



## Distinct patterns of food offering and co-feeding in rooks

CHRISTELLE SCHEID\*, JUDITH SCHMIDT†‡ & RONALD NOË\*

\*IPHC-DEPE, ULP, CNRS

†Konrad Lorenz Forschungsstelle, Gruenau im Almtal, Austria

‡Department of Behavioural Biology, University of Vienna, Austria

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Food sharing is widespread in animals and has received considerable attention because of its apparently altruistic nature. Sharing food includes different behaviours, notably offering food and co-feeding. In primates, food sharing between unrelated animals can largely be explained by reciprocity and harassment avoidance, while kin selection explains most instances of food sharing in cooperatively breeding birds. 'Costly signalling' has also been put forward as an explanation of food sharing in birds. A recent study on jackdaws, *Corvus monedula*, suggested that the costly signal of food sharing, notably offering food between juvenile birds, may play an essential role in the formation of pair bonds. We analysed food-sharing patterns in a group of juvenile rooks, *Corvus frugilegus* and found differences between the two modes of food sharing: offering food and co-feeding. Food offering was affected by dominance relationships and by gender, whereas co-feeding was reciprocated and occurred mainly between nestmates. We conclude that offering food and tolerating co-feeding have different functions in rooks: food offering acts as a costly signal directed to all members of the group whereas patterns of tolerating co-feeding were in line with both the reciprocity and pair-bonding hypotheses.

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In many cases the function of food sharing is no great mystery, notably in the context of reproduction, for example, parents feeding dependent offspring or monogamous birds feeding incubating partners. Other forms of food sharing are harder to explain within evolutionary theory because of their apparently altruistic nature. Examples include blood donations in vampire bats, *Desmodus rotundus* (Wilkinson 1984), sharing of meat and plant material in chimpanzees, *Pan troglodytes* (Boesch & Boesch 1989; de Waal 1989), and sharing of food between adult lion tamarins, *Leontopithecus rosalia* (Rapaport 2001), young ravens, *Corvus corax* (Heinrich 1988; Heinrich and Marzluff 1995) and juvenile jackdaws, *Corvus monedula* (de Kort et al. 2006; von Bayern et al. 2007). Two forms of food sharing should be distinguished: offering food to

another individual with the hand, mouth or beak, and co-feeding, which is feeding together around a source of food that could be monopolized. The functions of these two forms of sharing can be the same, but need not be. Several explanations for sharing between conspecifics that are neither closely related nor reproducing together have been put forward.

The first hypothesis is based on reciprocity (Trivers 1971), that is, food is shared because the receivers are likely to reciprocate in kind, as described for chimpanzees (de Waal 1997), capuchin monkeys, *Cebus apella* (de Waal 2000; Hauser et al. 2003) and vampire bats (Wilkinson 1984) or by giving other commodities, such as grooming (de Waal 1997) or support during conflicts (Mitani & Watts 2001). The latter phenomenon was labelled 'interchange' by Hemelrijk & Ek (1991) to distinguish it from 'reciprocity' which refers to the exchange of commodities of the same kind, for example, grooming for grooming or food for food.

A second explanation is based on costly signalling theory, which was introduced in the biological literature

Correspondence: C. Scheid, IPHC-DEPE, ULP, CNRS, 23 rue Becquerel, 67087 Strasbourg, France (email: [christelle.scheid@c-strasbourg.fr](mailto:christelle.scheid@c-strasbourg.fr)). J. Schmidt is at the Department of Behavioural Biology, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria.

by Zahavi (1975, 1977) and further developed by Grafen (1990a, b), but which has an older counterpart in the economic literature (Veblen 1899; Spence 1973). Zahavi (1990) suggested that offering food is a costly signal in Arabian babblers, *Turdoides squamiceps*. He found that food transfers were always directed down the hierarchy, while high-ranking individuals refused to take the food offered by lower-ranking birds. No direct food-for-food reciprocity was seen. It has been proposed that the advantages of such behaviour are related to the message conveyed by the costly signal. In a courtship context, several studies suggested that offering food signals the quality of the male and reflects his ability to forage and to provide food to the offspring (Wiggins & Morris 1986; Green & Krebs 1995). Females may then use courtship feeding to evaluate and choose a mate (Lack 1940; Helfenstein et al. 2003). In social species, offering food may signal the quality of an individual not only to the receiving party but also indirectly to bystanders of the interaction, thus improving the donor's 'reputation' as a food provider.

