

CROSSBILL FORAGING BEHAVIOR, BILL STRUCTURE, AND PATTERNS OF FOOD PROFITABILITY

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ABSTRACT.— The rate at which White-winged Crossbills (*Loxia leucoptera*) and Red Crossbills (*L. curvirostra*) extract and consume seeds from conifer cones was measured in the laboratory. White-winged Crossbills were more efficient than Red Crossbills at handling small seeds, but the converse was found for large seeds. Time required to extract seeds (interseed interval) from conifer cones depended on the stage of cone ripeness and was usually greater than seed-husking time. Interseed intervals were greatest, and intake rates (mg kernel ingested/sec) lowest, when cones were closed or when they were open, but had shed most of their seed. White-winged Crossbills were more efficient than Red Crossbills when foraging on spruce (*Picea* spp.) cones and when cones were open and full of seeds. Red Crossbills were more efficient while foraging on pine (*Pinus* spp.) cones and when seeds were difficult to extract from between cone scales. The differences in foraging efficiency were related to morphological differences between the two species; White-winged Crossbills have more slender, shallower, and less powerful bills than do Red Crossbills. The differences in foraging efficiency are consistent with patterns of crossbill distribution and conifer use in the field. Differences in bill structure may be related to increasing foraging efficiency during periods of food limitation. Differences in foraging efficiency among individual crossbills were consistent with the hypothesis that variation between the efficiency of individuals should be less when birds forage on foods used during periods of greatest food limitation than when they forage on foods used during less stressful times. Received 7 Nov. 1986, accepted 24 Feb. 1987.

A common assumption in avian foraging ecology is that differences in bill structure cause differences in foraging efficiency. Most foraging studies recognize two components of foraging behavior: search time and handling time (Pyke et al. 1977). For seed-eating birds, handling time is often assumed a constant for a given seed type (e.g., Pulliam 1980), whereas search time varies as a function of prey density. Among birds that feed on conifer seeds, time spent searching for conifer cones may contribute little to overall foraging time, and time spent husking a given seed type can be assumed constant. Time spent removing seeds from cones, however, may be the most variable and time consuming component of foraging. Furthermore, time spent removing seeds from cones may require more specific adaptation than that required to husk seeds. The correlation observed between the bill size of different species of crossbills (*Loxia* spp.) and the size of cones used (Griscom 1937; Lack 1944a, b, 1947; Southern

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TABLE 1
BILL AND BODY MEASUREMENTS OF WHITE-WINGED AND RED CROSSBILLS USED IN THE
EXPERIMENTS

	White-winged Crossbill	Red Crossbill	Ratio of WWC to RC
Bill depth (mm)	8.1 ± 0.1 ^a	9.6 ± 0.3	1:1.18
length (mm)	15.1 ± 0.7	16.6 ± 0.4	1:1.10
width (mm)	7.7 ± 0.4	10.4 ± 0.2	1:1.35
Wing length (mm) ^b	88.0	95.5	1:1.09
Body mass (g) ^c	26.4 ± 1.3	35.9 ± 1.7	1:1.36
Body mass ^{1/3}	2.98	3.30	1:1.11

^a $\bar{x} \pm SD$.

^b Based on measurements (middle of range) in Griscom (1937).

^c Weight at time of capture. White-winged Crossbills were caught in August; Red Crossbills were caught in late March and in early April. Winter weights are known to be higher than summer weights for cardueline finches (Newton 1972). Thus, the relative differences in mass probably are not as great as shown here.

1945) indicates that the procurement of seeds from cones has required specific adaptation.

In northeastern North America, White-winged Crossbills (*L. leucoptera*) most frequently forage on white spruce (*Picea glauca*), black spruce (*P. mariana*), and tamarack (*Larix laricina*); whereas Red Crossbills (*L. curvirostra*) most often forage on pines (*Pinus*), particularly white pine (*P. strobus*) (Benkman, in press). In the laboratory, I measured the efficiencies of both White-winged and Red crossbills foraging on the cones of seven species of conifers. Analyses of both intra- and interspecific differences in foraging efficiency were employed to interpret differences in bill structure and conifer use in the field, and to test the hypothesis that selection for bill structure has been strongest during periods of greatest food limitation. I describe the foraging behavior of crossbills to facilitate interpretation of the comparative foraging data. Elsewhere (Benkman, in press), I use foraging data gathered in the field to demonstrate that food profitability (mg kernel ingested/sec) influences crossbill diets, movements, and abundance.

METHODS

Three White-winged Crossbills (*L. l. leucoptera*) were captured in Laurentides Reserve, Quebec, in August 1984. Eight Red Crossbills were captured in Albany, New York, in April 1982 (Table 1, Fig. 1). The Red Crossbills studied in the laboratory represent the subspecies *L. c. bendirei* (based on body mass, wing chord, and bill depth, width, and length measurements; pers. obs., Dickerman 1986). When captured, all birds were in adult plumage, and at the time of the experiments, all birds were "after-hatching-year" birds.

