

Group Service in Macaques (*Macaca fuscata*), Capuchins (*Cebus apella*) and Marmosets (*Callithrix jacchus*): A Comparative Approach to Identifying Proactive Prosocial Motivations

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Proactive, that is, spontaneous, prosociality reflects a psychological interest in the welfare of others and has been reported in callitrichid monkeys, capuchin monkeys (*Cebus apella*), and humans, but not in chimpanzees. One explanation for the co-occurrence of proactive prosociality in these species is that it is linked to shared infant care (cooperative breeding); alternatively, it might merely reflect unusually high social tolerance or be mediated by advanced cognitive abilities. To date, distinguishing between these alternative explanations is difficult, partly because available evidence is restricted to only a handful of species and partly because methodological differences thwart comparisons across studies. Here, we present an experimental paradigm called group service, which allows estimation of both social tolerance and proactive prosociality in group settings. Its simplicity makes it intuitively plausible to subjects and allows testing a broad variety of species, including in zoos. We applied the test to independently breeding Japanese macaques (*Macaca fuscata*), cooperatively breeding common marmosets (*Callithrix jacchus*), and capuchin monkeys with an intermediate breeding system. Social tolerance was slightly higher in marmosets than capuchins and much higher in both compared to macaques, but only marmosets provided a service to other group members. Furthermore, we validated the group service paradigm in the common marmosets by comparing their performance to earlier data. Although our results are consistent with the cooperative breeding hypothesis, a comprehensive evaluation requires adding data from additional groups and species, which should be facilitated by the group service approach.

Keywords: group service, proactive prosociality, cooperative breeding, dictator games

Prosocial behaviors are activities that provide a benefit to others (Vonk et al., 2008). They can be caused by different motivations. A proactive, that is, spontaneous, motivation (i.e., proactive prosociality) reflects a genuine concern for the welfare of others, or the “other-regarding preferences” of economists (Fehr & Fischbacher, 2003). It plays a pervasive role in human prosocial behavior and is a fundamental element of human social organization (Henrich et al., 2005) and cognition (Burkart, Hrdy, & van Schaik, 2009; Hrdy, 2009; Tomasello, Carpenter, Call, Behne, & Moll, 2005).

Prosocial actions can also be motivated differently, for example, to get rid of a persistent beggar, or occur in response to signals of

need. In these cases, they are elicited or reactive rather than proactive (Jaeggi, Burkart, & van Schaik, 2010). The absence of proactive prosocial behavior in chimpanzees (see below), who rather show reactive prosociality (e.g., Melis et al., 2010; Warneken, Hare, Melis, Hanus, & Tomasello, 2007), led to the suggestion that the first might be uniquely human (e.g., Silk et al., 2005). However, recent studies documenting proactive prosociality in primate species less closely related to humans raise the question which convergent evolutionary forces were responsible for that distribution.

The presence of proactive prosociality can be assessed in non-human primates using provisioning games inspired by the dictator games economists play with humans (Camerer, 2003). In provisioning games, dyads of individuals are separated from their group and placed in adjacent or opposite experimental cages. Individuals in the donor role are given the opportunity to deliver food to the recipient in the other cage or not to do so, for example, by pulling one of two possible trays of an apparatus within reach. The behavioral choices in the presence of a potential recipient are then compared with those in the latter’s absence. If a prosocial effect emerges, additional controls are used to exclude other than proactive motivations.

Provisioning games have so far been played with chimpanzees, macaques, capuchin monkeys, and callitrichids. In chimpanzees no evidence for proactive prosociality has been reported (Jensen, Hare, Call, & Tomasello, 2006; Silk et al., 2005; Vonk et al., 2008), not even in mother-infant dyads (Yamamoto & Tanaka, in

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press). In macaques, the evidence is mixed (Colman, Liebold, & Boren, 1969; Mason & Hollis, 1962; Massen, van den Berg, Spruijt, Sterck, & Brosnan, 2010; Schaub, 1996). In capuchin monkeys, evidence for proactive prosociality was reported in constellations where subordinates played the donor role and dominants the recipient role (Lakshminarayanan & Santos, 2008; Takimoto, Kuroshima, & Fujita, 2010) or, in a token-exchange version of the game, in individuals preselected for their experience with token exchanges as well as their propensity to pay careful attention to others' behaviors (de Waal, Leimgruber, & Greenberg, 2008). In callitrichids, some studies reported positive evidence for cotton-top tamarins (Cronin, Schroeder, & Snowdon, 2010; Hauser, Chen, Chen, & Chuang, 2003) and common marmosets (Burkart, Fehr, Efferson, & van Schaik, 2007), but others did not (Cronin, Schroeder, Rothwell, Silk, & Snowdon, 2009; Stevens, 2010). Apart from the studies on chimpanzees, therefore, studies of the same species using this paradigm did not always yield consistent results.

Different hypotheses have been proposed to explain the emergence of proactive prosociality. First, the lack of a proactive motivation to benefit others in chimpanzees supported the idea that proactive prosociality might require levels of sociocognitive functioning only present in humans (e.g., Silk et al., 2005). Second, proactive prosociality might simply be an expression of high social tolerance (Yamamoto, Humle, & Tanaka, 2009). Social tolerance, that is, a low probability of attack when two animals are in close proximity in a particular context, is likely to be a necessary precondition for the emergence of proactive prosociality, and indeed for prosociality in general, since the latter usually requires individuals to be in close proximity. Nonetheless, it is less clear whether it is also a sufficient precondition. The third hypothesis posits that proactive prosociality may be linked to cooperative breeding (Burkart et al., 2007; Burkart et al., 2009; Burkart & van Schaik, 2010; Silk et al., 2005). Caregivers in independent breeders, that is, mothers, are in continuous direct contact with immatures, and reactive prosociality is thus sufficient, but the numerous caretakers in cooperative breeders are not, and often not even in constant proximity. Thus, for a smooth regulation of care such as carrying and provisioning, caregivers might have to proactively seek opportunities to offer help instead of simply responding to requests, signals of need, or even be coerced by dominant breeders (Burkart & van Schaik, 2010; Jaeggi et al., 2010). Consistent with this idea, food sharing under naturalistic conditions includes active provisioning in cooperatively breeding primates (proactive prosociality), but not in independently breeding ones (Brown, Almond, & van Bergen, 2004).

Evaluation of these hypotheses requires reliable and comparable measures of (a) the amount of allomaternal care, (b) social tolerance, and (c) the tendency to engage in proactive prosociality for a broad range of species. Although cooperative breeding is often considered a binary variable, in primates it is best seen as a continuum (Hrdy, 2009), and the degree and quality of allomaternal care in various species has recently been quantified for a large number of primate and other mammal species (Isler & van Schaik, 2011; Rowe, in press). Data on social tolerance and prosociality, however, is only available for very few species and often not directly comparable due to methodological differences. Social tolerance may well be a multilayered concept; here, we focus on the feeding context, which is arguably the most relevant (Hare,

Melis, Woods, Hastings, & Wrangham, 2007; Melis, Hare, & Tomasello, 2006).

