Voluntary food sharing in pinyon jays: the role of reciprocity and dominance

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Article history:

Received 1 February 2016

Initial acceptance 24 March 2016

Final acceptance 25 July 2016

Available online xxx

MS. number: A16-00087R

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Food sharing offers a clear example of prosocial behaviour, in which one individual's actions benefit another. Researchers have proposed a range of hypotheses that explain why food sharing may occur among unrelated individuals. Two such hypotheses, reciprocity and dominance, have been tested in many species, including fish, corvids, rats, bats and primates, showing that (1) recipients sometimes reciprocate sharing back to previous donors and (2) dominant individuals share more than subordinates. Although primates dominate the study of prosocial behaviour, active donation of food is actually quite rare in primates. In contrast, several corvid species spontaneously share food much more frequently. Here, we explored the role of reciprocity and dominance in spontaneous food sharing among male pinyon jays, *Gymnorhinus cyanocephalus*, a North American corvid species that exhibits high levels of social complexity. Unlike much of the previous work, we tested prosocial behaviour among unrelated, non-pair-bonded adults. We observed high levels of active sharing, and donors showed clear preferences with whom they shared. We found no evidence that pinyon jays reciprocated shares in either the short or long term. This was true for both sharing within dyads (direct reciprocity) and sharing irrespective of most recent partner identity (generalized reciprocity). However, dominance influenced sharing in one of our squads, with dominant individuals sharing more than subordinates. This study highlights corvids as a fruitful model for the study of the proximate mechanisms underlying naturally occurring prosocial behaviours.

Keywords:

corvid

direct reciprocity

dominance

food sharing

generalized reciprocity

prosocial behaviour

A flash of blue flits through the trees as a male pinyon jay, *Gymnorhinus cyanocephalus*, lands on the edge of the nest next to his mate. The female flaps her wings rapidly in a begging gesture, and the male offers her several seeds he collected. This example of food sharing offers a clear case of prosocial behaviour, in which an individual acts in a way that benefits another. When food sharing involves an immediate cost to the actor, either through a direct cost of acquiring the food or an opportunity cost of forgoing the chance to consume the food, it may also be considered altruistic. Food sharing among mates makes evolutionary sense because the cost borne by the male in giving up food is recouped by the fitness benefits associated with providing resources to the female, who will mate more readily or convert that energy into offspring (Galván & Sanz, 2011). Similarly, sharing with offspring and other relatives provides straightforward inclusive fitness benefits (Hamilton, 1963). Outside of these contexts, however, sharing poses an interesting evolutionary problem since by improving the welfare of another, it reduces the donor's relative fitness (Clutton-Brock, 2009; West, Griffin, & Gardner, 2007). Nevertheless, such cases of prosocial behaviours occur across a wide range of taxa, from fish (Pinto, Oates, Grutter, & Bshary, 2011) and bats (Carter & Wilkinson, 2013) to chimpanzees, *Pan troglodytes*, and bonobos, *Pan paniscus* (Crick, Suchak, Eppley, Campbell, & de Waal, 2013; Hare & Kwetuenda, 2010).

Researchers have explored a range of hypotheses that explains why altruistic behaviour such as food sharing may occur among unrelated individuals. For example, sharing may also benefit the actor by inducing reciprocity, signalling dominance, preventing harassment or enhancing reputation (Brown, Almond, & van Bergen, 2004; Jaeggi, Burkart, & van Schaik, 2010; Pinto et al., 2011; Stevens & Gilby, 2004). Reciprocity and dominance, in particular, have frequently been studied across a range of species. In reciprocity, donors recoup any cost of helping another individual by receiving help from that individual in the future (Trivers, 1971), whereas for dominance, costs of helping can be recouped by various signalling benefits, such as signalling the actor's superior dominance status and/or physiological state (Zahavi, 1995).

Reciprocating previous altruistic behaviour can occur in multiple ways and across multiple time scales. In direct reciprocity, donors reciprocate help from specific partners by helping only those partners

from whom they received help previously. Direct reciprocity can occur over both the short and long term. In the short term, a donor's decision to help requires short-term temporal contingency, a 'temporal relation between events' (Tiddi, Aureli, Polizzi di Sorrentino, Janson, & Schino, 2011). Female hamadryas baboons, *Papio hamadryas*, for example, are more likely to respond to the recruitment call of another individual if that individual groomed them recently (i.e. were groomed within 10–55 min prior to the call; Cheney, Moscovice, Heesen, Mundry, & Seyfarth, 2010). Over a longer timescale, individuals can reciprocate by helping most those from whom they received the most help ('relative reciprocity', in Hemelrijk, 1990). Japanese macaques, *Macaca fuscata*, for example, offer the most support to individuals that groomed them the most over the course of a year, even though grooming within the past half hour is not reciprocated (Schino, Polizzi di Sorrentino, & Tiddi, 2007). Although short-term reciprocity should scale to longer time periods, long-term reciprocity can occur without having short-term reciprocity. Fraser and Bugnyar (2012), for example, found that ravens, *Corvus corax*, reciprocate agonistic support over 2 years, but not within 1 week. Importantly, the main distinction between short-term and long-term direct reciprocity is the duration of the time gap between events. Although the exact timescales measured are often arbitrary (e.g. mere minutes to days for short-term reciprocity), analysis of long-term reciprocity often involves a comparison of many aggregated events, whereas short-term reciprocity is often analysed at a trial-by-trial basis.

A second form of reciprocity repays previous altruistic behaviour but not necessarily from a specific partner. In generalized reciprocity, donors help others when they have been helped in a previous interaction, irrespective of who helped them (Rutte & Taborsky, 2007). That is, a donor may help a current partner due to a previous positive interaction in which the donor received help. Unlike direct reciprocity, which requires, at the very least, identification and basic memory of previous partners and their interactions (Stevens, Cushman, & Hauser, 2005), generalized reciprocity could emerge through a simple cognitive mechanism 'give-what-you-get', where individuals reciprocate outcomes by 'paying it forward' (Leimgruber et al., 2014). In female rats, individuals cooperated more with an unknown partner following interactions in which they themselves had been helped by others (Rutte & Taborsky, 2007).

Similar results have been found in humans, who behave more generously or selfishly depending on whether they themselves received money or not (Gray et al., 2014; Stanca, 2009). In contrast, although vampire bats, *Desmodus rotundus*, and longtailed macaques, *Macaca fascicularis*, demonstrate direct reciprocity, neither show evidence of generalized reciprocity (Carter & Wilkinson, 2013; Majolo, Schino, & Aureli, 2012).

Another commonly explored functional explanation of food sharing is the role of one's position in a dominance hierarchy. Since food is often a rare and/or a highly desired resource, dominant individuals are usually the first and primary possessors. Dominance could influence sharing if dominant individuals share food to reinforce their dominance status or enhance social prestige (Kalishov, Zahavi, & Zahavi, 2005) or to reduce tension among the group (Schino, Scucchi, Maestripieri, & Turillazzi, 1988). Thus, sharing could occur primarily down the hierarchy, with dominants sharing the most food. Alternatively, subordinates may share food to curry future favours from dominants. For instance, subordinate primates exchange grooming for coalitionary support (Seyfarth, 1977; Seyfarth & Cheney, 1984) and subordinate fish help defend territories to avoid punishment (Bergmüller & Taborsky, 2005). Thus, one's position in a dominance hierarchy could influence food sharing in various ways.

