-verbal behavior was an
192 expressive movement of the limbs or head and body posture that was mechanically
193 ineffective, 2) the behavior was communicative by non-mechanical means (i.e. consistently
194 produced a change in the behavior of recipient or facilitated maintenance of activity, e.g.
195 grooming). Next, behavior had to be goal directed to be considered intentional [Bard, 1992;
196 Bates et al., 1979]. We used audience presence and visual attention to score the behavior as
197 intentional, following the example described by Tomasello et al. [1985]: 'a child might be
198 struggling to open a cabinet, crying and whining as s/he struggles. Seeing this, the mother
199 might come to the rescue and open the cabinet. This is a perlocutionary act because, while

200 communication may be said to have occurred, the "sender" (the child) did not intentionally
201 direct any behavior towards the mother. If, on the other hand, the child has turned its
202 attention from the cabinet to the mother and whined at her, the whining now becomes a
203 social-communicatory act with the intention of obtaining adult aid'.

204 In this dataset, all cases of gesturing included the presence of an audience within 10
205 meters. In addition, another criterion for defining intentionality (directing visual attention at
206 the recipient by the signaler) was fulfilled by the gestures. The mean percentage \pm SD [95%
207 CI] of cases of all gesture types associated with the presence of bodily orientation by the
208 signaller towards the recipient during the production of the gesture was $91.5 \pm 18.5\%$, [87,
209 95]. Finally, the criterion of communicative persistence was coded to identify intentional
210 gestures. Following the classification by Hobaiter and Byrne [2011b], persistence of
211 gesturing was scored when the chimpanzee produced one gesture or a gesture sequence, then
212 after a period of response waiting (1-5s) they produced another gesture. The details of
213 intentionality criteria scoring by each gesture type and each criterion separately can be found
214 in [Roberts and Roberts, 2018a]. Validation of the coding procedure was established by a
215 second coder who scored a random sample of 45 of the sequences of gestures for
216 concordance in function and modality. The Cohen's Kappa coefficient showed that reliability
217 was good for function ($K = 0.70$) and modality of gesturing ($K = 0.946$) [Bakeman and
218 Gottman, 1997]. A different sample of 50 sequences of gestures was coded by a second coder
219 for intentionality (response waiting and persistence) and the Cohen's Kappa coefficient
220 showed good reliability ($K = 0.74$).

221 Behavioral Data

222 Gesture events were scored in accordance to whether they occurred singly or in
223 sequences, defined as one or more than one gesture made consecutively by one individual,

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

244 For instance, if the unimodal communication produced by chimpanzee A towards
245 chimpanzee B (AB dyad) was one sequence consisting of three gestures and which contained
246 three different gesture types, and a single gesture containing one different gesture type, then
247 four gesture types would be recorded as directed from A to B. Then the rate of gestures, per
248 hour the AB dyad spent within 10 m, would be calculated to give the dyadic repertoire size

249 for A to B, i.e. the number of gesture types A produced towards B, per hour spent within 10
250 m of B. If a single gesture event was a combination of two gesture types of the same modality
251 type (e.g. two visual gestures), this would have been recorded as two gesture types. Given the
252 wide variety of multi-modal gestural sequences (sequences that contain some combination of
253 the four gestural modalities), also examining how different types of multi-modal gesture
254 sequences are associated with proximity was beyond the scope of this paper.

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

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

274 The dyadic association measure

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

277 $DA_{AB} = [(P10_{AB} * 2) * 60] / PSP_{AB} * 2$

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

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

280 2 = duration of instantaneous subsample interval in minutes

281 60 = the number of minutes in an hour

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

284 The dyadic communication measure

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

288 $CA_{AB} = (C_{AB} * 60) / P10_{AB} * 2$

289 where C_{AB} = the number of times A communicated with B when in close proximity (within
290 10 m) to B

291 $P10_{AB}$ = the number of times A was in close proximity (within 10 m) to B

292 2 = duration of instantaneous subsample interval in minutes

293 60 = the number of minutes in an hour

294 Attribute measures

295 Proximity between pairs of chimpanzees can be associated with biological factors such as the
296 reproductive status of the dyad, age, sex and kinship [Langergraber et al., 2009; Mitani et al.,
297 2002; Roberts and Roberts, 2016a; Roberts and Roberts, 2017; Roberts and Roberts, 2018a;

