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Public information cues affect the scrounging decisions of starlings

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Abstract. The foraging decisions that individuals make within groups should depend on the information available to them. An aviary experiment was conducted to examine whether a starling's, *Sturnus vulgaris*, decisions either to approach and feed from (scrounge) or to avoid the patches exploited by a partner bird are influenced by the information the partner provides. Both the type of information a subject could recognize and the point at which this information became available during the partner's exploitation of a patch were manipulated. Information concerning the quality of a patch was available in the form of a concealed colour cue and from the behaviour of the partner bird. The foraging environment was manipulated such that colour cues were either present or absent, and provided either correct or incorrect information concerning the presence of food. When cues corresponded with past foraging experience, test subjects responded selectively and profitably to the patch exploitations of the partner; they scrounged from a higher proportion of profitable patches than control birds, which lacked the ability to recognize colour cues. Test subjects also arrived more quickly at profitable patches that the partner bird discovered than did control birds; and consequently, were able to obtain more food at each food patch scrounged. Finally, test subjects avoided scrounging when the partner discovered empty patches and thus saved foraging time. Responding selectively to public information, therefore, allows an individual to compete more effectively for resources within a foraging group.

One of the major characteristics of group foraging is the sharing of information concerning each individual's foraging success (Clark & Mangel 1984, 1986). An individual that can recognize when another group member has discovered food can either choose to forage in similar types of locations (Krebs et al. 1972; Palameta 1989) or approach and feed from the discovered food source ('scrounge'; Barnard 1984; Giraldeau & Lefebvre 1986). In addition to providing such foraging benefits as a reduced variance in searching time (Caraco 1981; Pulliam & Millikan 1982; Caraco & Giraldeau 1991) and an increase in individual foraging rates (Pulliam & Millikan 1982; Clark & Mangel 1984), the use of information in foraging groups can potentially compensate for the costs of having to share food with others (Clark & Mangel 1984). For example, an individual that forages independently and ignores the successes of other group members will still have to share its own discoveries with them. Hence, each group member may monitor the activities of others and scrounge from their discoveries simply to avoid the cost of being the only individual that does not do so (Clark & Mangel 1984; Vickery et al. 1991).

Individuals that forage in groups for patchily distributed prey are thus faced with numerous foraging decisions. Not only must they use their own 'personal information' (Valone 1989) to decide whether to exploit patches enountered via their own foraging activities, but they must also decide how to respond to the 'public information' (Valone 1989) provided by the foraging activities of others in order to compete more effectively within the group. We studied starlings foraging in pairs in order to examine how the use of public information affects individual scrounging decisions and consequent foraging payoffs.

Types of Public Information

A group forager can potentially use several different kinds of public information, which can become available at different stages of the patch-exploitation process. In addition to noticing prey

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items when another individual has captured them, or observing its feeding behaviour (Drent & Swierstra 1977; Rabenold & Christensen 1979; Feare 1984), public information could become available even earlier in the form of slight behavioural changes that indicate when an individual has just discovered food or is about to capture a prey item (Metz et al. 1991). Behavioural cues may also be used to indicate the size and profitability of prey items before they are captured, as has been suggested for black-headed gulls, *Larus ridibundus*, scrounging worms from lapwings, *Vanellus vanellus* (Barnard & Stephens 1981; Thompson 1983). Similarly, certain patch characteristics that are exposed by another forager's exploitation of a patch (e.g. Heinrich & Collins 1983) could be used by an observing individual as cues to indicate the presence or absence of prey.

To date, few studies have investigated the types of public information that group foragers can use when making scrounging decisions, nor have they documented the advantages of using such information. Under competitive conditions in particular, it is likely that the ability to detect and predict the imminent discovery of food by another individual would provide a significant foraging advantage. The use of such public information should allow a forager to arrive at profitable patches more quickly and hence obtain a larger share of others' discoveries than one lacking this ability. Alternatively, recognizing when another individual is foraging unsuccessfully should enable a forager to avoid unprofitable or empty patches, a potentially important scrounging decision that has only recently been considered in group foraging studies (Benkman 1988).