Captive crossbills were housed in a 4 × 3 × 2.5 m indoor aviary that was partitioned with hardware cloth (1.2 cm mesh) into two sections. White-winged Crossbills were housed in one of the sections, which was approximately one half the volume of the adjacent section

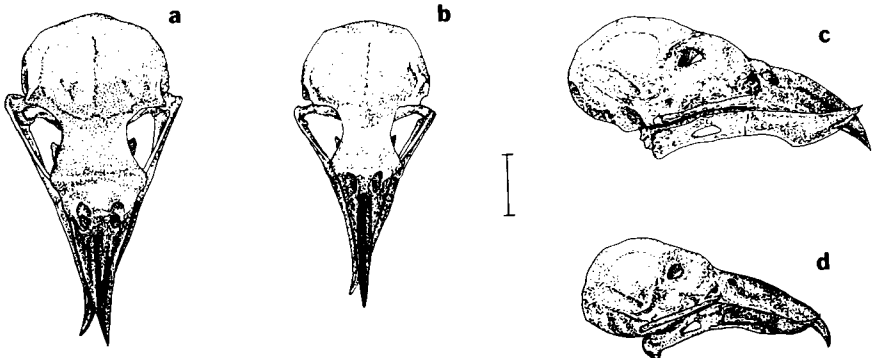


FIG. 1. Dorsal (a, b) and lateral (c, d) views of the bills and skulls of Red and White-winged Crossbills. Note the smaller and more slender bill of the White-winged Crossbill (b, d) as compared to the Red Crossbill (a, c). The bar equals 1 cm.

where Red Crossbills were housed. Crossbills were provided with fresh conifer branches every 3–7 days, with daily supplements of water, vitamins, grit, salt, limited quantities of commercial sunflower and thistle seeds, and conifer cones. Fresh cones were usually available to crossbills in the aviary. During the 6 months the experiments were conducted, most of the crossbills' diet consisted of conifer seeds, which the crossbills had to extract from cones.

Data were gathered for both species foraging on seven species of conifers (Fig. 2). The cones of these conifers represent both the size and structural variation of conifer cones found in northeastern North America. I chose cones that represented what I considered the average sizes and shapes for each species of conifer, except for pitch pine (*P. rigida*) whose cones appeared smaller than average. Every attempt was made to minimize structural variation among individual cones for each species, and the cone structure and seed number for each cone stage. Cones of the same species (usually from the same tree) and ripeness were given to both species of crossbills on the same day. Thus foraging efficiency differences between crossbills on a given conifer are largely attributable to differences between the crossbills rather than to differences among individual trees or cones.

Conifer cones vary in structure depending on ripeness: Cone scales were initially closed but eventually had wide gaps between them. After the scales spread apart (dehisce), seeds fall out. For each conifer, I selected cones with mature seed representing up to seven stages between closed cones to open cones. These cone stages, ranked in order of ripening phenology, are: (1) closed; (2) closed to a few scales opening; (3) a few to up to half of the scales opening; (4) all to nearly all scales open; (5) 14–22 seeds in open cone; (6) 7–13 seeds in open cone; and (7) 3–6 seeds in open cone. Stages not used were stage 1 for eastern hemlock (*Tsuga canadensis*), stage 2 for pitch pine, and stage 5 for jack pine (*P. banksiana*). Closed cones of each conifer species were gathered and either given to the crossbills within the next two to three days or they were stored in a refrigerator (2°C) until used. Open cones were obtained from either closed cones that were dried over a heat source or open cones that were gathered in the field. In both cases the open cones appeared similar. I created cones with progressively fewer seeds either by shaking open cones or by haphazardly removing seeds with forceps, or both. I placed seeds in empty cones of pitch pine to create its two cone stages with the fewest seeds. This was necessary because once pitch pine cones open, seeds shed rapidly from the cone.

Dry mass of seed kernels (female gametophyte and embryo) was measured with a Mettler

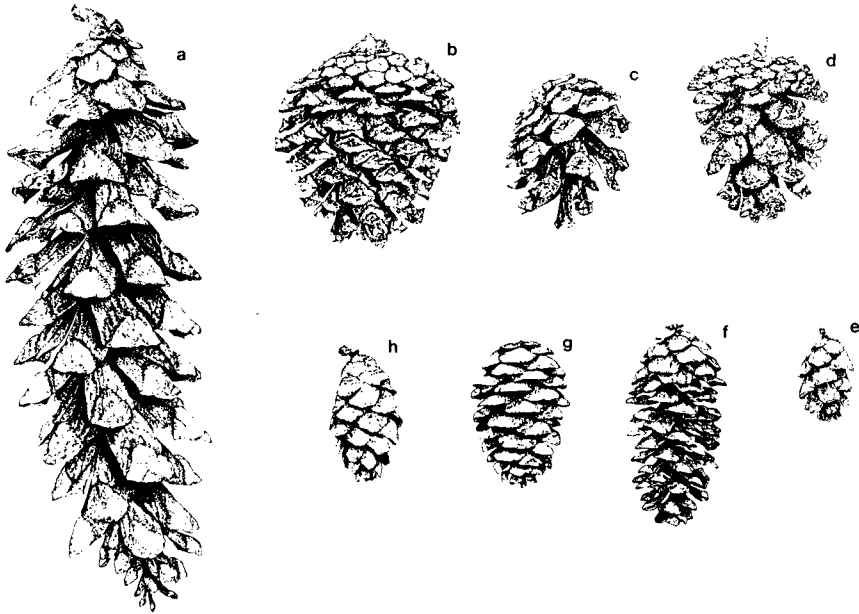


FIG. 2. Open cones of the seven species of conifers used in the experiments (a–c, e–h), plus red pine (d). Conifer cones: a = white pine, b = pitch pine, c = jack pine, d = red pine, e = eastern hemlock, f = white spruce, g = red spruce, and h = black spruce. The bar equals 1 cm.

