

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

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ABSTRACT

Food sharing offers a clear example of prosocial behavior, 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 behavior, 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 behavior 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 groups, 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 behaviors.

Keywords: corvid, dominance, food sharing, prosociality, reciprocity

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INTRODUCTION

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* behavior, in which individuals act 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 behaviors occur across a wide range of taxa, from fish (Pinto, Oates, Grutter, & Bshary, 2011) and bats (Carter & Wilkinson, 2013) to chimpanzees and bonobos (Crick, Suchak, Eppley, Campbell, & de Waal, 2013; Hare & Kwetuenda, 2010).

Researchers have explored a range of hypotheses that explains why altruistic behavior such as food sharing may occur among unrelated individuals. For example, sharing may also benefit the actor by inducing reciprocity, signaling 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 been frequently 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 signaling benefits, such as signaling the actor's superior dominance status and/or physiological state (Zahavi, 1995).

Reciprocating previous altruistic behavior 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, were more likely to respond to the recruitment call of another individual, if that individual had groomed them recently—*i.e.*, within the last 10 minutes (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, support most the individuals that groomed them the most over the course of a year even though grooming within the past half hour was not reciprocated (Schino, Polizzi Di Sorrentino, & Tiddi, 2007). Though short-term reciprocity should scale to longer time periods, long-term reciprocity can occur without having short-term reciprocity. Fraser & Bugnyar (2012), for example, found that ravens (*Corvus corax*) were more likely to reciprocate agonistic support over two years, but not within a week. Importantly, the main distinction between short-term and long-term direct reciprocity is the duration of the time gap between events. Though 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 analyzed at a trial-by-trial basis.

A second form of reciprocity repays previous altruistic behavior but not necessarily from a specific partner. In *generalized reciprocity*, donors help when helped with in the 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, though vampire bats (*Desmodus rotundus*) and long-tailed macaques (*Macaca fascicularis*) demonstrate direct reciprocity, neither showed 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 favors 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 used either 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 non-paired adult corvids voluntarily share monopolizable food with others, and, if so, why such behavior 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 creches of fledglings for several weeks before separating into pairs, extended family groups, and groups of non-breeding juveniles. (Marzluff & Balda, 1992). Thus, these jays form sub-groups 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 sub-group, repeatedly interact. Moreover, food sharing has

been linked to reciprocity in other corvids. Juvenile jackdaws (*Corvus monedula*), for example, gave food to those they received food from over the course of two weeks (de Kort et al., 2006). Though short-term reciprocity should scale to longer time periods, long-term reciprocity can occur without having short-term reciprocity. Fraser & Bugnyar (2012), for example, found that ravens (*Corvus corax*) were more likely to reciprocate agonistic support over two years, but not within a week. Thus, due to pinyon jay 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. Though 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 analyzed 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 eleven male pinyon jays (six in Squad 1 and five in Squad 2). Researchers captured all these birds in either Arizona or California (USFW 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 light:dark cycle. The University of Nebraska-Lincoln Institutional Animal Care and Use Committee approved this project (protocol #834) and the procedures conform to the ASAB/ABS Guidelines for the Use of Animals in Research. Subjects will continue to be 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 Lafaber'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 x 38.5 x 56.5 cm) in a room that was spatially and acoustically isolated from other birds (Figure 1). We placed a food cup filled with 50-70 g of pellet feed, 10-20 pine nuts, 1-4 peanuts, 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 (Figure 1). Thus, any food transfers required the donor present in or near the gap between cages.



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.

Experimenters observed the birds for a minimum of 20 minutes, at which point the session ended and birds returned to their home cages. At the 20-minute mark, we allowed sessions to continue up to 30 minutes 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 video recorded 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* in Von Bayern et al., 2007). When food fell from the donor into the recipient's cage but did not involve any physical interaction between the birds, we did not score them as sharing events. For any interactions that were ambiguous or where experimenters failed to live score, video recordings of all sessions allowed for confirmation that food items were actually transferred (as opposed to *play-sharing* in Von Bayern et al., 2007). 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. Though 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 five 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 one or two 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 2014 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 x 40 x 40 cm (Figure 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 (Figure 2a). Two barriers, one opaque and one transparent, on each side prevented birds from accessing the center 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 seconds. 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 center compartment (Figure 2b). One session lasted 3-5 minutes. 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 video recorded all dominance sessions for follow-up analysis.

