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Vicarious sampling: the use of personal and public information by starlings foraging in a simple patchy environment

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Abstract Group foragers may be able to assess patch quality more efficiently by paying attention to the sampling activities of conspecifics foraging in the same patch. In a previous field experiment, we showed that starlings foraging on patches of hidden food could use the successful foraging activities of others to help them assess patch quality. In order to determine whether a starling could also use another individual's lack of foraging success to assess and depart from empty patches more quickly, we carried out two experimental studies which compared the behaviour of captive starlings sampling artificial patches both when alone and when in pairs. Solitary starlings were first trained to assess patch quality in our experimental two-patch system, and were then tested on an empty patch both alone and with two types of partner bird. One partner sampled very few holes and thus provided a low amount of public information; the other sampled numerous holes and thus provided a high amount of public information. In experiment 1, we found no evidence of vicarious sampling. Subjects sampled a similar number of empty holes when alone as when with the low and high information partners; thus they continued to rely on their own personal information to make their patch departure decisions. In experiment 2, we modified the experimental patches, increasing the ease with which a bird could watch another's sampling activities, and increasing the difficulty of acquiring accurate personal sampling information. This time, subjects apparently did use public information, sampling fewer empty holes before departure when with the high-information partner than when with the low-information partner, and sampling fewer holes when with the low-information partner than when alone. We suggest that the degree to which personal and public information are used is likely to depend both on a forager's ability to remember where it has already sampled and on the type of environment in which foraging takes place.

Key words Social foraging · Patch sampling · Public information · *Sturnidae*

Introduction

It is increasingly acknowledged that the ability of animals to make profitable foraging decisions is constrained by incomplete foraging information (Stephens and Krebs 1986), and this is particularly true for patch departure decisions (Oaten 1977; Valone and Brown 1989). Rather than perfectly recognizing the quality of a resource patch upon encounter with it (e.g., Charnov 1976), a forager often has to rely on the sampling information it acquires while exploiting a patch in order to estimate patch quality and thus decide whether to continue exploiting the patch or to depart (Oaten 1977; Green 1980, 1984; McNamara 1982). How foragers should acquire different types of sampling information and make patch departure decisions has been the subject of much theoretical (Oaten 1977; Green 1980, 1984; McNamara and Houston 1980; Iwasa et al. 1981; McNamara 1982; Valone 1991) and empirical (Lima 1984, 1985; Kamil et al. 1988; Valone 1991, 1992) research.

Most patch departure research has focused on the decisions of solitary foragers, but because many animals forage socially, it is worth considering whether an animal will alter its foraging decisions depending upon the information it acquires from observing the activities of conspecifics foraging in the same patch. Such vicarious information use would provide group

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foragers with considerable foraging advantages, enabling them to avoid both the underutilization of rich patches and the overutilization of poor patches (Valone 1993). The use of social foraging information in a patch assessment context has only recently been considered in foraging models (Clark and Mangel 1984, 1986; Valone 1989, 1993). Like models of solitary patch estimation, these social patch-estimation models assume that individual group members form estimates of patch quality by combining their prior knowledge of the distribution of resources among patches in the environment with their current patch-sampling information (Green 1980; Iwasa et al. 1981; McNamara 1982). In addition to these two forms of "personal" information (Valone 1989), however, social patch assessment models assume that each individual's patch-sampling activities can be observed by other group members and used as a third, supplementary source of sampling information, known as "public" information (Valone 1989). Theoretically, a forager that has access to such public information should be able to assess the quality of a resource patch more efficiently than one relying on personal information alone (Clark and Mangel 1986).

To date, only two previous studies have tested for the use of public information in a patch assessment context. Valone and Giraldeau (1993) showed that pairs of captive budgerigars (*Melopsittacus undulatus*) used their own personal foraging information to estimate the quality of food patches, and completely disregarded the foraging success of their neighbours when making their patch departure decisions. In a similar field experiment, Templeton and Giraldeau (1995a) obtained evidence for the use of both personal and public information in groups of wild starlings (*Sturnus vulgaris*) foraging on a single experimental resource patch. In both cases, food was always present in the patches; thus information about patch quality was available in the form of feeding success. However, results of recent group foraging studies with captive birds suggest that it should be possible to acquire public information from a lack of foraging success as well. For example, in a producing and scrounging study, Templeton and Giraldeau (1995b) showed that starlings actively avoided scrounging from conspecifics that had discovered empty food containers. Similarly, Benkman (1988) found that red crossbills (*Loxia curvirostra*) tended not to visit trees where conspecifics were foraging unsuccessfully. Field experiments using model birds to recruit foragers have also shown that when a high proportion of non-foraging models are present in an area, fewer birds are attracted to that site (Krebs 1974; Drent and Swierstra 1977).

