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Social Tolerance in a Despotic Primate: Co-Feeding Between Consortship Partners in Rhesus Macaques

Constance Dubuc,[1,2,3]* Kelly D. Hughes,[4,5] Julie Cascio,[1] and Laurie R. Santos[6]

[1]*Département d'Anthropologie, Université de Montréal, C.P. 6128, succursale Centre-Ville, Montréal, Québec, Canada H3C 3J7*
[2]*Junior Research Group of "Primate Sexual Selection," Reproductive Biology Unit, German Primate Center, Goettingen, Germany*
[3]*Junior Research Group of "Primate Kin Selection," Department of Primatology, Max-Planck Institute for Evolutionary Anthropology, Germany*
[4]*Department of Anthropology, Yale University, New Haven, CT 06510*
[5]*Department of Brain and Cognitive Sciences, University of Rochester, Meliora Hall, Rochester, NY 14627*
[6]*Department of Psychology, Yale University, New Haven, CT 06510*

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ABSTRACT Food sharing among nonkin—one of the most fascinating cooperative behaviors in humans—is not widespread in nonhuman primates. Over the past few years, a large body of work has investigated the contexts in which primates cooperate and share food with unrelated individuals. This work has successfully demonstrated that species-specific differences in temperament constrain the extent to which food sharing emerges in experimental situations, with despotic species being less likely to share food than tolerant ones. However, little experimental work has examined the contexts that promote food sharing and cooperation within a species. Here, we examine whether one salient reproductive context—the consortship dyad—can allow the necessary social tolerance for co-feeding to emerge in an extremely despotic species, the rhesus macaque (*Macaca mulatta*). We gave naturally formed male–female rhesus macaque pairs access to a monopolizable food site in the free-ranging population at Cayo Santiago, Puerto Rico. Using this method, we were able to show that tolerated co-feeding between unrelated adults can take place in this despotic species. Specifically, our results show that consort pairs co-fed at the experimental food site more than nonconsort control pairs, leading females to obtain more food in this context. These results suggest that co-feeding is possible even in the most despotic of primate species, but perhaps only in contexts that specifically promote the necessary social tolerance. Researchers might profit from exploring whether other kinds of within-species contexts could also generate cooperative behaviors. Am J Phys Anthropol 148:73–80, 2012.

A hallmark of our species' cooperative nature—one that has been at the center of debates surrounding the evolution of cooperation and prosociality—is our propensity to share food with unrelated individuals (Gurven, 2004; Stevens and Gilby, 2004). Compared to other forms of cooperation, food sharing brings obvious benefits to the receiver and costs to the donor that can be estimated quantitatively. As food sharing is a trait shared across humans and animal species, analysis of food sharing can result in directly comparative data, to better understand the evolution of cooperation. In primates, food sharing has been defined as the voluntary transfer of defensible food-items by food-motivated individuals (Feistner and McGrew, 1989) or as the joint use of monopolizable food items, regardless of the method of transfer (Stevens and Gilby, 2004). However, although food sharing is common in humans, such sharing is relatively rare between unrelated individuals in other primates (Feistner and McGrew, 1989; Stevens and Gilby, 2004). As such, investigating the factors that allow food sharing to occur in primate species will help us reconstruct the evolution of this prevalent behavior in humans.

One way to better understand why food sharing has become so prevalent in our own species is to investigate the contexts in which different primate species share food: factors that affect whether primates passively share food (e.g., Jaeggi et al., 2010), cooperate to obtain food (e.g., Melis et al., 2006), and donate food to conspecifics (e.g., Silk et al., 2005). To date, research using experimental scenarios has demonstrated that species-specific differences in temperament constrain the extent to which primates succeed in cooperative tasks (see Hare et al., 2007 for discussion). For instance, several studies have observed that individuals from tolerant species (e.g., relaxed social relationships, high reconciliation tendencies) tend to behave prosocially on food donation tasks, selectively acting in ways that allow unrelated conspecifics to gain access to food (e.g., tufted capuchins, *Cebus apella*: de Waal et al., 2008; Lakshminarayanan

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*Correspondence to: Constance Dubuc, Department of Anthropology, New York University, Rufus D. Smith Hall, 25 Waverly Place, New York, NY 10003, USA. E-mail: constance.dubuc@nyu.edu