balance. Kernels were separated from the seed coats and dried at 60–65°C for 3–8 days, and then weighed. The mean kernel mass for each species was used to compute intake rates (mg kernel ingested/sec). Extensive samples of kernel mass were not made because mass varies relatively little within and between individual trees (Smith 1970; see also Haddon 1982).

Five cone scales from the midsection of mature and air-dried cones from each conifer species were removed and weighed to the nearest 0.1 mg with a Mettler balance. The midsection of a cone has the largest scales (see Fig. 2) and the highest seed concentration (Lyons 1956, pers. obs.). Cone scale width, length, and depth were measured to the nearest 0.1 mm with dial calipers. Scale width was measured at the widest part of the cone scale, and scale length was measured from the distal end of the seed scar to the tip of the scale. Scale depth was measured at the middle of the seed scar. Although these scale measurements are an inadequate characterization of all scales on a cone, they provide relative scale sizes of the different species.

Foraging data were measured for three male White-winged Crossbills and two male and two female Red Crossbills between 3 September 1984 and 11 February 1985. Observations of crossbills foraging on each conifer species lasted up to eight days and were preceded by at least one day of foraging on cones of the respective conifer species. There was no temporal increase in foraging efficiency that might have resulted from learning.

Crossbills were recorded foraging from early morning to early afternoon. They were deprived of seed for > 12 h before the experiments. On the day of the experiments, crossbills

were given 2–20 cones, with fewer cones given when total seed mass in the cones was large, and then foraging bouts were timed. Data in related studies demonstrate that feeding rates were usually higher for birds in the presence of other crossbills; therefore, during all timed bouts the other species of crossbill was present on the other side of the hardware cloth partition and at least one other conspecific was usually present in the same section with the bird being tested. A sufficient number of cones was given so that aggressive interactions were minimal.

Crossbills were observed through a one-way glass foraging less than 2 m distant in the same aviary in which they were housed. Foraging bouts were timed from when the bird began prying apart or probing between cone scales to when it finished consuming the last seed it obtained from the cone; crossbills usually did not consume all the seeds in the cones. Most often I counted the number of seeds consumed while timing the whole bout with a stopwatch. In some cases, I recorded both seed-husking times and interseed intervals with a computer programmed as an event recorder. Seed-husking time is the time from when the seed is initially held in the bill until the kernel is swallowed. Interseed interval is the time between the end of husking one seed to the beginning of husking the next seed. Interseed interval was obtained by subtracting mean seed-husking time from mean time per seed. I used a computer to record all bouts for the first cone stage of hemlock, the second cone stage of white spruce, the first three cone stages of black spruce and all cone stages of white pine. In all other cases a stopwatch was used. For conifer species for which I only used a stopwatch to record foraging bouts, I also used the computer to measure seed-husking time during separate bouts. In some cases, when > 30 seeds were consumed per cone, I terminated my recording of the bout before the last seed was eaten. This should not affect the results because in cases where 30 or more seeds were consumed per cone there was no correlation between number of seeds obtained per second and the number of seeds consumed (three cone stages of white spruce for each crossbill species; $r = -0.03$ to 0.34 ; $P > 0.1$ in all six cases). White pine cones have large quantities of pitch covering them; therefore, I also measured time spent removing pitch from the bill and adjacent feathers (e.g., bill wiping) during and immediately following seed extraction, as part of the bout. Measures of travel and search time were not attempted in the laboratory because in the field they usually represent <10% of total foraging time (pers. obs.) and would be difficult to simulate. Foraging bouts and seed husking were timed to the nearest 1.0 and 0.1 sec, respectively. The data presented are from crossbills consuming >20,000 seeds.

For all analyses, an ANOVA was used to determine if individual crossbills differed. In cases where individuals differed, all subsequent analyses that included those cases were based on the means of each individual. In cases where individuals did not differ, analyses were based on individual samples from each bird. To determine if interseed intervals and kernel intake rates differed both between crossbills and for each crossbill on the different conifers, an ANOVA was employed with cone stage as a covariate.

