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The use and misuse of public information by foraging red crossbills

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Group foragers may assess patch quality more efficiently by paying attention to the sampling behavior of group members foraging in the same patch (i.e., using "public information"). To determine whether red crossbills (*Loxia curvirostra*) use public information to aid their patch departure decisions, we conducted experiments that compared the sampling behavior of crossbills foraging on a two-patch system (one patch was always empty, one patch containing seeds) when alone, in pairs, and in flocks of three. When foraging alone, crossbills departed from empty patches in a way that was qualitatively consistent with energy maximization. We found evidence for the use of public information when crossbills were paired with two flock mates, but not when paired with one flock mate. When foraging with two flock mates, crossbills sampled approximately half the number of cones on the empty patch before departing as compared to when solitary. Furthermore, as expected if public information is used, the variance in both the number of cones and time spent on the empty patch decreased when crossbills foraged with two flock mates as compared to when alone. Although high frequencies of scrounging reduce the availability of public information, scrounging is usually uncommon in crossbills, apparently because they exploit divisible patches. Consequently, public information is likely to be important to crossbills in the wild. We also show that feeding performance is greatly diminished when the feeding performances of flock mates differ. This provides a mechanism that will favor assortative grouping by phenotype when phenotypes affect feeding performance, which may in turn promote speciation in some groups of animals. *Key words:* assortative flocking, crossbills, feeding performance, flocking, foraging behavior, *Loxia curvirostra,* optimal patch sampling, public information, speciation. *[Behav Ecol 10:54–62 (1999)]*

The benefits of sociality have been a central focus in behavioral ecology (Krebs and Davies, 1993). A potential benefit accrued from group foraging is improved resource, or patch, assessment (Clark and Mangel, 1984, 1986; Ruxton, 1995; Valone, 1989, 1993). According to models of group patch assessment, individual group members estimate patch quality by combining their prior knowledge of the distribution of prey with their current patch sampling information (Green, 1980; Iwasa et al., 1981; McNamara, 1982). Besides these two forms of "personal" information, group members use the patch sampling behavior of fellow group members, or "public" information (Valone, 1989), as a supplementary source of sampling information. A forager with access to public information could assess patch quality more efficiently than when relying on personal information alone (Clark and Mangel, 1986; Ruxton, 1995; Valone, 1989, 1993).

Although many studies have tested optimal patch assessment models for solitary foragers (Lima, 1984, 1985; Krebs and Kacelnik, 1991; Stephens and Krebs, 1986), few have tested the hypothesis of public information use. Templeton and Giraldeau (1995) found that starlings (*Sturnis vulgaris*) foraging at a feeder used both their own sampling and the successful sampling behavior of others to help assess patch quality. In a subsequent aviary study, Templeton and Giraldeau (1996) found that starlings used the lack of foraging success by partner birds to more rapidly assess patches and to depart from empty patches. A third study showed that pairs of budgerigars (*Melopsittacus undulatus*) used their own sampling information, but disregarded the foraging success of their neighbors when making patch departure decisions (Valone and Giraldeau, 1993). Thus, the use of public information in patch assessment has been found in one of the two species studied. Additional studies are needed on other species to determine the prevalence and potential importance of such behavior.

We used red crossbills (*Loxia curvirostra*) to test the use of public information because observations in the field and laboratory suggest that individuals are sensitive to the feeding behavior of flock mates (Benkman, 1988, personal observation), and crossbills flock year round (Benkman, 1997; Newton, 1972). Crossbills are specialized for foraging on seeds in conifer cones on trees (Benkman, 1993; Newton, 1972). When husking seeds, crossbills lift their bills from the cone (Benkman, 1997). This motion is distinctive and likely provides patch quality information (see Valone, 1989). In addition, crossbills can scan for predators (Benkman, 1997) and presumably observe the foraging behavior of flock mates while husking seeds.

We first tested whether solitary crossbills assess patch quality and depart from resource patches in a way that is consistent with energy maximization. The energy maximization solution was determined using Lima's (1985) patch assessment model. If crossbills were foraging in an energy-maximizing manner, then it could be assumed that changes in sampling behavior through time were not the result of crossbills acquiring additional experience. The assumption that crossbills should forage so as to maximize energy intake is reasonable given that crossbill foraging behavior in the wild is consistent with such an assumption (Benkman, 1987b, 1989), and much of the morphological variation between crossbills appears to be related to maximizing feeding intake rates on different species of conifers (Benkman, 1993; Benkman and Miller, 1996).

Second, we tested the hypothesis that crossbills assess food patches more efficiently by combining personal information gained from their own sampling behavior with public information acquired from observing the sampling behavior of flock mates on the same patch. We predicted that crossbills using public information should depart from poor patches sooner when foraging in flocks than when foraging alone. In

