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

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Many white-faced capuchin monkey dyads in Lomas Barbudal, Costa Rica, practise 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: (i) they involve an unusual intensity of focus on the partner, (ii) the behaviours have no immediate utilitarian purpose, (iii) they sometimes involve ‘sacred objects’, (iv) the distribution of these behaviours suggests that they are invented and spread via social learning, and (v) many behaviours in these rituals are repurposed from other behavioural domains (e.g. extractive foraging). However, in contrast with 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 9260 h of observation, ritual performance rate was uncorrelated with amount of time dyads spent in proximity but (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.

This article is part of the theme issue ‘Ritual renaissance: new insights into the most human of behaviours’.

## 1. Introduction

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

We refer to the capuchin social interactions described in this paper as ‘rituals’, defined as ‘learned behavioural sequences with no obvious immediate utilitarian purpose, composed of behavioural elements repurposed from other parts of the behavioural repertoire, characterized by a high degree of attentional focus by one or both partners on the other’s body and/or a (“sacred”) object jointly handled by the interactants’. This composite definition includes functionally relevant features from those used by sociologists, anthropologists, psychologists and ethologists to test hypotheses regarding the social functions of ritual; for discussion of ritual definitions across disciplines and whether the capuchin rituals described here meet those additional criteria, see electronic

supplementary material, table S1. The following two traits are particularly relevant for our definition, owing to their probable connection to social function:

- (1) *Quality of attentional focus*. The behaviours we describe here are prolonged (dyadic) social activities 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 (see Rossano's definition [1]). This intense focus on a particular partner, to the exclusion of other group members, calls to mind Collins' theory of interaction rituals [2], in which degree of attentional focus and 'emotional energy' directed to a partner informs the recipient about its current relative value to the actor.
- (2) *Use of sacred objects*. The objects (and partner body parts) handled in some of these rituals have no utilitarian value, e.g. they are neither food nor tools. Whether or not they have any symbolic value, qualifying as 'sacred objects', is a question of definition, but according to [3], an object, body part or individual can acquire sacred status by means of the repeated ritual performance.

Researchers of non-human primates have developed several hypotheses regarding the relationship between social relationships and rates of greeting rituals. Some hypotheses state that ritual performance is necessary to *establish or maintain social bonds*, perhaps by defining social roles and negotiating the terms of a social relationship, and predict that ritual performance will be associated with higher frequencies of time spent together, affiliative behaviours or cooperation [4]. Others state that these rituals are a way of *testing* important relationships critical to enhancing fitness [4–8], which leads to the predictions that bond tests will be more frequent when (i) there is a dearth of information regarding the state of the relationship, (ii) there is good reason to believe that the relationship is undergoing change (e.g. during a rank reversal), and (iii) the bond is solid enough that a Zahavian bond test would not be extremely risky, yet not so secure that there is no need to test it at all.

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

- (1) Rituals serve to establish and *maintain* social bonds:
  - (a) Rituals will be more frequent in dyads that
    - (i) spend the most time in proximity,
    - (ii) have higher relationship quality (RQ), and
    - (iii) cooperate most often in coalitionary aggression.
- (2) Rituals serve as Zahavian tests of social bonds [5]:
  - (a) Behavioural elements will entail some risk and/or discomfort.
  - (b) Rituals will be more frequent when state of a relationship is unclear (i.e. there should not be a positive linear correlation between the rate of ritual performance and time spent together, but rather, higher rates at intermediate rates of time spent in association).
  - (c) Rituals are predicted to be most often performed in dyads with good enough relationships to feel comfortable performing the intimate ritual, but not in relationships so completely free of conflict that they require no testing (i.e. highest rates of ritual

performance at upper intermediate values of RQ rather than at the highest end of the distribution).

- (3) Participation in rituals promotes group-wide solidarity:
  - (a) Rituals are expected to be performed simultaneously by many monkeys at once, exhibiting a form that is consistent among group-mates.

## 2. Study species and methods

### (a) 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 Perry and collaborators (see [9] for more details on the natural history of this species, and [10,11] 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].