RESULTS

Foraging Behavior

When feeding, crossbills usually orient themselves so that their lower mandible is directed parallel to the long axis of the cone scales (Fig. 3). The lower mandible curves slightly laterally, either to the left or right, whereas the upper mandible is directed more straightforward (Fig. 1). The tip of the lower mandible is placed against a cone scale (I call this scale the distal scale because it is toward the distal end of the cone relative to

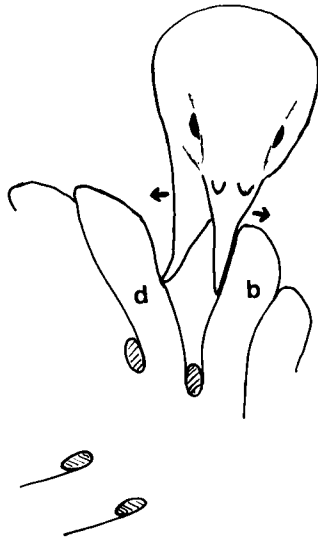


FIG. 3. A dorsal view of the head and mandibles of a Red Crossbill separating conifer cone scales. A median longitudinal section of the cone is illustrated. Note that the upper mandible rests parallel with the basal cone scale (b) and that only the tip of the lower mandible is positioned on the distal cone scale (d). Arrows point in the approximate directions in which forces are exerted by the mandibles. Seeds (4) are hatched, and the cone axis runs nearly perpendicularly to the "basal scale" in the figure. See text for further description.

the scale against which the upper mandible pushes [Fig. 3]). To create a gap between cone scales, the decurved and pointed upper mandible slides between the scales in a biting motion, often tearing tightly closed scales. After an initial gap is created, the jaws spread sideways (i.e., the lower jaw is abducted laterally in the direction that its tip points) so that the lateral surface of the upper mandible pushes the more basal scale away from the cone axis while the lower mandible presses against the distal scale (Fig. 3). Lateral abduction of the lower jaw takes place while the bill is slightly open (gaped). Lateral spread of the jaws widens and deepens the gap between the scales. The upper mandible again is driven deeper between the scale gap, and then the mandibles further separate the adjacent cone scales with a lateral abducting motion. The lower mandible pivots on the distal cone scale, whereas the upper mandible remains parallel with the more basal scale against which it pushes (Fig. 3). The upper mandible is relatively more active than the lower mandible, which often remains at the same site on the distal scale if the upper mandible has not penetrated very far. The tip of the laterally curved lower mandible provides a brace against the distal scale, providing a stable foundation for movement of

TABLE 2
SEED KERNEL MASSES AND HUSKING TIMES FOR WHITE-WINGED AND RED CROSSBILLS

	Kernel mass (mg)	Seed-husking time (sec)		<i>P</i> ^e
		White-winged Crossbill	Red Crossbill	
White spruce	1.6 ± 0.05 ^a (26) ^b	1.1 ± 0.05 ^c (1089) ^d	2.2 ± 0.11 (873)	<0.05
Black spruce	1.6 ± 0.05 (30)	0.9 ± 0.03 (401)	1.9 ± 0.06 (567)	<0.005
Tamarack	1.6 ± 0.05 (30)	1.2 ± 0.09 (212)	1.7 ± 0.07 (272)	NS
Red spruce	1.7 ± 0.06 (30)	0.9 ± 0.08 (58)	2.4 ± 0.09 (68)	<0.05
E. hemlock	2.1 ± 0.06 (20)	2.5 ± 0.15 (245)	1.6 ± 0.09 (184)	<0.05
Pitch pine	2.6 ± 0.12 (20)	2.0 ± 0.12 (55)	1.8 ± 0.04 (97)	NS
Jack pine	2.9 ± 0.08 (20)	1.6 ± 0.29 (19)	1.7 ± 0.06 (61)	NS
Red pine	5.9 ± 0.16 (30)	5.0 ± 0.33 (20)	2.6 ± 0.12 (156)	<0.005
White pine	13.7 ± 0.33 (19)	8.4 ± 0.40 (337)	2.6 ± 0.08 (587)	<0.005

^a $\bar{x} \pm SE$.

^b Sample sizes for kernel mass are number of kernels.

^c Seed-husking times are based on the means for each of three White-winged Crossbills and four Red Crossbills.

^d Because there are significant differences among individuals for at least one species of crossbill on all conifers but red pine (ANOVA, $P < 0.05$), pair-wise comparisons are based on the means of each individual (i.e., *N* equals 3 for White-winged Crossbills and 4 for Red Crossbills). The *N* presented is the total number of seeds husked.

^e Probability of a species difference using ANOVA.

the upper mandible. The consistency with which crossbills place their lower mandible against the distal scale has been noted previously (e.g., Tordoff 1954, Newton 1967) and is due to the different functions each mandible performs.

When the seed is exposed, the tongue is protruded and its spoon-shaped tip carries the loose seed to the bill to be husked. With thin-scaled cones the upper mandible is often used to hook the seed from between the scales, whereas on thick-scaled (or dry) cones, lateral abducting forces alone are usually sufficient to expose the seeds.

Crossbill handling behavior consists of two components: (1) extraction of seeds from cones (interseed interval or ISI) and (2) seed husking. The two components are analyzed separately below as ISI is mainly affected by cone structure, which varies with cone stage, whereas seed-husking time is influenced mainly by seed structure and size, which varies little with cone stage.