That solitary birds can use their own lack of foraging success as a source of personal sampling information has been demonstrated in two experimental studies of patch assessment behavior. Lima (1984) allowed free-ranging downy woodpeckers (*Picoides pubescens*) and captive starlings (Lima 1985) to forage in patchy environments where experimental patches were either empty or contained a fixed number of hidden food items randomly distributed among the holes of a patch. The problem for Lima's birds was to determine how many holes to sample unsuccessfully before giving the patch up as empty, and to do this in a way which maximized their long-term energy intake rate. Lima used a simple mathematical model (Oaten 1977; Green 1980) to predict the number of empty holes that a bird should sample before departure from a patch, and found that his birds' actual sampling behavior was in qualitative agreement with this number.

In this study, we asked the question: can group-foraging starlings use the unsuccessful sampling activities of neighboring birds as a source of supplementary information to aid in their assessment of and departure from empty patches? We carried out two experimental studies which compared the behavior of captive starlings sampling an empty patch both when alone and when in pairs. This required two key modifications to the original experimental design of Lima (1985). First, we had to create a situation where two birds would consistently sample the same patch at the same time. Thus, there were only two patches present per trial, to which we could control access. Secondly, unlike Lima's patches where the starlings had to peck covers off holes to check them, the holes in our experimental patches were designed to provide no visual cues that they had been checked. This was done to ensure that birds would not sample fewer holes when in pairs simply because there were fewer unchecked holes left to sample.

In the first part of each experiment, we examined whether solitary starlings would be able to assess patch quality in a two-patch system and whether their patch departure decisions could be predicted by Lima's patch assessment model. In the second part of each experiment, we tested the hypothesis that starlings would assess an empty patch more quickly by combining personal information obtained from their own unsuccessful sampling efforts, with public information obtained from observing the unsuccessful sampling efforts of a conspecific on the same patch. Because it was possible that a bird might automatically sample a patch less if another bird was present on the same patch, it was necessary to test subjects with two types of partner bird. One partner sampled very few holes and thus provided a low amount of sampling information; the other partner sampled numerous holes and thus provided a high amount of sampling information. We predicted that if the starlings used public information, they would sample fewer holes before departure when with the low-information partner than when alone, and even fewer holes when with the high-information partner.

Experiment 1

Methods

Subjects

Subjects were six experimentally naive, wild-caught adult starlings (four males and two females), randomly selected from a population of 30 birds that had been in captivity at least 3 months prior to the start of trials. Two additional birds, both female, were selected to act as partner birds during the second part of the experiment. When not being used in an experiment, birds were housed in groups of five in holding cages (107 × 62 × 92 cm) and maintained on an *ad libitum* diet consisting of a mixture of bread, dog food, and turkey starter crumbs, supplemented with cheese, mealworms, and mynah pellets ("8-in-1 tasty dinner with fruit"). During an experiment, subjects were maintained at 85% of their initial free-feeding body weights by providing supplemental food 30 min after each daily experimental session. Water was always available, and lighting was set on a 12-h day/night cycle.

Experimental environment

The foraging environment was located in an experimental room (2.4 × 2.7 × 3.0 m). Two patches were present per trial (Fig. 1a); these were long, rectangular pieces of foam (133 × 21 × 5 cm), separated by a vertical wooden barrier (84 × 135 cm). Each patch consisted of 30 numbered holes in a 2 × 15 array, with 4 cm separating each of the 15 pairs of holes and 2 cm between each member of a pair (Fig. 1a). Within each hole was a section of cardboard tubing 4 cm in diameter and 2.5 cm deep. Over the top of the tube was stretched a piece of opaque grey latex into which had been cut a 3.5-cm slit. A starling could only check a hole by probing its beak into the slit and opening its mouth (Fig. 1b). When the bird removed its beak, the cover returned to its original position, leaving little or no visual cues to indicate it had been checked.

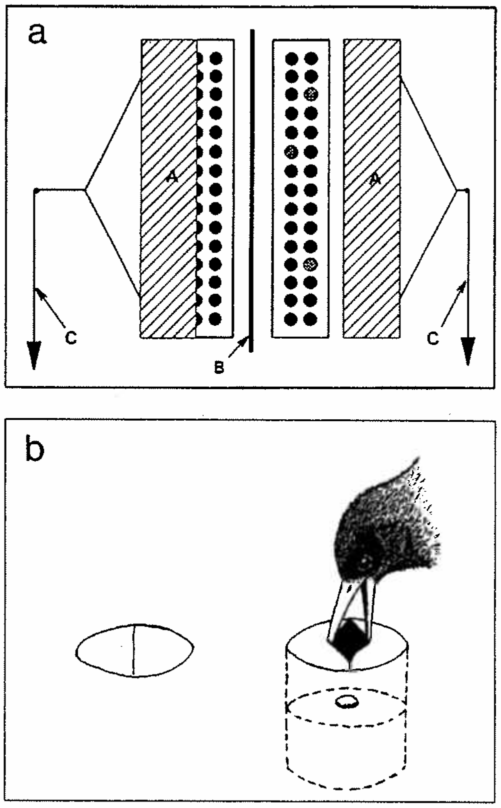

Fig 1 **a** Overview of the two experimental patches (*A* patch covers, *B* barrier, *C* pulley system controlling cover removal). **b** Detail of a starling sampling an experimental hole by probing its beak into a slit in the opaque latex cover