298 Roberts and Roberts, 2018b; Roberts and Roberts, 2016b]. The genetic relationships of this
299 community of chimpanzees have been previously determined and we used this information to
300 classify the dyads as maternally related or not [Reynolds, 2005]. Moreover, the age of most
301 of the subjects in the community is known from long term project records. Wild chimpanzees
302 reach physical and social maturity between ages 15 – 16 years old [Goodall, 1986]. We
303 classified dyads of chimpanzees as belonging to the same (5 years or less age difference) or a
304 different (above 5 years age difference) age class following previous studies [Mitani et al.,
305 2002]. The reproductive status was scored on the basis of the presence of the female sexual
306 swelling. Females who displayed swelling and were seen mating with the males were scored
307 as reproductively active – see ESM Table 1 for further explanation of the attribute variables
308 used in this study. In all analyses we controlled for these biological attributes.

309 Social network analysis:

310 The details of social network analysis have been previously described [Roberts and
311 Roberts, 2016a]. We entered weighted behavioral data into 12 rows and 12 columns
312 representing 12 focal chimpanzees. However, the weighted network matrices cannot
313 distinguish between ‘reciprocated’ and ‘one-sided’ relationships and therefore in order to
314 distinguish between different types of social relationships based on patterns of association,
315 three binary proximity networks were created with ‘1’, indicating a presence of a bond and
316 ‘0’ indicating absence of a bond. First, we created a binary proximity network, where dyads
317 of individuals who had values of proximity association equal or above the mean plus half SD
318 (who spent 30.3 or more minutes in close proximity, per hour spent in the same party), were
319 scored as 1 if the proximity was reciprocated (i.e. both A to B and B to A displayed values of
320 close proximity association equal or above 30.3 minutes duration - ‘preferred reciprocated
321 close proximity bonds’), whereas other dyads were scored as 0. Second, a binary network
322 was created, where dyads of individuals who had values of proximity association equal or

323 greater than the mean plus half SD, were scored as 1 when the proximity was non-
324 reciprocated (i.e. only A to B but not B to A had duration of proximity association equal or
325 above the 30.3 minutes - 'preferred, non-reciprocated close proximity bonds'), whereas other
326 dyads were scored as 0. Third, the binary proximity network was created, where dyads of
327 individuals who had values of proximity association equal or below the mean minus half SD
328 (who spent 16.23 or less minutes in close proximity to each other per hour spent in same
329 party), were scored as 1 ('non-preferred close proximity bonds'), whereas other dyads were
330 scored as 0.

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

348 For data transformation and analysis we used UCINET 6 for Windows [Borgatti et al.,
349 2014]. Social network matrices cannot be analysed by normal inferential statistical
350 techniques, as the observations that make up network data are not independent of each other.
351 Instead, a set of analysis using randomization (or permutation) have been developed where
352 the observed value is compared against a distribution of values generated by a large number
353 of random permutations of the networks. The p value is calculated by calculating the
354 proportion of random permutations in which a value as large (or as small) as the one observed
355 [Borgatti et al., 2013]. For analysis of relationships between different behavioural networks,
356 we used the Multiple Regression Quadratic Assignment Procedure (MRQAP) [Borgatti et al.,
357 2013]. This is similar to a standard regression model because it enables the association
358 between a number of predictor variables (gestural communication networks of different
359 modalities, control variables relating to sex and age) and a single outcome variable
360 (proximity network) to be examined. Among the different types of MRQAP regression, we
361 used the Double Dekker Semi Partialling MRQAP regression, as it is more robust against the
362 effects of network autocorrelation and skewness in the dataset [Dekker et al., 2007]. For this
363 analysis, 2,000 permutations were used. For the node level regressions we used a similar
364 procedure, using 10,000 random permutations to assess the effect of several predictor
365 variables (such as the outdegree of gestures and sex of focal chimpanzee) on the outcome
366 variable (the proximity outdegree). We used node-level regressions to examine the predictors
367 of proximity in degree by the dyadic repertoire in and outdegree. In these analyses the
368 average value of the proximity network matrix was taken to calculate the normalised degree
369 centrality for each individual chimpanzee ($N = 12$) [Croft et al., 2010]. The rate of the
370 behaviour directed by conspecifics towards the focal chimpanzee determines indegree of
371 given behavior, whilst outdegree indicates the rate of the behaviour directed by the focal
372 chimpanzee towards the conspecifics. In addition, the node-level regression was used to

373 examine the predictors of proximity indegree by individual repertoire size. In these analyses
374 the average value of the strong proximity bond network matrix, where dyads of individuals
375 who had values of proximity association equal or above the mean plus half SD, were scored
376 as 1 ('strong bonds') and taken to calculate the normalized degree centrality for each
377 individual chimpanzee (N = 12) [Croft et al., 2010]. Finally, we used Geary's C statistics to
378 examine the autocorrelation between attribute data (the total duration of observation) and
379 network data (gestural networks). This statistic has a value of 1 for no association, with
380 values of less than 1 indicating a positive association and values of more than 1 indicating a
381 negative association.

