# Patch assessment in foraging flocks of European starlings: evidence for the use of public information

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A field experiment was carried out to determine whether group-foraging starlings (*Sturnus vulgaris*) use public information to help them estimate the quality of an artificial resource patch and depart accordingly. Three kinds of information are potentially available in a group: patch-sample information, pre-harvest information, and public information. These three types of information can be combined into four patch assessment strategies: (1) patch-sample alone; (2) patch-sample and pre-harvest; (3) patch-sample and public; and (4) patch-sample, pre-harvest, and public. Depending on the foraging environment we presented to the starlings, each assessment strategy made a unique set of predictions concerning the patch departure decisions of pairs of birds based on differences in their foraging success. The environment was manipulated in two ways: by altering the variability in patch quality and by changing compatibility, the ease with which individual birds could simultaneously acquire both patch-sample and public information. Our observations on patch persistence and departure order demonstrate that the starlings used a combination of patch-sample and public information, but not pre-harvest information, to estimate the quality of the experimental patch. Moreover, our results suggest that starlings use public information only when it is easily available and ignore it under incompatible conditions. This study provides the first evidence of public information use in a patch assessment problem. *Key words:* group foraging, patch assessment, patch departure, personal information, public information, *Sturnus vulgaris*. *[Behav Ecol 6:65–72 (1995)]*

Animals foraging in groups are able to locate resource patches more quickly than solitary foragers, and this can occur via several mechanisms. They can use the activities of others to recognize either novel prey types (Galef, 1976; Turner, 1964) or the types of places that are likely to contain food (Krebs, 1973; Krebs et al., 1972; Palameta, 1989). They can also approach other group members and either feed in the same locations (Krebs, 1974; Waite, 1981) or scrounge from their discoveries (Barnard and Sibly, 1981; Giraldeau and Lefebvre, 1986). In addition to the simple recognition and location of foraging sites, however, Valone (1989) has suggested that group members can use one another's foraging activities as a supplementary source of information concerning patch quality to help them direct their patch departure decisions. By combining their own estimate of patch quality with an estimate obtained when paying attention to the success of conspecifics foraging in the same patch, group foragers could theoretically assess patch quality more quickly and accurately than solitary individuals (Clark and Mangel, 1984, 1986; Valone, 1989).

Three different sources of patch assessment information are potentially available to group foraging individuals (Valone, 1989). Two of these sources of information are "personal"; the third is "public." Personal information acquired during an individual's exploitation of the current patch is called "patch-sample" information (Valone, 1991, 1992), and it can include the number of food items obtained so far or the total time spent in the patch (Green, 1987; Iwasa et al., 1981). Any personal foraging information acquired before the exploitation of the current patch comprises the forager's past foraging experience and is called "pre-harvest" information (Valone, 1991, 1992; Valone and Giraldeau, 1993). This personal information can include knowledge of how patch quality varies in the environment (Green, 1980; McNamara and Houston, 1980; Oaten, 1977), as well as sensory information (Mitchell, 1989; Templeton, 1993) or the ability to remember patches that are temporally predictable in quality (Valone, 1991). Finally, public information can be acquired from monitoring the foraging success of other individuals feeding in the same patch (Templeton, 1993; Valone, 1989).

To date, only two aviary studies have investigated the process of patch assessment in foraging groups. Valone and Giraldeau (1993) examined the use of personal and public information in pairs of budgerigars (*Melopsittacus undulatus*) foraging for hidden seeds. Although the birds used both patch-sample and pre-harvest information, there was no evidence for the use of public information, perhaps because the small size of the seeds made it difficult to recognize others' foraging success while searching for their own food (Valone T, personal communication). Templeton (1993) also tested for the use of public information in pairs of starlings (*Sturnus vulgaris*) sampling empty patches in a highly clumped foraging environment. In this case, there was evidence of the use of public as well as personal information, but only on patches where individuals were able to forage adjacent to one another. How foragers respond to their own foraging success and that of others, therefore, may depend on the ease with which patch-sample and public information can be acquired simultaneously, as well as on the expected variability in patch quality.