Primate studies have provided a wealth of information on evolutionary pressures on food sharing (Jaeggi et al., 2010). Yet, most of the sharing events reported in primates are passive forms of sharing, such as tolerated theft, co-feeding or 'collect-near', where one individual obtains food previously discarded by another (Crick et al., 2013; Gilby, 2006; Stevens, 2004). Among primates, spontaneous and active transfer of food from one individual to another appears to be uncommon (Crick et al., 2013; Stevens, 2004). By contrast, many birds, including several species of corvids, spontaneously and actively share food (de Kort, Emery, & Clayton, 2003, 2006; Ostojić et al., 2014; Ostojić, Shaw, Cheke, & Clayton, 2013; Scheid, Schmidt, & Noë, 2008; von Bayern, de Kort, Clayton, & Emery, 2007). Corvids, therefore, may provide an ideal model system for understanding cognitive and evolutionary mechanisms underlying voluntary, active food sharing. The previous corvid studies, however, have either used pair-bonded individuals (Ostojić et al., 2014, 2013), or studied the role of food sharing among juveniles (de

Kort et al., 2003, 2006; Scheid et al., 2008; von Bayern et al., 2007). The current study investigates whether nonpaired adult corvids voluntarily share monopolizable food with others, and, if so, why such behaviour occurs.

Here, we tested three forms of reciprocity in conjunction with the role of dominance using a long-lived social corvid, the pinyon jay. Pinyon jays have a similar social structure to many primate species, forming large flocks of up to 500 members. After their offspring fledge, pinyon jays form communal crèches of fledglings for several weeks before separating into pairs, extended family groups and groups of nonbreeding juveniles (Marzluff & Balda, 1992). Thus, these jays form subgroups with related and unrelated individuals that coalesce with other groups and fission back to smaller groups. Spontaneous, active food sharing has been previously documented in pinyon jays between mating pairs, or from adults and juveniles to related nestlings and fledglings, including from unrelated males to fledglings (Marzluff & Balda, 1992).

Given their complex social structure and their spontaneous food sharing, even among unrelated individuals, pinyon jays provide an ideal study system for exploring the proximate and evolutionary underpinnings of food sharing (e.g. the role of reciprocity and dominance status). Notably, there are many opportunities for reciprocal food sharing to occur given that these jays are long-lived, and individuals from the same flock, particularly the same subgroup, repeatedly interact. Moreover, food sharing has been linked to reciprocity in other corvids. Juvenile jackdaws, *Corvus monedula*, for example, were observed to give food to those they received food from over the course of 2 weeks (de Kort et al., 2006). Thus, given the pinyon jay's social structure and evidence of reciprocity in other corvids, we tested whether short- or long-term direct reciprocity or generalized reciprocity explained any food sharing observed.

Pinyon jays form stable dominance hierarchies in both the field and captivity (Marzluff & Balda, 1992; Paz-y-Miño, Bond, Kamil, & Balda, 2004). Dominance status is more clearly defined in males, in which being dominant confers many benefits, such as better access to high-quality food and mates (Marzluff & Balda, 1992). This social structure allows us to test whether position in the dominance hierarchy influences sharing. Support for a role of dominance in corvid food sharing is mixed. Although

rooks, *Corvus frugilegus*, share more food down the dominance hierarchy to subordinates than up to dominant ones (Scheid et al., 2008), dominance does not seem to explain rates of food sharing observed in juvenile jackdaws (de Kort et al., 2006; von Bayern et al., 2007). We tested whether the dominant bird in a male–male dyad was more likely than the subordinate one to share food, perhaps to garnish prestige or signal dominance, as seen with Arabian babblers, *Turdoides squamiceps* (Kalishov et al., 2005).

In this study, we observed pairs of male pinyon jays in which we manipulated which individual had access to food. The jays exhibited numerous spontaneous, voluntary food transfers between partners. We then tested whether reciprocity and dominance influenced pinyon jay food sharing. Specifically, we analysed whether birds showed any short-term direct reciprocity, long-term direct reciprocity or generalized reciprocity. Given the high degree of interactions between pinyon jays, any of these reciprocity types could occur. Finally, we also examined whether the dominant bird within a dyad shared more often than the subordinate bird.

METHODS

Subjects

In the current study, we tested 11 male pinyon jays (six in Squad 1 and five in Squad 2). Researchers captured all these birds in either Arizona or California (United States Fish and Wildlife permit MB694205), between 1996 and 2011. Within each squad, most individuals were captured at different times and/or locations, minimizing the likelihood of high relatedness in pairs. All birds were individually housed since capture to control for social experience. Each squad was housed in the same room since 2011. Home rooms were kept at 22 °C with a 14:10 h light:dark cycle. The University of Nebraska-Lincoln Institutional Animal Care and Use Committee approved this project (protocol number 834) and all procedures conformed to the ASAB/ABS Guidelines for the use of animals in research. At the end of this study, subjects were maintained in our facility for future research.

Diet and Satiation Level

We maintained all individuals at 90% of their free-feeding weight and tested all birds prior to their daily afternoon feeding to elicit a high motivation for food. Thus, any food sharing was expected to be costly to the donor, and immediately beneficial to the recipient.

After completing the daily sessions, birds received their daily maintenance diet of Lafeber's Cockatiel and Parrot Pellets, as well as 2 g of mealworms if they had not had access to a food cup during experimental sessions (see Food Sharing: Procedure below). This helped maintain the recipients' weights at target level.

Food Sharing

Procedure

To test food sharing, we placed two pinyon jays in separate cages ($38.5 \times 38.5 \times 56.5$ cm) in a room that was spatially and acoustically isolated from other birds (Fig. 1). We placed a food cup filled with 50–70 g of pellet feed, 10–20 pine nuts, 1–4 peanuts and 2–6 g of mealworms in the cage of one bird ('donor') and no food in the cage of the other bird ('recipient'). Donors, therefore, could monopolize the food provided during testing.

We placed the donor and recipient cages 10–12 cm from each other such that the recipient could only obtain food directly from the donor's beak and not from reaching across the gap and into the food cup (Fig. 1). Thus, any food transfers required the donor present in or near the gap between cages.

Experimenters observed the birds for a minimum of 20 min, at which point the session ended and birds were returned to their home cages. At the 20 min mark, we allowed sessions to continue up to 30 min if the two individuals were interacting in any way (vocalizing back/forth, fighting, sharing food, etc.).

Experimenters scored each session in real time from outside the experimental room and videorecorded all sessions.

Food sharing definition

We defined food sharing as the transfer of food from the donor's beak or mouth to the beak or mouth of the recipient (see 'active giving'; von Bayern et al., 2007). When food fell from the donor's beak or mouth into the recipient's cage but did not involve any physical interaction between the birds, we did not score it as a sharing event. For any interactions that were ambiguous or where experimenters failed to live-score, we confirmed when food items were actually transferred (as opposed to 'play sharing'; von Bayern et al., 2007) from videorecordings. Thus, we only documented food transfers that were actively and voluntarily donated by the donor. We had an independent rater score food-sharing events for a randomly chosen subset of up to two sessions with sharing from each subject in every dyad in both squads. We calculated an inter-rater reliability of 0.89 ± 0.07 (intraclass correlation $\pm 95\%$ confidence interval) across both squads.