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and Santos, 2008; common marmoset, *Callithrix jacchus*: Burkart et al., 2007; cottontop tamarins, *Saguinus oedipus*: Cronin et al., 2010; but see Cronin et al., 2009, Stevens, 2010). In contrast, individuals from despotic species (e.g., strict dominance hierarchy, low reconciliation tendencies), like chimpanzees (*Pan troglodytes*) and rhesus macaques (*Macaca mulatta*), fail to do so, even when such donations pose no cost to the actor (Silk et al., 2005; Hare et al., 2007; Vonk et al., 2008; Chang et al., 2011; but see below). Comparative studies between closely related species also support the view that species-specific differences in temperament influence the ability to cooperate on a food donation task. Hare et al. (2007) observed that bonobos (*Pan paniscus*), a tolerant species, succeed more on a cooperative food pulling task than chimpanzees. Similarly, tolerant Tonkean macaques (*M. tonkeana*) successfully cooperated to retrieve hard-to-obtain food, but despotic rhesus macaques could not (Petit et al., 1992). Collectively, these results suggest that species-level differences in social tolerance greatly limit the extent to which primates cooperate, share, and act prosocially in experimental contexts.

At first glance, this interspecific account provided by experimental cooperation tasks appears to be in conflict with the evidence coming from more naturalistic field studies. Indeed, many reports of cooperation and food sharing stemmed from studies conducted on despotic chimpanzees: males of this species occasionally hunt in cooperative groups (e.g., Goodall, 1986; Boesch and Boesch, 1989; Mitani and Watts, 2001) and share meat with hunting partners, political allies, grooming partners, and potential mates (Mitani and Watts, 2001; Hockings et al., 2007; Gomes and Boesch, 2009; but see Gilby et al., 2010). Moreover, chimpanzees and other despotic species, such as the rhesus macaque, are known to allo-groom and provide coalitionary support (reviewed in Schino, 2007). In sum, even though it has been difficult to generate cooperation and food sharing experimentally in despotic species, evidence from the wild suggests that there are contexts under which such behaviors occur.

One way to reconcile the conflicting data about primate cooperation would be to explore which specific contexts promote social tolerance within a given species. Specifically, are there contexts in which a typically despotic species is prone to cooperation and sharing with unrelated conspecifics? Little work to date has addressed this issue, particularly in carefully controlled experimental settings. In a pioneering study, Melis et al. (2006) observed that although despotic chimpanzees rarely succeed on a cooperative food-pulling task, dyads that showed spontaneous interindividual tolerance outside the experiment were highly successful in cooperating on the task. These results suggest that contexts that naturally promote interindividual tolerance may allow individuals from despotic species to behave in a cooperative way. Furthermore, these results raise the question of how such social tolerance within dyads develops in the first place. In other words, are there certain reproductively relevant contexts that promote social tolerance within particular dyads in ways that increase cooperative behaviors, even in despotic species?

We decided to explore this issue by studying cooperative food sharing in the rhesus macaque. The rhesus macaque is considered to be one of the most despotic of all primate species (Maestripieri, 2007): in both males and females, conflicts are unidirectional, high-intensity aggressive interactions are common, and reconciliations are not frequent (see Thierry, 2006). Despite many decades of observation on this species, instances of food sharing by rhesus macaques are never reported in review articles (e.g., Feistner and McGrew, 1989; Stevens and Gilby, 2004). Indeed, some reviewers report that rhesus females often fail to share food with their dependent offspring (e.g., Feistner and McGrew, 1989; Maestripieri, 2007). Rhesus monkeys, however, do show some evidence of co-feeding at food patches; in these situations more than one female may eat simultaneously at a feeding site. However, given that proximity in rank is highly correlated to degree of relatedness between females (i.e., rank inherited from the mother; Sade, 1972) and that dominance hierarchy determines the order of access to food (Brennan and Anderson, 1988; Deutsh and Lee, 1991), one cannot rule out the possibility that copresence at feeding sites is linked to inclusive fitness and/or is forced on females of similar rank by the social context (e.g., de Waal, 1986; Kapsalis and Berman, 1996b). Accordingly, experimental work conducted in rhesus macaques' sister species, Japanese macaques (*M. fuscata*), another despotic species, showed that only closely related females (e.g., mother–daughter, sisters, or grandmother–granddaughter dyads) could tolerantly co-feed at a food site containing prized resource; such co-feeding behaviors were virtually absent between nonkin (Bélisle and Chapais, 2001). To date, it still remains unknown whether co-feeding can even occur between nonkin in despotic macaque species.