In this study we tested for the use of public in-

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**Table 1**

**Predictions of how differences in foraging success will influence both the order of patch departure of a focal pair of birds and the extra time spent by the second bird before its departure**

| | | Compatibility | |
|---|---|---|---|
| Information | Environment | Compatible | Incompatible |
| 1) Patch sample | Constant | L, + | L, + |
| | Variable | L, + | L, + |
| 2) Patch sample + Pre-harvest | Constant | S, + | S, + |
| | Variable | L, + | L, + |
| 3) Patch sample + Public | Constant | N, 0 | L, + |
| | Variable | N, 0 | L, + |
| 4) Patch sample + Pre-harvest + Public | Constant | N, 0 | S, + |
| | Variable | N, 0 | L, + |

Predictions apply to groups of individuals using different types of information to assess patch quality, as a function of the environmental variability and the compatibility between acquiring patch-sample and public information. L: less successful bird leaves first; S: more successful bird leaves first; N: differences in foraging success will not influence order of departure: +: the larger the difference in success, the longer the extra time spent on the patch by the second bird; 0: difference in success will not influence extra patch time of second bird.

formation in groups of starlings faced with a patch assessment problem in the field. We manipulated the ease with which patch-sample and public information could be acquired simultaneously (which we termed the "compatibility" between patch-sample and public information) by varying the height of opaque barriers within the experimental patch. When these barriers were high, it was difficult for starlings to observe other flock members and search for food at the same time; thus, in this condition, patch-sample and public information were considered to be "incompatible." When barriers were low, however, patch-sample and public information were considered to be "compatible." Patch quality was manipulated to be either constant or variable over trials.

Assuming that search would be random and that individuals would decide to leave a patch when their estimate of patch quality fell to some critical threshold level (Brown, 1988; Valone, 1989; Valone and Giraldeau, 1993), we predicted how the use of various combinations of pre-harvest, patch-sample, and public information would affect an individual's estimate of patch quality and its patch departure decisions. We then compared the birds' actual foraging behavior with the predictions by monitoring how individual differences in foraging success influenced patch departure decisions under different environmental conditions. The assumption that individuals will leave a patch when their estimate of patch quality drops to a certain threshold has some empirical support from the work of Tinbergen and Drent (1980), who showed that a starling would consistently abandon a site when its intake rate dropped below a particular threshold value. Whether all individuals will have the same threshold value is uncertain; however, it is not an unreasonable assumption, given that this threshold is considered to be a function of the benefits and costs experienced while foraging in a patch, which should be the same for all group members (Brown, 1988; Valone, 1989).

## Predictions

Valone and Giraldeau (1993) considered four assessment strategies that foragers could use to estimate the quality of a resource patch. In these strategies, to estimate patch quality foragers rely on patch-sample information either alone or in combination with pre-harvest information, public information, or both. We use this approach to generate predictions for each of the four assessment strategies when the foraging environment is variable or constant, and when patch-sample and public information are compatible or incompatible. The predictions for each of the four assessment strategies under the combined conditions of information compatibility and environmental variability are presented below, and are summarized in Table 1.

### *Strategy 1: patch-sample information alone*

In this assessment strategy, individual group members base their estimate of patch quality on patch-sample information alone, using their own average intake rate in the current patch (e.g., Tinbergen and Drent, 1980). At any point during the exploitation of the patch, group members can be ranked according to their foraging success (Valone, 1989). Thus, it is possible to consider any two individuals and make predictions concerning their relative patch persistence and departure order. The less successful of two foragers will have the lower estimate of patch quality and will reach the critical departure level first. The greater the difference in success between the two birds at the time of the less successful bird's departure, the longer the more successful individual will be expected to remain searching in the patch (Valone and Giraldeau, 1993). Neither the variability in patch quality nor the compatibility between patch-sample and public information should affect the birds' patch departure decisions.

### *Strategy 2: combining patch-sample and pre-harvest information*

Here, an individual's estimate of patch quality is a function of both its current foraging success and its prior knowledge of the variability in patch quality (Valone and Giraldeau, 1993). If patch quality is highly variable, patch-quality estimates will increase when resource items are found. If no resource items are found, however, patch-quality estimates will decline with the time spent searching (Green, 1987; Iwasa et al., 1981; Valone, 1989). Because the pre-harvest information of all group members should be similar (Lima, 1985; Templeton, 1993; Valone and Giraldeau, 1993), it is again possible to consider the foraging decisions of any two individuals. In this case, the less successful bird will be expected to depart first and, as the difference in foraging success between the two birds increases, the longer the more successful bird will remain searching in the patch after the first bird has departed (Valone and Giraldeau, 1993).