Seed Husking

White-winged Crossbills husked the smaller seeds of the spruces more rapidly than did Red Crossbills, whereas the converse was true on the larger seeds of the pines and hemlock (Table 2). Seed profitability, *Y* (mg kernel ingested/sec), remained constant for all seed sizes (*X*) for White-winged Crossbills ($Y = 1.52 - 0.002X$, $df = 7$, $r^2 = -0.0004$, $P = 0.96$),

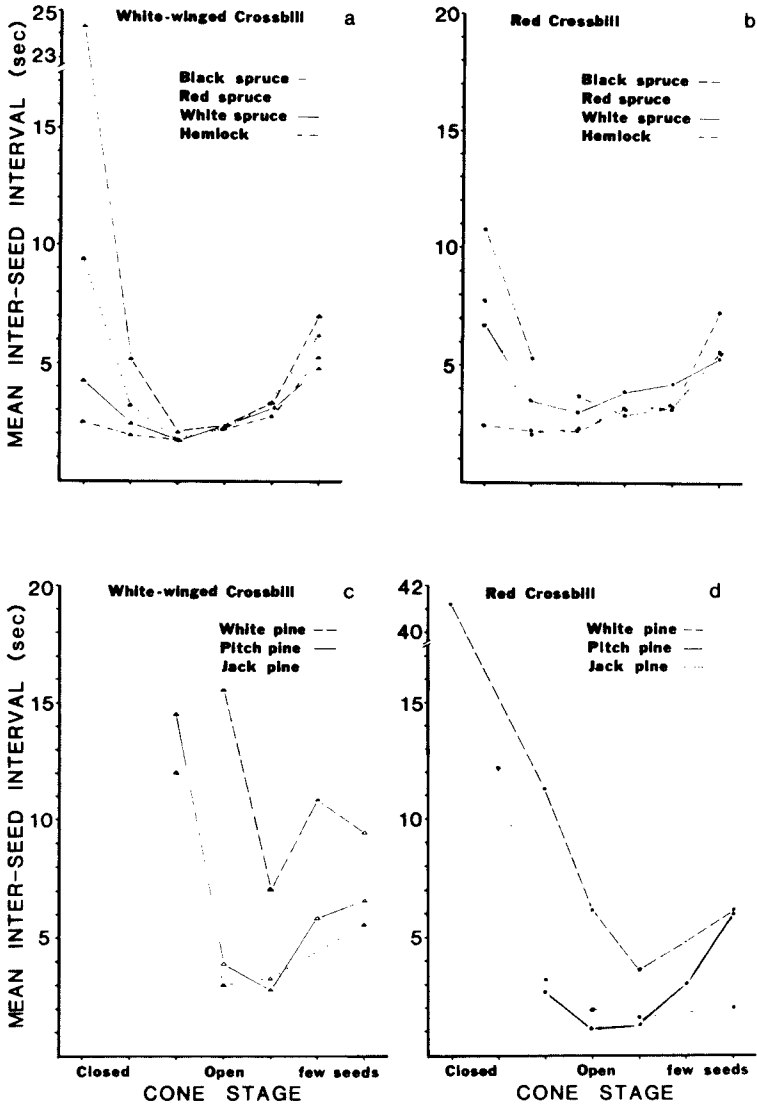


FIG. 4. Interseed intervals for crossbills foraging on different cone stages. (a) White-winged Crossbills foraging on hemlock and spruce. (b) Red Crossbills foraging on hemlock and spruce. (c) White-winged Crossbills foraging on pine. (d) Red Crossbills foraging on pine. Samples sizes are given in Figs. 5 and 6.

TABLE 3
CHARACTERISTICS OF SCALES FROM THE MIDDLE SECTION OF THE CONES OF EACH CONIFER SPECIES USED IN THE FORAGING EXPERIMENTS (CONES WERE MATURE, OPEN AND AIR-DRIED)^a

	Scale size (mm)			Mass (mg)
	Width ^b	Length ^c	Depth ^d	
E. hemlock	5.9 ± 0.21 ^e	4.8 ± 0.25	0.8 ± 0.04	10.3 ± 0.32
White spruce	9.0 ± 0.23	7.0 ± 0.68	0.8 ± 0.05	14.6 ± 1.68
Red spruce	11.2 ± 0.16	8.8 ± 0.39	1.1 ± 0.04	37.5 ± 0.56
Black spruce	7.6 ± 0.39	7.6 ± 0.18	1.5 ± 0.07	36.8 ± 3.41
Jack pine	7.8 ± 0.47	15.1 ± 0.74	0.9 ± 0.04	108.8 ± 13.52
Pitch pine	12.2 ± 0.45	13.5 ± 0.20	1.5 ± 0.23	126.5 ± 8.45
White pine	15.1 ± 0.21	22.4 ± 0.16	2.3 ± 0.33	182.6 ± 5.02

^a N = 5 for all measurements.

^b Greatest width of scale.

^c Distance from distal end of seed to cone scale tip.

^d Depth of scale at middle of seed scar on scale.

^e Mean ± SE.

but increased with seed size for Red Crossbills ($Y = 0.34 + 0.36X$, $df = 7$, $r^2 = 0.98$, $P < 0.0001$).

