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Flock size, food dispersion, and the feeding behavior of crossbills

C.W. Benkman

Department of Biological Sciences, State University of New York at Albany, 1400 Washington Avenue, Albany, NY 12222, USA

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Summary. Feeding rates of five captive red crossbills (*Loxia curvirostra*) were measured when they were foraging alone, and in flocks of two or four on three seed dispersion patterns. On the most strongly clumped seed dispersion, individuals had higher mean feeding rates and the smallest probability of starvation when in flocks of two than when alone or in flocks of four. Individuals in flocks of four had higher feeding rates on the weakly clumped seed dispersion than on the uniform and more clumped seed dispersions; there were no food finding benefits gained from flocking on the uniform seed dispersion and aggression increased as food became more clumped. Most recent work has assumed that flocking results in higher feeding rates only because time spent vigilant is reduced. Crossbills, however, did not visit more cones per unit time as flock size increased, as would be expected if less time was spent vigilant. Thus, any reductions in vigilance as flock size increased were countered by increases in other behaviours, such as those related to aggression. Consequently, the higher mean feeding rates of crossbills in flocks than when solitary is not attributable to reduced vigilance. The increase in mean and the decline in variance of feeding rates occurred because crossbills in flocks found good patches earlier, and possible by spending less time assessing poor patches.

Introduction

Flocking is thought to increase the efficiency with which individuals exploit patchily distributed prey (e.g. Krebs et al. 1972). Increases in flock size reduce both the mean and variance in the time required to locate food patches, because individuals in flocks may recognize when other flock members discover patches ("local enhancement"; e.g. Krebs et al. 1972). Sharing of patches and interference among flock members, however, may nullify the potential increase in mean feeding rates (Pulliam and Millikan 1982; Caraco and Pulliam 1984). As a result, the reduction in variance in feeding rates may be the main food finding advantage derived from flocking (Thompson et al. 1974; Krebs 1974; Baker et al. 1981; Caraco 1981; Pulliam and Millikan 1982; Caraco and Pulliam 1984; Ekman and Rosander 1987). In certain circumstances, however, mean feeding rates may be increased by foraging in flocks, such as when prey items are difficult to subdue (Schaller 1972), food patches are ephemeral (Pulliam and Millikan 1982), or meal size is less than patch size (Clark and Mangel 1984).

If mean feeding rates are enhanced by foraging in flocks, these gains may often result from reductions in antipredator behaviour, and much recent research on flocking has been on antipredator behaviour (e.g. Pulliam 1973, 1976; Caraco 1979; Caraco et al. 1980; Pulliam et al. 1982; Sullivan 1984; Glück 1987). These studies have demonstrated that flocking decreases an individual's time spent scanning, so that proportionately more time can be devoted to actual foraging.

Nevertheless, food finding benefits alone may increase mean feeding rates. Food finding benefits from flocking should be sensitive to food dispersion (Thompson et al. 1974), yet most of the experiments conducted so far have used extremely clumped food dispersions (Krebs et al. 1972; Baker et al. 1981; but see Krebs 1979). To test whether flocking can increase mean feeding rates I measured the number of seeds eaten per unit time of

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Present address: Department of Biology, Princeton University, Princeton, NJ 08544, USA

five captive red crossbills (*Loxia curvirostra*) foraging either alone, or in flocks of two or four. Three different patterns of food dispersion, from uniform to very clumped, were used.

Crossbills are ideal study animals because they (1) exploit seeds in conifer cones that vary in dispersion and are often abundant within patches (Newton 1967; Benkman, personal observation), (2) occur in flocks of various sizes year round (Benkman, personal observation), and (3) are very tame and take well to captivity (e.g. Tordoff 1954).

Methods

The crossbills were housed in a 2.8 × 4 × 2.7 m indoor aviary and were fed mostly conifer seeds in conifer cones. During the experiments crossbills foraged for Austrian pine (*Pinus nigra*) seeds located in pine cones that were attached to four wooden "trees". The trees were 1.9 m tall, and each had eight 37 cm long pieces of wooden dowling as side limbs. At each of four levels, 20 cm apart on the bole, two side limbs projected in opposite directions and perpendicular to adjacent levels. Eleven cm from the distal end of each limb was a 23 cm crossbranch. Open cones were mounted one cm from the end of each limb and 21 cm from the distal end of the main lateral branches, yielding a total of four cones per side limb and 32 cones per tree. Each cone was labelled with a numbered piece of folded tape that hung below the cone.