A third idea is that food can be shared under pressure. This phenomenon, now usually labelled 'harassment avoidance' (Stevens 2004), goes back to the idea of 'tolerated theft' first suggested by Blurton Jones (1984) and has been suggested as an explanation of food sharing in several animal species, for example, rhesus monkeys, *Macaca mulatta* (Hauser 1992), rooks, *Corvus frugilegus* (Emery 2004) and chimpanzees (Gilby 2006). These are species in which food possessors are often approached by beggars and it could be more costly to resist than to share the meal.

We studied food sharing in juvenile rooks, a Eurasian corvid that nests, roosts and forages in large flocks (Madge & Burn 1996). Examples of food sharing have been described in several corvid species (ravens: Heinrich 1988; jackdaws: de Kort et al. 2006; rooks: Emery 2004; Emery et al. 2007). de Kort et al. (2006) focused on patterns of food sharing in juvenile jackdaws and showed that the birds were sharing food with conspecifics independently of sex, kinship and dominance relationships. The authors concluded that food sharing in juvenile jackdaws was in accordance with both the reciprocity and harassment avoidance hypotheses. However, a complementary study (von Bayern et al. 2007) did not confirm the harassment avoidance hypothesis and explained reciprocity as a by-product of proximity. The authors suggested that the social signal hypothesis could not be rejected and that food sharing may be essential for the formation of social bonds between juvenile jackdaws.

Rooks have complex social relationships (Emery et al. 2007) and regularly share food with nonkin conspecifics (Emery 2004; Emery et al. 2007). Like jackdaws, they form pair bonds that can last for life (Coombs 1978). In the present study, we analysed patterns of food sharing in a group of captive juvenile rooks and assessed whether food transfers were in accordance with the hypotheses listed above. We predicted that if food sharing was in line with kin selection, the frequency of food shared among nestmates should be higher than expected by chance. If food sharing was in accordance with reciprocity, we should find a significant correlation between food

shared and food received, or in the case of interchange, we should find a correlation between food shared and preening received and/or food shared and help received during conflicts. If food sharing acts as a social signal, birds may share food more often with subordinate partners than with dominant ones. Finally, if food sharing between juvenile rooks plays a role in the formation of pair bonds, we should find that animals that frequently exchange food should form pair bonds later in life.

## METHODS

### Animals and Housing Conditions

The rooks used in this study were collected from a colony breeding on the campus of Cronenbourg in Strasbourg, France. In May 2006 we took 14 young birds from their nests when they were between 2 and 4 weeks old. They were hand reared and placed in an aviary as soon as they could fly. The group was composed of one triad of nestmates, three pairs of nestmates and five birds that had no nestmates. During hand rearing, nestmates were put together in a nestbox. Two of the five singletons (K, N) were in a box with a pair of nestmates, the third (M) was placed with another pair of nestmates and the other two singletons (T, S) were alone in a box (Table 1). The birds were identified with coloured rings on their legs and their sex was determined by genetic analysis of blood samples. The group was composed of 10 males and four females during period 1 (June–August 2006). However, between period 1 and period 2 (May–September 2007), two of the birds (S, A) died. The birds were housed in an external aviary (4 × 6 m and 2 m high), which was divided in half and an indoor room (4 × 2 m and 3 m high), which was divided into three compartments. The whole group always had access to all compartments. After they reached nutritional independence, the birds were fed

Table 1. Composition of the study group

Individual	Estimated week			Sex
	of hatching	Original nest	Nestbox	
T	14	1	1	M
S*	14	2	2	M
A*	15	3	3	M
E	15	3	3	M
J	15	3	3	F
H	15	4	4	M
V	15	4	4	F
O	15	5	5	M
I	16	5	5	F
P	17	6	6	F
B	17	6	6	M
K	17	7	6	M
N	17	8	6	M
M	15	9	5	M

The week of hatching was estimated on the basis of the developmental stage of the bird when captured. The same number in the 'original nest' or 'nestbox' columns indicates that birds were nestmates in their original nest and in their nestbox during hand rearing, respectively. M = male, F = female. Asterisks indicate birds that died during the study.

three times a day with cereals, cheese, eggs, meat and vegetables. They always had access to fresh water.