### (b) 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 libitum 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.

### (c) Dataset

The new data presented here are from 'Flakes' (FL) group, which fissioned from Abby's group (the original study group) in late 2003. Here, we analyse 9260 observation hours of data collected between 1 February 2004, when the group had become demographically stable, and 11 October 2018. The FL group was composed of two matriline, headed by matriarchs that are probably cousins, and contained five immigrant males, who arrived singly at different times during 2003–2004; two of these shared a natal group, and three were from outside the study area. These immigrant

males seemed to be 8–12 years old at the start of 2004. Over the course of the 15 years of observation, Flakes group included 53 individuals, ranging from 9 to 30 members at any given time (six monkeys were excluded from the analysis that died prior to six months of age).

The dataset consists of 446 social interaction ‘rituals’ and six failed attempts of monkeys to elicit joint interaction in a ritual. Thirty-seven (79%) of the 47 group members included in the analysis (17 of 20 females and 20 of 27 males), and 17% of the 762 co-resident dyads (40 female–female, 47 male–female and 46 male–male dyads) engaged in at least one ritual. Only 19 individuals (6 females, 13 males) composing 32 dyads (25 male–male and 7 male–female) participated in the most complex rituals (i.e. ‘games’). As more peripheral monkeys are more often missed in group scans, and because only a few individuals were the subjects of focal observations, total observation time varied among individuals. Observers spent much of each day collecting focal follows, so the probability of detecting rituals performed by focal subjects was higher than for non-focal animals. To correct for observation effort, we summed the number of group scans and point samples (collected at 2.5 min intervals during focal follows) for each member of the dyad on days when both members of the dyad were co-resident in the FL group.

#### (d) Measures

To test Hypotheses 1 and 2, we require measures for: physical proximity, RQ and coalition formation. Our measure of physical proximity is based on ‘group scans’ in which researchers wandered through the group, recording distance between the scanned monkey and other monkeys in proximity to it. We scored two individuals as being in physical proximity if they were less than 40 cm from one another (equivalent to an adult male body length, from nose to tailbase).

Our measure of RQ is based on observed social interactions during focal follows (when available) and ad libitum observations. The standard social interaction repertoire included 79 behaviours (some dyadic and some triadic) with clear emotional valences, i.e. participation would elicit at least in one of the participants positive or negative emotions, thereby affecting the ‘emotional energy’ (sensu Collins [2]) or the emotionally mediated ‘book-keeping’ of the rates and qualities of interactions [12] expected to influence the quality of future interactions of that dyad. Grooming, playing and forming a coalition are among the 42 behaviours expected to have a positive impact, whereas aggression and submission are among the 37 behaviours expected to have negative impact on RQ. We determined the relationship quality index (RQI) in the following way: we aggregated data into 10 min chunks. For each dyad and for each chunk, we assigned a score of 1 if there was at least one positive behaviour, and 0 if not. We repeated this for negative behaviours. The RQI for a given dyad-year consists of (a) the number of time-chunks with one or more positive impact behaviours, divided by the sum of (a) plus (b), the number of time-chunks with one or more negative impact behaviours. Thus,  $RQI = 0$  represents exclusively negative and  $RQI = 1$  exclusively positive ‘emotional energy’.

Our measure of coalition formation is based on ad libitum data, using only incidents of ‘overlords’, ‘cheek-to-cheek’ postures and ‘embraces’ (defined in [9]) against a common conspecific opponent. Although coalitions are fairly conspicuous behaviours; there is nonetheless some tendency to underreport

coalitions from peripheral group members. We accounted for this by creating an offset variable consisting of the number of group scans collected for individual A and individual B on days when they were co-resident. Because ad libitum observations were collected primarily as observers were wandering through the group collecting group scans, this should be a fairly accurate representation of the observability of these individuals.