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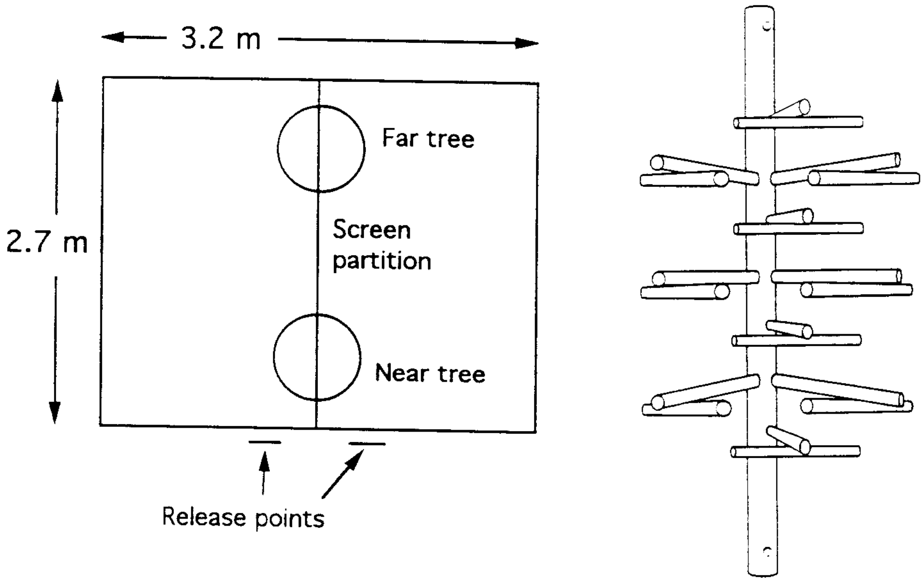

Figure 1
A schematic of the indoor aviary (left) and half a tree (right). Four open lodgepole pine cones (not shown) were mounted on each limb.

addition, the variance in patch departure time should be smaller when foraging in flocks than when foraging alone (Templeton and Giraldeau, 1995), although, unexplicably, a reduction in variation was not found in the study by Templeton and Giraldeau (1996).

Finally, we show that feeding performance is greatly diminished when the feeding performances of flock mates differ. This provides a mechanism favoring assortative grouping by phenotype when phenotype affects feeding performance (e.g., Benkman, 1993). Assortative grouping, in turn, could promote speciation in animals like crossbills, which flock year round (Benkman, 1992, 1997; Newton, 1972) and may choose mates from within their flock. This potentially important consequence of public information use has heretofore been unrecognized.

METHODS

Experiments were conducted in an aviary at the New Mexico State University Animal Care Facility from 20 May to 14 July 1996, from 13 September to 14 October 1996, and from 19 May to 2 June 1997. A 1.3-cm mesh hardware-cloth partition divided the aviary into two separate halves (Figure 1). We used two artificial trees to represent resource patches (Figure 1). Half of each tree was secured on one side of the screen partition and next to the other half to represent a single tree or resource patch. One tree was present near each end of the aviary (Figure 1). Each half-tree was 1.9 m tall and had ten 37-cm long pieces of wooden doweling as limbs. The limbs were arranged on seven different levels 15 cm apart on the bole. A 23-cm crossbranch was placed 11 cm from the distal end of each limb. Open lodgepole pine (*Pinus contorta*) cones were mounted 1 cm from the end of each limb and crossbranch and 21 cm from the distal end of the main lateral branches, yielding a total of 4 cones per limb and 40 cones per half tree. Each cone was uniquely labeled with a numbered piece of tape that hung below the cone. We used this setup because it roughly mimics a natural situation. This reduces the chance that not using public information was caused by unfamilar cues in an artificial environment.

Five wild-caught red crossbill [type 2 of Groth (1993)], which had lived in the right half of the aviary for nearly 3 years, were used in the experiments. Before the experiments, each crossbill was allowed to forage on the artificial trees for a total of 17 trials each. During the first two trials every cone contained three seeds. Next, each crossbill was allowed to forage when: 1 tree had no seeds and 1 tree had 3 seeds in each of 20 cones (5 trials); 1 tree had no seeds and 1 tree had 3 seeds in each of 8 cones (5 trials); and 1 tree had no seeds and 1 tree had 3 seeds in each of 4 cones (5 trials), which was the food distribution used in all subsequent trials for the focal crossbill. Crossbills were deprived of food for >15 h before each day of experiments.

On the right side of the aviary we conducted the experiment to test whether solitary crossbills depart from food patches (trees) in a way that maximizes energy. Only one tree had seeds during a trial. We selected the tree to contain seeds randomly, with the constraint that a tree could not contain food or be empty for more than three consecutive trials. When a tree contained food, four randomly selected cones (10% of cones) each contained three lodgepole pine seeds, with the requirement that the same cone could not contain food during two successive trials.

During the experiments, we released one crossbill into the right side of the aviary. To reduce the chance that differences between solitary and paired foraging were the result of changes in vigilance, a second crossbill occupied the left side of the aviary. This crossbill did not provide foraging information; it had a broken wing and was not provided with foraging substrates. A trial began when the crossbill landed on a tree and ended when the crossbill left or stopped foraging on the second tree. The termination of active foraging by crossbills was not the result of satiation; crossbills always foraged vigorously on food provided after the trials. Instead, crossbills apparently stopped foraging because seeds had been depleted and intake rates declined. At the end of a trial the lights were turned off, then the crossbill was caught and placed in a holding box while cones were emptied and the uneaten seeds counted. Trees were then restocked for the next trial. The mean intertrial interval for each individual crossbill ranged between 155 s and 178 s. Usually 15 consecutive trials were run per crossbill each day. We conducted between 89 and 191 solitary trials per crossbill.

While watching through a window, one of us (J.W.S.) recorded the number of cones sampled (crossbills peered into or probed with their bills) on each tree while another observer recorded, with a digital stopwatch, the time to the nearest second spent on each tree. We only analyzed data from the first tree visited. After each day of experiments, we analyzed the data to detect whether cone-sampling behavior had stabilized. To visualize the trends, we fit a cubic spline with λ set at 1000 to the data for the number of cones sampled and time spent on an empty tree. When the data appeared to stabilize, we used linear regression through the last 20 data points for three of the crossbills. We used a regression through the last 30 data points for two of the crossbills (47 and Yellow), because the number of cones sampled appeared to oscillate with no apparent overall upward or downward trend. We assumed cone-sampling behavior had stabilized and ended the trials when the slope of the regression did not differ from zero at $p > .5$.

