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SHORT COMMUNICATION

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Food offering in jackdaws (*Corvus monedula*)

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Abstract Food sharing among unrelated same-sex individuals has received considerable interest from primatologists and evolutionary biologists because of its apparent altruistic nature and implications for the evolution of complex social cognition. In contrast to primates, food sharing in birds has received relatively little attention. Here we describe three types of food sharing in jackdaws, with the initiative for the transfer either with the receiver or the giver. The latter situation is of particular interest because the food transfer takes place through active giving. Compared to primates, jackdaws show high rates of food sharing. Finally we discuss the implications of food sharing in jackdaws, and in birds in general.

Electronic Supplementary Material Supplementary material is available for this article if you access the article at http://dx.doi.org/10.1007/s00114-003-0419-2. A link in the frame on the left on that page takes you directly to the supplementary material.

Introduction

Food sharing is of great interest to evolutionary biologists because it seems to be altruistic behaviour that violates evolutionary principles. The term food sharing is used for a wide range of behaviours; from feeding offspring to tolerated theft and actively giving among peers (Perry and Rose 1994; Nishida and Turner 1996; Mitani and Watts 2001). Food sharing between non-related adults of the same sex seems to defy evolutionary theory, because explanations like inclusive fitness or courtship feeding are not applicable. How can food sharing among peers result in a positive fitness return for the sharing individual? Three explanations have been proposed. The first states that it is maintained through reciprocal altruism (Trivers 1971), a mechanism demonstrated in vampire bats (Wilkinson 1984). Vampire bats need to eat every day, but they are regularly unsuccessful in obtaining food. Through a reciprocal system of exchanging food between certain individuals, the risk of not obtaining food is reduced. A related explanation assumes that food sharing plays a role in coalition formation, where the gift of food is reciprocated by assistance in aggressive interactions with a third individual (Hemelrijk and Ek 1991; de Waal 1996). Finally, food sharing was suggested to increase the social prestige of the sharing individual, resulting in future positive fitness returns. In this case, food sharing is in the direct interest of the giver. For instance, in Arabian babblers (*Turdoides squamiceps*), high ranking individuals conspicuously feed lower ranking ones, but the receiver often declines the offer and rarely reciprocates (Zahavi and Zahavi 1997). An important analogy among these three explanations is that they require score keeping of who gives to whom, which has been suggested to be the origin of complex social systems in primates (de Waal 1996). Nevertheless, even among primates, food sharing is rare and it has been recorded in only a few species, the best studied cases being chimpanzees, *Pan troglodytes*, and capuchin monkeys, *Cebus* species (de Waal 1989, 2000; Rose 1997; Westergaard et al. 1998). Given the profound implications of food sharing on the evolution of complex social systems, including that of humans, we would like to draw attention to food sharing in birds, with special attention to jackdaws (*Corvus monedula*). Jackdaws, like jays, crows and ravens, belong to the family *Corvidae*, known for their highly developed cognitive skills (Mackintosh 1988; Clayton and Dickinson 1998; Emery and Clayton 2001; Stephens et al. 2002; Weir et al. 2002). Jackdaws breed in colonies and have complex

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social systems (Lorenz 1952). Here we report on different types of food sharing in jackdaws which are discussed in relation to food sharing in primates.

Methods

Two unrelated jackdaws in our laboratory share food regularly. Both are male, as was determined with a test based on polymerase chain reaction using DNA extracted from their feathers (cf. Griffiths et al. 1998). The two birds were taken from different nests that were 5 m apart, at approximately 20 and 25 days post-hatching and were housed together in a cage (91 cm wide × 76 cm deep × 91 cm height). Their maintenance diet consisted of scrambled eggs, dog biscuits, cheese, peanuts and various kinds of fruit. Their preferred food, however, is wax worms, which both birds take readily from the experimenter's hand. We took part in regular feeding sessions in which the birds were fed wax worms until they were satiated, i.e. after approximately 30 min or 35 worms each. These feeding sessions took place when the birds were between the age of 2 and 4 months, hence after nutritional independence. During these sessions, we recorded the number of wax worms that each bird took, and noted whether or not the wax worms were transferred and which individual eventually ate them.