Prosociality data from provisioning games often lacks consistency and is sometimes even contradictory, either with regard to other tests or with regard to the natural history of the species. For example, positive results in provisioning games have been reported in highly despotic long-tailed macaques (Massen et al., 2010) who under naturalistic conditions do not even passively share food (Brown et al., 2004). Jaeggi et al. (2010) provide a detailed review of this inconsistency of outcomes, both within and between species, and sometimes even when the same subjects are involved. This inconsistency suggests that provisioning games are highly sensitive to even marginal differences in methods. The most likely confounding factors are confusion by the use of counterintuitive apparatuses and the nature of the pay-off distribution offered to them (Rueth & Burkart, 2011), and anxiety caused by the separation from the rest of the group, particularly in highly interdependent species. Thus, understanding the evolutionary origin of proactive prosociality requires developing ecologically valid experimental paradigms that are more robust and will allow valid cross-species comparisons.

The aim of this article is to establish an experimental paradigm, the group service experiment, to assess social tolerance and proactive prosociality in a large variety of species that vary with regard to the extent of allomaternal care. The group service experiment is designed to be applied in both laboratory and zoo environments and has the advantages that (a) animals can be tested in their home enclosures, (b) it is not necessary to separate individuals from the group, and (c) it uses an intuitive experimental setup, easily learned by the subjects.

In the group service design, an apparatus is attached to the home cage, allowing an individual to provide food to the rest of the group, but not to itself (see Figure 1). Four phases with strictly predefined procedures that require the subjects to reach a criterion before they can pass on to the next phase of the experiment ensure the comparability of the data. In case that food is systematically provisioned in these initial sessions, an additional fifth phase allows one to further pinpoint the mechanisms responsible for these food deliveries. In particular we control for impulsivity (i.e., the inability to inhibit prepotent action tendencies), lack of understanding, and whether deliveries are proactive or reactive to solicitation in the form of begging and signaling need.

We applied the group service experiment to one group each of Japanese macaques, which are independent breeders (Mitani & Watts, 1997), capuchin monkeys, who show an intermediate breeding system (Fragaszy, Visalberghi, & Fedigan, 2004), and common marmosets, which are cooperative breeders (Digby, Ferrari, & Saltzman, 2007; see also Isler & van Schaik, 2011 and Rowe, in press for quantifications of allomaternal contributions). We predicted that the degree of allomaternal investment correlates with proactive prosociality and, to a lesser extent, with social tolerance, because social tolerance is likely to be favored by other factors as well, such as feeding ecology (van Schaik, 2003) or relatedness (Schülke & Ostner, 2008). If, alternatively, social tolerance predicts the presence of proactive prosociality, proactive prosociality should be higher in species with higher levels of social tolerance.

Finally, to validate whether the group service paradigm really assesses the same underlying propensity as dyadic provisioning games, we compared the performance of the marmosets in the

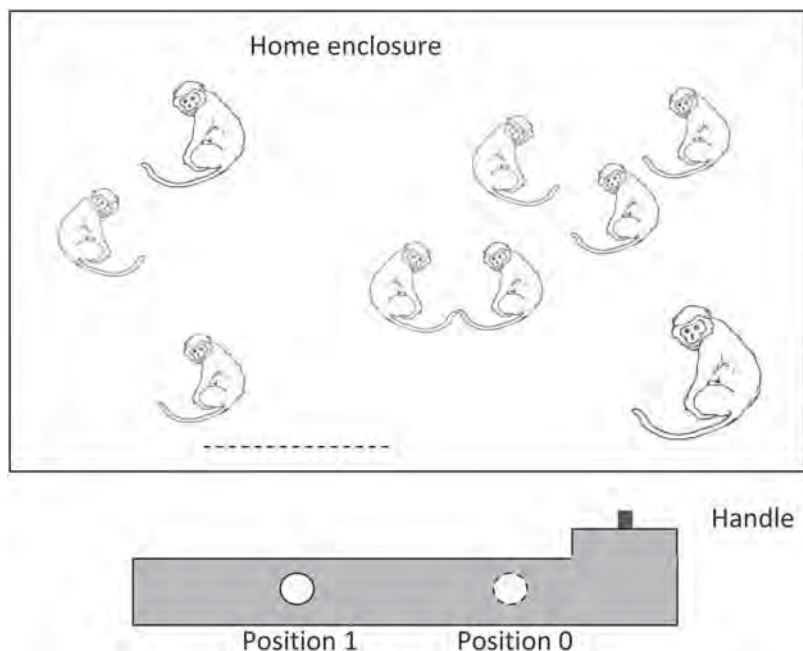


Figure 1. Apparatus and experimental setting of the group service experiment. Food can only be obtained from the food bowl in position 1 (black circle) if one subject pulls the board within reach and holds it because the apparatus slides back if the handle is released. With the food bowl in position 0 (dotted circle, training phase) subjects learn to handle the apparatus because they can pull and hold it with one hand and take the food with the other hand. In particular, they have to learn that the apparatus slides back if the handle is released. For phase V (control), a fine-meshed grid (dotted line) attached to the home-cage prevents individuals from taking the food when the board is pulled. If by pulling subjects indeed intend to provide food to recipients, rather than not being able to suppress this reaction, they would stop pulling the baited tray in this condition.

group service with data from provisioning games, using the same individuals (Burkart et al., 2007). If both tests assess proactive prosociality, these data sets should be correlated.

Method

Subjects

We tested three social groups of nonhuman primate species with different degrees of allomaternal investment: Japanese macaques (*Macaca fuscata*), capuchin monkeys (*Cebus apella*), and common marmosets (*Callithrix jacchus*). The macaques and the capuchin monkeys were tested at the Zoo al Maglio, TI, Switzerland, during June–July 2009, the marmosets at the Primate Station of the Anthropological Institute and Museum of the University of Zurich, Switzerland, during July 2009–January 2010.

The macaque group contained 10 individuals: two adult males, five adult females, two juvenile males, and one juvenile female. The group was organized in matriline and an additional infant of unknown sex was born during the experiment. Because of the absence of a fully grown dominant male, the most dominant individual (i.e., the one able to displace all other group members at any time and in any context) was an adult female, followed by her juvenile daughter (individuals 1 and 2 in Figure 3, left hand side). The capuchin group contained seven individuals: two adult males (the dominant one displaying distinct morphological features), two adult females, and three juvenile males, which were all offspring

from the dominant female (dominant individuals: one (female) and two (male) in Figure 3, middle). The marmoset group contained seven adult individuals: five males and two females, that is, a breeding pair¹ and their adult offspring (helpers; Figure 3, right hand side).

The animals were tested in the group between regular feedings. They were deprived of neither food nor water and the experiments did not interfere with the daily routines of cleaning and feeding. The macaques and the capuchin monkeys were kept in large, naturalistically structured outdoor cages connected to indoor shelters out of view of the zoo visitors. The marmosets were primarily housed in indoor cages but had regular access to outdoor cages; details can be found in Burkart and Heschl (2006).

¹ For common marmosets, dominance is difficult to be detected in food contexts and often fluctuates from one day to another. Thus, almost every individual can displace another one from a food source, including offspring their parents (who, in the reproductive context, are dominant over the other group members), or younger siblings older siblings. Indeed, current food motivation seems to be the best predictor for who displaces whom. An exception might be constellations in which offspring are housed together as a social group without parents (Burkart & Heschl, 2007). In an observational study, Furrer (2008) found that in the common marmoset group used in this study, the breeders have on average higher feeding priority when competition is relatively high (first feeding in the morning). We, therefore, considered the breeders as food-dominant to the other group members.

