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Ecological Monographs, Volume 57, Issue 3 (Sep., 1987), 251-267.

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FOOD PROFITABILITY AND THE FORAGING ECOLOGY OF CROSSBILLS¹

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Abstract. Observations over a two and a half year period in the Northeast United States and adjacent Canada indicate that White-winged Crossbills (*Loxia leucoptera*) and Red Crossbills (*L. curvirostra*) shift their diets among the seeds of various conifer species in a seasonal pattern. Both crossbill species forage on white spruce (*Picea glauca*) in late summer. White-winged Crossbills continue foraging on white spruce or tamarack (*Larix laricina*) until late autumn or winter, when they switch to black spruce (*P. mariana*). Red Crossbills switch to white pine (*Pinus strobus*) in early autumn and to red pine (*P. resinosa*) or other pines in winter or spring.

This pattern of diet shifts is consistent with the hypothesis that crossbills forage to maximize food intake rate. Profitability (milligrams of kernel ingested per second) was measured for crossbills foraging on each of these conifers by observing rates of seed ingestion in the field, and subsequently measuring dry seed kernel masses. Profitability for a given conifer increases as cones and seeds mature, then declines as seeds are shed from the cones. Because conifers differ in the timing of cone ripening, crossbills experience sequential peaks in profitability. Both crossbill species usually foraged predominately on the most profitable conifer species, with switches in conifer use coinciding with shifts in relative profitabilities. However, crossbills often forage on more than one conifer species at a time, even though intake rates might be maximized by foraging on only the most profitable conifer. Predation does not appear to influence diet selection and large-scale patterns of conifer use. Crossbill movements and patterns of abundance, both on local and continent-wide scales, are correlated with patterns of profitability.

Dietary overlap between crossbill species is greatest, often approaching 100%, in late summer when seed is most abundant. Overlap then declines rapidly when white pine cones open, and usually remains negligible most of the remainder of the year. Patterns of dietary overlap are a result of differences in profitability for each crossbill species that are largely inherent in the ripening phenology of conifer cones and seed accessibility, not seed depletion by crossbills. Interspecific competition is most likely between White-winged Crossbills and either the smallest form of the Red Crossbill or redpolls (*Carduelis* sp.) during the late winter of "invasion" years, which occur every 3–4 yr. Intraspecific competition is also likely to be most intense at these times.

Key words: conifers; crossbills; diet shifts; dietary overlap; foraging ecology; habitat use; *Loxia*; northeastern North America; *Picea*; *Pinus*; profitability; seeds.

INTRODUCTION

The rate at which food can be consumed, often termed food "profitability," is central to habitat selection, population dynamics, and competitive interactions. Most investigations addressing habitat selection and competitive interactions have measured, at most, food abundances, because profitability is difficult to measure. When food abundances have been measured, they often are translated into measures of food availability by making assumptions about abiotic factors, consumer morphology, or behavior (see Wiens 1984 for a review). Studies that have measured actual profitability,

in terms of energy gained per unit time foraging, have been successful in predicting and understanding habitat use (Gill and Wolf 1975, Goss-Custard 1977, 1981, Mittelbach 1981, Werner and Mittelbach 1981, Werner et al. 1983a). If measurements of profitability can be made, optimal foraging theory provides a mechanistic approach to studying diet selection, habitat use (Pyke et al. 1977, Krebs 1978), and diet overlap between species (Wolf et al. 1972, Werner 1977, 1984, Pulliam 1985).

Many researchers have suggested that the reduction in dietary overlap between species during periods of low food abundance is consistent with the occurrence of interspecific competition (Svårdson 1949; reviewed by Schoener 1982). However, simple measures of dietary contraction and overlap can have multiple interpretations unless actual patterns of food profitability

¹ Manuscript received 14 April 1986; revised 12 November 1986; accepted 20 November 1986.

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are measured. To date, patterns of food selection in relation to seasonal variation in food profitability have rarely been measured (Goss-Custard 1977, Schluter 1982a, Pulliam 1986), though such measures are critical to evaluating processes underlying habitat use, population dynamics, and the coexistence of species.

Determining the influence of food profitability on habitat use is easiest for species whose diet normally consists of foods differing little in nutrients, and for which there are a limited number of food types. Crossbills (*Loxia* spp.) satisfy these specifications; they consume little besides conifer seeds and these vary little in energy value (Smith 1968, 1970, Grodzinski and Sawicka-Kapusta 1970) or nutritive value (McKeever 1964, Jones and Earle 1966), and there are usually fewer than five conifer species in any given habitat. Furthermore, the movements of crossbills are thought to occur because of changes in profitability between the conifers most often used (Haapanen 1966, Newton 1970, 1972) and crossbill density has been found to be correlated with the size of conifer cone crops (Reinikainen 1937, Haapanen 1966).

Newton (1972) has summarized the qualitative patterns of conifer use for Red Crossbills (*L. curvirostra*) in Europe by relating conifer use and movements to patterns of conifer seed and cone ripening. Even though the actual foraging efficiencies of crossbills foraging in nature can be accurately measured, these measurements have not previously been reported, nor have the patterns of conifer use by crossbills in North America been adequately described. In this paper I describe the patterns of conifer seed profitability for both White-winged Crossbills (*L. leucoptera*) and Red Crossbills in northeastern North America and demonstrate how their conifer use, abundances, and movements are correlated with actual seed profitability. I then discuss for both crossbill species their patterns of conifer use, abundance, movement, dietary overlap, and periods of potential food limitation.

METHODS

Sites

Foraging data were gathered on crossbills from September 1982 to February 1985 in the coniferous forests of the northeastern United States and adjacent Canada. White-winged Crossbills were observed in the following four areas: along Chemin la Brulee near Mare du Sault in Laurentides Reserve, Quebec; Acadia National Park, Maine; near Wenlock Crossing, Vermont; and Algonquin Provincial Park, Ontario. Red Crossbills were observed at the Algonquin and Acadia sites, and on the Tongue Mountain Range, New York. Most observations of foraging crossbills were made along transects at the study sites. Conifer composition of the primary study sites (Table 1) was determined by recording, at 30–90 m intervals (depending on the transect length) along the transects, the species of the closest

cone-bearing conifer in each of four quadrants. At Otter Point–Blackwoods in Acadia National Park and Tongue Mountain no transects were established, but I estimated the frequency of each conifer species in the general areas where I located crossbills. For more details on these sites see Methods in Benkman (1985). Study sites were visited for 1–6 d at approximately monthly intervals when crossbills were present.

Conifer use and foraging rates

At all of the sites I walked or skied along dirt roads and trails, and, whenever crossbills were observed foraging, I recorded the time to the nearest minute, the number of crossbills, and the conifer species on which they were foraging. To provide a measure of the length of time foraging, I recorded the time the crossbills flew off or disappeared from view. When crossbills were too distant to observe foraging rates, I continued along the transect and the time the crossbills disappeared from view was recorded. My estimate for the amount of time spent foraging on each conifer species was made by multiplying the number of foraging individuals in each foraging flock by the number of minutes I observed them foraging on a particular conifer species. These products I call "bird-minutes." The total number of bird-minutes crossbills foraged on each conifer was the sum of the above products for each conifer species over a single visit to the site. The proportion of time spent foraging on a given conifer species is the number of bird-minutes foraging on the species of conifer divided by the total sum for all conifers.

If the crossbills were close enough to observe feeding rates, I attempted to record the number of seeds individual crossbills consumed during timed intervals. These intervals included time spent handling seeds and extracting them from cones and travel time between cones within trees. Travel time between trees was not included because it represented little of the total foraging time. Crossbills made more time-consuming long flights, but the relevance of these long flights to conifer use is problematic. Crossbills were timed from when they began foraging on a cone, or had just finished consuming a seed, to when they discarded the cone. When >10 seeds were obtained per cone I sometimes terminated recording data for that cone. This would not affect overall rates, because rate does not usually vary as a function of the number of seeds consumed from cones with >10 seeds (C. W. Benkman, *personal observation*). When <5 seeds were consumed per cone the timed interval often consisted of crossbills foraging on >1 cone. These timed intervals, whether including travel time or not, I term foraging bouts.

To account for travel time between cones within trees, I measured either foraging rates while crossbills foraged on more than one cone, including travel time in the total foraging time, or I measured both intercone travel time and the average amount of time spent foraging per cone. In the former case, feeding rate per

TABLE 1. Conifer composition and transect lengths at study sites.

Study site	Relative frequency of occurrence								Transect length (km)	No. trees (n)
	White spruce	Black spruce	Red spruce	Tamarack	Balsam fir	White pine	Red pine	Jack pine		
Laurentides Reserve										
Transect 1	0.07	0.44	—	0.33	0.15	—	—	—	2.0	72
Transect 2	0.02	0.44	—	0.02	0.52	—	—	—	1.4	52
Acadia National Park										
Wonderland	—	0.76	0.11	0.07	0.07	+	+	—	0.5	92
Ship Harbor	0.38	0.20	0.29	0.11	0.02	0.01	—	—	0.6	112
Otter Point	0.50	—	0.45	—	0.05	+	—	—	—	0*
Blackwoods	0.05	—	0.60	—	0.05	0.30	+	—	—	0*
Wenlock Crossing	+	0.62	0.33	0.02	0.04	+	—	—	1.2	52
Algonquin										
Achray 1	0.58	0.25	—	—	0.04	0.06	0.05	0.02	1.4	160
Achray 2	0.01	+	—	—	+	0.84	0.14	0.01	1.1	111
Tongue Mountain	—	—	0.10	—	—	0.55	0.35	—	—	0*

+, — Plus indicates species was present within 30 m of transect, but not sampled during tree census; minus indicates species not noted within 30 m of transect.

* The frequency of occurrence was estimated without censusing trees.

foraging bout was the number of seeds divided by time foraging, and in the latter case foraging rate was the average measured foraging rate multiplied by the average total time per cone divided by the sum of the mean time per cone and mean travel time. I did not measure travel time in all cases; thus I substituted the most appropriate times obtained from other sites or from different dates at the same site. All events were timed to at least the nearest 1.0 s with a stopwatch.

Characteristic bill movements accompany seed husking, which facilitates recording the number of seeds consumed. Crossbills consume only the seed kernel (cf. Gabrielson and Lincoln 1959) and the seed coat or empty seeds could often be seen when they were discarded. Before I began field work I had observed captive Red Crossbills remove >5000 seeds from cones of six species of conifer; I thus was able to distinguish crossbills handling full seeds (i.e., seeds with a seed kernel) from those handling empty seeds. Given sufficient light and proximity to foraging crossbills, accurate measurement of seed intake rates can be made. I used 10 × 50 binoculars and a 15–60× telescope, usually set at 20–30×, to observe crossbills. Nearly all timed foraging observations were made using a telescope.