382 Sampling effort:

383 In this study, a mean of 12.52 (range 8.33 – 18.63) hours of independent focal data
384 per individual subject was used to compute the dyadic repertoire size and sociality indices.
385 This mean value pertains only to the duration of 18-minute focal follows during which scan
386 samples were collected at 2 minute intervals during March and June 2008. This length of
387 observation of gestural communication of each focal subject in relation to social factors is
388 much greater than previously reported in studies that examined gestural communication (e.g.
389 3 – 5 hours of focal observation duration) [Hobaiter et al., 2017; Wilke et al., 2017]. Geary's
390 C statistic was used to examine the autocorrelations between the total duration of observation
391 for each focal chimpanzee and gesture networks. There was not a statistically significant
392 relationship between the total duration of observation and the networks for the repertoire size
393 of gestures overall ($C = 1.054$, $p = 0.402$) or any of the gesture modalities separately -
394 auditory long range gestures ($C = 0.412$, $p = 0.118$), auditory short range gestures ($C = 0.758$,
395 $p = 0.290$), visual gestures ($C = 0.756$, $p = 0.161$) and tactile gestures ($C = 1.029$, $p = 0.445$).
396 This suggests that the sampling duration for each dyad was not systematically related to the

397 gestural repertoire size observed in communication between that dyad, and that the sampling
398 duration was therefore sufficient.

399 **Results**

400 **Asymptote of repertoire size**

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

412 **How is dyadic repertoire size of gestures related to context?**

413 The definitions of gesture functions are given in ESM Table 2. Full details of all
414 models reported in this study can be found in ESM Tables 3 – 11. First, we examined the
415 relationship between the dyadic repertoire size of each modality of gestures and their
416 function. The details of gesture categorization according to modality and function can be
417 found in Table 2. Significant associations indicate that for pairs of chimpanzees, larger
418 gestural repertoire sizes were observed in specific contexts. The significant predictors of
419 repertoire size of long-range auditory gestures were gesture to receive groom ($r^2=0.504$,
420 $\beta=0.278$, $p = 0.028$), reassurance ($r^2=0.504$, $\beta=0.602$, $p = 0.049$), travel ($r^2=0.504$, $\beta=0.131$, p
421 $= 0.013$), copulation ($r^2=0.504$, $\beta=0.178$, $p = 0.011$) and high intensity panthoots ($r^2=0.504$,

422 $\beta=0.612$, $p = 0.010$). The significant predictors of repertoire size of short-range auditory
423 gestures were gestures to mutually groom ($r^2=0.926$, $\beta=0.795$, $p = 0.001$), gestures to receive
424 groom ($r^2=0.926$, $\beta=0.308$, $p = 0.001$), gestures to give groom ($r^2=0.926$, $\beta=0.222$, $p = 0.001$)
425 and gestures to play ($r^2=0.926$, $\beta=0.412$, $p = 0.001$). Moreover, the significant predictors of
426 repertoire size of tactile gestures were reassurance ($r^2=0.911$, $\beta=0.444$, $p = 0.018$), gestures to
427 play ($r^2=0.911$, $\beta=0.753$, $p = 0.001$) and greeting ($r^2=0.911$, $\beta=0.179$, $p = 0.002$). Finally, the
428 significant predictors of repertoire size of visual gestures were other threat ($r^2=0.918$,
429 $\beta=0.074$, $p = 0.037$), travel ($r^2=0.918$, $\beta=0.130$, $p = 0.001$), copulation ($r^2=0.911$, $\beta=0.173$, p
430 $= 0.001$), reassurance ($r^2=0.911$, $\beta=0.589$, $p = 0.012$), greeting ($r^2=0.911$, $\beta=0.426$, $p =$
431 0.001), gestures to receive groom ($r^2=0.911$, $\beta=0.204$, $p = 0.002$), play ($r^2=0.911$, $\beta=0.175$, p
432 $= 0.001$) and low intensity panthoot ($r^2=0.911$, $\beta=0.148$, $p = 0.001$).