One specific within-species context that could promote exactly the kind of social tolerance needed for successful food sharing between unrelated adults is the consortship dyad. Sexual consortships are short-term associations between a male and a sexually receptive female characterized by maintenance of close spatial proximity and an exchange of grooming and mating that can last up to several days (Carpenter, 1942; Lindburg, 1983; Manson, 1997). Consortships have long been thought to increase tolerance and cooperation between a male and his female partner (rhesus macaques: Carpenter, 1942; Altmann, 1962; Bernstein, 1963; Small, 1990; yellow baboons, *Papio cynocephalus*: Rasmussen, 1985; long-tailed macaques, *M. fascicularis*: van Noordwijk, 1985), but to date, this prediction has never been directly tested. We provide just such a direct test, hypothesizing that the level of close association required for a successful consortship might promote exactly the kind of tolerance needed for successful cooperation and food sharing. Accordingly, anecdotal reports have described cases in which rhesus macaques co-fed at monopolizable patches during consortship periods (Carpenter, 1942; Bernstein, 1963). Moreover, while Petit et al. (1992) did not observe any successful cases of cooperation between rhesus macaques trying to retrieve food from underneath a large rock in their experimental study, the authors did note that the only two attempts of cooperation observed involved a consortship dyad. On the basis of these anecdotes, we hypothesized that using male–female consort pairs may be an ideal way to study whether co-feeding can take place between unrelated adults. Moreover, using naturally occurring consort pairs can allow us to control for other confounding factors that might affect co-feeding, such as dominance rank, proximity, and relatedness. Because males of this species typically leave their natal group before reaching sexual maturity (Pusey and Packer, 1987), and females of this species avoid mating

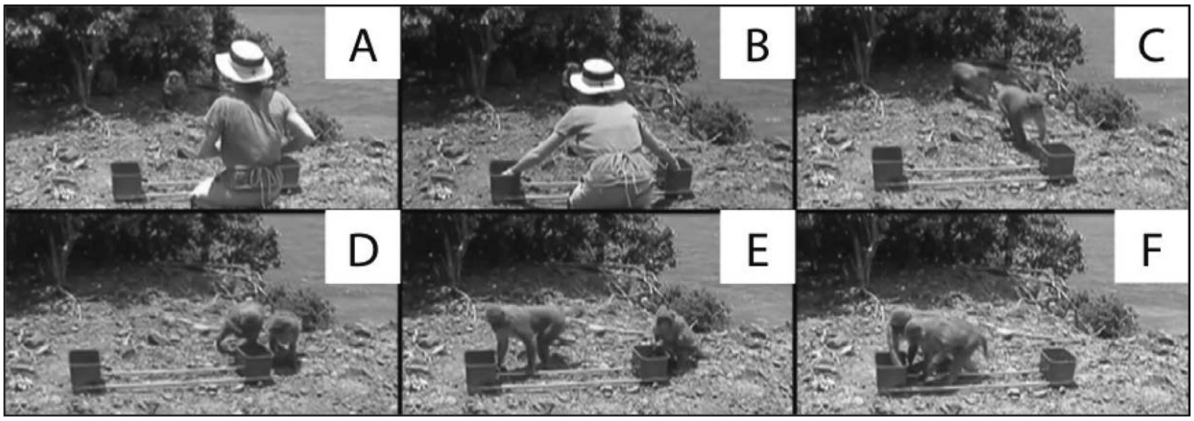

Fig. 1. Depiction of the experimental setup and procedure. An experimenter visibly dropped the pieces of coconut and walked away (**A** and **B**), allowing subjects to approach the apparatus (**C**–**F**). This represents an example of co-feeding between partners, with copresence at the same box and female joining the male at his box.

with closely related males (Paul, 2002; e.g., Manson and Perry, 1993), male–female consort dyads are unlikely to be related individuals.

Here, we investigated whether passive co-feeding can take place between unrelated adults in rhesus macaques. More specifically, we tested whether male rhesus macaques would be more inclined to tolerate their female consortship partner at feeding site. To explore this issue, we presented pairs from a free-ranging rhesus macaque population with the opportunity to passively share food. We approached naturally formed male–female pairs, in consort or not (control pairs), and presented them with a high-quality, monopolizable, and depletable food site (two buckets each containing two pieces of coconut).

METHOD

Field site and subjects

The study was conducted on one of the six social troops (Group V) of the free-ranging population of rhesus macaques living on Cayo Santiago (associated with the Caribbean Primate Research Center, CPRC), a 16-ha island off the coast of Puerto Rico (see Rawlins and Kessler, 1986 for details on population). Monkeys at this site are provisioned with chow and they forage for other foods naturally available on the island (e.g., coconuts, leaves, soil). We tested rhesus monkeys from Social Group V between June and July 2009, i.e., midway through the mating season (mid-March to September). At the time of the study, Group V contained 58 sexually mature individuals (>3-years old), 34 females and 24 males. All subjects were recognized individually. The group was composed of four matrilines, two large ones and two small ones. The highest-ranking matriline comprised 15 females; the second ranking one, three females; the third ranking one, 14 females; and the lowest-ranking one, two females. Maternal relatedness was provided by the CPRC and dominance relationships were established based on the outcome of dyadic agonistic interactions (see Brent et al., 2011).

