

# Social influences on foraging by rooks (*Corvus frugilegus*)

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## Summary

This study investigates the influence of social context on foraging by rooks. In Experiment 1, we show that rooks eat significantly more food in the presence of a conspecific than alone. Experiment 2 investigated the effect of social influences on rooks' preferences for specific foods. Birds were given two novel or two familiar foods, one of which they could observe a conspecific eating. Rooks selectively consumed the same food as the demonstrator when the foods were novel, but not when they were familiar. In Experiment 3, subjects could forage for familiar foods in each of two novel feeders, one of which was identical to the demonstrator's feeder. Subjects did not discriminate between the feeders, irrespective of whether or not the food contained within the feeder was visible.

*Keywords:* corvids, feeding behavior, rooks, social facilitation, social learning.

## Introduction

Adult humans consume up to 75% more food when others are eating compared to when dining alone, and the amount of food eaten correlates positively with the number of guests that are present (see Herman et al., 2003 for a review). The propensity to increase food consumption in the presence of co-eaters has traditionally been attributed to social facilitation (e.g., de Castro & de Castro, 1989; de Castro & Brewer, 1991; but see Pliner et al., 2006);

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an increase in the expression of a specific behaviour when in the presence of others who are engaging in the same behaviour (Clayton, 1978).

Increased food consumption in the presence of co-eaters has been documented throughout the animal kingdom (Table 1). Moreover, a study on pig-tailed macaques found that the ability to hear another individual eating was sufficient to enhance a subject's feeding rate (Ferrari et al., 2005). Ferrari and colleagues suggested that, in terms of the neurophysiological basis of socially facilitated feeding, the mirror neuron system might act to stimulate the production of a motor output that matches the observed/heard action (Ferrari et al., 2005).

Whilst the causal structure underlying socially facilitated feeding requires further investigation, one functional benefit of this phenomenon might be the increased acceptance of new foods by naïve individuals (Turner, 1965; Galef, 1993; Frigaszy & Visalberghi, 2004). By consuming unknown foods, animals risk illness or even death. This risk may explain why many species are initially reluctant to incorporate novel foods into their diet, a tendency described as food neophobia. Interactions with, or the presence of, feeding conspecifics are known to reduce food neophobia (e.g., marmosets, *Callithrix jacobs*, Voelkl et al., 2006; capuchins, *Cebus apella*, Visalberghi & Fragaszy, 1995; Visalberghi & Addessi, 2000; Addessi & Visalberghi, 2001) and to reinstate a preference for a previously devalued food (rats, *Rattus norvegicus*, Galef & Whiskin, 2000; Galef, 1986; hyaenas, *Crocuta crocuta*, Yoerg, 1991; cows, Angus & Hereford breeds, Ralphs et al., 1994; lambs, Provenza & Burritt, 1991). However, if socially facilitated feeding functions to foster novel food acceptance, rather than inflating food consumption generally, animals should selectively consume those new foods they have witnessed others eat (*specific* social facilitation; Visalberghi & Addessi, 2001).

The social transmission of novel food preferences by rats is well documented (see Galef, 1986 for review). After interacting with an individual who has recently eaten a distinctively flavoured food, naïve rats exhibit a preference for the same food as consumed by their conspecific demonstrator (Galef, 1988, 1996, 2001). Evidence for socially acquired novel food preferences in other animals, however, is not so clear. For example, when presented with two novel foods of varying colours, capuchins do not show a preference for the food of the same colour as that eaten by a demonstrator (Addessi & Visalberghi, 2001; see Addessi & Visalberghi, 2006, for the same finding in chimpanzees, *Pan troglodytes*).

**Table 1.** Species for which socially facilitated food consumption and the social facilitation of novel food consumption has been identified.

	Species
Delayed latency to consume novel foods	Blue jays, <i>Cyanocitta cristata</i> , Coppinger (1969). Capuchins, <i>Cebus apella</i> , Visalberghi et al. (2003). Marmosets, <i>Callithrix jacchus</i> , Voelkl et al. (2006). Mink, <i>Mustela vison</i> , Malmkvist et al. (2002). Ravens, <i>Corvus corax</i> , Heinrich (1988). Rhesus macaques, <i>Macaca mulatta</i> , Weiskrantz & Cowey (1963). Rats, <i>Rattus norvegicus</i> , Barnett (1958) & Galef (1970). Zebra finches, <i>Taeniopygia guttata</i> , Kelly & Marples (2004).
Socially facilitated food consumption	Budgerigars, <i>Melopsittacus undulates</i> , Soma & Hasegawa (2004). Canary, <i>Serinus canaries</i> , Cadieu et al. (1995). Capuchins, Galloway et al. (2005). Chaffinches, <i>Fringilla coelebs</i> , Turner (1965). Cows, <i>Bos taurus</i> , Phillips (2004). Red-billed weaverbirds, <i>Quelea quelea</i> , Lazarus (1979). Rhesus macaques, Harlow & Yudin (1933). Starlings, <i>Sturnus vulgaris</i> , Powell (1974). Yellow-faced Grassquit, <i>Tiaris olivaceam</i> , Black seedeater, <i>Sporophila aurita corvine</i> & White-collared seedeater, <i>Sporophila torquella</i> , Rubenstein et al. (1977). White Leghorn chickens, <i>Gallus domesticus</i> , Tolman (1964, 1967); Tolman & Wilson (1965); Keeling & Hurnik (1996).
Social facilitation of novel food consumption	Capuchins, Visalberghi & Adressi (2000, 2001); Visalberghi & Frigaszy (1995). Chacma baboons, <i>Papio ursinus</i> , Cambefort (1981). Cows, Ralphs et al. (1994). Domestic hens, Sherwin et al. (2002). Gerbils, <i>Meriones unguiculatus</i> , Forkman (1991). Lambs, <i>Ovis aries</i> , Thorhallsdottir et al. (1990). Merino sheep, Chapple & Wodzicka-Tomaszewska (1987). Marmosets, <i>Callithrix jacchus</i> , Vitale & Queyras (1997); Yamamoto & Lopez (2004); Schrauf et al. (2004). Rats, Galef (1993); Galef & Whiskin (2003); Galef (2000).