Manipulating Public Information

In our experiment, we examine how the availability of public information influences the scrounging decisions of captive European starlings, *Sturnus vulgaris*, foraging with one partner bird. We manipulated both the type of public information available to the subject and the time at which it was provided by the partner. Information concerning the quality of a patch was available from concealed colour cues and from the subsequent feeding behaviour of the partner bird. The environment was manipulated so that colour cues were present or absent, and provided either correct or incorrect foraging information. We document the use of colour cue and behavioural information and determine the effect these have on individual foraging payoffs.

METHODS

Subjects

Subjects were 18 wild-caught, adult starlings of known sex that had been in captivity for 6 months prior to the start of the experiment, and later released. These birds were randomly selected from a population of 25 starlings housed in groups of five in holding cages (107 × 62 × 92 cm). One additional female bird served as a foraging partner to each subject in the testing sessions. When not being used in an experiment, all birds were maintained on an ad libitum diet of insectivorous bird food and moistened mynah pellets ('8-in-1 Tasty Dinner with Fruit'). Water was always available and lighting was set on a 12:12 h light: dark cycle.

Experimental Task

The experimental patches were containers made of open-ended cardboard cylinders, 9 cm in diameter and 6·5 cm deep, set on their sides (Fig. 1a). Each container consisted of an 'information' compartment and a 'food' compartment, arranged so that the information compartment was accessed before the food compartment. Exploiting a container completely required accessing both compartments. Accessing the information compartment was termed 'opening', which required a single peck at a paper seal. Upon breaking the seal, the lid covering the front of the container fell open, revealing coloured tissue paper inside the lid and within the information compartment. Accessing the food compartment was termed 'checking', which the bird could accomplish by piercing through a heavy paper barrier placed at the rear of the information compartment.

Training I: Learning to Use Containers and Colour Cues

The 18 subjects were arbitrarily assigned to one of three treatments, with the constraint that each treatment group was composed of four males and two females. There were two treatment groups in

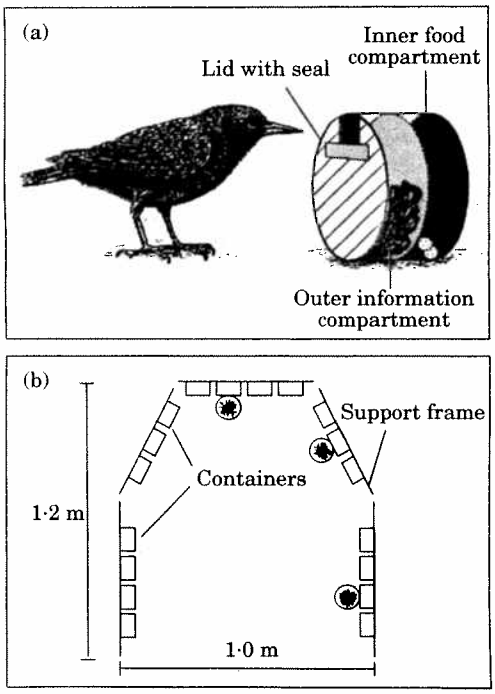

Figure 1. (a) Experimental container showing lid with paper seal; outer 'information' compartment with shredded tissue paper; and inner 'food' compartment with two pellets. (b) Top view of the experimental arena showing the 18 containers; three containers are open, revealing the shredded tissue paper on the inside of the opened lids.

which subjects were trained to recognize and respond to specific colour cues. In one group, the black test group, birds learned that black tissue paper always predicted the presence of food and that yellow always predicted its absence. In the other group, the yellow test group, the opposite association was learned. Control group birds learned that black and yellow did not provide any information on the presence or absence of food.

Starlings were first trained individually in cages (62 × 62 × 62 cm) to open and check single cueless containers; they usually became proficient at this task within 10 presentations. Once proficient, shredded tissue paper was added to the information compartment. For test subjects, only containers with the rewarded colour had food (two mynah pellets). For the control birds, each colour was associated with food 50% of the time. The birds received 10 presentations of single containers (five of each colour); then pairs of containers were presented, but birds were allowed to check only one of the two containers. Test subjects were required to meet a criterion of 10 successive decisions not to check a container with an unrewarded colour. The two experimental groups (total $N=12$) required an average ($\pm$ SE) of 59·2 ± 5·2 paired presentations over a 2–3-day period to meet this criterion. Control birds were not required to meet a criterion, but were given 2 days of presentations with food present 50% of the time in order to keep the amount of training between treatments approximately equal.