We used Lima's (1985) patch assessment model to solve for the rate-maximizing solution for each crossbill. This model assumes systematic search. Thus, we first calculated the cone revisitation rate for each crossbill and tested for systematic search as in Templeton and Giraldeau (1996). Lima's model uses both fixed and individually measured parameters. The fixed parameters were the probability that a patch (tree) contained food (0.5) and the number of cones with seeds in a patch with food (4). Three individually measured time parameters were estimated for each crossbill, including the time needed to search an empty cone (t_e), the time needed to search and handle a seed from a full cone (t_f), and the time needed to travel between patches (t_t). We determined the time to check an empty cone (t_e) for each crossbill by dividing the total time spent on an empty patch by the number of cones sampled averaged over the last 20 trials. An estimate of the time to search and eat from a full cone (t_f) was obtained for each crossbill from the last 20 food patches sampled as in Lima (1985:233):

$$t_f = \{[f - (b - m)t_e]/m\}/20,$$

where f represents the total time spent on the food patch, b represents the total number of cones checked, m represents the number of seeds found (0–12), and t_e is the estimate obtained above. Travel time (t_t) was estimated for each crossbill as one-half of the sum of the time taken to fly between trees (1 s) and the mean intertrial interval averaged over the last 20 trials. We used t tests to compare the observed mean number of cones sampled by each crossbill before departing the empty patch during the last 20 trials to its predicted individual rate-maximizing solution (Lima, 1985). We used paired t tests to determine if the crossbills as a group under- or oversampled cones. In addition, for each crossbill we calculated the percentage of optimum from sampling each of the observed numbers of cones (see Lima, 1985). The observed percentage of optimum for each crossbill was then calculated as the average percentage of optimum for the last 20 trials.

Following the experiments examining solitary sampling behavior, each crossbill was paired with another crossbill to test for the use of public information. This experiment duplicated the conditions in the first experiment, except that one crossbill was released into each side of the aviary simultaneously, and both halves of one tree had three seeds distributed in each of four randomly selected cones. If crossbills did not land on the same tree within 2 s of one another, then the trial was stopped. This accounted for few (<3) of the 332 trials. Data were collected from only the crossbill on the right side of the aviary. We tested each crossbill with at least two different partners. The mean intertrial interval for each crossbill was between 145 s and 175 s, which was approximately the same as for the solitary trials. Usually 10 consecutive trials were run per crossbill each day. Between 55 and 78 trials were conducted per crossbill. If crossbills used public information, then they should visit fewer cones and depart earlier from the empty tree when in flocks of two (hereafter pairs) than when alone (data from solitary trials). We used one-tailed, paired t tests to test for such differences.

We found no evidence of vicarious sampling in pairs; therefore, we modified the experimental design to create conditions that would be more favorable for vicarious sampling. We did this by using two partner crossbills instead of one and by doubling the number of cones with seeds on the left side from four to eight. Because of the different food distribution used during trio trials, the question of how public information affects the long-term rate of energy intake cannot be answered quantitatively. The change in the food distribution does not, however, confound whether or not crossbills were using public information to make patch departure decisions.

Data collection and analyses for flocks of three (hereafter trios) were identical to those using pairs. The only change was that one crossbill, 47, was not used in this experiment because it would not land on the tree simultaneously with the partner crossbills. We also recorded the number of seconds the two partner crossbills spent on the first tree. All three crossbills landed on the near tree within 2 s of each other in all trials. The mean intertrial interval for each crossbill ranged between 151 s and 162 s. Usually 15 consecutive trials were run per crossbill each day. We conducted between 90 and 169 trials per crossbill.

The screen partition allowed us to vary the quality of the two sides of a tree independently so that we could assess the importance of similarity in feeding performance. During this experiment, which was conducted 2 months after the trio trials, 11 consecutive trials were run per crossbill (as a focal crossbill) each day. Both sides of a given tree (see Figure 1) were either empty or full (similar feeding performances) in nine trials. In two trials, usually the fifth and tenth trial, one side of each tree was empty and the other side was full (different feeding performances). The two halves of each tree were different during only 2 of 11 trials because we were concerned that the crossbills might ignore or discount the sampling behavior of flock mates if such trials were more frequent. We repeated this experiment for a total of 100 to 108 trials per crossbill. During the 2 days before this experiment we conducted more than 20 trials with each crossbill as the focal bird (only ''similar feeding performance trials'') to refamiliarize the crossbills with the food dispersion.We compare data from this experiment to the last 20 solitary trials (when the empty tree was visited first). We used one-tailed, paired t tests for these statistical comparisons because we predicted a lower foraging efficiency when the two sides of a tree differed.

We repeated the experiments 10 months after the trio trials to assess further whether the changes between solitary and trio trials could have resulted from additional experience. The experiments were identical except that this time trio trials were conducted first and were immediately followed by solitary trials. Because all the paired t tests were conducted on the means of only four or five birds, we also present the power of the test (Sokal and Rohlf, 1981) when it was nonsignificant ($p > .05$).

