

# The Auk

A Quarterly Journal  
of Ornithology

Vol. 114 No. 2 April 1997

*The Auk* 114(2):163–178 + frontispiece, 1997

## FEEDING BEHAVIOR, FLOCK-SIZE DYNAMICS, AND VARIATION IN SEXUAL SELECTION IN CROSSBILLS

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**ABSTRACT.**—I present field data on feeding and scanning behavior of White-winged Crossbills (*Loxia leucoptera*) in relation to flock size. Feeding rates increased and individual levels of vigilance decreased as flock size increased from one to two. Further increases in flock size did not correspond with substantial reductions in individual vigilance, but did correspond with frequent agonistic interactions. As rates of agonistic interactions increased, feeding rates of subordinate age-sex classes (e.g. adult females) declined relative to those of dominant age-sex classes (e.g. adult males). Females (and immatures) may have reduced this effect by avoiding flocks composed mostly of adult males. Assortative flocking occurred in the nonbreeding period (late November to December), but during breeding periods (September and potentially rest of year) the numbers of each age-sex class tended to be positively correlated. Rates of agonistic interactions were higher when crossbills foraged on conifers whose cones were compactly dispersed. Flocks were smaller when rates of agonistic interactions were high and conifers had compact cone dispersions. Flock size increased as seed density declined. Larger flocks, with high levels of collective vigilance, were favored because feeding rate and the time spent scanning while seeds were husked also declined. Crossbills (*Loxia* spp.) that forage on small-crowned conifers are more sexually dichromatic and have other traits indicating stronger sexual selection than crossbills that forage on large-crowned conifers. I suggest that these differences result from differences in rates of agonistic interactions, which influence female feeding rates compared with male feeding rates, and likely have a differential effect on female mortality rates and the population sex ratio. *Received 21 June 1996, accepted 17 December 1996.*

FORAGING COSTS AND BENEFITS, as a function of group size, have been the focus of many studies (Bertram 1978; Pulliam and Millikan 1982; Clark and Mangel 1984, 1986; Pulliam and Caraco 1984; Terborgh and Janson 1986; Giraldeau 1988; Elgar 1989; Cresswell 1994; Saino 1994; Lima 1995a). Individuals can benefit from increasing flock size when higher levels of collective vigilance allow increased feeding rates because scanning rates are reduced (Pulliam 1973; Powell 1974; Caraco 1979a, b; Barnard

1980a; Elgar and Catterall 1981; Elgar et al. 1984; Sullivan 1984; Ekman 1987; Elgar 1987; Glück 1987; Lima 1987, 1988, 1995a; Catterall et al. 1992), predators are detected earlier (Powell 1974, Kenward 1978), predation risk is reduced (i.e. dilution effect; Bertram 1978, Foster and Treherne 1981, Dehn 1990), or the variance in finding food is reduced (Thompson et al. 1974, Baker et al. 1981, Pulliam and Millikan 1982, Ekman and Hake 1988). Certain costs also increase with group size. In particular, rates of agonistic interactions can increase with group size (Caraco 1979b, Elgar 1989), neutralizing benefits from larger groups. Especially important in this re-

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FRONTISPIECE. Male White-winged Crossbill in red spruce. Publication of this Frontispiece was supported by the Donald L. Bleitz Fund (photo by B. Henry/VIREO).

gard is the individual's dominance status (Ens and Goss-Custard 1984, Pulliam and Caraco 1984, Goss-Custard and Durell 1988).

A goal of these studies is to provide a mechanistic understanding of the main factors that influence group dynamics in the wild (Caraco et al. 1979a, b) and how these processes contribute to variation among populations and species. Few studies have attained this goal, however, in part because resource availability is difficult to quantify in the wild. Here, I present data from a field study of White-winged Crossbills (*Loxia leucoptera leucoptera*) for which it is easy to quantify food availability and for which a clear, direct functional link exists between the ecology and evolution of a species and its food resources, seeds in conifer cones (Benkman 1987a, b, 1989b, 1990, 1992, 1993a).

I initially focus on individual feeding rates and scanning behavior of different age and sex classes in relation to changes in flock size and rates of agonistic interactions. Although I have not seen a successful predation event in hundreds of hours observing crossbills, and successful predation may be rare, frequent scanning for predators is nevertheless advantageous (Lima 1992). The dilution effect, however, was likely relatively unimportant because predation rates were probably low on crossbills (but see Petty et al. 1995). Crossbills are unlikely to benefit much from the confusion effect (see Bertram 1978), because when predators attack, crossbills fly off in flocks that are not highly synchronized (pers. obs.).

After presenting the initial results, I further evaluate the patterns and hypotheses with data gathered during earlier studies (see Benkman 1987a, 1990). In particular, I use comparative data on feeding rates of males and females, sizes of foraging flocks, and rates of agonistic interactions for crossbills foraging on different conifers (i.e. different food dispersions). I then discuss how these processes might result in survivorship differences between the sexes, and how the conifers and their respective cone dispersions that different crossbills specialize upon might ultimately influence crossbill sex ratios. This, in turn, I relate to differences in the apparent intensity of sexual selection among different species and subspecies of crossbills.

#### METHODS

Between 5 September 1988 and 16 April 1989, I made extensive observations of White-winged Cross-

bills that foraged in red spruce (*Picea rubens*) and black spruce (*P. mariana*) forests in north-central New Brunswick (60 km east of Plaster Rock), Canada. Here, I report on crossbills foraging on an abundant cone crop of red spruce during 6 to 16 September and 18 November to 3 December. I focus on these two periods because I had extensive behavioral data, and during each period there was little change in cone structure that would influence feeding rates. For example, feeding rates did not vary with date in September ( $r = 0.057$ ,  $df = 158$ ,  $P = 0.33$ ) or in November/December (adults:  $r = 0.069$ ,  $df = 339$ ,  $P = 0.20$ ; immatures:  $r = 0.067$ ,  $df = 168$ ,  $P = 0.39$ ). This implies that crossbills had little effect on seed availability during the study. Crossbills foraged nearly exclusively on closed red spruce cones in September and mostly on open red spruce cones in November/December. Observations were made along a network of roads recently bulldozed in preparation for timber harvest the following summer.

Crossbills forage in the upper canopy, often climbing acrobatically on branch tips to reach cones (see Frontispiece). I used a 40× Questar telescope and 12× binoculars to observe crossbills, which usually were >30 m away and never seemed wary of me while I made observations. I recorded the number of seed kernels eaten (the husking of individual seeds could be observed) during timed intervals (see Benkman 1987a, b, 1993a; I timed crossbills feeding on 1,478 cones and eating 15,134 seeds). I define feeding rate as the number of seeds eaten per second from a single cone, with a minimum of five seeds consumed. Crossbills scan each time they lift their bills from cones to husk a seed. In addition, crossbills occasionally lift their heads to scan without husking a seed. These additional "scans" were included in total foraging time and also were analyzed separately for data gathered after 7 September (I did not record scanning time on 6 and 7 September). Foraging time was measured to the nearest 0.1 s with a digital stopwatch, and scanning time was estimated to the nearest 0.1 s.