Training II: Learning to Use the Foraging Arena

The experimental arena was situated in an indoor aviary (2·4 × 2·4 × 2·7 m). Eighteen containers were attached with velcro to vertical wooden supports (90 cm long × 17 cm high), which were arranged on the floor in a semi-circle (Fig. 1b) so that whenever a container was opened, the colour present in the information compartment would be visible from any point within the arena. Two birds of the same treatment group were trained together for five training trials. The pair to be trained was transferred to the aviary the day before arena training began. The five training sessions took place over 3 days: one session on the first day and two sessions on each of the following 2 days.

Food was distributed in a clumped fashion; only two of the 18 containers had food (six pellets each) in each treatment. The positioning of the two food containers was arbitrary, subject to the requirements that they were never adjacent to each other and they were never in the same position from one training trial to the next. For test subjects, the two containers with the rewarded colour contained food; the remaining 16 containers with the unrewarded colour were empty. For control birds, one container with yellow tissue paper and one with black tissue each contained food; the remaining eight black and eight yellow containers were empty. Containers were prepared outside of the aviary; the birds preferred to remain on a high perch while the containers were being attached to the sides of the arena.

During all stages of training and testing, each bird received 10 g of regular food mixture in a small dish 0·5 h after the last training trial of the

day. Subjects were deprived of food overnight from 2100 to 1300 hours, for a total of 16 h. At the end of the training period, the birds weighed 80–85% of their initial free-feeding body weight.

Testing

Testing alternated over the three treatment groups. We tested individual birds in the arena while paired with the same partner bird, whose function was to provide the subject with colour and behavioural cues. The partner was a subordinate female (LPW), chosen so that she would be more likely to allow subjects to scrounge from the containers she opened and less likely to scrounge from the subjects (e.g. Feare & Inglis 1979). Her subordinate status was established prior to the experiment using paired priority of access dominance trials involving LPW and four other birds from different groups with whom she would eventually be tested; with each bird, LPW had the longest latency to reach the criterion amount of feeding time. Like control subjects, LPW was trained to respond to both colours indiscriminately, thus she checked all containers irrespective of their colour cue. The partner bird was identified by a small dot of white paint applied to the top of her head. LPW acted as a partner bird 2 days in a row every 8 days for approximately 90 days total. Thus she was food-deprived in the same manner as the subjects for each 2-day period only; her weight during these 2-day periods dropped to between 80 and 85% of her free-feeding body weight.

A test started when one bird landed in the arena and lasted until all 18 containers had been opened and checked. We tested test and control subjects once in each of the three experimental environments at 1·5-h intervals in the following order: (1) 'informing', (2) 'uninforming' and (3) 'misinforming'. This testing order was necessary to avoid weakening the test subjects' previous training experience in the informing condition. In the informing environment, the concealed colour cues were in accord with the test subjects' past training experience, and thus provided them with correct information concerning the presence or absence of food. In the uninforming environment, colour cues were absent. In the misinforming environment, the colour cues were the opposite of past training experience; thus test subjects had incorrect information concerning the quality of a patch. Colour cues were meaningless to control birds in all three environments; hence this group controlled for any effect of testing order on the subjects' behaviour. In each environment, nine containers had food (two pellets each) and nine were empty. Positioning of food containers was random; however, there were never more than two containers of the same colour or quality in a row. All test trials were videotaped.

Data Collection

We defined six measures of individual responses to public information: (1) 'scrounging frequency', the number of containers opened by the partner that were scrounged by the subject, where scrounging was defined as the subject arriving at a container either while it was being opened and checked by the partner or within 1 s of the partner's departure; (2) 'scrounging efficiency', the proportion of total containers scrounged that contained food; (3) 'scrounging latency', the time between the partner first starting to check a food compartment and the subject's arrival; (4) 'scrounging payoff', the amount of food a subject obtained from scrounging at a food container (0 if it arrived after the partner had eaten both food pellets, 1 if it ate one pellet, and 2 if it ate both pellets); (5) 'avoiding frequency', the number of containers opened by the partner that were avoided by the subject in each environment; and (6) 'avoiding efficiency', the proportion of total containers avoided that were empty. A container was only considered to be 'avoided' when a subject either approached while the partner was checking a container, but interrupted its approach before scrounging (a 'break-off'); or when the subject watched the partner, but did not approach (an 'ignore'). A subject was only considered to be watching the partner if it paused for at least 1 s and turned its head towards the partner. We estimated the mean temporal cost of scrounging from an empty container by recording the time it took to check the food compartment of an empty container (i.e. from the first piercing of the inner barrier to departure); this was measured three times for each of the subjects and the partner bird.

