Title: Capuchin monkey rituals: an interdisciplinary study of form and function

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Abstract:

Many white-faced capuchin monkey dyads in Lomas Barbudal, Costa Rica, practice idiosyncratic interaction sequences that are not part of the species-typical behavioural repertoire. These interactions often include uncomfortable or risky elements. These interactions exhibit the following characteristics commonly featured in definitions of rituals in humans: (1) they involve an unusual intensity of focus on the partner, (2) the behaviours have no immediate utilitarian purpose, (3) they sometimes involve "sacred objects", (4) the distribution of these behaviours suggests that they are invented and spread via social learning, and (5) many behaviours in these rituals are repurposed from other behavioural domains (e.g. extractive foraging). However, in contrast to some definitions of ritual, capuchin rituals are not overly rigid in their form, nor do the sequences have specific opening and closing actions. In our 9,260 hours of observation, ritual performance rate was uncorrelated with amount of time dyads spent in proximity but is (modestly) associated with higher relationship quality and rate of coalition formation across dyads. Our results suggest that capuchin rituals serve a bond-testing rather than a bond-strengthening function. Ritual interactions are exclusively dyadic, and between-dyad consistency in form is low, casting doubt on the alternative hypothesis that they enhance group-wide solidarity.

Keywords: ritual, play, bond-testing, capuchin monkeys, social networks, social relationships

1. Introduction

28 A long-term field study of white-faced capuchin monkeys in Lomas Barbudal, Costa Rica has yielded a
29 rich observational record of highly idiosyncratic interaction sequences not found in the species-typical
30 behavioural repertoire. Here, we (a) give an account of these puzzling, apparently non-utilitarian social
31 interaction sequences practiced by some, but not all, capuchin monkey dyads, (b) determine whether these
32 behaviours qualify as rituals according to definitions of ritual in various disciplines, and (c) test
33 hypotheses regarding the possible function or communicative role these interactions might serve, by
34 examining the qualities of the behaviours themselves and the characteristics of the dyads performing
35 them.

36 We refer to the capuchin social interactions described in this paper as "rituals," defined as
37 "learned behavioural sequences with no obvious immediate utilitarian purpose, composed of behavioural
38 elements repurposed from other parts of the behavioural repertoire, characterized by a high degree of
39 attentional focus by one or both partners on the other's body and/or a ("sacred") object jointly handled by
40 the interactants." This composite definition includes functionally relevant features from those used by
41 sociologists, anthropologists, psychologists and ethologists to test hypotheses regarding the social
42 functions of ritual; for discussion of ritual definitions across disciplines and whether the capuchin rituals
43 described here meet those additional criteria, see ESM Table 1. The following two traits are particularly
44 relevant for our definition, due to their probable connection to social function:

45 1) *Quality of attentional focus*: The behaviours we describe here are prolonged (dyadic) social
46 activities involving a high degree of focus by one or both partners on the other's body and/or actions,
47 and/or an object jointly handled by the interactants, thereby diverting attention away from normal
48 activities such as foraging or vigilance (see Rossano's definition [1]). This intense focus on a particular
49 partner, to the exclusion of other group members, calls to mind Collins' theory of interaction rituals [2], in
50 which degree of attentional focus and "emotional energy" directed to a partner informs the recipient about
51 its current relative value to the actor.

52 2) *Use of sacred objects*: The objects (and partner body parts) handled in some of these rituals have
53 no utilitarian value, e.g. they are neither food nor tools. Whether or not they have any symbolic value,
54 qualifying as "sacred objects," is a question of definition, but according to [3], an object, body part, or
55 individual can acquire sacred status by means of the repeated ritual performance.

56   Researchers of nonhuman primates have developed several hypotheses regarding the relationship
57 between social relationships and rates of greeting rituals. Some hypotheses state that ritual performance is
58 necessary to *establish or maintain social bonds*, perhaps by defining social roles and negotiating the
59 terms of a social relationship, and predict that ritual performance will be associated with higher
60 frequencies of time spent together, affiliative behaviours, or cooperation [4]. Others state that these rituals
61 are a way of *testing* important relationships critical to enhancing fitness [4][5][6][7][8], which leads to the
62 predictions that bond tests will be more frequent when (a) there is a dearth of information regarding the
63 state of the relationship, (b) there is good reason to believe that the relationship is undergoing change (e.g.
64 during a rank reversal), and (c) the bond is solid enough that a Zahavian bond test won't be extremely
65 risky, yet not so secure that there is no need to test it at all.

66   To gain insight into the function of these rituals, we test the following hypotheses and predictions:

67   1) Rituals serve to establish and *maintain* social bonds:

68   a. Rituals will be more frequent in dyads that

69   i. spend the most time in proximity,

70   ii. have higher relationship quality, and

71   iii. cooperate most often in coalitionary aggression

72   2) Rituals serve as Zahavian tests of social bonds [5]:

73   a. Behavioural elements will entail some risk and/or discomfort

74   b. Rituals will be more frequent when state of a relationship is unclear (i.e. there should not
75   be a positive linear correlation between rate of ritual performance and time spent
76   together, but rather, higher rates at intermediate rates of time spent in association).

77   c. Rituals are predicted to be most often performed in dyads with good enough relationships
78   to feel comfortable performing the intimate ritual, but not in relationships so completely
79   free of conflict that they require no testing (i.e. highest rates of ritual performance at
80   upper intermediate values of relationship quality rather than at the highest end of the
81   distribution)

82   3) Participation in rituals promotes group-wide solidarity:

83   a. Rituals are expected to be performed simultaneously by many monkeys at once,
84   exhibiting a form that is consistent among group-mates

85

2. Study species and methods

2.1 Study population

Our subjects are wild, well-habituated white-faced capuchin monkeys (*Cebus capucinus*), residing in and near Lomas Barbudal Biological Reserve, in the tropical dry forests of northwestern Costa Rica. This population has been studied since 1990 by S. Perry and collaborators (see [9] for more details on the natural history of this species, and [10] and [11] for information on this longitudinal project, including the methods). White-faced capuchins are extraordinarily large-brained, long-lived New World primates living in stable multi-male, multi-female groups, characterized by female philopatry and male parallel dispersal; i.e. both sexes can maintain long-term bonds with same-sexed kin [9]. Their social behaviour is complex and characterized by a rich repertoire of signals for communicating about their social relationships, including both species-typical vocalizations and gestures, and innovative/learned gestures [9]. Cooperative interactions and alliances are key to the reproductive success of both sexes and pervade many aspects of capuchins' lives [9].

2.2 Data collection

Observers were instructed to record, in minute detail, descriptions of any social interaction (during focal and *ad libitum* observation) that was not composed exclusively of standard (i.e. species-typical) items in the ethogram in their normal context. Interaction descriptions were recorded in the field and later transcribed into a daily spreadsheet. Whenever possible, interactions were videotaped. Observers recorded participants' posture/bodily orientations, gaze directions, which body parts were in contact, any physical object that was handled as part of the interaction, and the social context (e.g. whether other monkeys were in proximity and whether they were paying attention). During *ad lib* observations, interaction start times were sometimes missed. Descriptions varied somewhat in level of detail, as the unpredictable form of these innovative interactions made it difficult to devise appropriate interobserver reliability measures. To increase reliability, two observers typically collect data from two different locations, thus mitigating the problem of foliage obscuring some parts of the interaction.

113   *2.3 Data set*

114   The new data presented here are from "Flakes" (FL) group, which fissioned from Abby's group (the

115   original study group) in late 2003. Here, we analyse 9,260 observation hours of data collected between

116   February 1, 2004, when the group had become demographically stable, until October 11, 2018. FL group

117   was composed of two matrilines, headed by matriarchs who are probably cousins, and contained five

118   immigrant males, who arrived singly at different times during 2003-2004; two of these shared a natal

119   group, and three were from outside the study area. These immigrant males seemed to be 8-12 years old at

120   the start of 2004. Over the course of the 15 years of observation, Flakes group included 53 individuals,

121   ranging from 9-30 members at any given time (six monkeys were excluded from the analysis who died

122   prior to 6 months of age).

123   The data set consists of 446 social interaction "rituals" and 6 failed attempts of monkeys to elicit

124   joint interaction in a ritual. Thirty-seven (79%) of the 47 group members included in the analysis (17 of

125   20 females and 20 of 27 males), and 17% of the 762 co-resident dyads (40 female-female, 47 male-female

126   and 46 male-male dyads) engaged in at least 1 ritual. Only 19 individuals (6 female, 13 males) comprising

127   32 dyads (25 male-male and 7 male-female) participated in the most complex rituals (i.e. "games"). As

128   more peripheral monkeys are more often missed in group scans, and because only a few individuals were

129   the subjects of focal observations, total observation time varies among individuals. Observers spent much

130   of each day collecting focal follows, so the probability of detecting rituals performed by focal subjects

131   was higher than for non-focal animals. To correct for observation effort, we summed the number of group

132   scans and point samples (collected at 2.5-min intervals during focal follows) for each member of the dyad

133   on days when both members of the dyad were co-resident in FL group.

134   *2.4 Measures*

135   To test hypotheses 1 and 2 we require measures for: physical proximity, relationship quality, and coalition

136   formation. Our measure of physical proximity is based on "group scans" in which researchers wandered

137   through the group, recording distance between the scanned monkey and other monkeys in proximity to it.