Because foraging crossbills were often difficult to locate, I usually recorded foraging behavior for as long as possible, unless I was conducting a census. During censuses I recorded foraging crossbills for <10 min, then continued the census. I attempted to measure foraging rates for as many individuals as possible. Foraging observations occasionally lasted up to an hour, and during this time usually >20 foraging bouts were recorded, encompassing many individuals on many trees. In most cases, data obtained on a given individ-

ual or on individuals foraging on a given tree comprised less than one-fourth of the total sample at a given site during a visit.

Censuses

I conducted censuses by walking (or skiing) slowly along a transect and recording all crossbills heard or seen. Censuses were usually completed before 1200. Crossbill abundance is given as the number of crossbills heard or seen per minute while I walked the transect.

Kernel mass and seed abundance

Conifer cones were gathered in the field to obtain samples for seed kernel masses. The cones were brought back to Albany, New York and stored for up to 3 mo at 2°C prior to removing seeds from the cones. Kernels (female gametophyte and embryo) were separated from the seed coats and immediately placed in a drying oven (60°–65°) for 3–8 d. The kernels were then weighed to the nearest 0.1–0.01 mg. Kernel sample sizes were usually 10 seeds from each of three trees per site. If kernel masses were not obtained from a given site, kernel masses of the appropriate species from the nearest site, or the average of the two closest sites, were substituted to compute intake rate. Intake rate (profitability) is defined as the dry mass of seed kernel consumed per second. Cones were also gathered to determine the number of full seeds per cone. The numbers of cones and trees sampled are presented whenever the number of seeds per cone is given.

Red Crossbill taxonomy

There is presently some confusion surrounding the taxonomy of Red Crossbills in North America (cf.

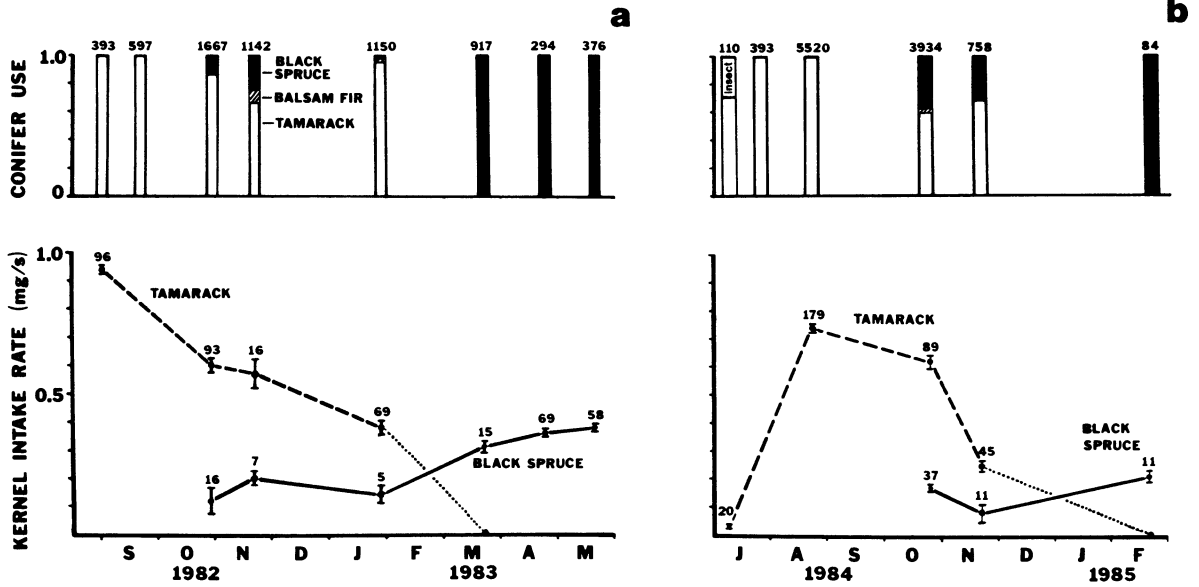


FIG. 1. The kernel intake rates ($\bar{X} \pm SE$) and proportion of time spent foraging on each conifer for White-winged Crossbills in 1982–1983 and in 1984–1985 at Laurentides Reserve, Quebec. (.....) shows estimated decline in intake rates, based on number of seeds per cone, after the last field records were taken. Sample size for foraging time is number of “bird-minutes” and sample size for intake rates is the number of foraging bouts (see Methods: Conifer Use and Foraging Rates).

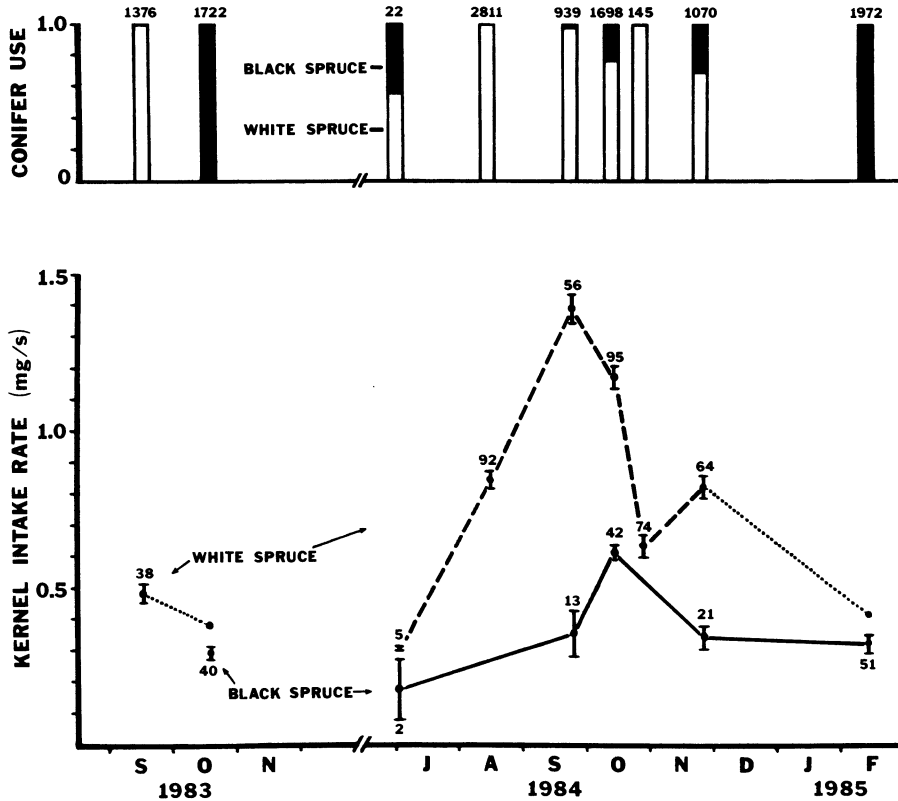


FIG. 2. The kernel intake rates ($\bar{X} \pm SE$) and proportion of time White-winged Crossbills spent foraging on white and black spruce at Wonderland–Ship Harbor in the autumn of 1983 and from July 1984 to February 1985. Tamarack was also foraged on along the Wonderland transect, but it is much less common (Table 1), so it is not included. Sample sizes and dotted line as in Fig. 1.

Griscom 1937, Monson and Phillips 1981, Groth 1984, R. Payne, *personal communication*). Monson and Phillips (1981) recognize four size classes in North America; I observed the three smallest size classes. Roughly following Monson and Phillips (1981), I will refer to the smallest size class as "*sitkensis*" (*L. c. minor* = *sitkensis*), the next larger size class as the medium size class (*L. c. neogaea*), and the next-to-largest size class as the large size class (*L. c. bendirei*). These three smallest size classes can be distinguished both by bill and body sizes (Monson and Phillips 1981). J. G. Groth (1984 and *personal communication*) has found a correlation between call notes and size, but it is not certain if these data support the size class divisions of Monson and Phillips (1981). I recognized the size classes by a combination of close observation, using a telescope, and by call notes. During the winter I was often able to compare Red Crossbills and White-winged Crossbills closely when both species went to the roads for salt and grit. The smallest size class of Red Crossbill is distinctly smaller than the White-winged Crossbill and the largest size class is considerably larger (see Griscom 1941). The largest size class I encountered has a distinctive call note (C. W. Benkman, *personal observation*) and was the most commonly observed size class. When more than one size class occurs in a given area, each size class appears usually to flock separately (C. W. Benkman, *personal observation*; J. Groth, *personal communication*). When I was not in the field I observed individuals of the large size class (*L. c. bendirei*; R. Dickerman, *personal communication*) daily for nearly 3 yr in captivity, and for the 1st yr one medium size class individual (*L. c. neogaea*; R. Dickerman, *personal communication*) was captive with them. After the winter of 1982–1983 I sent tape recordings of the call notes of Red Crossbills observed in the field to J. Groth to confirm call types. In the winter, especially 1984–1985, over 50 road-killed Red Crossbills from the study areas were examined. At all sites where Red Crossbills were observed, either specimens were examined or recordings were made or both.

RESULTS

Profitability and conifer use by White-winged Crossbills

Patterns of profitability were influenced most by cone ripening phenology. Intake rate on tamarack (*Larix laricina*) and white spruce (*Picea glauca*) increased from July to August and September (Figs. 1b, 2, and 3) as seed size increased to maturity and as cones began opening, then declined as seeds were shed from the cones (Figs. 1a, 1b, 2, and 3). Fig. 4 presents seed fall data from the literature. Tamarack and white spruce shed most of their seed between mid-September and early November. After cones opened, time per seed increased as the number of seeds per tamarack cone decreased (Fig. 5). This relationship was general for

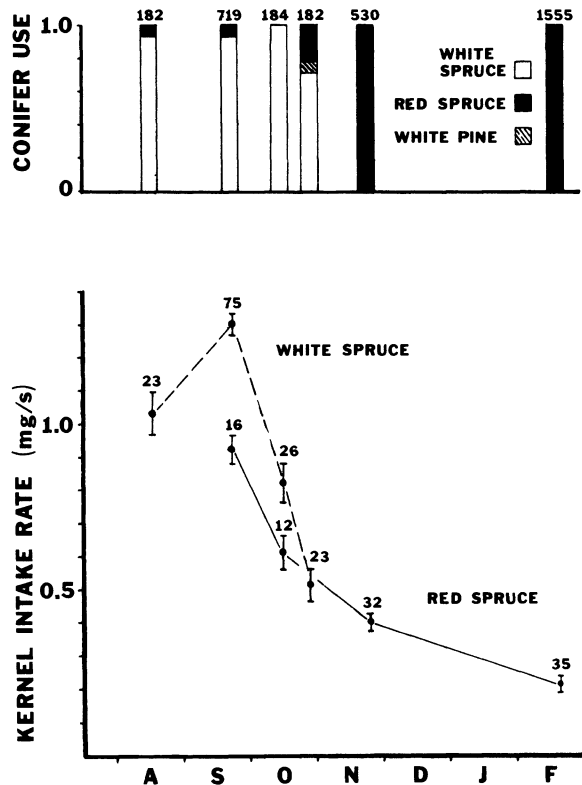


FIG. 3. The kernel intake rates ($\bar{X} \pm \text{SE}$) and proportion of time White-winged Crossbills spent foraging on each conifer at Otter Point-Blackwoods from August 1984 to February 1985. The mid-October intake rate data for red spruce were gathered near the Wonderland transect. Sample sizes are in Fig. 1.

crossbills foraging on open cones of all conifers (see Benkman 1987).