## Observations

Observations started as soon as all birds were placed in the aviary (end of May 2006) and continued until September 2007. We conducted 10 min focal animal samples (Altmann 1974). No bird was observed more than twice daily, with at least 1 h between two samples of the same individual. Focal samples were collected between 0800 and 1800 hours. The number of observations was evenly distributed over the day and across individuals. The identity and order of birds observed were randomly chosen before the observations started. A total of 250 h of focal observations were done by two observers (C.S. and T.H.). The interobserver concordance (Cohen 1960) for the frequency of behavioural elements was 91%. Focal observations were used notably to analyse instances of allopreening and of contact sitting. Allopreening was defined as one bird passing its beak through the feathers of another bird and contact sitting as two birds sitting closer than 5 cm from each other. In addition, we used ad libitum sampling (Altmann 1974) for food-sharing data, agonistic conflicts and coalitionary support, which was defined as the active intervention of third parties immediately during a conflict or in the 5 s following the agonistic interaction. We split the observation period into the 'juvenile phase' (period 1; 1 June–31 August 2006) and the 'adult phase' (period 2; 1 May 2007–30 September 2007). Food-sharing events were recorded exclusively during period 1. The data collected in period 2 were used to analyse frequencies of contact sitting after pairs were formed. Indeed rooks tend to form stable and often exclusive pairs in their first year of life (Emery et al. 2007). As two birds (A, S) died between period 1 and period 2, we excluded data from these two birds for the analysis that included the two periods.

## Single-feeder Trials

Between June and August 2006, 28 single-feeder trials (two or three trials per week) were conducted by T.H. and J.S. A bowl containing a large quantity of small food items (120 g of sausage cut into small cubes) was fixed on a wall of the outdoor aviary at a height of 30 cm. To reach the food, birds had to jump on a platform (20 × 20 × 20 cm) that was placed in front of the bowl. The size of the platform allowed only one bird at a time to take food from the bowl. No other food was available in the aviary during the trials. We recorded the order and the frequency (=producing) of passage on the platform for each bird. All food-sharing events were recorded until the bowl was empty, which was the case after 20 min on average.

## Data Analysis

We distinguished two modes of food sharing: offering food and co-feeding. During 'offering food' one bird

actively put the food item into the beak of another bird. We considered an interaction as 'co-feeding' when a bird in possession of food items that were easy to monopolize allowed another to approach and feed together. Food was considered as easy to monopolize if the bird could carry it in its beak. We excluded cases in which one of the birds showed threatening behaviour. We analysed offering-food events and co-feeding events separately. In both cases the 'donor' was the bird that was initially in possession of the food.

We analysed the food transfer data collected ad libitum outside trials and those collected during single-feeder trials separately. As we found the same patterns (Mantel  $Z$  test and Pearson  $r$  of matrix correlations: food offering:  $r = 0.90$ ,  $P = 0.0001$ ; co-feeding:  $r = 0.75$ ,  $P = 0.0001$ ), we combined the data from both methods in one matrix and conducted the statistics with this matrix. To see whether there was a difference in the frequency of food offering and of co-feeding across the 3 months of period 1, we split the data into three periods (June, July and August) and carried out a Friedman test. We used a Fisher's exact test to assess whether the gender of birds had an effect on the patterns of both food-sharing behaviours.

To test whether food sharing was in accordance with the reciprocity hypothesis, we carried out matrix correlations using the Mantel  $Z$  test with 10 000 permutations and Pearson  $r$  correlation. We also tested for interchange between both food offering and co-feeding and allopreening as well as lending support in conflicts.

We also carried out matrix correlations to assess the effect of familiarity on food-sharing rates. We used two measures of familiarity: (1) birds sharing the same box during the period of hand rearing and (2) birds originating from the same natal nest. A cell in the matrices contained a 1 for dyads from the same box or natal nest, respectively, and a 0 for all other dyads.

The dominance hierarchy was established using the Matman software package version 1.0 (Noldus, Wageningen, The Netherlands) based on all aggressive (threat, dominant posture) and submissive (avoid, submissive posture) interactions that occurred in period 1, during both focal animal and ad libitum observations. A total of 1234 agonistic interactions were recorded, all birds being involved. We found a highly linear hierarchy ( $h = 0.94$ ,  $P \leq 0.001$ ), males being dominant over females. We approached the question of the effect of dominance on food sharing in two steps. First we tested whether there was a correlation between the rank of the donor and the number of food items shared using a Spearman rank correlation test. Then we tested for the dominance relationship between donor and receiver by comparing the number of transfers directed up and down the dominance hierarchy using a Wilcoxon signed-ranks test. As all males were dominant over females and to exclude a confounding effect between sex and dominance, we also did these tests with the males only.