The purpose of the current study was to investigate whether rooks use social information to guide their feeding behaviour. There are three reasons why these birds might be particularly sensitive to the behaviour of others towards unknown foods. First, as omnivorous generalists rooks exploit a wide

variety of food, a factor that increases the chance they may ingest a toxic food (Goodwin, 1976; Cramp & Perrins, 1994). Indeed, the risks associated with novel food ingestion in rooks may be enhanced because, like other corvids, they eat carrion. Second, being highly social they are provided with opportunities to exploit social indicators of food palatability (Emery et al., 2007). Finally, like ravens (*Corvus corax*), rooks exhibit neophobia towards novel foods and objects (ravens, Heinrich, 1988; Kijne & Kotrschal, 2002; Stowe et al., 2006a; rooks, J. Dally, personal observations). A recent study of novel object exploration by ravens, however, found that object neophobia was moderated by social context. Specifically, the amount of time ravens spent close to, and manipulated new objects was significantly greater in the presence of a conspecific compared to when alone (Stowe et al., 2006b). Observing conspecifics interact with unknown foods might, therefore, reduce food neophobia in rooks and, thus, increase food consumption.

### Experiment 1

Experiment 1 explored the effect of social context (presence or absence of a conspecific) on the tendency for rooks to inspect and eat novel and familiar foods. Birds were provided with a novel and a familiar foodstuff in each of four conditions; Alone, in the presence of a conspecific (Social), in the presence of a conspecific eating a familiar food which was the same as (Social-Same), or different to (Social-Different), that given to the subject. One-hour later, the number and type of food items the subject had eaten, and/or discarded from the food bowl, were recorded.

Based on the observation that rooks, although social generalists, exhibit neophobia towards novel foods and objects, we made the following four predictions. First, irrespective of social condition, rooks would preferentially eat familiar foods. Second, that food consumption would be lowest in the Alone condition as conspecific presence often stimulates feeding (Table 1). Third, novel foods would be sampled most often in the social conditions, as in marmosets (Voelkl et al., 2006) and capuchins (Visalberghi & Fragaszy, 1995; Addessi & Visalberghi, 2001). Finally, we predicted that food consumption would be greatest in the Social-Same and Social-Different conditions in which a conspecific was both present and eating. However, based on the finding that the type of, albeit novel, food eaten by a demonstrator did not

moderate the feeding behaviour of another generalist omnivore, capuchins (Visalberghi & Addessi, 2000), we did not expect rooks' food consumption to differ significantly between these two conditions.

## **Materials and methods**

### *Subjects*

The subjects were twelve sexually mature rooks (10 females and 2 males). All birds were collected as nestlings and hand-raised at the University of Cambridge. The birds were group housed in an outside aviary (10 m wide  $\times$  3 m high  $\times$  20 m long). Experimental sessions were conducted in four adjacent test compartments (1 m long  $\times$  1 m wide  $\times$  2 m high) connected to the aviary. The test compartments were visually isolated from the main aviary, and physically separated from one another by internal wire mesh walls. The mesh walls meant that once inside a test compartment, adjacent compartments were visually accessible. On the morning of an experimental session, the birds entered the test compartments just prior to the provision of their maintenance diet (08.30 h), to ensure they were mildly hungry at test (09.00 h). Water was available ad libitum.

### *Procedure*

Four familiar foods and four novel foods were used in this experiment. Familiar foods were cooked egg yolk, fried egg-soaked bread, dog kibble and flapjack. Novel foods were pretzel, popcorn, banana and sliced black olives. In every experiment, novel foods were chosen because they are eaten by other captive corvids (A. von Bayern, personal communication, January 2006; C. Raby, personal communication, January 2006). As far as possible, all the foods were provided in 0.5 cm<sup>3</sup> pieces.

During test sessions, an opaque curtain was used to separate the four test compartments into two pairs, each pair of compartments being occluded from the other. At the start of a test session a rook entered one of the paired test compartments, and was presented with two 10 cm diameter metal food bowls placed 20 cm apart on a wooden shelf (79 cm  $\times$  44 cm). One bowl contained 40 pieces of a novel food and the other 40 pieces of a familiar food. Test sessions lasted for 1 h, during which time the birds were able to

feed freely. The number of food items was sufficient to ensure that the rooks' feeding behaviour was not constrained by the number of items available, and some pieces of food were always left uneaten at the end of the session.

As shown in Figure 1a, each bird was tested once in each of four conditions. In the Alone condition, the test compartment adjacent to the focal subject was empty, whereas in the other three conditions a conspecific was constantly present ('demonstrator'). In the Social condition, the demonstrator was simply present, whereas in the Social-Same condition the demonstrator was given a single food bowl containing 40 items of the familiar food being consumed by the test subject, and in the Social-Different condition the demonstrator was presented with 40 items of a familiar food, albeit of a different type to that being eaten by the test subject. All birds played the role of subject and demonstrator. The order in which the birds received the four test conditions was pseudo-randomised, such that no two birds were tested in the same condition on a single day. Similarly, food presentation was counter-balanced such that subjects were presented with the novel and familiar foods in every combination in each of the four conditions.