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

434 Across the 132 dyads, each chimpanzee dyad produced a mean 2.05 (overall range 0 – 40)
435 gesture types for each hour spent in close proximity. For each modality of gestures
436 separately, mean rate (overall range) of gesture type production was: auditory long range
437 (0.08; 0 - 5), auditory short range (0.07; 0 – 2.5), visual (0.57; 0 – 12.50) and tactile (0.15; 0 –
438 7.06). We used MRQAP to examine whether the gestural repertoire size for each dyad
439 predicted preferred reciprocated close proximity bonds, whilst controlling for sex, age,
440 kinship and reproductive similarity of the dyad. Including gestures of all modalities, overall a
441 larger gestural repertoire size significantly predicted the presence of a preferred reciprocated
442 close proximity bond ($r^2=0.087$, $\beta=0.196$, $p = 0.036$). We then examined whether the
443 repertoire size of each modality separately predicted preferred reciprocated close proximity
444 bonds (Fig. 2). A larger repertoire size of auditory short range gestures ($r^2=0.237$, $\beta=0.283$, p
445 $= 0.049$) and visual gestures ($r^2=0.237$, $\beta=0.433$, $p = 0.004$) predicted the presence of
446 preferred reciprocated close proximity bonds. In contrast, chimpanzee dyads that were less

447 likely to associate with each other through close proximity had a significantly larger
448 repertoire of tactile gestures ($r^2=0.237$, $\beta= - 0.380$, $p = 0.006$). Next, we examined whether
449 the gestural repertoire size for each dyad per each modality of gestures predicted presence of
450 preferred non-reciprocated close proximity bonds. There were no significant associations
451 between the repertoire size of any of the gestural modalities and the presence of this type of
452 bond. Finally, we examined whether the gestural repertoire size for each dyad per each
453 modality of gestures predicted presence of non-preferred close proximity bonds. A larger
454 repertoire size of tactile gestures ($r^2=0.131$, $\beta=0.263$, $p = 0.047$) predicted the presence of
455 non-preferred close proximity bonds, whereas visual gestures were negatively correlated with
456 this type of bond ($r^2=0.131$, $\beta= - 0.404$, $p = 0.002$).

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

458 We used node-level regressions to examine the predictors of proximity in degree by
459 the repertoire size of gestures overall and by the repertoire size of auditory long range,
460 auditory short range, visual and tactile gestures in and out degree. Here we controlled for the
461 duration of time spent in proximity to oestrus females, time spent in proximity to kin, and the
462 age and sex of the focal chimpanzee. When the overall gestural repertoire size was
463 considered, in degree proximity was significantly associated with the out-degree repertoire
464 size - that is the size of the gestural repertoire produced by the focal individual ($r^2=0.791$,
465 $\beta=0.763$, $p = 0.049$). When the repertoire size for each modality was considered in one
466 model, chimpanzees with a high proximity in degree had a high visual repertoire size
467 outdegree ($r^2=1$, $\beta=2.730$, $p = 0.041$). Thus focal chimpanzees that produced a greater variety
468 of visual gestures had higher rates of proximity to a greater number of conspecifics.

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

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

472 auditory long range (7.75; 3 - 14), auditory short range (2.16; 0 - 4), visual (25.41; 19 - 30)
473 and tactile (13.41; 7 - 19). The details of individual repertoire size of all gestures combined
474 and by modality is presented in ESM Table 12. Geary's C statistic was used to examine the
475 autocorrelations between individual repertoire size of each focal chimpanzee (all gestures
476 combined and per modality type) and the proximity networks ('preferred reciprocated close
477 proximity bonds', 'non-preferred close proximity bonds'). Overall, chimpanzees who had a
478 similar repertoire size of all gestures combined were more likely to have a preferred
479 reciprocated close proximity bonds with conspecifics (Geary's autocorrelation, $C = 0.481$, p
480 $= 0.044$). Chimpanzees who had dissimilar repertoire size of all gestures combined were
481 more likely to have a non-preferred close proximity bonds ($C = 1.346$, $p = 0.009$). However,
482 there were no significant relationships between the repertoire size of each modality of
483 gestures considered separately and proximity networks (ESM Table 13).