Classification of tested male–female pairs

Sexually receptive females (or receptive females) were identified in early morning and monitored in the following hours to determine whether they were in consort. A female was considered sexually receptive if she was seen engaged in mating activity (mating series and ejaculatory mounts) or with a sperm plug in her vagina. Mere presence of a receptive female in the tested pair was not sufficient for the pair to be considered as forming a consortship dyad. The term “dyad” refers the nature of the relationship between two individuals (e.g., consortship, mother-daughter, friends), while “pair” refers to two specific individuals that were tested. Male-receptive female pairs were considered in consortships if they were seen in close proximity or synchronizing their movements during two consecutive hours in the morning, before the experiments. We used 2 h because sexual associations last on average 88 min in rhesus macaques (Berard et al., 1994), and as such, any association between a male and an estrus female lasting more than this length could be considered a consortship with confidence. We also included as in consortship two pairs who were seen mating at the time of the experiment ($N = 2$) because we could not reject the possibility that they were a newly formed consortship; in one case, the pair was identified as a consortship the following morning. Because of the special consideration of these two pairs, we conducted a statistical analysis both with and without these data points. As analyses yielded similar results, only those including these data points are presented. Consortships lasted on average a total of 6.32 ± 5.16 days, whereas the average consortship estimated length in the morning before the trial was 4.25 ± 1.59 h.

Apparatus

The apparatus consisted of two red polystyrene boxes ($15 \times 20 \times 15$ cm^3) placed 80 cm apart and fixed to two polystyrene tubes (1.2 m) (Fig. 1). The distance between the boxes was small enough for a male to be able to monopolize the apparatus, but large enough to prevent him from searching for food in both boxes simultaneously, and thus allowing the female partner to use the remaining box. During the trial, two small pieces of coconut ($\sim$2.5 cm^3) were dropped in each box (two per box; Fig. 1B). We used a limited amount of food to ensure that the experimental context could generate competition among the partners while preventing interference by other group members. Coconut is a highly prized food, but its rarity on the island and the difficulty for rhesus to access it generates competition, even for small pieces. Each box was filled with 100 fresh leaves systematically collected from the same tree species on the island. The pieces of food were mixed among the leaves to increase searching time and trial duration (see details on procedure below).

Procedure

Experiments took place one to two times per week, in early afternoon (~1–2 PM), several hours after the macaques were fed chow (~7–8 AM), so that the animals were unlikely to be satiated at the time of the trial. Consortship pairs that had been identified earlier that morning were sought out, and nonconsortship pairs were identified opportunistically as they were encountered. All pairs sitting in proximity (i.e., $\leq$2 m if in proximity to the group; $\leq$5 m if isolated from the group) and outside the visual range of other monkeys were systematically tested. As such, all tested pairs were formed naturally. The subjects did not need to be interacting at the time of the trial and were classified as consortship or control pairs based on behaviors outside the experiments.

When a pair was found, an experimenter placed the apparatus in front of the pair (2–3 m distant and equidistant from both individuals), visibly dropped two pieces of food per box, mixed them among the leaves, and then walked away (~5 m) (Fig. 1A,B). Tests were aborted if a subject reached the apparatus while the experimenter was still presenting the apparatus, or if other individuals appeared. All experimental sessions were videotaped.

Forty-three pairs were tested, 22 consortships and 21 nonconsortship controls pairs, involving 28 different male–female pairs (consortships: $N = 16$, control pairs: $N = 16$) and including four tested in both contexts. Some pairs were selected but did not complete testing [subject approached before the presentation's completion ($N = 5$), interference from other monkeys ($N = 17$), or arrival of the group ($N = 3$)]. Note that all subjects showed interest toward the apparatus and no case of trial abortion involved a lack of interest or of participation of the subjects. Each pair was tested 3.0 ± 0.8 times (mean ± SD; consortships: 2.6 ± 0.6; control pairs: 2.5 ± 0.6). Ten different males were tested, including seven tested in both contexts (consortships: $N = 8$ males; control pairs: $N = 9$ males), and 20 different females, including five tested in both contexts (consortships: $N = 12$ females; control pairs: $N = 13$ females). Males were tested in 4.3 ± 3.06 trials (consortships: 2.8 ± 1.8 trials; control pairs: 2.3 ± 1.9 trials) and females, in 2.2 ± 2.0 trials (consortships: 1.8 ± 1.4 trials; control pairs: 1.6 ± 1.0 trials). The pairs formed by the seven males tested in both contexts (average per male ± SD: 5.0 ± 3.1) accounted for 35 trials, including 16 consortship (average per male: 2.4 ± 1.5) and 17 control nonconsortship pairs (2.4 ± 1.8). Males were tested on average with 3.1 ± 1.7 females (consortships: 1.9 ± 1.2; controls: 2.0 ± 1.2), for 15 different females tested.