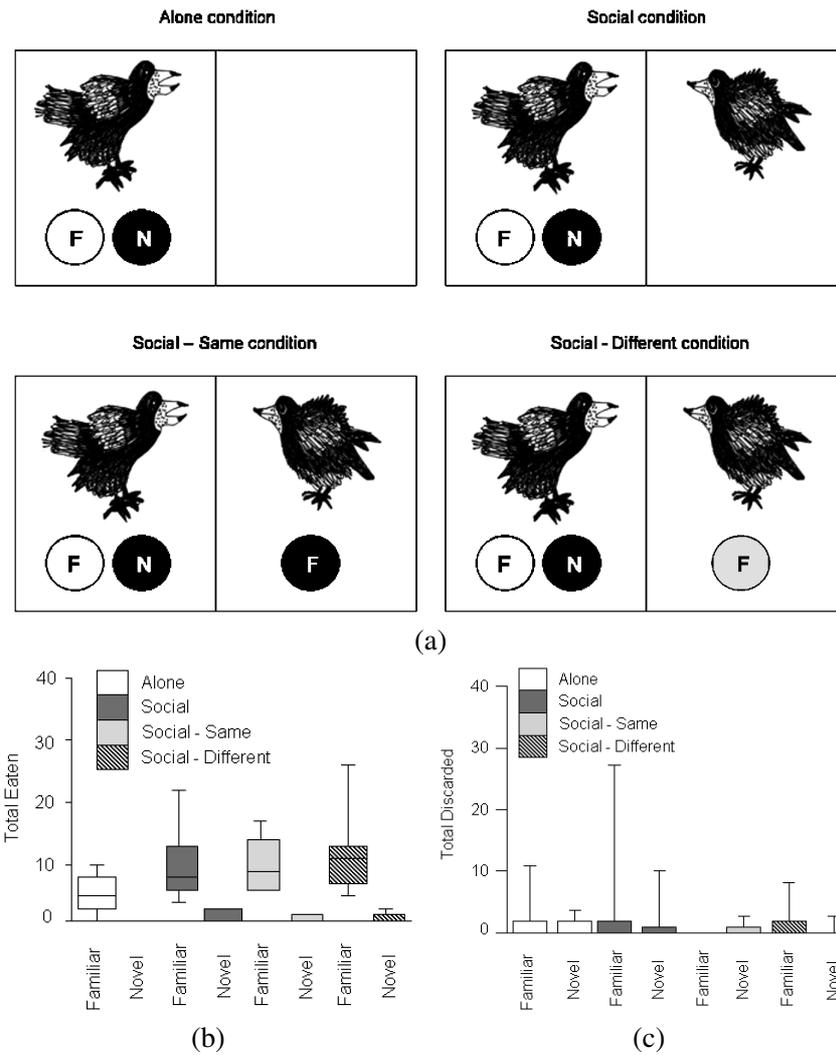
At the end of the 1-h test period, the food bowls were removed from the test compartment and the birds returned to the group. The experimenter recorded the number of Novel and Familiar food items that had been (a) discarded from the food bowl or (b) eaten.

#### *Statistical analysis*

Data was analysed using non-parametric statistics because it did not conform to assumptions of normality. Friedman's ANOVAs were used to compare (a) the number of items discarded in each condition (Alone, Social, Social-Same and Social-Different) and (b) the number of items eaten in each condition. Sign tests were conducted to compare the number of Novel and Familiar foods which were (a) eaten and (b) discarded in each of the four conditions. Alpha was set at 0.05 and  $p$  values were calculated for each test; medians and inter-quartile ranges (IQR) are reported throughout.

## **Results**

The rooks ate a significantly greater number of familiar food items relative to novel food items in all four conditions (see Figure 1b; Alone, Sign test;



**Figure 1.** (a) The experimental set-up for the Alone, Social, Social-Same and Social-Different conditions of Experiment 1. In each diagram, the subject is on the left hand side, and the demonstrator on the right. 'F' indicates a Familiar food and 'N' indicates a Novel food. In the Social-Same condition the same Familiar food was eaten by both the demonstrator and the subject. In the Social-Different condition the subject and demonstrator ate different Familiar foods (indicated by the different shading). (b) A box and whisker plot of the median (and IQRs) of the total number of items eaten by the subject in each condition of Experiment 1. (c) A box and whisker plot of the median (and IQRs) of the total number of items inspected and discarded by the subject in each condition of Experiment 1.

$S = 10/12$ ,  $p = 0.002$ ; Social, Sign test;  $S = 11/12$ ,  $p = 0.001$ , Social-Matched, Sign test;  $S = 12/12$ ,  $p = 0.001$ ; Social-Different, Sign test;  $S = 11/12$ ,  $p = 0.001$ ). Novel food items were never eaten in the Alone condition (Figure 1b).

The total number of food items eaten was lowest in the Alone condition (Figure 1b), a finding that appears to be responsible for the significant difference in food consumption across conditions (familiar food, Friedman's ANOVA,  $\chi^2_3 = 11.3$ ,  $p = 0.01$ ; novel food, Friedman's ANOVA,  $\chi^2_2 = 8.5$ ,  $p = 0.04$ ). When the Alone condition was removed from the analysis, no statistical difference was identified for the number of items eaten in each of the three social conditions (familiar food, Friedman's ANOVA,  $\chi^2_2 = 0.13$ ,  $p = 0.94$ ; novel food, Friedman's ANOVA,  $\chi^2_2 = 0.13$ ,  $p = 0.94$ ).