#### (e) Statistical analysis

The data were analysed in a series of three maximum-likelihood population-effects (MLPE) models. Like a Mantel test, MLPE models [13] assess the relationship between two matrices. However, the mixed effects parametrization (specifying the covariance structure of the matrices) accounts for non-independence among pairwise data in each matrix. The actual model is essentially a linear mixed effects model. The independent variable was the proximity index, the RQI or coalition count, divided by the sum total of group scans of the two coalition partners (as an observability adjustment). In all cases, the outcome variable was the count of rituals performed by this dyad, with the exposure being the sum total of group scans and point samples collected for the two partners in the ritual. Sample sizes of dyads were slightly smaller for the RQI model as a few dyads did not interact. We dropped infants less than six months of age from the coalition model, since they were never old enough to form coalitions. We use the `MLPE_rga()` function of the `ResistanceGA` package in R [14] (see electronic supplementary material, S4 for additional information).

### 3. Results

#### (a) Description of the behavioural phenomenon

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

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

- (1) inserting a finger into the orifice of a social partner (e.g. mouth, eye, nostril or ear), or vice versa (inserting the partner’s digits into one’s own orifices),
- (2) prying open a mouth or hand to conduct a detailed inspection of its contents,
- (3) passing an object (e.g. bark, leaves, flower, stick, green fruit or hair plucked from the partner’s body) back and

- forth from one partner to another, taking turns at the role of holding the object in hand or mouth, and extracting it (also with hands or mouth), in a very gentle ‘tug-o-war’,
- (4) clasping of hands, often with fingers interlaced,
  - (5) cupping the hand over some part of the partner’s face,
  - (6) sucking on some appendage belonging to the partner (e.g. tail, finger, toe, ear, nose or sometimes a clump of hair),
  - (7) using the partner’s back or belly as a drum to create loud, rhythmic noises.

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

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

The most complex interaction sequences were the ‘games’ which involved extracting an object from the hand or mouth of the partner (see electronic supplementary material, S2 for a video clip and a transcription of the interaction sequence). A particularly striking feature was the focus on physical objects (toys) that were extracted from interaction partners’ bodies. Sometimes, partner 1 would bite tufts of hair out of partner 2, who would then pry open the mouth of partner 1 to recover the hair. Using motor patterns typical of extractive foraging, the hair would then be passed back and forth amicably between the two partners. Other times, non-edible portions of plants were used as the game objects. Note that these objects had no nutritional value, and the monkeys were surrounded by similar objects, which could be more readily obtained. But it seemed that the object acquired value by virtue of the fact that monkey 1 had it in its possession (i.e. it acquired ‘sacred object’ status by virtue of the fact that it was being used in this ritual). The two monkeys would focus their attention on this object for several minutes (usually 10–30 min).

These interactions are readily interpretable from Heesen *et al.*’s [18] framework, which views social play as joint action, i.e. interactional achievements whereby the participants create a sense of togetherness. Those authors describe three phases of these interactions, including formalized openings and closings, which capuchin rituals generally lack. Instead, our monkeys almost always began and ended their interactions by merely approaching and leaving their partners. However, capuchin ritual behaviour typically includes the characteristics of the middle section (main body) of Heesen *et al.*’s sequence, described as negotiation of continuation of the activity, changes in type of interaction, role reversals, suspension of activities, and re-engagement of partner’s attention to the prior activity. Our subjects often initiate

role reversals or changes of activity by explicitly moving their partner’s hands to the part of the body where they want them to be. There are frequent examples of re-engagement of the partner’s attention, both in these rituals and in coalition formation (outside the context of rituals). In the toy and hair ‘games’, one partner will attempt to re-engage the attention of a partner whose attention has wandered, by spitting out the object and explicitly showing the partner that they have it, before either inserting it in their own mouth or holding it in front of the partner’s mouth. This is usually successful in re-establishing mutual participation. In a coalitionary context, when there is an asymmetry in affect and participation in attacking an opponent, the angrier monkey will sometimes tug on the body parts of the ally or bounce ferociously while in body contact with the ally, presumably to rev up the partner’s enthusiasm for the joint attack; these tactics are generally successful in creating more symmetric emotional engagement. Interestingly, in contrast with human children, young captive chimpanzees fail to re-engage human adult partners in activities following interruptions [19]. Possibly, the finding that capuchins and humans, but not chimpanzees, exhibit partner re-engagement is evidence of convergent evolution between capuchins and humans regarding awareness of joint commitment towards common goals among partners. This would be consistent with evidence indicating convergent human–capuchin evolution regarding the importance of coalitionary aggression.