As on tamarack and white spruce, intake rates on black spruce (*P. mariana*) were highest when cones were open and before many seeds had been shed (see Benkman 1987). In Laurentides, there was a small increase in intake rates during November due to some cones opening, but the largest increase occurred from March to May (Fig. 1a) when most black spruce cones opened (Fig. 4). At Wonderland-Ship Harbor (WSH), however, most black spruce cones opened in October (see Fig. 2).

Crossbills preferentially forage on the conifer species yielding the highest intake rate and changes in diet correspond to maximizing intake rate (Figs. 1, 2, and 3). During each of two years (1982–1983, 1984–1985) at Laurentides, White-winged Crossbills foraged mainly on tamarack when the intake rate on tamarack was highest and switched in winter to forage mostly on black spruce when the intake rate on tamarack fell below that on black spruce. At WSH, White-winged Crossbills exhibited similar shifts in intake rate and conifer selection as at Laurentides (Fig. 2), but at WSH

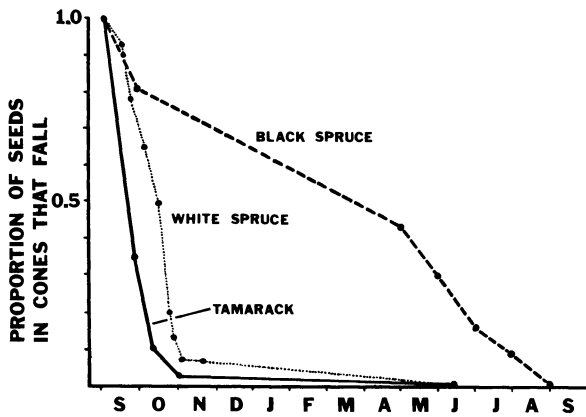


FIG. 4. The periods of seed fall for tamarack (Duncan 1954), white spruce (Roe 1946, Waldron 1965), and black spruce (Fowells 1965), based on seed trap data.

tamarack is much rarer (Table 1) and white spruce replaces tamarack in the White-winged Crossbill's diet. Data from Otter Point-Blackwoods (OPB), 15 km to the east of WSH, also indicate that White-winged Crossbills preferentially forage on the conifers with the highest profitabilities (Fig. 3). Black spruce is absent from OPB (Table 1) and there it is replaced in the diet by red spruce (*P. rubens*). Between August 1984 and early January 1985 White-winged Crossbills near Achray in Algonquin Provincial Park (hereafter Algonquin) foraged most efficiently on white spruce, and during my five visits to the site in 1984 they spent >80% of their time foraging on white spruce. However, in late February 1985, White-winged Crossbills foraged 61% of their time on black spruce, even though white spruce was more profitable. In February 1983, White-winged Crossbills at Achray had higher intake rates on white spruce than in February 1985, and in 1983 White-winged Crossbills foraged nearly 100% on white spruce, virtually ignoring black spruce.

Intake rates on tamarack and white spruce would have continued to decline after the last dates for which there are intake rate data, because the number of seeds per cone continued to decline. The dotted lines in Figs. 1 and 2 connect the last recorded intake rates to those estimated based on the number of seeds per cone (see Fig. 5). In March 1983 at Laurentides, there were on average 0.4 seeds per tamarack cone ($SE = 0.08$, $n = 95$ cones, 10 trees), and in February 1985 there were on average 0.1 seeds per cone ($SE = 0.05$, $n = 50$ cones, 5 trees). On 18–19 October 1983 at WSH, the mean number of seeds per white spruce cone was 2.0 ($SE = 0.47$, $n = 38$ cones, 5 trees). The estimated intake rate at WSH on 19 February 1985 was based on a mean of 2.3 seeds per cone ($SE = 1.69$, $n = 32$ cones, 3 trees). These seed densities were below that for which nearly all intake rate data were gathered. It is tenuous, therefore, to extrapolate with much precision the mean intake rates for these seed densities. Nevertheless, the

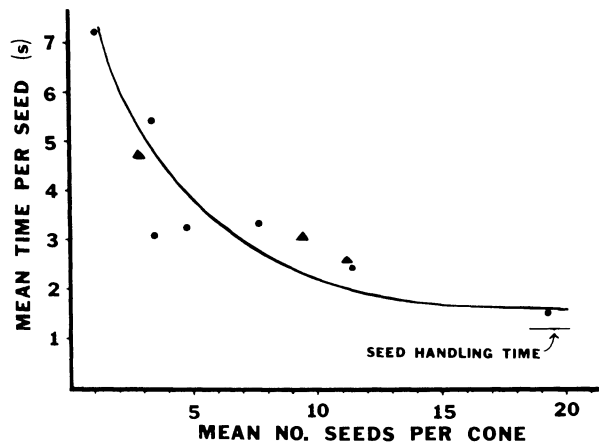


FIG. 5. The average times required for foraging White-winged Crossbills to obtain and handle (●) tamarack and (▲) white spruce seed, in relation to the mean seed density. Sample sizes for time per seed range from 16 to 179 bouts and 81 to 1310 seeds, respectively. The mean number of seeds per cone is usually based on samples of 10 cones from each of 5 trees. The mean handling time (short horizontal line), to which total time per seed declines asymptotically, is that for tamarack seeds ($SE = 0.12$, $n = 16$ seeds); it is on average slightly greater than that for white spruce seeds (Benkman 1987). The line was fitted by eye. When both time per seed (Y) and number of seeds per cone (X) are converted to their natural logarithms, there is a negative and significant relation ($Y = 2.04 - 0.48X$, $r = -0.92$, $P < .01$). Considering only tamarack yields a similar relationship ($Y = 2.05 - 0.51X$, $r = -0.93$, $P < .01$).

profitabilities of tamarack at Laurentides were undoubtedly less than that for black spruce. However, the estimates for WSH cannot be used to corroborate a switch in diet coinciding with a shift in relative profitabilities, but neither are they necessarily inconsistent with this prediction.

Patterns of White-winged Crossbill abundance

There were three periods of change in White-winged Crossbill abundance that coincided with shifts in conifer use and seed fall. The first period occurred in late October and November, which coincided with seed fall of tamarack and white spruce (Fig. 4). When profitabilities were high, White-winged Crossbills remained in the habitat (Fig. 6; see Fig. 1a) and often there were influxes of crossbills as at Achray (Fig. 7). On the six occasions when profitabilities were >0.4 mg/s in late October and November, White-winged Crossbills remained through winter at the site. On the two occasions when profitabilities were <0.40 mg/s, White-winged Crossbills emigrated. Most of the White-winged Crossbills apparently emigrated from Laurentides in late autumn 1984, because neither tamarack nor black spruce seed abundances and profitabilities were sufficient to support many crossbills through winter. For White-winged Crossbills to survive in January in Laurentides,

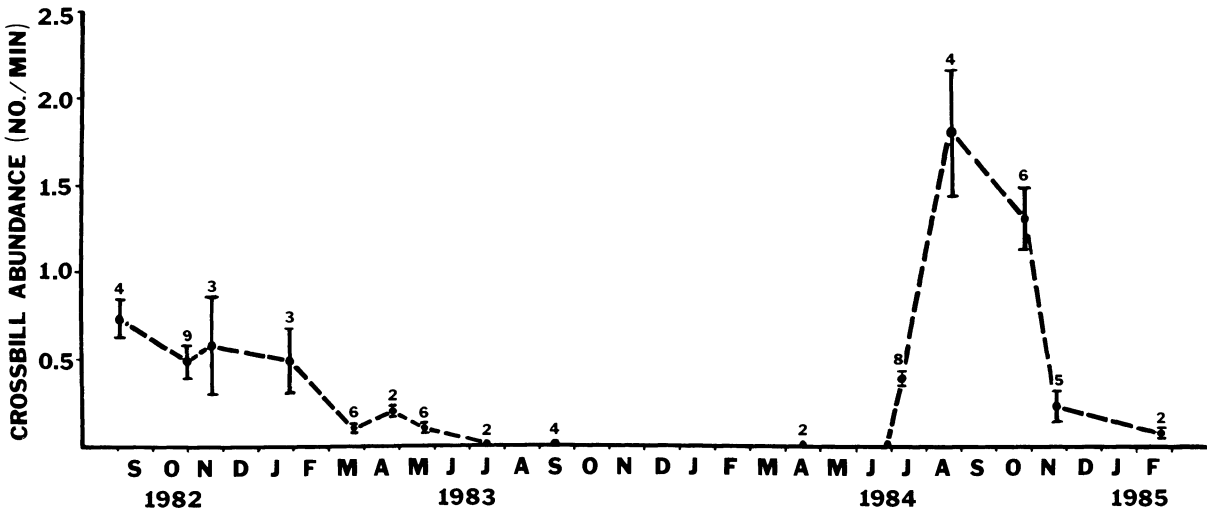


FIG. 6. The number of White-winged Crossbills ($\bar{X} \pm SE$) seen or heard per minute along transect 1 in Laurentides Reserve. Sample sizes are the number of censuses conducted.

