# SHORT COMMUNICATIONS

## Why White-winged Crossbills Do Not Defend Feeding Territories

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Most passerine bird species defend feeding territories while breeding (Welty 1975), but crossbills (*Loxia*) and many other cardueline finches (subfamily Carduelinae) do not (Newton 1972, Samson 1976). Instead, male crossbills usually defend only their mate and, at times, a small area around the nest. This type of defense probably deters extrapair copulations but does not reduce food consumption by conspecifics or other potential competitors, except possibly in the vicinity of the nest.

The absence of territoriality presumably arises when resources are indefensible or when no net benefit is accrued from defense (Brown 1964, Gill and Wolf 1975, Davies 1978). I hold the position that defense of food resources by White-winged Crossbills (*L. leucoptera*) would not increase their food intake rates, but instead would reduce intake rates.

I studied crossbills in the northeastern United States and adjacent Canada between September 1982 and February 1985. I measured foraging rates by counting the number of seeds eaten during timed intervals, measured with a stopwatch, and included both time spent foraging on cones and time traveling between cones. I used a telescope (usually 20–40×) to observe foraging crossbills. I determined the number of seeds per cone and the dry mass of the seed kernels (see Benkman 1987a for details on methods). Intake rate was defined as the mass of dry kernel consumed per unit time foraging; the specific caloric value of conifer seeds varies little within and among species (see Grodzinski and Sawicka-Kapusta 1970). If I observed nests or young being fed, then the population was considered to be breeding.

Intake rates varied little with changes in the number of seeds per cone in the range of intake rates for breeding crossbills (Fig. 1). The functional response (Holling 1959) was similar to the Holling type II functional response (Fig. 1; when converted to natural logarithms, $r = 0.87$, $n = 10$, $P < 0.005$).

On 24 occasions I measured foraging rates in populations containing breeding individuals. Foraging rates were greater than 0.6 mg/s for 19 (79%) of the samples, and 14 (58%) were greater than 0.8 mg/s. Thus, when White-winged Crossbills were breeding, intake rates generally were in the more asymptotic region where slight reductions in the number of seeds per cone would have had relatively little impact on intake rates (Fig. 1). On 3 of the 5 occasions when foraging rates of breeding populations were less than 0.6 mg/s, cones were opening and intake rates were increasing. At those times, seed accessibility increased during the whole nesting cycle and seeds were abundant, so that foraging rates would not have been affected in the short term by seed depletion (see Benkman 1987a, b). In sum, on 22 of the 24 (92%) occasions that crossbills were breeding, seed depletion would have had little immediate impact on intake rates. Further, because both cones and seeds are usually abundant when crossbills nest (Nethersole-Thompson 1975, pers. obs.), tremendous numbers of crossbills would be necessary to deplete seeds.

In addition to providing limited benefits, territorial defense would increase energy expenditure and interfere with flock formation. Crossbills often forage in flocks during nesting (pers. obs.). The inability to forage in flocks would have a considerable negative impact on intake rates because crossbills that forage in flocks have significantly higher intake rates than those foraging alone (Benkman in prep.). For example, in the field intake rates were 1.27 times greater for White-winged Crossbills in flocks than for single individuals ($t = 2.45$, df $= 106$, $P < 0.01$). Flocking in crossbills also may enhance predator detection. Moreover, the costs of territorial defense would be high and defense probably ineffective if conspecifics intrude in flocks (e.g. Orians 1961). The colonial-nesting tendencies of crossbills (Bailey et al. 1953, Nethersole-Thompson 1975, pers. obs.) may even promote flock formation.

Other factors that may reduce the benefits of territoriality and increase the benefits of flock foraging include large spatial and temporal variation in food resources (Horn 1968, Newton 1972, Pulliam and Millikan 1982). Seed availability, however, is unlikely to vary asynchronously among contiguous bird territories (e.g. Benkman et al. 1984). Further, conifer cones and trees are usually sufficiently dense where crossbills nest that a crossbill could occupy and defend a territory with enough seed for successful nesting.

Nevertheless, territorial defense could reduce seed depletion near the nest so that shorter distances need to be traversed when feeding nestlings. This advantage from territorial defense is minimized because crossbills can carry large amounts of seed during nest visits, and parents feed nestlings less frequently than once per hour (e.g. Bailey et al. 1953).

Foraging rates of breeding White-winged Crossbills would not necessarily be increased if they could gain exclusive rights to feeding territories. The energetic costs of territorial defense and reduced intake rates of foraging alone outweigh benefits gained from monopolizing a local food resource. All or part of these arguments may apply to Red Crossbills (*L. curvirostra*) and other seed-eating cardueline finches that

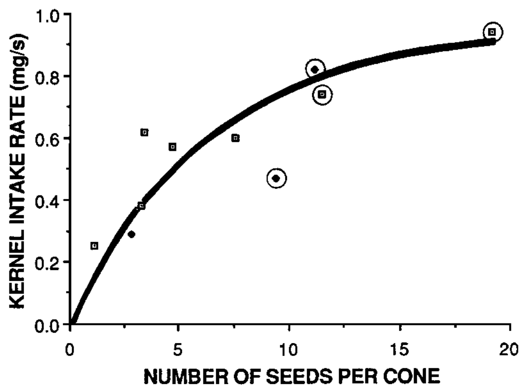


Fig. 1. Mean foraging rates of White-winged Crossbills in relation to the mean number of seeds per cone of tamarack (*Larix laricina*) (⊡) and white spruce (*Picea glauca*) (◆). Circled data points represent breeding populations, and those not circled represent nonbreeding populations. The curve was fitted by eye. Sample sizes for foraging rates range from 16 to 179 bouts and 81 to 1,310 seeds, respectively. The mean number of seeds per cone is usually based on samples of 10 cones from each of 5 trees. The one major exception is for the sample on white spruce, with 9.2 seeds per cone, which was based on cones from only 1 tree.

do not defend feeding territories while nesting; most birds may have a type II functional response when foraging on seeds (see Schluter 1984).

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