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

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

495 **Discussion**

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

512 A second key finding is that, individuals who directed a larger repertoire of gestures
513 at the recipient tended to remain in close proximity for longer. Further, different modalities of
514 gestures were differentially associated with proximity. Previous research described repertoire
515 of gestures and examined variation in overlap in gesture types in relation to characteristics of
516 social system [Roberts and Roberts, 2017]. However, in line with previous findings in
517 macaques [Maestriperi, 1999] this is the first study to show that repertoire size is also an
518 important dimension of chimpanzee sociality [Maestriperi, 1999]. Strong proximity bonds
519 were associated with a larger repertoire size of visual gestures, and of auditory short range
520 gestures. The analysis was based on the repertoire size per hour dyads spent in close

521 proximity, rather than the overall repertoire size of individuals. The significant association
522 between repertoire size and proximity therefore shows flexibility in the production of the
523 repertoire of gestures when associating with different interaction partners, with a greater
524 variety of gestures produced with strong proximity bonds. In contrast, if chimpanzees showed
525 less flexibility and produced their repertoire of gestures at the same rate with different
526 interaction partners, there would be no significant association between proximity and
527 repertoire size per hour spent with these different interaction partners.

528 Chimpanzees, in common with other primates, maintain a small number of close
529 social relationships, and it is these frequent interaction partners that are important in buffering
530 primates from the stresses of group living [Foerster et al., 2015; Lehmann and Boesch, 2009;
531 Mitani, 2009; Mitani et al., 2002; Muller and Mitani, 2005; Seyfarth and Cheney, 2013]. A
532 larger repertoire size of visual and auditory short-range gestures may operate in a similar way
533 to short-range, low intensity grunts in baboons, allowing for the regulation of social
534 relationships when in close proximity, using a visual or auditory short-range mode of
535 communication [Palombit et al., 1999]. However, because these gestures are more subtle or
536 less intense, they may be less efficient in coordinating social behaviour with conspecifics and
537 the recipient. Different gestures are associated with different ‘dominant responses’ by
538 recipients [Hobaiter and Byrne, 2014; Roberts et al., 2014a; Roberts et al., 2012a]. A more
539 varied repertoire of visual or auditory short-range gestures (i.e. greater complexity in the
540 gestural repertoire) may lead to a greater reduction in uncertainty in the recipient, as the
541 gesture can more precisely convey the communication goal. Using a greater variety of
542 gestures may make it more likely the recipient will respond appropriately to the gestures,
543 facilitating social interaction and allowing for close proximity to be maintained over longer
544 periods. This interpretation is consistent with previous findings from this population of
545 chimpanzees which showed that elaboration in gestural sequences is used more frequently if

546 the recipients' response to the initial visual gesture is not congruent with the communication
547 goal [Cartmill and Byrne, 2010; Liebal et al., 2004a; Roberts and Roberts, 2018a; Roberts et
548 al., 2013].

549 An increased repertoire size of visual gestures was associated with communication in
550 both affiliative (e.g. reassurance, greeting, receive groom, copulation) and antagonistic (e.g.
551 other threat) contexts and this wide range of contexts may require a corresponding large
552 repertoire size. Individuals that can use this extensive repertoire flexibly, and elaborate with
553 alternative gestures if the recipient does not respond appropriately [Leavens et al., 2005], may
554 be at selective advantage in eliciting appropriate responses from recipients [Roberts et al.,
555 2014a]. For example, subordinate chimpanzees use gestural communication to elicit matings
556 and flexibly adjust the modality of the gestural communication according to the presence and
557 visual attention of rival males [Roberts and Roberts, 2015]. Subordinate males with a larger
558 repertoire of gestures, and with greater flexibility in the production of those gestures, may be
559 at a selective advantage in soliciting matings.

560 In contrast to visual gestures, the repertoire size of tactile gestures was negatively
561 associated with the amount of time pairs of chimpanzees spent in close proximity. For these
562 social bonds, the diversity of the gestural repertoire may be less driven by the constraints
563 resulting from modality of gesture use. Instead, a larger repertoire of tactile gestures may
564 allow for more efficient resumption of social relationships after the lengthy periods of
565 separation chimpanzees experience due to the fission-fusion social structure [Dunbar and
566 Shultz, 2010]. When two chimpanzees meet after a period apart, they need to be able to
567 reestablish the social relationship and resolve any uncertainties that may have arisen due to
568 the period of absence – for example relating to changes in alliances, dominance status and
569 third party relationships [Amici et al., 2008]. The reduction in uncertainty associated with
570 greater communicative complexity (a larger repertoire size) in tactile gestures may therefore

571 be related to the nature of social relationship. A larger repertoire of tactile gestures was
572 associated with affiliative contexts (reassurance, gestures to play and greeting) and these
573 contexts are important in reestablishing social relationships with chimpanzees encountered
574 less frequently than the strong proximity bonds [Roberts and Roberts, 2016b]. Thus, large
575 repertoire of tactile gestures appears to be important for these partners were the individuals
576 maintain affiliative relationship but stay in proximity less often.

