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Food sharing in jackdaws, *Corvus monedula*: what, why and with whom?

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Food sharing is common in birds between mated pairs during courtship and by helpers at the nest in cooperatively breeding species. In contrast to primates, however, food sharing between peers in birds has received little attention. We explored the extent and pattern of food sharing in a group of juvenile jackdaws. The birds shared food with a number of individuals, regardless of sex and kinship. The frequency of food sharing and the number of recipients per donor decreased over time. Active food sharing, where the initiative for the transfer lies with the donor, appeared to be much more common in jackdaws than in any primate species studied so far. In addition, jackdaws shared more of a preferred food than of a less preferred food. Three functional explanations for food sharing between peers were tested: reciprocity, harassment avoidance and food sharing as a signal of social status. The results were consistent with reciprocity and harassment avoidance.

Food sharing between unrelated individuals outside of courtship is difficult to explain within an evolutionary framework because of its apparent altruistic nature. Furthermore, it has been argued that reciprocal altruism may be the underlying mechanism for active giving and taking of food between specific individuals. In primates, food sharing has received considerable attention, partly because the reciprocal nature of active food sharing may require advanced levels of cognition (Feistner & McGrew 1986; de Waal 1989, 1996, 1997; Hill & Kaplan 1993; de Waal & Berger 2000; Hauser et al. 2003; Brown et al. 2004). Emery & Clayton (2004) have argued that corvids (crows, jays, magpies and allies) may have similar levels of cognitive abilities to primates, but the food-sharing behaviour of corvids remains largely unexplored despite reports of it in several species (e.g. common ravens, *C. corax*: Heinrich 1988; Bugnyar & Kotrschal 2002; northwestern crows, *C. caurinus*: Verbeek & Butler 1981; jackdaws: de Kort et al. 2003; rooks, *C. frugilegus*: Emery 2004; western scrub-jays, *Aphelocoma californica*: de Kort et al. 2003). We examined food sharing in one of the social corvids, the jackdaw.

Food sharing has been defined as the transfer of a defendable food item from one food-motivated individual to another, excluding theft (Feistner & McGrew 1986) or joint use of monopolizable food items (Stevens & Gilby 2004). Both of these definitions use ambiguous terms such as 'defendable' and 'monopolizable' that are open to interpretation and that may depend on the relative fighting abilities and motivation of the individuals involved. Furthermore, in birds, food sharing is often used interchangeably with allofeeding. Allofeeding more commonly refers to the feeding of dependent young by parents or helpers at the nest in cooperatively breeding birds, or to courtship feeding by members of a mated pair. The functions and mechanisms of the types of food transfer denoted by allofeeding are well understood and ubiquitous in birds. In the current study, we focused on a type of food sharing that we defined as the transfer of a food item from the donor's beak to the recipient's beak between individuals of the same age class and outside the context of courtship.

In a preliminary study, two jackdaws shared a large proportion (14%) of a temporarily available and favoured food type (de Kort et al. 2003). Both jackdaws were males and they were not siblings, which suggested preclusion of explanations for food sharing such as courtship feeding (e.g. Tryjanowski & Hromada 2005) or inclusive fitness

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(Hamilton 1964). However, these observations were limited because the two birds had no choice with whom to share. The donor frequently initiated the food transfers, whereas donor-initiated food transfers are rare among primates (de Waal 1996). Food transfers initiated by donors are likely to be governed by different motivational mechanisms to those initiated by recipients (Stevens & Hauser 2005). The recipient's motivation for initiating food transfers is obviously the food itself. The motivation of a donor to initiate a food transfer is less clear, unless one presupposes a social incentive such as the formation or maintenance of an alliance partnership. Our first aim in the current study was to explore the social context under which juvenile jackdaws shared food, by observing which individuals shared with each other and whether the initiative for the transfer came from the donor or the recipient.

In our previous study, the jackdaws progressively reduced the frequency of food sharing until it reached a low, stable level around the age of 4 months posthatching (de Kort et al. 2003). Adult jackdaws continue to share food, but it is infrequent (personal observations) and not well understood. By describing the development of food sharing in juvenile jackdaws we aimed to gain insight into the relevance of food sharing in jackdaws, and explore further the previous, preliminary finding that food sharing decreases with age.