We analysed data with SYSTAT (Wilkinson 1990). All values reported are means ($\pm$ SE).

Table I. The mean (± SE) number of containers opened and checked by the partner in each of the test environments, as well as the significance levels of comparisons

	Informing	Uninforming	Misinforming	Environment comparison*
Test birds	9·3 (0·6)	10·0 (1·0)	9·4 (0·5)	NS
Controls	9·7 (1·1)	7·7 (0·7)	8·2 (1·1)	NS
Group comparison*	NS	NS	NS	

*Kolmogorov–Smirnov test between environments, and test and control birds.

RESULTS

There were no significant differences between black and yellow test groups in any of the three environments, so these results were combined. In virtually all trials, subject and partner landed within 1–2 s of each other, and remained in the foraging arena for 138·6 ± 14·7 s (N=54 trials) until all 18 containers had been opened and checked. The partner bird opened and checked a similar number of containers in the presence of test and control subjects in all three test environments, thus providing the subjects with a comparable number of opportunities to respond to public information (Table I). The behaviour of the partner was consistent over the 18 subjects; there was no difference between the number of scrounging opportunities provided to the first nine subjects and to the last nine subjects in each of the test environments (Kolmogorov–Smirnov test: NS).

Some of the opportunities provided by the partner were missed by both test and control birds when they were occupied with their own activities; however, when subjects were paying attention to LPW's activities, they responded either by scrounging from her or by avoiding her (Table II). Two-way repeated-measures ANOVAs (ANOVARs) were run separately for each of these three responses to public information (missing, scrounging, avoiding). There were no significant differences in the number of missed opportunities either between the two groups or over the three environments, indicating that birds in both groups had a comparable number of opportunities to respond more directly to public information (Table II). We consider these two types of scrounging decisions in turn.

Scrounging

When a subject scrounged, it displaced LPW from the container either physically or by vocalizing as it approached. Not all birds scrounged from the partner bird in all three environments; one of the 12 test birds and two of the six control birds never scrounged. However, the mean scrounging frequency (Table II) includes the data of these non-scrounging individuals. Test and control birds did not differ in their scrounging frequencies (two-way ANOVAR: $F_{1,16}$=1·007, P=0·331), although there was a tendency for the frequency of scrounging to be affected by the test

Table II. Responses by subjects to public information: mean (± SE) number of containers missed, scrounged, and avoided for each of the test environments

	Informing	Uninforming	Misinforming
Missed			
Test birds	5·5 (0·8)	6·3 (0·8)	5·5 (0·5)
Controls	7·8 (2·0)	5·7 (1·4)	5·0 (1·9)
Scrounged			
Test birds	1·3 (0·4)	2·9 (0·8)	2·7 (0·5)
Controls	1·3 (0·6)	1·2 (0·7)	2·2 (1·1)
Avoided			
Test birds	2·4 (0·3)	0·6 (0·2)	1·3 (0·3)
Controls	1·0 (0·4)	0·8 (0·4)	0·8 (0·3)

environment more in the test group than in the control group (group*environment interaction: $F_{2,32}=3{\cdot}138$, $P=0{\cdot}051$). Recognizer birds showed a significant increase in scrounging frequency over the three environments (one-way ANOVAR: $F_{2,22}=5{\cdot}325$, $P=0{\cdot}013$; Table II); this change was not significant in control birds, however ($F_{2,20}=0{\cdot}818$, $P=0{\cdot}469$; Table II).