Because crossbills were unbanded, I was uncertain as to individual identity. I attempted to record the feeding rates of a different crossbill on each successive foraging bout to reduce repeated samples from the same individual. When I knowingly recorded several bouts from the same individual (which was common in flocks of one, two and three), analyses were based on individual means. Although repeated measures from the same individual in different flocks were inevitable, the large number (>1,000) of crossbills in the area reduced the incidence of repeated measures from the same individual.

Time spent scanning may change with increasing flock size for several reasons (Elgar 1989). If time spent scanning is related to predator detection, then it should be inversely proportional to the estimated probability of detecting a predator when no additional scanning occurs except when husking seeds. That is, when the probability of detecting a predator is low,

such as in a small group, then individuals should devote additional time to scanning. To determine whether the changes in scanning time are consistent with predator detection, I estimate the probability of detecting a predator assuming that no additional time is spent scanning except when husking seeds (when crossbills extract seeds from cones their heads are oriented downward and their bills are between the cone scales). I used a method suggested by Hart and Lendrem (1984) to estimate the probability of detecting an avian predator (e.g. Sharp-shinned Hawk [*Accipiter striatus*], Merlin [*Falco columbarius*], Northern Shrike [*Lanius excubitor*]; Benkman 1992) in sufficient time to avoid predation. This model assumes that predator detection by a single bird is sufficient to alert all flock members. Although this may not apply to some species (Lima 1994b, 1995a, b), this assumption is reasonable because crossbills give alarm calls. I assumed that predators attack at random and independently of flock size. I used 0.30 as the proportion of time spent scanning by an individual crossbill. This was based on a mean seed husking time of  $0.92 \pm \text{SD of } 0.26 \text{ s}$  ( $n = 62$  seeds; data from aviary study in absence of predators [Benkman 1987b]) and a mean time between "scans" of  $2.19 \text{ s}$  ( $0.92/[0.92 + 2.19] = 0.30$ ). This assumes a feeding rate of 0.32 seeds per s, which slightly overestimates the feeding rates of crossbills in September (see Fig. 3) and slightly underestimates the feeding rates of adults in November/December in flocks of two or more (see Fig. 4). I also assumed crossbills "scanned" (i.e. husked seeds) independently of each other. The one unknown variable, tau, is the time from when an attacking predator can be detected to when it is so close that escape is no longer possible. I assumed tau ranges between 0.5 and 2.0 s (see Lima 1994a).

For all flocks I recorded the sex and age class of individuals and the number of individuals present (flock size) at about 5-min intervals. I distinguished age and sex classes by plumage coloration (see Benkman 1992). Few females were classified as first year. This may reflect the difficulty of aging females in the field. However, only 2 of the 26 females captured were first-year females. Although some first-year females were probably misidentified as adult females, first-year females undoubtedly were uncommon in this population. Flock size is the number of crossbills within one or several (usually no more than two) adjacent trees; sometimes crossbills fly back and forth between adjacent trees when foraging. When flock size fluctuated through time, I used the modal number as the flock size. Flocks of less than five individuals generally occurred within a single tree, and all individuals in these flocks likely provide each other with visual (flight) and/or auditory (alarm calls) information on predators (pers. obs.). Flocks of five or more were combined, except where noted, because my count for larger groups often fluctuated as crossbills moved about the canopy, and two and even more trees were sometimes occupied so that the efficiency with which

information on predators can be transmitted between individual birds inevitably declines (see Elgar et al. 1984, Lima and Zollner 1996).

Agonistic interactions (see Benkman 1992 for description of behavior) were recorded, and the age and sex class of the dominant (usually the initiator; see Bekoff and Scott 1989) and subordinate were identified whenever possible. Data on agonistic interactions that resulted in displacement (most agonistic interactions) are presented from a total of 1,286 min of observing foraging flocks during 6 to 19 September and between 18 November and 3 December. I missed some agonistic interactions because I could not see all individuals in the flock when observing through a telescope. This results in an underestimation of the rate of interactions, especially as flock size increased.

Eighty-three White-winged Crossbills, including eight streaked immatures of unknown sex, were captured with a mist net. The net was set on 10, 12, and 17 September 1988 where crossbills and other cardueline finches were coming to the ground for salt and grit. Each crossbill was aged and sexed (see Benkman 1992), and body mass, wing length, and several bill dimensions were measured (only bill depth is reported here; see Benkman 1992).

I used parametric statistical tests when the data (untransformed or ln-transformed) were normally distributed (Wilks' Lambda test) and the variances across groups did not differ significantly (Bartlett's test). Otherwise, I used nonparametric tests. I used JMP 3.1 (SAS 1994) for all analyses. Dispersion statistics reported for means are  $\pm 1 \text{ SE}$ .

## RESULTS

*Scanning behavior relative to flock size.*—The probability of detecting a predator in sufficient time to avoid predation for three values of tau (the time from when an attacking predator can first be detected to when it is so close that escape is no longer possible) is shown in Figure 1. The probability of detecting a predator early enough to escape begins to level off near 1.0 at flock sizes between two and four. This suggests that the benefit from spending additional time scanning (besides when husking seeds) to detect predators decreases rapidly as flocks increase from one to three individuals. If crossbills scan (aside from when they are husking seeds) mainly to detect predators, then the time spent scanning should decrease as flock size increases from one to two or three individuals, but not with further increases in flock size.

In support of this prediction, the number of seconds spent scanning per seed consumed decreased significantly as flock size increased from one to two in both September (Kruskal-Wallis

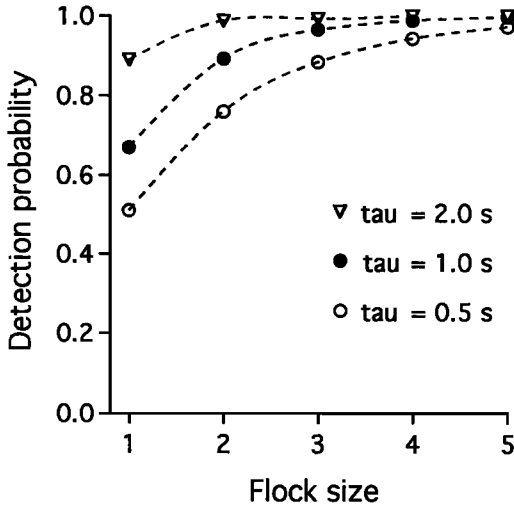


FIG. 1. Estimated probability of detecting a predator in sufficient time to avoid predation in relation to flock size.

test,  $\chi^2 = 4.95$ ,  $df = 1$ ,  $P = 0.026$ ; Fig. 2A) and November/December ( $\chi^2 = 5.47$ ,  $df = 1$ ,  $P = 0.019$ ; Fig. 2B), but not with further increases in flock size ( $P_s > 0.20$ ; Fig. 2). It should also be noted that the increase in scanning behavior for solitary individuals versus individuals in larger flocks (Fig. 2) underestimated the increase in vigilance because solitary crossbills appeared to spend more time husking individual seeds (pers. obs.).