Our third aim was to explore whether food sharing in jackdaws is related to the value of the food (de Waal 1996). Humans (Kaplan & Hill 1985), chimpanzees, *Pan troglodytes*. (Mitani & Watts 2001) and capuchins, *Cebus apella* (Rose 1997) tend to share preferred meat more than less preferred vegetable matter. If the act of sharing has a social function, for instance to elicit reciprocity or to enhance one's social status, then a gift of high quality may be more effective than a gift of low quality (de Waal 1997). Regardless of why food sharing should be more common with preferred foods, we tested whether jackdaws shared more high-quality food than food of a lower quality.

Our last aim was to test whether the pattern of food sharing in jackdaws was consistent with adaptive explanations for the apparent altruism of food sharing. Three explanations have been commonly proposed to explain food sharing. The reciprocal altruism hypothesis suggests that a cooperative act increases the probability of benefiting from cooperation in future interactions (Trivers 1971). Recurrent interactions between specific individuals may result in associative bonds with fitness benefits for the participating individuals. Others (Hauser et al. 2003; Stevens & Hauser 2004) have contested the view that reciprocity underlies food sharing because reciprocity requires the animals to inhibit temporal discounting (the devaluation of future rewards relative to current ones), and temporal discounting has not conclusively been identified in any species other than humans (Stevens 2004). Harassment avoidance has been proposed as an alternative system that precludes the problem of delayed benefits, since both donor and recipient gain direct benefits (Blurton Jones 1987; Stevens & Stephens 2002; Stevens 2004). By relinquishing part of its food, the donor may stop the harassment and be able to consume its own food.

A third explanation for the prevalence of food sharing is that it constitutes a costly social signal, either as a ritualized display to affirm dominance status (Rijksen 1978) or as a signal to enhance the social prestige of the donor (Zahavi 1975, 1990). According to the social prestige hypothesis, competition expresses itself through altruism, where the most competitive individual will be most altruistic (Roberts 1998; Lotem et al. 1999) and therefore will share food most actively. Both the dominance affirmation and social prestige hypotheses predict that an individual should not accept a food offer from a lower-ranking individual and that more dominant individuals will share food more often. Hence, if food offers serve as social signals, then higher-ranking individuals would be more likely to feed lower-ranking individuals than vice versa.

METHODS

Subjects

Jackdaws are a semicolonial, highly social and long-lived species of the temperate regions of western Eurasia (Roëll 1977; Cramp & Perrins 1994). Despite this colonial social structure, extrapair copulations are seldom observed and jackdaws are thought to pair for life (Henderson et al. 2000). The birds in this study ($N = 12$) were collected from nests in chimney pots or tree holes from three colonies around Cambridge, U.K., 20–25 days posthatching, under an English Nature permit, and were subsequently hand reared until nutritional independence. The group consisted of four pairs of siblings and four birds that had no siblings in the nest. Two of the 12 birds were female. Ten birds were 6–8 weeks old at the start of the experiment. The remaining two birds were 1 year old and had participated in an earlier study on food sharing in jackdaws (de Kort et al. 2003). All birds were nutritionally independent at the start of the experiment.

Before fledging, the 10 nestlings were kept in three cat transport boxes and fed with Roudybush special bird mix. After fledging, the 10 juveniles joined the two adults in an indoor aviary (3×2.5 m and 2 m high) for the duration of the study. Water and the maintenance diet (egg, dog biscuits, potatoes, meat, cheese, various fruits, cereals and nuts and mixed birdseed) were available ad libitum. The birds were kept at a photoperiod of 12:12 h and at a room temperature of 20°C. After the experiment, the jackdaws were moved to a large outdoor aviary.

Social Behaviour

We assessed social behaviour patterns during eight 45-min observation periods that took place in the same period as the feeding trials (see below). To enhance social activity and to allow assessment of relative dominance position within the group, we placed a bowl with 50 mealworms (larvae of *Tenebrio molitor*) in the centre of the aviary at the start of each observation period. The size of the bowl permitted access by only one bird at a time (cf. Verhulst & Salomons 2004). The average order of access to the bowl over subsequent trials was interpreted as equivalent to the dominance rank order. A second measure of dominance rank was based on the number of aggressive interactions (displacements and pecks resulting in one bird moving away) won relative to the total number of aggressive interactions between two individuals.