Interseed Interval

Hemlock and spruce.—ISI's were largest and their differences among hemlock and spruce greatest when the cones were closed or when few seeds remained in the cones (Fig. 4A, B). When cones of hemlock and the three species of spruce were open and filled with seeds, the ISI's for White-winged Crossbills were very similar (Fig. 4A). As cone scale size increased, the effect on ISI of cones being closed increased. Cone scale mass and depth increased in the following progression: hemlock, white spruce, red spruce (*P. rubens*), and black spruce (Table 3, Fig. 2). For White-winged Crossbills foraging on the first cone stage of hemlock and the three spruces (N = 4), ISI was most highly correlated with scale depth ($r = 0.99$), then mass ($r = 0.76$), length ($r = 0.48$), and width ($r = 0.03$). The relative importance of scale thickness in impeding White-winged Crossbills can be seen by comparing red spruce to black spruce. Red spruce has wider and longer cone scales than does black spruce. Black spruce seeds, however, were generally less accessible than those of red spruce, in large part because black spruce has thicker cone scales and was thus more resistant to forces exerted by crossbills.

The effect of cone stage, with conifer species the covariate, was significant for both White-winged Crossbills ($F = 58.1$, $df = 5,62$, $P < 0.0001$) and Red Crossbills ($F = 50.2$, $df = 5,85$, $P < 0.0001$) (Fig. 4A, B). The

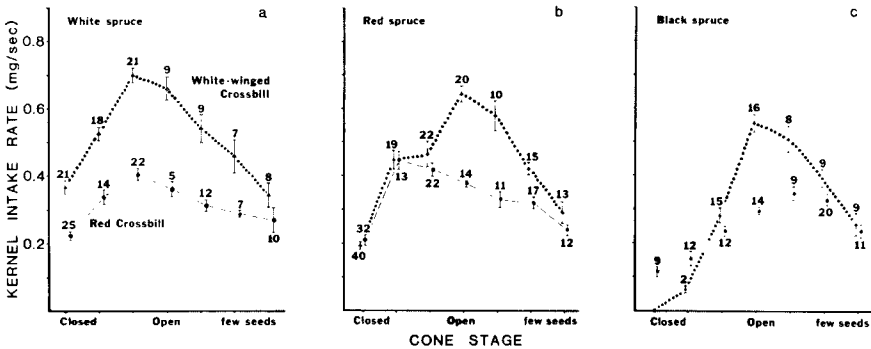


FIG. 5. Mean (\pm SE) kernel intake rates of White-winged Crossbills (triangles connected by dotted lines) and Red Crossbills (closed circles connected by dashed lines) foraging on cones of three species of spruce. Cone ripening progresses to the right. Sample sizes are the number of cones; total number of seeds was >3000 for each crossbill species.

one cone stage for which White-winged Crossbills had lower ISI's than Red Crossbills was when cones were open and nearly full of seeds.

Pine.—Red Crossbills extracted seeds more rapidly than did White-winged Crossbills from the cones of jack pine ($F = 7.7$, $df = 1,25$, $P = 0.01$), pitch pine ($F = 12.6$, $df = 1,27$, $P < 0.002$), and white pine ($F = 18.1$, $df = 1,16$, $P < 0.001$), and for each pine species Red Crossbills extracted seeds from one to three earlier cone stages than did White-winged Crossbills (Fig. 4C, D). For both crossbill species, the differences in ISI was greater among pines ($F = 8.1$, $df = 2,31$, $P = 0.002$ for White-winged Crossbills; $F = 12.1$, $df = 2,46$, $P < 0.0001$ for Red Crossbills) than among hemlock and spruces ($F = 2.0$, $df = 3,64$, $P = 0.12$ for White-winged Crossbills; $F = 2.3$, $df = 3,87$, $P = 0.08$ for Red Crossbills). This was apparently related to the greater absolute differences in cone scale structure and mass among pines than among hemlock and spruces (Table 3, Fig. 2). For both crossbill species, ISI was greater on white pine than on either jack pine or pitch pine; however, the ISI for the latter two pines was similar for both White-winged Crossbills ($F = 0.03$, $df = 1,24$, $P = 0.86$) and Red Crossbills ($F = 0.14$, $df = 1,32$, $P = 0.71$). The thicker and longer cone scales of white pine (Table 3, Fig. 2) probably caused the higher ISI's. These data imply that (1) White-winged Crossbills were impeded more by the relatively long and massive pine cone scales than were Red Crossbills, and (2) the bill of the Red Crossbill, as compared to that of the White-winged Crossbill, appeared to be particularly well adapted for extracting seeds that were relatively inaccessible.