Apparatus and Materials

The apparatus consists of a board placed parallel to the outer mesh of the home cage (see Figure 1), upon which a food bowl can be attached in variable positions. The food bowl cannot be reached directly by the subjects, but can be pulled within reach through a handle on one side of the board. However, the board slides back out of reach as soon as the handle is released because it is mounted on inclined rails that run perpendicularly to the mesh. Thus, in order to obtain the food, an individual has to pull the board within reach, keep it in place with one hand and take the food with the other hand. However, when the distance between the handle and the food bowl is more than two arm's lengths, the only way to obtain food is when one individual pulls and holds onto the handle and another group member grabs it. Favorite food items were used and were chosen according to group preferences that were established prior to the test. Importantly, the food items had to be highly preferred by all members of the group.

Procedure

The group service experiment consisted of five phases described below.

Phase I: Habituation. The aim of phase I was to habituate the subjects to the presence of the experimenter and the apparatus. The board was fixed on the apparatus close to the enclosure in such a way that the subjects could directly access the food bowl in position 0 (see Figure 1) without pulling. Pieces of favorite foods (10 times the number of animals in the group per day) were provided sequentially during 5 days, or until every subject had taken at least three pieces. The piece of food was held up by the experimenter, who simultaneously attracted the subjects' attention verbally ("look here!") before placing it in the bowl. This attention-getting procedure assured that all subject groups would equally pay attention to the setting, independent of cage size, and was used in all phases of the experiment. If necessary, dominant individuals were distracted from the apparatus by a second experimenter to make sure that all individuals would approach the apparatus.

Phase II: Social tolerance. To assess social tolerance, 35 pieces of favorite food were placed one at a time on the apparatus within reaching distance, as in phase I, during two consecutive days. We recorded the percentage of food items received by each group member and calculated the evenness of this distribution (Pielou, 1977), as a measure of how equitable food was obtained by group members, and thus, how good the odds of subordinates are of having access to the food. When food was shared (passively or actively), it was counted as food received by both group members involved, independent of the amount of food eaten by each individual.

Phase III: Training. The aim of phase III was that subjects learned to pull the handle and to understand that the handle had to be held in order to take the food. The board was now in its original position, at some distance from the enclosure, such that only the handle could be reached. Criterion was reached when the subjects were able to pull the handle and hold it with one hand and take food with the second hand, with the food bowl placed one arm length away from the handle (Figure 1, position 0). Pieces of food were provided until each subject was successful in pulling food

within reach for itself in at least seven trials (again, if necessary after distracting dominant individuals). For individuals who had difficulties in learning the task, intermediate steps (i.e., placing the food on top of the handle, directly in front of the handle, near the handle with increasing distances to it, and finally in the food bowl) were introduced.

Phase IV: Group service. Phase IV assessed whether subjects would provide food to group members, even though this meant that they had to move away from the food to pull and hold the handle, and thus were not able to get anything for themselves. The food bowl was placed in position 1, that is, four arm's lengths away from the handle. We alternately ran five test sessions and five control sessions.

Each session consisted of 70 trials, interrupted with motivation trials on every sixth trial (resulting in a total of 84 trials, including the very first trial which also was a motivation trial). During motivation trials, a piece of food was placed in position 0 and could be obtained by individual effort. These motivation trials were introduced to make sure that the animals were interested in the reward until the end, and would continue to pay attention to the experimental setup. If no one would take the food in more than two successive motivation trials, the session was ended by the experimenter.

During test sessions, the food bowl was baited at the beginning of each trial by holding up the food item, attracting the group's attention by a vocal attention getter ("look here!") and conspicuously placing the food item in the bowl. The trial ended either when the food had been provided to a group member or after 1 minute from the beginning of the trial. If no food was taken in a trial, the experimenter held up the food item from the bowl again, showed it demonstratively to the group, attracted their attention vocally and placed it again in the food bowl, thereby starting the next trial.

During control sessions, the food bowls were not baited with food but instead, the experimenter held up a small stick, touched the bowl with it audibly and simultaneously used the same verbal attention getter as during the experimental trials. This control served to exclude the possibility that pulling occurred simply to explore the apparatus itself, or as play behavior.

Phase IV provides a functional, ecologically valid measure of whether provisioning of group members occurs or not in a naturalistic setting. However, because it does not allow us to dissect the exact mechanism involved with the same accuracy as in traditional dyadic provisioning games, we added the following phase.

Phase V: Mechanism and validation of the group service approach. If sustained provisioning occurs in phase IV, it could still be argued that transfers occurred by mistake because the pulling subjects didn't understand that they wouldn't be able to obtain the food themselves, and did not learn this during the five test sessions. Even though the animals had the opportunity to learn that pulling with food in position 1 was never rewarded, it could be argued, especially for smaller-brained species such as callitrichids (Deaner, Isler, Burkart, & van Schaik, 2007), that 350 trials are not sufficient to learn so. In the final phase V, we tested this understanding for those groups that showed sustained provisioning in phase IV (i.e., approximately stable rates over the five test sessions, rather than rates declining to zero). Phase V was identical to phase IV, except that now access to the food bowl was blocked by a fine-meshed grid attached to the home cage in front of position

1 (Figure 1, dotted line), still allowing for visual and olfactory cues. Thus, even if the tray was pulled to within reach, no one could ever obtain the food. We again ran five test sessions (position 1 baited) and five control sessions (position 1 empty) with the grid always in place, on alternating days. Each session consisted of 70 trials and additional motivation trials interspersed after every sixth trail (during motivation trials, food was available and accessible in position 0). If pulling the tray baited in position 1 occurred for any reason other than intentionally providing food (e.g., a persistent inability to inhibit pulling the baited tray due to the salient visual and olfactory cues), it should continue at the same level as during phase IV. However, if pulling in phase IV occurred to provide food to group members, pulling in phase V should decrease over time more consistently than in phase IV.

Finally, we compared the results from the group service experiment with earlier results on proactive prosociality in the same group of common marmosets (Burkart et al., 2007), in order to assess whether the group service paradigm indeed measures the same as dyadic provisioning games.

Analyses

The behavior of the animals was coded during the experiments with paper and pencil, but was also videotaped and the recordings used to verify the data of phase II, IV, and V of the experiment. Statistical analyses were performed in SPSS. As estimate for social tolerance in the food context, we calculated the evenness of the

distribution of food pieces obtained and consumed by each individual during phase II. We used Pielou's J' as evenness measure (Pielou, 1977), which is calculated as $H'/H'_{\max}$, where H' is the number derived from the Shannon diversity index and $H'_{\max}$ is the maximum value of H' . J' is thus constrained between 0 and 1, with 0 indicating a maximally unequal distribution and 1 indicating a perfectly equal distribution. Phase IV, the core of the group service experiments, was analyzed according to the decision tree shown in Figure 2.