*Alternative explanations for scanning-time/flock-size relationships.*—We need to consider alternative hypotheses before concluding that time spent scanning declined in larger flocks because of an increase in number of individuals scanning (Elgar 1989, Roberts 1996). First, time spent scanning may decline with temperature (e.g. Pravosudov and Grubb 1995). Although I observed few crossbills foraging alone, none was observed during particularly warm days or during the afternoon when temperatures were warmest. However, scanning rates did decrease between September and November/December as temperature declined. Time spent scanning per seed in flocks of five or more was significantly lower in November/December (adults:  $\bar{x} = 0.045 \pm 0.007$  s,  $n = 261$ ; adults and immatures combined:  $\bar{x} = 0.047 \pm 0.006$  s,  $n = 412$ ), when daytime temperatures often did not exceed  $0^\circ\text{C}$ , than in September ( $\bar{x} = 0.099 \pm 0.014$  s,  $n = 160$ ; Kruskal-Wallis test,  $\chi^2 = 9.80$ ,  $df = 1$ ,  $P = 0.002$ , and  $\chi^2 = 13.51$ ,  $df = 1$ ,  $P = 0.0002$ ,

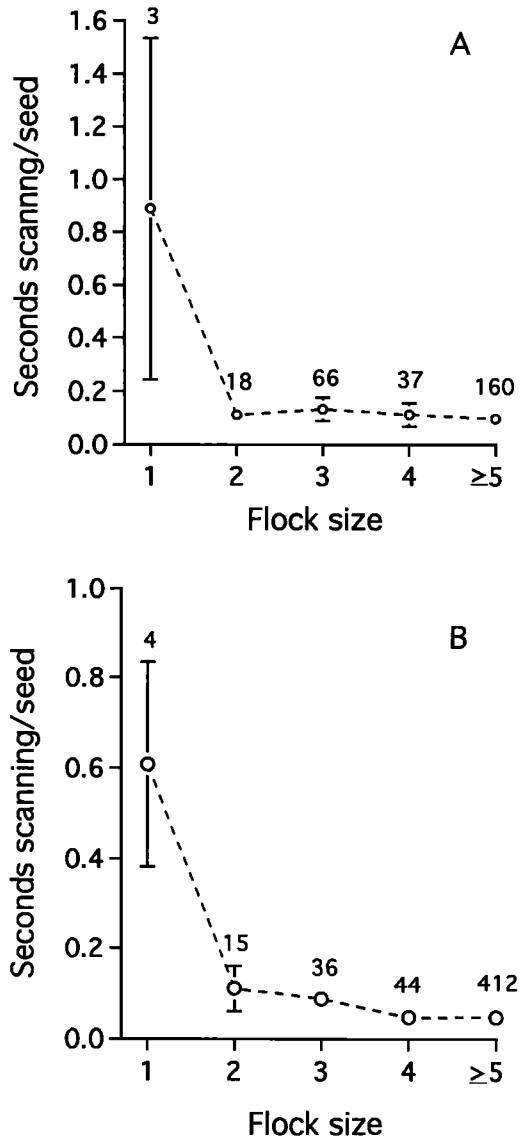


FIG. 2. Seconds scanning per seed ( $\bar{x} \pm \text{SE}$ ), besides when husking seeds, of White-winged Crossbills foraging on red spruce in relation to flock size (A) during 6 to 16 September and (B) between 18 November and 3 December 1988 in New Brunswick. Numbers above points are number of feeding bouts sampled.

respectively), when daytime temperatures usually exceeded  $10^\circ\text{C}$ .

A second explanation for variation in time spent scanning relative to flock size is covariation between flock size and the density, quality, or availability of food (see Elgar 1989). This hypothesis is unlikely because: (1) the total number of seeds removed from a cone (a direct mea-

sure of cone or resource quality; Benkman 1987a, b, 1989b, 1990) was not correlated with flock size ( $r = -0.09$ ,  $n = 20$ ,  $P = 0.71$ ; sample size is small and only from September because I usually terminated a foraging bout after 10 seeds were eaten); (2) feeding rates leveled off as the number of seeds per cone increased (Benkman 1987a, 1990), and only when the number of seeds per red spruce cone declined below about 20 did feeding rate begin to decrease (Benkman 1987b; crossbills removed an average of 37 seeds per cone in September); (3) crossbills did not defend feeding territories (Benkman 1988b, 1992), they selected trees in a manner consistent with maximizing food intake rates, and they left low-quality trees quickly (Benkman 1987a); and (4) feeding rates varied within a single tree in relation to changes in flock size. For example, foraging data were gathered on a flock of six and then on a solitary individual after the other five individuals flew off. The mean feeding rate for adult females declined (although not significantly) from 0.28 to 0.19 seeds per s ( $t = 1.30$ ,  $df = 7$ ,  $P = 0.23$ ).

Third, variation in the distance to cover from feeding sites has been related to variation in time spent scanning (Lima 1987, Elgar 1989, Lazarus and Symonds 1992). Because crossbills usually fly up and away from predators rather than into cover (Benkman 1992), a more important variable might be foraging height in the tree rather than distance to cover. Crossbills that forage at lower heights might be more vulnerable to predators (see Ekman 1986) and therefore may scan more frequently. Because crossbills usually foraged within 2 m of the top of a tree except in the largest flocks (pers. obs.), crossbills in larger flocks should on average scan more, not less (Fig. 2).

Fourth, individuals on the edge of a flock may be more vigilant than those at the center. If this factor was operating, then the decline in time spent scanning should have continued with increases in flock size above two and should not, as I found, have been restricted mainly to the increase in flock size from one to two individuals.

Fifth, variation in age-sex composition with flock size may influence the time spent scanning among different flock sizes. The time spent scanning, however, did not differ among age-sex classes. For example, time spent scanning per seed did not differ among age-sex classes in flocks of five or more in September ( $\chi^2 = 3.21$ ,

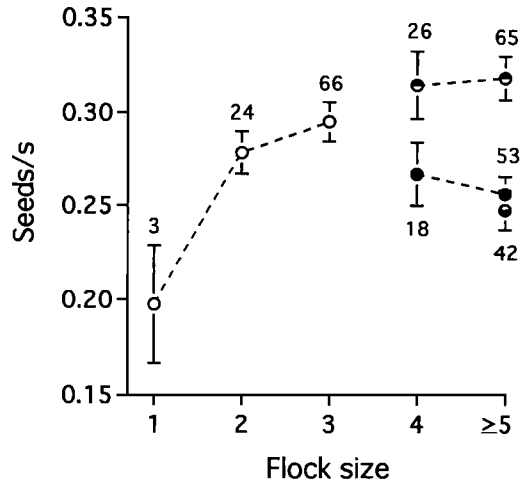


FIG. 3. Feeding rates ( $\bar{x} \pm SE$ ) of White-winged Crossbills foraging on red spruce in relation to flock size during 6 to 16 September in New Brunswick. Open circles represent all age and sex classes combined for flock sizes of 1 to 3. Adult males (circle with top half filled), adult females (solid circle), and first-year males (circle with bottom half filled) are distinguished in flock sizes of four or more (see text). Numbers above or below points are number of feeding bouts sampled.

$df = 2$ ,  $P = 0.20$ ) or November/December ( $\chi^2 = 3.90$ ,  $df = 3$ ,  $P = 0.27$ ).