RESULTS

Solitary foraging

Cone-sampling behavior

The number of cones sampled on the empty tree varied among crossbills through time but stabilized at between 16 and 21 cones for 4 of the 5 crossbills (Figure 2). The mean time spent on the empty patch declined through time for all five of the crossbills (Figure 3; $r < -.46$, $p < .0001$ for three crossbills, $r < -.21$, $p < .14$ for two crossbills). This decrease resulted largely from the decline in mean time spent per cone

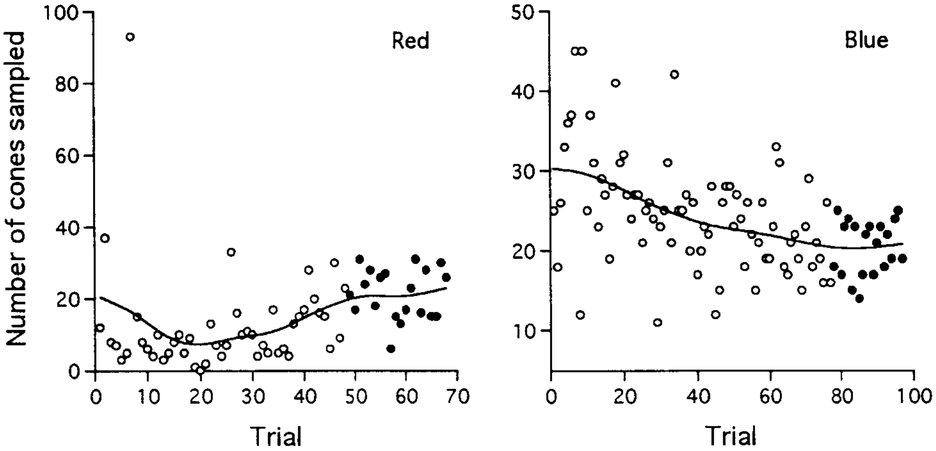

Figure 2
Number of cones sampled on the empty tree in relation to trial number for two of the crossbills. These two crossbills were chosen to show the variation between crossbills. The curves are cubic splines (λ = 1000). The solid circles represent the last 20 trials.

(Figure 4; $r < -.71$, $p < .0001$ for all crossbills), indicating that the crossbills became more proficient at sampling cones.

As crossbills converged upon their predicted optima, their propensity to miss the full tree decreased, or the number of cones sampled on the empty tree declined, but without a reduction in the probability of getting seeds on the full tree. For example, two crossbills (Red and 52) significantly increased the number of empty cones sampled before leaving a tree [Figure 2; $r = .41$, $F = 44.56$, df = 64, $p < .0001$ (with two outliers removed); $r = .14$, $F = 6.12$, df = 39, $p = .018$; respectively] and thereby reduced their probability of not getting seeds on the full tree when it was the first tree visited (logistic regressions: $\chi^2 = 21.22$, df = 1, $p = .0001$; $\chi^2 = 12.0$, df = 1, $p = .0005$, respectively). One crossbill (Blue) significantly decreased the number of cones sampled (Figure 2; $r = .47$, $F = 21.20$, df = 95, $p < .0001$) without experiencing a reduction in the probability of finding seeds on the full tree (logistic regression: $\chi^2 = 0.02$, df = 1, $p = .89$).

Optimal patch sampling

Crossbills foraged systematically, which is assumed by Lima's (1985) patch estimation model. Crossbills resampled significantly fewer cones than expected for random search ($t = -5.78$, df = 4, $p = .004$), and did not differ significantly from zero revisits expected for perfectly systematic search ($t = 1.88$, df = 4, $p = .13$, power = 0.49).

During the last 20 trials, crossbills were not optimal in the sense that each crossbill left the empty tree after visiting a distribution of cones (Table 1) rather than a single optimal number as predicted. In addition, three of the five crossbills (47, Red, Yellow) differed significantly from their predicted optima (Table 1). Nevertheless, crossbills were in approximate agreement with their predicted optima (Table 1), with the sampling behavior of four of the five crossbills representing 90% or more of their optima. Overall, crossbills did not consistently over- or undersample cones (Table 1; $t = -1.22$, df = 4, $p = .29$, power = 0.36).

The number of cones sampled by solitary crossbills on the empty tree during the 1996 trials was not significantly different from that of the 1997 trials ($t = 0.84$, df = 3, $p = .46$, power = 0.29). Within-bird comparisons revealed that the number of cones sampled on the empty tree differed significantly between 1996 and 1997 for only one (Yellow) of the four crossbills (Table 1). Yellow's cone-sampling behavior in 1997 was much closer to its predicted optimum than in 1996. These data indicate that further changes in behavior when in flocks are unlikely to result from additional learning.

Pairs

We found no evidence for the use of public information when crossbills were paired with one other crossbill. Neither the number of cones sampled (Figure 5a) nor the number of seconds spent on the empty tree (Figure 5b) differed significantly between crossbills foraging alone or in pairs ($t = -0.72$, df = 4, $p = .26$, power > 0.99; $t = 0.58$, df = 4, $p = .30$, power = 0.27; respectively). Time spent sampling each cone decreased for three of the five crossbills when foraging in