Finally, we looked for the role of food sharing in pair formation by comparing matrices of offering food and co-feeding for period 1 with a matrix of frequencies of contact sitting for period 2 when pairs were formed.

Matrix correlations were carried out with Matman (Vries et al. 1993). Wilcoxon tests and Spearman correlations were calculated by hand according to Siegel & Castellan (1988). All tests were two tailed with  $\alpha < 0.05$ . The alpha levels were corrected for the use of the same data in multiple tests according to Benjamini & Yekutieli (2001) following Narum (2006).

### Ethical Note

We had permits from the Direction Départementale de l'Agriculture et de la Forêt to take birds from the wild and from the Direction Départementale des Services Vétérinaires to do experimental work with them. The birds remained in captivity after this study to be used in similar research. For the DNA sexing, 0.2 ml of blood was taken from the brachial vein. Birds were immediately released after this procedure which lasted no more than 5 min.

## RESULTS

### General Patterns

#### Offering food

The feeding of flockmates started 2 weeks after fledging (end of May 2006) and occurred regularly during period 1. There was no significant difference in the frequency of food items offered across the 3 months of period 1 (Friedman test:  $F_r = 4.05$ ,  $P = 0.1$ ). All birds were involved in food sharing but not all in the same way. Five individuals acted both as donor and as receiver, four were donors exclusively and five received food but never donated. The four females of the group were among the latter. Food offering was observed significantly more often in males than in females (Fisher's exact test:  $N = 14$ ,  $P = 0.005$ ). The number of food items offered ( $N = 120$ ) was very variable across donors and ranged between one and 44 transfers. The four exclusive donors were the birds that offered the highest number of food items to others. Although donors shared with one to three recipients, they showed a strong preference for one among them (ranging from 73% to 92% of the donor's food transfers). Recipients were fed by one to four different donors. There were few signs of offering food under pressure: recipients approached the food owner and begged in 29% of cases of food offers and no other forms of harassment were observed.

#### Co-feeding

Co-feeding ( $N = 83$ ) was seen for the first time about 4 weeks after fledging. No significant differences in the frequency of co-feeding were found for the 3 months of period 1 (Friedman test:  $F_r = 4.95$ ,  $P = 0.1$ ). Eleven birds played the role of both donor and receiver in co-feeding acts; two female individuals acted only as receivers but never as donors and one male as donor but never as receiver. We found no significant gender difference in the tendency to co-feed (Fisher's exact test:  $N = 14$ ,  $P = 0.07$ ). Most birds co-fed with one to three flockmates, but one individual shared with as many as seven others.

All birds had between one and four donors. In 33% of cases, owners shared after begging by the recipient.

### Reciprocity

Food was transferred in both directions in only one of 23 dyads in which it was offered, while five of 23 dyads in which we observed co-feeding were bidirectional, which means that both members of the dyad played the roles of donor and receiver over the 3 months of observation. During period 1, we observed 139 instances of allopreening and 41 cases of help received during conflicts. Table 2 summarizes our analysis of reciprocity using matrix statistics. We found no significant correlation between offering food and food received either for preening received or for help received. After correction ( $\alpha' = 0.02$ ), the only significant form of reciprocity we found was mutual tolerance of co-feeding. The interpretation of these results is open to debate since we chose only one of several possible methods of correcting the alpha level and the  $P$  values and the corrected error rate are similar. However, it is more important to point out that the significant and near-significant results were due to a few dyads, which should lead to caution when drawing conclusions at the group level.

### Dominance Effects

Concerning single-feeder trials, we found a significant correlation between producing (=frequency of visits to the feeder) and the rank of birds (Spearman correlation:  $r_s = 0.73$ ,  $N = 14$ ,  $P = 0.005$ ). Thus for the analysis of dominance effects on food sharing patterns, we corrected food transfers for producing, by dividing the number of food transfers by the frequency of visits to the feeder.