138   We scored two individuals as being in physical proximity if they were <40cm of one another (equivalent

139   to an adult male body length, from nose to tailbase).

140   Our measure of relationship quality (RQ) is based on observed social interactions during focal

141   follows (when available) and *ad libitum* observations. The standard social interaction repertoire included

142   79 behaviours (some dyadic and some triadic) with clear emotional valences, i.e. participation would

143 elicit at least in one of the participants positive or negative emotions, thereby affecting the "emotional

144 energy" (sensu Collins [2]) or the emotionally-mediated "book-keeping" of the rates and qualities of

145 interactions [12] expected to influence the quality of future interactions of that dyad. Grooming, playing,

146 and forming a coalition are among the 42 behaviours expected to have a positive impact, whereas

147 aggression and submission are among the 37 behaviours expected to have negative impact on relationship

148 quality. We determined the relationship quality index (RQI) in the following way: we aggregated data

149 into 10-minute chunks. For each dyad and for each chunk, we assigned a score of 1 if there was at least

150 one positive behaviour, and 0 if not. We repeated this for negative behaviours. The RQI for a given dyad-

151 year consists of (a) the number of time-chunks with one or more positive impact behaviours, divided by

152 the sum of (a) plus (b) the number of time-chunks with one or more negative impact behaviours. Thus,

153 RQI=0 represents exclusively negative and RQI=1 exclusively positive "emotional energy".

154   Our measure of coalition formation is based on *ad libitum* data, using only incidents of

155 "overlords", "cheek-to-cheek" postures, and "embraces" (defined in [9]) against a common conspecific

156 opponent. Although coalitions are fairly conspicuous behaviours, there is nonetheless some tendency to

157 underreport coalitions from peripheral group members. We accounted for this by creating an offset

158 variable consisting of the number of group scans collected for individual A and individual B on days

159 when they were co-resident. Because *ad libitum* observations were collected primarily as observers were

160 wandering through the group collecting group scans, this should be a fairly accurate representation of the

161 observability of these individuals.

162

163 *2.5 Statistical analysis*

164 The data were analysed in a series of three MLPE models. Like a Mantel test, MLPE models [13] assess

165 the relationship between two matrices. However, the mixed effects parameterization (specifying the

166 covariance structure of the matrices) accounts for non-independence among pairwise data in each matrix.

167 The actual model is essentially a linear mixed effects model. The independent variable was the proximity

168 index, the relationship quality index (RQI), or coalition count, divided by the sum total of group scans of

169 the two coalition partners (as an observability adjustment). In all cases, the outcome variable was the

170 count of rituals performed by this dyad, with the exposure being the sum total of group scans and point

171 samples collected on the two partners in the ritual. Sample sizes of dyads were slightly smaller for the

172 RQI model as a few dyads did not interact. We dropped infants <6 months of age from the coalition

173 model, since they were never old enough to form coalitions. We use the MLPE_rga() function of the
174 ResistanceGA package in R [14] (see ESM section 4 for additional information).

175

3. Results

3.1 Description of the behavioural phenomenon

178 Most of the social interactions that comprise a dyadic relationship in white-faced capuchins consist of
179 species-typical interactions common to primates generally: e.g. grooming, hugging, and rough-and-
180 tumble play (chasing, wrestling, biting, hitting, "play face"), submission (cowering, avoiding),
181 aggression, infant care behaviours and sexual interactions, plus a few species-specific behaviours such as
182 coalitionary recruitment signals, courtship "dances" and vocal signals of benign intent or aggressive intent
183 (vocal threats)[15]. However, in addition to these species-typical behaviours, white-faced capuchins often
184 invent new forms of social interaction, devising rituals that are often unique in their subtle details to a
185 specific individual or dyad [6][16]. There is inter-individual variation in the propensity to invent such
186 rituals; in a prior 5-year study of innovation in this population, only 84 of 234 individuals (36%) were
187 members of dyads that invented a new social interaction ritual [16].

188   The following behavioural elements were commonly included in novel social rituals created by
189 the monkeys in Flakes group:

190   (1) Inserting a finger into the orifice of a social partner (e.g. mouth, eye, nostril, or ear), or vice
191 versa (inserting the partner's digits into one's own orifices),

192   (2) Prying open a mouth or hand to conduct a detailed inspection of its contents,

193   (3) Passing an object (e.g. bark, leaves, flower, stick, green fruit, or hair plucked from the
194 partner's body) back and forth from one partner to another, taking turns at the role of holding the object in
195 hand or mouth, and extracting it (also with hands or mouth), in a very gentle "tug-o-war",

196   (4) Clasping of hands, often with fingers interlaced,

197   (5) Cupping the hand over some part of the partner's face,

198   (6) Sucking on some appendage belonging to the partner (e.g. tail, finger, toe, ear, nose, or
199   sometimes a clump of hair),

200   (7) Using the partner's back or belly as a drum to create loud, rhythmic noises.

201   Note that elements 1-3 above seem to be borrowed from the extractive foraging repertoire and applied to
202   a partner's body rather than to a substrate potentially containing food. The repurposing of elements from
203   one portion of the behavioural repertoire in another section of the repertoire is commonly discussed as a
204   feature of rituals by early researchers of animal ritual [17].

205   Of the 446 individual instances of rituals described in our sample, 49% involved placing the
206   fingers in or on the nose, 54% involved insertion of fingers in the partner's mouth, 14% involved passing
207   a "toy" back and forth between mouths or hands, 5% involved biting hair out of a partner who then tried
208   to retrieve it, 7% involved insertion of fingers into a partner's eye, 7% included "dental exams," 1%
209   included "back-whacking," and 4% involved some creative way of kissing, sucking or chewing on a
210   partner. Many rituals included additional features that were more idiosyncratic to an individual or a dyad.

211   The most complex interaction sequences were the "games" that involved extracting an object
212   from the hand or mouth of the partner (see ESM section 2 for a video clip and a transcription of the
213   interaction sequence). A particularly striking feature was the focus on physical objects ("toys") that were
214   extracted from interaction partners' bodies. Sometimes partner 1 would bite tufts of hair out of partner 2,
215   who would then pry open the mouth of partner 1 to recover the hair. Using motor patterns typical of
216   extractive foraging, the hair would then be passed back and forth amicably between the two partners.
217   Other times, non-edible portions of plants were used as the game objects. Note that these objects had no
218   nutritional value, and the monkeys were surrounded by similar objects, which could be more readily
219   obtained. But it seemed that the object acquired value by virtue of the fact that monkey 1 had it in its
220   possession (i.e. it acquired "sacred object" status by virtue of the fact that it was being used in this ritual).
221   The two monkeys would focus their attention on this object for several minutes (usually 10-30 min).

222   These interactions are readily interpretable from Heesen et al's [18] framework that views social
223   play as joint action, i.e. interactional achievements whereby the participants create a sense of
224   togetherness. They describe three phases of these interactions, including formalized openings and
225   closings, which capuchin rituals generally lack. Instead, our monkeys almost always began and ended
226   their interactions by merely approaching and leaving their partners. However, capuchin ritual behaviour
227   typically includes the characteristics of the middle section ("main body") of Heesen et al.'s sequence,

228 described as negotiation of continuation of the activity, changes in type of interaction, role reversals,

229 suspension of activities, and re-engagement of partner's attention to the prior activity. Our subjects often

230 initiate role reversals or changes of activity by explicitly moving their partner's hands to the part of the

231 body where they want them to be. There are frequent examples of re-engagement of the partner's

232 attention, both in these rituals and in coalition formation (outside the context of rituals). In the toy and

233 hair "games," one partner will attempt to re-engage the attention of a partner whose attention has

234 wandered, by spitting out the object and explicitly showing the partner that they have it, before either

235 inserting it in their own mouth, or holding it in front of the partner's mouth. This is usually successful in

236 re-establishing mutual participation. In a coalitionary context, when there is an asymmetry in affect and

237 participation in attacking an opponent, the angrier monkey will sometimes tug on the body parts of the

238 ally or bounce ferociously while in body contact with the ally, presumably to rev up the partner's

239 enthusiasm for the joint attack; these tactics are generally successful in creating more symmetric

240 emotional engagement. Interestingly, in contrast to human children, young captive chimpanzees fail to re-

241 engage human adult partners in activities following interruptions [19]. Possibly, the finding that

242 capuchins and humans, but not chimpanzees, exhibit partner re-engagement is evidence of convergent

243 evolution between capuchins and humans regarding awareness of joint commitment towards common

244 goals among partners. This would be consistent with evidence indicating convergent human-capuchin

245 evolution regarding the importance of coalitionary aggression.

246 We observed considerable variation in (a) the ways various combinations of the basic behavioural

247 elements described above were incorporated into a dyadic ritual, (b) the posture and gaze direction of the

248 participants, (c) the extent to which dyads were temporally consistent in the form of their rituals, (d) the

249 extent to which there was symmetric emotional engagement, and (e) the degree of turn-taking for those

250 rituals that had multiple roles. However, structural commonalities in the rituals have led us to hypothesize

251 that they share a common function (as bond-testing signals [6]) and/or ontogenetic process. Capuchin

252 monkeys normally behave at a rapid pace, both in their destructive foraging style and in their social

253 interactions (e.g. rapid-fire grooming exchanges). Even while resting, their visual attention typically

254 wanders, seeking new foraging opportunities or monitoring others' social interactions. In striking

255 contrast, their more creative social rituals proceed via slow, deliberate movements, and the participants'

256 faces bear almost trance-like expressions. Although participants rarely make eye-to-eye visual contact,

257 one or both monkeys focuses visual attention on some body part of its partner, often for several minutes at

258 a time. Sometimes both participants focus their attention jointly on an object. The amount of time and the

259 sustained focus devoted to these rituals suggests that the two ritual partners value one another highly.