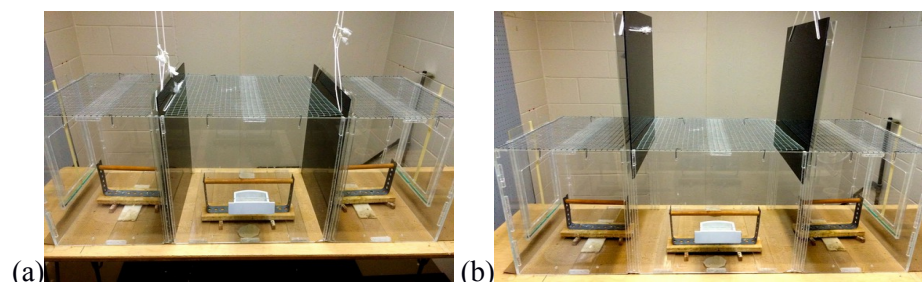


Figure 2: *Dominance encounter box.* The food cup in the middle contained a peanut glued to the bottom. Birds started sessions in chambers on either side of the center chamber without visual access to the food or other bird (a). We removed the barriers simultaneously to release the birds into the center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

A previous experiment from January 2011 to May 2012 used the same two squads and involved placing individuals in both a group and dyadic setting to measure dominance relationships (Bond unpublished data). 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) version 3.3.0. Data and R code are available in the Supplementary Materials and will be uploaded on the Dryad data repository (<http://datadryad.org/>).

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 fit the quantity of food shared (count data distributions *e.g.*, poisson and negative binomial) agreed with the sharing vs. no-sharing binomial GLMM and are therefore not further addressed. We used a binomial distribution generalized linear mixed model (GLMM) with a binary response variable (donor shares or donor does not share). The current partner's previous behavior (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.*, is donor in the current trial but was a 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, and 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 most with whom it received the most from and least with whom it received 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 analyzed 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 200 to 72 sessions for Squad 2. We then conducted a GLMM with previous partner behavior (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

Due to non-independence 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

Though 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 1-3 food items shared (49.5%). Though we observed more food sharing in Squad 2, this was primarily due to one individual, ID#423 (Figure 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, though most dyads exhibited bi-directional 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.

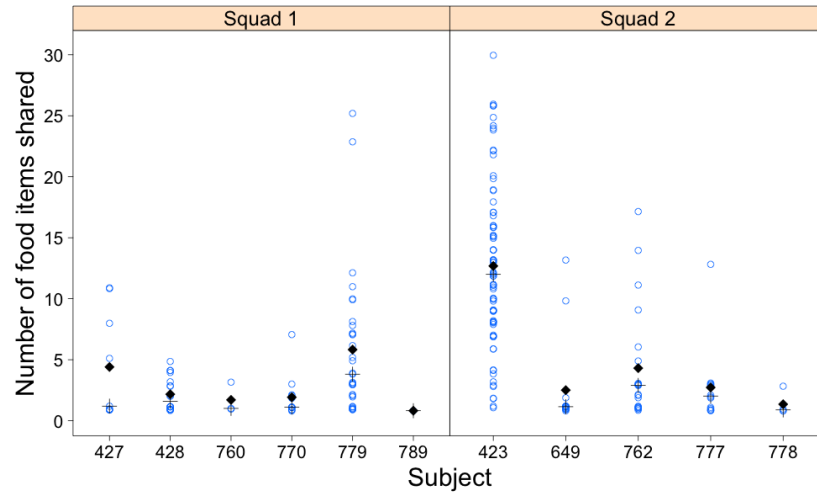


Figure 3: Number of food items shared per session for each donor. Birds vary in the amount of food shared across all partners for Squad 1 and Squad 2. Each point represents the amount of sharing that occurred in an individual session. Data shown here include only sessions in which at least one item was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

Table 1: Sharing matrices. Values represent total numbers of food items shared by row donor to column recipient.

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							

Table 2: Dominance matrices. Values represent the proportion of times the row individual obtained food prior to the column individual.

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							

Variation in sharing

Donors varied greatly in their total number of shares (Table 1). Though 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 (Figure 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 behavior predicts that individuals should reciprocate in kind: *i.e.*, they should share following previous sharing but not share following no sharing. In other words, current behavior 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 cluster around 0, suggesting that individuals do not appear to share more following previous sharing than following no sharing for either direct or generalized reciprocity (Figure 4). Moreover, both squads show comparably low variance, indicating little to no squad differences in reciprocity. Thus, at least visually, it does not appear that our birds' sharing behavior is contingent on previously being shared with. To more formally test for direct and generalized reciprocity, we conducted GLMMs (see below).

