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The importance of mature conifers to red crossbills in southeast Alaska

William C. Holimon [a], Craig W. Benkman [a,*], Mary F. Willson [b]

[a] Department of Biology, New Mexico State University, Las Cruces, NM 88003, USA
[b] Forestry Sciences Laboratory, 2770 Sherwood Lane, Juneau, AK 99801, USA

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Abstract

Red crossbills (*Loxia curvirostra*) in southeast Alaska feed mostly on seeds in the cones of western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*). During a year of poor cone production, red crossbills did not forage in young stands. Within mature stands, crossbills tended to forage preferentially on trees with large cone crops. These favored trees were also the larger and older trees because cone production increases with tree size. The avoidance of young stands is especially pronounced during poor seed years and may be related to the absence of mature trees containing numerous cones with many seeds. We suggest that mature stands are critical for maintaining crossbill populations and possibly other conifer seed-eating species. © 1998 Elsevier Science B.V.

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1. Introduction

Many species whose food intermittently fails in a given area are 'extinction prone' (Terborgh and Winter, 1980; Janzen, 1986). One food source that fails at irregular intervals, often over extensive areas, is conifer seeds (Newton, 1972; Benkman, 1993a). Although no conifer seed specialist is known to have gone extinct recently, one conifer seed specialist, the Newfoundland red crossbill (*Loxia curvirostra percna*), is likely to be on the verge of extinction (Benkman, 1989, 1993c; Pimm, 1990) and other crossbills are likely to become increasingly imperiled because logging reduces seed abundance (Benkman, 1993a).

Crossbills wander nomadically to exploit spatiotemporally varying conifer seed crops (Newton, 1972; Bock and Lepthien, 1976; Benkman, 1987a, 1992). Crossbills accumulate in areas of large cone crops (Reinikainen, 1937; Newton, 1972; Benkman, 1987a, 1992); as a result, the size and areal extent of the cone crop have tremendous impacts on the size of crossbill populations (Benkman, 1992). Conifer seeds are especially critical to crossbills because they are inefficient at using alternative foods compared to less specialized finches (Benkman, 1988). When conifer cone crops fail, therefore, crossbills may suffer high mortality (Newton, 1972; Benkman, 1992). This reliance on conifer seeds, however,

* Corresponding author. Tel.: +1-505-646-2541; fax: +1-505-646-5665; e-mail: cbenkman@nmsu.edu.

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makes crossbills vulnerable to any factor that reduces the size and areal extent of cone crops. Logging is one such factor (Benkman, 1993a).

The goal of this study was to determine (a) the association between stand age and cone production, and (b) the use of trees by crossbills in relation to stand age and to the number of cones produced by western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*). We focus on red crossbill conifer use in relation to individual tree and stand-level characteristics rather than in relation to landscape characteristics. This is justified by the observation that crossbills readily fly great distances (Benkman, 1992), and, as a consequence, can potentially select individual trees from among many stands within a day or just a few trees from one stand. In addition, a recent study (McGarigal and McComb, 1995) found little evidence that landscape structure affected red crossbill abundances in coastal forests in the Pacific Northwest.

We chose this area in southeast Alaska for two reasons. First, one species of red crossbill (type 3 of Groth (1993)) is adapted specifically for foraging on seeds in the cones of western hemlock and relies on the hemlock forests along the coastal belt (Benkman, 1993b). Second, logging has eliminated most of the old-growth temperate rain forests in the Pacific Northwest. Only 10% of the original old-growth stands remain in western Oregon and Washington (Norse, 1990). Two-thirds of the coastal temperate watersheds in British Columbia have been logged (Beebe, 1991). In southeast Alaska, only two percent of the most productive old-growth stands remain because of extensive clearcutting that began in the 1950s (O'Clair et al., 1992).

2. Materials and methods

2.1. Site description and surveys

Crossbill and cone surveys were conducted by one of us (WCH) on 1.6-km transects along logging roads (measured by odometer) and foot trails (measured by pedometer) in mature (> 150 yrs old) and young (20–30 yrs old) stands. Transects were established in 19 stands in the following areas: three mature stands and three young stands near both Thorne Bay, Prince of Wales Island and Petersburg, Mitkof Island; three mature stands and one young stand near Sitka, Baranof Island; and three mature stands near Juneau on the mainland. No stands of intermediate age were available because large-scale clearcutting started in the 1950s in southeast Alaska (O'Clair et al., 1992). Younger stands were not always available for surveys because some study areas were not clearcut until recently.

We conducted crossbill surveys three times during 1995 and at least once in 1994 along each transect. We recorded whether individuals were perched, foraging, or flying. When we observed crossbills on other occasions, we recorded their behavior and associated habitat. All observations were made between 5 June and 9 August, 1994 and between 30 May and 25 July, 1995.