Four pairs were tested in both contexts, for a total of 11 trials (average per pair: 2.8 ± 0.9), including five consortships (1.3 ± 0.5) and six control nonconsort pairs (1.5 ± 0.6). These pairs were formed by three males tested in 3.7 ± 1.5 trials (consortships: 1.7 ± 0.6; control pairs: 2.0 ± 1.0), and four females tested in 2.8 ± 1.0 trials (consortships: 1.3 ± 0.5; control pairs: 1.5 ± 0.6). One male was tested with two females in five trials (consortships: two trials; control: three trials). None of the six control trials include cases of receptive females tested outside a consortship.

No mother–son or brother–sister dyads were tested, but one aunt–nephew dyad was tested in a control nonconsort pair, a level of relatedness considered to be beyond the kin nepotism threshold for despotic macaque species (Kapsalis and Berman, 1996a; Bélisle and Chapais, 2001; Chapais et al., 2001). Females of all four matrilines were represented in our sample: 10 females of the highest-ranking matriline were tested in 15 trials (consortships: $N = 8$ trials; control pairs: $N = 7$ trials), two females of the second-ranking, in five trials (consortships: $N = 1$ trial; control pairs: $N = 4$ trials), seven females of the third-ranking, in 19 trials (consortships: $N = 11$ trials; control pairs: $N = 8$ trials) and one female of the lowest-ranking, in four trials (consortships: $N = 2$ trials; control pairs: $N = 2$ trials).

Coding

We coded for 1) copresence of the partners at the apparatus and at the same box, 2) the number of pieces of food obtained by each individual, and 3) the emission of agonistic behaviors (threats and submissions). A subject was considered as being at the apparatus if it was at arm-length distance from a box and could see its content. Copresence was considered to take place if the two individuals were "peacefully" present at the apparatus at the same time for at least one second (i.e., without immediate retreat, aggression, or submission).

One experimenter coded the sessions during and after the experiments, with the aid of digital videos. A second experimenter blind to the pair type coded the digital videos as well. Agreement across coders was high (presence at the apparatus/box at the same time: 95.2%, kappa coefficient = 0.912, $P < 0.001$; number of pieces food obtained by both partners: 100%, kappa coefficient = 1.000, $P = 0.0$; presence of submissions: 85.3%, kappa coefficient = 0.742, $P < 0.001$; presence of aggressions: 90.5%, kappa coefficient = 0.529, $P = 0.001$). Initial coding from the first experimenter was systematically used in the analysis.

Statistical analysis

We performed Wilcoxon signed-rank to test our hypothesis that females were more likely to tolerantly cofeed with the tested male in consortship dyads than in control nonconsort pairs. Specifically, we compare the proportions of tests in which females reached the apparatus/box at the same time as the male, obtained food, and emitted submissive behaviors differed between consortship dyads and consort pairs for the seven males who were tested in both contexts. Statistical analyses were undertaken in SPSS 15.0. All analyses were two tailed, and significance levels were set at $P < 0.05$.

RESULTS

Access to the apparatus

Males approached to within arm-length's reach of the apparatus in all 43 trials, while females only went to the apparatus in 23 trials (53.5%). Sessions lasted on average 45.3 s (median: 23.5, range: 4–237 s); males stayed an average of 32.2 s (median: 16.5, range: 2–194 s) at the apparatus and females that approached the