We found a significant correlation between the rank of the donor and the number of food items offered ( $r_s = 0.89$ ,  $N = 14$ ,  $P = 0.001$ ), suggesting that high-ranking individuals offered more food items than low-ranking ones. This correlation remained significant when we considered only the data from focal and ad libitum observations outside the trials with a single feeder ( $r_s = 0.67$ ,  $N = 14$ ,  $P = 0.02$ ) and when only males were taken into account in the analysis ( $r_s = 0.75$ ,  $N = 10$ ,  $P = 0.02$ ). In line with this finding we also found that the birds were

Table 2. Summary of the reciprocity analysis

	Same act reciprocated		Interchange with			
			Allopreening		Coalitional support	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Offering food	-0.017	0.47	0.011	0.21	0.017	0.18
Co-feeding	<b>0.33</b>	<b>0.002</b>	0.18	0.025	0.018	0.026

The results of matrix correlations are listed. Significant result (after correction for multiple tests) is marked in bold.

more likely to offer food to a subordinate group member than to a dominant one (Wilcoxon signed-ranks test:  $T = 43.5$ ,  $N = 9$ ,  $P = 0.006$ ; males only:  $T = 41$ ,  $N = 9$ ,  $P = 0.027$ ; Fig. 1). In contrast, we did not find a significant correlation between the rank of donors and the number of co-feeding events ( $r_s = 0.37$ ,  $N = 14$ ,  $P = 0.2$ ). Moreover, for co-feedings, birds did not share food significantly more often with subordinate partners than with dominant partners (Wilcoxon signed-ranks test:  $T = 56.5$ ,  $N = 12$ ,  $P = 0.1$ ; Fig. 1).

### Familiarity

Nestmates were always included in the set of recipients for the nine birds that had a nestmate in the group, both in the case of offering food and co-feeding. We obtained the same results irrespective of the parameter for familiarity chosen, sharing the same natal nest or the same box. Matrix statistics also revealed significant positive correlations between familiarity and co-feeding (Pearson correlation: box:  $r = 0.34$ ,  $N = 14$ ,  $P = 0.002$ ; natal nest:  $r = 0.19$ ,  $N = 14$ ,  $P = 0.04$ ) suggesting that birds did co-feed with their nestmates more often than expected by chance. However, for offering food, the results were not significant (box:  $r = 0.09$ ,  $N = 14$ ,  $P = 0.12$ ; natal nest:  $r = 0.09$ ,  $N = 14$ ,  $P = 0.09$ ).

### Pair Bonding

During period 2, four pairs (two male–male and two male–female) were formed, none of them by nestmates from the same natal nest. We observed 132 instances of contact sitting during period 2. Pairs spent a median of 84% (first and third quartiles: 65 and 100) of their ‘contact sitting time’, with their partner. We found no significant correlation between the matrices of offering food and the frequency of contact sitting (Pearson correlation:  $r = 0.03$ ,  $N = 14$ ,  $P = 0.13$ ). Indeed, none of the four pairs was formed by a donor and its preferred receiver (the

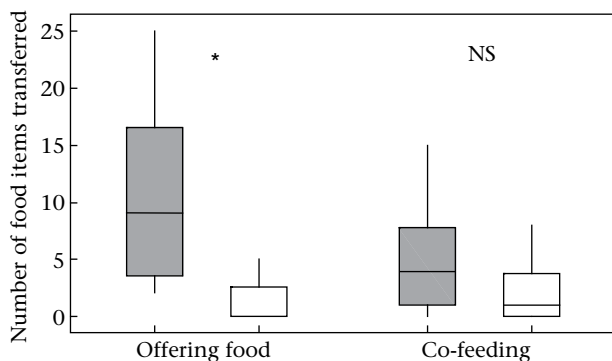
individual to which the donor transferred about 80% of all food items). However, matrix statistics revealed a positive correlation between co-feeding events and frequency of contact sitting ( $r = 0.28$ ,  $N = 14$ ,  $P = 0.017$ ).

## DISCUSSION

We found clear differences between offering food and co-feeding in our analyses of the correlations with rank and dominance, as well as familiarity and pair bonding. Moreover, the gender of the donors appeared to play a role in food offering but not in co-feeding. Our results for reciprocity and interchange with allopreening and support in conflicts suggested only a weak difference between the two modes of sharing. Finally, for both behaviours, we found little evidence for sharing food under pressure. The differences observed between the patterns of offering food and co-feeding may result from donors selecting the recipients with whom they want to share when offering food. The selected recipients were not necessarily nestmates as there was no correlation with the familiarity matrices. In contrast, instances of co-feeding followed an approach by the recipients who preferentially approached affiliated group members. Thus the different patterns of food offering and co-feeding may reflect differences in motivation of food owners and birds looking for food.