We observed considerable variation in (i) the ways various combinations of the basic behavioural elements described above were incorporated into a dyadic ritual, (ii) the posture and gaze direction of the participants, (iii) the extent to which dyads were temporally consistent in the form of their rituals, (iv) the extent to which there was symmetric emotional engagement, and (v) the degree of turn-taking for those rituals that had multiple roles. However, structural commonalities in the rituals have led us to hypothesize that they share a common function (as bond-testing signals [6]) and/or ontogenetic process. Capuchin monkeys normally behave at a rapid pace, both in their destructive foraging style and in their social interactions (e.g. rapid-fire grooming exchanges). Even while resting, their visual attention typically wanders, seeking new foraging opportunities or monitoring others’ social interactions. In striking contrast, their more creative social rituals proceed via slow, deliberate movements, and the participants’ faces bear almost trance-like expressions. Although participants rarely make eye-to-eye visual contact, one or both monkeys focuses visual attention on some body part of its partner, often for several minutes at a time. Sometimes, both participants focus their attention jointly on an object. The amount of time and the sustained focus devoted to these rituals suggests that the two ritual partners value one another highly. Another common feature of these interactions is that they typically involve some risk or discomfort, e.g. a finger in someone’s mouth where it is at risk of being injured by teeth, or a finger in another monkey’s eye socket, so that a quick movement could scratch the cornea. One monkey often twists another’s body into positions that look distinctly uncomfortable. The monkeys’ enthusiasm for these uncomfortable and/or risky interactions is consistent with Zahavi’s ‘testing of a bond’ theory [5]. Behaviours that are risky, uncomfortable or disgusting will seem aversive when received from a non-favoured partner, but pleasurable when received from a favoured partner; the emotional response

**Table 1.** Results of three separate MLPE models predicting ritual rate.

	model 1: proximity	model 2: RQI	model 3: coalitions
intercept	0.019	0.008	0.019
estimate	−0.0014	0.089	0.11
s.e.	0.035	0.040	0.04
<i>p</i>	0.967	0.027	0.004
95% CI	−0.07–0.07	0.01–0.17	0.04–0.19
$\sigma^2$	0.90	0.89	0.89
$\tau_{00}$ individual	0.05	0.06	0.05
ICC	0.05	0.06	0.05
<i>N</i> individuals, dyads	45 762	45 693	42 676

elicited by the bond-testing behaviour informs the tester about the state of the relationship. This theory (minus the emphasis on risk/discomfort as an adaptive design feature in the ritual) closely mirrors Collins' ideas about interaction rituals, in which partners assess one another's behavioural responses to their interactions with them, obtaining useful information about their relationship status and how the partner feels about them, relative to other partner options [2].

### (b) Who performs these rituals, what are the performing dyads' characteristics and what does this tell us about ultimate function?

We find that individual capuchins were first seen to participate in some sort of ritual (game or non-game) 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 mean age of 3.2 years (0.7–7.3 years), with one female never becoming an active participant (see electronic supplementary material, §S5 for additional information). The absence of these behaviours in younger individuals suggests that learning is involved in their production.

Table 1 presents the results of the three MLPE models used to predict ritual rates; graphical representations of these data are found in electronic supplementary material, §S4, figure S1, along with other details of the analysis. The ICC and  $\tau$  values indicate that individual idiosyncrasy did not explain much of the variance in ritual rates. The proportion of time a dyad spends in proximity is not a strong predictor of ritual rate; this is inconsistent with Hypothesis 1 (bond establishment and maintenance), but not necessarily inconsistent with the 'bond-testing' hypothesis (Hypothesis 2). Consistent with both hypotheses, those dyads with higher quality relationships were slightly more likely to perform rituals. However, consistent more with the bond-testing than the bond maintenance hypothesis, dyads were more likely to perform 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% of 212 dyads for which RQI  $\geq$  0.9); none of the 14 dyads with RQI < 0.3 performed a ritual. Finally, the model using coalition formation rate as a fixed effect demonstrates a positive (though modest) relationship between coalition formation rate and rate of ritual performance; this is consistent with both Hypotheses 1 and 2.