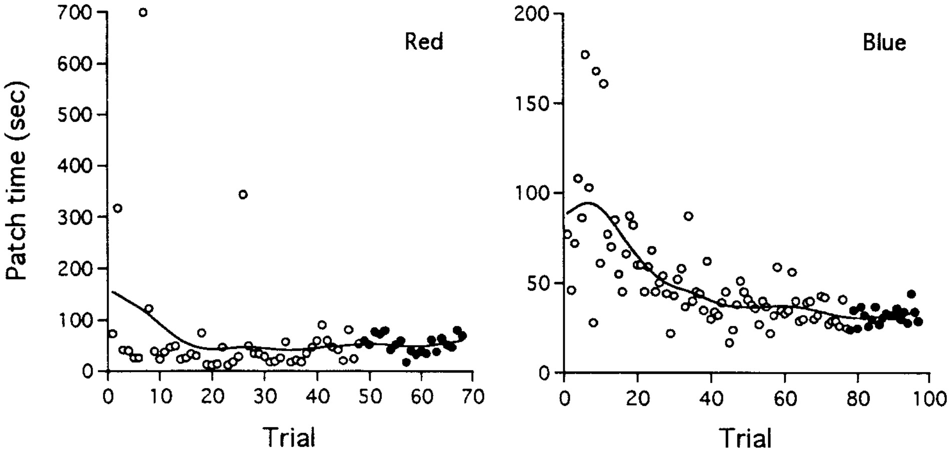

Figure 3
The number of seconds spent on the empty tree in relation to trial number for two of the crossbills. The curves are cubic splines (λ = 1000). The solid circles represent the last 20 trials.

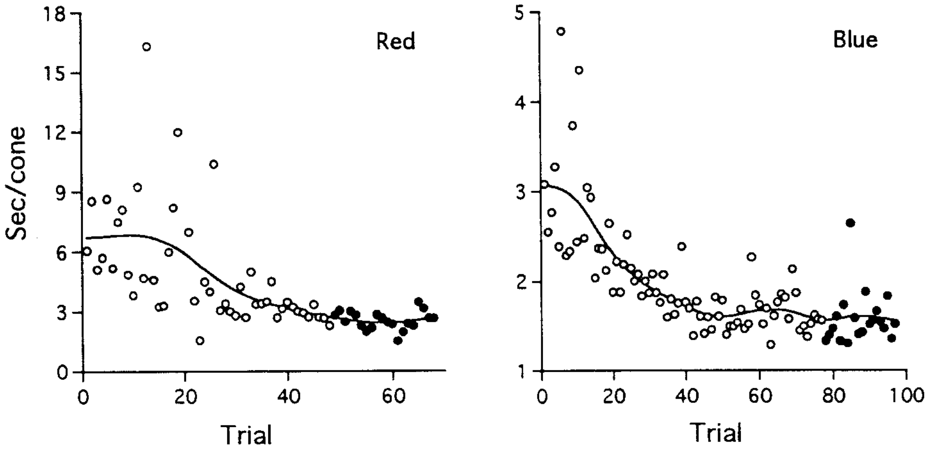

Figure 4
The number seconds spent sampling a cone on the empty tree in relation to trial number for two of the crossbills (all five crossbills showed the same pattern). The curves are cubic splines ($\lambda = 1000$). The solid circles represent the last 20 trials.

pairs as compared to when foraging alone, but this change was not significant ($t = 1.20$, df = 4, $p = .30$, power = 0.37).

Trios

Two lines of evidence show that crossbills in trios used public information to assess patch quality. First, the crossbills sampled significantly fewer cones and spent significantly less time on the empty tree when foraging in trios than when foraging alone (Figure 5; $t = 3.80$, df = 3, $p = .02$; $t = 4.66$, df = 3, $p = .01$; respectively). These differences were also highly significant within each crossbill (all $p < .004$). Furthermore, these comparisons were significant ($p < .05$) when data from solitary trials following trio trials (1997 data) were used. Some of the decline in time spent sampling is in part related to the decrease in time spent sampling each cone when foraging in trios as compared to when foraging alone. However, this change was not significant ($t = 1.25$, df = 3, $p = .30$, power = 0.36). Because the time per cone was virtually identical for crossbills in pairs and trios ($t = -0.04$, df = 3, $p = .97$, power = 0.17), the decline between solitary crossbills (two crossbills present but only one foraging) and those in trios cannot be attributed to a change in vigilance as flock size increased. Second, the variance in both the number of cones sampled and time spent on the empty tree decreased significantly for two and three of the crossbills (Levene's tests: $p < .02$), respectively, when foraging in trios as compared to when foraging alone.

Several crossbills also benefited on the good tree by foraging in a flock. For example, three of the four crossbills ate more seeds on the full tree when foraging in trios as compared to when foraging alone, although this trend was not significant ($t = -0.71$, df = 3, $p = .27$, power = 0.26). At the very least, by sampling fewer empty cones before leaving a tree when in trios than when alone, crossbills were not more likely to miss seeds in a full tree (Fisher's Exact tests: all $p > .5$).

Half of tree had seeds but the other half did not

When the near tree was empty for the focal crossbill but had seeds on the other side, the focal crossbill sampled between 1.6 and 4.1 times as many cones before departing than when both halves of the tree were empty (Figure 6a; $t = 3.82$, df = 3, $p = .016$). This suggests that the focal crossbill observed its flock mates eating seeds and behaved more like its side of the tree contained seeds.

When the near tree contained seeds on the focal crossbill's side but not on the other side, the focal crossbill sampled significantly fewer cones (Figure 6b; $t = 5.93$, df = 3, $p = .005$), and as a result they found significantly fewer seeds than when both sides of the tree contained seeds (Figure 6c; $t = 7.81$, df = 3, $p = .002$). The focal crossbill would often leave the full tree before getting any seeds because its flock mates did not find seeds. Sometimes the focal crossbill would even leave the full tree after it found seeds in one or two cones. In contrast, when both sides of the near tree contained seeds, the focal crossbill would consistently remain and sample most of the cones (Figure 6b) and eat most or all of the seeds (Figure 6c).