If variance in patch quality is low, on the other hand, patch assessment models (Green, 1987; Iwasa et al., 1981; Valone, 1989) have shown that patch quality estimates will either decrease with each resource item obtained, in what is essentially a patch-depletion effect (constant environment), or will decrease with the time spent in the patch independent of the number of resource items obtained (random environment). In the former case, the more successful forager will have the lower estimate of patch quality and will depart first; whereas in the latter case, differences in foraging success should not influence the order of patch departure.

### *Strategy 3: combining patch-sample and public information*

Assuming that foragers weight patch-sample and public information equally (Clark and Mangel, 1986; Valone and Giraldeau, 1993), all group members should have approximately the same estimate of patch quality at any point in time under compatible foraging conditions. Because the same information is shared by all, it is still valid to consider the departure decisions of any two group members. Thus, when personal and public information are compatible, differences in foraging success between the two birds will affect neither the order of patch departure nor the extra patch time of the second bird to depart (Valone and Giraldeau, 1993). However, when personal and public information are incompatible, we expect foragers to be able to use only patch-sample information (predictions comparable to those for strategy 1). The assumption of equal weighting of information is arbitrary, but has some support from Templeton (1993) who showed that when another bird provided public information, captive starlings spent half as much time sampling empty patches as they did when alone.

### *Strategy 4: combining patch-sample, pre-harvest, and public information*

We again assume that group members have the same pre-harvest information and that they weight the three sources of information equally, such that all individuals possess the same patch-quality estimates (Valone and Giraldeau, 1993). Foragers are therefore expected to behave in the same manner as those using strategy 3 when patch-sample and public information are compatible. In contrast, when these two sources of information are incompatible, foragers will be expected to be able to use only patch-sample and pre-harvest information (predictions comparable to those for strategy 2).

## METHODS

The study was conducted during February and March 1992 on a third floor balcony of a three-story apartment building in Montréal, Québec, Canada. The balcony was situated on the northeast corner of the building and therefore received little to no direct sunlight. During trials, we placed a single experimental patch on a wooden platform (1 $m^2$) attached to the balcony railing. We videotaped trials with a Sony Handycam from a window overlooking the balcony.

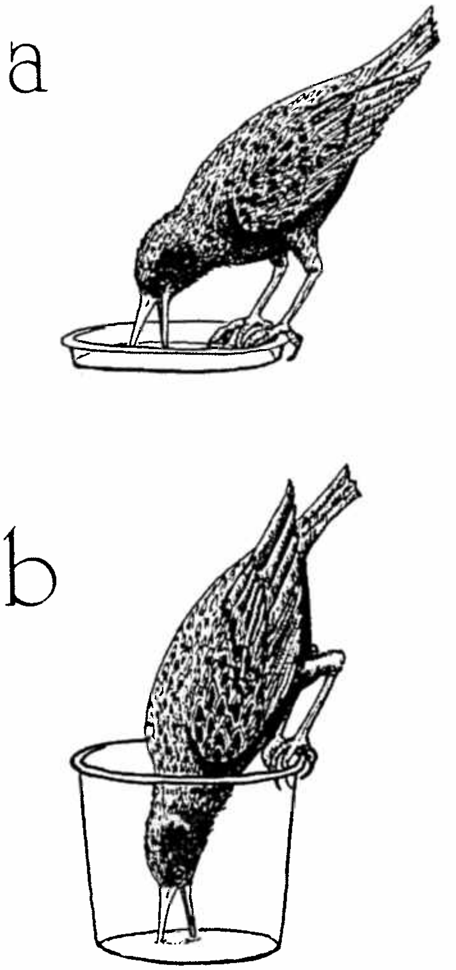

**Figure 1**
(a) Starling sampling a single low cup in the "compatible" condition; the bird's eyes remain above the rim of the cup at all times. (b) Starling sampling a single high cup in the "incompatible" condition: the head of the bird is well below the rim of the cup during sampling.