## 4. Discussion

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

### (a) Comparisons of form and proximate causes

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

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

### (b) Function, and the relationship between form and function

Whereas some theories regarding the evolution of ritual have focused more on the benefits relating to working memory [1], others (e.g.[2,5]) have focused more on how the quality of the

attention itself can serve as a signal of the partner's current emotional and motivational state, which is relevant to assessing commitment to their relationship. It has been hypothesized, both for many types of human rituals (e.g. religious rituals [20–23]) and for some types of non-human rituals (e.g. [4,6–8]), that ritual serves a social bonding function, enhancing feelings of solidarity, trust and desire to collaborate or at least testing commitment to a particular group or partner(s). Although testing these functional hypotheses is difficult in both humans and non-humans, the evidence from capuchins is generally consistent with the idea that capuchin dyadic rituals serve a bond-testing function. An important difference is that whereas most human rituals seem designed to promote group-wide solidarity, capuchin (and other non-human primate) rituals seem to operate at the dyadic level [20], which has important implications for the relationship between form and function of rituals. Although capuchins do seem to have a strong sense of group identity (as exhibited by their xenophobia and collaborative aggression towards members of neighbouring capuchin groups [11]), we have seen no examples of capuchin rituals in which all group members perform actions in strict unison, and capuchins very rarely cooperate as an entire group. Current theorizing about the function of ritual in humans also emphasizes the value of ritual for promoting adherence to group-specific social norms; possibly, capuchins lack such social norms.

The degree of rigidity in the form and ordering of the ritual actions is often considered a necessary diagnostic feature for rituals [22], and examination of this feature might provide insights into function. When a ritual's function is group-wide bonding/identification, promoting group-wide cooperation, we should expect group-wide uniformity in the performance of a ritual. Our data make us sceptical that this is the function of capuchin rituals. In the capuchin dataset, there was considerable inter-individual and between-dyad variation in the behavioural elements included in the ritual repertoire, and there was between-dyad variation in the level of mutual engagement and role reversals as well; electronic supplementary material, §S3 describes some of this variation, discussing case studies of the ritual networks for four individuals. Capuchin rituals are more likely to be designed by natural and cultural selection to test and/or strengthen dyadic bonds, enabling individual monkeys and dyads to understand where they stand with regard to commitment and cooperation compared with other individuals and dyads within their social group. If this is correct, then we should expect to see high within-dyad uniformity, but less between-dyad uniformity than is seen in human rituals that are performed in groups. Indeed, following the logic of [6], between-dyad variation in the form of a ritual may be a design feature. The time required to devise a unique dyadic ritual would be non-transferable to other dyads, creating an opportunity cost that serves as an honest signal of commitment to that particular dyadic partner. Reminders of unique dyad-specific games played exclusively with a particular partner might create links between the past, present and future of that dyadic relationship (a phenomenon akin to 'traditionalism' [22]), in which the dyad-specific ritual behaviour may help create a mental representation of the social relationship. If this functional hypothesis is correct, then we would expect the following pattern of variation in capuchins: (i) increasing homogeneity within each dyadic ritual, as the

partners come to an agreement of what roles and behavioural sequences characterize their unique dyadic ritual, (ii) greater within-dyad homogeneity in form than between-dyadic homogeneity in form, even for dyads including one of the same individuals, (iii) absence of within-group homogeneity in form, aside from the trivial similarities that come from the fact that independent inventions of rituals are constrained by the types of building blocks existing in the 'zone of latent solutions' [24] for the species, and the obvious advantages of including behavioural elements that have Zahavian bond-testing qualities (i.e. are risky or uncomfortable for dyads with poor quality relationships) [5]. Unfortunately, our dataset currently includes insufficient numbers of rituals for most dyads to test these hypotheses.