260 Another common feature of these interactions is that they typically involve some risk or discomfort, e.g. a

261   finger in someone's mouth where it is at risk of being injured by teeth, or a finger in another monkey's

262   eye socket, so that a quick movement could scratch the cornea. One monkey often twists another's body

263   into positions that look distinctly uncomfortable. The monkeys' enthusiasm for these uncomfortable

264   and/or risky interactions is consistent with Zahavi's "testing of a bond" theory [5]. Behaviours that are

265   risky, uncomfortable or disgusting will seem aversive when received from a non-favoured partner, but

266   pleasurable when received from a favoured partner; the emotional response elicited by the bond-testing

267   behaviour informs the tester about the state of the relationship. This theory (minus the emphasis on

268   risk/discomfort as an adaptive design feature in the ritual) closely mirrors Collins' ideas about interaction

269   rituals, in which partners assess one another's behavioural responses to their interactions with them,

270   obtaining useful information about their relationship status and how the partner feels about them, relative

271   to other partner options [2].

272

273   *3.2 Who performs these rituals, what are the performing dyads' characteristics, and what does this tell us*

274   *about ultimate function?*

275   We find that individual capuchins were first seen to participate in some sort of ritual (game or non-game)

276   at a mean age of 1.9 years (range 0.1-4.8 years), but were first seen to be active participants in games at a

277   mean age of 3.2 years (0.7-7.3 years), with one female never becoming an active participant (see ESM

278   section 5 for additional information). The absence of these behaviours in younger individuals suggests

279   that learning is involved in their production.

280   Table 1 presents the results of the three MLPE models used to predict ritual rates; graphical

281   representations of these data are found in the ESM, Section 4 Figure 1, along with other details of the

282   analysis. The ICC and tau values indicate that individual idiosyncracy did not explain much of the

283   variance in ritual rates. The proportion of time a dyad spends in proximity is not a strong predictor of

284   ritual rate; this is inconsistent with Hypothesis 1 ("bond establishment and maintenance"), but not

285   necessarily inconsistent with the "bond-testing" hypothesis (H2). Consistent with both hypotheses, those

286   dyads with higher quality relationships were slightly more likely to perform rituals. However, consistent

287   more with the bond-testing than the bond maintenance hypothesis, dyads were more likely to perform

288   rituals if they were in the range of RQI=0.7-0.9 (30% of 254 dyads) than in the highest RQ values (7.5%

289   of 212 dyads for which RQI $\geq$ 0.9); none of the 14 dyads with RQI <.3 performed a ritual. Finally, the

290   model using coalition formation rate as a fixed effect demonstrates a positive (though modest)

291 relationship between coalition formation rate and rate of ritual performance; this is consistent with both
292 Hypotheses 1 and 2.

293

294 **4. Discussion**

295 In the previous sections we have described some unusual behavioural sequences observed in white-faced
296 capuchin monkeys and provided an argument for calling these "rituals." Our analysis supports the notion
297 that these behaviours are relevant for dyadic bond-testing. In the following section we compare the
298 observed rituals with human rituals and analyse form and function.

299

300 *4.1 Comparisons of form and proximate causes:*

301 The form of the capuchin rituals described here bears some resemblance to other nonhuman primate
302 rituals (e.g. baboon greetings) and to many types of human interaction rituals. As far as we can tell in the
303 absence of similar methodologies across studies, it seems that the degree of behavioural variability in
304 capuchin rituals is somewhat greater (i.e. less rigid and rule-bound) than in human rituals. The
305 exaggeration of movement so typical of more species-stereotypical mammalian rituals (e.g. displays) is
306 absent in capuchins. There is less obvious "framing" of the onset of rituals in capuchins than in humans,
307 or even in baboons [8]. Though most of the dyadic rituals described in this paper start in the context of
308 grooming, resting in contact, or slow motion play, there is no one behavioural or contextual element that
309 reliably signals that a ritual is beginning or ending, even within a single dyad. It seems likely that the
310 proximate trigger for these rituals is the monkeys' perceived need for information about the status of the
311 relationship, but we do not currently have a means of testing that hypothesis.

312   A commonality between capuchin rituals and human rituals is the attentional focus, which is
313 often focused on a "sacred object," i.e. an object that gains its value from the emotional charge acquired
314 via its use in the ritual, rather than from any intrinsic utilitarian value ([20][21][2][3]). An important
315 difference, however, is that the symbolic meaning of sacred objects in human rituals continues outside the
316 context of the ritual; as far as we can tell, this is not true in capuchins.

317

318   *4.2 Function, and the relationship between form and function:*

319   Whereas some theories regarding the evolution of ritual have focused more on the benefits relating to
320   working memory [1], others (e.g.[2][5]) have focused more on how the quality of the attention itself can
321   serve as a signal of the partner's current emotional and motivational state, which is relevant to assessing
322   commitment to their relationship. It has been hypothesized, both for many types of human rituals (e.g.
323   religious rituals [22][20][23][21]) and for some types of nonhuman rituals (e.g. [8][7][6][4]), that ritual
324   serves a social bonding function, enhancing feelings of solidarity, trust and desire to collaborate, or at
325   least testing commitment to a particular group or partner(s). Although testing these functional hypotheses
326   is difficult in both humans and nonhumans, the evidence from capuchins is generally consistent with the
327   idea that capuchin dyadic rituals serve a bond-testing function. An important difference is that whereas
328   most human rituals seem designed to promote group-wide solidarity, capuchin (and other nonhuman
329   primate) rituals seem to operate at the dyadic level [20], which has important implications for the
330   relationship between form and function of rituals. Although capuchins do seem to have a strong sense of
331   group identity (as exhibited by their xenophobia and collaborative aggression towards members of
332   neighbouring capuchins groups [11]), we have seen no examples of capuchin rituals in which all group
333   members perform actions in strict unison, and capuchins very rarely cooperate as an entire group. Current
334   theorizing about the function of ritual in humans also emphasizes the value of ritual for promoting
335   adherence to group-specific social norms; possibly, capuchins lack such social norms.

336   The degree of rigidity in the form and ordering of the ritual actions is often considered a
337   necessary diagnostic feature for rituals [22], and examination of this feature might provide insights into
338   function. When a ritual's function is group-wide bonding/identification, promoting group-wide
339   cooperation, we should expect group-wide uniformity in the performance of a ritual. Our data make us
340   sceptical that this is the function of capuchin rituals. In the capuchin data set, there was considerable
341   inter-individual and between-dyad variation in the behavioural elements included in the ritual repertoire,
342   and there was between-dyad variation in the level of mutual engagement and role reversals as well; ESM
343   section 3 describes some of this variation, discussing case studies of the ritual networks for 4 individuals.
344   Capuchin rituals are more likely to be designed by natural and cultural selection to test and/or strengthen
345   dyadic bonds, enabling individual monkeys and dyads to understand where they stand with regard to
346   commitment and cooperation compared with other individuals and dyads within their social group. If this
347   is correct, then we should expect to see high within-dyad uniformity, but less between-dyad uniformity
348   than is seen in human rituals that are performed in groups. Indeed, following the logic of [6], between-
349   dyad variation in the form of a ritual may be a design feature. The time required to devise a unique dyadic

350 ritual would be non-transferable to other dyads, creating an opportunity cost that serves as an honest

351 signal of commitment to that particular dyadic partner. Reminders of unique dyad-specific games played

352 exclusively with a particular partner might create links between the past, present, and future of that dyadic

353 relationship (a phenomenon akin to "traditionalism" [22]), in which the dyad-specific ritual behaviour

354 may help create a mental representation of the social relationship. If this functional hypothesis is correct,

355 then we would expect the following pattern of variation in capuchins: (a) increasing homogeneity within

356 each dyadic ritual, as the partners come to an agreement of what roles and behavioural sequences

357 characterize their unique dyadic ritual, (b) greater within-dyad homogeneity in form than between-dyadic

358 homogeneity in form, even for dyads including one of the same individuals, (c) absence of within-group

359 homogeneity in form, aside from the trivial similarities that come from the fact that independent

360 inventions of rituals are constrained by the types of building blocks existing in the "Zone of Latent

361 Solutions" [24] for the species, and the obvious advantages of including behavioural elements that have

362 Zahavian bond-testing qualities (i.e. are risky or uncomfortable for dyads with poor quality relationships)

363 [5]. Unfortunately our data set currently includes insufficient numbers of rituals for most dyads to test

364 these hypotheses.