Experimental Sessions

Squad 1

We formed all possible dyads ($N=15$) from six male pinyon jays. We conducted a total of 450 sessions (30 pairings for each of the 15 dyads) from May to December 2013. Within each dyad, we alternated donor and recipient roles at every pairing. We tested each of the 15 dyads before repeating any dyad. We also randomized the order of dyads for each complete round. We tested all birds once daily about five times per week; thus, each bird was either a potential donor or potential recipient on any given day. Although roles reversed within a dyad, a bird could be in the same role with another partner on consecutive days. No bird experienced the same role for more than two consecutive sessions, regardless of partner.

Dyads in Squad 1 interacted with each other after a minimum of 5 days, since all individuals interacted with specific partners again only after cycling through all other partners. This timing made short-term direct reciprocity difficult due to memory interference from sessions with other partners (Stevens et al., 2005). For generalized reciprocity, however, donors would only have to remember what occurred in their previous session as a recipient, which was 1–2 days before. Thus, this design facilitated the use of generalized reciprocity more than direct reciprocity.

Squad 2

We formed all possible dyads ($N=10$) from five male pinyon jays in Squad 2. We conducted a total of 403 sessions (roughly 40 pairings for each of the 10 dyads) from May to September 2014. We ran dyads twice daily, reversing the donor/recipient roles in the second pairing of the day. For example, in the morning, if Bird A was paired as the donor with Bird B, then in the afternoon, B would be the donor with A. In contrast to Squad 1, the timing of Squad 2's experimental sessions allowed for a greater possibility of direct reciprocity by reducing memory interference from other pairings. All other aspects of the experimental procedure were identical to Squad 1.

Dominance

To assess dominance, we placed both squads in pairwise competitive interactions over food in an encounter box, $100 \times 40 \times 40$ cm (Fig. 2). In these encounters, two birds competed over access to a peanut glued to the bottom of a food cup. Two birds were placed in a three-compartment chamber, one in the left chamber and the other on the right (Fig. 2a). Two barriers, one opaque and one transparent, on each side prevented birds from accessing the centre food compartment. A pulley system allowed experimenters to lift the barriers without being in the room.

In a dominance session, we first raised both opaque barriers but left the transparent barriers in place for 15 s. This gave the birds visual access to each other and the food cup. Then, we raised both the

transparent barriers simultaneously, giving both birds access to the centre compartment (Fig. 2b). One session lasted 3–5 min. Each dyad experienced nine total sessions for Squad 1 (three prior to experiment, six after), and 12 for Squad 2 (nine prior to experiment, three after). We videorecorded all dominance sessions for follow-up analyses.

A previous experiment from January 2011 to May 2012 used the same two squads and involved placing individuals in both a group and a dyadic setting to measure dominance relationships (Bond & Kamil, n.d.). Individuals within a squad were therefore already familiar with one another and had an established dominance hierarchy that remained consistent both over time as well as when tested in dyads versus together in a group.

Data Analysis

For all analyses we used R Statistical Software (R Core Team, 2016) v.3.3.0. Data and R code are available in the Supplementary Materials and will be uploaded on the Dryad data repository (<http://dx.doi.org/10.5061/dryad.g977f>).

Variation in sharing

To test whether donors preferentially shared more with specific individuals rather than with everyone equally, we calculated each donor's variance in the total number of sharing events across partners. High variance indicates that donors shared more with some partners and less with others, while low variance suggests equal sharing among all partners. By summing these six individual values for Squad 1, and five values for Squad 2, we obtained a total observed variance for each squad. This value was compared against a null random distribution (see Randomization tests below).

Short-term direct reciprocity

To investigate short-term direct reciprocity, we tested whether a partner's sharing or lack of sharing in the most recent session predicted the donor's sharing in the current session. Results from more complicated models that fitted the quantity of food shared (count data distributions, e.g. Poisson and negative binomial) agreed with the sharing versus no-sharing binomial generalized linear mixed model (GLMM) and are therefore not further addressed. We used a binomial distribution GLMM with a binary response variable (donor shares or donor does not share). The current partner's previous behaviour (share or no share) was a fixed effect and donor identity (six in Squad 1, five in Squad 2) and dyad identity (15 in Squad 1, 10 in Squad 2) were included as random effects. The combination of these random effects accounts for the interdependency among data points because donors occurred in multiple dyads. For both squads, we included only trials in which the donor switched roles in the previous trial (i.e. donor in the current trial but recipient in the previous trial for that dyad). Models using recipient identity as an additional random effect contained little to no variance and so were omitted from analyses. All models used the 'glmer' function in R from package 'lme4' (Bates, Maechler, Bolker, & Walker 2014).

Long-term direct reciprocity

To investigate long-term direct reciprocity, we tested whether individuals shared most with those whom they received the most from over the course of the experiment. This was done by calculating, for each individual, the observed Spearman rank correlation of shares given to each partner and shares received by those same partners (rowwise correlation in de Vries, 1993). Thus, a coefficient of 1 suggests that an individual shared the most with the individual that it received the most from and least with the individual that it received the least from. To obtain an overall correlation, we averaged the six individual values for Squad 1 and the five values for Squad 2. Thus, this value represents the degree to which individuals in each squad tended to share most with the partners from which they received most. We tested long-term direct reciprocity by comparing our observed values to a null random distribution (see Randomization tests below).

Generalized reciprocity

For generalized reciprocity, we conducted a similar GLMM analysis as used for short-term direct reciprocity. Unlike direct reciprocity, where the response variable was calculated from within each dyad, generalized reciprocity was based on sharing (or not) from whichever partner a donor most recently interacted with. Importantly, we only analysed sessions in which current donors were recipients in their previous session. This was only necessary for the generalized reciprocity analysis, since roles alternated within dyad. Additionally, we excluded afternoon sessions from Squad 2, since they involved the same dyads that were tested in the morning and, therefore, would be examples of direct rather than generalized reciprocity. Thus, we only used morning sessions in which the current partner differed from the partner in the previous interaction. This reduced the number of sessions from 350 for the direct reciprocity analysis to 229 for the generalized reciprocity analysis for Squad 1, and from 200 to 72 sessions for Squad 2. We then conducted a GLMM with previous partner behaviour (share or no share) as the response variable and donor and dyad identity as random effects.

Dominance

We calculated within-dyad (i.e. each pair of individuals) dominance as the proportion of dominance encounters in which each individual was first to consume any food. Thus, our dominance value was a proportion ranging from 0 (never first to consume, ‘strongly subordinate’) to 1 (always first to consume, ‘strongly dominant’). To test whether the direction of sharing occurred up the hierarchy from subordinates to dominants, or down the hierarchy from dominants to subordinates, we binarized both the sharing and dominance matrices. Within each dyad, we scored the individual that shared the most food as 1, and the other individual as 0. Similarly for the dominance matrix, we scored the more dominant individual as 1, and the more subordinate as 0.

We calculated a correlation of our sharing matrix with the corresponding values in the dominance matrix. To test the effect of dominance, we compared our observed value against its null random distribution (see Randomization tests below).