We distinguished three distinct types of food transfer: (1) the receiver steals the worm from the possessor without retaliation (Tolerated theft), (2) the receiver begs and the possessor responds by putting the food in the begger's bill (Begging), (3) the possessor initiates the transfer by pecking at the bill of the receiver (Giving, Electronic Supplementary Material S1).

Outside these feeding sessions the birds were deprived of wax worms, although they had unlimited access to their maintenance diet and water.

Results

We provided 32 feeding sessions, with one session per day during the period 15 June to 30 July 2002. During this time the birds received a total of 2,189 wax worms. Of the 1,112 wax worms that bird A received, it transferred 16% to bird B, while bird B shared with bird A 12% of the 1,077 wax worms it received. Of the total number of transfers from bird A to B, A initiated 32% (Giving), responded to B in 43% (Begging), and allowed B to steal in 25% (Tolerated theft). Bird B initiated 30%, responded to begging in 27%, and tolerated theft in 43% of the transfers from B to A. The overall transfer ratio was unequal, with bird A transferring more to bird B than vice versa. However, the difference seems to be age related. Bird B is approximately 5 days older than bird A. In the first half of the sessions the difference was pronounced, with bird A sharing twice as much as bird B, while in the second half of the trials the difference disappeared. In general, the birds were not satiated when transferring food. Bird A ate on average 55% of the wax worms it received during a feeding session after it shared the first one, while for bird B this was 71%.

Discussion

These two jackdaws share a large proportion of their food and they tend do so well before they are satiated, i.e. before the wax worms have lost their incentive value. A striking observation is that a large proportion (31%) of the food transfers in these jackdaws is initiated by the possessor. Descriptions of primates actively sharing food (initiated by the giver) are few and far between. Food transfers initiated by the possessor were reported for capuchin monkeys, but they constituted a very small percentage (0.3%) of the total number of transfers (de Waal 1997). In contrast, active food sharing has been observed in natural situations in several bird species from a wide range of taxa (e.g. Arabian babbler, *Turdoidus squamiceps*, Carlisle and Zahavi 1986; red-throated caracara, *Daptrius americanus*, Thiollay 1991; pied starling, *Spreo bicolor*, Craig 1988; pied kingfisher, *Ceryle rudis*, Reyer 1986; and two corvids; northwestern crow, *Corvus caurinus*, Verbeek and Butler 1981; and common raven, *Corvus corax*, Bugnyar and Kotrschal 2002).

Food sharing between these jackdaws may be an early manifestation of behaviour that is important in adult life, i.e. courtship feeding, or it may be an unusual behaviour that has resulted from being raised in captivity. However, anecdotal field observations indicate that adult jackdaws allofeed outside the breeding season (S. Tebbich, personal communication), suggesting that it is not restricted to a courtship context or to captive birds. Furthermore, other corvid species in our laboratory, i.e. rooks (*Corvus frugilegus*) and western scrub jays (*Aphelocoma californica*) not only share, but they actively transfer food from the possessor to the receiver. This suggests that food offering may be a corvid-wide trait. Interestingly, although the scrub-jays are housed in separate cages adjacent to one another, certain birds actively feed their neighbour through the wire mesh that separates them (see Electronic Supplementary Material S2). In both species, food sharing takes place irrespective of sex and therefore cannot be explained as courtship behaviour.

A functional explanation for food sharing, and more specifically food offering in chimpanzees, is the important role it plays in affiliative relationships (Nishida and Hosaka 1996). The observations of food sharing in these jackdaws, and indeed in other corvid species as well, suggests that it plays a role in affiliative behaviour. In one particularly striking and illustrative instance of food sharing, these jackdaws were perched next to each other. Bird A dropped a wax worm. Bird B descended, picked up the wax worm, and offered it to bird A, who ate it. A further measure of the affiliation between these jackdaws is the permanent close proximity between the two birds. Even when released into the flight area they spend all their time together. However, fully understanding the significance and implications of food sharing in jackdaws requires further laboratory and field observations and using a large sample size.

Given the emphasis on food sharing in the primatology literature, there is surprisingly little stress on food sharing in other taxa, notably social species of birds. The occurrence of food sharing in unrelated taxa, such as primates, corvids and bats, indicates that it is most probably analogous rather than homologous in its evolutionary origin. Interestingly, all species that do demonstrate food sharing among adults have complex social systems. This suggests that food sharing may be crucial to the evolution of social cognition and complex social systems in vertebrates.

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