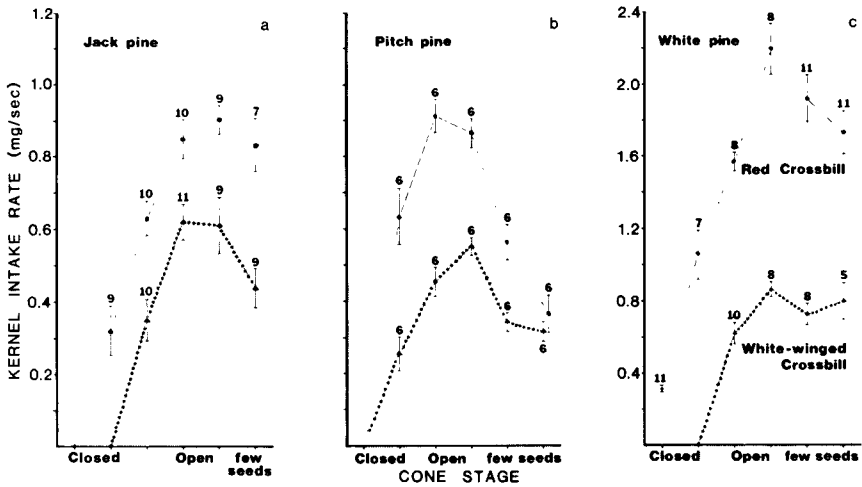


FIG. 6. Mean (\pm SE) kernel intake rates of White-winged and Red crossbills foraging on cones of three species of pines. Symbols as in Fig. 5. Total number of seeds was >1400 for White-winged Crossbills and >2600 for Red Crossbills.

Intake Rates

In both species profitability increased as cones opened, then declined as seeds were shed from the cones of all seven conifer species (Figs. 5 and 6) as a result of variation in seed accessibility (Fig. 4). Because ISI was both more variable and usually greater at any given cone stage than seed-husking time, ISI contributed relatively more to patterns of profitability. On most conifer species, individuals within each crossbill species did not differ significantly in intake rates (Table 4).

Hemlock and spruce.—Red Crossbills had slightly higher intake rates on hemlock than did White-winged Crossbills ($F = 4.9$, $df = 1,39$, $P = 0.03$). On average, White-winged Crossbills had slightly lower intake rates, and Red Crossbills had slightly higher intake rates on hemlock than their respective intake rates on white spruce (see Fig. 5A). White-winged Crossbills were more efficient than Red Crossbills on white spruce ($F = 41.5$, $df = 1,42$, $P < 0.0001$), red spruce ($F = 55.4$, $df = 1,246$, $P < 0.0001$), and black spruce ($F = 9.7$, $df = 1,135$, $P < 0.005$).

On closed white spruce cones, White-winged Crossbills foraged more efficiently than did Red Crossbills (Fig. 5A), but the foraging efficiency of White-winged Crossbills as compared to that for Red Crossbills was similar on the first and second cone stages of red spruce (Fig. 5B), and it was

TABLE 4
ANOVA FOR DIFFERENCES AMONG THREE WHITE-WINGED CROSSBILLS AND FOUR RED
CROSSBILLS WHEN FORAGING ON SEVEN SPECIES OF CONIFERS (CONE STAGE WAS A
COVARIATE)

	df	F-ratio	P
White-winged Crossbill			
Eastern hemlock	2,146	2.6	0.076
White spruce	2,89	0.9	0.404
Red spruce	2,139	1.4	0.244
Black spruce	2,53	0.1	0.932
Jack pine	2,35	7.2	0.002
Pitch pine	2,26	0.8	0.442
White pine	1,32	0.4	0.516
Red Crossbill			
Eastern hemlock	3,146	19.6	0.0001
White spruce	3,90	6.9	0.0003
Red spruce	3,135	0.9	0.435
Black spruce	3,82	1.4	0.258
Jack pine	3,41	0.6	0.628
Pitch pine	2,26	2.1	0.138
White pine	3,36	1.6	0.202

less on the first two cone stages of black spruce (White-winged Crossbills could not extract seed from the first cone stage) (Fig. 5C). Cone scale depth and difficulty of extracting seeds from closed cones increased from white to red to black spruce.

White-winged Crossbills were more efficient than Red Crossbills when spruce cones were open and full of seeds (Figs. 5A–C), because White-winged Crossbills required less time to handle spruce seed (Table 2) and secure them from the cones (Fig. 4). White-winged Crossbill and Red Crossbill intake rates converged when few seeds remained in spruce cones. The few remaining seeds were difficult to extract because they were usually secured between the most closed cone scales.

Pine. — Red Crossbills had higher intake rates than White-winged Crossbills did on jack pine ($F = 14.1$, $df = 1,29$, $P < 0.001$), pitch pine ($F = 96.5$, $df = 1,50$, $P < 0.0001$), and white pine ($F = 276.2$, $df = 1,74$, $P < 0.0001$) (Figs. 6A–C). Neither crossbill species extracted seeds from closed jack and pitch pine cones; crossbills require a gap between the scales into which they slide their bills to separate the scales. The similarity between the intake rates of White-winged and Red crossbills on the last two cone stages of pitch pine, in contrast to those on the other pines, is probably

an artifact of my methods for creating these two cone stages for pitch pine (see Methods). Red Crossbills removed seeds from closed white pine by shredding the relatively soft cone scales. Red Crossbills often removed pieces of white pine seed kernel from the shredded cones, rather than the whole seed. As the complete kernel was not always removed, the intake rate was over-estimated for closed white pine cones; for estimates of profitability I assumed whole kernels were consumed. Red Crossbills extracted seeds from an earlier cone stage of jack pine than pitch pine because it was apparently easier to separate the thinner and less massive cone scales of jack pine (Table 3). The second cone stage of white pine was cones with scales just separating; Red Crossbills easily separated the cone scales apart to expose the underlying seeds, but White-winged Crossbills could not.