577 As well as the large amount of variation in levels of proximity between pairs of
578 chimpanzees, there was also a large amount of variation in the number of proximity bonds
579 chimpanzees maintained with others. Individual chimpanzees that had a larger repertoire of
580 visual gestures had a larger number of proximity bonds. Maintaining and communicating
581 with a larger number of social partners places both cognitive and time demands on
582 individuals [Dunbar, 1993; Lehmann and Dunbar, 2009] because of the need to remember
583 and track past and present relationships and use this information to flexibly produce and
584 respond appropriately to gestural communication. This is particularly the case when
585 responding to visual signals when manipulating information about a larger number of social
586 relationships. The efficiency of social coordination may limit the number of relationships that
587 could be maintained with a restricted repertoire of gestures, but a larger repertoire allows for
588 more efficient coordination with the receiver, and thus more efficient communication by
589 signallers [Shannon et al., 1951]. The mean repertoire size for visual gestures (25 gesture
590 types) was greater than all the other modalities combined and using this large repertoire size
591 flexibly to communicate with the recipients may allow individual chimpanzees to maintain a
592 larger number of proximity bonds. Individuals with a larger repertoire of visual gestures may
593 be better equipped to regulate social interactions and manage the tensions of social life, for
594 example when feeding on patchy food sources such as figs where chimpanzees are forced
595 into close proximity for extended periods of time. In contrast, the size of the repertoire of

596 tactile or loud auditory gestures was not significantly related to the size of the proximity
597 network. These gestures might be more intense and therefore the mere frequency of use of the
598 gestures, rather than the size of the repertoire, may be sufficient to maintain the larger
599 number of weaker relationships in the network.

600 The findings of this study are in line with previous research showing that chimpanzees
601 show considerable flexibility in gestural communication [Gillespie-Lynch et al. 2013;
602 Hopkins and Wesley, 2002; Liebal et al., 2004b; Masur, 1982; Nishida, 1980; Schneider et
603 al., 2012; Schneider et al., 2017; Tomasello et al., 1994], have a large and varied gestural
604 repertoire [Hobaiter and Byrne, 2011a; Liebal et al., 2004a; Roberts et al., 2014a; Roberts et
605 al., 2012b; Tomasello et al., 1985], and that several different features of gestural
606 communication are related to sociality [Roberts and Roberts, 2018a; Roberts and Roberts,
607 2018b]. However, the study was based on 12 focal individuals and whilst network analysis
608 allows for the analysis of relationships at the level of the dyad rather than the individual
609 [Borgatti et al., 2013], the findings of this study should be replicated on a larger sample. All
610 the great ape species [Byrne et al., 2017] and some monkey species [Maestriperi, 1999] have
611 a varied repertoire of gestural communication and future research on how the size of this
612 gestural repertoire relates to sociality is needed to determine whether the association between
613 repertoire size and proximity is found across different populations of the same species, and
614 across different species.

615 A second area for future research is to examine the relative importance of similarity of
616 repertoire size of two individuals for maintaining proximity. Whilst this study showed overall
617 similarity in the individual repertoire size of chimpanzees is associated with proximity, it did
618 not examine whether two chimpanzees both with a small repertoire size spent longer in
619 proximity than two chimpanzees both with a large repertoire size. Examining this question
620 will provide further insights into whether it is specifically larger repertoire sizes that allow

621 pair of chimpanzees to maintain proximity for longer durations of time, or whether the
622 overlap in repertoire size between individuals is more important in maintaining proximity.