The artificial patch was a shallow plastic tray (68 × 42 × 3.5 cm) filled with sand (3 cm deep) into which were sunk 40 opaque plastic cups (8 cm diam) with the bottoms cut out. They were arranged in five rows of eight cups attached with masking tape. The cups were cut to create either a compatible patch with all cups 3.5 cm high (0.5 cm above the sand surface, Figure 1a) or an incompatible patch with all cups 10 cm high (7 cm above the sand, Figure 1b). Cups contained a maximum of one orange cheddar cheese pellet (0.23 ± 0.04 g), hidden below the sand surface.

Over the 2-week period before setting up the platform, we trapped 31 starlings on the balcony in a pull-string trap. These birds were sexed, weighed, banded with unique color combinations, and marked on the head with a dot of nontoxic acrylic paint before being released. To attract as many different starlings as possible to the experimental patch and to give them foraging experience in both incompatible and compatible conditions, we placed the patch on the platform for 4.5 h each morning for a two-week period before the start of the experiment. For the first two days of this period, each cup contained a cheese pellet, clearly visible on the sand surface. Following each visit by starlings, the patch was removed and replenished indoors. After the first two days, we gradually covered the pellets until the starlings immediately began to probe in the sand on their arrival at the patch. Once the birds consistently searched in the sand, patch quality was varied so that there were either 40 pellets (with $p = .4$) or zero pellets (with $p = .6$, $\bar{X} = 16$ pellets), with the constraint that there were no more than three patches in a row of the same quality. This was done to prevent the extinction of patch visits whenever empty patches were encountered.

### Experimental environments and procedure

The two experimental environments, *variable* and *constant*, provided an average of 16 pellets per patch presentation. In the variable environment, there were three patch types: empty, poor, and rich, each of which occurred randomly in 33% of the trials, with the constraint that there were no more than three of a given patch type in a row. An empty patch contained no cheese pellets; a poor patch, eight pellets, randomly distributed among the 40 cups; and a rich patch, 40 pellets. Half of each of these three patch types were presented in the compatible condition; the other half, in the incompatible condition. In the constant environment, the patch always contained 16 pellets per trial, randomly distributed among the 40 cups. Again, in half the trials, the patch was in the compatible condition; in the other half, it was in the incompatible condition.

A trial was defined as at least one bird visiting the patch and probing in at least one cup; a trial was terminated when the bird(s) departed from the patch. Daily trials began one-half hour after sunrise and continued until approximately 1230 h, which allowed a maximum of 16 trials per day. After the last trial of the day, we spread mixed food (grated cheese, turkey starter crumbs, bread crumbs, and bologna sausage) on the platform for the afternoon. We ran 130 consecutive trials in each environment, with 2 days between the two environmental conditions during which time mixed food was available on the balcony in the morning. The variable environment was available first; the constant environment, second.

### Data collection and analyses

We collected data from videotapes of the last 60 trials in each environment. Only data from patches where food was present were used. We selected pairs of focal birds randomly from among the first four individuals to arrive at a patch, with the requirements that: (1) the second focal bird arrived within 4 s of the first; (2) no pellets had been discovered by another individual before the arrival of both members of the focal pair; (3) both members of the pair actively searched for pellets; and (4) the second member of the pair to depart did not obtain any pellets after the first bird's departure (so that its departure decision would be based on information acquired before the first bird's departure).

The data collected from each focal pair of birds included: the time at which each bird landed on the patch; the time at which each bird left the patch; the number of pellets each bird consumed until the first bird's departure; and the total number of birds foraging on the patch at the same time as the focal pair. We also recorded the time to probe in both low and high cups using data from 10 birds in each environment, five birds for each of high and low cups. We determined whether the birds probed cups randomly by recording the number of reprobes made by individual birds in the first 30 cups probed, again using data from 10 birds in each environment. We then compared the observed number of reprobes with the number expected for both random and systematic search (e.g., Templeton, 1993; Valone, 1992).