Randomization tests

Given the nonindependence of our data associated with donors occurring in multiple dyads, we used randomization tests to compare each observed value to a null random distribution (de Vries, 1993; Manly, 2006; Sokal & Rohlf, 2011). For our tests of variation across partners and long-term direct reciprocity, we used 10 000 permutations in which each individual's total number of shares was held constant but the distribution of those shares was randomly allocated across all partners. This method allowed us to maintain individual baseline differences in propensity to share food while allowing all other aspects to vary. For our test of dominance, we used 10 000 permutations of the binarized sharing matrix that randomly shuffled bird identity in both the row and column to create a null distribution. This randomization kept the existing sharing structure constant but randomly assigned individuals in the matrix.

RESULTS

Spontaneous Food Sharing

Although food was easily monopolizable, we observed many instances of spontaneous food sharing. In 450 total sessions for Squad 1, 75 sessions resulted in sharing (16.7%) with 288 food items given. In 403 total sessions for Squad 2, 131 sessions resulted in sharing (32.5%) with 1149 food items given. Of 206 sessions with sharing (combining data across squads), 102 contained one to three food items shared (49.5%). Although we observed more food sharing in Squad 2, this was primarily due to one individual, ID 423 (Fig. 3). This bird shared 977 of the 1149 food items shared (85%) in 77 of the 131 sessions with sharing (58.8%).

Lastly, of the 25 dyads (15 from Squad 1 and 10 from Squad 2), both birds in the pair shared with each other in 14 dyads (56%), only one bird shared in 10 dyads (40%), and no sharing from either bird

occurred in one dyad (4%). Thus, although most dyads exhibited bidirectional sharing, they varied in sharing rates. We included random effects for donor and dyad identity in our short-term analyses to account for these differences.

Variation in Sharing

Donors varied greatly in their total number of shares (Table 1). Although some individuals (e.g. 760, 778 and 789) rarely shared, others (e.g. 423 and 779) shared abundantly. Moreover, donors did not randomly distribute those shares across recipients (Supplementary Fig. S1); in both squads, the observed within-donor variance in number of shares across recipients exceeded the variance expected by chance (Squad 1: variance = 1660.4, $P < 0.01$; Squad 2: variance = 2220.1, $P < 0.01$). Thus, donors shared more with some individuals than with others.

Reciprocity

Reciprocal behaviour predicts that individuals should reciprocate in kind: that is, they should share following previous sharing but not share following no sharing. In other words, current behaviour should be contingent on what occurred previously. To illustrate whether individuals behaved contingently, we calculated the proportion of trials in which each individual shared following trials in which he had been shared with (reciprocity would predict a proportion of 1). We then calculated the proportion of trials in which the individual shared following trials in which he had not been shared with (reciprocity would predict a proportion of 0). Subtracting the latter from the former yields a value ranging from 1 to -1. A value of 1 means the individual reciprocated every trial where there was previous sharing and did not share following every trial where there was no previous sharing (perfect reciprocity). A value of -1 means, in every trial, the individual did not share following sharing but did share following no

sharing. Values near 0 mean that previous sharing did not influence current sharing. We calculated these values for both direct and generalized reciprocity.

These individual measures of reciprocity clustered around 0, suggesting that individuals did not share more following previous sharing than following no sharing for either direct or generalized reciprocity (Fig. 4). Moreover, both squads showed comparably low variance, indicating little to no squad differences in reciprocity. Thus, at least visually, a bird's sharing behaviour did not appear to be contingent on whether it had previously been shared with. To test for direct and generalized reciprocity more formally, we conducted GLMMs (see below).

Short-term direct reciprocity

In Squad 1, all dyads were shuffled through prior to repeating any single dyad, which likely imposed memory demands that would make direct reciprocity difficult. Conversely, in Squad 2, dyads were run twice daily with donor and recipient roles reversed, which lightened memory constraints on direct reciprocity since individuals only needed to remember a partner's behaviour from earlier in the day. However, a GLMM analysis showed that the probability of a donor sharing with a specific recipient did not depend on whether the recipient shared in the previous interaction in Squad 1 ($\beta = -0.15 \pm 0.49$, $P = 0.76$) or in Squad 2 ($\beta = 0.68 \pm 0.74$, $P = 0.36$). Thus, after accounting for differences in sharing rates in donors and dyads, there was no evidence that pinyon jays shared based on whether a specific partner shared in the previous interaction.

Long-term direct reciprocity

Although we found no evidence that exchange of food depends on actions in the short term, it could depend on long-term interactions through long-term direct reciprocity. Randomization tests comparing our observed value to a null distribution (Supplementary Fig. S2) showed no evidence that the rank ordering of partners with which an individual shared correlated with the ordering of partners who

shared with that individual (mean Spearman rowwise correlations: Squad 1: $r_s = 0.26$, $P = 0.11$; Squad 2: $r_s = 0.14$, $P = 0.30$).

Generalized reciprocity

The probability of a donor sharing with a recipient did not depend on what occurred in the previous session of that donor in Squad 1 (GLMM: $\beta = 0.60 \pm 0.73$, $P = 0.41$) or in Squad 2 ($\beta = -0.75 \pm 1.18$, $P = 0.52$). Thus, after accounting for differences in sharing rates in donors and dyads, we found no evidence that pinyon jays decided whether to share based on what occurred in the previous interaction regardless of partner.

Dominance

A randomization test (Supplementary Fig. S3) showed no correlation between within-dyad dominance and within-dyad sharing for Squad 1 ($r = -0.30$, $P = 0.31$) but a positive correlation for Squad 2 ($r = 0.51$, $P < 0.01$). Thus, within dyads, dominant individuals in Squad 2 shared more food than subordinates.

DISCUSSION

In this study we investigated active food sharing in two squads of male adult pinyon jays and found that, on average, sharing occurred in 24% of sessions, although individuals varied greatly in their sharing rates. This sharing rate supports de Kort et al.'s (2006) contention that active food sharing occurs more frequently in corvids than in many primates (capuchin monkeys: 1.6%; chimpanzees: 0.2%; bonobos: 2.7%; de Waal, 1996). Pinyon jays did not share indiscriminately, however. Donors shared with some individuals more than others. Pinyon jays, therefore, provide a novel model system to test the evolutionary factors influencing spontaneous, active food sharing.

To test the factors that may account for the distribution of sharing across partners, we investigated the effects of reciprocity and dominance on sharing. We found no evidence that pinyon jays use recent past interactions to decide whether to share. Moreover, in the long term, individuals were not more likely to share more with those that shared most with them. Dominance, however, may have played a role in one of the squads, with the dominant individual within each dyad sharing more often than the subordinate one.

Implications

Reciprocity

Our pinyon jays showed no evidence of sharing contingent on recent past interactions. This was true even in Squad 2 where donor and recipient roles reversed within a dyad on the same day, thereby reducing memory constraints on direct reciprocity. Thus, it appears these jays do not punish cheaters or reward cooperators as is expected from hypotheses requiring short-term temporal contingency. Moreover, we did not find any evidence for the correlation between shares given and received over the course of the experiment (long-term direct reciprocity).