365

366 *4.4 Ontogenetic and phylogenetic aspects:*

367 In both human religious rituals and nonhuman rituals, elements of feeding, drinking, and washing

368 behaviours are often introduced into new contexts, i.e. taken from their original functional context and

369 repurposed for communicative means. In the case of capuchin rituals, most of the behaviours come from

370 the behavioural domains of (a) grooming, (b) extractive foraging (prying open or probing into holes and

371 crevices with fingers, substituting a social partner's body parts for the plant parts upon which these

372 actions are performed in a foraging context), or (c) food sharing/tolerated theft (in which an individual

373 exhibits close-range inspection of another's hands or mouth and gently attempts to remove a piece of the

374 food from the monkey in possession of the food; in the ritual case, a non-food item is substituted for

375 food). When these behavioural elements are applied in the context of ritual, the presumed original

376 functions of these actions (e.g. hygiene, in the case of grooming; nutritional gain, in the case of extractive

377 foraging and tolerated food theft) are replaced by a new function, presumably related to the establishment,

378 maintenance and/or testing of social bonds. It is not entirely clear on what time scale (ontogenetic or

379 phylogenetic) this repurposing occurs in capuchins. Because not all individuals express the same rituals,

380 and these rituals are generally developed and expressed later in life, it is likely that most individuals

381 independently invent these rituals by repurposing behavioural elements and subsequently socially

382 transmit them to partners via ontogenetic ritualization, i.e. that the borrowing occurs within the lifetime of

383 an individual. Given the similarities in form across so many individuals and dyads, it seems likely that

384 capuchins as a species (or genus) have evolved a proclivity to prefer to borrow these particular kinds of

385 behaviours (i.e. elements from the grooming, extractive foraging and food transfer repertoires) rather than

386 other behaviour types, due in part to the fact that they are descended from a long evolutionary line of

387 animals that relies on extractive foraging and social learning about food that occurs in a scrounging

388 context; this would be more of a phylogenetic argument.

389

390 *4.5 Comparisons with human playground rituals:*

391 Besides these characteristics that are commonly aspects of definitions of ritual, the behaviours we

392 describe here have additional characteristics that are part of Burghardt's [25] definition of *play*: (1) They

393 appear to be *spontaneous, pleasurable, rewarding and voluntary* for at least one, and almost always both,

394 members of the dyad performing them. (2) They are performed *in the absence of any obvious acute or*

395 *chronic stress*, when the participants seem relatively relaxed. (3) *Elements are often repeated* within a

396 single ritual performance or in subsequent performances by the same dyad, but not typically in rigid

397 rhythmic or stereotypic form. Lack of immediate purpose is also a feature of definitions of both play and

398 ritual [25]. In some ways, capuchin rituals resemble human children's playground rituals. Merker [26]

399 points out that whereas the motor details of children's' rituals are mainly arbitrary with respect to

400 function, there is social pressure to do things in a particular way, and the propensity to care about these

401 details, i.e. to conform, has a bond-testing function. That is, the obligatory stereotypy of the rituals makes

402 it obvious when mistakes (deviations) occur, and to avoid making such mistakes, it is necessary to invest

403 much time in practice. Learning the details of a dyadic or group greeting ritual, for instance, requires that

404 the individual pay close attention over long periods of time and practice; this is a costly way of indicating

405 investment in the relationship(s). Capuchin rituals are simpler than children's hand-clapping games or

406 secret handshakes, but they too seem to require extensive practice at mastering arbitrary details. The

407 patterning of behavioural variation suggests that participants recall their usual roles with particular

408 partners and repeat them, as if reaffirming their roles in this particular relationship.

409

410 **5. Conclusions**:

The capuchin dyadic interaction rituals described here are characterized by a strong attentional focus on the partner's body and/or a "sacred object", repurposing of behavioural elements from the extractive foraging repertoire, and incorporation of risky or uncomfortable behaviours. The form of these behaviours makes them ideal as Zahavian bond testing rituals, but is also consistent with a bond maintenance hypothesis. The patterning of which dyads performs these rituals most often best supports the bond-testing hypothesis. The group solidarity hypothesis is supported neither by the form of the rituals (which are highly variable between dyads within the same group), nor by the temporal aspects, as these rituals are performed by dyads in isolation, rather than by many monkeys simultaneously. Although there is a fairly high degree of consistency within dyad regarding the behaviours performed, there is more creativity, less rhythm, and less precise replication of behavioural elements than is consistent with many definitions of ritual in the ethology, psychology and anthropology literatures.

446

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505

506   Table 1: Results of 3 separate MLPE models predicting ritual rate.

507

	Model 1: Proximity	Model 2: RQI	Model 3: Coalitions
intercept	0.019	0.008	0.019
estimate	-0.0014	0.089	0.11
SE	0.035	0.040	0.04
P	0.967	0.027	0.004
95% CI	-0.07–0.07	0.01-0.17	0.04-0.19
σ_2	0.90	0.89	0.89
$\tau_{00\ individual}$	0.05	0.06	0.05
ICC	0.05	0.06	0.05
N individuals, dyads	45, 762	45, 693	42, 676

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Capuchin monkey rituals: an interdisciplinary study of form and function

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ESM 1. On the definitions of ritual

1. Definitions across academic disciplines

There is very little consensus among researchers, either within or between disciplines, about what a ritual is. However, several features appear repeatedly in these definitions. In Table ESM1, we present a sample of some common definitional features of ritual associated with particular disciplines. The features selected as being important in these definitions probably have some loose association with the putative function of ritual that is attributed by the researchers. The fourth column in Table ESM1 lists the putative function of ritual that is named in studies for which this feature is an essential part of the definition of ritual. Note, however, that in some definitions certain features are claimed to be indispensable and others optional, and that the claimed link between definitional feature (form) and function is made explicit in some, but not all of these studies, most of which were not designed with such an evolutionary analysis in mind. This is not an exhaustive literature review, of the many elements found in definitions of ritual, nor of the researchers using these definitions. Instead, it is meant as a rough guide demonstrating some of the cross-disciplinary linkages in definitions and theorizing regarding the function of ritual that we came across.

2. How do observed capuchin rituals correspond to our definitional features?

Here we describe how the characteristics of the capuchin monkey behaviours that we designate as "rituals" in the Results section correspond to these proposed attributes in our definition:

3) *Quality of attentional focus*: The behaviours described here are prolonged (dyadic) social activities sometimes lasting up to an hour, involving a high degree of focus by one or both partners on the other's body and/or actions, and/or an object jointly handled by the interactants, thereby diverting attention away from normal activities such as foraging or vigilance (as in Rossano's definition of ritual [1]). This intense focus on a particular partner, to the exclusion of other group members, is reminiscent of Collins' theory of interaction rituals [2], in which degree of attentional focus and "emotional

546   energy" directed to a partner provides information to the recipient about its current
547   relative value to the actor.
548   4) *Lack of immediate utilitarian purpose*: These behaviours have no obvious utilitarian
549   purpose, i.e. they do not seem to enhance food-acquisition, safety or health in any
550   obvious, immediate way, though they may serve a communicative purpose.
551   5) *Sacred objects*: Similarly, the objects (and partner body parts) handled in some of these
552   rituals have no utilitarian value, e.g. they are neither food nor tools. Whether or not
553   they have any symbolic value, qualifying as "sacred objects," depends on how this term
554   is defined (see discussions by Durkheim [3], Goffman [4] and Collins [2]), but it seems
555   unlikely that the objects retain this symbolic value after the ritual is over.
556   6) *Learned behaviours*: We infer that these behaviours have a learned component because
557   they are not performed by all individuals in the population and are not produced during
558   early development. They could hypothetically appear in an individual repertoire via
559   innovation or social learning (probably via ontogenetic ritualization:[5]).
560   7) *Repurposing of behavioural elements found elsewhere in the repertoire:* Scholars of both
561   ritual and play [4][6][7] have noted that complex animal rituals, like human rituals, often
562   involve the transfer of behavioural elements and stimuli from one behavioural domain
563   to a new (social) context.

564 Importantly, we do **not** emphasize *rigidity of form or repetition* in our definition, although this
565 attribute comprises a core feature of many scholars' definitions of ritual (e.g.[8][9]), nor is
566 *function* a critical part of our definition. However, we did choose to focus on those definitional
567 aspects used by scholars who study the implications of ritual for social relationships (Table
568 ESM1). Although some degree of repetition and constancy of form is clearly involved in ritual,
569 both human and nonhuman, we argue that rituals may serve multiple functions, and that the
570 optimal degree of flexibility vs. rigidity in form may depend on the function of the ritual.
571 There was insufficient space to discuss definitional aspects needed for testing some alternative
572 hypotheses, e.g. that the capuchin rituals we describe function to detect and react to inferred
573 threats [9], or the idea that capuchin rituals contain symbolic content relevant to detecting or
574 enforcing social norms violations. However, the lack of precisely repeated, rhythmic,
575 compulsive actions is incompatible with the Hazards Precautions Hypothesis and the social
576 norms hypothesis. Furthermore, there is no obvious display of moral outrage or shame in
577 response to deviations from the typical form that a dyad's ritual has, nor is there currently any
578 solid evidence for social norms in capuchins.
579
580

Definitional feature of ritual	Intellectual tradition(s)*	Reference examples	Proposed ritual function**	Present in capuchins
Distinction between the sacred and the profane	ANTH, SOC	[3][4][10][8]	b, c, e	?
Shared group emotion	SOC	[2][3]	e	No?
Feedback between mood and joint focus; shift in emotional energy within a dyad	ETHO, SCO	[2][11]	c, d, e	Yes
Breaking ritual proprieties results in moral uneasiness	SOC	[10][4]	b	Probably not
Repurposing of behaviors evolved for other purposes	ETHO	[12][6]	c	Yes
Exaggeration and stereotypy (sort of like formalism)	ETHO, PSY, perhaps ANTH	[9][10][8][13]	a, b, c	Only slightly
Traditionalism, i.e. repetition of activities from an earlier period	ANTH	[8]	b, c	Yes
Disciplined, rigid repetition, often rhythmic	PSY	[9][8][13][6]	a, maybe b	Only slightly
Lack of rational motivation, no obvious immediate function	ANTH, ETH, PSY, SOC	[9][10]	a, b, c, d, e	Yes
Compulsiveness	PSY	[9]	a	No?
Framing of the act	ANTH	[8][14]	(various)	No
Symbolism	ANTH, SOC	[3][4][2][10][8][14]	b, c, e	Probably only during the ritual

Table ESM1. Elements commonly found in definitions of ritual across disciplines.