The trees were placed in the corners of a square within the room, with each side 1.6 m long, and with the bole of each tree 63 cm from the nearest wall. Prior to each trial 64 seeds were individually placed between the scales of the cones. The crossbills had to be next to the cone to locate seeds.

Three seed dispersions were used. In the uniform seed dispersion each tree held 16 seeds and two of the four cones on each side limb held one randomly placed seed. In the moderately clumped seed dispersion one tree held 31 seeds and the other three trees held 11 seeds each (31:11 seed dispersion). Within each tree, the distribution of seeds among cones conformed to a Poisson distribution. The cones containing seeds differed between trials. The tree containing 31 seeds was determined randomly with the constraint that, for a given crossbill, the high seed density tree could be the same for no more than two consecutive trials. The most clumped dispersion had 49 seeds in one tree and five seeds in each of the other three trees (49:5 seed dispersion). Within each tree, the distribution of seeds among cones conformed to a Poisson distribution. The average number of seeds per cone within a tree ranged from 0.16 (5 seeds/32 cones) to 1.53 (49 seeds/32 cones). This range is within the range of seed densities red crossbills commonly encounter in nature. For example, in Ontario, Canada, red crossbills foraged on white pine (*P. strobus*) cones from October 1984 when the mean number of seeds per cone was greater than 10 to mid January 1985 when the number of seeds per cone had declined to a mean of 0.19 (range 0.067–0.38; $n = 3$ trees [40 cones]; see Benkman 1987).

Flock sizes of one, two, and four were used. These flock, sizes are common in nature, representing 50 percent of red crossbill foraging flocks (74 of 148 flocks, median flock size = 3) that I observed from 1982 to 1985 in North America (see Benkman 1987).

Crossbills were deprived of food overnight for more than 14 h prior to the experiments and trials were completed before 1300 hours. To avoid satiation, individual crossbills were tested a maximum of one, two, and four times a day during trials of solitary crossbills, and flocks of two and four, respectively. Usually an individual crossbill consumed less than 60 seeds in all trials during a day, yet when given unlimited access to seeds, individual crossbills consumed over 150 seeds in less than 15 min.

During trials with solitary crossbills, I recorded with a tape recorder, while watching through a one-way window, each cone visited and the time when a seed was eaten. During trials for flocks of two and four, I recorded the same information for a pre-selected crossbill, while another observer recorded times when a second pre-selected crossbill obtained seeds. Trials began when the first crossbill landed on a tree, which usually was immediately after the trees were placed in the aviary. All aggressive interactions involving the two focal crossbills were recorded. Because the social hierarchy among the crossbills was not linear, relative dominance effects for an individual were scored as the number of dominant interactions per 1000 s minus the number of subordinate interactions per 1000 s.

Trials were terminated when the crossbills stopped foraging or after all or nearly all of the seeds had been depleted. All trees were then immediately withdrawn from the aviary and all remaining seeds were removed. The number of seeds remaining was recorded. For trials of solitary crossbills and flocks of two, every seed should have been accounted, for, but not for flocks of four. Usually all 64 seeds were accounted for, but occasionally fewer and rarely more were recorded. Inaccuracy in the number of recorded seeds occurred because, for example when several seeds were husked in rapid succession the number of seeds actually consumed may have been over- or under-estimated. If the deviation from 64 was greater than three (5% of total), the trial was discarded.

The sequence of trials, in terms of seed dispersion/flock size, and number of trials (*n*) were as follows: uniform/one (21), uniform/four (53), 31:11/one (40), 31:11/four (77), 49:5/one (38), 49:5/four (71), and 49:5/two (54). All trials for a given seed dispersion/flock size were completed before the next combination was tested.

A total of five different crossbills were used in the experiments. All five possible flocks of four birds were usually tested each day in a temporal sequence that changed systematically from day to day. All crossbills were followed in roughly equal numbers of trials in each flock size. For flocks of two, half of each individual's trials were with a dominant and half with a subordinate. Dominance relations between individuals, as determined by aggressive interactions (i.e., supplantings, chases), were constant during the study and subordinate individuals rarely unequivocally displaced dominants (see also Tordoff 1954).

The cumulative number of seeds eaten at 30 s intervals between 30 and 180 s were compared between seed dispersions and flock sizes. Detailed analyses of longer periods were not done because nearly all seeds were depleted within 150–180 s during flock trials. Unless noted otherwise, tests for differences in means were *t*-tests for paired comparisons on the means of each individual (i.e., $n = 5$) and tests for differences in variances were *F*-tests on the variances of single individuals.