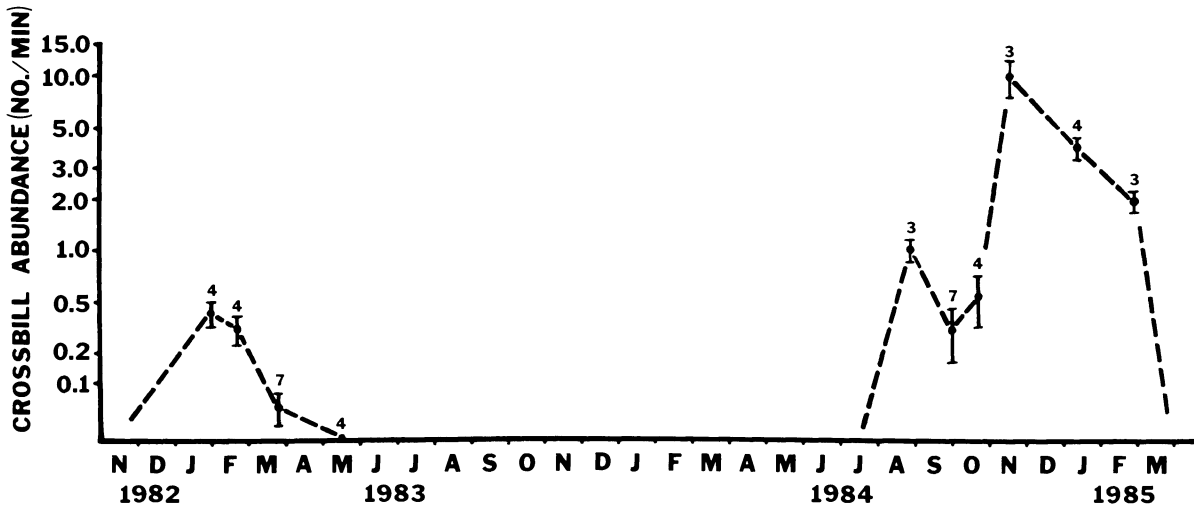


FIG. 7. White-winged Crossbill abundances ($\bar{X} \pm SE$) along transect Achray 1 (in Algonquin Provincial Park) from February 1983 to February 1985. In 1982 and 1984, White-winged Crossbills began arriving in the Park in November and July, respectively. Between May 1983 and mid-July 1984 no censuses were made, but during this period White-winged Crossbills were rare in the Park (Algonquin Provincial Park records). Note nonlinear scale of ordinate. Sample sizes are the number of censuses conducted.

I estimate that a male must have at least an average intake rate of 0.21 mg/s while foraging (see Benkman 1985 for calculations and assumptions), which would result if there is an average of one seed per tamarack cone (see Fig. 4). On 20 February 1985, there was only a mean of 0.14 seeds per tamarack cone, which would not have been sufficient to support crossbills (Fig. 1b). On this same day, White-winged Crossbills had a mean intake rate of 0.21 mg/s when foraging on black spruce (I estimate that male White-winged Crossbills require an intake rate of at least 0.17 mg/s to survive in February). To maintain an intake rate this high through winter on black spruce, White-winged Crossbills prob-

ably must occur in low densities and forage selectively on partly open cones.

Crossbills were responsible for some of the reduction in the number of seeds per cone. For example, the more rapid decline in the proportion of seeds remaining in cones in 1984 compared with the decline in 1982 at Laurentides (Fig. 8) was due, in part, to both higher White-winged Crossbill densities (Fig. 6) and a lower initial number of seeds per cone in 1984 ($\bar{X} = 11.5$ seeds per cone, $SE = 0.62$, $n = 50$ cones, 5 trees) than in 1982 ($\bar{X} = 19.2$ seeds per cone, $SE = 0.69$, $n = 38$ cones, >8 trees).

The second period when White-winged Crossbills

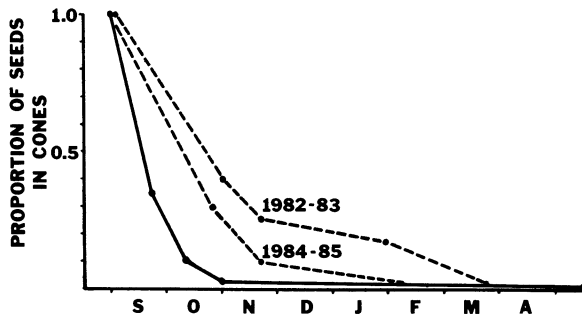


FIG. 8. This figure shows both the timing of seed fall for tamarack (—) as presented in Fig. 4 and the actual measured proportional decline in the number of seeds per tamarack cone (---) at Laurentides Reserve in 1982–1983 and 1984–1985. The difference between the seed density curves and the seed fall curve is an estimate of the proportion of seeds that do not fall to the ground (as measured by seed traps) and are consumed mainly by White-winged Crossbills.

frequently shifted habitats was in late February and March. This shift coincided with the decline in profitability of tamarack and white spruce and the switch from foraging on tamarack and white spruce to black spruce. White-winged Crossbills emigrated from Achray in March 1983 when the average number of seeds per white spruce cone declined from 9.4 on 1 February to 0.5 on 25 March ($SE = 1.54$, $n = 17$ cones, 1 tree, and $SE = 0.21$, $n = 51$ cones, 5 trees, respectively). Similarly, in late February and March 1985 White-winged Crossbills emigrated from Achray (Fig. 7) and the rest of Algonquin when intake rates declined from a mean of 0.46 mg/s on 21–22 January to 0.29 mg/s on 22–25 February ($SE = 0.04$, $n = 46$ foraging bouts, and $SE = 0.07$, $n = 12$ foraging bouts, respectively). Between 13 and 19 March large numbers of White-winged Crossbills were observed moving west past the Long Point Bird Observatory on Lake Erie, Ontario, ≈ 420 km southwest of Achray (Weir 1985c). The switch in conifer use in Laurentides (Fig. 1a) caused a decline in White-winged Crossbill abundance along transect 1 (Fig. 6) where tamarack was common (Table 1).

The third period of movement by White-winged Crossbills coincided with the switch from foraging on open black spruce cones to foraging on developing tamarack and white spruce cones in June and July. Immigration into habitats containing large developing tamarack and white spruce cone crops often occurred at this time, such as in Laurentides in 1984; White-winged Crossbills were absent from Laurentides on 29 June 1984 (R. Ouellet, *personal communication*), then by 6 July hundreds had arrived (Fig. 6) and foraged on the abundant developing tamarack cone crop. In both 1983 and 1984, White-winged Crossbills arrived in Acadia in mid to late June (W. Townsend, *personal communication*). In 1984, White-winged Crossbills were first noted in Algonquin on 17 July (R. Tozer, *personal communication*). In July 1984, White-winged Cross-

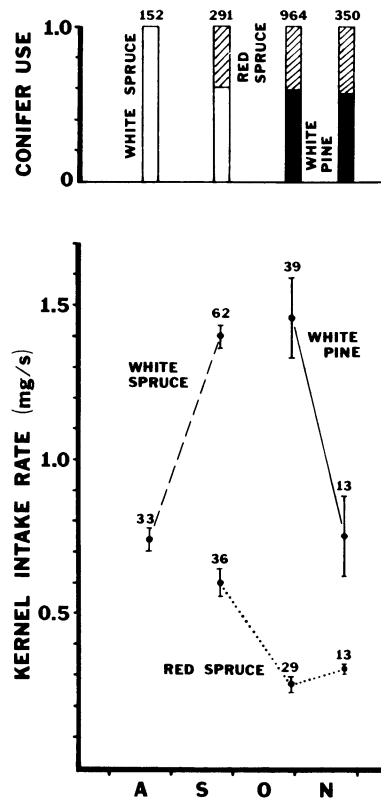


FIG. 9. The intake rates ($\bar{X} \pm SE$) and proportion of time spent foraging on each conifer by Red Crossbills at Otter Point-Blackwoods in 1984. Sample sizes as in Fig. 1. See Results: Profitability and Conifer Use by Red Crossbills for further explanation.

bills at WSH foraged for seed in black spruce cones that had opened in the autumn of 1983 and on developing white spruce cones (see Fig. 2). White-winged Crossbills emigrated from Laurentides in mid-May to June 1983 (Fig. 6) because there was a virtual absence of developing tamarack cones.

Algonquin Provincial Park records, kept since 1960, indicate that the temporal pattern of White-winged Crossbill residency in 1982–1983 was repeated in 1964–1965 and 1974–1975, and the pattern found in 1984–1985 occurred in 1960–1961 and 1978–1979.

Profitability and conifer use by Red Crossbills

Red Crossbills at OPB and Achray foraged most frequently on the conifers yielding the highest intake rates (Figs. 9 and 10). At OPB, Red Crossbills (mostly medium size class) switched from foraging on white spruce to white pine (*Pinus strobus*) when profitabilities shifted, but the crossbills continued to include red spruce in their diet even though it provided lower profitabilities (Fig. 9). As at OPB, Red Crossbills (mostly large size class) at Achray (Fig. 10) switched from foraging on white spruce to white pine in autumn, coinciding

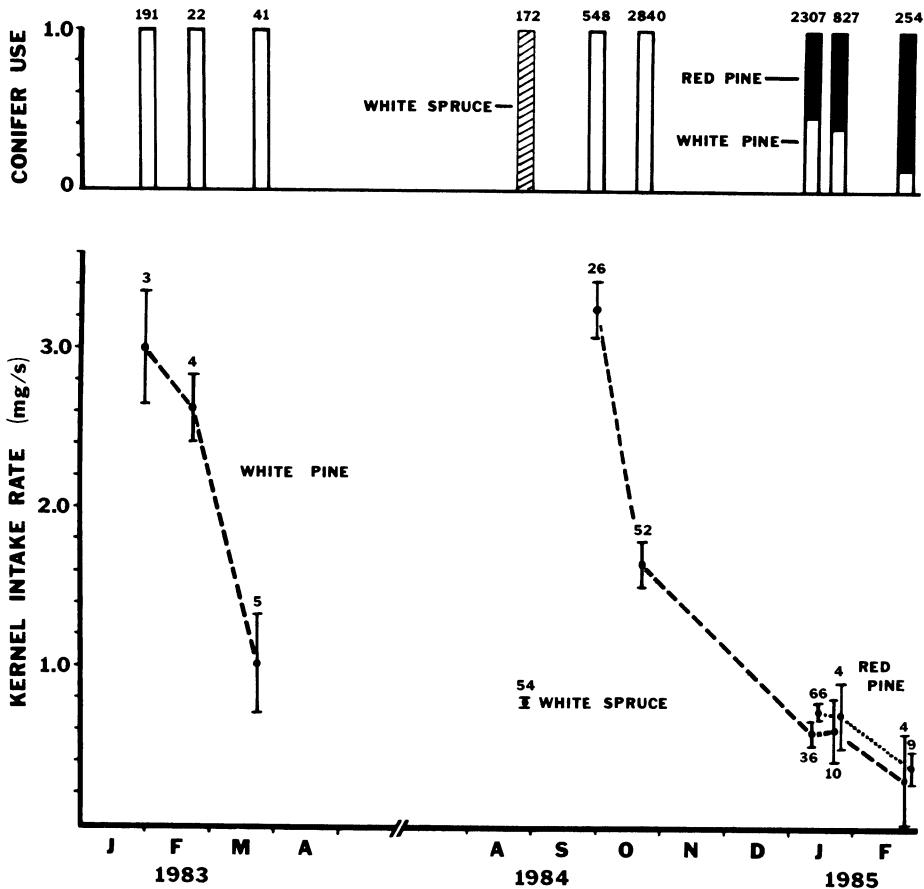


FIG. 10. The intake rates ($\bar{X} \pm SE$) and proportion of time spent foraging on each conifer by Red Crossbills near Achray. Sample sizes as in Fig. 1. See Results: Profitability and Conifer Use by Red Crossbills for further explanation.

with the opening of the white pine cones between mid-September and mid-October. When white pine cones are closed, Red Crossbills have intake rates of ≈ 0.4 mg/s (Benkman 1987), which is less than their intake rate on white spruce, but intake rates increase rapidly as white pine cones open. White spruce cones opened in early September and intake rates would have declined as seeds were shed (see Fig. 3; note decline of intake rate for White-winged Crossbills foraging on white spruce at OPB after Red Crossbills switched to white pine). Thus, the shift in use from white spruce to white pine occurred when intake rates were declining on white spruce and increasing on white pine and coincided with a change in relative profitabilities.