Table 1
Predicted, optimal, and observed number of cones samples by five red crossbills on the empty tree

Bird	Optimal no. of cones sampled[a]	No. of cones sampled, 1996		p[b]	Mean no. of cones sampled, 1997	p[c]
		Mean (SD)	% of optimum			
47	20	15.6 (5.5)	92.3	.002	—	—
52	16	19.0 (8.5)	89.9	.136	22.8	.290
Red	17	21.4 (7.0)	94.4	.012	21.9	.564
Blue	20	20.5 (3.4)	98.9	.562	17.2	.157
Yellow	20	32.6 (9.0)	65.8	<.001	17.7	<.001

[a] Estimates based on Lima's (1985) model.

[b] t tests comparing the observed number of cones sampled to the predicted optima.

[c] t tests (df = 33–37) comparing the number of cones sampled by solitary crossbills during 1996 to that during 1997.

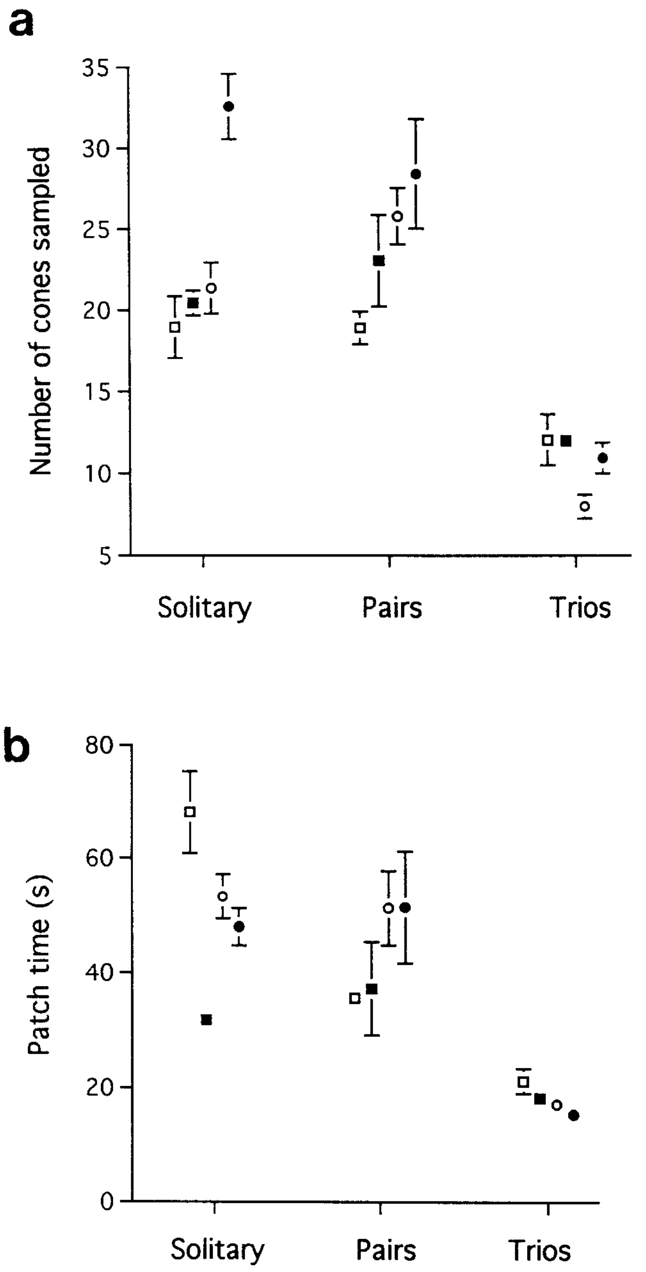

Figure 5
(a) Mean (±SE) number of cones sampled and (b) seconds spent on the empty tree during the last 20 trials. "Solitary" refers to when the focal crossbill foraged alone. "Pairs" and "trios" refer to when the focal crossbill foraged with one and two partners, respectively. Each symbol represents a different crossbill. SE bars are not visible in several cases because they are covered by the symbol.

DISCUSSION

The results of this study agree with theoretical (Clark and Mangel, 1984, 1986; Valone, 1989, 1993) and recent experimental results (Templeton and Giraldeau, 1995, 1996) that group foragers may use the foraging behavior of fellow group members to help assess patch quality and guide patch departure decisions. By using public information, crossbills accurately assessed an empty patch in about half the time and visited about half as many cones as when alone. This shows that by paying attention to the unsuccessful sampling behavior of flock mates, crossbills can assess poor patches more quickly and therefore spend less time in unprofitable areas. The benefits of using public information, in addition to local enhancement (Benkman, 1988) and collective vigilance (Benkman, 1997), should favor flocking in crossbills.

The results of these experiments further suggest that public information may be more valuable in assessing poor than good patches. However, because patches were of contrasting quality (seeds or no seeds), the importance of public information use during assessment of good patches may have been underestimated. Public information may be more valuable on good patches when the differences between patches are less extreme. For example, if good patches vary in quality, crossbills using public information may depart more rapidly from "poor" good patches. Crossbills clearly used public information in the form of foraging success and also the lack of foraging success, as was demonstrated when one half of a tree contained seeds but the other half did not.