Training

A new subject was released into the experimental room with the two partner birds and given *ad libitum* food for 1 day. The partner birds and food were then removed and training began the next day. The subject was first provided with a small, eight-hole training patch (30 × 21 × 5 cm), sprinkled with 5 g of regular food mixture. Once the food was consumed, one mynah pellet was suspended in the slit of each hole cover; the pellet would fall into the hole when pecked, prompting the starlings to pry apart the covers to obtain the pellet. This was repeated three times, and the subject was then food-deprived overnight for 15 h.

On the 2nd day of training, the two experimental patches were stocked with three pellets each, placed in the arena on either side of the barrier, and covered with a strip of cardboard. One cover was removed, and once the bird had obtained the three pellets, the other cover was removed and the bird was allowed to forage on the second patch (Fig. 1a). This procedure was repeated several times, with the second cover being removed earlier and earlier until the bird would remain foraging on the first patch without being disturbed.

Part 1: solitary sampling

Procedure

Each subject received a total of 100 trials over a 4-day period. In any given trial, each patch had a 0.5 probability of being uncovered first and a 0.5 probability of containing food, with the constraint that a patch could not contain food or be empty more than three trials in a row. When a patch did contain food, only three randomly-selected holes contained one mynah pellet (0.12 ± 0.01 g) each; the same hole could not contain food from one trial to the next. Trials were videotaped with a Sony Handycam.

A trial started as soon as the subject stepped onto the first patch and ended once it had stepped off the second patch, at which point the experimenter entered the aviary and removed the patches. Any remaining pellets were then removed from the patches and the next set of holes were stocked with fresh pellets as necessary. The intertrial interval was 5 min. A mean of 28.3 ± 2.7 trials were run per day for the first 3 days.

On the 4th day, a naive starling was released into the aviary with the subject 15 min before the start of the last 15 trials. This was done in preparation for paired sampling (part 2); it allowed the subject to get used to another bird being in the arena during the presentation of patches and it prevented the subject from associating the presence of another bird with empty patches (patches were always empty during paired sampling). The naive bird, which was fed to satiation prior to its release into the aviary, tended to sit on top of the barrier during trials and occasionally landed beside the patch on which the subject was foraging.

Data collection and analyses

Solitary sampling data were collected from videotapes of each bird. Only the sampling behavior on the first patch visited in each trial was recorded. Rate-maximizing sampling solutions were determined for each individual using Lima's patch assessment model (Lima

1985), which includes both fixed and individually-measured time parameters. The fixed parameters were: the probability that a patch contained food, 0.5; and the number of pellets in a food patch, 3. We obtained estimates of the three time parameters for each individual. The time to check an empty hole (t_e) was calculated by dividing the total time spent on an empty patch by the number of holes checked (Lima 1985). The mean for each bird, taken over the last 20 empty patches visited, was our estimate of its t_e. An estimate of the time to check and eat from a full hole t_f was obtained for each bird from the mean t_f over the last 20 food patches visited, using the following formula with each patch (Lima 1985): $t_f = [f-(b-m)t_e]/m$, where f represents the total time spent on the food patch, b represents the total number of holes checked, m represents the number of pellets found (1, 2, or 3); and t_e is the estimate obtained above.

Travel time (t_t) was estimated by taking the average of a bird's mean inter-patch travel time and the five minute inter-trial interval (e.g., Cuthill et al. 1990). Inter-patch travel time was defined as the time between a starling lifting its head from the last hole checked on the first patch until the beak touched the first hole checked on the second patch. We obtained mean inter-patch travel time from the last 20 videotaped trials of each subject, the times being determined to the nearest 0.1 s using a stopwatch. Inter-trial times were not measured specifically for each bird; we therefore used 300 s as a reasonable estimate of the inter-trial interval.

The observed mean number of holes sampled by each bird on empty patches in the last block of trials was compared with the individual rate-maximizing sampling solutions, using paired t-tests. Unless otherwise noted, square-root transformations were carried out on all data before analyses with SYSTAT (Wilkinson 1990). All values are reported as means ± SE.