There is no a priori reason to select any time prior to seed depletion as the appropriate time for analysis. Instead, the question of interest is what flock size provides an individual crossbill with the highest mean feeding rate; that crossbills forage in a manner that comes close to maximizing feeding rate is evident from both conifer use patterns (Benkman 1987) and the time of departure from individual tamarack (*Larix laricina*) cones (Benkman, in press) in the field. What is critical, therefore, is the maximum marginal feeding rate (e.g. Charnov 1976; Stephens and Krebs 1986) obtained in the set of 4 trees in the experiments. It is assumed that in nature similar sets of trees would be repeated; in nature, individual crossbills often visit ≫20 trees in the course of a day (Benkman, personal observation). Individual survivorship may also be influenced by variance in feeding rate (e.g. Pulliam and Millikan 1982). Variance in feeding rates is examined separately of mean intake rates in the Results, but in the Discussion both means and variances will be examined simultaneously to determine the flock size maximizing survivorship.

The feeding rates of individuals progressively increased during the solitary and flock trials on the uniform seed dispersion implying learning. Such a result was not found on the other seed dispersions. Data from early trials on the uniform dispersion, therefore, are not presented. Because there appeared to be two periods of learning, first when alone and then when in flocks, I later tested one bird (WF) three times on the uniform seed dispersion. WF's mean feeding rates were substantially higher than its pre-flock rates on the uniform seed dispersion, although they were nearly identical to those when solitary on the other two seed dispersions. Consequently, the data for solitary birds on the uniform dispersion are not presented. On the other hand, indentical mean feeding rates for solitary individuals are expected since the mean number of seeds per cone was identical in all three seed dispersions. This also implies that after the initial learning, feeding behaviour stabilized.

Results

31:11 seed dispersion

Individual crossbills in fours consumed significantly more seeds after 60 s (Paired *t*-test, $t_4 = 3.18$, $P < 0.05$) and had higher marginal feeding rates than did solitary foragers (Fig. 1b). Feeding rates diminished with time for crossbills in fours so that after 180 s the number of seeds consumed were less for flock members than for solitary crossbills (Paired *t*-test, $t_4 = 4.62$, $P < 0.01$). Feeding rates for solitary crossbills did not decline until after 210 to 270 s, depending on the individual.

The variance in seed intake for each individual in flocks of four was compared to its variance in seed intake when alone after each 30 s interval from 30 to 180 s. This resulted in 6 comparisons (*F*-tests) for each of 5 individuals for a total of 30 comparisons. The variances in seed intakes for individual crossbills in flocks of four on the 31:11 seed dispersion were similar to those when alone (Fig. 1b, *F*-tests, $df = 8{,}15$ or $8{,}16$, $P > 0.05$ in 29 of 30 comparisons).

49:5 seed dispersion

Crossbills in flocks of two consumed more seeds during the different time intervals than when alone (Paired *t*-test, $P < 0.02$, except after 180 s) or when in flocks of four (Paired *t*-test, $P < 0.05$, except after 60 and 90 s) on the 49:5 seed dispersion (Fig. 1c). Seed intake was greater for individual crossbills in flocks of four than when alone after 30 s (Paired *t*-test, $t_4 = 3.16$, $P < 0.05$), but by 150 s solitary crossbills had a higher total intake (Paired *t*-test, $t_4 = 5.61$, $P < 0.01$, Fig. 1c).