At the first level of analysis, we assessed *whether food deliveries occurred at all*. If they did, we assessed *whether pulling was more frequent during test versus control sessions*. In each trial, each individual who pulled at least once was coded as pulling, without taking multiple pulls into account (because multiple pulls mostly occurred in bouts rather than independently). Deliberate pulling aimed at providing food is only suggested if pulling is more frequent in test sessions. Otherwise, further analysis is not necessary but may be continued to confirm this conclusion. If there is no difference, or if pulling is more frequent in the control phase, this is most likely due to subordinates only having the opportunity to access and sample the apparatus during control trials when dominant individuals stop monopolizing the apparatus. This is expected in species with very steep dominance hierarchies, where subordinates are behaviorally inhibited by dominants to a considerable degree (Drea & Wallen, 1999; Drea, 1998) and have to focus on

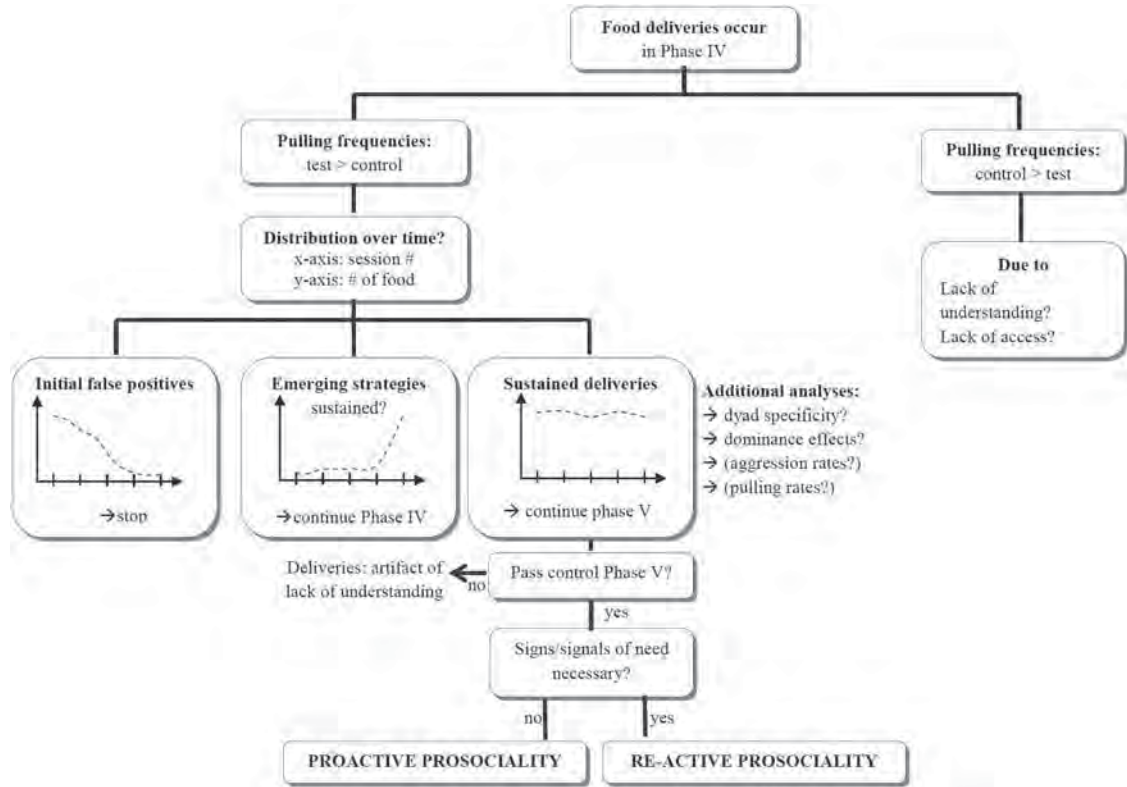


Figure 2. Overview of the analyses of phase IV if food provisioning to group members occurs. The aims are (a) to determine whether provisioning reflects a prosocial behavior or results as artifact of the experimental setup and if so, (b) to narrow down the motivational mechanism involved. See text for details.

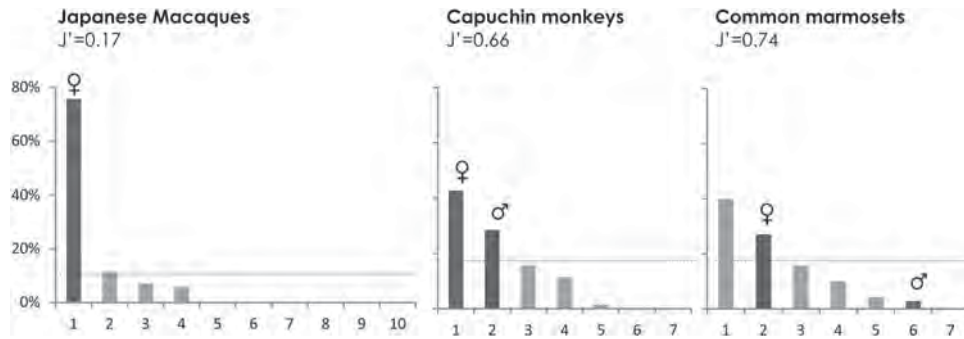


Figure 3. Phase II, social tolerance. Percentage of food items obtained by each individual during phase II. Individuals in dark gray are dominant in their group (or the breeding pair in the common marmosets). Stippled lines indicate expected values if all group members obtained equal amounts of food.

potential attacks from dominants rather than the task (e.g., pay attention to whether or not there is food on the apparatus) even when having access to the apparatus.

In a next step, we analyzed the trials in which food provisioning actually occurred. Such trials require coordinated pulling, where the tray is pulled long enough to allow a recipient to take the food and the puller shows sufficient tolerance to let the recipient take the food. We focused in particular on the *distribution of coordinated pulling over time*. First, if they only occur at the beginning and decrease over the test sessions, this is most likely due to initial false positives where pullers in reality tried to obtain the food for themselves. Second, if coordinated pulling is low in the beginning but increases over time, or increases again after an initial drop, adding additional test sessions is necessary to establish whether coordinated pulling is sustained (although the mechanism is probably different from that in the next pattern). Finally, if high rates of coordinated pulling are sustained over time, true prosocial pulling is most likely. The only alternative can be controlled for in phase V, namely that the individuals continue to produce false positives because they do not understand (or learn during 350 trials) that they will not obtain the food for themselves.

If coordinated pulling is sustained over the five test sessions, additional information can be obtained by comparing the pattern of transfers to background data of the study group (e.g., whether the *direction of food provisioning* is linked to dominance status, or whether coordinated pulling is *dyad specific*) and more detailed behavioral analyses of the food transfers. Behavioral analyses may include the proportion of food transfers accompanied by *agonistic interactions*, for example, pullers attacking recipients after they have taken the food, despite previously pulling for them. However, cross-species comparisons of pulling rates may be misleading (see discussion). Depending on how often the apparatus is visited, *quantitative analyses of pulling rates* can produce an approximation to the provisioning games reviewed above, by comparing the pulling rates of an individual when one or more potential recipients are present at the place where food potentially will be delivered versus its pulling rate when it is alone in front of the apparatus.

Finally, if pulling was due to a proactive, rather than reactive, prosocial motivation, *solicitation* (i.e., *begging*) and *signaling of need* (e.g., *conspicuous reaching attempts*) should not be necessary for the prosocial behavior of pulling the tray.

Results

Habituation (Phase I)

The habituation phase lasted 2 days in the common marmosets, 7 days in the capuchin monkeys and 9 days in the macaques. Ad libitum observations suggest that these differences were due to dominance effects rather than to neophobic reactions toward the experimenter and the board. Some dominant individuals had to be distracted in the capuchin monkeys by a second experimenter; in the macaques, two additional experimenters were necessary as well as presenting the board during regular feedings.

Social Tolerance (Phase II)

Figure 3 shows the percentage of directly accessible food pieces obtained by each individual during both test sessions. The evenness of this distribution was used as a proxy for social tolerance and was highest in common marmosets (Pielous's $J' = .74$), similar capuchin monkeys ($J' = .66$) but lower in Japanese macaques ($J' = .32$).