Results and discussion

Sampling behavior

By the last 20 trials, significantly fewer holes were sampled on empty patches (26.5 ± 0.4) than on food patches (29.0 ± 0.5); paired *t*-test, $t = 4.6$, $df = 5$, $P = 0.006$), indicating that the birds were discriminating between them. Before we could compare the sampling behavior on empty patches with the rate-maximizing sampling solution, however, we first had to confirm that each bird was sampling systematically (probing each hole only once). We did this by finding the mean number of reprobes made in the first 26 probes on each of the last 10 empty patches visited. If the birds were sampling systematically, the number of holes reprobed should be zero regardless of the total number of holes sampled. If the birds were randomly sampling holes, however, they would be expected to average 8.1 reprobes in the first 26 probes. The subjects were found to have a mean of 0.17 ± 0.2 reprobes in 26 probes. This was significantly less than expected for random search ($t = 8.2$, $df = 5$, $P < 0.001$), and not significantly different from the zero reprobes expected for systematic search ($t = 0.4$, $df = 5$, $P > 0.5$).

Observed versus predicted sampling decisions

The time parameters required to calculate the rate-maximizing sampling solutions were estimated separately for each individual. The birds took 0.52 ± 0.01 s to check an empty hole, and 1.91 ± 0.28 s to check a full hole and handle the pellet. The mean inter-patch travel time was 3.06 ± 0.65 s; and as noted above, inter-trial time was 300 s for each bird. Owing both to the similarity among the individual birds' time parameter scores and to the insensitivity of the model's rate-maximizing sampling solution (Lima 1985), all subjects were found to have the same predicted sampling solution: 25.0 ± 0.0 holes. The observed mean number of holes sampled on empty patches in the last 20 trials (26.5 ± 0.4 holes) was slightly but significantly higher than this predicted number (paired *t*-test, $t = 3.5$, $df = 5$, $P < 0.017$). However, because the starlings did not exhibit a fixed sampling solution, we also used a slightly modified version of Lima's model (Green 1990) to compare the payoffs our starlings actually received with the payoffs they could have received if only the predicted number of empty holes had been sampled. By this method, the birds' mean intake rate was found to be 99.1% of the intake rate that would have been achieved by a perfectly rate-maximizing forager.

The results from part 1 suggest that the starlings were able to acquire personal information from their unsuccessful sampling activities and that they used this information in a rate-maximizing fashion when assessing patch quality in our experimental two-patch system.

Part 2: paired sampling

Following the 100 trials examining solitary sampling behavior, subjects were paired with partner birds and tested for the use of public sampling information on an empty patch. We predicted that if the subjects did sample vicariously, they would sample fewer holes when with the low-information partner than when alone, and even fewer holes when with the high-information partner.

Information partners

During training and testing sessions, the two partner birds were housed individually in cages (61 × 60 × 62 cm) in visual contact with one another. Each partner was trained to provide different amounts of sampling information when it sampled the empty right-hand (test) patch with the subject. The "high-information" partner was trained to learn that only one, randomly-chosen hole contained food. Thus, this partner probed many holes during a test trial. The "low-information" partner, on the other hand, learned to probe only three well-spaced holes (positions 3, 16, and 25), each of which had a small blue dot on the cover (the dots were meaningless to the other birds). The spacing of the holes ensured that this partner moved over the entire patch, so that the only difference between the partners was the amount of sampling information they provided. During training, zero to three of these marked holes contained a pellet. The left-hand patch never contained food, and the partners learned never to visit it.

Procedure

Each subject was given a set of three consecutive trials in each of three test conditions: (1) alone; (2) paired with the low information partner; and (3) paired with the high information partner. The order of these testing conditions was arranged in a Latin square design over subjects. During test trials, both patches were empty, and the cover of the test patch was always removed first. In each test trial, the subject and partner were required to land on the test patch within three seconds of one another; if this did not occur, the trial was interrupted and a retest followed immediately. Before each set of test trials, a subject was given a set of three food trials in the presence of a naive, satiated starling. Three pellets were present in each patch in the first trial, and in only one of the patches in the other two food trials. The purpose of these food trials was to help the subject maintain a relatively constant hunger level over the testing period and also to prevent the extinction of its sampling behavior that could result from repeated exposures to empty patches during testing. A total of nine food trials and nine test trials were run on a test day. Within each set of food or test trials, there was a five minute inter-trial interval. Sets of trials were run every 30 min.

Data collection and analyses

Test trials were videotaped, and the number of empty holes sampled as well as the time spent on the test patch during each trial was recorded for both subject and partner birds. Subject data were summarized as mean scores per test condition and analyzed with a one-way repeated measures analysis of variance (ANOVAR) over the three conditions; high and low information partner data were summarized as mean scores per subject and compared with paired *t*-tests. Appropriate transformations of data were carried out before analyses; all data are reported as means ± SE.