The nearest cone-bearing conifer in each 90° quarter of the compass was identified at 0.32-km intervals along the transects. We used a diameter tape to measure the diameter at breast height (DBH) of each tree, and we used 8.5 × 44 mm binoculars to count the number of cones seen from one side of the tree; we use this number as an estimate of the number of cones per tree. All cones were counted in 1994, but only developing (green) cones were counted in 1995.

Because log transformations did not normalize the data, we used Kruskal–Wallis tests to compare the average number of cones per cone-bearing tree in stands of different ages. We used linear regressions to determine if the number of cones was related to DBH for specific sites in 1994. Combined 1994 data from the two stand ages at specific study sites met the assumptions of the model, although combined data for all sites did not. Thus, we restricted linear regressions to specific sites, and nonparametric Spearman rank correlations for all sites combined. Regression analyses were not done on 1995 data because the median number of cones per tree was zero for nine of the 10 possible species–site combinations. A Spearman rank correlation was used on the data from the one species–site combination where the median number of cones per tree was greater than zero (median = 100 cones). We used a Kolmogorov–Smirnov test for goodness-of-fit to determine if there was a non-random association between the number of cones on a tree and use by foraging flocks of crossbills in 1994; crossbills were much

Table 1
Correlations between the number of cones and diameter at breast height in conifer stands in southeast Alaska in 1994

Location	Sitka spruce			Western hemlock		
	r	*P*	*n*	*r*	*P*	*n*
Prince of Wales Island	0.86	0.0002	13	0.65	0.0005	14
Mitkof Island	0.86	0.0001	46	0.10	0.99	11
Baranof Island	0.72	0.0001	26	0.46	0.05	19
Juneau	0.44	0.0240	26	0.84	0.16	4

less common in 1995 and were not observed foraging.

3. Results

Two lines of evidence show that cone production increased with tree size. First, the number of cones produced was positively correlated with DBH in Sitka spruce (Table 1, Fig. 1a; r_s 0.76, $n = 111$, $P < 0.0001$) and western hemlock (Table 1, Fig. 1b;

Table 2
The number of cones counted per cone-bearing tree from sites in southeast Alaska where both young and mature stands were surveyed

Species/year	Young stand			Mature stand			P[a]
	$\bar{x}$	SE	n	$\bar{x}$	SE	n	
Sitka spruce							
1994	145	25	45	840	87	66	< 0.001
1995	8	2	37	15	3	19	0.007
Western hemlock							
1994	2342	580	9	4887	623	35	0.056
1995	219	71	18	464	108	32	0.019

[a] Kruskal–Wallis tests were conducted on $\log_{10}$-transformed data.

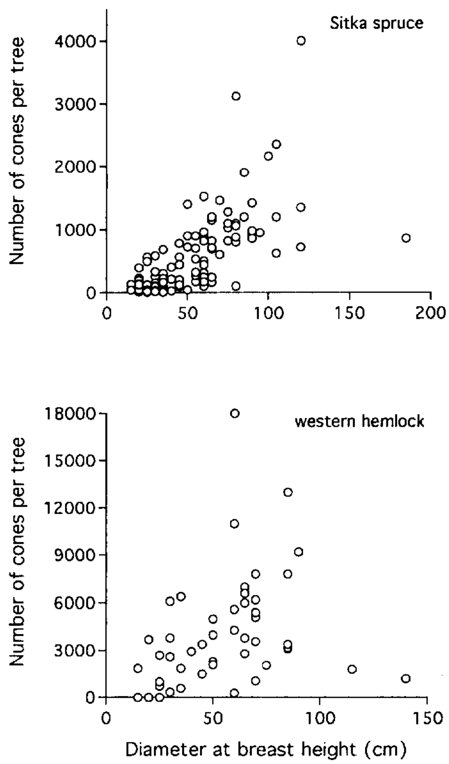

Fig. 1. Number of cones per Sitka spruce tree (above) and western hemlock tree (below) in relation to diameter at breast height (DBH) for all sites combined in 1994.

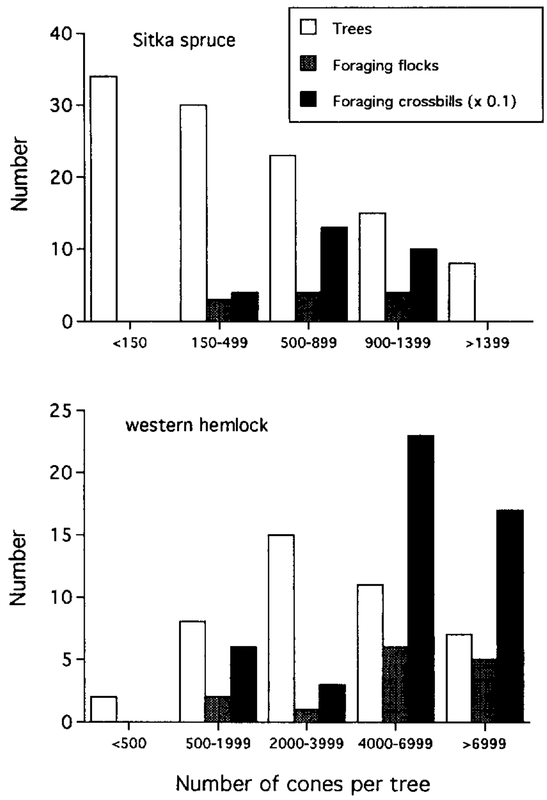

Fig. 2. The number of trees, foraging crossbill flocks, and number of foraging crossbills in relation to the number of cones per Sitka spruce tree (above) and western hemlock tree (below) in mature stands.