We also assessed affiliative behaviour patterns, that is, allopreening, bill twining, cofeeding (i.e. simultaneous feeding from the same source) and joined manipulation of an object. An instance of one of these affiliative behaviours terminated when the distance between the two individuals involved was beyond the reach of each other's beak. For example, when a bird was preening another individual and they moved away from one another before resuming preening, we considered these separate cases of allopreening.

Feeding Trials

The jackdaws received 28 feeding trials between 25 June and 8 August 2003. During a trial, the experimenter entered the aviary where the birds were housed together. One bird at a time received 10 food items consecutively, after which a second bird received 10 food items, and so on until all birds had received the same treatment. The order in which individuals received the food items was randomized before the trials. Between trials, the food items alternated between corn or waxworms (larvae of the wax moth, *Galleria mellonella*). The birds did not receive corn or waxworms outside the feeding trials. The maintenance diet was available ad libitum during and outside the trials.

For each food item provided to a focal bird, we recorded whether the bird ate the item or transferred it to another bird. Transfers were divided into two categories: recipient-initiated transfers and donor-initiated transfers. We considered a transfer recipient initiated either when the recipient took the food item directly from the beak of the donor or when the donor put the food item on the floor while handling it and the recipient took the item from underneath the possessor. When a possessor dropped a food item, or moved away from it and another bird retrieved the food item, we did not consider this a transfer. A transfer was deemed donor initiated when a donor put the food item directly into the beak of the recipient. We further recorded whether donor-initiated transfers were preceded by begging behaviour by the recipient.

Development of Food Transfer

To analyse the developmental pattern of food transfer we combined trials 1–7 into period 1 and trials 8–14 into period 2. We compared the total number of transfers, the total number of recipients per donor and the number of transfers per recipient for the two periods, by using a general linear model (GLM) repeated measures design. If food sharing in jackdaws can be explained by inclusive fitness, then most transfers should take place between siblings. For each period, we calculated the average number of transfers between siblings and nonsiblings corrected for the ratio of siblings to nonsiblings present for each individual. The four birds that did not have siblings were excluded from the kinship analysis. Since the birds were housed in three cat boxes during hand rearing, they may have perceived their cat box mates as siblings. Therefore, we also analysed the relative number of food transfers between cat box mates. Finally, if food transfer is an aspect of courtship then most transfers should take place between the sexes. To assess the effect of sex on transfer rate, we calculated the relative average number of transfers between males and females. We then used a GLM repeated measures design with period as within-subject factor and either kin, cat box or sex as between-subject factors to test for their effects on transfer rates.

Transfers of Specific Food Types

We also tested the effect of food type on the transfer rate in jackdaws, by using a GLM repeated measures design with period and food type as within-subject factors. Before the first trial, we established a preference ranking by allowing each individual to choose between a piece of corn and a waxworm 10 times consecutively. This procedure was repeated after the last trial to assess whether the preference had changed. To test whether there was more begging for waxworms than for pieces of corn, we compared the average total frequency of begging over all trials for the two food types. Similarly, we compared the frequency of donor-initiated transfers for the two food types separately. Donor-initiated transfers concern a subset of the total number of transfers and these data did not follow a normal distribution. Therefore, we used two-tailed Wilcoxon signed-ranks tests for these analyses.

Hypothesis Testing

We tested three hypotheses for adaptive explanations of food sharing on the summed number of transfers for both food items over the 28 trials.

Reciprocal altruism

Reciprocal altruism was tested with an actor–receiver model (Hemelrijk 1990b), which assumes that a recipient reciprocates to a previous donor. We tested for reciprocity with the total number of transfers (donor initiated and recipient initiated) and separately with just the donor-initiated data. We also examined interchange, that is, the exchange of different kinds of favours using allopreening as the alternative currency to food. We assessed the level of interchange by correlating the donor-initiated transfers with the instances of allopreening. The reciprocity hypothesis predicts a positive correlation between the two.

Harassment avoidance

To assess the degree of harassment, we used the exposure of the possessor to begging birds during the feeding trials. For each food item that the possessor received from the experimenter, we noted whether begging occurred. The total amount of begging received from a specific individual across all trials was then correlated with the total number of food items that a donor actively shared with the begging individual.

Food offers as social signals

To test whether food sharing may be explained by social signalling, we examined whether more donor-initiated transfers took place from dominant to subordinate individuals, regardless of their absolute rank order, than vice versa. We also tested whether higher-ranking individuals generally initiated more transfers than did lower-ranking ones.