623 Overall the results of this study may provide new insights into gestural theories of
624 language evolution, by demonstrating a link between flexibility in use of a larger repertoire of
625 gestures and the maintenance of different types of social bonds. A key challenge in large and
626 complex social groups, both for primates and our hominin ancestors, is managing an
627 increasingly differentiated set of social relationships, consisting of a set of strongly bonded
628 regular interaction partners and also a more numerous set of weakly-bonded individuals with
629 less regular interaction [Dunbar, 2012]. This is a particularly issue in fission-fusion systems
630 that characterize many primate species and are also likely to have been present through much
631 of hominin evolution [Amici et al., 2008; Anderson et al., 2002]. Further, interaction with
632 these social partners occurs across a wide range of both affiliative and agnostic contexts. A
633 larger repertoire of gestural communication, and being able to use this larger repertoire in a
634 flexible way, may help to meet the time and cognitive challenges involved in sociality by
635 increasing efficiency of communication suitable for maintaining close proximity with others.
636 This reduction in uncertainty may allow for individuals to maintain closer proximity over
637 longer periods of time. Human language is characterized by both an extensive repertoire and
638 flexibility in how that repertoire is used [Burling, 1993]. Given the strong association
639 between individual variation in the strength of social bonds and fitness outcomes [Silk et al.,
640 2009] an increasing repertoire of gestural communication, and flexibility in employing that
641 repertoire with varied social partners and across multiple contexts, may have played an
642 important role in the evolution of complex communication in both primates and humans.

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651 **Conflict of interest**

652 Authors have no conflict of interest to declare

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

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

939 Notes. ^a Alpha female; ^b Alpha male.

940 Dominance based on unidirectional pant-grunt calls

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

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

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

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

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

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

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

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

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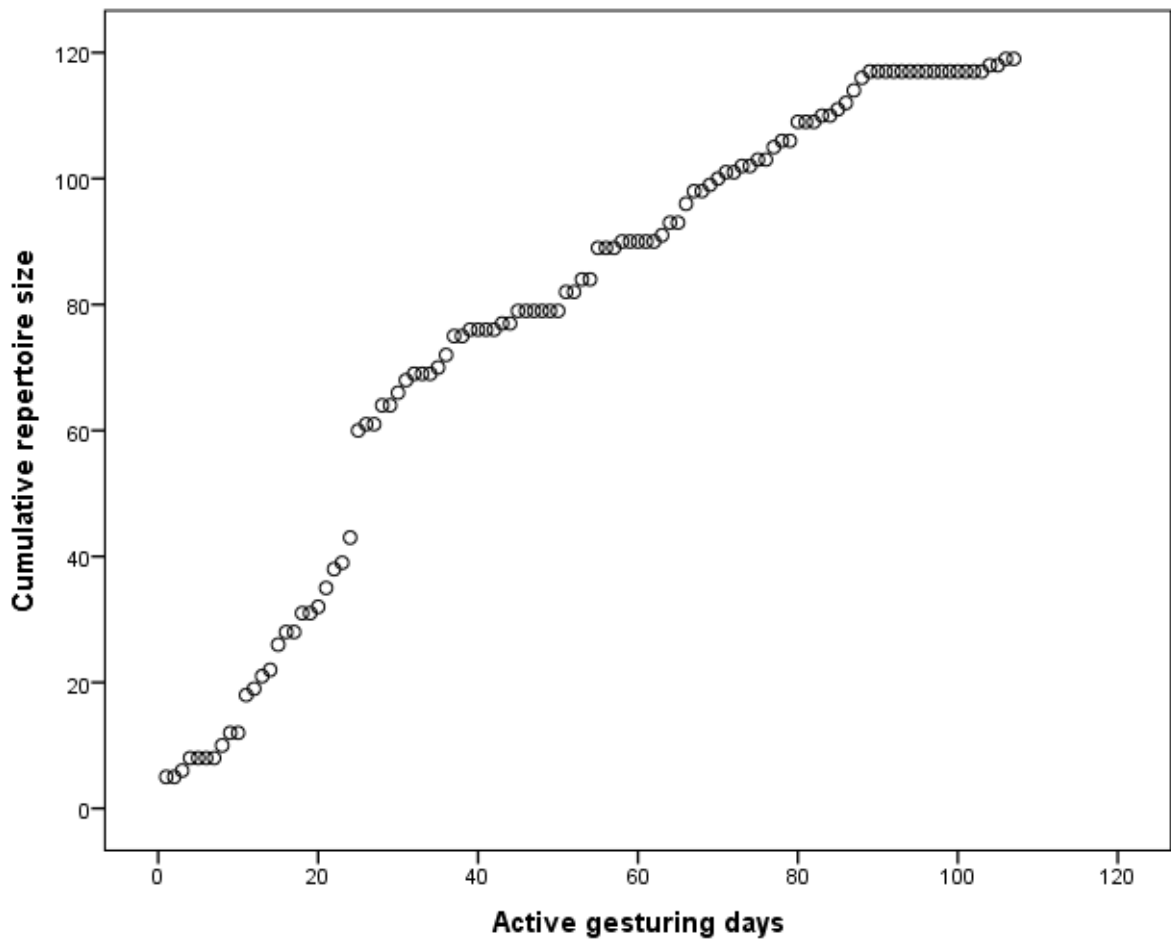
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955 **Figure titles**