In the macaques, 87% of the food was monopolized by the dominant female and her daughter (a fully grown adult male was absent in this group). Similarly, the dominant male and female in the capuchin monkeys together monopolized 70% of all food items. In the common marmosets, the dominant (i.e., breeding) individuals obtained 30% of all food items. The two marmosets who obtained most food (individual 1 = adult male helper, individual 2 = female breeder) received 67% of all food items. Food sharing (i.e., others also ate from the food taken by an individual) only occurred in common marmosets and took the form of an adult son picking up the food, emitting food calls and letting his mother take it (four times).

Training (Phase III)

The training phase lasted 2 days for the marmosets, and 6 days for both the capuchin monkeys and the macaques. Dominant individuals had to be distracted in the same way as in the habituation phase. In the marmosets, a female helper who was about to be expelled from the group was tested separately in an adjacent enclosure.

Group Service (Phase IV): Prosociality

In all species, food was taken during all motivation trials. Thus, data for all species is available and analyzed separately below, according to Figure 2.

Macaques. Successful food deliveries occurred in 7.7% of all trials (see Table 1). Overall, individuals didn't pull the tray more often in test sessions versus control sessions (Wilcoxon signed-ranks test $z = -1.523$, $p = .123$). Four subjects never pulled the tray, three individuals pulled more often during test sessions ($\chi^2(1) =$ varying between 6.7 and 12.6, $p < .006$), two individuals pulled equally during test and control sessions, and one individual tended to pull more often during control sessions, $\chi^2(1) = 3.05$, $p = .08$. Over the five test sessions, overall deliveries gradually dropped to 0% (see Figure 4). Individual contributions to the food deliveries, and who obtained the food, are shown in Table 2; the evenness of this distribution in comparison to the other two test species is shown in Table 3.

This first analysis suggests a lack of deliberate food provisioning in this macaque group. We nevertheless analyzed the data further. According to Figure 2, we analyzed successful food deliveries with regard to (a) the direction and dyad specificity of the delivery and (b) whether agonistic behaviors were involved (open mouth threat, lunging at).

Sixteen deliveries were performed by individuals who pulled more in the test condition compared to the control condition and may thus potentially reflect proactive prosociality. Eight deliveries went from dominant to subordinate, and eight from subordinate to dominant (see also Table 1). Thirteen of these deliveries occurred within the dominant mother-daughter dyad, suggesting high dyad-specificity.

In eight instances of all deliveries, providers showed overt agonistic behaviors to the recipient during or immediately after pulling. As expected in a despotic society, agonistic behaviors toward recipients exclusively occurred when food was provisioned from dominant individuals to subordinates. From the 16 deliveries by individuals who pulled more in test conditions, five went from the highest ranking female to her daughter, four of which were

followed by agonistic behaviors toward the daughter. Eight more deliveries occurred in the same dyad and went from the daughter to the mother, not followed by agonism.

Capuchin monkeys. Successful food deliveries occurred in 3.1% of all trials (see Table 1). All deliveries occurred in the first test session, after which deliveries dropped to 0% (see Figure 5). They tended to pull the tray more often in test session versus control session (Wilcoxon signed-ranks test $z = -1.897$, $p = .058$). One subject (subordinate adult female) never pulled the tray, the two adult males in the group pulled equally often in test and control sessions, $\chi^2(1) = 1.14$, *ns*, and the other adult female pulled more often in test sessions, $\chi^2(1) = 4.5$, $p = .034$. The 2- and 3-year-old males pulled more often in test sessions ($\chi^2(1) > 4.26$, $p < .038$) and the 1-year-old male never pulled. Individual contributions to the food deliveries, and who obtained the food, are shown in Table 4; the evenness of this distribution in comparison to the other two test species is shown in Table 2. Since no more deliveries occurred in the remaining four test sessions, no further analyses were performed.

Common marmosets. Successful food deliveries occurred in 60.9% of all trials (see Table 1). They pulled the tray more often in test sessions versus control sessions (Wilcoxon signed-ranks test $z = -2.197$, $p = .028$). All but one individual pulled more often during test sessions ($\chi^2(1) =$ varying between 16 and 87, $p < .0003$). The remaining individual, a female helper, was about to be expelled from the group during the test period. She pulled nine times during control trials and once during a test trial, $\chi^2(1) = 6.4$, $p < .01$, which resulted in a successful food delivery. Thus, 99.7% of all food deliveries occurred by individuals who pulled significantly more in the test sessions.

Over the five test sessions, overall deliveries remained stable, ranging between 54% and 71% (see Figure 4). Sustained pulling over all test sessions, combined with higher pulling rates in test versus control sessions, is consistent with prosocial provisioning in this group.

The distribution across group members of both food deliveries and food receipts (see Table 5) was more equal than in the other

Table 1
Number of Food Deliveries, Pulls in Test Sessions and Pulls in Control Sessions in the Macaques, the Capuchins, and the Marmosets. S = Subject

	Macaques (<i>n</i> = 10)			Capuchins (<i>n</i> = 7)			Marmosets (<i>n</i> = 7)		
	Food deliveries	Pulls test	pulls control	Food deliveries	Pulls test	pulls control	Food deliveries	pulls test	pulls control
S1	5	20	3	2	7	1	41	87	0
S2	11	74	44	(0)	(7)	(8)	41	48	16
S3	0	19	6	7	17	5	36	73	16
S4	(5)	(13)	(10)	2	27	12	54	97	4
S5	(2)	(12)	(10)	(0)	(0)	(0)	32	51	3
S6	(4)	(34)	(50)	(0)	(1)	(0)	12	20	1
S7	(0)	(0)	(0)	0	17	5	(1)	(1)	(9)
S8	(0)	(0)	(0)						
S9	(0)	(0)	(1)						
S10	(0)	(3)	(1)						
Total	27	175	125	11	76	31	214	377	49

Note. The order of the subjects corresponds to that in Figure 3. In brackets and italics: Individuals who did not pull significantly more during test conditions.

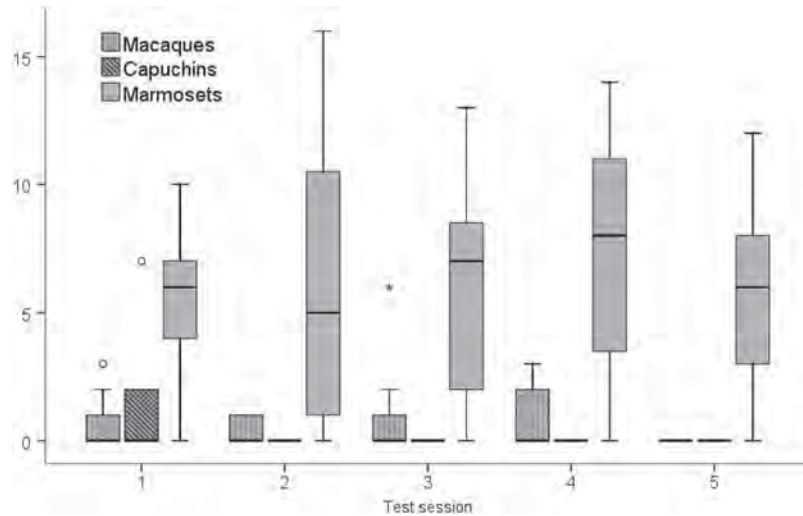


Figure 4. Phase IV: Successful food deliveries over time (median, lower, and upper quartile, sample minimum and maximum, and outliers). In macaques and capuchin monkeys, the frequency of successful food deliveries decreased over the five test sessions and dropped to zero, while it stayed high in the marmosets. Successful food delivery requires coordinated pulling, which is timed with the presence of a potential recipient and is not stopped before the food has been taken successfully.

two species (see Table 3). Due to the constantly high density of animals around the board, it is unlikely that donors had significant control over who received the food. High rates of delivery despite of this lack of control suggest no or only low dyad specificity of proactive prosociality in this marmoset group. The amount of food delivered and received was correlated ($Rho(7) = 0.883, p = .008$), but this reflected different levels of participation in the task rather than dyad specificity.