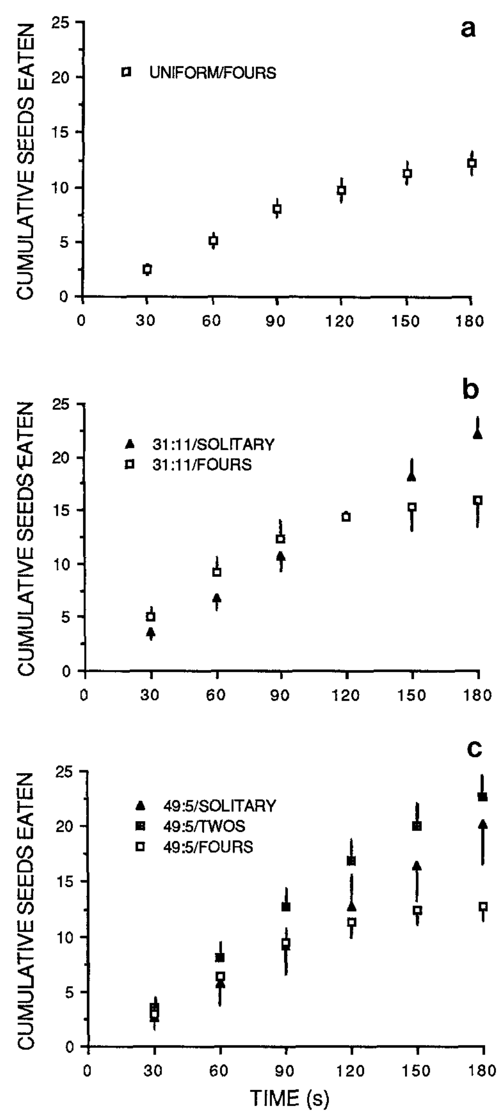

Fig. 1a–c. The mean number of seeds eaten after different time intervals on (**a**) the uniform seed dispersion, (**b**) the 31:11 seed dispersion, and (**c**) the 49:5 seed dispersion. The bars extending either up or down from the means represent one SD. Means and SD's are based on the mean and SD's for each for five individuals, respectively

Variance in seed intake for individual crossbills decreased significantly as flock size increased from one to two (Fig. 1c, *F*-tests, $df = 7{,}14$ or $8{,}14\text{-}15$, $P < 0.05$ in 12 of 30 comparisons) and from two to four (*F*-tests, $df = 14{,}10\text{-}11$ or $15{,}12$, $P < 0.05$ in 12 of 30 comparisons). Variance in individual seed intake also declined significantly as flock size increased from one to four (*F*-tests, $df = 7{,}10\text{-}11$ or $8{,}10\text{-}12$, $P < 0.05$ in 15 of 30 comparisons).

Comparisons between seed dispersions

There were no significant differences between the mean seed intake of solitary crossbills on the 31:11 and 49:5 seed dispersions (Fig. 1, Paired *t*-tests, $P > 0.1$), except after 30 s (Paired *t*-test, $t_4 = 4.32$, $P < 0.02$). The variances in seed intake for solitary crossbills, however, were significantly larger (*F*-tests, $df = 7\text{–}8,8$, $P < 0.05$) on the 49:5 seed dispersion than on the 33:11 seed dispersion at all time intervals for three of the crossbills, but not for WF (4 of 6 cases $P > 0.05$) or for UM (all 6 cases $P > 0.1$).

The mean seed intake for crossbills in fours on the 49:5 seed dispersion did not differ from those on the uniform seed dispersion (Paired *t*-tests, $P > 0.05$), but they were both significantly less than those on the 31:11 seed dispersion at all time intervals (Paired *t*-tests, $P < 0.02$).

Foraging and vigilance behaviour

Changes in seed intake rates between individuals in different flock sizes did not occur because of changes in the rate at which cones were visited. For example, crossbills in flocks of two had higher seed intake rates than when they were alone on the 49:5 seed dispersion, but the rate at which cones were visited did not differ between individuals in twos and when alone ($F_{1,84} = 1.00$, $P = 0.32$, with the number of seeds eaten as a covariate). Similar results were also found between individuals foraging alone and in fours on both the 31:11 seed dispersion ($F_{1,74} = 1.02$, $P = 0.32$) and the 49:5 seed dispersion ($F_{1,64} = 0.20$, $P = 0.66$). If scanning decreased with increased flock size, then more time should have been available for feeding and as a result more cones should have been visited per unit time. Although crossbills did not appear to devote time to non-foraging related activities (e.g. preening) during the experiments, crossbills did not visit more cones per unit time as flock size increased. This implies that any reduction in scanning behaviour as flock size increased was countered by increases in time spent on other activities, such as aggression. This interpretation is further supported by data on seed intake rates. For instance, crossbills in flocks of two and four compared to when alone did not have consistently higher or lower seed intake rates when on trees with the same seed density (Fig. 2). As an aside, these feeding rates represent a range of about 0.26 to 3.1 mg of kernel (dry weight) per s, which equals the range of feeding rates for red crossbills in nature (Benkman 1987).