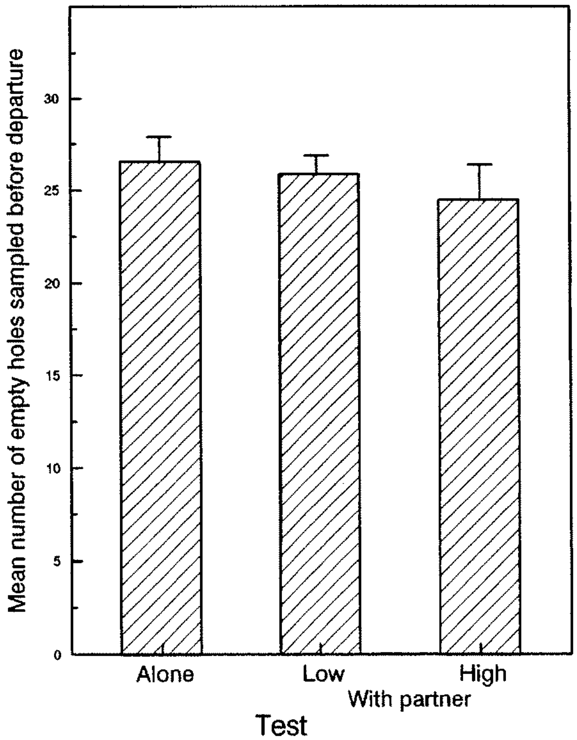

Fig 2 Mean (+SE) number of empty holes sampled by subjects before departure from the empty test patch under the three test conditions: alone, paired with the low-information partner, and paired with the high-information partner (experiment 1, part 2)

Results and discussion

In 31 of the 36 (86%) test trials in which subjects were paired with partners, the subject and partner landed on the test patch within 1 s of one another. In only two of these test trials did the partner bird not land within the three-second time limit, but retests were successful.

We found no evidence for the use of public information on the test patch (Fig. 2). Subjects sampled a similar number of empty holes before departing for the other patch when alone as when with the low and high information partners (square-root transformed data, $F = 0.9$, $df = 2{,}10$, $P = 0.407$). The subjects had a slightly lower probing rate when with the low (1.9 ± 0.1 probes/s) and high (1.9 ± 0.1 probes/s) information partners than when alone (2.1 ± 0.1 probes/s). However, this difference was not significant (log-transformed data, $F = 2.4$, $df = 2{,}10$, $P = 0.141$).

The lack of public information use was not a consequence of poor partner performance. With each subject, the high partner consistently probed at over twice the rate (1.8 ± 0.1 probes/s) of the low partner (0.8 ± 0.1 probes/s; paired *t*-test on log-transformed data: $t = 11.1$, $df = 5$, $P < 0.001$). The high partner also consistently made more probes (17.3 ± 1.9) before departure than did the low partner (5.1 ± 0.8; square-root transformed data, $t = 6.7$, $df = 5$, $P = 0.001$). On all test trials, both partner birds left before the subject.

In summary, the results of experiment 1 indicate that solitary starlings were able to use their personal sampling information to assess empty patches in a rate-maximizing fashion in our experimental two-patch system. When foraging in pairs however, the starlings made no use of public sampling information and continued to rely on personal information alone to make their patch departure decisions. There are two possible explanations for this lack of vicarious sampling. The first is that it may have been too difficult for the starlings to sample the patch and watch the partner bird simultaneously. This was found to be an important factor affecting vicarious sampling in a field experiment on patch assessment in wild starlings (Templeton and Giraldeau 1995a) in which we manipulated the height of visual barriers within the experimental patch. We found that starlings would make use of public information, but only when personal information could be acquired at the same time. In the present study, the array of the holes on the long, narrow patch meant that the partner bird was occasionally either just in front of, or just behind the subject (though in most cases, the two birds sampled towards one another), which would have made it difficult for the subject to watch the partner bird while sampling. Secondly, the linear array of holes also meant that subjects sampled the patch in an extremely methodical manner, sampling the first pair of holes from right to left, the next pair from left to right, and so on. This meant that the subjects were able to sample the patch almost perfectly systematically, making it easy for them to acquire accurate personal information about the state of the patch. Thus, public information was perhaps neither useful, nor required.

Both of these explanations imply that the lack of vicarious sampling may simply have been an effect of the geometry of the experimental patch. In order to create conditions which would be more favorable for vicarious sampling, therefore, we decided to modify the experimental patches in such a way that it would be both easier to watch a partner bird, and more difficult to acquire accurate personal sampling information. As described below, patches in experiment 2 had a square array of holes which we assumed would increase both the difficulty of keeping track of holes already sampled and the ease of watching the partner bird.

Experiment 2

Methods

The methods used in this experiment were comparable to those for experiment 1 and are summarized below.

Subjects

Subjects were five experimentally-naive, wild-caught adult starlings (four males and one female). These birds had been in captivity at least three months prior to testing and were selected randomly from a population of 20 experimentally naive starlings. The partner birds used during part 2 were the same as those used in experiment 1.

Experimental environment

The two patches were square pieces of foam (45 × 45 × 5 cm), separated by a wooden barrier. Each patch consisted of 30 numbered holes in a 6 × 5 array, with 3 cm separating each hole. The top of the cardboard tube in each hole was covered with a piece of opaque grey latex into which had been cut a 4-cm slit, as in experiment 1 (Fig. 1b).