We defined the more successful member of a focal pair as the bird that had eaten more pellets than the other at the time of the first bird's departure. Cases where both members of a pair were equally successful were omitted from the analyses. We compared the observed orders of departure of less and more successful birds to those predicted by each assessment strategy (Table 1) using binomial tests. When the direction was predicted a priori, a one-tailed test was used; when no direction was predicted, a two-tailed test was used. To test the predictions concerning the extra patch time of the second individual to depart, we categorized as "small" or "large" (e.g., Valone and Giraldeau, 1993) the degree to which members of a pair differed in their foraging success, using the median difference in success as the cutoff point. We then compared these departure time data to the predictions of the assessment strategy that was most strongly supported by the results of departure order (Table 1), using one- and two-tailed $t$ tests. Data were analyzed with SYSTAT (Wilkinson, 1990). Unless otherwise stated, all values reported in the text are means ± SE.

## RESULTS

We conducted a mean of 10.0 (range 5–16) trials per day in the constant environment and a mean of 11.6 (range 6–15) trials per day in the variable environment. Each series of 130 trials was completed after 13 days and 11 days for the constant and variable environments, respectively. During the last 60-trial period from which data were collected, mean daily temperature was not significantly different between the constant (−12.7°C ± 0.5°C) and variable (−10.9°C ± 1.4°C) environments ($N = 20$ trials each environment, log-transformed data, $t = 1.145$, df = 38, $p = .259$).

Of the starlings captured before the start of the experiment, 14 were male (89.9 ± 1.1 g), and 17 were female (86.8 ± 1.8 g). Only five marked birds were seen again, however, and these just occasionally; thus, the use of known individuals for data collection was precluded. Up to 14 starlings were observed to forage on the patch at one time and an estimated 30 to 50 starlings were regularly observed to feed on the platform following the last trial of the day. Starlings generally arrived at the patch within 10–15 min of it being placed on the platform (constant environment: 6.0 ± 2.5 min; variable environment: 10.9 ± 2.5 min, $N = 20$ trials each). There was a slight tendency for more birds to be present in the variable than in the constant environment (Table 2; two-way ANOVA on square-root transformed data, $F = 3.827$, df = 1,36, $p = .058$); however, group size remained relatively constant within a trial, with all birds tending to arrive within 10 s of the first bird's arrival. The starlings checked a mean of 48.0 ± 7.2 and 40.6 ± 11.1 cups per trial in the constant and variable environ-

Table 2

**Mean (±SE) number of birds foraging on the patch, the mean time required to probe each cup, the mean latency for the second bird of a focal pair to arrive, and the mean time focal pairs spent together on the patch as a function of the environmental variability and the compatibility between acquiring patch-sample and public information**

| | Constant environment | | Variable environment | |
|---|---|---|---|---|
| | Compatible | Incompatible | Compatible | Incompatible |
| Mean number of birds on patch per trial | 5.5 (0.7) | 4.3 (1.4) | 6.5 (1.0) | 6.8 (1.1) |
| Mean time to probe each cup (s) | 1.3 (0.2) | 1.7 (0.3) | 1.2 (0.1) | 1.8 (0.2) |
| Mean arrival latency of 2nd focal bird (s) | 1.5 (0.3) | 1.6 (0.3) | 1.4 (0.2) | 1.7 (0.3) |
| Mean time focal pairs together on patch (s) | 60.1 (11.6) | 84.5 (8.9) | 57.7(16.5) | 59.3 (13.7) |

ments, respectively ($N = 20$ in both cases). Birds in both environments took significantly longer to check high cups than low cups (Table 2; log-transformed data, $F = 10.897$, df = 1,16, $p = .005$). Once the birds located a cheese pellet, handling times were quite short (0.7 ± 0.1 s, $N = 10$). Most starlings actively searched for pellets, and also appeared to direct visual scans toward their flockmates; these scans occasionally led to scrounging attempts, though usually they were not successful.

Because of the poor return rate of marked individuals, it was necessary to use data from randomly chosen pairs of unmarked focal birds: 10 pairs for each of the four environment-compatibility combinations, one pair per trial. For the variable environment, we used five pairs of birds from each of the poor and rich patch types. In over 90% of the focal pairs, the second bird arrived within 3 s of the first. The mean arrival latency of second birds did not differ between environments (two-way ANOVA on log-transformed data, $F = 0.130$, df = 1,36, $p = .720$) or compatibility conditions ($F = 0.914$, df = 1,36, $p = .345$, Table 2). Focal birds foraged together for approximately 1 min before one of them departed (Table 2); they were not always adjacent to one another during this time. Again, the time spent together on the patch was not significantly affected by either the type of environment (log-transformed data, $F = 2.905$, df = 1,36, $p = .097$) or the compatibility condition ($F = 1.735$, df = 1,36, $p = .196$).