581

582

583   *ANTH=anthropology, SOC=sociology, ETH=ethology, PSY=psychology

584   ** a: detection of and reaction to inferred fitness threats,

585   b: transmission and maintenance of social norms,

586   c: communication about/definition of social roles,

587   d: testing of dyadic social bonds,

588   e: establishing society-wide solidarity

589

590

591   ESM 2. Transcription of video clips demonstrating rituals

592   **3. LBMP-Capuchin_Monkey_Rituals-Clip1.m4v**
593   The following example (and accompanying video) depict a ritual often performed by two
594   immigrant males (BL and QJ), in which they take turns passing a "toy" (in this case a piece of
595   bark, i.e. something that is not food) back and forth, each earnestly attempting to retrieve the
596   "sacred object" from the other's hand or mouth. Because they were born outside the study
597   area, we do not know their exact ages, but they appear to be the same age (within a year of
598   one another); BL joined Flakes in September 2004, group 5.5 months after QJ joined. They
599   started devising rituals together in May 2005, initially giving one another "dental exams" which
600   involved inserting their fingers in one another's mouths. In February 2006 they started using
601   one another's hair as an object to pass back and forth, and by March 2006 they were also using
602   "toys" such as the bark used in this example. They were mutually enthusiastic practitioners of
603   these rituals until BL emigrated in November 2009. At the time of this particular interaction, QJ
604   is the 2nd ranked male and BL the 3rd-ranked male in the group.
605   April 22, 2004, 9:10 am:
606   At the start of the video, BL has his finger in QJ's mouth (QJ on the right, BL on the left). BL uses
607   his mouth and hand to try to pry QJ's mouth open. QJ has a piece of bark in his mouth. [It isn't
608   obvious that this is bark until later in the clip.] QJ grabs BL's hand (the one in his mouth) and
609   removes BL's hand from QJ's mouth. QJ takes the piece of bark out of his mouth to show BL,
610   perhaps to encourage BL to play the game. QJ is still holding BL's hand. QJ puts the bark back in
611   QJ's mouth (or tries), but BL grabs QJ's hand and tries to open it to extract what is there. They
612   let go of one another's hands, and then BL grabs QJ's face, one hand braced against QJ forehead
613   and the other prying QJ's mouth open. BL uses his hand and mouth to pry open QJ's mouth,
614   using enough force to make QJ's body sway. QJ adjusts BL's hand in QJ's mouth. Now BL uses
615   both hands to pry QJ's mouth open. BL gets the bark (or part of it) out of QJ's mouth and puts it
616   in BL's mouth. Now each of them is using a hand to try to get bark from the other's mouth. At
617   9:12:23, BL finally removes his hands, and QJ uses both hands to open BL's mouth. BL pries QJ's
618   hands from BL's face. They hold hands, and BL tries to extract the bark from QJ's hand. QJ tries
619   to get things out of BL's hands. QJ succeeds in getting the bark from BL's hand and puts it back
620   in QJ's mouth. BL is still working hard to get something out of QJ's other hand. BL gets a piece of
621   QJ's bark and puts it in BL's mouth. QJ grabs BL's other hand and puts the bark in QJ's mouth.
622   QJ grabs something from BL's lips and brings it to QJ's mouth. BL lets some more bark protrude
623   from BL's mouth to show QJ, and QJ grabs that too, putting it in QJ's mouth. BL grabs QJ's head,
624   turning it to face BL, and tries to pull the same bark from QJ's mouth, using enough force to
625   twist QJ's body around a bit. BL's finger seems to be clamped in QJ's mouth. QJ eyes are closing.
626   BL uses both his mouth and hands to try to open QJ's mouth; QJ's eyes are still closed. QJ grabs
627   BL's hand and pulls it out of QJ's mouth. QJ grabs BL's face and tries to open BL's mouth. QJ
628   seems to be chewing something. QJ's finger is lodged in BL's mouth. QJ tries to pull something
629   from BL's mouth, using both hands. When they are trying to get bark out of the other's mouth,
630   their visual attention is focused on the mouth rather than the eyes of the partner, throughout
631   this interaction. QJ finally gets the bark out of BL's mouth, puts it in QJ's mouth, and chews it.
632   BL immediately tries to retrieve it from QJ's mouth. BL removes his hands and lies on his side,

633 presenting for grooming while facing QJ. QJ tries to open BL's mouth with both hands. BL holds
634 QJ's hands. BL inserts his hand in QJ's mouth, then turns his attention to QJ's hands, trying to
635 pry one open. QJ tries to open BL's hands. Their foreheads touch as they both focus on
636 watching one another's hand manipulations. QJ gets something out of BL's hands, pops it in his
637 (QJ's) mouth, and chews it. BL immediately tries to get it out of QJ's mouth. BL uses both hands
638 to try to open QJ's mouth, using much force. Finally, BL removes the bark and puts it in BL's
639 mouth. QJ scratches, then tries to open BL's mouth. QJ removes his hand and scratches again.
640 QJ sticks his finger in BL's mouth. QJ uses both hands to pry open BL's mouth. He fails, and BL
641 uses both hands to try to open QJ's mouth. BL gets something out of QJ's mouth and chews it
642 but continues to try to open QJ's mouth. BL scratches his own head and drops his hands. QJ
643 tries to pry open BL's hand. BL's attention strays, and he looks off in the distance. QJ jerks BL's
644 hand, as if to demand his attention. QJ lies down as if presenting for grooming but keeps his
645 grip on BL's hand. BL puts something in BL's mouth. QJ tries to remove the bark from BL's
646 mouth with one hand, but while still reclining. Then QJ uses both hands. QJ stretches, inviting
647 grooming. BL grooms QJ's chest. BL stops grooming and turns away from QJ. BL is still playing
648 with the bark. QJ grabs BL's tail and tugs it 3 times, but BL doesn't turn around. BL self-grooms
649 and turns back to face QJ. BL flops down, presenting for grooming to QJ. It is not clear who ends
650 the interaction sequence, because the video clip ends here, at 9:22.

651 **4. LBMP-Capuchin_Monkey_Rituals-Clip2.mov**

652 March 13, 2012:

653 In this clip we see Minstrel ('MI', the alpha female) and her maternal half-sister Mead ('ME',
654 who is two years younger), performing a ritual that is highly typical of their relationship (see
655 section 3 of the ESM for more details regarding their relationship). Minstrel, on the left, is
656 clutching Mead's hand and inserting it in her (Minstrel's) mouth. Mead reclines, passively
657 accepting this. Minstrel readjusts Mead's finger, inserting it deeper into her mouth on the other
658 side, and then switches back to the original position. This is just one of multiple clips from this
659 ritual, but it is fairly typical both of this bout and of the relationship more generally.

660

661 ## ESM 3. Between-dyad variation in ritual performance, case studies

662 As can be seen by visually inspecting the tab called "ritual_details" in the RawData.xlsx file,
663 there was considerable variation between dyads regarding the elements incorporated into their
664 rituals, and also variation in the degree of mutual enthusiasm/engagement. Limited space
665 precludes presentation of the data for all dyads, but here we present some illustrative cases
666 from individuals who contributed large sample sizes to the data set, focusing on the behaviour
667 of four individuals: two immigrant males (QJ and NP) and two females (sisters ME & MI).
668 NP, a highly peripheral and shy male, contributed 57 rituals to the data set (2 of them failed
669 attempts to engage others), and participated in rituals with 15 different monkeys, though he
670 focused primarily on three of the older juvenile males. Of his 57 rituals, 5 involved insertion of
671 fingers in or on the nose, 20 involved insertion of fingers in mouths, 3 were "dental exams", 3
672 involved eye-poking, 2 involved sucking a body part other than the finger, and the rest were
673 games in which an object (hair in 12 cases, a "toy" in 27 cases) were passed back and forth.
674 Comparison of the network diagrams for physical proximity and ritual performance (Section 6,