Testing for recurrent interactions between individuals requires matrix comparisons to avoid interdependence of data points. We calculated the TauKr statistic (Hemelrijk 1990a) implemented in the program Matrix Tester (C. Hemelrijk, unpublished software), which provides a measure of correlation between cells in a matrix. In the TauKr calculation each cell in the matrix is compared only to other cells in the same row and therefore corrects for individual variation between the actors in the matrix. Significance levels of the TauKr statistic are calculated with Mantel's permutation method. All tests were conducted with 10 000 permutations. When the analysis concerned transfers of the same currency, the matrix was correlated with its transposed version. When the analysis concerned different currencies (e.g. food and allopreening), the actor matrix (actor in rows) was correlated with the receiver matrix (receiver in rows) of transfers in the other currency.

RESULTS

Food Transfers

The jackdaws received 3118 food items of which they transferred 11.1% (Table 1). Of the transfers, 26% were donor initiated and 74% were recipient initiated. There was no increase in recipient-initiated transfers for food items towards the end of a trial (GLM: $F_{11,9} = 0.37$, $P = 0.95$). However, a donor was significantly more likely to initiate a transfer towards the end of a trial than at the beginning ($F_{11,9} = 2.5$, $P = 0.01$; Fig. 1).

Patterns of Food Transfer

The total number of transfers was higher in the first period (trials 1−7) than in the second period (trials 8−14; GLM: $F_{1,11} = 15.9$, $P < 0.002$), but the birds also reduced the number of recipients that they shared with across the two periods ($F_{1,11} = 14.1$, $P < 0.003$; Fig. 2). The reduction in the number of shared food items was mainly due to a reduction in the number of individuals that a donor shared with, given that the average number of food items that a donor transferred to one recipient remained stable over the two periods ($F_{1,11} = 0.90$, $P = 0.36$). The two birds that were 1 year older than the other birds transferred a total of nine and 16 items across all trials combined, and the 10 juveniles transferred 14−69 items. Thus, the younger birds showed a considerable range in transfer rate, and the older birds' transfer rate was at the lower end of that range.

Table 1. Number of waxworms and pieces of corn in the four behavioural categories

Behaviour	Waxworm	Corn	Total
Consume	1251	1385	2636
Recipient initiated	196	59	255
Donor initiated	77	13	90
Discard	47	90	137
Total	1571	1547	3118

Consume: consumed by the focal individual; recipient initiated: recipient-initiated transfer; donor initiated: donor-initiated transfer; discard: number of items discarded.

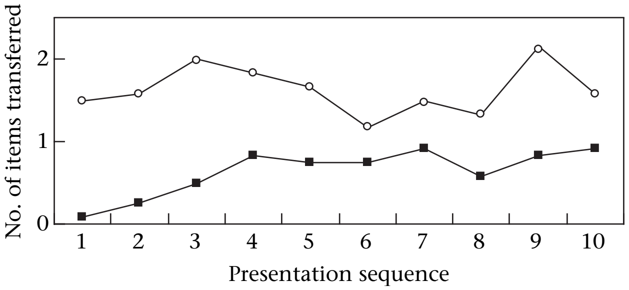

Figure 1. The average number of recipient-initiated food transfers (○) and donor-initiated food transfers (■) in relation to the sequential position of the food item in the trial.

We found no effect of kinship on food transfer rate (GLM: $F_{1,7} = 2.37$, $P = 0.15$) and there was no interaction between kinship and period ($F_{1,7} = 0.08$, $P = 0.93$). Individuals that had been reared in the same cat box did not transfer more items to one another than to individuals reared in other cat boxes ($F_{1,11} = 1.3$, $P = 0.27$). There was no overall effect of sex ($F_{1,11} = 0.39$, $P = 0.54$) on the number of food transfers and no an interaction between period and sex ($F_{1,11} = 0.23$, $P = 0.63$).

Effects of Food Type

The jackdaws showed a preference for waxworms over corn both before the first trial (Wilcoxon signed-ranks test: $T = 66$, $N = 12$, $P = 0.034$) and after the last trial ($T = 78$, $N = 12$, $P < 0.001$). Overall, both donor- and recipient-initiated transfers contained more waxworms than pieces of corn (repeated measures GLM: $F_{1,11} = 20.7$, $P = 0.001$; Fig. 3). However, there was a significant interaction between period and food type ($F_{1,11} = 10.2$, $P = 0.008$), indicating that the high number of waxworm transfers in the first block of trials decreased in later trials. When analysed separately there were significantly more donor-initiated waxworm transfers than donor-initiated corn transfers (Wilcoxon signed-ranks test: $T = 78$, $N = 12$, $P < 0.001$; Fig. 4), and there was no difference in the amount of begging for the two food types ($T = 57.5$, $N = 12$, $P = 0.16$).