Agonistic reactions occurred in 32% of food deliveries, ranging from 22% (Test 1) to 44% (Test 4). In contrast to macaques, agonistic reactions toward recipients were not exclusively performed by dominants. Indeed, in the four subjects that provisioned both to dominant and subordinate group mates, aggression rates toward dominants were not higher than toward subordinates (Wilcoxon signed-ranks test $z = 0, p = 1$, Test Session 4 and 5). While three of these subjects did not direct more agonism toward subordinates or dominants (Fisher's

exact test $p = 1, 1$ and 0.25 , respectively), one even had a higher propensity to do so toward dominants ($p = .01$).

Since begging, the most obvious signal of need, did not occur in the marmosets, we quantified reaching attempts. In the first test session, reaching occurred in approximately two thirds of all trials. However, it did not increase tray pulling; instead it decreased it, that is, pulling rates in trials with reaching were lower compared to trials without reaching (Wilcoxon signed-ranks test $z = 1.997, p = .046$, Figure 5). In the last test session, when mistakes or lack of understanding had become increasingly unlikely, and which is therefore most representative, no reaching attempts did occur. Thus, signaling of need in a highly conspicuous way was not necessary for coordinated pulling.

Finally, we compared the successful deliveries of all three species. The marmosets delivered more food to group members in all five test sessions (Kruskal-Wallis: $\chi^2(2) =$ varying between 9.1

Table 2
Distribution of Food Deliveries in Japanese Macaques (Food Given vs. Received)

	AF	JF	AM	AF	AF	AM	AF	AF	JM	JM	Total given
AF	—	5	0	0	0	0	0	0	0	0	5
JF	8	—	0	0	0	3	0	0	0	0	11
AM	0	0	—	0	0	0	0	0	0	0	0
(AF)	(0)	(0)	(0)	—	(5)	(0)	(0)	(0)	(0)	(0)	(5)
(AF)	(0)	(0)	(0)	(1)	—	(1)	(0)	(0)	(0)	(0)	(2)
(AM)	(0)	(2)	(1)	(0)	(0)	—	(0)	(0)	(1)	(0)	(4)
(AF)	(0)	(0)	(0)	(0)	(0)	(0)	—	(0)	(0)	(0)	(0)
(AF)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	—	(0)	(0)	(0)
(JM)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	—	(0)	(0)
(JM)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	—	(0)
Total received	8	7	1	1	5	4	0	0	1	0	27

Note. The order of the subjects corresponds to that in Figure 3; F = female; M = male; A = adult; J = juvenile. In brackets and italics: Individuals who did not pull significantly more during test condition.

Table 3
Evenness of the Distribution (Pielou's J') of Food Given and Received

	Macaques	Capuchin monkeys	Common marmosets
Food given	0.56	0.34	0.89
Food received	0.64	0.12	0.83

Note. J' varies between 0 (unequal distribution) and 1 (all subjects participated equally to the distribution).

and 14.5, p = varying between 0.01 and 0.002 for the five sessions).

Mechanism and Validation of the Group Service Approach (phase V)

In the control phase V, the access to the recipient food bowl was always blocked by a fine-meshed grid; everything else was identical to phase IV. This allowed the animals to see and smell the reward on the bowl, but not to grab it once it was pulled within reach. This phase was only reached by the marmosets. We tested the subjects S1, S3, and S4 because after the death of the breeding male, the group had to be separated and the remaining animals were no longer available for testing. S1, S3, and S4 accounted for 60.5% of all deliveries in phase IV.

From the second (S1: $\chi^2(1) = 23.1, p < .001$; S4: $\chi^2(1) = 23, p < .001$) and third (S3: $\chi^2(1) = 10, p = .002$) test session on, the animals pulled the tray less frequently than in phase IV and pulling dropped to minimal levels thereafter (see Figure 6). Thus, the marmosets quickly adjusted to the situation when pulling did not produce any benefit to anybody and stopped pulling, indicating that in Phase IV, they had correctly understood the consequence of their pulls.

Finally, we compared the results to an earlier study (Burkart et al., 2007) in which the individuals from the same group of common marmosets had been tested dyadically in a provisioning game. For 22 dyads, constituted by six individuals, data for both studies was available. As expected due to the lack of control over recipients in the group service experiment, results were not correlated at the dyadic level, ($r = .073, n = 22, p = .74$). We also compared the data at the

individual level. Individual data for the provisioning game was calculated as average prosociality across different dyad partners. For the group service experiment, we again took the most reliable data from the last test session and calculated the ratio of pieces of food given and received, in order to control for food motivation, and therefore probability of being close to the apparatus. At the individual level, there was a good correspondence between the two studies, given the small sample size ($r = .779, n = 6, p = .068$).

Table 6 gives an overview of the main results for all three species.

Discussion

The aim of this study was to develop a novel experimental approach to investigate proactive prosociality and social tolerance, the group-service paradigm. It was designed to provide a tool for assessing social tolerance and proactive prosociality across as many species possible, in order to obtain comparable data across a broad range of species. Such a database will enable us to distinguish between different, nonexclusive hypotheses proposed for the evolution of proactive prosociality. The main focus in designing these experiments were (a) to produce truly comparable data by setting up a standardized paradigm with a cognitively undemanding apparatus and procedure, and (b) to keep experimental manipulations at a minimum in order to be able to also test animals in nonlaboratory settings, in particular in zoos, where separation of individuals is usually not possible.

We applied the group service paradigm to three initial test species, the independently breeding Japanese macaques, the capuchin monkeys which show an intermediate breeding system, and the cooperatively breeding common marmosets. Social tolerance was highest in the common marmosets, almost equally high in the capuchin monkeys, but much lower in the Japanese macaques. Prosociality, in the form of sustained, coordinated pulling that led to food delivery, was only found in the common marmosets, and additional analyses and the results in phase V suggest that this provisioning occurred proactively. This preliminary pattern is consistent with the cooperative breeding hypothesis of proactive prosociality, but not with the effects of social tolerance or socio-cognitive abilities. However, a more solid evaluation requires data from additional species.

Table 4
Distribution of Food Deliveries in Capuchin Monkeys (Food Given vs. Received)

	AF	AM	JM	JM	JM	AM	AF	Total given
AF	—	0	0	2	0	0	0	2
AM	(0)	—	(0)	(0)	(0)	(0)	(0)	(0)
JM	7	0	—	0	0	0	0	7
JM	2	0	0	—	0	0	0	2
JM	(0)	(0)	(0)	(0)	—	(0)	(0)	(0)
AF	(0)	(0)	(0)	(0)	(0)	—	(0)	(0)
AM	0	0	0	0	0	0	—	0
Total received	9	0	0	2	0	0	0	11

Note. The order of the subjects corresponds to that in Figure 3; F = female; M = male; A = adult; J = juvenile. In brackets and italics: Individuals who did not pull significantly more during test condition.