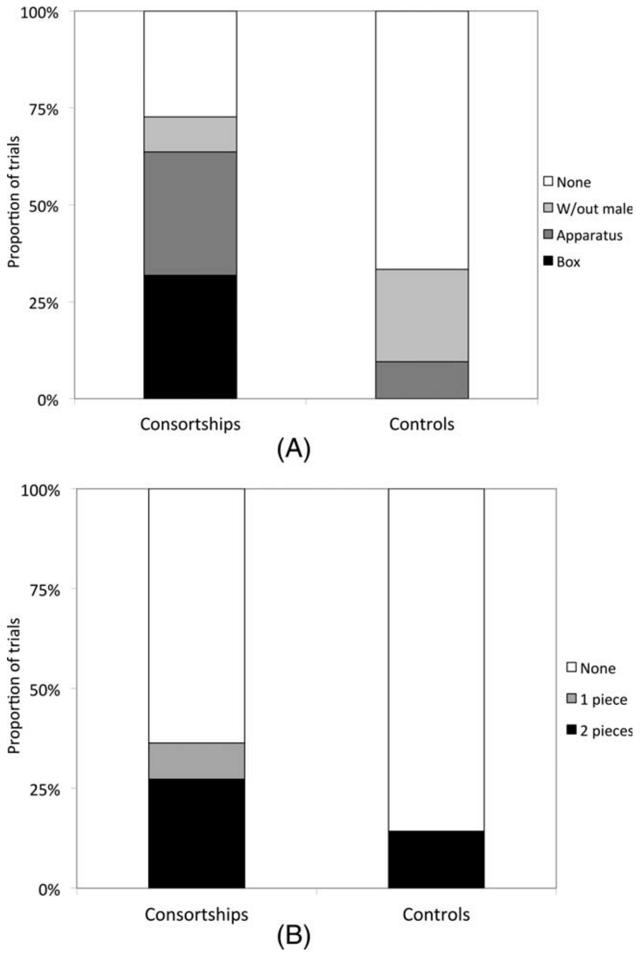

Fig. 2. Comparison of the occurrence of co-feeding between consort pairs and nonconsort control pairs. (**A**) Proportion of the 43 tests in which copresence at the apparatus occurred. "None": only the male went to the apparatus; "without male": the female went to the apparatus, but only when the male was absent; "apparatus": the male and female were at the apparatus simultaneously, but always at different boxes; "box": the male and female went to the same box simultaneously. (**B**) Number of pieces of fruit obtained by the female.

apparatus, an average of 26.7 s (median: 11.5 s, range: 1–137 s).

Females went to the apparatus more frequently in the consortship than in the control nonconsort context ($Z = -2.207$, $N = 7$, $P = 0.027$; Figs. 2a and 3): consorting females went to the apparatus in 16 out of 22 trials (72.7%), while other females went in seven out of 21 (33.3%).

Copresence of the partners

Copresence at the apparatus occurred in 16 out of 43 trials (37.2%) (11 different pairs; eight males, seven females) and copresence at the box, in seven (16.3%) (six pairs; six males, four females). When copresence occurred, partners were simultaneously at the apparatus and at the same box for an average of 11.8 s (median: 5.0 s, range: 1–69 s) and 4.4 s (median: 3.0 s; range: 1–8 s), respectively.

Copresence at the apparatus and at the box occurred more frequently in consortships than in control nonconsort pairs (apparatus: $Z = -2.410$, $N = 7$, $P = 0.016$; box: $Z = -2.032$, $N = 7$, $P = 0.042$; Figs. 2a and 3). Consorting females went to the apparatus at the same time as the male in 14 out of 22 trials (63.6%; 10 pairs; eight males, six females), and at the same box, in seven trials (31.8%; six pairs; six males, four females). In contrast, females in control pairs went to the apparatus at the same time as the male in two out of 21 trials (9.5%; two pairs; two males, two females), with no instances of copresence at the same box (0%). As such, male–female pairs were within arm-length's distance of the same box only in the consortship dyads. When females approached the apparatus, consortship partners were at the apparatus at the same time for 12.9 s (median: 5 s; range: 1–69 s), while nonconsort pairs, for 3.5 s (median: 3.5 s; range: 2–5 s).

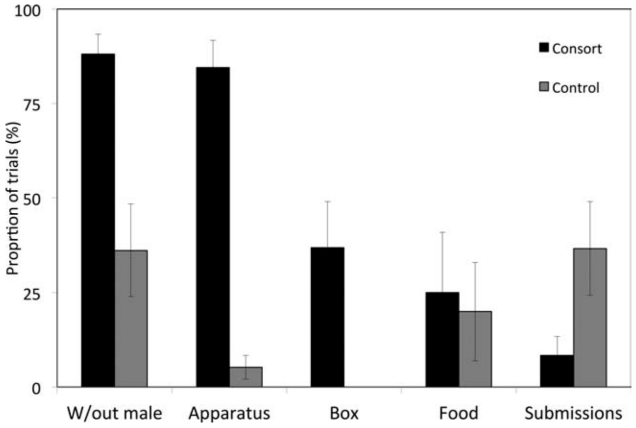

Fig. 3. Comparison of the proportion of the 35 tests in which co-feeding occurred between consort pairs and nonconsort control pairs for the seven males who have been tested in both contexts. "Without male": the female went to the apparatus, but only when the male was absent; "apparatus": the male and female were at the apparatus simultaneously, but always at different boxes; "box": the male and female went to the same box simultaneously; "food": the female obtained at least one piece of food, "submission": the female submitted to the male during the trial.