Finally, if the decline in vigilance resulted from a reduction in the risk of predation (i.e. the dilution effect), then vigilance should have been proportional to the reciprocal of flock size (Roberts 1996). Vigilance was not inversely proportional to flock size. Instead, vigilance declined more sharply than the reciprocal of flock size between solitary crossbills and flocks of two, and then leveled off in flocks of two or more (Fig. 2). I conclude that time spent scanning per seed declined in larger flocks because of an increase in number of individuals scanning.

**Feeding rates.**—The decrease in scanning time as flock size increases from one to two (Fig. 2) should result in increased feeding rates. The feeding rates of individuals in flocks of two were significantly higher than those of solitary birds in September ( $t = 2.35$ ,  $df = 25$ ,  $P = 0.027$ ; Fig. 3), and adults in flocks of two tended to have higher feeding rates (although not significant) than did solitary adults in November/December ( $t = 1.82$ ,  $df = 12$ ,  $P = 0.094$ ; Fig. 4). In addition, feeding rates of adults in flocks of three were significantly higher than those of solitary adults ( $t = 2.73$ ,  $df = 28$ ,  $P = 0.01$ ).

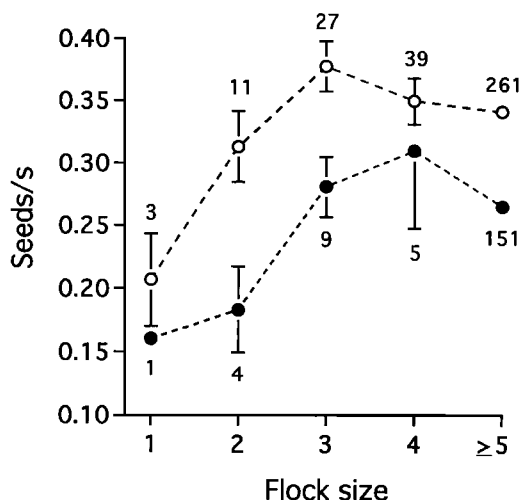


FIG. 4. Feeding rates ( $\bar{x} \pm SE$ ) of White-winged Crossbills foraging on red spruce in relation to flock size between 18 November and 3 December 1988 in New Brunswick. Open circles: adults; solid circles: immatures. Numbers above or below points are number of feeding bouts sampled.

In September, feeding rates did not differ significantly among flock sizes of two, three, four, or five or more (ANOVA,  $F = 0.91$ ,  $df = 3$  and  $291$ ,  $P = 0.44$ ; Fig. 3), nor did feeding rates differ among age-sex classes in flocks of two, three, or four (ANOVAs,  $P > 0.05$ ). However, feeding rates differed among age-sex classes in flocks of five or more (ANOVA on ln-transformed data,  $F = 13.62$ ,  $df = 2$  and  $157$ ,  $P < 0.0001$ ; Fig. 3). The feeding rates of adult males were significantly greater than those of adult females and first-year males (Tukey-Kramer test for pairwise comparisons,  $P < 0.001$ ), whereas the feeding rates of adult females did not differ significantly from those of first-year males ( $P > 0.05$ ).

Feeding rates in November/December were similar to those in September (Fig. 4). In contrast to September, however, many streaked immature crossbills were present in November/December. Most of these immature birds had fledged in the previous four months (see Benkman 1990, 1992). In addition, the "first-year males" from September had subsequently molted into adult plumage. Thus, four age-sex classes were distinguishable in November/December: adult males, adult females, streaked immature males, and streaked immature females. Adult crossbills (excluding because of small sample sizes solitary crossbills and those in pairs) had significantly greater feeding rates

than immatures (two-way ANOVA,  $F = 6.42$ ,  $df = 1$  and  $486$ ,  $P = 0.012$ ; Fig. 4), but the effect of flock size was insignificant ( $F = 0.58$ ,  $df = 2$  and  $486$ ,  $P = 0.56$ ). The interaction between flock size and age (adult vs. immature) also was not significant ( $F = 0.44$ ,  $df = 2$  and  $486$ ,  $P = 0.65$ ). Although males tended to have higher feeding rates than females, in flocks of five or more, feeding rates were statistically equal between the sexes within adults ( $t = 1.35$ ,  $df = 259$ ,  $P = 0.18$ ) and within immatures ( $t = 0.66$ ,  $df = 149$ ,  $P = 0.51$ ).

Differences in feeding rate among the three age-sex classes in September may have resulted from differences in bill morphology or experience. This explanation is unlikely for several reasons. First, the 13 first-year males captured in this study had a mean bill depth of  $8.05 \pm 0.06$  mm, whereas the mean bill depth of 29 adult males was  $8.07 \pm 0.04$  mm (see Benkman 1992). Second, crossbill feeding behavior is not particularly complex (Benkman 1992) and should not require a year (i.e. the age of first-year males) to learn (see Marchetti and Price 1989). Finally, feeding rates did not differ among the three age-sex classes in flocks of less than five (two-way ANOVA,  $F = 2.73$ ,  $df = 2$  and  $110$ ,  $P = 0.07$ ). In November/December, however, the higher feeding rates of adults than immatures (Fig. 4) probably resulted from the inexperience of immatures (<5 months old) and perhaps differences in morphology.

*Feeding rates and agonistic interactions.*—The low feeding rates of first-year males and adult females relative to adult males in larger flock sizes in September may have resulted from an increase in the rate of agonistic interactions as flock size increased (Fig. 5A). The decline in feeding rates from adult males to adult females and first-year males might correspond with decreasing dominance or increasing rates of being displaced. Adult males consistently were dominant to adult females and first-year males (binomial test,  $P < 0.05$ ; Table 1) and tended to be displaced in interactions about half as often as adult females and first-year males (Table 2). The slight decline in feeding rates in larger flocks in November/December (Fig. 4) also may be related to the frequent agonistic interactions in larger flocks (Fig. 5B). Although males were consistently dominant to females in November/December, feeding rates did not differ between the sexes.