Red Crossbills shifted foraging from white pine to red pine (*P. resinosa*) at Achray when white pine seed profitability declined substantially (Fig. 10). In 1982–1983 the white pine cone crop was heavier than in 1984–1985, which resulted in higher intake rates on white pine and a lack of a dietary shift to red pine as in 1985. On Tongue Mountain in 1983–1984, Red Crossbills (large size class) foraged on white pine in late November, then by January switched to red pine (C. W. Benkman, *personal observation*). Apparently,

the white pine seed crop was even poorer than at Achray in either 1982–1983 or 1984–1985, because on 28 January 1984 Red Crossbills were only observed to forage on red pine and they had a mean intake rate of 0.50 mg/s ($SE = 0.102$, $n = 14$ bouts); compare to Fig. 10. Intake rates on red pine cones were usually < 0.7 mg/s. At both Achray and Tongue Mountain there were many red pine to forage on, but there were few at OPB (Table 1). Thus, when white pine seed profitability declined between November and February, Red Crossbills switched to red pine at Achray and Tongue Mountain, but they emigrated at OPB.

Algonquin records indicate that Red Crossbills were present near Achray by early July in both 1982 and 1984 and that Red Crossbill abundance and residency patterns in 1960–1961 and 1972–1973 were similar to those found in 1984–1985.

Seeds are much more accessible in open white pine cones than in open red pine cones (Benkman 1985), but white pine cones shed their seeds more rapidly after their cones begin to open in autumn than does red pine (Fig. 11). By late winter or early spring red pine holds a higher proportion of its seeds in its cones than does white pine. Thus, even though a given red pine seed

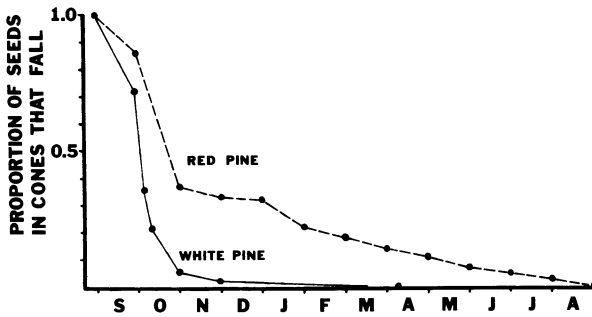


FIG. 11. The periods of seed fall for white pine (Graber 1971) and red pine (Sims and Campbell 1970) based on seed trap data. Cones of both pines begin opening in autumn, but red pine cones open more gradually and seed is released over a more extended period.

is smaller and less accessible than a white pine seed, the greater number of seeds per red pine cone can make red pine more profitable for Red Crossbills. In late summer, when white and red pine cones are closed, their seeds are much less accessible than the seeds of the much smaller white and red spruce cones (Benkman 1987); at this time crossbills forage on spruce.

Differences in body and bill sizes of Red Crossbills may further contribute to variation in the observed patterns of conifer use and seed profitability between sites. The Red Crossbills at OPB were smaller (medium size class) than those at Achray (large size class) and medium sized Red Crossbills may be slightly less efficient on white pine. They did appear to take longer to handle the large white pine seeds than the large-billed Red Crossbills at Achray, but this was not quantified. In the laboratory, however, the mean seed handling time of white pine seeds was $1.35 \times$ as great for an individual of the medium size class as that for the mean for five large sized individuals ($t = 4.32$, $df = 170$, $P < .005$). The even smaller White-winged Crossbill required $3.3 \times$ as long to handle white pine seeds as the large sized Red Crossbills (Benkman 1987).

In sum, the most profitable conifer was foraged on $>90\%$ of the time on 22 of 35 occasions (63%) for White-winged Crossbills and on 7 of 13 occasions (54%) for Red Crossbills. For 83 and 85% of the samples White-winged and Red Crossbills, respectively, foraged on the most profitable conifer $>60\%$ of the time.

DISCUSSION

Patterns of conifer seed profitability

Profitability contributes significantly to patterns of crossbill conifer use, and patterns of profitability determine, in large part, local habitat use and movement. Conifer seed profitability depends on cone structure, timing of cone opening and seed release, and, of course, seed mass. Profitability usually peaks as cones open (see Newton 1967, 1972, Nethersole-Thompson 1975), when both seed accessibility and the number of seeds

per cone are high (Benkman 1987). Crossbills show consistent switches in conifer use because of regular differences in patterns of profitability between conifer species. However, due to differences in crossbill bill morphology, which influence foraging efficiency (Benkman 1987), White-winged Crossbills differ from Red Crossbills in conifer use.

Conifer use is variable between years and locations because profitability, for a given conifer, varies temporally and spatially. After cones open, profitability decreases as the number of seeds per cone diminishes. The rate at which profitability declines varies with the initial number of seeds per cone and weather conditions. Higher initial numbers of seeds per cone usually result in profitabilities that remain higher for longer periods of time after cones open. Because seeds per cone and cone abundance are positively correlated (Smith and Balda 1979), large cone crops usually correspond to extended periods of high profitability. This, for example, may explain the variable timing of White-winged Crossbills switching from tamarack and white spruce to black spruce and of Red Crossbills switching from white pine to red pine. Autumn weather conditions can also influence seed fall; cool moist weather can delay white pine seed fall several weeks (Graber 1971) and red pine seed fall several months (Cayford 1964). Since both climatic and growing conditions vary geographically, patterns of profitability may differ within a given conifer species from region to region. Variation between areas in profitability is further amplified by geographic variation in both cone opening patterns (e.g., black spruce [this study], pitch pine [*P. rigida*; Givnish 1981]) and seed mass (C. W. Benkman, *personal observation*; Sorensen and Miles 1978).

Different areas have different conifer compositions that further influence a habitat's pattern of profitability. In general, from mid or late summer to the following spring, crossbills forage on cones with progressively less accessible seed. This pattern occurs because "tougher" cones usually hold their seed longer; if seed is held for extended periods, more seed defenses are required to deter vertebrate seed predators (e.g., Smith 1970, Benkman et al. 1984). The fewer conifer species present, the shorter the time period during which profitability is likely to be sufficient to support crossbills. Whether crossbills occupy a habitat for extended periods depends on both the number and composition of conifer species present and the synchrony of cone crops in a habitat.

In a given area large cone crops are usually synchronous within either (1) pines or (2) spruces, tamarack, and hemlock (*Tsuga*), but less frequently between these two groups (Smith and Balda 1979). This difference between the cone production of these two groups apparently occurs because they differ in the time period between cone bud formation and seed maturation: 2 yr for pines, 1 yr for spruce, tamarack, and hemlock. Thus, for each crossbill species, a given habitat is more

likely to be either good for extended periods during bumper cone crops or very poor during periods of cone failure.

Both the magnitude of and variation in abundance of crossbills is likely influenced by the distribution and diversity of conifers (also see Bock and Bock 1974, Bock 1982). The geographic distribution of crossbills (Newton 1972) coincides with that of conifers in the Pinaceae, except in the southeastern United States outside of the Appalachian Mountains and in China (see Critchfield and Little 1966). Habitats in these two areas either contain only a single species of conifer (*Pinus massoniana* in China; Critchfield and Little 1966) or one to three species of pines with similar seed-shedding phenologies (C. W. Benkman, *personal observation*). In either case it is doubtful if there is sufficient seed to support crossbills for extended periods within a year or between years.

The timing of switches between conifers

Mittelbach (1981) found that bluegill sunfish (*Lepomis macrochirus*) switched from vegetated to open habitats as the relative profitabilities shifted between these habitats. Time lags on the order of 2 wk were found between the shift in relative profitabilities and the actual switch by the sunfish. The lag in switching by bluegills was attributed to learning or experience in the "new" habitats (also see Werner et al. 1981). Learning effects in crossbills, given the extent of sampling observed, would not result in much of a lag for several reasons. First, crossbill foraging efficiency rapidly reaches an asymptote after foraging on <20 cones of a given conifer species (C. W. Benkman, *personal observation*). Second, conifer use is influenced by the combined assessment of many members in feeding flocks (C. W. Benkman, *personal observation*), which probably increases the accuracy of assessment of conifer profitability (see Krebs et al. 1972). Third, crossbills often switch conifer types within a habitat and they regularly cover long distances during a day.

The intervals between which I gathered data were usually greater than a month. This precludes a detailed evaluation of the actual extent to which crossbills track variation in profitability among conifer species. In those cases where the intervals were a month or less (Figs. 2, 3, 9, and 10) crossbills switched conifer use in a manner consistent with maximizing energy intake.

Predation and habitat use

Predation pressure on crossbills could also affect conifer use by crossbills. Recent work on bluegill sunfish has demonstrated the importance of predation risk on habitat selection (Werner et al. 1983b). Crossbills often forage in exposed positions on the outer limbs of conifers where predation risks could be high. Avian predators of crossbills include Sharp-shinned Hawk (*Accipiter striatus*), Northern Merlin (*Falco columbarius*), Peregrine Falcon (*F. peregrinus*), and Northern Shrike

(*Lanius excubitor*) (Austin 1968, Cade et al. 1968, C. W. Benkman, *personal observation*).

Different conifers provide crossbills with refuge from predators to various degrees. Crossbills are more visible in tamarack, especially in winter after its needles are shed, and may be less concealed from predators when foraging on this species. However, there is no consistent trend of White-winged Crossbills foraging on tamarack less than predicted from intake rates measured after needle loss than before needle loss (Fig. 1).

Conifer use by White-winged Crossbills

The annual cycle of the White-winged Crossbill is tied to patterns of profitability. In late June and July, the cones of all conifers are developing, with seed in cones of tamarack and white spruce being the most accessible. Large cone crops of these two species of conifers, and possibly red spruce in the southern part of the White-winged Crossbill's range, are searched for in summer. Seed in cones of the other conifer species are less accessible (e.g., black spruce and pines; Benkman 1987). White-winged Crossbills cannot remove seeds from developing black spruce cones, but in July seeds often still remain in cones from the previous year. White-winged Crossbills frequently arrive in a given area in June and July (C. W. Benkman, *personal observation*; A. Erskine, *personal communication*). For example, in 1984, White-winged Crossbills began arriving in areas of large tamarack or white spruce cone crops from mid to late June (Acadia National Park, northern New Brunswick, and Laurentides) to mid to late July (Algonquin and Adirondack Mountains, New York).