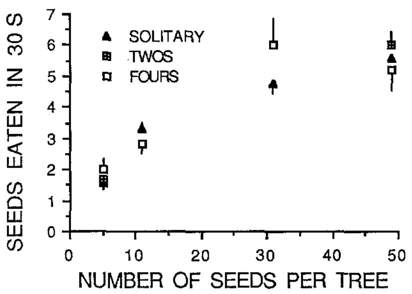

Fig. 2. The mean number of seeds consumed by individual crossbills during the first 30 seconds on trees with different numbers of seeds. The bars extending either up or down from the means represent one SE. Means are based on the means for each individual. The mean intake rates were not significantly different (Paired *t*-tests, $P > 0.05$) for all comparisons within trees, except between individuals in flocks of two and four on trees with 49 seeds

Local enhancement

An increase in intake rate could result if individuals join other flock members when they locate the tree with the most seeds (i.e. "local enhancement"). Indeed, crossbills in flocks of two experienced a reduction in time to begin foraging on the tree with 49 seeds, *T*, as compared to when alone (Table 1). The reduction in *T* as flock size increases should be, at best, inversely proportional to flock size (see Caraco and Pulliam 1984). This assumes that all flock members immediately go to the good tree after the first bird locates it, and that there is little aggression between birds. The mean interval between which a crossbill first obtained a seed on the tree with 49 seeds and the other crossbill landing on that tree was 23.1 s (median = 12.4 s, SD = 21.7, $n = 17$). Because there was about a 20 s lag between the time when the first crossbill located the high seed density tree and the time the second crossbill began foraging on the tree, *T* for individuals in flocks of two should have been greater than half of that for solitary crossbills (see Caraco and Pulliam 1984). Instead, *T* for individuals in flocks of two was nearly 10 s less than half of the that for solitary crossbills (Table 1). A reduction in *T* to less than half of that for solitary crossbills could arise if, in addition to local enhancement, crossbills in flocks of two could both more rapidly assess poor patches and avoid them than when alone. This hypothesis cannot be directly confirmed.

Determining whether *T* for individuals in flocks of two was significantly less than half of *T* for solitary crossbills is not straightforward because the distributions contain a large class of zero values and are not normally distributed. In one fourth

Table 1. The time (in seconds) required to locate the tree with 49 seeds (*T*). Sample sizes (*n*) are the number of trials

Bird[b]	Flock size[a]								
	1			2			4		
	$\bar{x}$	SD	(*n*)	$\bar{x}$	SD	(*n*)	$\bar{x}$	SD	(*n*)
BF	81.2	82.70	(7)	27.5	32.73	(17)	51.2	35.05	(5)
YF	100.8	87.35	(8)	35.0	44.49	(11)	47.0	24.05	(6)
WF	80.5	71.39	(8)	44.7	32.70	(15)	47.2	37.45	(7)
YM	72.3	74.27	(8)	30.0	42.61	(16)	30.1	29.93	(6)
UM	72.7	77.51	(7)	28.5	27.90	(13)	26.9	18.16	(6)
Overall[c]	81.7	75.16	(38)	33.0	35.90	(72)	40.3	29.50	(30)

[a] Within each flock size, there were no differences between individuals ($P>0.4$, Kruskal-Wallis test)

[b] Individuals are ranked from the most frequent subordinate relative to being a dominant (BF), to the most frequent dominant relative to being a subordinate (UM);

[c] Both the means and variances were greater for solitary crossbills than when they were in twos (Paired *t*-test, $t_4=9.27$, $P<0.001$ and *F*-tests, $P<0.05$ for each crossbill, respectively) or fours (Paired *t*-test, $t_4=9.55$, $P<0.001$ and *F*-tests, $P<0.05$ for all but WF [$F_{7,8}=3.6$, $0.1>P>0.05$], respectively). The means and variances did not differ statistically ($P>0.05$) between crossbills in flocks of two and four

of the trials *T* equaled zero. This is expected by chance because there were four trees and a crossbill has a one in four chance of landing on the tree containing most of the seeds. Cases where *T* equaled zero were ignored because the proportion of zeros did not differ between solitary crossbills and crossbills in flocks of two ($\chi_1^2=0.40$, $P>0.1$). The values of *T* for solitary individuals were divided in half and compared to values of *T* for individuals in flocks of two. For crossbills in flocks of two *T* was significantly less than half of that for solitary crossbills ($\chi_1^2=4.14$, $P=0.04$, Kruskal-Wallis test).

There was also significantly less variance in *T* for crossbills in flocks of two than when alone (Table 1). The variance in *T* was approximately proportional to $1/n^2$, where *n* is flock size, as hypothesized by Caraco (1981).