Reciprocity did not account for the patterns of sharing observed in these data, which leaves open the question of why donors share preferentially with some individuals and not others. Given the maladaptive nature of willingly giving away valuable resources, an alternative adaptive mechanism, beyond reciprocity or dominance, may account for these patterns of sharing. The high degree of sociality observed in pinyon jays suggests one possibility: sharing functions as an affiliative behaviour that builds and reinforces affiliative relationships. This function is seen in other corvids, whereby sharing forms and strengthens social bonds in both juvenile jackdaws and rooks (Scheid et al., 2008; von Bayern et al., 2007). Such affiliative relationships can provide adaptive benefits to many group-living animals (Seyfarth & Cheney, 2012), and networks with strong bonds between specific individuals are conducive to the evolution of cooperation in a population (Nowak, 2006). In feral horses, *Equus ferus caballus*, for

example, strong social bonds enhance mares' foal birthrate and survival, and reduce harassment from males (Cameron, Setsaas, & Linklater, 2009). Likewise, infant survival increases in female savannah baboons (*P. cynocephalus*), as their social integration within the group increases (Silk, Alberts, & Altmann, 2003). Thus, the costs of acting prosocially may be recouped by benefits obtained from the social bond.

In a similar experiment, capuchin (*Cebus apella*) donors shared more food with long-term, socially bonded partners than with those that had previously shared with them (Sabbatini et al., 2012). Likewise, zebra finches, *Taeniopygia guttata*, maintained high levels of cooperation in an iterated Prisoner's Dilemma game, but only when interacting with partners with whom they were socially bonded (St-Pierre, Larose, & Dubois, 2009). Thus, existing affiliative relationships are important to consider when evaluating reciprocity. In fact, although de Kort et al. (2006) initially suggested long-term direct reciprocity was important among juvenile jackdaws, a follow-up study suggests this reciprocity effect is a by-product of repeatedly interacting with preferred social partners and ending relationships with other individuals (von Bayern et al., 2007). Given these findings in other corvids, pinyon jay food sharing may also function as an important social behaviour, although not necessarily as a result of reciprocal exchange. Social bonds could facilitate the maintenance of prosociality if bonded individuals preferentially direct these behaviours towards each other over other individuals (Schino & Aureli, 2009; Wang, Suri, & Watts, 2012), as is seen in Trinidadian guppies, *Poecilia reticulata* (Croft et al., 2005; Wilson et al., 2014). Since our birds were individually housed, affiliative behaviours outside the experiment could not have facilitated social bond formation; however, the preferential sharing we observed might reflect the development of a social bond. Indeed, individuals within each squad had been paired with one another for a prior study (1–2 years prior) that measured dominance hierarchies and were thus familiar with one another (Bond & Kamil, n.d.).

Dominance

In Squad 2, but not Squad 1, the dominant individuals in a dyad shared more food than subordinates did. This dominance effect may occur because Squad 2 donors share food as a reinforcing signal of their dominance status (e.g. a costly signal; Zahavi, 1995), which mirrors most primate studies in which dominant individuals exhibit more prosocial behaviours than subordinate ones (Cronin, 2012). In nature, dominant individuals may share food to maintain high status either directly by advertising their own ability to obtain resources, or indirectly by reducing social tension in other individuals, thereby maintaining social group cohesion. With the current data, we cannot distinguish between these explanations, although our individual housing of the pinyon jays reduces the opportunity for social tension to arise. Future work is needed to understand the context dependency of dominance on food sharing.

One possible reason for the squad difference is that the Squad 2 effect was spurious. In this squad, individuals exhibited a perfectly linear dominance hierarchy (Table 2), and the pattern of sharing matched the dominance hierarchy almost perfectly. Thus, although Bird 423 shared the most and was dominant in all of his dyads, he alone did not drive the dominance effect. Alternatively, our measure of dominance might not accurately reflect the true dominance relationship of our dyads. We consider this unlikely since both our dominance and food-sharing sessions involved interacting near food, and displacement of subordinates by dominants around a food source is a behaviour observed in wild pinyon jays (Marzluff & Balda, 1992).

Another possible reason for the squad difference is that the social composition of individuals in a group is critical to the determining the reliance on dominance. Food sharing in longtailed macaques, for example, occurs primarily from dominants to subordinates, and subordinates will withhold giving food when only one partner is present (Massen, van den Berg, Spruijt, & Sterck, 2010). However, subordinates will give food to the highest-ranking partner if given a choice between two individuals (Massen, Luyten, Spruijt, & Sterck, 2011). Thus, the role of dominance in food sharing could depend on the social partners present. Although our birds only experienced one partner at any given time, it is possible that Squad 2

birds exhibited a different reliance on dominance than Squad 1 birds. This is supported by the observation that Squad 2 showed a more linear dominance hierarchy than Squad 1.

Given the constraints in our laboratory, individuals in Squad 1 experienced only three dominance sessions prior to the sharing experiment, whereas Squad 2 experienced nine prior sessions. Thus, although individuals within each squad had the same amount of overall exposure to each other, the dominance encounters for Squad 2 may have been more salient. The increased number of dominance sessions prior to starting the current experiment could have increased Squad 2's attention to dominance and subsequently led to the observed dominance effect. Such an effect could occur, if for instance, dominant individuals gain more benefits from sharing when the salience of the dominance relationships is high. For example, dominant individuals may reinforce their superior rank through sharing, but only when subordinate recipients have had recent interactions with them, thereby reducing memory constraints.

Finally, it is plausible that our dominance effect was not due to dominance per se, but rather, due to some other correlate of dominance. For example, perhaps dominant individuals are more active around food, as compared to subordinates, thereby increasing the likelihood of having food near a potential recipient. If this leads to increased opportunities for sharing, then dominance would seem to correlate with sharing merely as a by-product of increased interactions with food. Nevertheless, it is not currently possible to disambiguate the reason underlying the squad difference; therefore, future studies should aim to understand the situations under which dominance does and does not play a role in prosocial behaviour.

Limitations and Future Directions

In this study, we used only males because female dominance status is less clearly defined in pinyon jay groups (Marzluff & Balda, 1992). However, the use of all males only allows for male–male interactions and, thus, our results do not provide insight into either male–female or female–female interactions. At least for interactions among males and females, observations of wild pinyon jays suggest that food sharing from males to females functions as courtship and pair bonding (Marzluff & Balda,

1992). As for other interaction types, in a previous study we paired other individuals in the same food-sharing context and have observed sharing between many types of dyads (e.g. females to males, food-deprived to satiated individuals, and younger to older individuals; Duque & Stevens, 2013). Thus, while we know that food sharing can occur across many relationship types, not just between males as shown here, future research could formally test whether the functions of food sharing among these various dyad types are the same, or whether they differ in some aspects.

Another potential limitation is the individual housing of our birds. We intentionally housed our birds individually to control for the subjects' experiences outside of the experiment. Although individual housing allowed us to have a more consistent and controlled social environment, it does not mimic the natural composition of groups or natural interactions among individuals in the wild. Moreover, housing in groups likely allows for the formation of stronger social relationships, which can, in turn, influence sharing. For example, stronger social relationships may increase the likelihood of finding reciprocity if partners reciprocate with partners. Housing could potentially influence dominance hierarchy formation, as well. Previous work with our jays, however, shows that they do form similar dominance hierarchies when tested in isolated dyads versus in a more naturalistic group-setting aviary (Paz-y-Miño et al., 2004). Although individual housing allowed us to remove possible confounds to examining reciprocity and dominance, future work with more natural living conditions may provide insights into alternative explanations such as social bonding.