By early November, seed fall of most tamarack and white spruce is complete (Fig. 4), and at this time White-winged Crossbills may depart. This decision appears to be based, in part, on their intake rate. On the two occasions in October and November when White-winged Crossbill intake rates were <0.40 mg/s they dispersed, but on the six other occasions when they had intake rates >0.40 mg/s they remained resident.

White-winged Crossbills often switch to forage on black spruce between October and late winter. Black spruce cones open later in the year than white spruce, red spruce, or tamarack (Fowells 1965; C. W. Benkman, *personal observation*), and seeds are often available in black spruce through the following summer (Chai and Hansen 1952; this study). From late winter to spring, black spruce cones open in Quebec and possibly throughout much of the northern boreal forests of Canada (Vincent 1965). This provides a seed source for White-winged Crossbills when the other conifers usually taken have lost most of their seed. When tamarack or white spruce holds a lot of seed, White-winged Crossbills do not switch as early to black spruce (also see Sealy et al. 1980). However, by March both tamarack and white spruce (and red spruce) usually have lost most of their seed and White-winged Crossbills

rely on black spruce. The emigration from areas of black spruce in late spring does not appear to be based as much on intake rates as on the presence or absence of developing tamarack or white spruce cone crops; intake rates in mid-May 1983 on black spruce in Laurentides were sufficient for adults to support fledglings (see Fig. 1a), yet from mid-May to June crossbills emigrated. By summer, black spruce sheds most of its seed. The early summer movements of European Red Crossbills also coincide with diet shifts (Haapanen 1966, Newton 1970, 1972).

Large-scale movements are probably linked to patterns of profitability. Irruptions of White-winged Crossbills into areas south of their normal range usually occur in late October and November (Roberts 1936, Bagg and Eliot 1937, Griscom 1937, Stewart and Robbins 1958, Baird 1964, Austin 1968, Bull 1974, Kane 1982, Eckert 1983), which coincides with tamarack and white spruce seed fall. This was also the period when White-winged Crossbills left Acadia in 1983 and Laurentides in 1984 and large movements were noted at Wenlock Crossing (C. W. Benkman, *personal observation*) and Algonquin. During morning counts on 18 to 22 November 1984 on Manitoulin Island in Lake Huron, the number of migrating White-winged Crossbills ranged from 500 to 10 000 (Weir 1985a). Also, irruptions of other boreal seed-eating birds, such as Boreal Chickadees (*Parus hudsonicus*; Yunick 1984), often are first noted in late October and November. Eastern hemlock (*T. canadensis*) frequently holds seed well into winter, and White-winged Crossbills often forage on hemlock during winter in invasion years (e.g., Bagg and Eliot 1937, Griscom 1937, 1941, Palmer 1949, Stone 1949, Kane 1982). White-winged Crossbills usually leave invasion areas from late February to April (Allen 1864 quoted in Bagg and Eliot 1937, Roberts 1936, Stewart and Robbins 1958, Austin 1968, Bull 1974, Kane 1982, Eckert 1983), which coincides with the opening of black spruce in the boreal forests. How long White-winged Crossbills linger in invasion areas and the timing of irruptions, however, probably depends on local profitabilities (Svårdson 1957).

Conifer use by Red Crossbills

For at least two reasons, Red Crossbills have a more complicated pattern of conifer use than do White-winged Crossbills: (1) Red Crossbills have more powerful bills than White-winged Crossbills, which enable them to utilize efficiently more species of conifers over a wider range of cone stages (see Benkman 1987); (2) There are at least three size classes of Red Crossbill in eastern North America that differ in bill morphology, which at times cause the different size classes to have different foraging efficiencies and conifer use patterns.

In late summer, Red Crossbills, like White-winged Crossbills, breed while foraging on white spruce. But the large size class is much more efficient on pine than are White-winged Crossbills (see Benkman 1987); thus,

when white pine cones begin opening in September and October, Red Crossbills switch to foraging on white pine. If red pine is present, they may subsequently switch to it when its profitability becomes greater than that for white pine. White or red pine is often used into spring. If white and red pine seeds are no longer sufficient to support Red Crossbills, they may emigrate as early as November (e.g., Red Crossbills at Highlands, North Carolina in 1983; D. McNair, *personal communication*). White pine seed is important for crossbills throughout much of the East (Southeastern states: Murray 1971, LeGrand and Hamel 1980; New York and Maine: this study; Ontario: Lawrence 1949, Ross and Ross 1950, this study).

From winter to late spring and summer, seed from a variety of conifers may be consumed. Pitch pine cones open, most often after fire (Fowells 1965), in late autumn or in early spring (C. W. Benkman, *personal observation*). In some areas in the East, pitch pine and Virginia pine (*P. virginiana*) seed can be an important winter and spring seed source (November to April for Virginia pine; Patuxent stomach card file; also see Bagg and Eliot 1937, Hall 1983, Leck 1984). Jack pine (*P. banksiana*) cones often open in late spring (C. W. Benkman, *personal observation*), or after fire (Fowells 1965). Red Crossbills utilize jack pine seeds during summer (H. Ouellet, *personal communication*) and probably often forage for seed in opening jack pine cones. During May and June, Red Crossbills can forage on staminate cones until profitability increases for developing cones (pistillate).

Most of the above discussion pertains to the large size class of the Red Crossbill that occurs in the Northeast and probably also to the medium size class. The medium size class, however, may rely more on spruce and hemlock than the large size class. In the western mountains, Jollie (1953) reported that Red Crossbills of the large size class occurred most commonly while breeding in areas of ponderosa pine (*P. ponderosa*), whereas Red Crossbills that had wing measurements similar to the medium size class resided during breeding in forests consisting of the Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*P. contorta*), and western white pine (*P. monticola*) three conifers whose cones have thinner scales than those of ponderosa pine.

The North American Red Crossbill that has the smallest bill, "sitkensis," also occurs in the Northeast (Griscom 1937, Bull 1974; C. W. Benkman, *personal observation*) and it appears to forage mainly on eastern hemlock. "Sitkensis" foraged on hemlock from December to the end of February along the Highway 60 Corridor on the west side of Algonquin Provincial Park (C. W. Benkman, *personal observation*; >20 road kills). On this side of the Park hemlock is very abundant; white pine is also common, but it had a poor cone crop. On the east side of the Park, at Achray, the pine cone crop was good and the large size class of Red Crossbill was common. In the southern Adirondacks

of New York, "sitkensis" bred while foraging on hemlock in January and February 1985 (C. W. Benkman, *personal observation*; >50 road kills) and remained until late March (R. Yunick, *personal communication*). Eastern hemlock is abundant in the Huron Mountains of Michigan and "sitkensis" is relatively common there (R. Payne, *personal communication*).

Spatial scale of movements

On what spatial scale do White-winged Crossbills move? The emigration of White-winged Crossbills from Laurentides in October and November 1984 coincided with increases 550 km to the southwest at Algonquin and 340 km to the south in northern Vermont (also see Weir 1985*b*), but it is not known whether these were the same individuals.

Some temporal changes in White-winged Crossbill abundances may have resulted from continent-wide movements. In the spring of 1983 White-winged Crossbills emigrated from both Laurentides and Algonquin and were largely absent from eastern and most of western North America until the summer of 1984 (National Audubon Society 1984). The one exception to the general absence of White-winged Crossbills in the East was along the coast of northern Maine and in Newfoundland; during late summer and autumn there were small numbers along the coast of Maine and in the winter of 1983–1984 White-winged Crossbills were common in Newfoundland where there was a large spruce cone crop (Forster 1984, Heil 1984). During this same period White-winged Crossbills were extremely numerous in the Yukon and central Alaska. In the Yukon there was a "cone crop of the century" and White-winged Crossbills were abundant between autumn 1983 and spring 1984 (Grünberg 1984, 1985). In central Alaska there was a large white spruce cone crop (Gibson 1984*b*) and White-winged Crossbills were common there from autumn 1983 (Gibson 1984*a*) to spring 1984 when they bred commonly (Gibson 1984*c*). By 1 June 1984 there was a large movement of White-winged Crossbills out of central Alaska (Gibson 1984*d*) and presumably out of the Yukon, since few were apparently noted in summer and autumn 1984 (Grünberg 1985). Large influxes of White-winged Crossbills, >3600 km to the east southeast were observed by early July in Laurentides (Fig. 6) and in mid-July in Algonquin (Fig. 7). These White-winged Crossbills may have moved across the boreal forests from Alaska and the Yukon to Ontario and Quebec in about a month. White-winged Crossbills that may have been part of the movement out of Alaska and the Yukon arrived in June and July in Alberta (Gollop 1984), Washington (Rogers 1984), Nevada (Kingery 1984), Wyoming (Kingery 1984), New Mexico (Hubbard 1984), and Michigan (Tessen 1984). White-winged Crossbills began showing up along the coast of Maine and New Brunswick by mid-June (this study; Tingley 1984). These crossbills

arrived earlier than those in Ontario and Quebec because they probably originated in Newfoundland and other eastern Maritime locations and thus had to traverse <1200 km. A year later in mid-June 1985 there was a large northwesterly movement of >1000 White-winged Crossbills in northwest Ontario (Veit 1985).

These changes in abundance indicate that White-winged Crossbills move across the continent following the belt of boreal forest (see Rowe 1972) in search of large conifer cone crops; transcontinental movements by another cardueline finch, the redpoll (*Carduelis* sp.), have been recorded (Troy 1983). This type of movement, largely southeast and northwest, across the boreal forests of North America is analogous to the "pendulum flights" reported for Red Crossbills in Eurasia (Svärdson 1957). Because of the difficulty in recognizing forms of the Red Crossbill, it is not so obvious on what scale Red Crossbills may move in North America. However, "sitkensis" may regularly make movements between the Pacific Northwest, including Alaska, and the Great Lakes region.

Population limitation, diet overlap, and competition

Griscom (1937) stated that the two most important factors influencing White-winged Crossbill and Red Crossbill distributions in North America are their dependence on conifer seed crops and the effect of competition between the two crossbill species. For interspecific competition to be important, not only must there be overlap in conifer seed use, but diet overlap must occur for seeds limiting either population size or growth. Smith and Balda (1979) have argued that competitive exclusion is rare among conifer seed-eating animals. Their argument rests on the contention that potential competitors rarely rely on similar foods or strategies to harvest conifer seeds when they are most limiting. However, crossbills forage on conifer seeds throughout the year and use similar exploitation strategies to harvest conifer seed.