Feeding rates and aggression

T for the subordinate individual in the pair did not differ significantly from that for the dominant on the 49:5 seed dispersion (Paired *t*-test, $t_{17}=0.27$, $P>0.5$). Consequently, crossbills foraging in the presence of a dominant did not have significantly different intake rates from those when foraging in the presence of a subordinate (Kruskal-Wallis tests for each crossbill, $P>0.05$), nor was there even a tendency for intake rates to be higher when foraging with a subordinate than with a dominant.

Crossbills in flocks of four on the 49:5 seed dispersion had a lower mean intake rate than they did when in flocks of two because higher rates of aggression in the former resulted in an increase in *T* for subordinates. Rates of aggression were over seven times greater between individuals in flocks of four (16.2 aggressive interactions per crossbill per 1000 s) than in flocks of two (2.3 aggressive interactions per crossbill per 1000 s; Paired *t*-test, $t_4=3.90$, $P<0.02$). Although *T* was not significantly larger for individuals in flocks of four than when in flocks of two (Table 1), higher rates of aggression in fours resulted in increases in *T* for subordinates relative to that for dominants. In fact, the difference between the rate at which a crossbill was dominant and the rate at which it was subordinate in interactions was negatively correlated with the amount of increase in *T* between flocks of two and four (Fig. 3; $r=-0.99$, $n=5$, $P<0.01$).

The intake rates for crossbills in flocks of four may have been lower on the 49:5 seed dispersion than on the 31:11 seed dispersion (Fig. 1) because, in part, the rate of aggression among crossbills in flocks of four on the 49:5 seed dispersion (16.2 aggressive interactions per crossbill per 1000 s) was over six times greater than on the 31:11 seed dispersion (2.5 aggressive interactions per crossbill per 1000 s; Paired *t*-test, $t_4=3.60$, $P<0.05$).

Cone revisitation and systematic foraging

Interference did not cause crossbills to revisit a higher number of cones in flocks of four than when alone (Table 2), and thus reduce the efficiency at

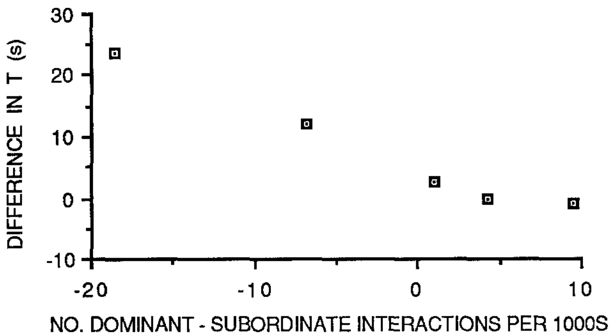

Fig. 3. The effect of aggression on the time to begin foraging on the tree with 49 seeds (*T*) for crossbills in flocks of four relative to when in flocks of two. The abscissa is the mean *T* for an individual when in a flock of four minus its *T* when in a flock of two (see Table 1). The ordinate is the rate at which an individual interacted aggressively as a dominant minus the rate at which it was subordinate in interactions. Each point represents a different bird

which cones were searched. The large number of revisits on trees with 49 seeds (Table 2) was mainly due to many successive revisits after most of the cones had been visited. If the analysis was confined to the period before three consecutive cones were revisited, then solitary crossbills revisited only 3.1 cones (SD = 2.1) after an average of 20.6 different cones had been visited (13% revisitation rate). On trees with 49 seeds, flock members revisited only an average of 0.8 cones (SD = 1.1) after an average of 12.7 different cones (SD = 5.4) had been visited (6% revisitation rate).

The linear cumulative intake of solitary crossbills (Fig. 1) implies that crossbills forage systematically. The mean number of seeds eaten by solitary crossbills did not differ during the 30 s intervals between 30 and 180 s on the 31:11 dispersion ($F_{4,20} = 0.70$, $P = 0.60$) or on the 49:5 dispersion ($F_{4,20} = 1.11$, $P = 0.38$). Further demonstrating that crossbills visited cones systematically, solitary crossbills on trees with five seeds did not revisit any cones during 42 of the 102 cases where the average number of different cones visited was 15.1 (SD = 6.4). In one case WF, when in a flock of four and on a tree with five seeds, visited all 32 cones before revisiting a single cone! Whether crossbills avoided cones visited by other crossbills could not be determined from the data.