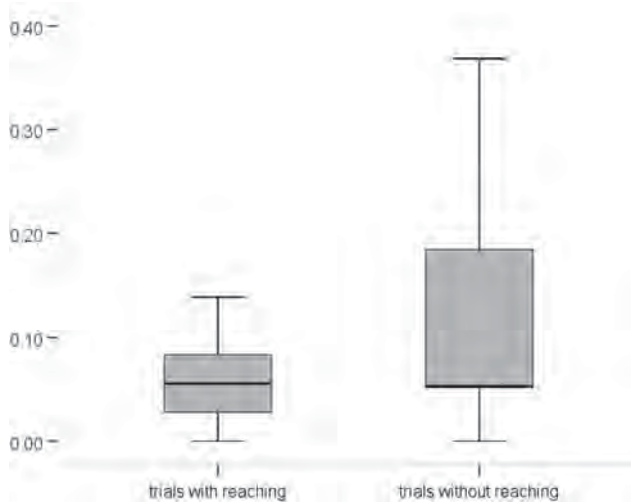


Figure 5. Phase IV: Pulling rates (median, lower and upper quartile, sample minimum and maximum, and outliers) during the first test session in common marmosets, in trials with and without reaching. Attempts to reach for the food by potential recipients are not a prerequisite for coordinated pulling by subjects (formal begging does not occur in this species). Indeed, pulling rates are higher in trials in which no reaching occurred compared to trials in which reaching occurred. Reaching attempts decreased over test sessions and were absent in Test Session 5, but coordinated pulling persisted nonetheless.

What Is Measured by the Group Service Paradigm?

A crucial question is whether the group service approach really measures proactive, that is, spontaneous prosociality. Indeed, sustained provisioning of group members in phase IV, the core of the group-service approach, serves as a quick screening for the occurrence of prosocial behavior in a given species. If no prosocial behavior emerges in this phase, it is futile to further ask for underlying mechanisms. If prosocial behavior emerges and is sustained over time, one needs to address what proximate, motivational mechanisms are involved. We will now discuss potential proximate mechanisms, as well as ways to distinguish between them, including (a) a lack of understanding, (b) social facilitation, (c) expectation of reciprocation, (d) reputation seeking, (e) re-

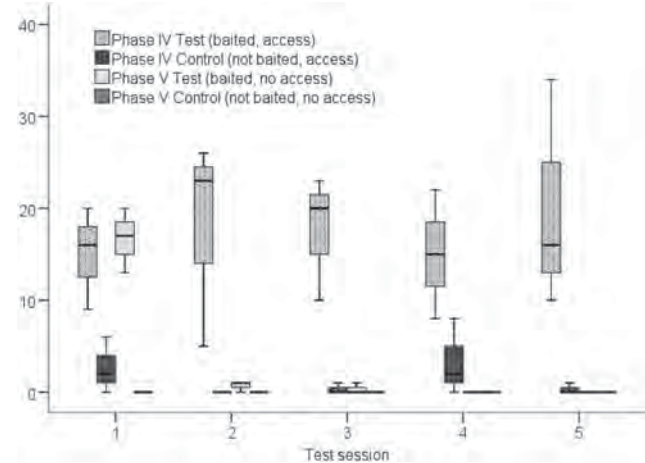


Figure 6. Number of pulls by common marmosets during phase IV (food delivery possible) and phase V (fine-mesh grid in front of receiver positions prevents taking, but not seeing the food). The boxplots indicate median, lower and upper quartile, sample minimum and maximum, and outliers). Test = food is placed on the board, Control = food bowl is only touched but not baited. Sustained pulling over all test sessions only occurred when recipients could access the food, but not when the board was not baited or when the baited board could not be accessed.

sponse to signaling, begging or harassment, (f), empathetic concern, and (g) proactive, unsolicited prosociality.

A lack of understanding of the consequences of pulling the apparatus is obviously an important alternative to exclude. Sustained, rather than declining rates of provisioning is a first indication that subjects understand the consequences of their pulling. Additional certainty can be obtained by adding the control condition from phase V. In this control, we essentially repeated the procedure of phase IV, except that physical access to the reward, once pulled within reach, was blocked by a fine-meshed grid. This grid, however, allowed visual and olfactory access to the food reward. If these powerful stimuli prevent subjects from learning that the food reward can never be reached by anybody, pulling rates should be in the same range as in phase IV when the food could be obtained by conspecifics. Thus, a lack of understanding can be experimentally excluded in the group-service context. The

Table 5
Distribution of Food Deliveries in Common Marmosets (Food Given vs. Received)

	Male helper	Female breeder	Male helper	Male helper	Male helper	Male breeder	Female helper	Total given
Male helper	—	9	9	14	4	5	0	41
Female breeder	25	—	2	6	2	6	0	41
Male helper	15	5	—	7	6	3	0	36
Male helper	22	18	7	—	5	2	0	54
Male helper	10	10	5	7	—	0	0	32
Male breeder	7	3	1	1	0	—	0	12
(Female helper)	(0)	(0)	(0)	(0)	(1)	(0)	—	(1)
Total received	79	45	24	35	18	16	0	217

Note. The order of the subjects corresponds to that in Figure 3. In brackets and italics: Individuals who did not pull significantly more during test condition.

Table 6
Summary of the Main Results

	Food deliveries in phase IV?	Pulling frequencies: test > control?	Sustained deliveries?	Pass control phase V?	Signs/Signals of need necessary?	Proactive Prosociality?
Macaques	yes	(yes)	no	—	—	no
Capuchin monkeys	yes	(yes)	no	—	—	no
Marmosets	yes	yes	yes	yes	no	yes

Note. Brackets indicate that higher pulling frequencies in test sessions were found at the group level, but not for all individuals that contributed to food deliveries.

marmoset results in this setting show that even these small-brained monkeys are able to understand the consequences of pulling and that their sustained provisioning was not a lack of inhibition of the pulling response.

Social facilitation has been evoked as an alternative to prosociality in provisioning games, where the reaction in the presence of a potential recipient is compared to the one in its absence (e.g., Cronin et al., 2010). The design of the group-service experiment excludes social facilitation because group composition is not manipulated. The exclusion of a lack of understanding and social facilitation as mechanisms leading to sustained provisioning suggests that donors indeed pulled the tray to make food available to recipients. In the common marmosets, this conclusion is further supported by the correlation of the results in the group service experiment with previous results from a provisioning game with the same individuals (Burkart et al., 2007). Nevertheless, this does not necessarily imply that the motivational force to provide food to the rest of the group was proactive.

Another possible mechanism is that individuals do so because they *expect reciprocation in the future*. Whether it is ever possible to exclude expectation effects experimentally has been extensively debated in human studies (Trivers, 2006; West, El Mouden, & Gardner, 2010). However, calculated reciprocation is cognitively demanding (Stevens, Cushman, & Hauser, 2005; Stevens & Hauser, 2005) and unlikely to occur in most nonhuman primates (Dufour, Pelé, Neumann, Thierry, & Call, 2009; Dufour, Pelé, Sterck, & Thierry, 2007; Melis, Hare, & Tomasello, 2008), which generally use some friendship indicator or emotionally based bookkeeping to generate approximately reciprocal exchanges (Schino & Aureli, 2009). Thus, the extreme rarity of calculated reciprocity in nonhuman primates, perhaps because it is cognitively demanding, makes it unlikely to be responsible for prosocial pulling in the group service experiment in many species.