In each condition, a similar number of familiar and novel food items were discarded from the food bowls (Figure 1c; Friedman's ANOVA,  $\chi^2_3 = 4.6$ ,  $p = 0.20$ ). There was no significant preference to discard novel or familiar items (Alone, Sign test;  $S = 3/12$ ,  $p = 0.99$ ; Social, Sign test;  $S = 3/12$ ,  $p = 0.99$ ; Social-Matched, Sign test;  $S = 0/12$ ,  $p = 0.50$ ; Social-Different, Sign test;  $S = 3/12$ ,  $p = 0.25$ ).

## Discussion

The findings of Experiment 1 upheld three of our predictions and provided partial support for the fourth. First, the rooks predominantly ate familiar foods in every condition. Second, feeding was elevated in the presence of a conspecific. Third, novel food items were only sampled in the three social conditions. Finally, in the presence of a co-eater, the amount of familiar food ingested was similar irrespective of whether it was the same as (Social-Same condition), or different to (Social-Different condition) that of the demonstrator. Contrary to our final prediction, however, food consumption in the presence of a feeding demonstrator was not significantly greater than in the Social condition when a conspecific was present but not feeding.

The birds' overwhelming preference to consume familiar foods in this experiment cannot be attributed to an inherent aversion to the novel foods. Indeed, rooks discarded novel food items in every condition. Marples & Kelly (1999) have argued that the latency to inspect a novel food provides an index of neophobia, but that the time-period between a food's initial inspection

and its full incorporation into the diet results from the psychologically distinct process of 'dietary conservatism' (see also Marples et al., 1998; Kelly & Marples, 2004). The rooks' reluctance to consume the novel food in this experiment may have been exacerbated by the consistent presence of familiar foods.

According to the traditional definition of social facilitation, an increase in a subject's feeding rate would only be defined as such if it were temporally concurrent with another individual's feeding behaviour (Clayton, 1978). This definition would become particularly appropriate should the actions of mirror neurons underpin the facilitated response (Ferrari et al., 2005). The tendency for rooks to increase feeding in the presence of a non-feeding conspecific should, therefore, be attributed to an elevated motivation to feed rather than an effect of social facilitation. Indeed, rather than facilitating eating *per se*, the presence of a conspecific might have decreased subjects' stress levels, increasing feeding rates as a corollary.

Irrespective of the specific processes involved, these results support the suggestion that conspecific presence enhances an animal's inclination to sample novel foods (Turner, 1965; Galef, 1993; Fragaszy & Visalberghi, 2004). Hungry animals might be expected to be most likely to use social cues as indicators of food palatability in the absence of known foods. We, therefore, conducted a second experiment in which the rooks were exposed to a choice of novel foods or familiar foods.

## **Experiment 2**

Experiment 2 assessed the specificity of social information use and feeding preferences in rooks. Social learning theory predicts that animals should utilise social information in situations where they do not possess adequate personal information (Boyd & Richerson, 1985), and that an individual's reliance on social information should increase as the costs associated with acquiring personal information increase (Laland, 2004; Kendal et al., 2005). The question in this experiment, therefore, was whether after observing a demonstrator eating a particular novel or familiar food, would rooks use this social information to inform their own food choice?

Novel food ingestion is associated with a risk of poisoning or even death. We, therefore, predicted that, when faced only with novel foods, naïve individuals would exploit social information and predominantly eat the same

food as a conspecific demonstrator. By contrast, as individuals would be informed as to the palatability of familiar foods, and have formed a personal preference or dislike for them, we did not expect the rooks' choice of familiar foods to be affected by the feeding behaviour of a demonstrator.

## **Materials and methods**

### *Subjects*

The same twelve birds were used in Experiment 2, 11 birds (1 male, 10 females) acted as test subjects and 1 bird (male) as a demonstrator.

### *Procedure*

Prior to testing, the demonstrator was given three 1-h training sessions in which it was given the opportunity to eat two novel foods (Tesco Prawn Crackers<sup>®</sup> and Tesco 'Breakfast Boulders'<sup>®</sup>). By the end of the third session, the demonstrator was readily eating both foods.

The experimental apparatus and procedure were identical to those described for the Social-Same condition of Experiment 1 in all but two respects. First, the novel foods were Prawn crackers<sup>®</sup> and Breakfast Boulders<sup>®</sup>, and the familiar foods were cooked egg yolk and dog kibble. Second, each bird was given a single test session in each of two conditions: Novel and Familiar. In the Novel condition, as in Experiment 1, the test subject was presented with two metal food bowls, one containing 40 pieces of Prawn Crackers<sup>®</sup>, and the other 40 pieces of Breakfast Boulders<sup>®</sup>. The demonstrator was presented with a bowl containing 40 pieces of one of the foods (Prawn Crackers<sup>®</sup> or Breakfast Boulders<sup>®</sup>). The procedure for the Familiar condition was identical to that of the Novel condition except that familiar foods were used. Food presentations were counter-balanced such that, in the Novel condition, six subjects witnessed the demonstrator eating Prawn Crackers<sup>®</sup> and five subjects observed the demonstrator eating Breakfast Boulders<sup>®</sup>. Similarly, in the Familiar condition, six subjects witnessed the demonstrator eating dog kibbles and five rooks observed their conspecific eating cooked egg yolk.