Part 1: solitary sampling

Procedure

The procedure was completely analogous to that used in part I of experiment 1.

Data collection and analyses

Solitary foraging data were collected from videotapes of the last 20 trials for each individual as described in experiment 1.

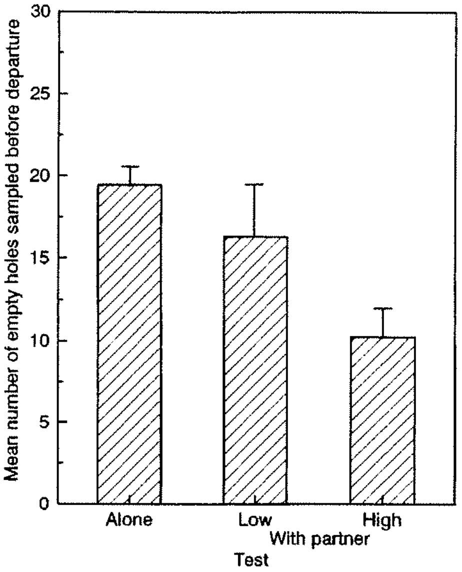

Fig 3 Mean (+SE) number of empty holes sampled by subjects before departure from the empty test patch under the three test conditions: alone, paired with the low-information partner, and paired with the high-information partner (experiment 2, Part 2)

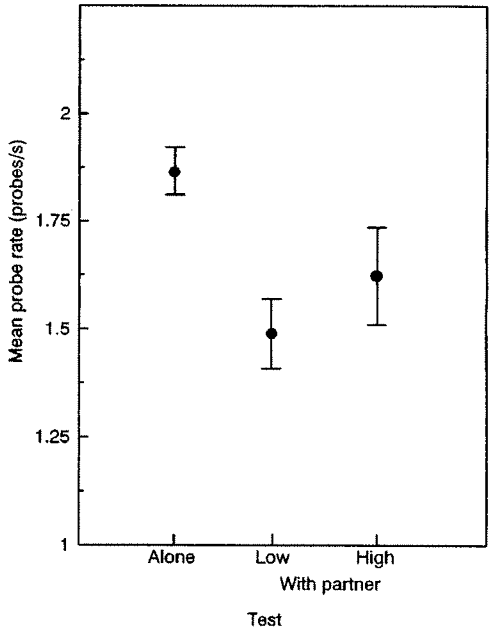

Fig 4 Mean (± SE) rate of sampling (empty holes probed per second) under the three test conditions: alone, paired with the low-information partner, and paired with the high-information partner (experiment 2, part 2)

Results and discussion

Sampling behavior

By the end of the solitary sampling trials, the birds were sampling fewer holes on empty patches (17.2 ± 0.7) than on food patches (30.5 ± 1.3; paired *t*-test, $t = 11.6$, $df = 4$, $P < 0.001$), indicating that they were discriminating between them. To determine whether the birds were sampling systematically, at least by the end of the solitary trials, we compared the number of reprobes observed on empty patches with the number expected for both systematic and random search. We did this by recording the mean number of reprobes made in 17 total probes on each of the last 10 empty patches visited. The mean number of reprobes in 17 probes was 0.7 ± 0.2. This was significantly less than the 3.5 reprobes expected for random search ($t = 5.7$, $df = 4$, $P < 0.01$), and not significantly higher than the zero reprobes expected for systematic search ($t = 1.5$, $df = 4$, $P > 0.1$). Therefore, the birds were considered to be sampling reasonably systematically, at least by the end of the solitary sampling trials.

Observed versus predicted sampling decisions

The time parameters required to calculate the rate-maximizing sampling solutions were estimated separately for each individual. The mean time to check an empty hole was 0.59 ± 0.01 s, and 2.17 ± 0.35 s to check a full hole and eat the pellet. Average travel time was calculated to be 151.3 ± 0.4 s for both conditions. The predicted number of empty holes to sample was calculated for each bird separately, and all birds were found to have the same predicted number: 25 holes. However, the observed mean number of holes sampled on the last 10 empty patches visited (17.2 ± 0.7 holes) was markedly lower than 25 (paired *t*-test: $t = 11.8$, $df = 4$, $P < 0.001$).

The birds in this second experiment clearly used their personal sampling information to discriminate between food and empty patches; however, they departed from empty patches much earlier than predicted by the rate-maximizing sampling solution. This finding suggests that these birds were departing from the new square patches on the basis of a less accurate estimate of patch quality, perhaps because of a reduced ability to keep track of holes already sampled. Although the birds in experiment 2 were found to be sampling reasonably systematically by the end of solitary trials, this was likely due to the fact that they were also sampling fewer total holes by this stage (17 as opposed to 26 in experiment 1). Indeed, a post hoc comparison of sampling errors (percent reprobes) made on the last 20 empty patches visited by solitary starlings in the two experiments confirms that it was more difficult to keep track of holes already sampled on the square patches; significantly more sampling errors were made in experiment 2 (8.0 ± 1.2%) than in experiment 1 (1.8 ± 1.2%; *t*-test, arcsine square-root transformed data: $t = 3.8$, $df = 9$, $P = 0.007$).