Hypotheses About the Function of Food Sharing

Reciprocity

The matrix comparison of food transfers showed a significant correlation (TauKr = 0.390, $N = 12$, $P < 0.001$),

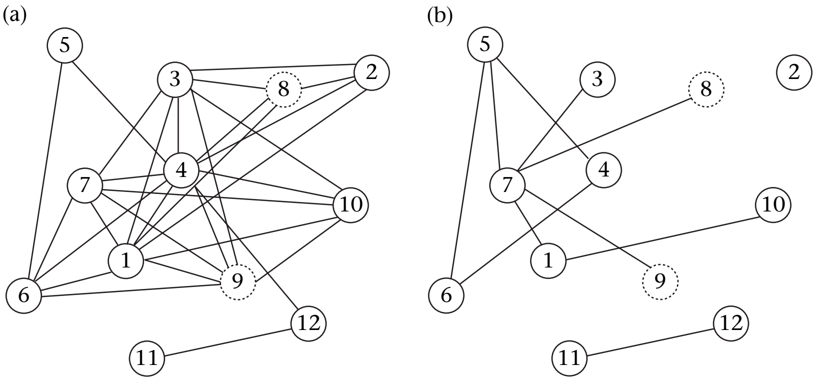

Figure 2. Sociogram for jackdaws ($N = 12$) showing mutual food transfers in (a) period 1 and (b) period 2. Circles connected by a line indicate individuals that transferred food to each other. Dotted circles: females; full circles: males. Individuals 11 and 12 were 1 year old; the remaining birds were juveniles.

which indicates that the jackdaws transferred food items to the individuals from whom they had received food. The results are thus consistent with food-for-food reciprocity as an explanation for food sharing in jackdaws. The reciprocal transfer of food between particular individuals may be the result of a symmetry-based relationship, where individual X associates most frequently with individual Y and therefore, when food transfers take place, they transfer to one another. We controlled for this possibility by removing the effect of proximity on food transfers. As a measure of proximity, we used the summed number of cases of three affiliative behaviour types: cofeeding, bill twining and joint manipulation of an object. Matrix Tester allows one to test for a correlation between two matrices while correcting for a third matrix. When the food transfer matrix was corrected for affiliative behaviour (cofeeding, bill twining and joint manipulation of an object) the reciprocation remained significant (TauKr $= 0.181$, $N = 12$, $P = 0.027$). The matrix comparison showed no correlation between donor-initiated transfers (TauKr $= 0.06$, $N = 12$, $P = 0.26$). However, the donor-initiated transfer matrix was correlated with the allopreening matrix (TauKr $= 0.275$, $N = 12$, $P = 0.002$).

Harassment avoidance

There was a significant positive relation between donor-initiated transfers and begging by the recipient (TauKr $= 0.323$, $N = 12$, $P = 0.001$). When begging was controlled for in the reciprocity calculation for total food transfers, the correlation was nonsignificant (TauKr $= 0.143$, $N = 12$, $P = 0.06$).

Food offers as social signals

Dominance rank based on the two assessment methods, rank order of access to the food bowl and displacements won, was strongly correlated (Spearman rank correlation: $r_S = 0.85$, $N = 12$, $P < 0.001$). There was no relation between the number of donor-initiated transfers and the donor's dominance rank ($r_S = -0.463$, $N = 12$, $P = 0.13$). We found no evidence that donor-initiated transfers occur unidirectionally from dominant to subordinate individuals (GLM: $F_{1,11} = 0.13$, $P > 0.7$).

DISCUSSION

This study produced four main results. First, juvenile jackdaws shared food regularly with more than one individual, and donors initiated a large proportion of the transfers. Second, these jackdaws reduced the frequency of food sharing and the number of recipients during the 2 months of this study. Third, jackdaws shared significantly more highly preferred food than less preferred food.