Lastly, another limitation of this study is the small sample size: we tested 11 individuals, six in one squad and five in another. This sample size may not have been sufficient to detect reciprocity if individuals only reciprocate occasionally (and thus produce a low effect size). Nevertheless, this sample size is comparable to or larger than other studies of food sharing and tests of reciprocity in corvids and primates (de Kort et al., 2003; de Kort et al., 2006; Ostojić et al., 2014; Ostojić et al., 2013; Sabbatini et al., 2012; Scheid et al., 2008; Schwab et al., 2012; von Bayern et al., 2007). Furthermore, we utilized a complete round-robin design, allowing us to form 15 and 10 dyads in Squad 1 and 2, respectively. Thus, we attempted to capture dyadic differences individuals may naturally encounter.

In this study we examined the exchange of a single ‘currency’: food for food. As has been observed in other studies, however, individuals may exchange prosocial behaviours for different services, such as grooming in exchange for food (Schino & Aureli, 2009). Indeed, among corvids, grooming is exchanged for food sharing in jackdaws (de Kort et al., 2006) and for agonistic support in ravens (Fraser & Bugnyar, 2012). Among wild pinyon jays, males courtship-feed their pair-bonded females, which is equivalent to exchanging food for mating opportunities (Marzluff & Balda, 1992). Lastly, as was alluded to with social bonds, it could be that donors share with socially bonded partners and receive other, nonfood, benefits in return. Since we individually housed our birds, it was improbable that any other exchanges occurred. More naturalistic housing that is representative of social interactions in the wild could allow for a more flexible exchange of currencies.

Our dyadic setting also artificially imposed a forced partner choice, in which donors could not decide with whom to interact. In the wild, individuals can choose to interact with specific individuals from the group. This is particularly true in highly social species, including pinyon jays, where the frequent interaction of individuals could facilitate the selection of preferred partners. Indeed, the selection of partners can be an evolutionarily stable strategy in maintaining prosocial behaviour within a group (Noë & Hammerstein, 1994) and can play an integral role in determining cooperative interactions (Bshary & Noë, 2003). Therefore, in addition to the exchange of other currencies, more natural groupings could allow pinyon jays to preferentially associate with specific individuals.

Lastly, our study manipulated which of two birds had access to food to test naturalistic, spontaneous food sharing. Other studies have used more controlled manipulations, such as tools or operant tasks to distribute food (Di Lascio, Nyffeler, Bshary, & Bugnyar, 2013; Rutte & Taborsky, 2007; Stephens, McLinn, & Stevens, 2002; Stevens & Stephens, 2004). Although such designs have been criticized as artificial (Noë, 2006), they may prove valuable in understanding the factors that influence sharing. Controlling the behaviour of the food donor, in particular, provides a powerful test of direct reciprocity by manipulating the contingency of behaviours (Stephens et al., 2002). Now that we have

demonstrated spontaneous food sharing in pinyon jays, future work can more directly manipulate the sharing environment to test further factors influencing their sharing.

Conclusion

In this study we documented a high degree of sharing behaviour among male pinyon jays. Individuals varied greatly in their propensity to share, and, within individuals, shares were not distributed randomly. Rather, sharing individuals gave more food to some individuals than to others. Although other animals have been shown to reciprocate prosocial behaviours, the variation of food sharing observed in this study was not explained by short- or long-term reciprocity. Dominance, on the other hand, may play role, with dominant individuals sharing more than subordinates; however, this was only observed in one of our squads. The variation in whether or not and with whom a donor will share provides a valuable model for testing mechanisms that maintain prosocial behaviour.

Acknowledgments

We thank Amy Ort, Alan Bond, Al Kamil and the EEB Behavior Group at the University of Nebraska-Lincoln for their thoughtful feedback on many drafts. Particular thanks to Dai Shizuka and Colby Tanner for many comments and assistance with statistical analyses. Lastly, thanks to the Avian Cognition Lab undergraduates (Victoria Contreras, Jasmine Emerick, Sanjaya Roy, Matt Schmitt, Aotian Yang, Vitor Oliveira, Treavor Heeney, Whitney Lechner and Holly Ahmann) who were integral to the entire process, and laboratory technicians Marianna Burks and Jesse Baumann for maintaining the bird colony. This research was supported in part by National Science Foundation Graduate Research Fellowship Program funding (DGE-10410000).

References

- Bergmüller, R., & Taborsky, M. (2005). Experimental manipulation of helping in a cooperative breeder: Helpers 'pay to stay' by pre-emptive appeasement. *Animal Behaviour*, 69, 19–28.
<http://doi.org/10.1016/j.anbehav.2004.05.009>
- Brown, G. R., Almond, R. E. A., & van Bergen, Y. (2004). Begging, stealing, and offering: Food transfer in nonhuman primates. *Advances in the Study of Behavior*, 34, 265–295.
[http://doi.org/10.1016/S0065-3454\(04\)34007-6](http://doi.org/10.1016/S0065-3454(04)34007-6)
- Bond, A. & Kamil, A. (n.d.). [Measured individuals' ability to learn dominance relationships of unfamiliar individuals through transitive inference]. Unpublished raw data.
- Bshary, R., & Noë, R. (2003). Biological markets. The ubiquitous influence of partner choice on the dynamics of cleaner fish: Client reef fish interactions. In P. Hammerstein (Ed.), *Genetic and cultural evolution* (pp. 167–184). Cambridge, MA: MIT Press.
- Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences of the United States of America*, 106(33), 13850–13853. <http://doi.org/10.1073/pnas.0900639106>
- Carter, G. G., & Wilkinson, G. S. (2013). Food sharing in vampire bats: Reciprocal help predicts donations more than relatedness or harassment. *Proceedings of the Royal Society B: Biological Sciences*, 280(1753), 20122573. <http://doi.org/10.1098/rspb.2012.2573>
- Cheney, D. L., Moscovice, L. R., Heesen, M., Mundry, R., & Seyfarth, R. M. (2010). Contingent cooperation between wild female baboons. *Proceedings of the National Academy of Sciences of the United States of America*, 107(21), 9562–9566. <http://doi.org/10.1073/pnas.1001862107>
- Clutton-Brock, T. (2009). Cooperation between non-kin in animal societies. *Nature*, 462(7269), 51–57.
<http://doi.org/10.1038/nature08366>

- Crick, J., Suchak, M., Eppley, T. M., Campbell, M. W., & de Waal, F. B. M. (2013). The roles of food quality and sex in chimpanzee sharing behavior (*Pan troglodytes*). *Behaviour*, 150(11), 1203–1224. <http://doi.org/10.1163/1568539X-00003087>
- Croft, D. P., James, R., Thomas, P. O. R., Hathaway, C., Mawdsley, D., Laland, K. N., et al. (2005). Social structure and co-operative interactions in a wild population of guppies (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology*, 59(5), 644–650. <http://doi.org/10.1007/s00265-005-0091-y>
- Cronin, K. A. (2012). Prosocial behaviour in animals: The influence of social relationships, communication and rewards. *Animal Behaviour*, 84, 1085–1093. <http://doi.org/10.1016/j.anbehav.2012.08.009>
- de Kort, S. R., Emery, N. J., & Clayton, N. S. (2003). Food offering in jackdaws. *Naturwissenschaften*, 90(5), 238–240. <http://doi.org/10.1007/s00114-003-0419-2>
- de Kort, S. R., Emery, N. J., & Clayton, N. S. (2006). Food sharing in jackdaws, *Corvus monedula*: What, why and with whom? *Animal Behaviour*, 72, 297–304. <http://doi.org/10.1016/j.anbehav.2005.10.016>
- de Vries, H. (1993). The rowwise correlation between two proximity matrices and the partial rowwise correlation. *Psychometrika*, 58(1), 53–69. <http://doi.org/10.1007/BF02294470>
- de Waal, F. B. M. (1996). *Good natured: The origins of right and wrong in humans and other animals*. Cambridge, MA: Harvard University Press.
- Di Lascio, F., Nyffeler, F., Bshary, R., & Bugnyar, T. (2013). Ravens (*Corvus corax*) are indifferent to the gains of conspecific recipients or human partners in experimental tasks. *Animal Cognition*, 16(1), 35–43. <http://doi.org/10.1007/s10071-012-0548-0>
- Duque, J. F. & Stevens, J. R. (2013, March). *Pinyon jays voluntarily share food with others....sometimes? Factors influencing prosocial behavior*. Poster presented at the meeting of the Comparative Cognition Conference Melbourne, Fl. Abstract retrieved from http://www.comparativecognition.org/CO3_2013_Final_Program.pdf