Alternative explanations

Three alternatives to public information use could account for the above results. First, the apparent vicarious sampling may have been an artifact of the experimental design. During solitary trials a full tree had three seeds in each of four cones (10% of cones) on the right side of the aviary. During trio trials the full tree also had three seeds in each of four cones on the right side of the aviary, while on the left side of the aviary (where two partner crossbills were released) the full tree had three seeds in each of eight cones (20% of cones). Because all crossbills acted as partner crossbills about two-thirds of the time, crossbills may have started basing their patch departure decisions on this new eight-cone food distribution. However, the results from the 1997 experiments argue against this alternative. When experiments were repeated in 1997, trio trials were conducted first, immediately followed by solitary trials. If the crossbills were leaving the empty tree earlier when in trios because of this new eight-cone distribution, then we would have expected the number of cones sampled on the empty tree to increase over time during solitary trials when the crossbills foraged exclusively on the four-cone distribution. During the first 15 solitary trials the crossbills showed no evidence of progressive learning and were sampling approximately the same mean number of cones during the 1997 solitary trials as during their 1996 solitary trials (Table 1). This suggests that the results were not artifacts of the experimental design.

A second alternative is that the focal crossbill considered its partners to be competitors and foraged faster to avoid competition (Clark and Mangel, 1986; Shaw et al., 1995). We attempted to eliminate this possibility by separating the focal crossbill from the partner crossbills by a screen partition. Three lines of evidence indicate that the decline in both the time spent and the number of cones sampled between crossbills foraging alone and in trios was not the result of competition. (1) This alternative hypothesis predicts that crossbills should spend less time sampling cones, not sample fewer cones. Yet crossbills sampled only about half as many cones when in trios as compared to when solitary. (2) Cone-sampling rates should have increased as flock size increased from two to three, yet there was virtually no difference ($\Delta = 0.005$ s/cone) between the overall means when foraging in pairs and trios. (3) In the experiment when the focal crossbill's side was empty but the other side had seeds, the focal crossbill sampled significantly more cones than when both halves were empty. The focal crossbill even tended to sample more cones than when alone (Figure 6a). If the results were due simply to competition, then the focal crossbill should have sampled fewer or the same number of cones, not more cones. Con-

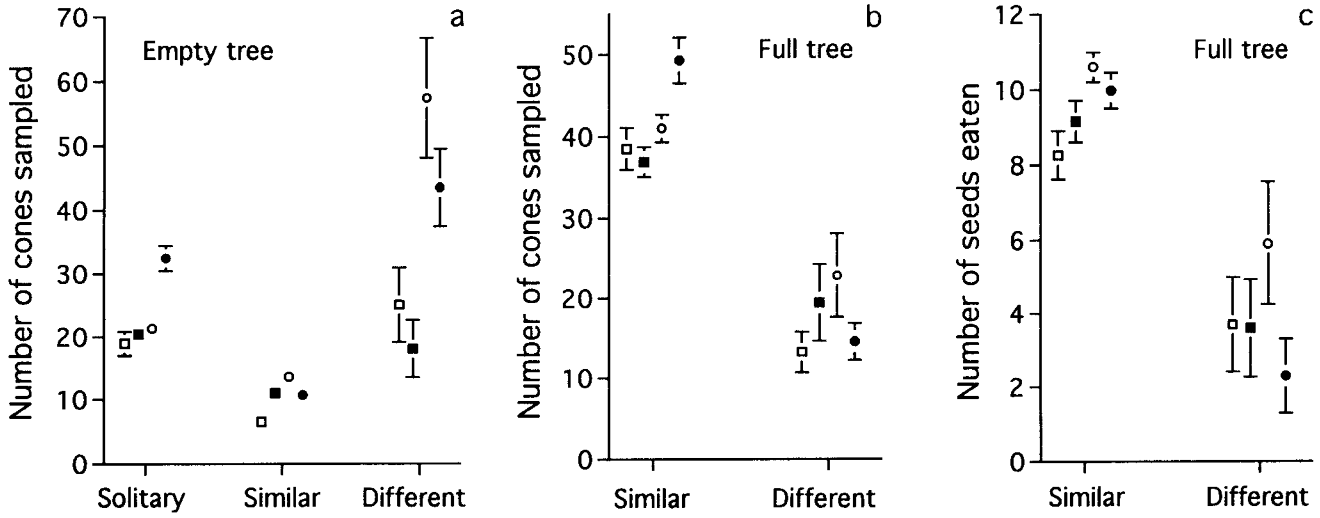

Figure 6
(a) The mean number of cones sampled (±SE) by the focal crossbill when the first tree it landed on was the empty tree. The number of cones sampled includes resampled cones. "Solitary" refers to when the focal bird foraged alone. "Similar" refers to trials when both sides of a given tree were either empty or full of seeds. "Different" refers to trials when one side of a tree was empty and the other side was full. Each symbol represents a different crossbill. Sample sizes were 20 trials per bird for solitary trials, 37–48 trials per bird for "similar" trials, and 10 trials per bird for "different" trials. SE bars are not visible in several cases because they are covered by the symbol. (b, c) The mean numbers of cones sampled and seeds eaten (±SE) by the focal crossbill when the first tree it landed on was the full tree. Sample sizes were 38–43 trials per bird for "similar" trials and 10 trials per bird for "different" trials.

versely, when the focal crossbill's side had seeds but the other side was empty, the focal crossbill sampled significantly fewer cones than when both sides had seeds (Figure 6b). If differences were the result of competition, then the focal bird should have stayed longer, not shorter, on the good half because the partner birds left early. These results indicate that the alternative hypothesis of competition does not apply, quite possibly because the screen provided an effective barrier.