Part 2: paired sampling

Following the 100 solitary trials measuring the use of personal sampling information, subjects were paired with partner birds and tested for the use of public information. The procedure and data analyses were completely analogous to those used in part 2 of experiment 1.

Results and discussion

In 22 of the 30 test trials with a partner (73%), the subject and partner landed within 1 s of one another. In only four of the remaining eight test trials (each time with a different subject), one or the other of the partner birds did not land within the 3-s time limit. In these cases, retest attempts were unsuccessful, with the partner bird refusing to land. Therefore, for four of the five subjects, it was necessary to obtain mean test scores from two rather than three successful trials in one of the paired test conditions.

The sampling behavior of subjects in the three test conditions is presented in Fig. 3. A significant difference in the number of empty holes sampled over the three test conditions implies that subjects were indeed using public sampling information to direct their patch departure decisions (square-root transformed data, $F = 9.1$, $df = 2{,}8$, $P = 0.01$). As predicted, subjects sampled significantly fewer holes before departure from the empty test patch when with the high information partner than when alone (one-tailed test, $F = 18.5$, $df = 1$, $P = 0.005$, Bonferroni-adjusted level of sigificance set at $P = 0.02$, Fig. 3). They also sampled significantly fewer holes when with the high-information partner than when with the lowinformation partner (one-tailed test, $F = 10.4$, $df = 1$, $P = 0.016$).

Probing rates of the subjects differed significantly among the three test conditions (log-transformed data, $F = 10.5$, $df = 2{,}8$, $P = 0.006$, Fig. 4). Subjects had significantly lower probing rates when with partner birds than when alone ($F = 15.9$, $df = 1$, $P = 0.016$), which suggests that the subjects were paying attention to the partners' sampling activities.

The sampling behavior of the two partner birds confirmed that they were providing different amounts of sampling information to the subjects. With each subject, the high information partner consistently probed at over twice the rate (1.7 ± 0.1 probes/s) of the low information partner (0.8 ± 0.1 probes/s; paired *t*-test, log-transformed data: $t = 6.6$, $df = 4$, $P = 0.003$). In addition, the high information partner consistently made more probes (10.3 ± 2.1) before each subject departed than the low information partner made before it departed (4.0 ± 0.5; paired *t*-test, square-root transformed data: $t = 3.4$, $df = 4$, $P = 0.028$).

These results are consistent with the predictions for vicarious sampling behavior, and suggest that the starlings were not only paying attention to the activities of the partner birds, but that they were responding appropriately to the public information provided.

Discussion

Our study provides some of the first experimental evidence for the ability of group foragers to use a lack of foraging success as a source of public information in a patch assessment context. This ability would clearly be advantageous in the field, where recognizing the unsuccessful foraging activities of other group members would allow starlings to assess and abandon poor patches more quickly and thus waste less time in unprofitable areas (Tinbergen and Drent 1980).

The results of the present study extend the findings of Templeton and Giraldeau (1995a), which showed that wild, group foraging starlings can also use the successful foraging activities of others to help them assess the quality of a resource patch and make their patch departure decisions. Taken together, the results from these two studies are consistent with theoretical suggestions (Clark and Mangel 1984, 1986; Valone 1989) that public information may be used by group foragers to aid in the assessment of patch quality. This study also provides some support for the assumption that foragers will weight personal and public information equally (Clark and Mangel 1984; Valone and Giraldeau 1993; Templeton and Giraldeau 1995a); the fact that subjects sampled approximately half as many holes when with the high-information partner as they did when alone implies that they treated the sampling information provided by the partner as equivalent to their own sampling information.

Alternative explanations

One potential alternative explanation for the apparent use of public information in experiment 2 is that the subjects viewed the high-information partner as a "stronger" competitor than the low-information partner, and thus departed earlier to avoid this competition. Three key observations argue against this possibility. First, if the starlings in experiment 2 had merely been treating the partners as competitors, then the starlings in experiment 1 should also have done so, spending less time on the patch when a partner bird was present. This was not the case. Second, if the subjects had responded to the partner birds as competitors, their probing rates would have been expected to increase, in a variation on the "milkshake effect" of Clarke and Mangel (1986). Increased probing rates would also have been expected by the "vigilance effect" (Bertram 1978). This effect predicts a decline in individual vigilance levels and a consequent increase in individual probing rates as the number of foragers in a group increases, an effect which has been noted in wild starlings foraging in small flocks (Jennings and Evans 1980; Keys and Dugatkin 1990). Rather than increasing their probing rates, however, the subjects in experiment 2 probed at significantly lower rates when with partner birds than when alone, which implies that they were in fact paying attention to the partners' sampling activities. This observation is compatible with the view that vigilance and foraging are mutually exclusive activities, whether the vigilance is to watch for predators or to watch the foraging activities of others (Lazarus 1979; Pulliam et al. 1982; Lendrem 1984; Vickery et al. 1991).