Potential period of population limitation.—The period between tamarack and white spruce seed fall in late autumn and the opening of black spruce cones in late winter is when profitability is lowest relative to energy demands for White-winged Crossbills; seeds in closed black spruce cones are inaccessible (Benkman 1987) and seed densities in tamarack and white spruce cones can decline to low levels. After early November, crossbills are often responsible for most further declines in tamarack and possibly white spruce seed abundance (Fig. 8), with seed reductions substantially increasing the time per seed during foraging (Fig. 5) and reducing intake rate. Food limitation on a local scale is most likely during this period of relatively high energy demands and low profitability. Later in winter, black spruce cones begin opening and seeds become sufficiently accessible that White-winged Crossbills can meet their energy demands more easily. Similar pat-

terns of food limitation in winter are likely for Red Crossbills, but for the large size class, white pine should be substituted for tamarack and white spruce, and red pine and other late-opening pines substituted for black spruce.

Conifer cone crops vary by several orders of magnitude between years, with intervals of 2–10 yr between good cone crops (Fowells 1965). As a result of this variation, crossbills rarely occur commonly in the same area two years in succession (e.g., Figs. 6 and 7). Cone crops fail over large regions every 2–4 yr, and at these times there are large irruptions of crossbills from their normal range (Griscom 1937, Newton 1970, 1972, Bock and Lepthien 1976). These cone crop failures correspond to periods of severe food limitation for White-winged Crossbill populations on a large geographic scale (Newton 1970, 1972). Because of spatial variation in seed crops, some local populations are likely to be food limited in any given year. In the northern boreal forests, black spruce is probably the most important seed source for White-winged Crossbills during cone failures because black spruce cone crops are the least variable and rarely fail (Fowells 1965) and seeds are held in open to partially open cones for years at a time (Chai and Hansen 1952).

Partially open black spruce cones may represent the type of cone which the White-winged Crossbill is best adapted to use (Benkman 1987). White-winged Crossbills can slide their slender bills more rapidly, and probably with less effort, between the slightly open black spruce cone scales than can Red Crossbills with their wider bills.

Period of food overlap.—Differences in diet or habitat use are often greatest during periods of food limitation (Newton 1967, 1972, Smith et al. 1978, Schluter 1982b, Schoener 1982). Food overlap between White-winged and Red Crossbills is highest in summer when both species forage on white spruce. For both crossbill species in late summer, intake rates are higher on white spruce than on all other conifers, except possibly on tamarack for White-winged Crossbills. Pullianen (1972) also reported high diet overlap between three species of crossbill in northeast Lapland during July and August. Late summer and early autumn is when seed is most abundant and least limiting. During the rest of the year the diets of both species of crossbills diverge because each crossbill species is best adapted for procuring and handling seeds from different species of conifer (see Benkman 1987).

There are large differences between White-winged and Red Crossbills in foraging efficiency that make it unlikely that both species can profitably forage on the same conifers when seed is most limiting. When diets diverge in autumn the change in conifer use is primarily in response to cone ripening patterns, not seed depletion by crossbills. Diets diverge both when seeds are abundant and readily available in winter (seed does not limit population size and nesting may occur), as

well as when seeds are more limiting (see Schluter 1982a, b for similar interpretations of patterns of seed use by Darwin's finches). Therefore, interspecific competition has little impact on major patterns of conifer use. Nevertheless, seed depletion by the other species may limit diet breadth and possibly population size. For example, when spruce and tamarack seeds are scarce, White-winged Crossbills may be able to subsist on abundant white pine seed. Depletion of white pine seed by Red Crossbills, however, may make white pine seed unprofitable for White-winged Crossbills (also see Benkman 1987).

If there is competition between White-winged and Red Crossbills, "sitkensis" is more likely affected than the large size class of Red Crossbill. The winter diet of "sitkensis" consists primarily of hemlock (in the East), which can be an important winter seed source for White-winged Crossbills, particularly when other seed sources are depleted; use of hemlock seed appears to coincide with years of high crossbill abundances and invasions. Large numbers of crossbills foraging on a seed source that already may be low makes competition more likely. In Alaska, where both White-winged Crossbills and "sitkensis" regularly occur, they are largely allopatric (Gabrielson and Lincoln 1959).

In some winters, Common Redpolls (*C. flammea*) forage predominately for tamarack and white spruce seeds (C. W. Benkman, *personal observation*; also see Todd 1963, Smith 1979, Sealy et al. 1980). Redpolls apparently forage on conifer seeds mainly when they are in the southern parts of their winter range (Smith 1979, also see Antikainen et al. 1980, Götmark 1982). This occurs during invasion years, which in North America coincide with those years when seed is most limiting for crossbills. Redpolls are efficient at procuring and consuming tamarack and white spruce seed (C. W. Benkman, *personal observation*). Redpolls were very abundant in Laurentides in November 1984 and were seen to consume only tamarack seed. Redpolls, therefore, potentially contribute to depleting what can be a limiting resource for White-winged Crossbills.

CONCLUSIONS

The diets and population movements of crossbills are correlated with patterns of profitability (food intake rate) while foraging on conifer cones. Because of regular patterns of profitability for both White-winged and Red Crossbills, and differences between crossbill species due to different morphologies, many patterns of crossbill diets and movements can be understood. Dietary overlap between White-winged and Red Crossbills is highest in late summer, when seed abundance is greatest, and overlap declines rapidly in early autumn well before seed is most limiting. Competition between White-winged Crossbills and the large size class of Red Crossbill in northeast North America is probably infrequent. However, competition between White-winged Cross-

bills and either the smallest size class of Red Crossbill or redpolls is likely and may occur irregularly, coinciding with continent-wide cone failures.

ACKNOWLEDGMENTS

K. Johnson and Drs. R. Pulliam, K. Able, J. Brown, J. Gilliam, D. Schluter, J. N. M. Smith, and L. Wolf read and made constructive comments on this manuscript. Many people informed me of crossbill sightings including D. Strickland, R. Tozer, W. Townsend, W. Russell, J. Peterson, A. Erskine, M. Metcalf, F. Oatman, R. Ouellet, D. Christie, D. Kimball, R. Yunick, and D. Keefer. C. Cardinal at Laurentides Reserve and R. Tozer and D. Strickland at Algonquin Provincial Park were particularly helpful in enabling me to conduct research and providing me with accommodations during particularly harsh conditions. C. Schell allowed me to conduct research in Acadia National Park. Financial support was provided, in part, by grants from the Frank Chapman Memorial Fund and SUNYA Benevolent Foundation to the author and NSF Grants DEB-13017 and DEB-8206936 to R. Pulliam. I am most thankful to all those mentioned above and to those I have failed to mention. They all helped make my research possible and memorable.

LITERATURE CITED

- Antikainen, E., U. Skaren, J. Toivanen, and M. Ukkonen. 1980. Urpianisen *Acanthis flammea* vaellusaikainen joukkopesintä Pohjois-Savossa keväällä 1979 (Summary: The nomadic breeding of the Redpoll *Acanthis flammea* in 1979 in North Savo, Finland). *Ornis Fennica* 57:124-131.
- Austin, O. L. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows and allies. Part I. United States National Museum Bulletin 237.
- Bagg, A. C., and S. A. Eliot, Jr. 1937. Birds of the Connecticut Valley in Massachusetts. The Hampshire Bookshop, Northampton, Massachusetts, USA.
- Baird, J. 1964. The changing seasons: a summary of the fall season, 1963; early movements of boreal birds. *Audubon Field Notes* 18:4-6.
- Benkman, C. W. 1985. The foraging ecology of crossbills in eastern North America. Dissertation. State University of New York, Albany, New York, USA.
- . 1987. Crossbill foraging behavior, bill structure, and patterns of food profitability. *Wilson Bulletin* 99, in press.
- Benkman, C. W., R. P. Balda, and C. C. Smith. 1984. Adaptations for seed dispersal and the compromises due to seed predation in limber pine. *Ecology* 65:632-642.
- Bock, C. E. 1982. Factors influencing winter distribution and abundance of Townsend's Solitaire. *Wilson Bulletin* 94:297-302.
- Bock, C. E., and J. H. Bock. 1974. Geographical ecology of the Acorn Woodpecker: diversity versus abundance of resources. *American Naturalist* 108:694-698.
- Bock, C. E., and L. W. Lepthien. 1976. Synchronous eruptions of boreal seed-eating birds. *American Naturalist* 110:559-571.
- Bull, J. 1974. Birds of New York State. Doubleday/Natural History Press, Garden City, New York, USA.
- Cade, T. J., C. M. White, and J. R. Haugh. 1968. Peregrines and pesticides in Alaska. *Condor* 70:170-178.
- Cayford, J. H. 1964. Red pine seedfall in southeastern Manitoba. *Forestry Chronicles* 40:78-85.
- Chai, T. S., and H. L. Hansen. 1952. Characteristics of black spruce seed from cones of different ages. Minnesota Forestry Notes 2, University of Minnesota, St. Paul, Minnesota, USA.
- Critchfield, W. B., and E. L. Little, Jr. 1966. Geographic distribution of the pines of the world. Miscellaneous Publication 991, United States Department of Agriculture, Washington, D.C., USA.
- Duncan, D. P. 1954. A study of some of the factors affecting the natural regeneration of tamarack (*Larix laricina*) in Minnesota. *Ecology* 35:498-521.
- Eckert, K. R. 1983. A birder's guide to Minnesota. The Pine Knot, Cloquet, Minnesota, USA.
- Forster, R. A. 1984. Northeastern maritime region. *American Birds* 38:177-179.
- Fowells, H. A. 1965. Silvics of forest trees of the United States. Agricultural Handbook Number 271, United States Department of Agriculture, Washington, D.C., USA.
- Gabrielson, I. N., and F. C. Lincoln. 1959. Birds of Alaska. Stackpole, Harrisburg, Pennsylvania, USA.
- Gibson, D. D. 1984a. Alaska region. *American Birds* 38:234-236.
- . 1984b. Alaska region. *American Birds* 38:348-349.
- . 1984c. Alaska region. *American Birds* 38:947-948.
- . 1984d. Alaska region. *American Birds* 38:1052-1053.
- Gill, F. B., and L. L. Wolf. 1975. Foraging strategies and energetics of east African sunbirds at mistletoe flowers. *American Naturalist* 109:491-510.
- Givnish, T. J. 1981. Serotiny, geography, and fire in the Pine Barrens of New Jersey. *Evolution* 35:101-123.
- Gollop, J. B. 1984. Prairie provinces region. *American Birds* 38:1031-1033.
- Goss-Custard, J. D. 1977. Predator responses and prey mortality in Redshank, *Tringa totanus* (L.), and a preferred prey, *Corophium volutator* (Pallas). *Journal of Animal Ecology* 46:21-35.
- . 1981. Feeding behavior of Redshank, *Tringa totanus*, and optimal foraging theory. Pages 115-133 in A. C. Kamil and T. D. Sargent, editors. Foraging behavior. Garland, STPM, New York, New York, USA.
- Götmark, F. 1982. Gräsiskans *Carduelis flammea* förekomst i södra Sverige under "sydhäckningsåret" 1975. Summary: Irruptive breeding of the Redpoll, *Carduelis flammea*, in south Sweden in 1975. *Vår Fågelvärld* 41:315-322.
- Graber, R. E. 1971. Natural seed fall in white pine (*Pinus strobus* L.) stands of varying density. United States Forest Service Research Note NE-119.
- Griscom, L. 1937. A monographic study of the Red Crossbill. Proceedings of the Boston Society of Natural History 41:77-210.
- . 1941. Second flight of the Sitka Crossbill to Massachusetts. *Auk* 58:411-413.
- Grodzinski, W., and K. Sawicka-Kapusta. 1970. Energy values of tree-seeds eaten by small mammals. *Oikos* 21:52-58.
- Groth, J. G. 1984. Vocalizations and morphology of the Red Crossbill (*Loxia curvirostra* L.) in the southern Appalachians. Thesis. Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.
- Grünberg, H. 1984. Northwestern Canada region. *American Birds* 38:336-337.
- . 1985. Northwestern Canada region. *American Birds* 39:77-78.
- Haapenen, A. 1966. Bird fauna of the Finnish forests in relation to forest succession. *Annales Zoologici Fennici* 3:176-200.
- Hall, G. A. 1983. West Virginia birds, distribution and ecology. Special Publication of the Carnegie Museum of Natural History Number 7.
- Heil, R. S. 1984. Northwestern maritime region. *American Birds* 38:293-296.
- Hubbard, J. P. 1984. New Mexico. *American Birds* 38:1050-1052.
- Jollie, M. 1953. Plumages, molt, and racial status of Red Crossbills in northern Idaho. *Condor* 55:193-197.