Similarly, *reputation seeking* could motivate individuals to provide food for the group. Reputation seeking can be viewed as a generalization of calculated reciprocity from the dyadic context to the group context, and has for example been seen responsible for meat sharing in human hunter-gatherer societies (Hawkes & Bird, 2002). Reputation seeking can either be a direct, psychological motive, but also explain prosocial behavior at a more ultimate level. In this case, prosocial behavior might be regulated at the proximate level by a concern for the wellbeing of others, but ultimately be present because it increases the donor's reputation within its group. Disentangling these possibilities is not straightforward, even in humans. In the group service context, reputation seeking would be evident if a subject is more likely to provide food for the rest of the group the larger the audience attending to the

event is. However, to date there is no evidence for such reputation motivation among nonhuman primates in any context, and cognitive demands may be argued to be even higher than for calculated reciprocity.

If providing food to the rest of the group is underlain by a proactive motivation, the impetus to do so must come from the donor. It should thus also occur in the absence of *signaling, begging or harassment* by potential recipients. Many results suggest that prosocial behaviors in chimpanzees are reactive, that is, they only occur as response to signaling, begging or harassment (Jaeggi et al., 2010; Melis et al., 2011; but see Hare & Kwetuenda, 2010 for bonobos), whereas at least some studies indicate that they also occur independent of signs and signals in common marmosets (Burkart et al., 2007), capuchin monkeys (Takimoto et al., 2010), and human toddlers (Rueth & Burkart, 2011). To date it is unclear why in some studies, including the present one, negative effects of reaching attempts on prosocial behavior have been reported (Burkart et al., 2007; Cronin et al., 2009; Takimoto et al., 2010). Regardless, in the present study, explicit begging was absent in the marmosets, and signaling need by reaching attempts was not necessary to elicit prosocial pulling.

Closely related to the responsiveness toward prompting by recipients is the possibility that providing food is related to an *empathetic concern*, that is, an understanding of the need of group members. Cognitive empathetic concern is particularly relevant in targeted helping situations, where helpful individuals have to understand the specific needs and goals of the recipient under the current environmental constraints. This cognitive requirement of targeted helping may explain why reports so far are strongest for chimpanzees (reviewed in Jaeggi et al., 2010), who arguably show particularly high levels of nonhuman primate cognitive ability, including mentalizing (Barnes, Hill, Langer, Martinez, & Santos, 2008). However, since targeted helping necessarily includes prompting by the recipient (or at least correctly perceiving and interpreting signs of need), such instances are not suitable to solve the question whether food delivery is regulated by a proactive motivation. Food provisioning is probably cognitively less demanding than targeted helping, since the naturalistic situation is that all individuals always need food, including the subject. As a consequence, no discrepancy between own need and that of others will arise. Indeed, an appreciation of others being food-interested can even be developmentally canalized. It is important to note, however, that no matter how an individual comes to *understand* that the other needs something (i.e., through contagion, empathic concern, or innate mechanisms), this appreciation of the other's need is not sufficient by itself to also *motivate* the subject to take

action to fulfill this need, and therefore does not constitute a complete alternative mechanism for prosocial behavior.

In sum, the group service approach makes it possible to precisely pin down whether individuals pull the apparatus *in order* to provide food to others, and thus, show prosocial behavior. It also makes it possible to acquire insight in the motivation behind this behavior, in particular by excluding the most likely alternative mechanisms. In the present study, a proactive prosocial motivation is the most plausible explanation for the prosocial behavior shown by the marmosets.

Advantages and Limitations of the Group Service Approach

The group-service approach has been developed to provide data on many groups of many species that will allow us to disentangle competing hypotheses that purport to explain the evolutionary origin of proactive prosociality. It focuses on prosocial behaviors that occur in the natural group context because this is the context in which selection takes place. In other words, rather than assessing the potential of a species to engage in prosociality, we aim at establishing how prevalent proactive prosociality really is under naturalistic conditions. This focus is particularly relevant because further cognitive consequences of cooperative breeding can only be expected if prosociality prevails at the group or at least subgroup level (Burkart et al., 2009; Burkart & van Schaik, 2010).

Furthermore, any potentially disruptive effect of separating individuals from their group can be excluded. Such effects are present in dyadic provisioning games and may be most pronounced for highly interdependent species, which are arguably also most likely to show proactive prosociality. Additionally, the group approach allows testing species in various settings, including nonlaboratory settings where no handling is possible.

The group approach also has its limitations. It often cannot provide independent individual data for all group members, or data of specific dyadic constellations. Such individual and dyadic data are particularly suitable to provide a proof-of-principle, that is, to find out whether proactive prosociality ever occurs in a given species, albeit only under ideal conditions that are rarely ever met in nature. However, individual or dyadic approaches are less suitable to obtain a biologically valid estimation of the prevalence of spontaneous prosociality under naturalistic situations. The lack of prosociality in capuchin monkeys in the present study, for example, is at odds with other reports in the literature (de Waal, et al., 2008; Lakshminarayanan & Santos, 2008; Takimoto et al., 2010). It may indicate that prosociality in capuchin monkeys is expressed only when specific dyads are separated from the rest of the group. The two approaches can thus be viewed as complementary.

For the present purpose, we reported per capita pulling rates. However, per capita data points from the group service experiment are not quite independent when individuals compete over the opportunities to pull. The relatively low percentage of actual pulling events suggests the absence of such competition, but it may occur at higher levels than the ones seen here. Thus, unpublished data from another marmoset group shows that when the most actively providing individual in the group was removed, the overall provisioning rate remained stable at 75% provisioning, because other individuals step in. Moreover, per capita rates cannot readily

be compared between groups of very different sizes. For a broader comparative analysis, which is the ultimate scope of the group service approach, it may, therefore, be more suitable to use group-level data, where each social group is considered as one data point. Of course, focusing on groups rather than individuals drastically reduces effective sample size. To infer species differences with certainty, it will therefore be necessary to test multiple groups per species, and to demonstrate that variation within species is clearly smaller than between species.

Prima facie, detailed behavioral analyses during the trials may add crucial insights, for example, the proportion of food transfers accompanied by agonistic interactions. While such analyses are useful for understanding within-species variation, it is important to stress that a direct comparison of the rate of such interactions between species might be misleading. On the one hand, subordinates in more despotic systems are more likely not to react due to deference even if they did not intend dominants to take the food (Drea, 1998), while subordinates in more egalitarian systems might be able to show their frustration in agonistic acts even toward more dominant group members (Furrer, 2008). On the other hand, potential prosocial motivations necessarily have to be integrated with self-interested motives which might produce counterintuitive situations, for example, that individuals perfectly understand the experimental situation and intentionally pull the tray in a coordinated way to make food available for the group, but then nevertheless become frustrated when others, and not they themselves, obtain it.

Disentangling the selection pressures on proactive prosociality requires a considerable amount of research effort, and the group service approach should help to channel efforts by different research groups to facilitate the comparability of results. Indeed, the authors are happy to provide additional methodological details or other support on request. Given the crucial role that the emergence of prosociality played for human evolution (Burkart, Hrdy & van Schaik, 2009; Hrdy, 2009) we believe that it is worth making this effort and encourage researchers to contribute to this endeavor by contributing group service data from their own study species.

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