### *Statistical analysis*

Wilcoxon's signed rank tests were used to compare (a) the total number of items the focal subject ate during the Novel and Familiar conditions and (b) the number of items eaten by the demonstrator in both conditions. Sign tests were used to compare the number of food items eaten by the subject that were the same as, or different to the food eaten by the demonstrator in both the Novel and Familiar conditions.

## **Results**

### *Subjects*

The total number of food items eaten did not differ statistically between the two test conditions (Novel, median = 6.0, IQR = 8.5, Familiar, median = 10, IQR = 9.8; Wilcoxon's test,  $Z = 1.7$ ,  $p = 0.08$ ). There was a significant preference to eat the same food as the demonstrator in the Novel (Figure 2b, Sign test;  $S = 9/12$ ,  $p < 0.004$ ), but not the Familiar condition (Sign test;  $S = 6/12$ ,  $p = 0.99$ ).

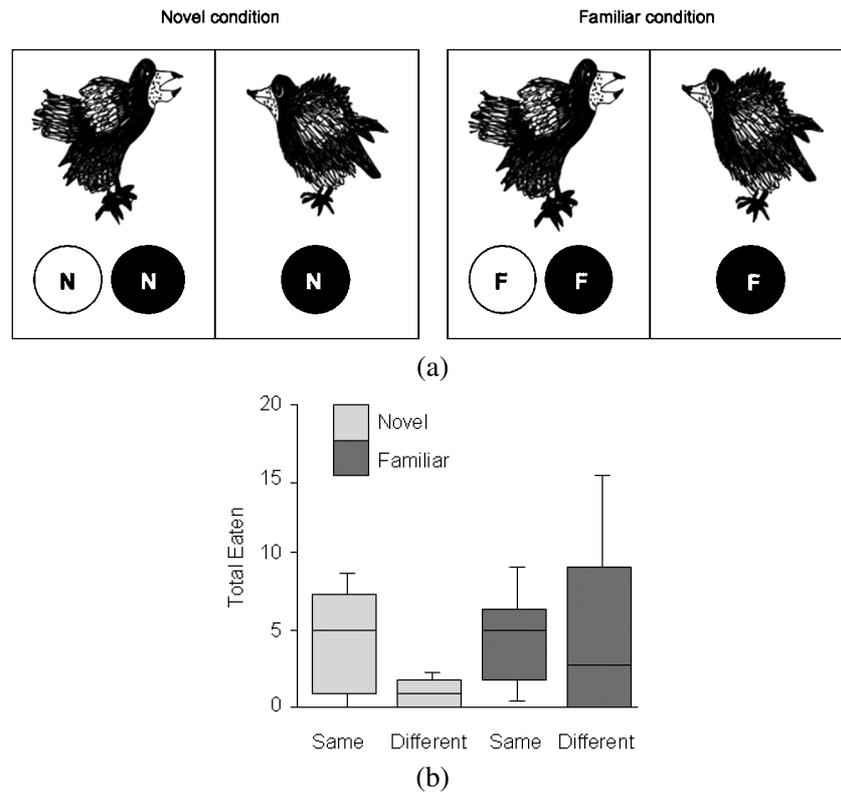
### *Demonstrators*

The number of items eaten by the demonstrator did not differ between the two conditions (Novel, median = 7.0, IQR = 3.8; Familiar, median = 7.0, IQR = 6.7; Wilcoxon's test,  $Z = 0.8$ ,  $p = 0.41$ ).

## **Discussion**

The results of Experiment 2 supported our prediction that rooks would use social information to guide their choice of novel, but not familiar, foods. It is important to note that the demonstrator consumed a similar number of food items in both the Familiar and the Novel condition. It, therefore, appears unlikely that the rooks' proclivity to eat the same food as the demonstrator in the Novel condition, but not in the Familiar condition, results from differences in the demonstrator's feeding behaviour.

There are at least two reasons why the birds might have exhibited a preference for the same food as the demonstrator in the Novel condition but not



**Figure 2.** (a) The experimental set-up for the Novel and Familiar conditions of Experiment 2. In each diagram the subject is on the left hand side and the demonstrator on the right. In the Familiar condition the subject was given two familiar foods ('F'), one of which was the same as the demonstrator's food (shaded circle) and one was different (white circle). Similarly, in the Novel condition, one of the subject's novel foods (N) was the same as the demonstrator's (shaded circle) and one was different (white circle). Note that the experimental set-up for the Food Visible and Food Invisible conditions of Experiment 3 was identical to that depicted for the Novel condition of this experiment except that (a) novel foods were replaced with novel 'open' feeders in the Food Visible condition and (b) closed containers in the Food Invisible condition. All containers held a familiar food. (b) A box and whisker plot of the median (and IQRs) number of items that were eaten by the subject that were the same as, or different to, the food eaten by the demonstrator in both the Novel and Familiar conditions of Experiment 2.

the Familiar condition. First, the birds' prior experience of the foods in the Familiar condition may have rendered socially available information redundant, whereas the demonstrator's actions in the Novel condition may have provided an indicator to an unknown food's palatability.

The differential use of personal and social information during foraging has been examined in a number of animal species (see Kendal et al., 2005 for a review). In a study of food patch assessment by starlings, Templeton and Giraldeau (1996) found that naïve individuals ignored public information pertaining to the quality of a food patch when personal information was relatively easy to collect, but when foraging patches were made more complex, birds increasingly utilised information provided by conspecific demonstrators. The differential use of public and private information by starlings accords with the central assumptions of social learning theory; the use of public information increased as the costs associated with acquiring accurate personal information increased (Boyd & Richerson, 1985). The rooks' feeding behaviour in the current experiment also aligns with social learning theory. That is, when individuals lacked personal information pertaining to food safety (Novel condition) they used social information to guide their feeding behaviour. By contrast, personally acquired information may be more reliable than socially acquired information, so the birds based their food choice on personal past experience whenever possible (Familiar condition).