675 Fig. 2) highlights how extensive NP's ritual network was, despite his low rates of physical
676 association with his group-mates.
677 QJ, an immigrant male who became the alpha male in 2007, was a far more socially central
678 male than NP, and contributed 92 rituals to the data set. These were spread over 21 monkeys
679 (11 females, 10 males), all but two of whom (the eldest females of each matriline) were
680 younger than him. His most frequent partner by far was BL, an unrelated adult male who
681 performed 21 rituals with him (one of them displayed in the ESM video clip LBMP-
682 Capuchin_Monkey_Rituals-Clip1.mv4); all involved some sort of exploration of the partner's
683 mouth, and 9 involved a "toy" or hair game; in general, his rituals with BL were characterized by
684 a high degree of turn-taking and mutual engagement. He also performed 5 or more rituals each
685 with TU (an unrelated male), his son YJ, and his three daughters (BW, LD and IE). His
686 relationship with his daughter BW was noteworthy for the active role she played in
687 manipulating various parts of QJ's head. In only one of these was an object involved (in which
688 BW was trying to remove hair from QJ's mouth).
689 The dyad consisting of Minstrel (MI, alpha female) and her half-sister Mead (ME, 2 years
690 younger than Minstrel), contributed 72 rituals to the data set beginning in Feb 2004 when
691 Mead was 4 years old and ending in January 2015. There was remarkable similarity in form
692 across these events. Typically, Minstrel grabbed her sister's hand and inserted Mead's fingers
693 into Minstrel's nostrils and/or mouth. In all cases in which we were certain of the initiator, it
694 was Minstrel; Minstrel terminated the interaction in 57% of the 30 instances for which we felt
695 comfortable designating a terminator. Although Mead was an involved participant for the
696 grooming portion of the ritual, she was far less engaged in the portion that involved insertion of
697 her fingers in Minstrel's orifices. Mead either lay there passively until Minstrel was done with
698 her fingers, or, in some cases, actively resisted the interaction, struggling to adopt more
699 comfortable positions than those favoured by Minstrel. In only three cases did Mead attempt to
700 insert Minstrel's finger in Mead's mouth or nose. This pair was a sharp contrast to some of the
701 male-male dyads (such as QJ-BL, described in the ESM, section 2) that had more complex rituals
702 characterized by high emotional engagement on both sides, and active turn-taking in which
703 roles were reversed. This contrast is evident by comparing the two video clips called LBMP-
704 Capuchin_Monkey_Rituals-Clip1.m4v and LBMP-Capuchin_Monkey_Rituals-Clip2.mov in the
705 ESM.
706 Interestingly, although Mead seemed unenthusiastic about hand-sniffing and finger-sucking
707 with Minstrel and almost exclusively had the role of "finger-donor", she practiced these
708 behaviours with several younger members of her family, and took the role of the more active
709 participant (taking their fingers and inserting them into her mouth or nose, despite some
710 resistance from them). Mead had 15 other relationships with one more ritual. In only three of
711 these did she sometimes assume the role of the monkey whose finger was sucked or sniffed. In
712 at least 8 of these relationships, it was clear that Mead was directing the action, and taking the
713 hands of her partners to insert in her nose or mouth. Although it would be tempting, based on
714 the patterning of Mead's interactions alone, to say that dominance rank or age was the factor
715 determining who sniffed or sucked on whose body parts, this pattern did not hold true for the
716 group more generally. Intriguingly, HE, the male who was alpha male from 2004-2007 (and who
717 remained in the group after being deposed) participated in a ritual only once, as a passive

718 participant with his son, even though all of the other adult and adolescent males were
719 enthusiastic practitioners.

ESM 4. Analyses of predictors of which dyads perform rituals

721 In order to better understand what characteristics of dyads predict propensity to engage in
722 these rituals, we conducted several analyses aimed at examining the relationship between
723 ritual performance and (a) proportion of time spent in 1 body length (i.e. a measure of both
724 affiliation and of the amount of information the dyad has about the current status of its
725 relationship), (b) relationship quality (i.e. the likelihood that something nice, rather than
726 something aversive, will happen when the two come into proximity), and (c) coalition
727 formation. If rituals help to build or maintain social bonds, then all three of these variables are
728 expected to be correlated. If the rituals function as bond tests, then the predicted distribution is
729 somewhat different, with the highest rates of ritual performance **not** expected at one end of
730 the distribution for all three predictor variables.
731 Bond-tests are expected primarily when (a) partners do not have current information about
732 their relationship status (i.e. not in the pairs who spend the most time together), and (b) when
733 partners have a sufficiently trusting and long-term relationship that performing risky acts is not
734 very frightening, but not so secure that there is no point in testing the bond. The predictions
735 regarding the relationship between the bond-testing hypothesis and *rate* of ritual performance
736 are less clear, but more *successful* bond tests are expected to be associated with higher rates of
737 coalition formation, and most of the rituals in the sample were successful.
738 Our relationship quality index (RQI) varies from 0 to 1, with 1 representing entirely
739 affiliative/cooperative interactions and 0 representing entirely negative interactions (see main
740 text for further detail). The coalitions index is the number of 10-minute chunks of time in which
741 a dyad forms a coalition, divided by the total number of times monkey 1 and monkey 2 were
742 scanned in group scans, to adjust for probability of observing these individuals during ad lib
743 observations. Given the sometimes large number of group scans per individual, we divided the
744 total group scans by 1000, and so, our coalition index represents the number of observed
745 coalitions per 1000 observations. The reason for lumping behaviours within 10-minute time
746 intervals is that individuals likely adjust emotional energy in a more bout-like fashion. E.g. they
747 recall losing a fight to a particular monkey, but probably they don't feel much worse for having
748 been slapped 7 times, as opposed to 4 times, within the time period of a 4-minute fight.
749 Examination of Figure 1a reveals that, consistent with the bond-testing hypothesis and
750 inconsistent with the bonding hypothesis, most of the high values for rate of ritual performance
751 are in the lower regions of the proximity index, i.e. in those pairs that spend little time together
752 and hence may lack information about the current state of their relationship. In Fig. 1b, the
753 distribution of data points is fairly consistent with both hypotheses, but more so with the bond-
754 testing hypothesis. Note that most of the high values for ritual performance are between 0.7
755 and 0.9 on the RQI scale, i.e. a zone in which dyads have pretty amiable relationships, but there
756 are fewer high scores for ritual rate in the zone between 0.9 and 1.0 (highest quality
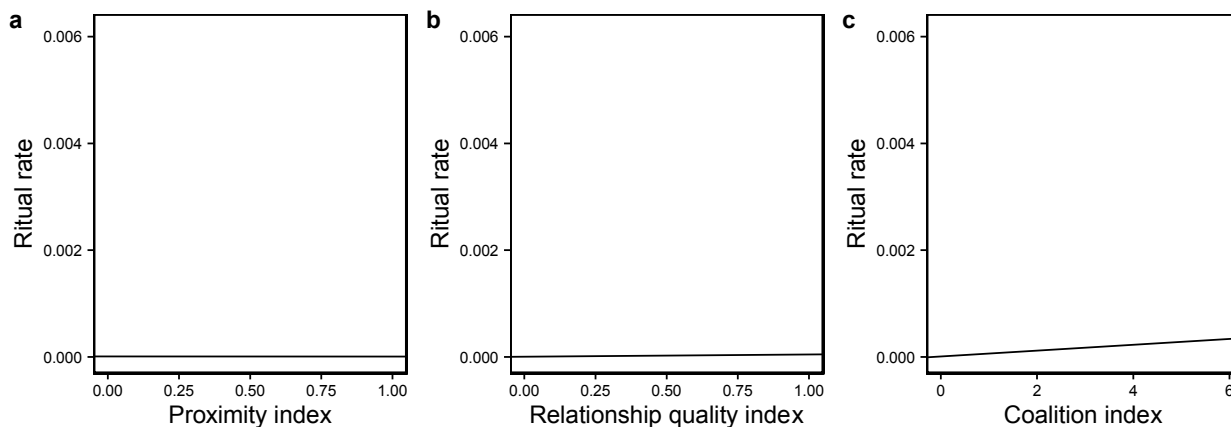757 relationships),despite the fact that ~ 30% of dyads have RQI > 0.9.

Figure 1. Graphical representations of the relationship between ritual performance rate and (a) physical proximity index, (b) relationship quality index, and (c) coalition index.

758   This data set was challenging to analyse for five reasons: (1) Most dyads had values of zero, for
759   ritual counts and counts of coalition formation; (2) Dyads are not independent of one another
760   because the same individual can be a member of multiple dyads; (3) There are missing values
761   when constructing a matrix in which each monkey's name is represented in the row and column
762   headings, because not all possible dyads were co-resident in the group; (4) The use of *ad*
763   *libitum* data for calculating ritual and coalition rates was a problem because we do not have
764   precise estimates of how much time each individual was observed, and not all individuals are
765   equally easy to observe; and (5) Behavioural sampling density was insufficiently high to permit
766   subdivision of the data set into chunks of time that we intuitively thought would be appropriate
767   for tracking temporal changes in relationship quality and ritual performance rate. We did not
768   find a single analytical approach that satisfactorily dealt with all of these issues. Therefore, we
769   analysed the data set in several different ways.

770   ## 5. ESM 4.1 Mixed effects negative binomial regression

771   Our first approach was to conduct *mixed effects negative binomial regression models* (in Stata
772   13.1), with crossed random effects for monkey 1 and monkey 2 (i.e. the two members of each
773   dyad). The results were similar to those described in the next paragraph, and also for the MLPE
774   models, i.e. no significant effect of proximity, with slight (but statistically significant) positive
775   effects of RQI and coalition rate on the rate of ritual performance. However, we were not
776   satisfied with how these models handle the effects of the monkey identities.