The birds in the constant environment reprobed a mean of 8.2 ± 1.0 cups. This was not significantly different from the 8.4 reprobes expected for random search ($t = 0.06$, df = 9, $p > .2$), and was significantly higher than the zero reprobes expected for systematic search ($t = 2.37$, df = 9, $p < .05$). Similarly, birds in the variable environment reprobed a mean of 9.6 ± 0.9 cups. This again was not significantly different from random search ($t = 0.38$, df = 9, $p > .2$), and was significantly higher than systematic search ($t = 3.05$, df = 9, $p < .02$).

### Individual foraging success and departure order

In compatible foraging conditions, there was no significant relationship between the relative foraging success of a focal pair and their order of patch departure (Table 3). This finding is consistent with both assessment strategies 3 and 4 (Table 1). In incompatible foraging conditions, however, there were significantly more cases where the less successful member of the focal pair left first in the variable environment; a similar trend was also observed in the constant environment (Table 3). Thus, these results provide the strongest support for assessment strategy 3 (Table 1).

### Differences in foraging success and extra patch time

The median difference in foraging success between less and more successful birds was 2.0 pellets in the variable environment, and 1.5 pellets in the constant environment. Therefore, we defined two pellets to be the cutoff point between small (≤2) and large (>2) differences in foraging success. We found no relationship between the magnitude of the difference in foraging success and the second birds' extra patch time under compatible foraging conditions (Table 4). In contrast, when foraging conditions were incompatible, the extra patch time of the more successful birds was markedly longer when

Table 3

**Number of trials in which the bird that departs first is either equally, less, or more successful than the other in each environment–compatibility combination**

| | Constant environment | | Variable environment | |
|---|---|---|---|---|
| | Compatible | Incompatible | Compatible | Incompatible |
| Equally successful | 2 | 1 | 1 | 1 |
| Less successful departs first | 4 | 7 | 4 | 8 |
| More successful departs first | 4 | 2 | 5 | 1 |
| Significance level | $p = 1.0^a$ | $p = .09^b$ | $p = 1.0^a$ | $p = .02^b$ |

$p$ values correspond to comparisons between observations and the most closely matching set of predictions.

[a] Two tailed binomial test.

[b] One-tailed binomial test.

there were large differences in foraging success than when there were small differences in success, and this was true for both environments (Table 4). Thus, these results are consistent with the predictions of assessment strategy 3 (Table 1).

To confirm that differences in departure times were not affected by differences in foraging group size, we reanalyzed these data, taking this potentially confounding factor into account. For the compatible condition, data from both the constant and variable environments were combined and analyzed with a two-way ANOVA, testing for the effects of both group size and differences in foraging success. We classified group size as small when there were four birds or fewer present (including the focal pair), or large (more than four birds); differences in success between focal birds were classified as before. We found no significant effect of either group size (log-transformed data; $F = 0.095$, df = 1,13, $p = .762$), or difference in success ($F = 0.009$, df = 1,13, $p = .926$) on extra patch time, nor was there a significant interaction. For the incompatible condition, a two-way ANOVA was precluded due to insufficient sample sizes. Therefore, two $t$ tests were performed on data from the constant and variable environments combined. We first tested for an effect of group size while holding the"difference in success" category constant, and found no significant effect (log-transformed data; $t = .559$, df = 7, $p = .594$). We then tested for an effect of difference in success, while holding the group size category constant, and found a significant effect ($t = -4.155$, df = 8, $p = .003$). These results are consistent with those presented in Table 4, and indicate that differences in departure times of focal birds were not confounded by differences in flock size.