If the decline in feeding rates in larger flocks

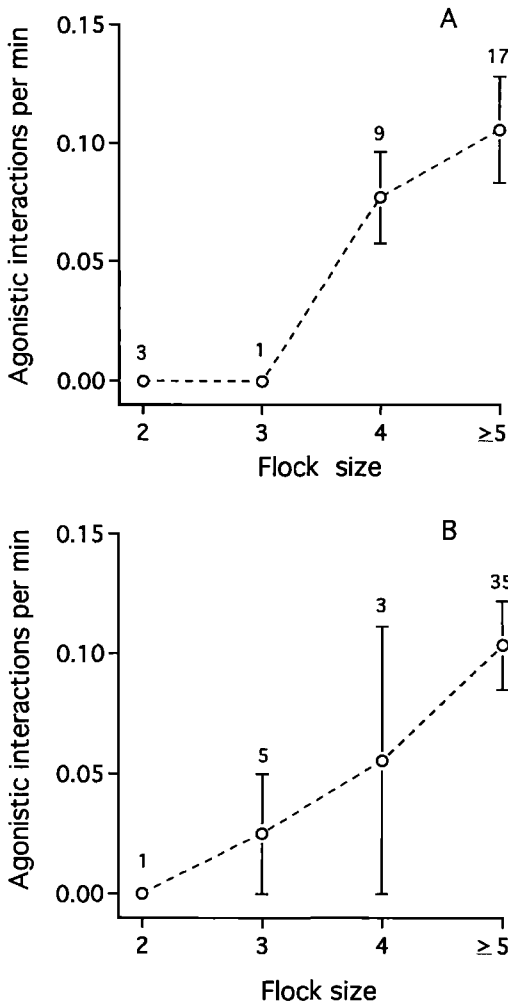


FIG. 5. Rates of agonistic interactions ( $\bar{x} \pm SE$ ) in relation to flock size (A) during 6 to 19 September and (B) between 18 November and 3 December. Numbers above points are number of flocks sampled. The number of interactions per min did not increase significantly among flock sizes greater than five in September ( $r = 0.005$ ,  $df = 10$ ,  $P = 0.99$ ) or November/December ( $r = 0.16$ ,  $df = 33$ ,  $P = 0.33$ ). The rates of agonistic interactions per individual were unrelated to flock size ( $\geq 3$  individuals) in September ( $r = 0.30$ ,  $df = 24$ ,  $P = 0.14$ ) and November/December ( $r = 0.10$ ,  $df = 41$ ,  $P = 0.54$ ).

is the result of agonistic interactions, then feeding rates should decline as rates of agonistic interactions increase. In particular, the feeding rates of females (subordinates) should decline in relation to the feeding rates of males (dominants). This is exactly what I found when data from earlier studies (Benkman unpubl. data) of

TABLE 1. Outcomes of agonistic interactions between age-sex classes of White-winged Crossbills observed for 617 min, 6 to 19 September 1988.

Subordinate individual	Dominant individual			Totals
	Adult male	First-year male	Adult female	
Adult male	12	1	—	13
First-year male	9	1	2	12
Adult female	18	9	5	32
Totals	39	11	7	57

White-winged Crossbills and Red Crossbills (*Loxia curvirostra*) are included with data from this study (Table 3, Fig. 6). Females feed at progressively slower rates compared with males ( $y$  = the ratio of female feeding rate to male feeding rate) as rates of agonistic interactions ( $x$ ) increase ( $y = 1.03 - 1.06x$ ;  $F = 37.23$ ,  $df = 3$ ,  $r^2 = 0.93$ ,  $P = 0.009$ ). Moreover, the intercept approximates one ( $1.03 \pm 0.03$ ), which shows that differences in feeding rates between males and females arise because of agonistic interactions, and not because of intrinsic differences in feeding abilities.

Subordinate individuals should avoid flocks with large numbers of dominant individuals to avoid displacement and the concomitant reduction in feeding rates. However, the number of adult females and first-year males tended to be positively correlated with the number of adult males within a flock (females:  $r = 0.30$ ,  $n = 21$ ,  $P = 0.19$ ; first-year males:  $r = 0.43$ ,  $n = 18$ ,  $P = 0.077$ ) in September. In addition, the number of adult females also tended to be positively correlated with the number of first-year males ( $r = 0.36$ ,  $n = 20$ ,  $P = 0.12$ ). Consequently, the proportion of individuals in each sex class is similar in the different flock sizes. This suggests that neither adult females nor first-year males avoid flocks with large numbers of adult males. It also indicates that the changes in feeding rates be-

TABLE 2. Rates of agonistic interactions ( $\bar{x} \pm SE$ ) for age-sex classes in flocks of  $\geq 4$  White-winged Crossbills, 6 to 19 September 1988 ( $n$  = number of flocks).

	Interactions per individual per min <sup>a</sup>		<i>n</i>
	Total	When subordinate	
Adult males	0.038 $\pm$ 0.010	0.009 $\pm$ 0.004	20
First-year males	0.042 $\pm$ 0.011	0.019 $\pm$ 0.008	20
Adult females	0.025 $\pm$ 0.006	0.020 $\pm$ 0.005	23

<sup>a</sup> Rates did not differ significantly among age-sex classes (Kruskal-Wallis test,  $P_s > 0.30$ ).



TABLE 3. Rates of agonistic interactions and individual feeding rates ( $\bar{x} \pm \text{SE}$  in each case) in flocks of  $\geq 4$  crossbills foraging on five species of conifers.

Conifer	Agonistic interactions			Feeding rate (seeds per s)				
	No. per min <sup>a</sup>	n <sup>b</sup>	Obs. <sup>c</sup>	Male	n <sup>d</sup>	Female	n <sup>d</sup>	Ratio female:male
White-winged Crossbill								
Tamarack	0.01 $\pm$ 0.01	14	414	0.53 $\pm$ 0.01	52	0.51 $\pm$ 0.01	34	0.96
White spruce	0.04 $\pm$ 0.02	11	135	0.41 $\pm$ 0.02	52	0.41 $\pm$ 0.02	41	0.98
Red spruce	0.10 $\pm$ 0.01	64	1,098	0.34 $\pm$ 0.01	209	0.31 $\pm$ 0.01	253	0.92
Black spruce	0.32 $\pm$ 0.06	13	149	0.24 $\pm$ 0.03	12	0.16 $\pm$ 0.04	4	0.68
Red Crossbill								
Red pine	0.05 $\pm$ 0.02	11	183	0.15 $\pm$ 0.01	25	0.16 $\pm$ 0.01	19	1.03

<sup>a</sup> Interaction rates differed significantly among White-winged Crossbills foraging on each of the three species of spruce and between those foraging on tamarack vs. red and black spruce (Kruskal-Wallis tests,  $P_s < 0.05$ ). Interaction rates differed significantly ( $P < 0.005$ ) between Red Crossbills (in red pines) and White-winged Crossbills foraging on black spruce (but not when foraging on the other three conifer species).

<sup>b</sup> Number of flocks.

<sup>c</sup> Total no. min of observations.

<sup>d</sup> No. of individuals.

tween different flock sizes in September (Fig. 3) were not the result of changes in flock composition.

In November/December, the number of immatures in a flock was negatively correlated with the number of adult males ( $r = -0.52$ ,  $n = 17$ ,  $P = 0.03$ ) and tended to be positively correlated with the number of adult females ( $r = 0.43$ ,  $n = 17$ ,  $P = 0.088$ ). This suggests that immatures avoid adult males, which often displace other flock members, but associate with adult females, which rarely displace other flock members (Tables 1 and 2). Similarly, the number of adult

females also tended to be negatively correlated with the number of adult males in November/December ( $r = -0.34$ ,  $n = 22$ ,  $P = 0.13$ ). This may explain why feeding rates did not differ significantly between adult males and adult females in November/December; females (and immatures) may avoid reduced feeding rates by avoiding males and joining flocks composed mostly of females. On the other hand, the positive association between the number of adult males and both adult females and first-year males in flocks in September may account for why females and first-year males have lower feeding rates than adult males in larger flocks (Fig. 3).