$r_s = 0.42$, $n = 48$, $P = 0.003$) in 1994. Similarly, there was a significant positive correlation in the one species–site combination in 1995 where the median number of cones per tree was greater than zero (western hemlock on Prince of Wales Island: $r_s = 0.32$, $n = 51$, $P = 0.022$). Second, the average number of cones per cone-bearing tree was significantly greater in mature stands (> 150 yrs old) than in young stands (20–30 yrs old) for Sitka spruce and western hemlock in both 1994 and 1995 (Table 2).

Red crossbills were observed to forage or perch only in mature stands ($n = 306$ flocks, 2167 individuals). Within mature stands, flocks of red crossbills tended to forage more frequently on trees with many cones (Fig. 2; Kolmogorov–Smirnov tests, $P < 0.1$ for crossbill flocks in relation to the number of cones on trees for Sitka spruce and for western hemlock; analyses based on individual birds were highly significant [Chi-square tests, $P < 0.0001$], but individuals are not strictly the independent unit).

4. Discussion

Larger and presumably older conifers (Husch et al., 1972, pp. 295–298) in southeast Alaska produce more cones than younger conifers. This is consistent with studies on other conifers (Fowells and Schubert, 1956; Fowells, 1965; Linhart and Mitton, 1985; Shearer, 1986). For example, old-growth Douglas-fir (*Pseudotsuga menziesii*) produces 20 to 30 times more cones than 50 to 100-yr-old second growth (Burns and Honkala, 1990).

Red crossbills in southeast Alaska responded to differences in cone production by foraging preferentially in mature stands where cone production was greater than in young stands. Similarly, red crossbills were more abundant in older than in younger forests in Finland (Helle and Järvinen, 1986), northern California (Raphael et al., 1988), and southern Washington (Manuwal and Huff, 1987; Huff et al., 1991; Manuwal, 1991). One likely explanation for the preponderant, if not exclusive, use of mature stands is that crossbills prefer to forage on trees with larger cone crops. Young stands, therefore, are avoided because most trees in these stands produce small numbers of cones. Thirty (67%) of 45 Sitka spruce trees within young stands each had fewer than 150 cones in 1994. This is less than the number cones on the spruce trees foraged upon by crossbills in mature stands (Fig. 2). Likewise, eight (89%) of nine western hemlock trees within young stands had fewer than 4000 cones in 1994. This is less than the number of cones on the hemlock trees foraged on by 11 of the 14 crossbill flocks in mature stands (Fig. 2).

Crossbills may favor trees with larger cone crops for at least two possible reasons. First, the size of the cone crop is generally positively correlated with the number of seeds per cone (e.g., Smith and Balda, 1979), which in turn influences crossbill foraging efficiency (Benkman, 1987b, 1990). The especially pronounced preferences of crossbills for mature stands over younger stands during years of poor cone crops (Manuwal and Huff, 1987; Huff et al., 1991; this study) may be the result of young stands producing insufficient cones and seeds to support even a few crossbills for extended periods (see Benkman, 1987a, 1992). Second, travel time between cones for crossbills increases as the density of cones decreases in the canopy of a tree. However, whether within-canopy densities of cones differed between young and mature stands is unknown. The greater number of cones in the mature stands may merely reflect the relative differences in the volume of the canopies in the different stands. A higher within-tree density of cones might explain why crossbills tended to preferentially forage on trees with many cones within mature stands (see also Christensen et al., 1991). Whatever the actual mechanism underlying the avoidance of young stands, mature stands are clearly important for the conservation of crossbill populations and other conifer seed-eating animals (see also Benkman, 1993a).

In sum, crossbills avoid conifers in young stands apparently because they produce smaller cone crops with fewer seeds per cone. Young stands may be unsuitable for crossbills during years of extensive cone failures such as during the years of this study; cone crops fail over large regions every two to four years (Newton, 1972; Bock and Lepthien, 1976) and may fail every 10 yrs in southeast Alaska (Willett, 1921; Harris, 1962; Benkman, unpublished data). Crossbills accumulated in the few areas in southeast Alaska where at least small cone crops were produced (Holimon, 1996). In these areas, however, young stands were avoided by crossbills even when these stands represented some of the few areas where cones were produced. Thus, during the occasional extensive cone failures, which is when food is also most limiting to crossbills (Newton, 1972; Benkman, 1992), only mature stands can support crossbills for extended periods.

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