### (c) Ontogenetic and phylogenetic aspects

In both human religious rituals and non-human rituals, elements of feeding, drinking and washing behaviours are often introduced into new contexts, i.e. taken from their original functional context and repurposed for communicative means. In the case of capuchin rituals, most of the behaviours come from the behavioural domains of (i) grooming, (ii) extractive foraging (prying open or probing into holes and crevices with fingers, substituting a social partner's body parts for the plant parts upon which these actions are performed in a foraging context) or (iii) food sharing/tolerated theft (in which an individual exhibits close-range inspection of another's hands or mouth and gently attempts to remove a piece of the food from the monkey in possession of the food; in the ritual case, a non-food item is substituted for food). When these behavioural elements are applied in the context of ritual, the presumed original functions of these actions (e.g. hygiene, in the case of grooming; nutritional gain, in the case of extractive foraging and tolerated food theft) are replaced by a new function, presumably related to the establishment, maintenance and/or testing of social bonds. It is not entirely clear on what time scale (ontogenetic or phylogenetic) this repurposing occurs in capuchins. Because not all individuals express the same rituals, and these rituals are generally developed and expressed later in life, it is likely that most individuals independently invent these rituals by repurposing behavioural elements, and subsequently socially transmit them to partners via ontogenetic ritualization, i.e. that the borrowing occurs within the lifetime of an individual. Given the similarities in form across so many individuals and dyads, it seems likely that capuchins as a species (or genus) have evolved a proclivity to prefer to borrow these particular kinds of behaviours (i.e. elements from the grooming, extractive foraging and food transfer repertoires) rather than other behaviour types, owing in part to the fact that they are descended from a long evolutionary line of animals that relies on extractive foraging and social learning about food that occurs in a scrounging context; this would be more of a phylogenetic argument.

### (d) Comparisons with human playground rituals

Besides these characteristics that are commonly aspects of definitions of ritual, the behaviours we describe here have additional characteristics that are part of Burghardt's [25] definition of *play*: (i) They appear to be *spontaneous, pleasurable, rewarding and voluntary* for at least one, and almost always both, members of the dyad performing them. (ii) They are

performed *in the absence of any obvious acute or chronic stress*, when the participants seem relatively relaxed. (iii) *Elements are often repeated* within a single ritual performance or in subsequent performances by the same dyad, but not typically in rigid rhythmic or stereotypic form. The lack of immediate purpose is also a feature of definitions of both play and ritual [25]. In some ways, capuchin rituals resemble human children's playground rituals. Merker [26] points out that whereas the motor details of children's rituals are mainly arbitrary with respect to function, there is social pressure to do things in a particular way, and the propensity to care about these details, i.e. to conform, has a bond-testing function. That is, the obligatory stereotypy of the rituals makes it obvious when mistakes (deviations) occur, and to avoid making such mistakes, it is necessary to invest much time in practise. Learning the details of a dyadic or group greeting ritual, for instance, requires that the individual pay close attention over long periods of time and practise; this is a costly way of indicating investment in the relationship(s). Capuchin rituals are simpler than children's hand-clapping games or secret handshakes, but they too seem to require extensive practise at mastering arbitrary details. The patterning of behavioural variation suggests that participants recall their usual roles with particular partners and repeat them, as if reaffirming their roles in this particular relationship.

## 5. Conclusion

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 a 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.

**Ethics.** The data were collected in accordance with the Animal Behavior Society Guidelines for the Use of Animals in Research, and the protocol was approved by UCLA's Animal Research Committee, under approval numbers ARC # 2005-084 and 2016-022. Research permits in Costa Rica were obtained biannually from MINAE-SINAC-ACAT.

**Data accessibility.** The data upon which these findings are based, along with the R code and Stata code for conducting the statistical analyses, are provided in the electronic supplementary material.

**Authors' contributions.** S.P. designed the study, collected and coded the data and wrote most of the manuscript. Both authors contributed to the quantitative analysis. M.S. wrote the R code, created the figures and assisted in the drafting of the manuscript.

**Competing interests.** We declare we have no competing interests.

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