If only the 11 trials involving the four pairs which were tested in both contexts are considered, similar results are obtained. Consorting females went to the apparatus at the same time as the male in four of five trials (80.0%; three pairs; three males, three females), including two cases at the same box (40.0%; two pairs; two males, two females), while in contrast, females in control pairs went to the apparatus at the same time as the male in one out of six trials (16.7%; one pair), with no instances of copresence at the same box (0%). In other words, in two out of four pairs, the female only went to the apparatus in the consort context (three trials; two males, two females), including two instances at the same box (two pairs; two males, two females). In the other pairs, both formed by the same male, the female did not go to the apparatus in either context in one case (two trials), and went to the apparatus in two out of three trials in the other, one in both contexts (three trials; one consort, two controls).

Females reached the apparatus after the male in 11 out of 16 cases in which copresence at the apparatus occurred (68.8%). All the five remaining cases involved females in consort: the female arrived first at the apparatus and remained once the male joined. As for copresence at the same box, females joined the males at their box in six of seven trials (85.7%).

Food obtained by the female

Females obtained food in only 11 out of the 43 trials (25.7%). Females never obtained more than two pieces of fruit (Fig. 2b). Relative to control nonconsort females, females in consort obtained food more often ($Z = -2.263$, $N = 7$, $P = 0.039$; Fig. 3): consorting females obtained food in eight out of 22 trials (36.4%; six pairs; six males, three females), and nonconsort females, in three out of 21 (14.3%; three pairs; three males, three females). Among the four pairs who were tested in both contexts, the female obtained food in two trials involving the same pair, both in the consort context and both with copresence at the apparatus, including one at the same box.

Consortship and control nonconsort females seem to have used different tactics to obtain food. All cases in which consorting females obtained food involved copresence of the partners at the apparatus ($N = 4$) or at the box ($N = 4$). In contrast, only one case in which a nonconsort female obtained food involved copresence at the apparatus. In the two other cases, the female used the early arrival tactic: she reached the apparatus, took food, and left the apparatus before the males' initial arrival.

Agonistic behaviors

Agonistic behaviors were rarely observed at the apparatus and were of relatively low intensity. Females acted submissively to the males in 10 of the 23 trials when they went to the apparatus (43.5%), which involved only displacement and avoidance. Consorting females were submissive less often than females in control pairs; consorting females submitted in four out of 16 trials (25%), while control nonconsort females submitted in six out of seven (85.7%), although the difference is not significant ($Z = -1.490$, $N = 7$, $P = 0.136$; Fig. 3). Males only threatened females three times, with one instance toward a consort female partner.

DISCUSSION

By testing naturally formed male–female consortship pairs, we found that rhesus macaques are capable of tolerated co-feeding at a monopolizable feeding site. These observations corroborate previous reports demonstrating the importance of interindividual tolerance in the development of cooperative behaviors (Melis et al., 2006) and show that such tolerance does not only apply to chimpanzee cooperation. This work, however, goes beyond these previous findings to suggest that such within-species tolerance can actually be generated across a variety of specific individuals in a reproductively relevant context. As predicted, most instances of co-feeding involved consortship dyads; females in consort were more likely to reach the experimental feeding site, to be in close proximity with the male at the apparatus and to obtain food than control females. In contrast, nonconsort females went to the apparatus less frequently and almost never at the same time as the males. The most common way nonconsort females obtained food was by rushing in and out of the feeding patch to obtain food before the male arrived (e.g., Dubuc and Chapais, 2007). These findings highlight that the social tolerance needed for cooperation can occur between unrelated adults even in a highly despotic primate species, at least within reproductively relevant dyads. The fact that co-feeding also occurred between nonconsort pairs in few instances hints that other contexts or factors might generate social tolerance in despotic species as well, for example, male–female friendship (see Chapais, 1986; Hill, 1987) or interindividual differences.

The idea that consortship promotes social tolerance in rhesus macaques is supported by anecdotal observations of co-feeding between consortship partners in some previous studies (Carpenter, 1942; Bernstein, 1963) and by an observation reported in an experimental study investigating rhesus' ability to cooperate at a food task (Petit et al., 1992). In the experimental study, Petit and coworkers observed only two instances of cooperation attempts across 296 trials, both of which involving the members of a consortship dyad (Petit et al., 1992). In fact, there are hints that sexual associations might promote the social tolerance needed for food sharing across a number of primate species. For instance, food sharing between consortship partners has recently been reported in orangutans (*Pongo pongo*), a solitary species (van Noordwijk and van Schaik, 2009). Similarly, primate researchers have long observed food sharing within the context of pair-bonded partners, which can be seen as an extension of consortship (e.g., siamangs, *Symphalangus syndactylus*: Chivers, 1974; owl monkeys, *Aotus azarai*: Wolovich et al., 2007). Sexual associations may also promote the necessary social tolerance for food sharing and cooperation in other animal groups as well. For example, St-Pierre et al. (2009) demonstrated that in zebra finches (*Taeniopygia guttata*), only pair-bonded pairs were able to cooperate in a task involving food. Collectively, these results support a long proposed view that consortship is a context that commonly promotes social tolerance and cooperation (Carpenter, 1942; Bernstein, 1963; Rasmussen, 1985; van Noordwijk, 1985; Small, 1990).