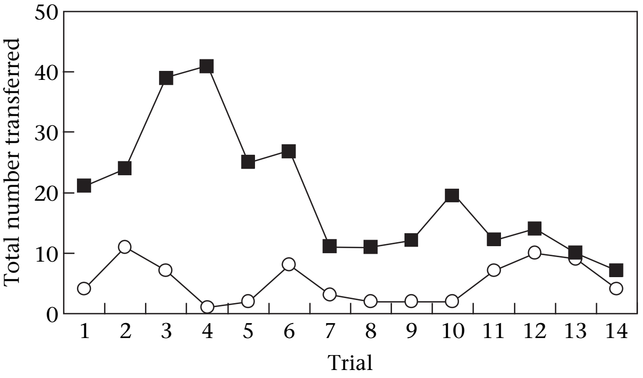

Figure 3. The total number of food transfers involving corn (○) and waxworm (■) over 14 consecutive trials for 12 jackdaws.

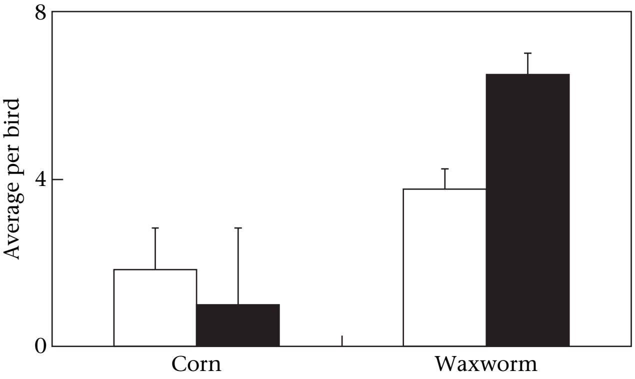

Figure 4. The mean + SEM number of instances of begging (☐) and instances of active giving of corn or waxworms (■) ($N = 12$ jackdaws).

Finally, the results were consistent with two of three proposed explanations for food sharing, reciprocity and harassment avoidance. We discuss each of these findings in turn.

The jackdaws transferred 11.1% of temporarily available food items to one another. These food transfers cannot be explained through inclusive fitness or as courtship displays. An inclusive fitness explanation for food transfers predicts more transfers between siblings than between unrelated individuals but the transfer rate was no different between siblings and nonsiblings. Food sharing may also be explained as courtship behaviour and in that context it is common in many bird species. If food sharing is an aspect of courtship then it should be more frequent between males and females than between same-sex individuals. The jackdaws did not show more food sharing between the sexes, but this may result from the biased sex ratio in our group. In addition, by analysing the data over different periods, we showed that food transfers between males and females did not increase with time as one would predict if food sharing served a courtship function.

The frequency of food sharing and the number of individuals with whom each donor shared decreased over time. However, the number of items transferred to each recipient remained constant. Over time, food sharing became more focused on specific individuals and was restricted to only one or two recipients by the age of 4 months posthatching. Furthermore, the two adult birds transferred fewer food items than did juvenile birds, suggesting that this decline in the frequency of food sharing was a developmental effect. There was also considerable variation between birds in the number of individuals with whom a jackdaw shared (Fig. 2), which may contribute to socialization in this species.

The pattern of food transfer in the jackdaws in our study is consistent with both the reciprocity and harassment avoidance hypotheses, but not with the social status hypothesis. In support of the reciprocity hypothesis, individuals transferred food mainly to those from whom they received food. It seems unlikely that these reciprocal exchanges occurred purely because of proximity. Although the jackdaws shared with an average of three individuals, some birds shared with eight of 11 potential recipients during one feeding trial, which suggests that many of the transfers could not have been based on proximity. The donor typically offered food to three individuals before giving a food item to a recipient, indicating that donors move around just before giving food, and they do not necessarily give the food to the closest individual. Furthermore, although there was a correlation between the total numbers of food transfers given and received, this was not the case for donor-initiated transfers alone. However, there was a positive relation between donor-initiated transfers and allopreening, which is similar to grooming in primates (Byrne 1995). Allopreening in jackdaws is usually directed to the head, which the recipient cannot reach itself, and this probably has fitness benefits for the recipient by reducing parasite load (e.g. Hart & Hart 1992).

The harassment avoidance hypothesis suggests that cooperation expressed by food sharing can be explained by mutualism, where both individuals benefit immediately from the interaction. The recipient's benefit is obtaining food and the donor's benefit is being able to consume the food without being disturbed. We found a positive relation between the amount of begging to which a bird was exposed and the amount of food that it shared with the begging individual.