The second reason for the rooks' propensity to selectively eat the same novel, but not familiar, food as the demonstrator may have resulted from an interaction between the intrinsic attractiveness of the two foods and a socially-induced preference for the food consumed by the demonstrator. To elucidate, Galef & Whiskin (1998) found that the extent to which the dietary choices of Norway rats were subject to social influence depended on the relative attractiveness of the available foods; the greater the intrinsic preference for one food over the other, the lower the likelihood that a socially acquired preference for one of the two foods could be induced. Consequently, if the two foods used in the Familiar condition of Experiment 2 differed significantly in (a) intrinsic palatability or (b) preference before the experiment, we might not expect to see a socially induced preference for one of the foods, and indeed we did not. Similarly, if we assume that the two foods in the Novel condition were equally attractive, neither having been previously encountered, this explanation suggests that we would be more likely to see a socially-induced preference.

Unfortunately, we have been unable to tease these two explanations apart. A subsequent preference test, where the birds were given the two familiar foods and allowed to eat them both, identified a significant preference for one of the two familiar foods (egg yolk) over the other (dog kibble; Wilcoxon's

test,  $Z = 2.6$ ,  $p = 0.01$ ). To ascertain whether the results of Experiment 2 were attributable to an effect of novelty versus familiarity, or to a bias in preference for one of the two foods in the Familiar condition, it would be necessary to repeat the Familiar condition with two equally preferred foods. After repeated attempts to find two such foods, however, it became apparent that the birds always preferred one food over another. Consequently, in Experiment 3, we investigated the possibility that, in the Novel condition, the preference to consume the food being eaten by the demonstrator might be attributable to a general tendency to engage in the same behaviour as conspecifics in a novel situation, rather than a specific response to a novel food.

### Experiment 3

If rooks use social cues to inform novel food exploitation, they might benefit from attending to the visual attributes of objects from which others feed. By basing foraging decisions solely on facets of novelty such as the outer appearance of a food resource, however, individuals may miss opportunities to access ephemeral resources. Consider that rooks scavenge for food at a motorway service station (Benyon, 2003). By avoiding familiar foods because they are contained within novel containers (e.g., different rubbish bins), individuals would not only forego access to food, but would increase the level of competition at previously exploited foraging sites.

The presence of conspecifics is known to facilitate the exploitation of food contained in novel feeders (e.g., zebra finches, *Taeniopygia guttata*, Coleman & Mellgren, 1994), and socially induced preferences for specific food sites have been identified for a number of species (e.g., zebra finches, Benskin et al., 2002; Burmese fowl, *Gallus gallus spadecius*, McQuoid & Galef, 1992, 1993). To investigate whether rooks use social information when foraging in novel sites, birds were given the opportunity to observe a conspecific eating a preferred food (mealworms, *Tenebrio molitor*) from a novel feeder in each of two conditions. In both conditions the naïve subject was presented with two novel feeders, which also contained mealworms, one of which was identical to that given to the demonstrator. In the Food Visible condition, the food contained in the feeder was constantly visible to the naïve subject. By contrast, in the Food Invisible condition the birds had to place their head inside the feeder in order to access the food. We predicted that (a)

rooks would utilize the information provided by the demonstrator in the Food Invisible condition as they would be uninformed as to the content of the feeder, but that (b) if rooks use others' foraging behaviour to guide their consumption of specifically novel food, and if the visible presence of a familiar food acts to reduce novel object neophobia, both food containers would be treated similarly in the Food Visible condition.

## **Materials and methods**

### *Subjects and procedure*

The subjects, apparatus and procedure were identical to those described for Experiment 2 (Figure 2a) in all but the following respects.

Prior to testing, the demonstrator was given sixteen 1-h training sessions in which it was given the opportunity to eat from one of four novel feeders. Two of the feeders were 'open' such that the food they contained was constantly visible (4 training sessions each), whereas the demonstrator needed to put its head inside the other two 'closed' feeders in order to see and access the food (5 training sessions each). By the end of the sixteenth session, the demonstrator was readily eating from all 4 containers. Each test subject was given a single test session in each of two conditions: Food Visible and Food Invisible. In the Food Visible condition, the demonstrator was presented with a single 'open' feeder and the test subject two 'open' feeders, one of which was identical to that of the demonstrator, but neither of which the test subject had seen previously. All feeders were baited with 10 mealworms, a familiar and highly preferred food, and feeder presentations were counter-balanced such that half the birds observed the demonstrator with feeder A and half with feeder B. The procedure for the Food Invisible condition was identical to that of the Food Visible condition except that 'closed' feeders were used, such that the food contained within the feeder could not be observed unless the subject placed its head inside of the feeder itself.

### *Statistical analysis*

Wilcoxon's signed rank tests were used to compare (a) the total number of items the focal subject ate during the Food Visible and Food Invisible conditions, (b) the latency to first touch a feeder in the Food Visible and Food

Invisible conditions and (c) the number of items eaten by the demonstrator in both conditions. Sign tests were used to compare the number of food items eaten from, and the latency to first touch the feeder that was the same as, or different to that presented to the demonstrator in both the Food Visible and Food Invisible conditions.