Discussion

Local enhancement

Crossbills in flocks of two and four required less time to locate the high seed density tree (*T*) than solitaires, implying that individuals were able to recognize when others had located this tree. Local enhancement has been demonstrated for great tits (*Parus major*) (Krebs et al. 1972). Several cues may have been used by crossbills to detect the high seed density tree. Crossbills may have responded to the length of time that other crossbills remained on the tree, an accumulation of crossbills on the tree (see Krebs 1974), the reduced movement between cones by crossbills on the tree, or the consumption of seeds by crossbills. Although these hypotheses are not mutually exclusive, crossbills, probably relied most on the foraging behaviour of individuals on cones. These cues should give the quickest assessment of the trees and are consistent with the relatively short time interval (median time = 12.4 s) between the first crossbill foraging on the tree with many seeds and the second crossbill of the pair beginning to forage on it. Other observations in the laboratory suggest that crossbills detect seed consumption by other crossbills (Benkman, personal observation). For example, when I fed the crossbills securely closed conifer cones the most dominant crossbill (UM) would often remain perched while the other crossbills pried apart the cones. However, the first crossbill to obtain seeds was almost invariably displaced by UM.

Individuals in flocks may be able to more rapidly assess both poor and good patches than can solitary birds. For instance, individuals in flocks may depart from poor patches sooner or avoid poor patches where other birds were observed to find few seeds. As a result, *T* may decline more

Table 2. Cone revisitation rates for crossbills in flocks of four and when alone on the 49:5 seed dispersion. Sample sizes (*n*) are the number of trees visited

Flock size	5 seeds/tree						49 seeds/tree					
	No. cones visited			No. cones revisited			No. cones visited			No. cones revisited		
	$\bar{x}$	SD	(*n*)	$\bar{x}$	(%)	SD	$\bar{x}$	SD	(*n*)	$\bar{x}$	(%)	SD
1	18.2	6.3	102	1.4	(7)	1.7	27.3	4.2	37	11.3	(29)	6.4
4	14.1	4.4	64	0.8	(5)	1.3	14.6	6.6	28	2.5	(15)	3.6

rapidly than just proportionately to 1/*n*, with increases in flock size (*n*).

Flock size and food dispersion

Flocking increased mean intake rates, but this depended on the size of the flock relative to the food patch size. For example, when flock size increased from one to two on the 49:5 seed dispersion the mean time to locate a patch and its variance were reduced. In this case the patch was sufficiently large so that aggression did not exclude flock members from the patch and all flock members gained from local enhancement. However, as flock size increased to four, aggression increased, and only a fraction of the flock could forage on the patch at any given time (also see Krebs et al. 1972; Baker et al. 1981). This decreased the benefit from local enhancement and reduced intake rates. Thus, the flock size maximizing individual intake rates depended on patch size (see Thompson et al. 1974; Clark and Mangel 1984). If patch size was reduced, presumably the flock size maximizing average individual intake rates would have been smaller (Thompson et al. 1974). In nature, food patches (trees) are larger and can accomodate more individuals with less aggressive interactions than in the aviary. Indeed, flock sizes of foraging and nonbreeding red crossbills average 8.0 individuals in nature (SE = 0.9, *n* = 67 flocks; see Benkman 1987).

Intake rates for individuals in larger flocks should increase as patchiness increases and then decline (Thompson et al. 1974). Consistent with this hypothesis, individuals in flocks of four had higher intake rates on the 31:11 seed dispersion than on either the uniform or 49:5 seed dispersions.

Reductions in patch size relative to flock size may also result in greater asymmetries among feeding rates for individuals differing in dominance status. As flock size increased from two to four on the 49:5 seed dispersion, crossbills that were subordinate more often than dominant (usually the aggressor) had the largest increases in *T*. The crossbill least often subordinate (UM), was also the crossbill that had the smallest decline in feeding rate as flock size increased from two to four. Presumably, if patch size had been reduced further, or flock size increased, asymmetries in intake rates would have been more pronounced (e.g. Baker et al. 1981). If flocks are often larger than optimal (Clark and Mangel 1984) then dominants suffer least. In late winter seed is most limiting for crossbills (Benkman 1987) and foraging can be concentrated in a few trees where aggressive interactions may be frequent (Benkman, personal observation).