Although begging seems to contribute to food transfers in jackdaws, the donor's costs of being exposed to begging are unclear. The donors in our study actively appeared to avoid the begging individual by moving away from it. Furthermore, unlike in chimpanzees, where begging rarely results in forceful claiming of another's food (de Waal 2005), begging in jackdaws often precedes the begging bird forcefully trying to obtain the food item from the possessor. The possessor may avoid this struggle by sharing food with the begging individual.

The hypothesis that giving food signals social status was not supported by this study. Both the prestige-enhancing and dominance-affirming hypotheses of social status predict that active giving takes place only from dominant to subordinate, but in jackdaws active giving took place from subordinates to dominants and vice versa. Jackdaws actively gave more of a preferred food type (waxworm) than of a less preferred food type (corn), but the begging rates for the two food types did not differ. Thus, there was an excess of active giving of waxworms that cannot be explained by the recipients' soliciting behaviour. Food sharing in corvids may facilitate formation and maintenance of social bonds between specific individuals regardless of sex (Emery 2004). Thus, the food offer may not be a social signal of status directed at other group members, but rather may be a signal of positive intent towards the recipient. This hypothesis is supported by the finding that the jackdaws reduced the number of individuals with whom they shared over time.

Food sharing and especially donor-initiated transfers appear to be more common in jackdaws than in the primates studied so far. One obvious difference between the behavioural repertoires of primates and birds may underlie the higher rate of active food sharing in birds. In contrast to mammals, most altricial bird species actively provide solid food to their young. Perhaps jackdaws have to learn with whom to share in preparation for courtship and rearing of young. As juveniles, they may display active giving in an unfocused form that becomes more focused during maturation. Jamieson (1989) suggested that allofeeding by juvenile helpers in communal breeding species may be the result of early exposure to the relevant stimuli (begging birds) for eliciting provisioning behaviour. In other words, allofeeding may be a by-product of delayed dispersal. An important difference between food sharing in jackdaws and helping behaviour in cooperative breeders, however, is that cooperative breeders provision individuals of a younger generation, whereas in jackdaws we found sharing between peers. In addition, a large proportion of the food transfers in jackdaws were initiated by donors and were not a response to gaping or begging, which refutes the idea that food sharing in jackdaws is a maladaptive behavioural response to stimuli that are out of context.

A striking aspect of the food transfers in jackdaws was the proportion of transfers initiated by the donor. With respect to food sharing in primates, de Waal (1989, page

434) stated that: 'the process observed in nonhuman primates falls short of at least one characteristic of human food-sharing: voluntary handing over of food is virtually absent'. Indeed, for three primate species studied, the proportion of donor-initiated transfers remained below 3%, but for jackdaws this proportion was 26% of total number of transfers. (chimpanzee: 0.2%, $N = 2377$ transfers; bonobo, *Pan paniscus*: 2.7%, $N = 598$ transfers; capuchin: 1.6%, $N = 931$ transfers; de Waal 1996; jackdaw: 26%, $N = 346$ transfers; this study).

The jackdaws were more likely to transfer food actively after they had eaten several items, indicating that satiation affected donor-initiated transfers. Nevertheless, the motivation for actively transferring food remains difficult to explain from a learning perspective. If reciprocity is the mechanism that underlies active giving of food, then this behaviour needs to be acquired and maintained through delayed reinforcement, since donors do not receive immediate rewards. Instead, donors have to wait until recipients return the favour later. Learning through delayed reinforcement is not thought to operate when the stimulus and conditioned response are separated by more than a few seconds (e.g. Grice 1948). Other aspects of the delayed reward, such as temporal discounting and memory for who gave previously, may pose further cognitive constraints on active sharing (Cheney & Seyfarth 1992; Stevens & Hauser 2004). These cognitive constraints apply mainly to donor-initiated transfers, since recipient-initiated transfers (tolerated theft) can be explained through direct stimulus—reward mechanisms operating on the receiver and do not need to rely on memory of previous interactions or recognition of individuals. Recipient-initiated transfers require the inhibition of defence behaviour from donors, but this inhibition could be motivated at least partly by a harassment avoidance mechanism. Given that the cognitive constraints on cooperation in the form of food sharing mainly apply to donor-initiated transfers, these donor-initiated favours need to be separated from recipient-solicited favours in studies that examine cooperation in relation to cognition.

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