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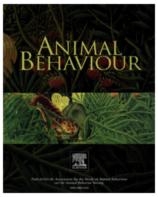

Voluntary food sharing in pinyon jays: the role of reciprocity and dominance

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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.

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. For 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).

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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, Ward, & Norton, 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 (von Bayern, de Kort, Clayton, & Emery, 2007; de Kort, Emery & Clayton, 2003, 2006; Ostojić et al., 2014; Ostojić, Shaw, Cheke, & Clayton, 2013; Scheid, Schmidt, & Noë, 2008). 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 (von Bayern et al., 2007; de Kort et al., 2003, 2006; Scheid et al., 2008). 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. Lastly, 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, Emery, & Clayton, 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 (von Bayern et al., 2007; de Kort et al., 2006). We tested whether