## Results

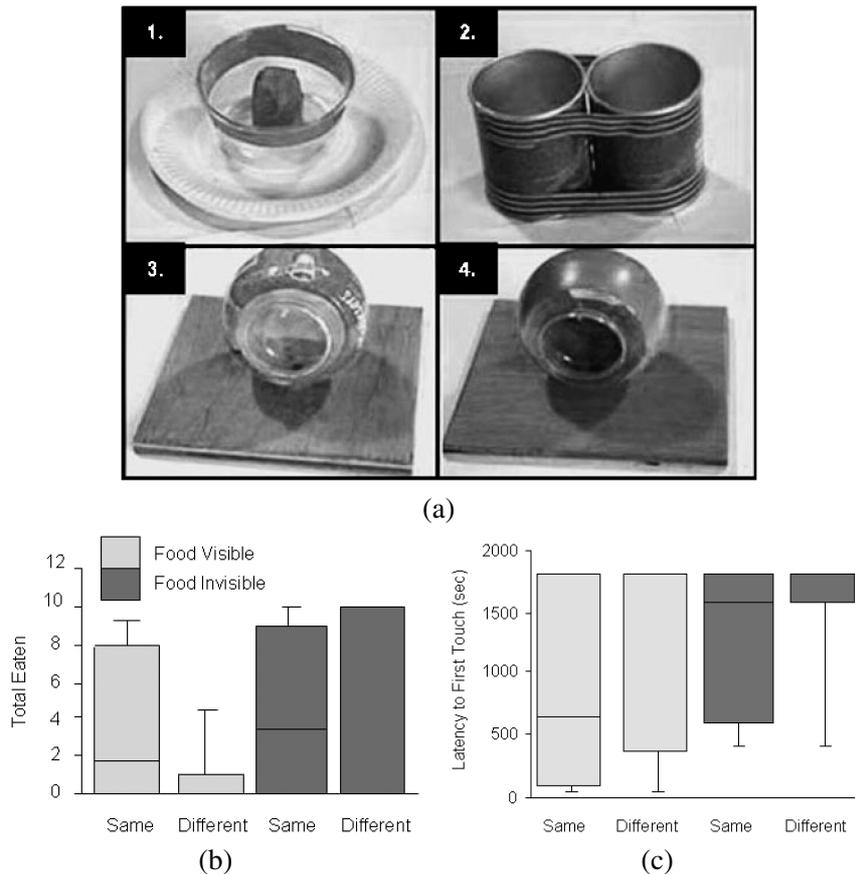
No statistical differences were identified in the number of items eaten from either feeder in the Food Visible (Figure 3a; Sign test,  $S = 5/10$ ,  $p = 0.45$ ) and Food Invisible conditions (Sign test,  $2/10$ ,  $p = 0.69$ ), nor did the total number of items eaten in the two test conditions differ statistically (Food Visible, median = 3.5, IQR = 17, Food Invisible, median = 2.0, IQR = 9.0; Wilcoxon's test,  $Z = 0.7$ ,  $p = 0.48$ ). Similarly, the number of items eaten by the demonstrator did not differ statistically between either condition (Food Visible, median = 7.3, IQR = 8.4; Food Invisible, median = 4.4, IQR = 5.7; Wilcoxon's test,  $Z = 0.8$ ,  $p = 0.41$ ).

The time taken to first touch a feeder was significantly shorter in the Food Visible condition compared to the Food Invisible condition (Figure 3b; Wilcoxon's test,  $Z = 2.2$ ,  $p = 0.03$ ). However, the latency until subjects first touched the feeder that was the same as, or different to the feeder given to the demonstrator was not statistically different in either the Food Visible (Sign test,  $S = 5/10$ ,  $p = 0.45$ ), or Food Invisible condition (Sign test,  $S = 2/10$ ,  $p = 0.69$ ).

## Discussion

There were two principal findings from this experiment. First, subjects did not exhibit a significant preference to eat from, or touch, the feeder that was identical to that of the demonstrator in either the Food Visible or Food Invisible condition. Second, naïve birds were significantly quicker to touch open feeders relative to closed feeders.

The decreased latency before the birds first touched the open feeders relative to the closed feeders suggests that, as predicted, the visual presence of a familiar food moderates the degree of neophobia elicited by novel objects. Considering the relative increase in neophobia elicited by the closed feeders,



**Figure 3.** (a) The feeders used in Experiment 3. Feeders 1 and 2 are the open feeders used in the Food Visible condition, 3 and 4 are the closed feeders in the Food Invisible condition. (b) A box and whisker plot of the median (and IQRs) number of items that were eaten from the novel feeder that was the same as, or different to, that of the demonstrator in the Food Visible and Food Invisible conditions of Experiment 3. (c) A box and whisker plot of the median (and IQRs) latency (in s) to touch the novel feeder that was the same as, or different to, that of the demonstrator in the Food Visible and Food Invisible conditions of Experiment 3.

it was initially surprising that the rooks did not exhibit a socially-induced preference to feed from, or touch, the same feeder as the demonstrator in the Food Invisible condition. However, as the closed feeders were identical in all but colour, it is possible that the actions of the demonstrator simply motivated the observer to direct their feeding behaviour towards functionally similar objects. This account is supported by the fact that in the Food Invisi-

ble condition no observer ever inspected either feeder before the demonstrator. Indeed, on the occasion that a demonstrator did not consume any items the observer never approached either feeder.