- Jones, Q., and F. R. Earle. 1966. Chemical analysis of seeds II: oil and protein content of 759 species. *Economic Botany* **20**:127-155.
- Kane, R. 1982. 1981-82 White-winged Crossbill invasion in New Jersey. *New Jersey Audubon* **8**:22-23.
- Kingery, H. E. 1984. Mountain west region. *American Birds* **38**:1044-1047.
- Krebs, J. R. 1978. Optimal foraging: decision rules for predators. Pages 23-63 in J. R. Krebs and N. B. Davies, editors. *Behavioural ecology*. Blackwell Scientific, London, England.
- Krebs, J. R., M. H. MacRoberts, and J. M. Cullen. 1972. Flocking and feeding in the Great Tit *Parus major*—an experimental study. *Ibis* **114**:507-530.
- Lawrence, L. de K. 1949. The Red Crossbills at Pimisi Bay, Ontario. *Canadian Field-Naturalist* **63**:147-160.
- Leck, C. F. 1984. The status and distribution of New Jersey's birds. Rutgers University Press, New Brunswick, New Jersey, USA.
- LeGrand, H. E., Jr., and P. B. Hamel. 1980. Bird-habitat associations on Southeastern forest lands. Clemson University, Clemson, South Carolina, USA.
- McKeever, S. 1964. Food habits of the pine squirrel in northeastern California. *Journal of Wildlife Management* **28**:402-404.
- Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* **62**:1370-1386.
- Monson, G., and A. R. Phillips. 1981. Annotated checklist of birds of Arizona. Second edition. University of Arizona Press, Tucson, Arizona, USA.
- Murray, J. W. 1971. Notes on Red Crossbills near Blacksburg, Virginia. *Raven* **42**:46-47.
- National Audubon Society. 1984. *American Birds* **38**.
- Nethersole-Thompson, D. 1975. Pine Crossbills: a Scottish contribution. T. and A. D. Poyer, Berkhamsted, England.
- Newton, I. 1967. The adaptive radiation and feeding ecology of some British finches. *Ibis* **109**:33-98.
- . 1970. Irruptions of crossbills in Europe. Pages 337-357 in A. Watson, editor. *Animal populations in relation to their food resources*. Blackwell Scientific, Oxford, England.
- . 1972. *Finches*. Collins, London, England.
- Palmer, R. S. 1949. Maine birds. *Bulletin of the Museum of Comparative Zoology, Cambridge, Massachusetts, USA*.
- Pulliaainen, E. 1972. Summer nutrition of crossbills (*Loxia pytyopsittacus*, *L. curvirostra* and *L. leucoptera*) in northeast Lapland. *Annales Zoologici Fennici* **9**:28-31.
- Pulliam, H. R. 1985. Foraging efficiency, resource partitioning, and the coexistence of sparrow species. *Ecology* **66**:1829-1836.
- . 1986. Niche expansion and contraction in a variable environment. *American Zoologist* **26**:71-79.
- Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology* **52**:137-154.
- Reinikainen, A. 1937. The irregular migration of the crossbill (*L. c. curvirostra*) and their relation to the cone crop of the conifers. *Ornis Fennica* **14**:55-64.
- Roberts, T. S. 1936. *The birds of Minnesota*. Second edition. Volume II. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Roe, E. I. 1946. Extended periods of seedfall of white spruce and balsam fir. Technical Note Number 261, Lake States Forest Experiment Station, St. Paul, Minnesota, USA.
- Rogers, T. H. 1984. Northern Rocky Mountain-Intermountain region. *American Birds* **38**:1041-1044.
- Ross, E. G., and V. M. Ross. 1950. Nesting of the Red Crossbill in Pakenham Township, Lanark County, Ontario. *Canadian Field-Naturalist* **64**:32-34.
- Rowe, J. S. 1972. *Forest regions of Canada*. Forestry Service Publication 1300, Department of Environment, Ottawa, Ontario, Canada.
- Schluter, D. 1982a. Seed and patch selection by Galapagos ground finches: relation to foraging efficiency and food supply. *Ecology* **63**:1106-1120.
- . 1982b. Distributions of Galapagos ground finches along an altitudinal gradient: the importance of food supply. *Ecology* **63**:1504-1517.
- Schoener, T. W. 1982. The controversy over interspecific competition. *American Scientist* **70**:586-595.
- Sealy, S. G., D. A. Sexton, and K. M. Collins. 1980. Observations of a White-winged Crossbill invasion of south-eastern Manitoba. *Wilson Bulletin* **92**:114-116.
- Sims, H. P., and G. D. Campbell. 1970. Red pine seedfall in a southeastern Manitoba stand. Department of Fisheries and Forests Publication 1267, Canadian Forest Service, Ottawa, Ontario, Canada.
- Smith, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels, *Tamiasciurus*. *Ecological Monographs* **38**:31-63.
- . 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. *Ecological Monographs* **40**:349-371.
- Smith, C. C., and R. P. Balda. 1979. Competition among insects, birds and mammals for conifer seeds. *American Zoologist* **19**:1065-1083.
- Smith, J. N. M., P. R. Grant, B. R. Grant, I. J. Abbott, and L. K. Abbott. 1978. Seasonal variation in feeding habits of Darwin's ground finches. *Ecology* **59**:1137-1150.
- Smith, K. G. 1979. Common Redpolls using spruce seeds in northern Utah. *Wilson Bulletin* **91**:621-623.
- Sorensen, F. C., and R. S. Miles. 1978. Cone and seed weight relationships in Douglas-fir from western and central Oregon. *Ecology* **59**:641-644.
- Stewart, R. E., and C. S. Robbins. 1958. *Birds of Maryland and District of Columbia*. United States Fish and Wildlife Service, North American Fauna Number **62**.
- Stone, R. H. 1949. In the hemlocks at Wolf Hollow. *Feathers* **11**:5-6.
- Svårdson, G. 1949. Competition and habitat selection in birds. *Oikos* **1**:157-174.
- . 1957. The "invasion" type of bird migration. *British Birds* **50**:314-343.
- Tessen, D. D. 1984. Western Great Lakes Region. *American Birds* **38**:1022-1024.
- Tingley, S. I. 1984. Northeastern maritime region. *American Birds* **38**:997-999.
- Todd, W. E. C. 1963. *Birds of the Labrador Peninsula and adjacent areas*. University of Toronto Press, Toronto, Ontario, Canada.
- Troy, D. M. 1983. Recaptures of redpolls: movements of an irruptive species. *Journal of Field Ornithology* **54**:146-151.
- USDA (United States Department of Agriculture). 1974. *Seeds of woody plants in the United States*. Agricultural Handbook Number **450**.
- Veit, R. R. 1985. The changing seasons. *American Birds* **39**:879-884.
- Vincent, A. B. 1965. *Black spruce: a review of its silvics, ecology and silviculture*. Publication 1100, Canadian Department of Forestry, Ottawa, Ontario, Canada.
- Waldron, R. M. 1965. Cone production and seedfall in a mature white spruce stand. *Forestry Chronicle* **41**:314-329.
- Weir, R. 1985a. Ontario Region. *American Birds* **39**:48-50.
- . 1985b. Ontario Region. *American Birds* **39**:161-164.
- . 1985c. Ontario Region. *American Birds* **39**:291-296.
- Werner, E. E. 1977. Species packing and niche comple-

- mentarity in three sunfishes. *American Naturalist* **111**:553–578.
- . 1984. The mechanisms of species interactions and community organization in fish. Pages 360–382 *in* D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, editors. *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, New Jersey, USA.
- Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983*b*. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* **64**:1540–1548.
- Werner, E. E., and G. G. Mittelbach. 1981. Optimal foraging: field test of diet choice and habitat switching. *American Zoologist* **21**:813–829.
- Werner, E. E., G. G. Mittelbach, and D. J. Hall. 1981. The role of foraging profitability and experience in habitat use by the bluegill sunfish. *Ecology* **62**:116–125.
- Werner, E. E., G. G. Mittelbach, D. J. Hall, and J. F. Gilliam. 1983*a*. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. *Ecology* **64**:1525–1539.
- Wiens, J. A. 1984. Resource systems, populations, and communities. Pages 397–436 *in* P. W. Price, C. N. Slobodkinoff, and W. S. Gaud, editors. *A new ecology: novel approaches to interactive systems*. John Wiley and Sons, New York, New York, USA.
- Wolf, L. L., F. R. Hainsworth, and F. G. Stiles. 1972. Energetics of foraging: rate and efficiency of nectar extraction by hummingbirds. *Science* **176**:1351–1352.
- Yunick, R. P. 1984. An assessment of the irruptive status of the Boreal Chickadee in New York state. *Journal of Field Ornithology* **55**:31–37.