Because some subjects did not scrounge in all three environments and because test subjects all performed equally well in the informing environment (Fig. 2a), the amount of variation required for parametric statistics was insufficient; thus, scrounging efficiency was analysed with a Friedman 'two-way ANOVA', the non-parametric equivalent of ANOVAR (Wilkinson 1990). Test birds experienced a reduction in scrounging efficiency over the three environments (Friedman $\chi^2=10{\cdot}889$, $df=2$, $P=0{\cdot}004$; Fig. 2a). Control birds, on the other hand, experienced no significant change in scrounging efficiency (Friedman $\chi^2=1{\cdot}750$, $df=2$, $P=0{\cdot}417$; Fig. 2a). In the informing environment, all the containers from which test subjects scrounged contained food. Thus, test subjects made a significantly higher proportion of correct responses than did control birds in the same environment (Mann–Whitney U-test: $U=22{\cdot}5$, $df=1$, $P=0{\cdot}010$; Fig. 2a).

A two-way ANOVAR on scrounging latencies revealed a significant interaction between group and test environment (log-transformed data: $F_{2,14}=7{\cdot}0$, $P<0{\cdot}001$). Test birds showed a significant change in their scrounging latencies over the three environments (one-way ANOVAR: $F_{2,10}=11{\cdot}521$, $P=0{\cdot}003$), whereas no effect was detected in control birds ($F_{2,4}=0{\cdot}949$, $P=0{\cdot}460$; Fig. 2b). In the informing environment, test birds arrived at the partner's discoveries more quickly than control birds (log-transformed data: $t=-5{\cdot}690$, $df=13$, $P<0{\cdot}001$; Fig. 2b). However, the mean scrounging latencies of test birds in both the uninforming and misinforming environments were significantly higher than in the informing environment (contrasts subsequent to one-way ANOVAR: $F_1=22{\cdot}461$, $P=0{\cdot}005$; $F_1=22{\cdot}552$, $P=0{\cdot}005$, respectively, Bonferroni-adjusted level of significance set at $P=0{\cdot}02$).

The test birds' scrounging payoffs reflected the change in scrounging latencies over the three environments, with a significant interaction occurring between group and test environment (square-root transformed data, two-way ANOVAR: $F_{2,14}=16{\cdot}029$, $P<0{\cdot}001$). There was a highly significant change in test birds' scrounging payoffs over the three environments ($F_{2,12}=48{\cdot}059$, $P<0{\cdot}001$; Fig. 2c); but the three control birds that scrounged from food containers obtained similar scrounging payoffs in each of the three environments ($F_{2,4}=1{\cdot}3$, $P=0{\cdot}4$). In the informing

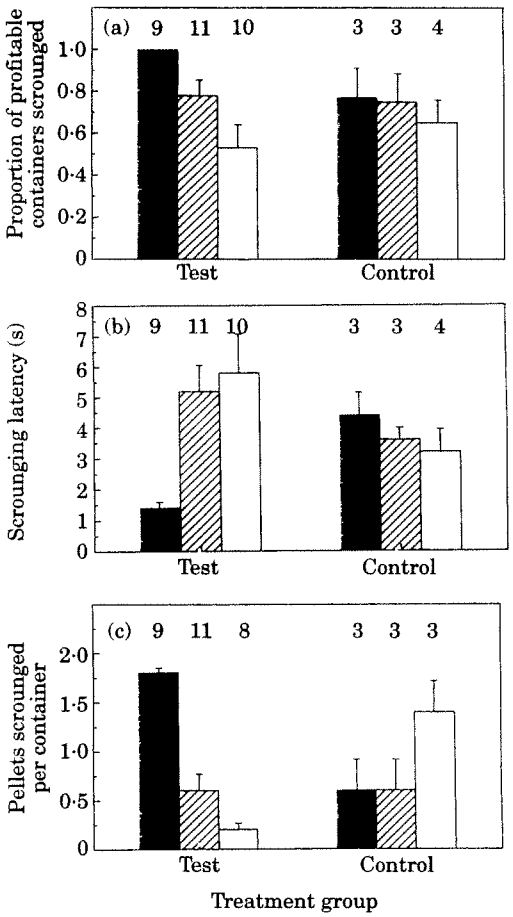

Figure 2. (a) Mean (+SE) proportion of profitable containers scrounged by test and control subjects in each of the three experimental environments. (b) Mean (+SE) latency for test and control subjects to scrounge from the partner after the partner started to check a container in each of the three test environments. (c) Mean (+SE) number of pellets scrounged by test and control subjects from each profitable container in each of the three test environments. ■: Informing; ▨: uninforming; □: misinforming. Sample sizes are given above each bar; numbers differ because some individuals scrounged from food containers in some environments but not in others.

environment, recognizers obtained significantly greater scrounging payoffs than control birds ($t=3{\cdot}912$, $df=10$, $P=0{\cdot}003$; Fig. 2c).