*Food dispersion and rates of agonistic interactions.*—If a high rate of agonistic interactions depresses feeding rates, what influences the rate of agonistic interactions? In the wild, rates of agonistic interactions are highest on black spruce (Table 3), which has cones that are compactly located within a small cylinder about a meter tall and less than a meter wide within the narrow crown (Fig. 7; Caron and Powell 1992; also see Fowells 1965:292 for photographs). Moreover, when White-winged Crossbills forage on black spruce, they often remove the cones and fly to adjacent trees to forage (pers. obs.). This behavior reduces agonistic interactions within the narrow crown and is rare when crossbills forage on other conifer species. In red spruce, the cones are much more widely dispersed and the crown is much larger than in black spruce (Fig. 7; Strickland 1987, pers. obs.). Perhaps as a result of this difference, rates of agonistic interactions in flocks of four or more

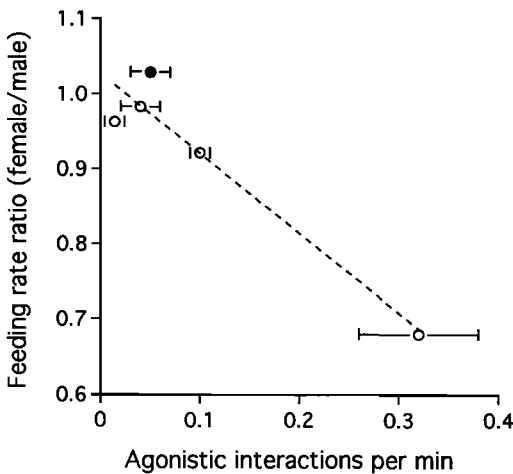


FIG. 6. The ratio of female:male feeding rates in relation to rate of agonistic interactions ( $\bar{x} \pm \text{SE}$ ). Open circles: White-winged Crossbills; solid circle: Red Crossbills. Data are from Table 3. Dashed line represents the best-fit linear regression.

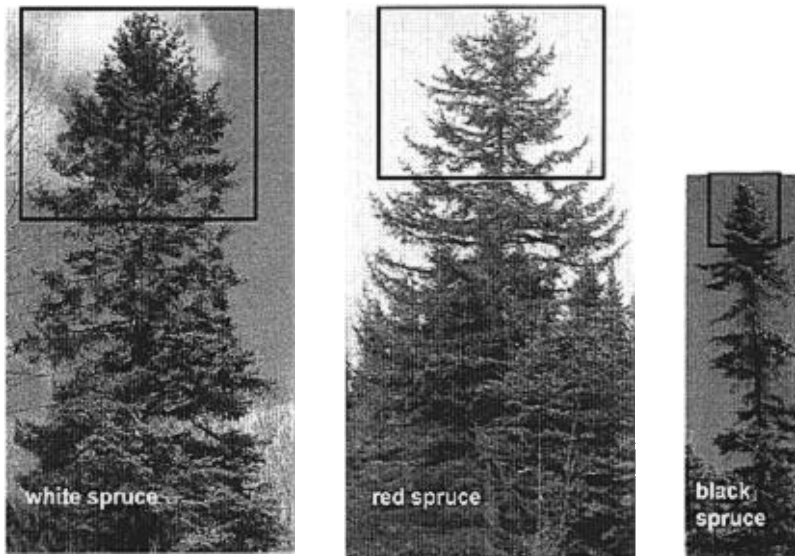


FIG. 7. The tops of three species of spruce (from Strickland [1987] with permission). Rectangles enclose areas where cones are concentrated (cones are restricted mostly to the outer canopy). White and red spruce reach heights of 30 m; black spruce about 10 m.

are lower on red spruce than on black spruce (Table 3; Kruskal-Wallis test,  $P < 0.05$ ). As in the red spruce, white spruce (*Picea glauca*) cones are dispersed throughout a large crown, but white spruce cones tend to be more abundant (see Powell 1975). In addition, white spruce branches are more continuous (Fig. 7), and the cones appear to be more uniformly dispersed in space than are red spruce cones. Rates of agonistic interactions in flocks of four or more are even lower on white spruce than on red spruce (Table 3; Kruskal-Wallis test,  $P < 0.05$ ). Similarly, rates of agonistic interactions are very low on two other species of conifers, tamarack (*Larix laricina*) and red pine (*Pinus resinosa*; Table 3), whose cones are widely dispersed throughout large crowns. This is consistent with the hypothesis that agonistic interactions increase as the food dispersion becomes more clumped.

**Flock-size dynamics.**—When agonistic interactions are more frequent, many individuals (especially females and immatures) should avoid large flocks, and average flock size should be smaller. Indeed, crossbill flock sizes decrease as rates of agonistic interactions increase in flocks of four or more (Fig. 8). This may seem to contradict data in Figure 5, which show that rates of agonistic interactions increase with flock size. Rates of agonistic interactions do increase within increasing flock size (Fig. 5), but the rates

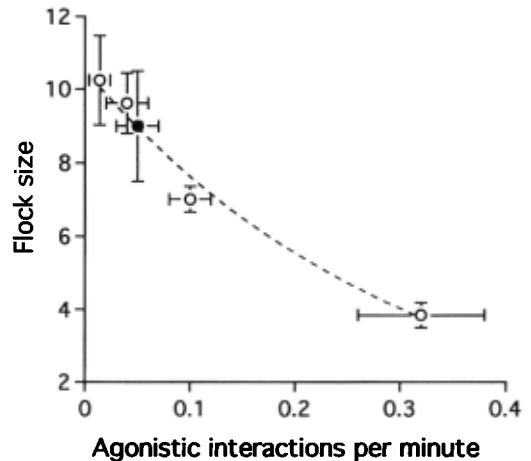


FIG. 8. Flock size in relation to the number of agonistic interactions per min ( $\bar{x} \pm \text{SE}$  in each case) for White-winged Crossbills foraging on tamarack and three species of spruce (open circles), and for Red Crossbills foraging on red pine (solid circle). The dashed curve is an exponential function (flock size =  $10.69 \cdot 10^{0.015[\text{interactions}/100 \text{ min}]}$ ,  $r^2 = 0.985$ ,  $df = 3$ ,  $P < 0.001$ ). Sample sizes: 48 flocks on tamarack, 92 flocks on white spruce, 124 flocks on red spruce, 32 flocks on black spruce, and 17 flocks on red pine. Data for flock sizes restricted to periods when birds foraged mostly on the respective conifer. Data on agonistic interactions are from Table 3.

of agonistic interactions reach higher levels in flocks of four or more individuals in conifers with smaller canopies. Thus, it is the rate of agonistic interactions in flocks of four or more that apparently influences average flock size (Fig. 8).

Although increased rates of agonistic interactions favor smaller flock sizes, increasing risk of predation should favor larger flock sizes (Pulliam 1973, Caraco et al. 1980). As the time interval between husking seeds increases (i.e. seed density declines; see Benkman 1987a, 1990), the proportion of time spent scanning decreases (given that crossbills scan when husking seeds), and the probability of detecting a predator will level off at larger flock sizes (see Fig. 1). Thus, flock size should increase as feeding rates decrease. Because the dispersion of cones influences the rate of agonistic interactions and flock size, the appropriate data to test this hypothesis are those on crossbills foraging on a single species of conifer.