777   ## 6. ESM 4.2 Negative binomial regression model

778   Our second approach, adapted from the econometrics literature, was to analyse the data using
779   a series of 3 *negative binomial regression models* (in Stata 13.1) in which the independent
780   variable of interest was (a) the proximity index, (b) the relationship quality index (RQI), or (c)
781   coalition index. Each of these models also had a fixed effects intercept for each individual
782   monkey, i.e. a dummy variable was created that represented whether each individual monkey
783   was represented in that dyad. The outcome variable, in all cases, was the count of rituals
784   performed by this dyad, with the exposure being the sum total of group scans and point
785   samples collected on the two partners in the ritual. For the proximity and RQI models, we also
786   ran versions in which each row was a dyad-year (i.e. having repeated measures for each dyad),

787   because we were concerned that the quality of relationships might change over time and that
788   this variation (and its relationship to ritual performance rate) would be lost by lumping over
789   such large time periods. In these models that had repeated measures for dyads, we clustered
790   robust SE on dyads.
791   The model for RQI (lumping all years together) had 693 observations (some had to be dropped
792   due to zero social interactions). There was a significant positive relationship between RQI and
793   ritual rates (coeff.=2.18, SE=0.38, z=5.8, P<0.001, 95% CI 1.44-2.92). Results were similar when
794   each data point was a dyad-year (coeff.= 0.76, robust SE=0.17, z=4.36, P<0.001, 95%CI 0.42-
795   1.10).
796   The model in which proximity was used to predict ritual rate was more perplexing. When the
797   data set was analysed as a single unit of time, the coefficient was 7.37, SE=2.11, z=3.50,
798   P<0.001, 95% CI 3.24-11.50); this positive relationship only occurred in very low values of the
799   proximity index starting to level off or decline around the value of x=0.02. Visual inspection of
800   the graphical output indicated that even if there was a statistically significant relationship, it
801   was not biologically significant. This result was an outlier in that other modelling approaches
802   did not find a significant effect of proximity. In the model in which each data point was a dyad-
803   year, the strength of this statistical association was much weaker (coefficient=0.82, robust
804   SE=0.89, z=0.92, P=0.36, 95%CI -0.93-2.56).
805   The coalition index was positively associated with ritual rates (coeff=0.37, SE=0.16, z=2.28,
806   P=0.02, 95%CI 0.053-0.696). There were several extreme values, both for dyads that form many
807   rituals but no coalitions and vice versa. The code for running these models in Stata is included in
808   the ESM.

809   ## 7. ESM 4.3 Mantel test

810   However, none of these previous approaches preserved dyadic information. We used two
811   further tests that preserve this information: Mantel test and MLPE models. The Mantel test
812   compares two matrices. Our raw data are column entries of, e.g. ritual rates, for various dyads.
813   We turned these values into matrices by creating an empty square matrix with row and column
814   numbers that were equal to the number of unique identifiers in all dyads. We then filled in the
815   column information in the correct cell for each dyad.
816   The Mantel test provides a Z-statistic, which is equal to the sum of the products of the
817   corresponding elements of each matrix:

818
$$Z = \sum_{ij} X_{ij}Y_{ij} \text{ where } i \neq j .$$

819   However, this value is highly dependent on the scale of the data. Therefore, we also calculated
820   the Pearson correlation coefficient between the two matrices X and Y as

821
$$\rho_{X,Y} = \frac{cov(X,Y)}{\sigma_X \sigma_Y}$$

822   The Mantel test permutates one of the two matrices repeatedly. With each permutation, a
823   correlation coefficient between the two matrices is calculated. This provides a distribution of
824   correlation coefficients based on random permutations. The p value then represents the
825   chance that the actual observed correlation coefficient between the two original matrices is
826   based on chance. In ESM Table 2, we summarize the results of the Mantel test we ran. Again,
827   the results show that proximity has no effect on ritual count, whereas relationship quality has a

828 small but significant, and coalitions a larger and significant effect. However, because the Mantel
829 test does not accept missing data, we had to create matrices that contained structural zeros for
830 those dyads that were not co-resident. This is not ideal, which led us to the final set of models.
831 These models originated in landscape genetics, called Maximum Likelihood Population Effects
832 (MLPE) mixed effects models. Like a Mantel test, MLPE models assess the relationship between
833 two matrices. The mixed effects parameterization of MLPEs (specifying the covariance structure
834 of the matrices) accounts for non-independence among pairwise data in each matrix (see e.g.
835 [15][16]). Additionally, we could remove dyads that were non-co-resident, which avoided the
836 use of structural zeros. We used the MLPE_rga() function of the ResistanceGA package in R [17].
837 The actual model is essentially a linear mixed effects model. The results are shown in Table 1 in
838 the main text.

839

840   **ESM Table 2**. Mantel test results. Results shown are
841   for 5,000 permutations of the matrix pair in each row.

	Z	Coefficient	p
Ritual ~ Proximity	0.003	0.006	0.227
Ritual ~ RQI	0.077	0.022	< 0.001
Ritual ~ Coalition	0.048	0.127	< 0.01

842

843 ESM 5. How and when are individuals inducted into the network of ritual
844   participants?

845 To investigate this, we examined the ritual participation histories for the 17 monkeys (7 female,
846 10 male) who were immatures when first observed to participate in the toy and/or hair games,
847 i.e. the rituals exhibiting the most complexity and requiring the most active participation. They
848 were first seen to participate in some sort of ritual (game or non-game) at the mean age of 1.9
849 yrs of age (range 0.1-4.8 yrs), but were first seen to be active participants in games at a mean
850 age of 3.2 years (0.7-7.3 yrs), with one female never becoming an active participant. In all but
851 one case, the older monkey who served as a "tutor" (i.e. the other participant) was a male. For
852 the 7 females, the "tutor" (i.e. the older monkey who was the other participant) was her
853 (probable) father in 5 cases, an unrelated adult male in one case, and a female relative in the
854 other case. Males had a wider variety of "tutors", all of them male, including 2 fathers, 3
855 unrelated adult males, and in some cases other juvenile males very close to them in age.

856 ESM 6. Social network analyses, for visualization of the relationship between
857   time spent in association and ritual performance

858 Networks were constructed and analysed in R (Core Team, 2019), using the igraph package [18].
859 We created three networks, based on proximity, rituals, and games (Figure 2A-C respectively).
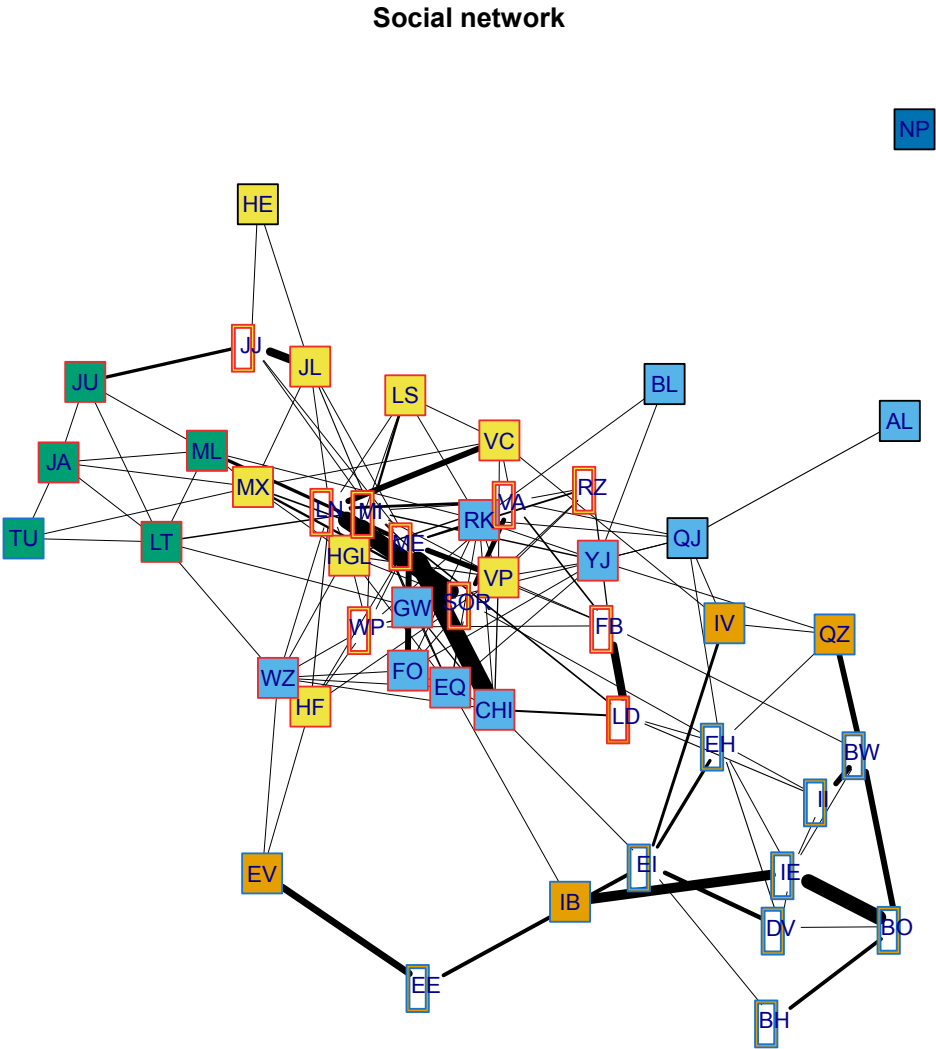860 For the social network, we calculated the proximity index, PI, as:

861
$$PI = \frac{s_{AB}}{s_A + s_B}$$

862   Where s_{AB} is the number of scans where monkey 1 and monkey 2 where in one or less body
863   length distance from each other and s_A and s_B is the number of group scans where each
864   monkey was spotted. We only consider scans where both individuals were co-resident in the
865   same group to avoid inflating the denominator with scans where the monkeys resided in
866   completely different groups.
867   In Figures 2A-C, circle nodes represent females and square nodes represent males that belong
868   to one of the two matrilines (blue borders for the subordinate matriline and red for the
869   dominant matriline) or have migrated into Flakes group (black border). In A, nodes are coloured
870   based on the results of the greedy community detection algorithm of the igraph package. This
871   algorithm is trying to find dense subgraphs by optimizing the networks modularity score. Edge
872   weights correspond to the proximity index of each dyad. In B and C, edge weights represent the
873   relative frequency with which monkeys engage in all rituals (B) and games (C). To make
874   comparison between graphs easier, node positions (based on the Fruchterman-Reingold layout
875   in Fig. 2A) were preserved in Fig. 2B and Fig. 2C.
876   Visual inspection of the proximity network (Fig. 2A) highlights the fact that matriline members
877   tend to cluster together, with immigrant males being less social (aside from the alpha male,
878   who was HE till the end of 2007, QJ through mid-2016, and finally MX). However, the diagrams
879   showing frequency of ritual participation show that some of the most isolated immigrant males
880   (e.g. NP) are active ritual participants, particularly with regard to the games. Fig. 3 also
881   highlights the lack of correspondence between social centrality and ritual participation.
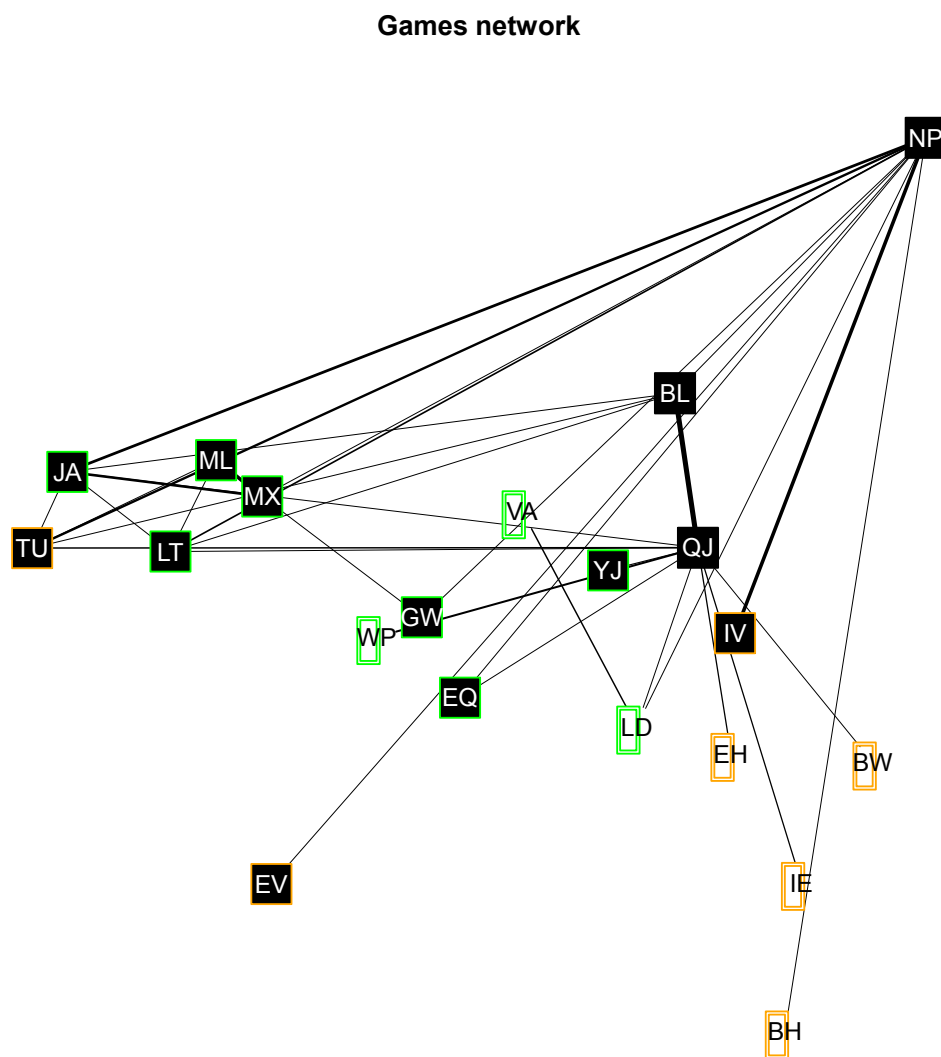
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Social network

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886   **Figure 2A.** Network based on proximity.

Rituals network

Figure 2B. Network based on all rituals

891

Games network

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893
894   **Figure 2C.** Network based just on games portion of the rituals data set
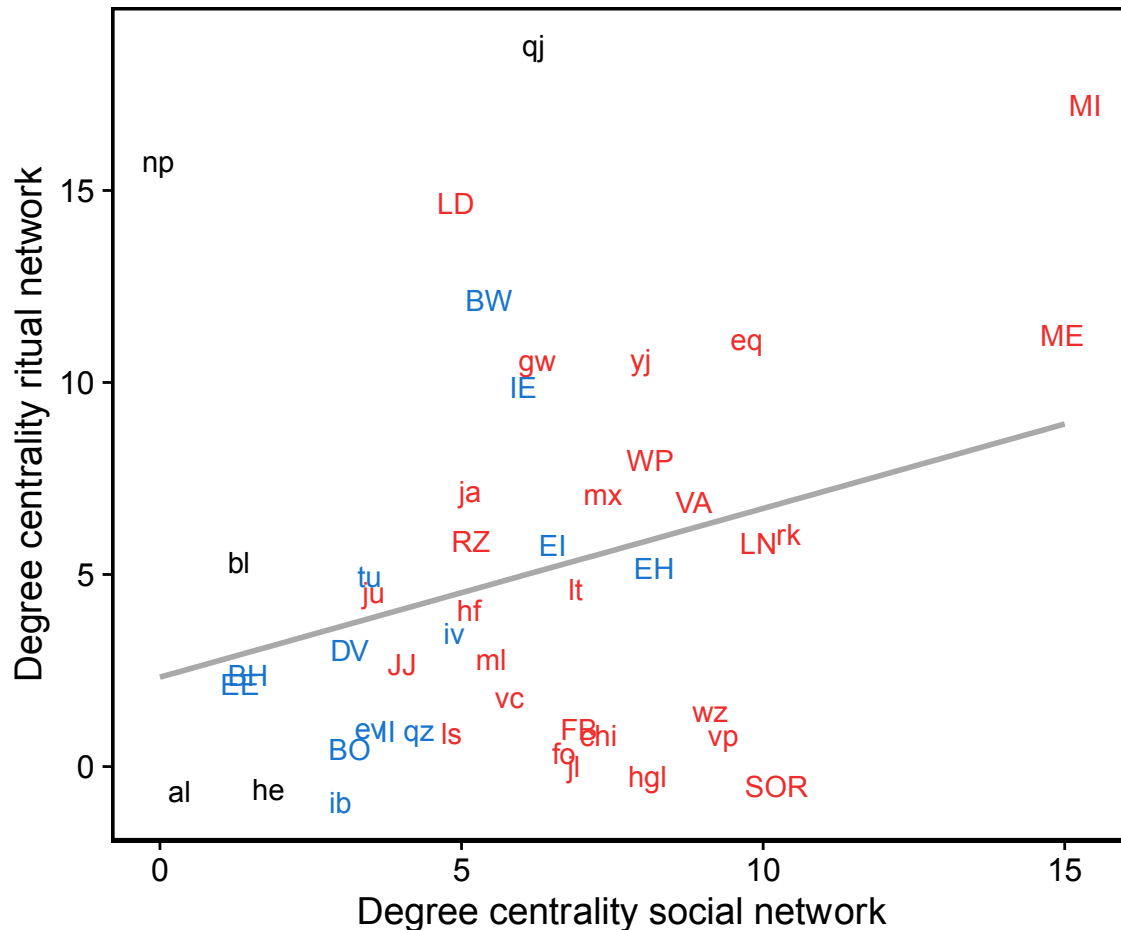895
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903 **Figure 3.** The number of individuals with whom a monkey performs rituals (y-axis) is
904 uncorrelated to the number of individuals they regularly interact with (degree centrality, x-
905 axis). There is a slight upwards trend, but it is not significant (regression line in grey, adjusted
906 R^2=0.06, p=0.06). Males are represented by lowercase letters and females by uppercase letters.
907 Members of the two matrilines are represented by blue (subordinate) and red (dominant), and
908 immigrants by black letters.
909
910

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