Avoiding

Of all avoiding events, 39% of those made by test birds and 32% made by control birds were ignores; the rest were break-offs. Subjects rarely showed either type of avoidance behaviour when colour cue information was lacking, as was indicated by the low avoiding frequency per trial shown both by test birds in the uninforming environment, and by control birds in all three environments (Table II). This change in avoidance behaviour according to the availability of colour cues resulted in a significant group*test environment interaction (two-way ANOVAR on square-root transformed data: $F_{2,32}=6{\cdot}849$, $P=0{\cdot}003$).

Subjects could incorrectly avoid the partner if she was exploiting a food container, or correctly avoid her if she was exploiting an empty container. Because subjects rarely exhibited avoidance behaviour when colour cue information was lacking, our analysis of avoiding efficiency was limited to test birds in the informing and misinforming environments, where colour cues were available. Avoiding efficiency was significantly higher in the informing environment (proportion correct= $0{\cdot}9 \pm 0{\cdot}1$) than in the misforming environment (proportion correct=$0{\cdot}2 \pm 0{\cdot}1$; Wilcoxon paired-sample test: $z=-2{\cdot}64$, $N=8$, $P=0{\cdot}008$). The temporal cost of checking the food compartment of an empty container was $6{\cdot}4 \pm 1{\cdot}1$ s ($N=19$, including the partner); because test birds correctly avoided scrounging 2·4 times on average in the informing environment (Table II), this corresponded to a saving in search time of over 12 s, more than 10% of the mean trial time.

DISCUSSION

Our study has demonstrated that starlings can respond selectively to the information generated by the patch exploitations of a foraging companion, and that the ability to recognize different foraging cues can have important consequences for individual foraging success. When colour cues provided accurate information, a higher proportion of the containers scrounged by test birds contained food than did those scrounged by control birds; and because test birds could respond more quickly to successful public information than could control birds, they were able to obtain more food on average when they scrounged from these food patches. Test birds were also able to avoid scrounging at empty containers and consequently saved a considerable amount of foraging time. These findings provide the first experimental support for suggestions made in previous field studies that group foragers can use several different types of public foraging information to make different scrounging decisions (Rabenold & Christensen 1979; Barnard & Stephens 1981; Greene 1987). In addition, our results suggest that the quality of the information available to an individual may influence its ability to compete effectively for resources within a foraging group.

A few caveats are in order when drawing comparisons between the results of this study and typical group foraging situations. First, the social context of our experiment used only two birds. In a foraging situation involving more than two birds, the ability to recognize the success of another individual as quickly as possible would be important, not only because it would enable a bird to arrive in time to obtain at least a share of the find, but also because it would allow it to obtain a greater proportion of the discovery than an individual lacking the ability to recognize foraging cues that become available early in the patch exploitation process. Under typical foraging conditions, it is likely that all group members will in fact be 'recognizers'; thus, all should arrive at profitable discoveries at approximately the same time, and receive similar payoffs. This would be equivalent to the Nash equilibrium proposed by Clark & Mangel (1984), where every group member monitors everyone else's foraging success and therefore all receive the same payoffs.

Second, the fact that our partner bird was always the same individual could also be considered to be somewhat unrealistic if different starlings reacted differently to the discovery of food. But previous work suggests that individuals expect others to respond to the same foraging conditions as they would themselves. For example, nectivorous bats, *Leptonycteris sanborni*, feeding on desert agaves, *Agave palmeri*, depart when the nectar drops below a certain threshold level. The first bat to assess a flower's depletion and depart is followed by its companions, which

do not check the flower themselves to confirm that the first bat has made the correct decision (Howell 1979).