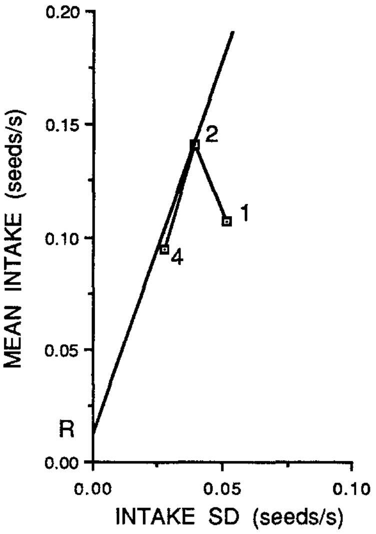

Fig. 4. The combinations of mean and their standard deviations in intake for individuals foraging on the 49:5 seed dispersion after 120 s. The numbers represent flock size. *R* is the estimated minimum necessary intake to meet daily energy demands based on standard allometric equations (Walsberg 1983) and specific caloric value of conifer seed kernels. See text for interpretation

At these times, subordinate crossbills may have lower intake rates and, consequently, suffer higher mortality than dominant crossbills.

Both the mean and variance in intake rates may influence survivorship (Pulliam and Millikan 1982; Stephens and Charnov 1982; Stephens and Krebs 1986). Many temperate birds should maximize the probability that their intake during the day will be adequate for surviving the night (minimizing "energetic shortfall"; Stephens and Charnov 1982). Stephens and Charnov (1982) have shown that the combination of mean and variance minimizing energetic shortfall can be determined graphically (Fig. 4). The combination of mean and standard deviation in the feasible set minimizing energetic shortfall is that which is on the line with the maximum slope drawn from the point on the mean intake axis representing the minimum required intake (*R*). In this example individuals in a flock of two would have a smaller chance of energetic shortfall than those when alone or in a flock of four; the intercept of the line connecting the combinations for individuals in flocks of four and two is less than zero. If *R* is larger than about 0.25 seeds/s, solitary individuals have a smaller probability of energetic shortfall relative to individuals in flocks of two. In this example *R* is relatively small because Austrian pine seed kernels (15.5 mg/seed) are larger than most seeds consumed by crossbills (1–13 mg/seed; see Benkman 1987). In winter *R* may commonly be in the range of 0.05 and 0.15 seeds/s.

Patch quality and aggession

The rate of aggression for individuals in flocks of four on the 31:11 seed dispersion was similar to that for flocks of two on the 49:5 seed dispersion. This suggests that not only is patch size important in determining aggression rates (the high quality patch was one tree in each case), but also the difference in quality between patches. Intake rates were over three times higher on trees with 49 seeds than on trees with 5 seeds, whereas intake rates on trees with 31 seeds were less than 1.5 times those on trees with 11 seeds (Fig. 2). As differences in intake rates between patches decline the net payoff from access to the high quality patch decreases and interference on the high quality patch may diminish (see Ewald 1985). Consistent with this, aggression between crossbills in flocks was less frequent on trees with 31 seeds in the 31:11 seed dispersion than on trees with 49 seeds in the 49:5 seed dispersion. This may explain why intake rates tended to be higher for crossbills in flocks of four on trees with 31 seeds than on trees with 49 seeds (Fig. 2; Paired *t*-test, $t_4 = 0.64$, $P > 0.05$).

Scanning behaviour

Crossbills in flocks of two or four did not move faster between cones than when alone as would be expected if time spent scanning by individuals decreased as flock size increased. However, scanning behaviour was not measured directly. Thus, individual scanning rates may have declined as flock size increased, but the decline in scanning for predators may have been replaced with watching other flock members (see Knight and Knight 1986) and increases in time spent on aggression as flock size increased. Nevertheless, a decrease in scanning behaviour is not a sufficient explanation for increases in feeding rate with increases in flock size.

Individuals may also increase their rate of seed consumption in flocks (see Lendrem 1984), possibly to reduce the effect of seed depletion by other flock members (Clark and Mangel 1986). This, like the reduction in scanning behaviour, should result in higher cone visitation rates for individuals in flocks than when alone. Such a result, however, was not found. Alternatively, the apparent lack of a reduction in scanning rates as flock size increased may have resulted, in part, because crossbills did not scan much in the predator-free indoor aviary; the crossbills had been housed in the aviary for over a year when the experiments began. It may be possible to isolate food finding benefits from antipredator benefits for birds in aviaries by holding birds in wire cages during solitary trials.

In summary, even though interference among individuals and more rapid depletion of patches by flocks tends to depress feeding rates, flocking can potentially increase the rate and reduce the variance at which food is obtained because of local enhancement and the improved ability to avoid and possibly assess poor patches. Reduction in vigilance as flock size increases may result in further increases in mean intake rates, but such a result was not pronounced in this study.

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