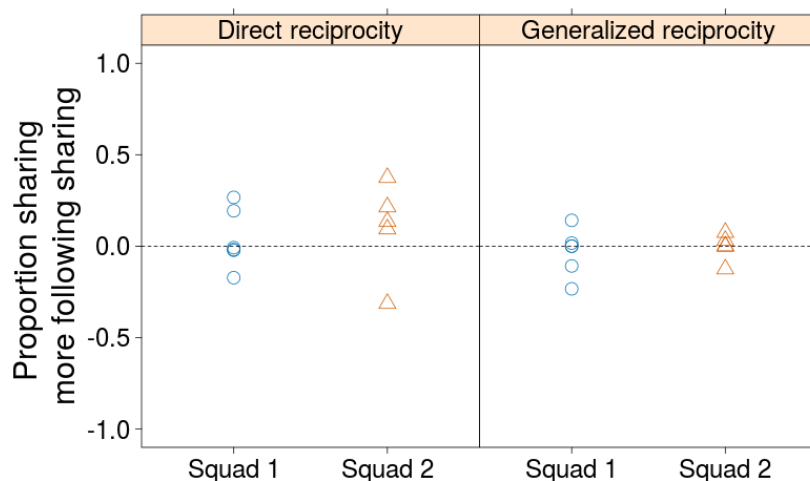


Figure 4: *Measures of reciprocal sharing.* Each point represents the difference between an individual's proportion of trials in which he shared following a previous share and his proportion of trials in which he shared following a no sharing.

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 behavior 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 is no evidence that pinyon jays share based on whether a specific partner shared in the previous interaction.

Long-term direct reciprocity

Though there is 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 (Figure 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, there is no evidence that pinyon jays decided whether to share based on what occurred in the previous interaction regardless of partner.

Dominance

A randomization test (Figure 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, though 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 behavior 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 (*Papio 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, though 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 behavior, though not necessarily as a result of reciprocal exchange. Social bonds could facilitate the maintenance of prosociality if bonded individuals preferentially direct these behaviors toward 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 behaviors 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 unpublished data).

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 behaviors 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, though 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 is spurious. In this squad, individuals exhibit a perfectly linear dominance hierarchy (Table 2), and the pattern of sharing matches the dominance hierarchy almost perfectly. Thus, although #423 shares the most and is dominant in all of its dyads, he alone does not drive the dominance effect. Alternatively, our measure of dominance might not accurately reflect the true dominance relationship of our dyads. We find this unlikely since both our dominance and food sharing sessions involve interacting near food, and displacement of subordinates by dominants around a food source is a behavior observed in wild pinyon jays (Marzluff and 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 long-tailed 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. Though our birds only experience one partner at any given time, it is possible that Squad 2 birds exhibit a different reliance on dominance than Squad 1. This is supported by the observation that Squad 2 shows a more linear dominance hierarchy than Squad 1.

Due to constraints in the lab, 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 this squad'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 is 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. Nonetheless, 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 behavior.

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 and Stevens unpublished data). 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 the subjects' experiences outside of the experiment. Though 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). Though 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, 2006; Ostojić et al., 2014, 2013; Sabbatini et al., 2012; Scheid et al., 2008; Schwab et al., 2012; von Bayern et al., 2007). Further, 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 behaviors for different services, such as grooming in exchange for food (Schino and Aureli 2009). Indeed, among corvids, grooming was exchanged for food sharing in jackdaws (de Kort et al., 2006) and 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, non-food, 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 others 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 selecting of partners can be an evolutionarily stable strategy in maintaining prosocial behavior 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, 2012; Rutte & Taborsky, 2007; Stephens, McLinn, & Stevens, 2002; Stevens & Stephens, 2004). Though such designs have been criticized as artificial (Noë, 2006), they may prove valuable in understanding the factors that influence sharing. Controlling the behavior of the food donor, in particular, provides a powerful test of direct reciprocity by manipulating the contingency of behaviors (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 behavior 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. Though other animals have been shown to reciprocate prosocial behaviors, 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 behavior.

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