White-winged Crossbills remained at approximately constant abundances along a 2-km transect in the Laurentian Mountains, Quebec as feeding rates on tamarack declined between 28 October 1982 and 29 January 1983 (Benkman 1987a). As predicted if reduced scanning rates favor larger flock sizes, flock size increased as feeding rates declined, and the time between seeds increased (Fig. 9). An alternative explanation is that flock size increased in response to an increase in predators (e.g. Caraco et al. 1980). This explanation is unlikely because Northern Shrikes were present throughout the period, and *Accipiter* hawks were only observed in October (Benkman unpubl. data). Another explanation for the increase in flock size is that agonistic interactions decreased because less time was available for nonfeeding activities as feeding rates declined (and temperature and day length decreased; e.g. Pulliam et al. 1974, Caraco 1979b). I did not record agonistic interactions consistently in 1982 and 1983; however, based on other data for crossbills foraging on tamarack (Table 3), agonistic interactions were probably rare. In addition, feeding rates of males and females (seeds/s) on tamarack from 28 to 31 October 1982 were virtually identical (males:  $\bar{x} = 0.44 \pm 0.03$ ,  $n = 21$ ; females:  $\bar{x} = 0.45 \pm 0.05$ ,  $n = 11$ ), which implies low rates of agonistic interactions (see Fig. 6). Thus, the increase in flock size probably does not result from a decrease in the allocation of time to aggression.

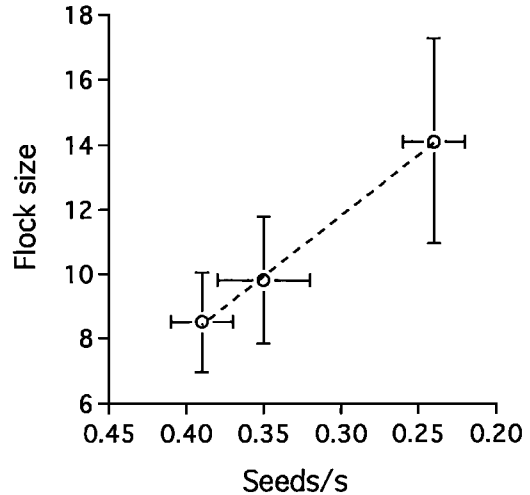


FIG. 9. Flock size in relation to feeding rates ( $\bar{x} \pm$  SE in each case) for White-winged Crossbills foraging on tamarack in the Laurentian Mountains, Quebec. Note that the values on abscissa decrease to right. The least squares linear regression between flock size ( $y$ ) and feeding rate ( $x$ ) was significant ( $y = 23.12 - 37.71x$ ;  $F = 738.5$ ,  $df = 1$ ,  $r^2 = 0.999$ ,  $P = 0.023$ ). Sample sizes for the three periods from left to right: 28 October to 1 November 1982 (64 feeding bouts and 23 flocks); 21 to 23 November 1982 (16 feeding bouts and 13 flocks); 27 to 29 January 1983 (67 feeding bouts and 12 flocks).

#### DISCUSSION

*Feeding, scanning, and agonistic behavior.*—The relationship between feeding rate and flock size in White-winged Crossbills is the same as that predicted by theory and documented in several other studies (Caraco 1979a, b; Pulliam and Caraco 1984; Clark and Mangel 1984, 1986; Elgar 1987; Giraldeau 1988; Saino 1994). Initially, feeding rates increase with increasing flock size from one to two or three individuals (Figs. 3 and 4). This increase coincides with a decline in scanning time (Fig. 2) and is most consistent with the hypothesis that crossbills feed faster by reducing vigilance time as the number of individuals scanning for predators increases (Pulliam 1973, Powell 1974, Caraco 1979b, Inglis and Lazarus 1981, Sullivan 1984, Glück 1987, Elgar 1989, Lima and Dill 1990, Saino 1994). Larger flock sizes could allow further reductions in vigilance and increases in feeding rates, but such benefits are not evident from my data.

The decline in feeding rates as flock size increased beyond three individuals for all but

adult males in September is most consistent with the increased incidence of agonistic interactions. An increase in agonistic interactions as flock size increases has been found in other studies (e.g. Caraco 1979b, Barnard 1980b, Wilkinson 1982, Elgar 1987, Saino 1994) and has been related to declines in feeding rates (e.g. Elgar 1987, Saino 1994). Because subordinate individuals spend additional time avoiding dominants (e.g. Caraco 1979b, Ens and Goss-Custard 1984), or scan more than dominant individuals (Ekman 1987; Waite 1987a, b; but see Hogstad 1988) to avoid displacement (Knight and Skagen 1988), subordinate individuals especially should suffer from increases in agonistic interactions. In fact, subordinates often have lower feeding rates than dominants (Murton et al. 1971, Baker et al. 1981, Millikan et al. 1985, Ens and Goss-Custard 1984, Theimer 1987, Waite 1987a, Goss-Custard and Durell 1988, Caraco et al. 1989, Smith and Metcalfe 1994).

This leaves unanswered the question of why subordinate individuals like females do not always flock assortatively and avoid adult males (see Metcalfe 1986). Assortative flocking occurred in November/December, but not in September. This difference may have resulted from the different breeding status of crossbills during the two periods. When crossbills breed (as in September), or may soon breed, males and females are likely to associate. Because White-winged Crossbills nest opportunistically nearly year-round (Benkman 1990, 1992), females presumably benefit from associating with males much of the year even though they may have lower feeding rates. Late November/December is the one period when breeding is uncommon (Benkman 1990, 1992), and this was when females tended to avoid males. Immatures may not be so constrained, although they may breed during their first year (Benkman 1992).

*Flock-size dynamics.*—Two main factors affect flock size in crossbills. First, the availability of seeds, which determines the interval between husking seeds (see Benkman 1987a, 1990), influences how rapidly the probability of detecting a predator levels off with increasing flock size (see Fig. 1). As seed availability declines, the relative benefits of larger flock sizes increase because of enhanced predator detection, which allows crossbills to feed at a faster rate. Similarly, the consistently lower feeding rates of nonbreeding crossbills compared with breeding crossbills

(Benkman 1990) also may explain why flock sizes average larger for nonbreeding crossbills than for breeding crossbills (see Benkman 1992).

Second, as food becomes more clumped, aggression increases and feeding rates of females (i.e. subordinates) decline compared with those of males (i.e. dominants; Fig. 6). Similar results have been found for brown capuchins (*Cebus apella*; Terborgh and Janson 1986; also see Whitten 1983, Theimer 1987). This, in turn, affects the benefits from foraging in large flocks. As cones become more clumped in space, rates of agonistic interactions increase and flock sizes decline. Likewise, variation in food dispersion has been shown to affect rates of agonistic interactions (Conder 1949, Prescott 1987, Benkman 1988a) and flock size in other species (Ekman 1987, Elgar 1987, Pearson 1989).