Third, the focal crossbill may have departed earlier simply because it followed the first partner crossbill to leave the empty tree (e.g., Valone, 1993). This hypothesis, like the public information use hypothesis, predicts a decrease in the average time (and variance) to depart from the empty tree. However, unlike the public information use hypothesis, it predicts that the distributions of times spent on the empty tree for trios should fall within those of solitary birds. This was not found. Considering all the data from the four crossbills, solitary crossbills never spent less than 17 s on the empty tree (n = 80 trials), whereas in trios the focal crossbills spent less than 17 s on the empty tree during nearly half of the trials (36 of 80 trials). This could in part result because the two partner crossbills should be able to more rapidly sample and assess their half of tree and hence leave earlier. However, this is not an adequate explanation because the focal crossbill sometimes left the empty tree first (focal crossbills left first on 17 of the 80 trio trials), including 7 times before 17 s was spent on the tree. In addition, if the focal crossbill was simply following the first partner crossbill, the interval between the leaving times should be small. Although in many cases the interval was 1–2 s, the focal crossbill left 5 s or more later on 24 of the 63 trials when the focal crossbill followed. In sum, focal crossbills did not just simply follow the first partner crossbill to leave. However, patch departure by other crossbills is probably an important additional cue for foraging crossbills because it signals the bird's assessment of the patch as empty or unprofitable.

Scrounging and producing in crossbills

Equally critical to demonstrating the occurrence of a behavior is determining whether the behavior is important to the animal in the wild. A first step is to determine whether conditions in the wild likely favor the use of public information. Giraldeau (1997) has suggested that foraging groups often provide minimal public information because some individuals may not provide sampling information ("scroungers") (Barnard and Sibly, 1981). The presence of specialized scroungers is expected to be related to the extent to which resources are divisible (Giraldeau et al., 1990). When food is indivisible, whole parcels of food can be obtained at a reduced cost by scrounging (Thompson, 1986). However, when food patches are divisible, "producing" provides a consistently larger share of each patch (Giraldeau et al., 1990; Vickery et al., 1991). The producer's advantage may prevent individuals from specializing as scroungers (Giraldeau et al., 1990).

Cones within a tree are divisible for crossbills, but seeds within a cone are indivisible. Thus, whether a scrounging strategy will be favored in crossbills depends on what scale of patchiness is most important in crossbills. Three lines of evidence indicate that variation among trees is the most important level of patchiness to crossbills. First, variation in cones among trees is substantially greater than that found within trees (Benkman, unpublished data). Second, crossbills in the wild rarely displace individuals to scrounge from cones foraged on by other crossbills; scrounging rarely occurs more frequently than once every 60 min in flocks of two or more (Benkman, unpublished data; see Benkman, 1997). Finally, a crossbill must sample a cone to decide whether it is profitable and by doing so eats some seeds. A scrounger that usurps a sampled cone gets a partially depleted cone. By forgoing sampling, the scrounger has missed the opportunity to eat seeds and the opportunity to discover its own equally profitable cone during the time that it was watching other producers. Specialized scrounging, therefore, is unlikely to provide net benefits to crossbills. Consequently, crossbills are likely to conform to the assumption of equal search and equal sharing of food characterized by the social foraging models, which predict public information use (Clark and Mangel, 1984, 1986).

Misleading public information, assortative flocking, and speciation

Finally, the results of our study suggest that the value of using public information depends critically on the similarity between the feeding performances of flock mates. When feeding performances differ between flock mates, public information can be misleading. For example, some patches might be poor for some individuals but good for others because of differences in trophic structures between individuals. Consequently, an individual for which a patch is poor might remain longer on this patch if it uses the feeding performance of flock mates to help assess patch quality. Conversely, an individual for which the patch is good might leave the patch prematurely if it uses public information. These are exactly the results we found in our experiments. This implies that public information should be most valuable to foragers in single- or mixed-species flocks when feeding performances are similar between individuals. Likewise, it has been hypothesized that individuals in flocks might compromise their feeding rates to remain with the group if other benefits acrue (Hutto, 1988; Valone, 1993). Our study is the first to experimentally demonstrate such an effect.

Previous studies on factors favoring assortative grouping have concentrated on the disadvantages to less competitive phenotypes and to odd individuals that might be preferentially preyed upon by predators (Peuhkuri, 1997, and references therein). These provide very different mechanisms favoring assortative grouping from the one proposed here, which arises from public information use.

In red crossbills, slight differences in bill depth (<0.5 mm) or palate structure can have substantial effects on feeding performance (Benkman, 1987a, 1993; Benkman and Miller, 1996), which in turn result in pronounced differences in conifer use (Benkman, 1987b, 1993). Differences in feeding performance between morphologically similar red crossbills should favor assortative flocking in relation to bill size and palate structure. Given that public information is likely important to crossbills for patch assessment in the wild, selection favoring assortative flocking may be great. In addition, flock members with similar morphologies will have similar patch preferences and durations of patch use, resulting in flock cohesiveness (see Hutto, 1988; Valone, 1993). Increased flock cohesion should be favored because remaining in a flock has a variety of benefits to crossbills (Benkman, 1988, 1992, 1997).

Selection favoring assortative flocking could also promote reproductive isolation and could have been critical in the evolution of different ecological species or host races of red crossbills, especially if they evolved in sympatry (Benkman, 1993; Bush, 1994). Because the different ecological species or host races of red crossbills are so similar in appearance (Groth, 1993), selection may have even favored vocalizations that rapidly identify trophic morphology. This might explain why the eight different taxa of red crossbills in North America (Groth, 1993) are described as ‘‘call types.’’ Observations in the wild indicate that crossbills flock assortatively by call type (CWB, personal observation), but this has yet to be adequately quantified. Whether the use of public information might favor assortative grouping and contribute to speciation in other taxa is unknown. Such potentially important consequences, however, warrant increased study of public information in other animals.

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