Our results provide support for a ‘signalling’ function of offering food. Food was offered significantly more often by the dominant member of a dyad than by the subordinate member and there was also a positive correlation between the rank of the donor and the number of food items offered. The fact that food was more accessible for higher-ranking birds, and therefore these birds could act as donors more often, does not seem to explain this pattern since we also found it in our observations when food was offered ad libitum. No such significant effect of dominance was found for co-feeding, which means that this behaviour is unlikely to fulfil the same signalling function as offering food. It is remarkable, however, that high-ranking animals did tolerate animals lower in rank feeding beside them. Co-feeding was, however, linked to pair bonding at a late stage and tended to be paid back in kind or in alternative currencies, such as preening and support in conflicts. The latter results were not statistically significant after correction for the use of the same data sets in multiple tests. However, the lack of a significant correlation between food sharing and preening or help does not exclude the interchange hypothesis, as other currencies may be exchanged.

The suggestion that offering food acts as a signal in birds is not new. Males may feed their partners to signal their quality (Helfenstein et al. 2003) or their ability to provide food to the future offspring (Wiggins & Morris 1986). Offering food among members of the same sex also suggests that this behaviour acts as a costly signal (Zahavi 1990; Gintis et al. 2001; Kalishov et al. 2005). In the present study, we found that only males offered food to others, and although the sample size is too small to draw general conclusions, it suggests that there is a sex bias in this trait.



**Figure 1.** Number of food items transferred to subordinate (grey) and dominant (white) partners, for offering food and co-feeding. Boxes represent the interquartile range, bars within boxes are median values, and whiskers indicate the 5th and 95th percentiles. \* $P \leq 0.01$ , Wilcoxon signed-ranks test.

However, males fed not only females but also other males, which indicates that this behaviour cannot be considered exclusively as courtship feeding. Nevertheless, it is possible that this pattern is due to the biased sex ratio of our study group.

Our results are very different from those obtained for jackdaws (de Kort et al. 2006; von Bayern et al. 2007). de Kort et al. (2006) suggested that food sharing in jackdaws was in accordance with the reciprocity and harassment avoidance hypotheses. However, a second study of food sharing in juvenile jackdaws by the same research group (von Bayern et al. 2007) arrived at different conclusions. Sharing food, and especially offering food, played an essential role in the formation of pair bonds because offering food mainly took place between future pairmates. The authors proposed that offering food could act as a costly signal directed simultaneously towards a potential social partner as well as to the group. We found no obvious relationship between offering food and pair formation and therefore tentatively assume that offering food in our rooks was used to convey a message to the flock in general, for example, about the quality of the donor.

There are at least three possible explanations for the differences observed between the present study on rooks and the two studies on jackdaws mentioned above. First, there is a difference in terminology and definitions. Our 'food offering' corresponds to 'donor-initiated transfers' in de Kort et al.'s (2006) study but co-feeding does not correspond to 'recipient-initiated transfer'. Indeed 'recipient-initiated transfers' were tolerated theft, whereas co-feeding refers to two birds feeding together from a small source of food. Second, our findings may reflect species-specific differences. Food sharing among juveniles may play a different role in these two species although rooks and jackdaws are phylogenetically closely related (Haring et al. 2007). Third, the discrepancies may be caused by differences in methods. In both jackdaw studies each subject was handed pieces of food one after the other by an experimenter. After offering 10 food items to the first bird, the experimenter gave 10 pieces to a second bird and so on until all birds were fed. These differences between experimental set-up may have important consequences for food-sharing patterns. First, when only one bird of the group is handling food, the attention of all other group members is directed to this single bird. As a consequence, there is considerable pressure on this single individual and harassment may be frequent. Second, the jackdaws were fed at the place where they were sitting. In this situation, a bird is more likely to feed another one close by. This can result, as suggested by von Bayern et al. (2007), in reciprocity as a by-product of proximity (symmetry-based reciprocity, de Waal 2000). The fact that our birds could obtain food items ad libitum also means that all could pass the point at which they were satiated, which obviously varies between individuals. This means that larger, and often higher-ranking, birds also had the opportunity to share a surplus. This may have led to more frequent observations of offering food by high-ranking birds in our study.

Our results support the idea that juvenile rooks offer food to flockmates as a costly social signal of quality. We

did not find evidence for a role in pair formation. In contrast, co-feeding appeared to be a form of tolerance around food that occurs mainly between affiliated individuals and is correlated with subsequent pair formation. Our study does not allow inferences about the cause–effect relationship: sharing could be instrumental in pair bonding or animals that are mutually attracted to each other could share more than others. Our conclusions differ from two previous studies that addressed similar questions (de Kort et al. 2006; von Bayern et al. 2007). We suggest that these differences are due to differences in experimental procedures rather than to fundamental differences between species or populations.

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