## DISCUSSION

This field experiment is the first study to provide evidence that foragers use the successful foraging activities of others to help them assess the quality of a resource patch and make their patch-departure decisions. It supports the empirical suggestion of Tinbergen and Drent (1980) that starlings may pay attention to the sampling activities of others when they assess patch quality, and it also confirms the theoretical suggestions of Clark and Mangel (1984, 1986) and Valone (1989) that foragers can combine their own patch-sample information with public information to aid their estimations of patch quality. These results extend the findings of Templeton (1993), which demonstrated that captive starlings recognized the unsuccessful foraging activities of conspecifics and used this information in combination with both patch-sample and pre-harvest information to aid in their assessment of experimental patches. Taken together, these studies show that when personal and public information are compatible, group foraging starlings are alert and sensitive to the foraging rates of other flock members and will use this information in combination with their own to direct their patch-departure decisions.

Our results indicate that group foraging starlings used a combination of patch-sample and public information to assess the quality of the experimental resource patch. Differences in individual foraging success were related to the order of patch departure only when patch-sample and public information were incompatible; in this condition, less successful members of focal pairs left first more often than more successful birds in both constant and variable environments. Thus, when access to public information was visually impeded, the birds relied on their patch-sample information alone to make their patch departure decisions. In the compatible condition, however, foraging differences were not related to the order of patch departure in either environment, suggesting that all birds had similar estimates of patch quality at their departure as a result of sharing each other's information on foraging success (Clark and Mangel, 1986; Valone, 1989).

When public information was incompatible with patch-sample information, the extra time spent on the patch by the more successful individuals was positively associated with the degree to which members of focal pairs differed in foraging success; this was true for both environments. This indicates that there was no sharing of information and that only personal, patch-sample information was used. In the compatible condition, however, the extra times spent on the patch were not related to differences in foraging success. Thus, the birds had similar estimates of patch quality at their departure despite individual differences in personal foraging success. These findings are consistent with those of departure order, and again imply that the starlings paid attention to the foraging activities of neighboring birds, at least under compatible foraging conditions.

It is worth considering the possibility that the results obtained in the incompatible foraging condition may have been due to some effect of cup height other than the reduced visibility of one's foraging companions. Both a reduced ability to maneuver on the high cups and a reduced ability to scan for predators when probing in high cups might well influence a bird's foraging decisions. One potential effect of cup height might be to increase the critical departure threshold (Brown, 1988; Valone, 1989) such that birds would tend to depart from the incompatible patch earlier, at higher estimates of patch quality. However, this effect would have been the same for both more and less successful individuals, such that departure order should not have been affected. In fact, we found that focal pairs tended to spend slightly more time together on incompatible than on compatible patches (Table 2), which suggests that the critical departure threshold did not increase under incompatible conditions and that the birds were just as willing to forage in high cups as in low cups.

The behavior of the birds on the experimental patch made it clear that they were paying attention to the activities of others. This attention took the form of visual scans directed toward other group members and occasional scrounging attempts when a cheese pellet was seen in another bird's beak. These scrounging attempts were rarely successful, however, because of the manner in which pellets were distributed among the cups. Both Templeton (1993) and Templeton and Giraldeau (in press) document the activities of group foraging starlings as they search for food, and provide direct evidence that starlings do indeed watch and respond to the activities of others.

Table 4

**Mean duration (s) of the second focal bird's extra patch time (±SE) before departure from the test patch as a function of within-pair differences in foraging success for each environment–compatibility combination**

| | Compatible[a] | | Incompatible[b] | |
|---|---|---|---|---|
| Difference | ≤2 pellets | >2 pellets | ≤2 pellets | >2 pellets |
| Constant environment | 7.0 ± 3.8 | 8.9 ± 4.1 | 1.6 ± 0.8 | 37.4 ± 3.7 |
| *t* test | $t = -0.779$, df = 6, $p = .5$ | | $t = 5.445$, df = 5, $p = .002$ | |
| Variable environment | 3.7 ± 1.1 | 1.8 ± 1.2 | 7.5 ± 0.9 | 26.0 ± 9.9 |
| *t* test | $t = 1.246$, df = 7, $p > .2$ | | $t = -3.495$, df = 6, $p = .007$ | |

Results of *t*-tests on log-transformed data, testing the predictions of assessment strategy 3, are shown below each pair of mean durations. Only cases where the less successful bird left first are included in the analyses for the incompatible condition, as required to test the predictions of assessment strategy 3.