*Sex differences in feeding rates, male-biased sex ratios, and sexual selection.*—Female crossbills often have lower feeding rates than males (Table 3). Lower feeding rates require females to spend additional time foraging, which may result in greater vulnerability to predation. Females also will have lower survival rates than males if they are less able to meet their daily energy requirements. Females are smaller than males (mean body mass =  $24.4 \pm 0.2$  g vs.  $26.0 \pm 0.1$  g, respectively; Benkman 1992), and daily energy demand is proportional to body mass<sup>0.6052</sup> (Walsberg 1983). Therefore, whenever female feeding rates are less than 96% of those of males, females will require more time to meet their daily energy demands (assuming that dominants and subordinates have similar mass-specific metabolic requirements; see Hogstad 1987, Bryant and Newton 1994, Reinertsen and Hogstad 1994, Cristol 1995). Female feeding rates were less than 96% of those of males when foraging on red and black spruce (Table 3). During winter when feeding rates decline to near the minimum necessary to survive a day (Benkman 1987a, 1992), females will be especially prone to starvation. Many studies have found that subordinate individuals have lower survivorship than dominant individuals (Baker and Fox 1978, Kikkawa 1980, Garnett 1981, Ekman and Askenmo 1984, Arcese and Smith 1985, Koivula and Orell 1988), or that individuals with lower feeding rates have lower survivorship (Dittus 1977).

Lower survival rates for females could result in a male-biased sex ratio. Indeed, the sex ratio

of North American White-winged Crossbills (*L. leucoptera leucoptera*) is male biased (1.30 males:1 female; data from Benkman [1992, unpubl. data] and P. Deviche [pers. comm.]) and differs significantly from 1:1 ( $\chi^2 = 9.43$ ,  $df = 1$ ,  $P < 0.005$ ).

An alternative explanation for a male-biased sex ratio is that females suffer greater mortality because they devote more effort to reproduction than do males (see Breitwisch 1989). Reproductive effort has not been completely quantified for crossbills. However, males provide a substantial amount of the food for the young and for the incubating and brooding female (Benkman 1990, 1992 and references therein). Furthermore, after the young fledge, males feed the fledglings at least as much as do the females, and females often desert the fledglings while the male still provides cares for them (Benkman 1989c). Indeed, it is the relative scarcity of females that enables them to exact large amounts of paternal care of offspring (Benkman 1989c; also see Breitwisch 1989). Thus, differential mortality and the male-biased sex ratio are unlikely the result of differential parental investment. This is consistent with many studies of monogamous birds (Breitwisch 1989), including other cardueline finches (Shreeve 1980, Breitwisch 1989).

If agonistic interactions depress feeding rates in females, which in turn cause females to survive less well, then food dispersion (which influences the frequency of agonistic interactions) ultimately may be responsible for the biased sex ratio. Crossbills that rely on widely dispersed cones, such as those in many pines (*Pinus* spp.), should have lower rates of aggression, more similar feeding rates among males and females, and less male-biased sex ratios than crossbills relying on cones that are tightly clustered in narrow crowns. North American White-winged Crossbills specialize on cones that lie within the narrow crown of black spruce (Benkman 1987a, 1987b, 1992), whereas most Red Crossbills forage on more widely dispersed cones (Benkman pers. obs.). Consequently, Red Crossbills should have lower rates of agonistic interactions (see Table 3) and less male-biased sex ratios than White-winged Crossbills. Unfortunately, the available data on sex ratios are inadequate to test this hypothesis.

An alternative method to test this hypothesis is to compare the extent of sexual selection as evidenced by male coloration or sexual dichromatism. Especially in monogamous species like

crossbills, heavily male-biased sex ratios should lead to greater opportunities for sexual selection and brighter male coloration (Andersson 1994, Hill et al. 1994, Kvarnemo and Ahnesjö 1996). Therefore, crossbills that specialize on conifers with more clumped cone dispersions should have a greater preponderance of males and be more sexually dichromatic. As predicted, male North American White-winged Crossbills have brighter and more contrasting plumage than the two other subspecies of White-winged Crossbills, which specialize on conifers with widely dispersed cones (i.e. *L. l. megaplaga* in Hispaniola and *L. l. bifasciata* in Eurasia that specialize on pine and larch, respectively; Newton 1972; Benkman 1992, 1994). Similarly, male Red Crossbills in North America that specialize on the widely dispersed cones of pines, Douglas-fir (*Pseudotsuga menziesii*), and western hemlock (*Tsuga heterophylla*; Benkman 1993a) are drab (pers. obs.; see Austin 1968), have small testes (Manville 1941, T. P. Hahn pers. comm.), and relatively simple courtship displays (Benkman 1992, pers. obs.) compared with North American White-winged Crossbills. In contrast to these Red Crossbills, the Newfoundland Red Crossbill (*L. c. percna*), like the North American White-winged Crossbill, specializes on black spruce (Benkman 1989a, 1993b). As predicted, male Newfoundland Red Crossbills have red coloration that is "deeper, richer and more brilliant" than any other North American Red Crossbill (Austin 1968:498).

Alternative explanations for variation in sexual dichromatism among crossbills, such as variation in migratory status (Fitzpatrick 1994), predation intensity (Promislow et al. 1992), palatability (Baker and Parker 1979), body size (Andersson 1994), and parasite loads (Hamilton and Zuk 1982) are inadequate to account for the observed variation. First, nearly all crossbills are nomadic, and variation in sexual dichromatism among crossbills is unrelated to the extent of movements. For example, one island endemic is strongly sexually dichromatic (i.e. Newfoundland Red Crossbill), whereas another (i.e. Hispaniolan White-winged Crossbill) is less sexually dichromatic (see above). Second, predator abundance is not lower in the northern boreal forests of North America, where White-winged Crossbills are relatively strongly sexually dichromatic, than in the pine forests of Hispaniola (pers. obs.). Third, given that crossbills sometimes are preferentially harvested by

hawks (Petty et al. 1995), the bright coloration of males is unlikely to represent aposematic coloration. Fourth, sexual dichromatism is not correlated with body size. For example, the smallest White-winged Crossbill is the most sexually dichromatic (Benkman 1992), whereas the most sexually dichromatic New World Red Crossbill is among the largest of the New World crossbills. Fifth, data are inadequate to evaluate the incidence of parasites among crossbills. The incidence of blood parasites, however, is not correlated with plumage dichromatism in 19 other species of cardueline finches (A. V. Badyaev pers. comm.; also see Seutin 1994).

In summary, clumped food resources (i.e. cone dispersion) lead to higher rates of agonistic interactions and lower feeding rates in female crossbills relative to males. Females may then suffer greater mortality, which results in a more male-biased sex ratio. The more male-biased sex ratio leads to a greater intensity of sexual selection and brighter males.

#### ACKNOWLEDGMENTS

I was supported by two Frank Chapman Memorial Grants and a NSF Postdoctoral Fellowship in Environmental Biology while conducting field work. C. Cardinal at Laurentides Reserve, Quebec, and R. Tozer and D. Strickland at Algonquin Provincial Park, were especially helpful in enabling me to conduct the research. P. Deviche graciously provided sex-ratio data; G. Head helped compute detection probabilities; and T. Caraco, M. Elgar, A. Knox, G. Roberts, J. C. Senar, and two anonymous reviewers made many helpful comments on the manuscript.

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Associate Editor: J. Ekman