One potential confound in our study, though, is the possibility that females were more willing to take risks to obtain food when they were sexually receptive. Under this account, the increased co-feeding we observed in consortship dyads would have resulted from increased female temerity rather than from increased male tolerance. There are reasons to question this possibility. Indeed, previous evidence hints that while in consortship, receptive female cercopithecines enjoy similar or even higher access than they do outside the receptive period (Japanese macaques: Matsubara and Sprague, 2004; yellow baboons, *P. cynocephalus*: Rasmussen, 1985), suggesting that females in consortship dyads were not hungrier than females tested in the control situation. Moreover, human females, for example, are less willing to take risks around the timing of ovulation than at other times of the ovarian cycle (Chavanne and Gallup, 1998; Bröder and Hohmann, 2003). One way to see whether female receptivity was a factor is to take a more careful look at our results. Within the 21 control nonconsort pairs we tested, we had four cases involving a receptive female. Of those, co-feeding occurred in only one case; in all other cases, the female never approached the apparatus during the trial. Moreover, while co-feeding did not occur in all consortship pairs, we observed that some nonreceptive females went to the apparatus, again suggesting that factors other than receptivity were needed for co-feeding in male–female pairs to occur. In the future, work on the proximate factors that allow for increased co-feeding in reproductive contexts may illuminate this question.

Another potential alternative explanation of our data is that consortship partners showed high levels of social tolerance because they also had a special relationship (i.e., friendship) outside the sexual context. Under this view, it is friendship not consortship alone that could increase tolerance needed for co-feeding. There are a few reasons to doubt that this explanation fully explains our results. First, it is unlikely that our consortship dyads mainly involved closely bonded male–female pairs because previous research has shown that rhesus macaque male–female "friendships" result in less rather than more sexual activity between the partners (Chapais, 1986; Hill, 1990; Manson, 1995). Second, if the consort dyads we tested were involved in close male–female relationships outside the consort period, then these male–female dyads would also have been likely tested for the control condition since, by definition, friends spend more time in close proximity than nonfriends. In contrast, we observed very few instances of pairs being tested in both the consortship context and the nonconsortship context (only four pairs of 28), suggesting that the specific consort dyads we approached did not spend much time in close proximity outside this period.

However, even though we believe that pairs differences in friendship could not fully account for the pattern of results we observed, it remains highly possible that consortship is not the only within-species context that gives rise to social tolerance and food sharing. Indeed, it is likely that factors common in other types of relationships (e.g., increased grooming and proximity) can affect the emergence of tolerance as well. Increases in cooperative tendencies like those that we observed in consortship dyads could also arise in the contexts of other types of relationships, such as in friendships (e.g., Kapsalis and Berman, 1996b).

If, as our study suggests, some specific contexts generate tolerance in despotic species, this could reconcile the apparent discrepancies of previous experimental findings. Indeed, researchers have suggested that human-like cooperative tendencies arose from the requirements of being a cooperative-breeding primate species (Burkart et al., 2007). Recent work has challenged this view, observing that a species' status as a cooperative breeder does not always predict prosocial tendencies (Cronin et al., 2009; Stevens, 2010), and conversely, that noncooperative-breeding species can act prosocially (de Waal et al., 2008; Hare and Kwetuenda, 2010; Lakshminarayanan and Santos, 2008). Considering factors that can generate tolerance within-species might provide a way to reconcile this cooperative-breeding account with the available data on primate prosocial behavior. For instance, perhaps social units formed in cooperative-breeding species have a higher proportion of reproductively relevant dyads that promote social tolerance than those of other species. This would explain why accounts of cooperation and prosociality are more frequent but yet not systematic in cooperatively breeding species, while rare but not absent in other species. More work is needed to test this idea and identify which specific dyads and within-group contexts have the potential to generate social tolerance.

In sum, our results show that specific contexts can generate the necessary tolerance for food sharing to emerge in a despotic primate species. As such, species' differences in temperament might limit but not prevent the expression of cooperation, food sharing, and prosociality in primates. More work is required to identify whether other contexts lead to such tolerance and to identify the proximate mechanisms that generate it. Future studies investigating the social and cognitive abilities required for individuals to succeed at cooperative tasks in animals should take into account the degree of familiarity between the tested subjects and the nature of their relationship in the analysis and experimental design.

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