A third, albeit anecdotal, observation also argues against the early departures of the subjects as being merely a response to increased competition. While being tested with a subject on an "empty" patch in experiment 2, the low-information partner found the remains of a pellet that had mistakenly been left behind from a previous food trial. The subject immediately rushed over to the partner, checked the same now-empty hole, and then proceeded to check more holes than it checked on average when sampling an empty patch alone. This trial was discounted due to the error, but it implied both that the subject was paying attention to the partner's sampling activities, and that it used the partner's discovery to conclude that the patch apparently did contain food.

It is also worth considering the possibility that the change in patch geometry between experiments 1 and 2 forced subjects and their partners into closer proximity in the latter experiment and that it was this increased intrusion into each others' personal space that may have led to the earlier departures observed in experiment 2. Several factors are inconsistent with this hypothesis, however. First, there was no indication that birds came any closer to one another on the second patch type. Indeed, birds were often closer to each other on the first, linear patch, due to the fact that they either were "beak-to-tail", or had to squeeze past one another to continue sampling (J.J.T., personal observation); despite this, subjects sampled the patch as much as they did when alone. Second, even if the birds had been closer to each other on the square patch type, one would expect the intrusion of the partner to affect departures in the low and high information conditions equally. This was not the case.

Factors affecting vicarious sampling

We have shown that starlings pay attention to the unsuccessful sampling activities of other individuals in the same patch and that they will use this vicariously acquired public information in combination with their own personal information to recognize and depart from empty patches more quickly. The degree to which starlings will sample vicariously, however, appears to depend on at least two factors: (1) the ease with which personal and public information can be acquired simultaneously, and (2) the difficulty of obtaining accurate personal sampling information. When the array of holes in the experimental patches was linear (experiment 1), the subjects showed no evidence of vicarious sampling, preferring to rely on personal information alone to make their patch departure decisions. Only when we modified the experimental patches so that the array of holes was square (experiment 2) did we obtain evidence for the use of public information. The importance of the first factor, visual compatibility between personal and public information, has already been demonstrated clearly in a field experiment in which we manipulated the ability of starlings to watch each other on an experimental patch by altering the height of visual barriers (Templeton and Giraldeau 1995a). In the present study, evidence for a difference in visual compatibility between the two patch types is only indirect. However, by showing that it was more difficult to sample the patches accurately in experiment 2, we provide some strong evidence that the second factor, accuracy of personal sampling information, may play an important role in the degree to which foragers rely on public information.

Accuracy of patch assessment

Although we cannot rule out the possibility that the increase in vicarious sampling observed between the first and second experiments was due at least in part to a change in the ease with which subjects could watch the partner bird, we have much stronger evidence that the observed increase was related to an increase in the difficulty of acquiring accurate personal sampling information. Two observations support this view. First, solitary subjects in part 1 of experiment 2 were found to sample empty patches significantly less than predicted by the rate-maximizing sampling solution, which suggests that they were departing from these patches with some degree of uncertainty about the quality of the patch. Second, they also made more sampling errors, reprobing a higher percentage of holes than they did on patches in experiment 1, which implies that these inaccurate assessments of patch quality were likely due to a reduced ability to keep track of holes already sampled.

In an evolutionary model of social learning, Boyd and Richerson (1988) have suggested that as it becomes more difficult to acquire accurate information, asocial (trial and error) learning should decline and social learning should increase. A similar conclusion was reached by Gibson and Höglund (1992) in the context of mate choice, where animals must assess the quality of potential mates as opposed to resource patches. They proposed that as the costs of mate assessment increase, the extent of personal sampling should be expected to decrease, with a concomitant increase in vicarious sampling. Such a pattern was observed in the present study. The higher probability of reprobes in experiment 2 meant that it was more difficult to assess patch quality accurately. Here, subjects not only reduced their use of personal information by sampling empty patches less than* when solitary, but they also responded appropriately to the available public information when in the presence of partner birds, which they did not do in experiment 1.

*predicted

In order to examine specifically how the cost of acquiring accurate information influences individual sampling behavior, it will be necessary to alter sampling costs experimentally to determine what effects these manipulations have on patch assessment and departure decisions (Templeton 1993). Both the type of environment in which foraging takes place, and the limits on the ability of a forager to remember where it has already sampled might well be expected to play important roles in the extent to which foragers will rely on both personal and public sources of information.

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