Third, our comparison of scrounging payoffs between test and control subjects in this study depended on the subordinate partner allowing them to displace her from the containers she opened. In the field, however, payoffs to scroungers would be influenced both by the status of producing individuals, and by the availability of food at patches. If producers all defended their discovered resources, or if resource patches were all large and ephemeral, the advantages of early scrounging would be lost. The results of this study, however, should still be relevant to group-foraging situations where patches can either be usurped, or shared with the producer until depleted.

Although colour cues themselves perhaps cannot strictly be considered 'public' information in the same way that a change in the behaviour of a foraging individual might be used to indicate the presence or absence of food, this does not mean that the foraging problem faced by our starlings was not a social one. The presence of the partner bird was necessary not only to open containers and reveal the colour cues, but to act as foraging competitor as well. For example, if the partner had not been present and containers had just opened by themselves, there would have been no need for solitary subjects to arrive quickly at profitable containers and consequently no difference between the payoffs obtained by test and control birds. The presence of the partner, therefore, made arrival times crucial to an individual's scrounging payoffs. In the present study, however, our aim was not to argue that animals can use colour cues as public information. We simply used colour cues as a substitute for behavioural cues in order to illustrate the advantages of being able to respond to public information early in the patch exploitation process.

Implications for Producer–Scrounger Systems

The potential for foragers to arrive at discovered food patches more quickly and thereby obtain more food has important implications for information use in producer–scrounger systems, where 'producers' actively search for their own food and 'scroungers' feed from producers' discoveries (Barnard & Sibly 1981; Giraldeau et al. 1990). For example, previous studies have suggested that producers often enjoy a larger share of their discoveries in the form of a 'producer's advantage' (Caraco 1987; Giraldeau et al. 1990; Vickery et al. 1991). The size of this advantage, however, may depend on the availability of informational cues indicating the success of the producer to a potential scrounger.

Dominant individuals might be most likely to learn to recognize such cues; their ability to displace others from food patches means that they would have the most to gain from public information. This, in turn, could lead dominant individuals to begin specializing at scrounging (Baker et al. 1981; Rohwer & Ewald 1981), especially if there are costs to using both personal and public information concurrently (Vickery et al. 1991).

Recognizing a Lack of Foraging Success

The ability to respond selectively to public information meant not only that test starlings had a higher scrounging efficiency than control birds, but that they also had a higher avoiding efficiency. This suggests that animals are just as likely to use public information about a lack of foraging success when directing their foraging decisions, rather than simply not noticing it as has often been assumed implicitly by earlier group foraging studies. This finding contrasts with those of previous experimental studies examining information use in groups. Krebs et al. (1972) and Krebs (1973) found that great tits, *Parus major*, black-capped chickadees, *P. atricapillus*, and chestnut-backed chickadees, *P. rufescens*, were just as likely to approach an unsuccessful bird as they were to approach a successful one, perhaps because the birds had not yet learned how to discriminate between successful and unsuccessful foraging on the novel tasks, or because the time wasted on such errors was low. Until recently, the only indication that animals may be capable of using public information about unsuccessful foraging has been Benkman's (1988) intriguing, but nevertheless indirect evidence that red crossbills, *Loxia curvirostra*, may be able to recognize a lack of foraging success in others and use this information to avoid poor patches.

In natural group-foraging situations, the advantages of recognizing a lack of foraging success should be considerable. The time saved could be spent not only in an individual's own search for

food, but in monitoring the potentially successful discoveries of other group members. In environments where food patches of the same type and quality may be found together in the same locations, recognizing unsuccessful information would allow a forager both to avoid exploiting similar patch types (Benkman 1988) and to depart from such unprofitable areas more quickly (Templeton 1993).

The conventional view of group foraging assumes that group members monitor each other's foraging behaviour, but exactly what information they use has not previously been considered. Our results suggest that group foragers are likely to invest considerable effort not only in detecting the foraging success of other individuals as quickly as possible but also in detecting their lack of success. No doubt other individual foraging decisions such as patch residence times, patch sampling and prey choice give rise to similar forms of information exploitation in foraging groups that researchers have only recently begun to consider (e.g. Palameta 1989; Krebs & Inman 1992; Templeton 1993).

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