[a] Two-tailed test.

[b] One-tailed test.

## Lack of pre-harvest information use

Unlike Valone and Giraldeau's (1993) budgerigars, the order of patch departure of the starlings was not influenced by the amount of variation in the two environments, indicating that they were not using pre-harvest information to aid in their estimation of patch quality (Table 1). This result should not be taken to indicate that starlings are incapable of learning the distribution of food among patches, however. On the contrary, Lima (1985) and Templeton (1993) have shown that solitary starlings use both patch-sample and pre-harvest information to direct their patch-departure decisions when given extended experience in experimental environments.

At least three explanations are possible for the lack of use of pre-harvest information in the present study, and all relate to the difficulty the birds may have had in accurately learning the distribution of food in both environments. First, the fact that marked birds appeared at the patch only occasionally suggests that at least some unmarked focal birds may also have visited the patch irregularly; thus, some birds may have had insufficient experience with each experimental environment. Second, we had no control over the arrival times of different individuals, thus if a bird arrived later than the majority of the birds during a trial, its experience on the patch would not likely reflect the original patch quality (unless the patch was empty at the start). Finally, because the experiment was performed on free-ranging wild birds, they would have had access to other sources of food, further reducing the likelihood of their accurately learning the specific distribution of food in each of the experimental environments in a short period of time. It is possible that if we had established our experimental patch earlier in the winter, the starlings might have been more likely to make use of pre-harvest information. Both Bray et al. (1975) and Feare (1984) have reported that individual starlings overwintering in a given area consistently use the same daily feeding sites, at least if they started to use these sites at the beginning of the winter.

## Compatibility between personal and public information

Although our study documents the use of public information, it also suggests that the use of this information is contingent upon its costs. When we increased the height of the cups, we increased the difficulty of acquiring patch-sample and public information simultaneously. In this condition, then, paying attention to others meant forfeiting the opportunity to search for pellets. Rather than pay this cost, the starlings simply ignored the available public information and relied on patch-sample information alone. This finding implies that theories dealing with public information use, whether in the context of patch estimation (Clark and Mangel, 1984, 1986; Valone, 1989), producing and scrounging (Barnard and Sibly, 1981), or cultural transmission, can no longer ignore the costs associated with the acquisition of public information. In addition to "lost opportunity" costs (Stephens and Krebs, 1986), these costs could include a reduced efficiency at acquiring patch-sample information (Vickery et al., 1991) as well as the extra energy expended to acquire public information.

The fact that birds did not depart simultaneously when foraging in the compatible condition implies that there was still some degree of incompatibility between sampling cups and watching others, even in this condition. Paradoxically, this incompatibility could have been an effect of group size. Although our predictions concerning patch departure assume implicitly that there will be no group size effects, Valone (1989) points out that in large groups it might be difficult for a bird to keep track of the activities of all other individuals, particularly when the positions of some individuals might block the view of others and interfere with the transfer of public information. If group size did indeed affect the transfer of information in our study, we might expect this to have been reflected in the differences in departure times of focal pairs, with larger group sizes being associated with greater differences in departure times. However, we found no effect of group size under either compatible or incompatible conditions.

Under natural foraging conditions several factors in addition to group size might limit the transfer of information between individuals. Along with physical barriers such as tall grasses or boulders, the size of prey items may make it difficult to recognize the foraging success of a neighbor (Metcalfe, 1984; Valone and Giraldeau, 1993). As well, the difficulty of the foraging task could influence the ease with which a forager can pay attention to the activities of others and still forage with a reasonable level of efficiency (Lawrence, 1985; Lima, 1987; Vickery et al., 1991). In the field, therefore, it might be predicted that the departure decisions of individuals in foraging groups will depend on ecological factors such as characteristics of the foraging environment or the foraging task. For example, greater differences in individual departure times should be expected when foraging conditions are incompatible than when they are compatible. However, if group cohesion is also important (e.g., Cody, 1971; Hutto, 1988), the simultaneous departure of group members from a patch may occur even when foraging conditions make the acquisition of personal and public information incompatible. In such cases, individual foragers may have to rely on alternative cues, such as auditory signals between group members, to remain within the group (Valone T, personal communication).

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