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

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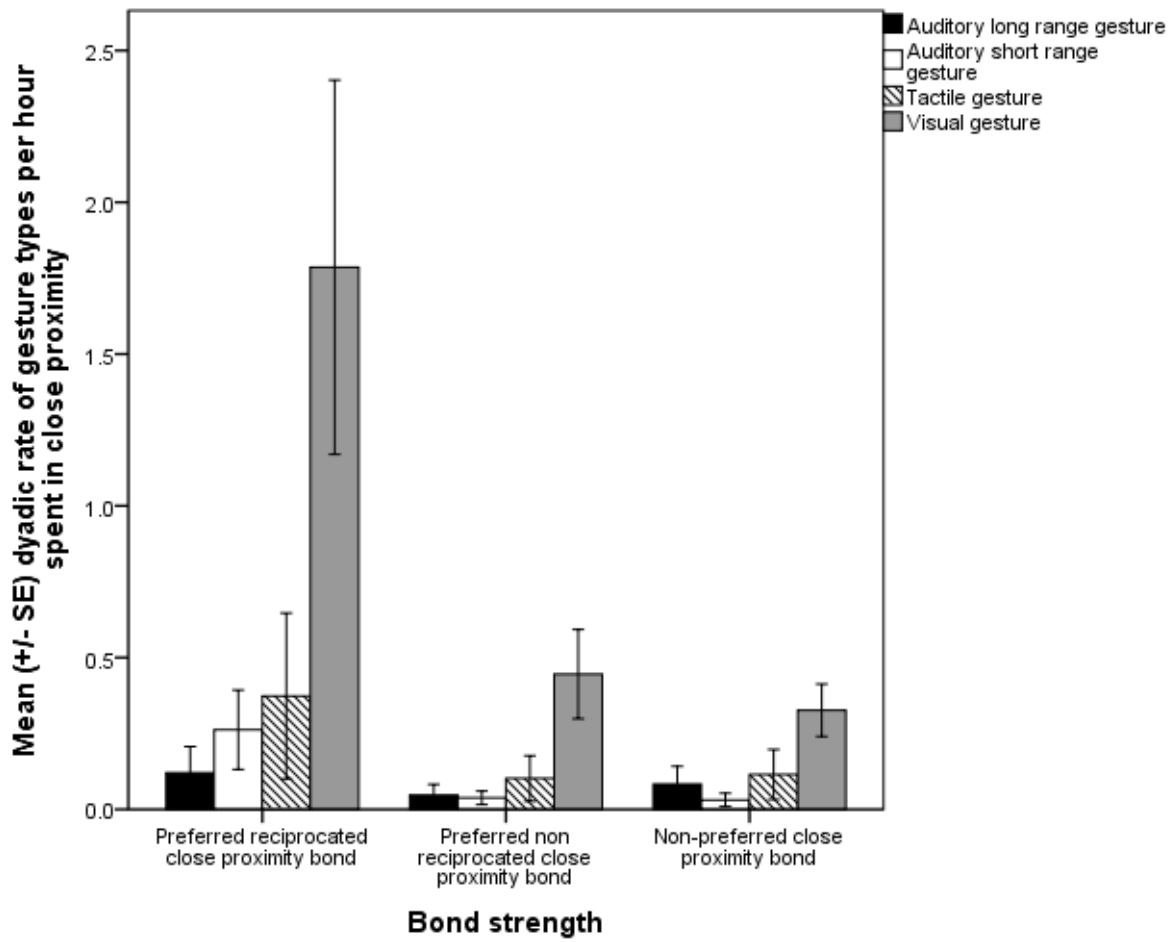


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964 Fig. 2 Mean rate of gesture repertoire production across four modalities, per hour dyad spent
965 in close proximity (within 10m).



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