- Fraser, O. N., & Bugnyar, T. (2012). Reciprocity of agonistic support in ravens. *Animal Behaviour*, 83, 171–177. <http://doi.org/10.1016/j.anbehav.2011.10.023>
- Galván, I., & Sanz, J. J. (2011). Mate-feeding has evolved as a compensatory energetic strategy that affects breeding success in birds. *Behavioral Ecology*, 22(5), 1088–1095. <http://doi.org/10.1093/beheco/arr094>
- Gilby, I. C. (2006). Meat sharing among the Gombe chimpanzees: Harassment and reciprocal exchange. *Animal Behaviour*, 71, 953–963. <http://doi.org/10.1016/j.anbehav.2005.09.009>
- Gray, K., Ward, A. F., & Norton, M. I. (2014). Paying it forward: Generalized reciprocity and the limits of generosity. *Journal of Experimental Psychology: General*, 143(1), 247–254. <http://doi.org/10.1037/a0031047>
- Hamilton, W. D. (1963). The evolution of altruistic behavior. *American Naturalist*, 97(896), 354–356. <http://doi.org/10.1086/497114>
- Hare, B., & Kwetuenda, S. (2010). Bonobos voluntarily share their own food with others. *Current Biology*, 20(5), R230–R231. <http://doi.org/10.1016/j.cub.2009.12.038>
- Hemelrijk, C. K. (1990). Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. *Animal Behaviour*, 39, 1013–1029. [http://doi.org/http://dx.doi.org/10.1016/S0003-3472\(05\)80775-4](http://doi.org/http://dx.doi.org/10.1016/S0003-3472(05)80775-4)
- Jaeggi, A. V., Burkart, J. M., & van Schaik, C. P. (2010). On the psychology of cooperation in humans and other primates: Combining the natural history and experimental evidence of prosociality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1553), 2723–2735. <http://doi.org/10.1098/rstb.2010.0118>
- Kalishov, A., Zahavi, A., & Zahavi, A. (2005). Allofeeding in Arabian babblers (*Turdoides squamiceps*). *Journal of Ornithology*, 146(2), 141–150. <http://doi.org/10.1007/s10336-005-0073-x>
- Leimgruber, K. L., Ward, A. F., Widness, J., Norton, M. I., Olson, K. R., Gray, K., et al. (2014). Give what you get: Capuchin monkeys (*Cebus apella*) and 4-year-old children pay forward positive

- and negative outcomes to conspecifics. *PLoS One*, 9(1), e87035.
<http://doi.org/10.1371/journal.pone.0087035>
- Majolo, B., Schino, G., & Aureli, F. (2012). The relative prevalence of direct, indirect and generalized reciprocity in macaque grooming exchanges. *Animal Behaviour*, 83, 763–771.
<http://doi.org/10.1016/j.anbehav.2011.12.026>
- Manly, B. F. J. (2006). *Randomization, bootstrap and Monte Carlo methods in biology* (3rd ed.). Boca Raton, FL: Chapman & Hall/CRC Press.
- Marzluff, J. M., & Balda, R. P. (1992). *The Pinyon jay: Behavioral ecology of a colonial and cooperative corvid*. London, U.K.: T&AD Poyser.
- Massen, J. J. M., Luyten, I., Spruijt, B., & Sterck, E. (2011). Benefiting friends or dominants: prosocial choices mainly depend on rank position in long-tailed macaques. *Primates*, 52(3), 237–247.
<http://doi.org/10.1007/s10329-011-0244-8>
- Massen, J. J. M., van den Berg, L. M., Spruijt, B. M., & Sterck, E. H. M. (2010). Generous leaders and selfish underdogs: Pro-sociality in despotic macaques. *PLoS One*, 5(3), e9734.
<http://doi.org/10.1371/journal.pone.0009734>
- Noë, R. (2006). Cooperation experiments: Coordination through communication versus acting apart together. *Animal Behaviour*, 71, 1–18. <http://doi.org/10.1016/j.anbehav.2005.03.037>
- Noë, R., & Hammerstein, P. (1994). Biological markets: Supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology*, 35(1), 1–11. <http://doi.org/10.1007/BF00167053>
- Nowak, M. A. (2006). Five rules for the evolution of cooperation. *Science*, 314(5805), 1560–1563.
- Ostojić, L., Legg, E. W., Shaw, R. C., Cheke, L. G., Mendl, M., & Clayton, N. S. (2014). Can male Eurasian jays disengage from their own current desire to feed the female what she wants? *Biology Letters*, 10(3), 20140042. <http://doi.org/10.1098/rsbl.2014.0042>
- Ostojić, L., Shaw, R. C., Cheke, L. G., & Clayton, N. S. (2013). Evidence suggesting that desire-state attribution may govern food sharing in Eurasian jays. *Proceedings of the National Academy of*

- Sciences of the United States of America*, 110(10), 4123–4128.
<http://doi.org/10.1073/pnas.1209926110>
- Paz-y-Miño, G., Bond, A. B., Kamil, A. C., & Balda, R. P. (2004). Pinyon jays use transitive inference to predict social dominance. *Nature*, 430(7001), 778–781. <http://doi.org/10.1038/nature02723>
- Pinto, A., Oates, J., Grutter, A., & Bshary, R. (2011). Cleaner wrasses *Labroides dimidiatus* are more cooperative in the presence of an audience. *Current Biology*, 21(13), 1140–1144.
<http://doi.org/10.1016/j.cub.2011.05.021>
- Rutte, C., & Taborsky, M. (2007). Generalized reciprocity in rats. *PLoS Biology*, 5(7), e196.
<http://doi.org/10.1371/journal.pbio.0050196>
- Sabbatini, G., Vizioli, A. D. B., Visalberghi, E., & Schino, G. (2012). Food transfers in capuchin monkeys: An experiment on partner choice. *Biology Letters*, 8(5), 757–759.
<http://doi.org/10.1098/rsbl.2012.0534>
- Scheid, C., Schmidt, J., & Noë, R. (2008). Distinct patterns of food offering and co-feeding in rooks. *Animal Behaviour*, 76, 1701–1707. <http://doi.org/10.1016/j.anbehav.2008.07.023>
- Schino, G., & Aureli, F. (2009). Reciprocal altruism in primates: partner choice, cognition, and emotions. *Advances in the Study of Behavior*, 39, 45–69. [http://doi.org/10.1016/S0065-3454\(09\)39002-6](http://doi.org/10.1016/S0065-3454(09)39002-6)
- Schino, G., Polizzi di Sorrentino, E., & Tiddi, B. (2007). Grooming and coalitions in Japanese macaques (*Macaca fuscata*): Partner choice and the time frame reciprocation. *Journal of Comparative Psychology*, 121(2), 181–188. <http://doi.org/10.1037/0735-7036.121.2.181>
- Schino, G., Scucchi, S., Maestripieri, D., & Turillazzi, P. G. (1988). Allogrooming as a tension-reduction mechanism: A behavioral approach. *American Journal of Primatology*, 16(1), 43–50.
<http://doi.org/10.1002/ajp.1350160106>
- Schwab, C., Swoboda, R., Kotrschal, K., & Bugnyar, T. (2012). Recipients Affect prosocial and altruistic choices in jackdaws, *Corvus monedula*. *PLoS One*, 7(4), e34922.
<http://doi.org/10.1371/journal.pone.0034922>

- Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, 65(4), 671–698. [http://doi.org/10.1016/0022-5193\(77\)90015-7](http://doi.org/10.1016/0022-5193(77)90015-7)
- Seyfarth, R. M., & Cheney, D. L. (1984). Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature*, 308(5959), 541–543. <http://doi.org/10.1038/308541a0>
- Seyfarth, R. M., & Cheney, D. L. (2012). The Evolutionary origins of friendship. *Annual Review of Psychology*, 63(1), 153–177. <http://doi.org/10.1146/annurev-psych-120710-100337>
- Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science*, 302(5648), 1231–1234. <http://doi.org/10.1126/science.1088580>
- Sokal, R. R., & Rohlf, F. J. (2011). *Biometry* (4th ed.). New York, NY: W. H. Freeman.
- Stanca, L. (2009). Measuring indirect reciprocity: Whose back do we scratch? *Journal of Economic Psychology*, 30(2), 190–202. <http://doi.org/10.1016/j.joep.2008.07.010>
- Stephens, D. W., McLinn, C. M., & Stevens, J. R. (2002). Discounting and reciprocity in an iterated prisoner's dilemma. *Science*, 298(5601), 2216–2218. <http://doi.org/10.1126/science.1078498>
- Stevens, J. R. (2004). The selfish nature of generosity: Harassment and food sharing in primates. *Proceedings of the Royal Society B: Biological Sciences*, 271(1538), 451–456. <http://doi.org/10.1098/rspb.2003.2625>
- Stevens, J. R., Cushman, F. A., & Hauser, M. D. (2005). Evolving the Psychological mechanisms for cooperation. *Annual Review of Ecology, Evolution, and Systematics*, 36, 499–518. <http://doi.org/10.2307/30033814>
- Stevens, J. R., & Gilby, I. C. (2004). A conceptual framework for nonkin food sharing: timing and currency of benefits. *Animal Behaviour*, 67(4), 603–614. <http://doi.org/10.1016/j.anbehav.2003.04.012>
- Stevens, J. R., & Stephens, D. W. (2004). The economic basis of cooperation: Tradeoffs between selfishness and generosity. *Behavioral Ecology*, 15(2), 255–261. <http://doi.org/10.1093/beheco/arh006>

- St-Pierre, A., Larose, K., & Dubois, F. (2009). Long-term social bonds promote cooperation in the iterated Prisoner's Dilemma. *Proceedings of the Royal Society =B: Biological Sciences*, 276(1676), 4223–4228. <http://doi.org/10.1098/rspb.2009.1156>
- Tiddi, B., Aureli, F., Polizzi di Sorrentino, E., Janson, C. H., & Schino, G. (2011). Grooming for tolerance? Two mechanisms of exchange in wild tufted capuchin monkeys. *Behavioral Ecology*, 22(3), 663–669. <http://doi.org/10.1093/beheco/arr028>
- Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, 46(1), 35–57.
- von Bayern, A. M. P., de Kort, S. R., Clayton, N. S., & Emery, N. J. (2007). The role of food- and object-sharing in the development of social bonds in juvenile jackdaws (*Corvus monedula*). *Behaviour*, 144(6), 711–733. <http://doi.org/10.1163/156853907781347826>
- Wang, J., Suri, S., & Watts, D. J. (2012). Cooperation and assortativity with dynamic partner updating. *Proceedings of the National Academy of Sciences of the United States of America*, 109(36), 14363–14368. <http://doi.org/10.1073/pnas.1120867109>
- West, S. A., Griffin, A. S., & Gardner, A. (2007). Evolutionary explanations for cooperation. *Current Biology*, 17(16), R661–R672. <http://doi.org/10.1016/j.cub.2007.06.004>
- Wilson, A., Krause, J., James, R., Croft, D. P., Ramnarine, I. W., Borner, K. K., et al. (2014). Dynamic social networks in guppies (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology*, 68(6), 915–925. <http://doi.org/10.1007/s00265-014-1704-0>
- Zahavi, A. (1995). Altruism as a handicap: The limitations of kin selection and reciprocity. *Journal of Avian Biology*, 26(1), 1–3. <http://doi.org/10.2307/3677205>

Table 1

Sharing matrices

Squad 1							Squad 2					
	427	428	760	770	779	789		423	649	762	777	778
427		1	2	1	35	1	423		242	214	275	246
428	4		11	1	19	2	649	7		0	17	13
760	0	3		1	1	0	762	1	13		74	2
770	3	19	0		2	1	777	37	2	0		0
779	34	71	1	0		74	778	4	1	0	1	
789	0	1	0	0	0							

Values represent total numbers of food items shared by row donor to column recipient.

Table 2

Dominance matrices

Squad 1							Squad 2					
	427	428	760	770	779	789		423	649	762	777	778
427		0.89	1	1	1	1	423		0.83	1	1	1
428	0.11		1	0.83	0.78	1	649	0.17		0.75	0.67	1
760	0	0		0.17	0.25	0.22	762	0	0.25		0.58	0.83
770	0	0.17	0.83		0.33	0.33	777	0	0.33	0.42		0.67
779	0	0.22	0.75	0.67		0.22	778	0	0	0.17	0.33	
789	0	0	0.78	0.67	0.78							

Values represent the proportion of times the row individual obtained food prior to the column individual.

Figure 1. Food sharing apparatus. One bird, the potential donor, had access to food. The gap between the cages prevented the other bird, the potential recipient, from obtaining food by himself. Thus, transfers could only occur if the donor voluntarily reached through the gap and offered food.

Figure 2. Dominance encounter box. The food cup in the middle contained a peanut glued to the bottom. Birds started sessions in chambers on either side of the centre chamber without visual access to the food or other bird (a). We removed the barriers simultaneously to release the birds into the centre chamber (b). The first bird to obtain a piece of peanut was coded as ‘dominant’ for that specific session.

Figure 3. Number of food items shared per session for each donor. Birds vary in the amount of food shared across all partners for Squad 1 and Squad 2. Each point represents the amount of sharing that occurred in an individual session. Data shown here include only sessions in which at least one item was shared. For each individual, the diamond represents the mean and cross is the median.

Figure 4. Measures of reciprocal sharing. Each point represents the difference between an individual’s proportion of trials in which he shared following a previous share and his proportion of trials in which he shared following a no sharing.

(a)

(b)

Proportion sharing
more following sharing