The finding that observer rooks did not inspect either feeder before the demonstrator in the Food Invisible condition of Experiment 3 initially appears at odds with the finding that, in the Social condition of Experiment 1, rooks increased food consumption in the presence of conspecifics. However, unlike the Food Invisible condition in the current experiment, but similarly to the Food Visible condition, the visual presence of a familiar food in the Social condition of Experiment 1 may have been sufficient to elicit food-directed responses.

### General discussion

There are three key findings from these experiments. First, feeding by rooks appears to be influenced by social context; the birds ate significantly more food in the presence of a conspecific compared to when alone (Experiment 1). Second, when observing a conspecific eat a specific novel food, naive birds preferentially ate the same food as that eaten by the demonstrator (Experiment 2). Finally, when feeding from novel objects, rooks do not match their choice of feeder to that of a demonstrator (Experiment 3).

One reason for increased food consumption in the presence of others, at least in species that live in groups, might be the reduced need for every individual to engage in vigilant behaviours such as scanning for potential predators (e.g., Caraco et al., 1980). Indeed, Laland (2004) suggested that when threatened with predation, animals might benefit by exploiting socially available information as to food palatability rather than individually assessing that same food source. If individual risk is perceived to decrease in social situations, this might explain the rooks' proclivity to increase food consumption in the presence of a conspecific, irrespective of whether the demonstrator was or was not also feeding (Experiment 1; but see a recent study on Norwegian rats which found that subjects were least likely to use social information to guide novel food choice when confronted with a direct cue of predation threat; Galef & Whiskin, 2006).

The finding that, in Experiment 2, conspecific foraging behaviour induced a specific novel food preference is particularly intriguing. Mason & Reiding (1981) reported a similar finding for red-winged blackbirds (*Agelaius*

*phoeniceus*). It has since been observed, however, that although the black-birds did exhibit a preference to consume the same novel food as a conspecific, they had prior experience of observing the demonstrator eating this food. This raises the possibility that the birds were expressing a preference to eat relatively familiar, rather than novel foods. In the current study, relative familiarity cannot be invoked as an explanation for the tendency for naïve rooks to predominantly eat the same novel food as a conspecific, as birds only witnessed a demonstrator eating each novel food once, and this occurred concurrently with their opportunity to eat the same, or different novel food.

The finding that rooks appear to utilize social cues to inform novel food choice (Experiment 2), but not the exploitation of familiar food contained within a novel feeder (Experiment 3), makes intuitive sense if we consider the risks associated with the two variables in the context of social learning theory. In Experiment 2, the costs associated with acquiring personal information through trial-and-error learning were relatively high, because novel foods have the potential to induce sickness, or even death. Consequently, individuals would benefit from exploiting social information pertaining to the palatability of unknown foods. By contrast, in Experiment 3 individuals already possessed personal information regarding the palatability of the food (mealworms) contained within the feeders, and the need for social information would, therefore, be reduced (see Kendal et al., 2005 for a review of social learning theory).

Recent studies by Bugnyar and colleagues have found that object exploration in ravens is not only affected by social context (the presence or absence of conspecifics), but also by the sex of, and relationship between, individuals present (e.g., Stowe et al., 2006a; Schwab et al., 2007). For example, in the presence of a dominant male, subordinate ravens approach novel objects first, whereas, when paired with a female, dominant males approach novel objects significantly faster than their conspecific (Stowe et al., 2006b). Unfortunately, we were unable to conduct an analysis in terms of the sex, and relative dominance, of the observer and demonstrator rooks in each experimental trial for two reasons. First, the sex ratio of the rooks was heavily biased (2 males and 10 females), and second, the demonstrator in Experiment 2 and Experiment 3 was always the dominant male.

But why might rooks be particularly sensitive to the behaviour of others towards novel foods? One possibility is that the birds' omnivorous diet has

acted as a catalyst to promote the exploitation of novel food sources, whilst providing an inbuilt 'safety-net' to reduce the risk of consuming toxic or unpalatable foods. A comprehensive investigation of novel food consumption in another omnivore, however, has failed to identify any specific effects of social facilitation (capuchins, see Fragaszy & Visalberghi, 2004 for a review).

Although studies of captive capuchins have not identified any evidence for the social transmission of novel food preferences (Addessi & Visalberghi, 2001), their experience of humans may be key in shaping their response towards unknown food. Capuchins in the Brasilia National Park, Brazil (Visalberghi et al., 2003) have habituated to humans and commonly explore objects that are associated with food (e.g., knapsacks, plastic bags, rubbish bins). By contrast, capuchins in the National Park of Iguazu, Argentina have little human experience (Sabbatini et al., 2007). This difference in human contact appears to have resulted in divergent responses to food novelty. Whilst Iguazu capuchins approach familiar foods significantly faster than novel foods or objects, Brasilia capuchins treat all foods alike, approaching novel and familiar foods with the same latency irrespective of whether or not a novel object was also present.

The proclivity by corvids to colonize urban areas (Coombs, 1978) might be expected to increase their exposure to dietary hazards. Yet a study on house sparrows (*Passer domesticus*), found that birds from a population that was actively invading a city (Colon, Panama) more readily approached and consumed novel foods compared to a population of birds that had been resident in one city (Princeton, NJ, USA) for more than 150 years (Martin II & Fitzgerald, 2005). This propensity for an invasive species to exhibit reduced food neophobia is consistent with Sol et al.'s (2002) argument that an inclination to readily taste new foods will significantly increase the likelihood that a species will survive in a novel environment. We suggest that by predominantly sampling novel foods they have witnessed others eat, rooks may have struck a behavioural balance between increasing their chance of survival in new environments, and reducing the chance of consuming foods that may have a detrimental effect on their health.

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