White-winged Crossbills had higher maximum intake rates when foraging on spruce than on jack and pitch pines, but White-winged Crossbills had their highest intake rates on white pine. However, although all 3 White-winged Crossbills foraged on all other conifers, only 2 of the 3 foraged on white pine cones. The pitch covering the outer surface of the cone apparently deterred the one White-winged Crossbill from foraging. Furthermore, the two individuals that did forage on white pines dropped small pieces of seed kernel that were broken off large kernels. This resulted in lower intake rates for White-winged Crossbills on white pine than is indicated in Figure 6C.

DISCUSSION

Foraging behavior and morphology.—It has long been assumed that small-billed crossbills forage relatively more efficiently on small conifer cones and that large-billed crossbills forage relatively more efficiently on large conifer cones (Griscom 1937; Lack 1944a, b; Southern 1945; Newton 1972). That large-billed crossbills are more efficient on large cones than small-billed crossbills is supported by Niethammer's (1937, cited in Lack 1944b and Newton 1967) observations of the largest billed crossbill, the Parrot Crossbill (*L. pytyopsittacus*), foraging more efficiently on pine cones than the Red Crossbill. My data support these contentions and observations. White-winged Crossbills have smaller bills than Red Crossbills in terms of depth, length, and width (Table 1, Fig. 1). These morphological differences result in differences in foraging efficiency.

Bill depth influences biting force (Bock 1966). Deep bills are usually thought to be critical for husking hard seeds (Grant 1981). Red Crossbills have deeper bills (Fig. 1) and, in fact, husk larger, harder seeds more efficiently than do White-winged Crossbills. The width of the palatine grooves of the horny palate is also essential for securing seeds in the bill

while seeds are husked (Ziswiler 1965, Newton 1967). The White-winged Crossbill's slender upper mandible has relatively narrow palatine grooves (pers. obs.), which likely is one reason that White-winged Crossbills husk small seeds more efficiently than do Red Crossbills. As seed size increases, White-winged Crossbills have increasing difficulty mandibulating seeds and cracking seed coats; therefore, seed-husking time increases. The wider palatine grooves and deeper bills enable Red Crossbills to crack and remove seed coats from large seeds efficiently.

White-winged Crossbills are most efficient at extracting seeds from between thin and relatively short cone scales, especially when the cones are at least partially open. The slender upper mandible of the White-winged Crossbill is well suited both for sliding rapidly between and for hooking seeds free from between the thin scales of spruce and tamarack cones. White-winged Crossbills rely less on powerful lateral abduction of their mandibles to separate adjacent cone scales to expose seeds than do Red Crossbills. However, White-winged Crossbills are affected more by differences in cone structure than are Red Crossbills. As cone scale mass increases, from hemlock to white pine, the range of cone stages for which White-winged Crossbills have high intake rates diminishes.

The deeper and wider bill of the Red Crossbill enables them to harvest seeds from a wide range of cone structures, including seeds secured between thick cone scales. Greater depth throughout most of the bill's length should enable Red Crossbills to exert a more powerful bite at the tip of their mandibles than can White-winged Crossbills. A powerful bite is essential to creating gaps between cone scales without openings; gaps between the scales are necessary for the mandibles to be inserted between the scales. The deeper and wider bill of the Red Crossbill enables it to separate the closed cone scales of pines and black spruce more efficiently than White-winged Crossbills.

As the length and thickness of cone scales increase, greater bill strength and probing ability are required to secure seeds. A deep and wide bill provides power, but greater probing capacity requires either a long bill or a protrusible tongue. Red Crossbills have only slightly longer bills than do White-winged Crossbills, and, compared to differences in other bill dimensions, Red Crossbills have relatively short bills that are proportional to the cube of their body mass (Table 1). Red Crossbills, and probably other large-billed crossbills such as the Parrot Crossbill, have increased probing ability by evolving relatively long tongues. The ratio of tongue length (tip of fleshy part of tongue to posterior tip of basihyal for two dried tongues of each species) to bill length is 1.00 and 0.67 for Red and White-winged crossbills, respectively. (See Benkman 1985 for more detailed discussion.)

Conifer use, distribution, and bill structure.—The relative intake rates on the different conifers underlie the differences in distribution and conifer use between the two species of crossbills. In nature, crossbills forage mainly on the most profitable conifer species (Benkman, in press). White-winged Crossbills occur primarily in habitats dominated by spruce, and when in mixed conifer forests, they rarely forage on pines. Red Crossbills are found most often in habitats characterized by pines and, when in mixed conifer forests, they forage mostly on pine.

Bill structure is best suited for using efficiently those foods available during periods of greatest food limitation. For example, studies on Galápagos finches have shown that natural selection on bill structure is greatest during periods of extreme food limitation (Boag and Grant 1981, Price et al. 1984), and that bill structure is most strongly related to diets during the periods of food limitation (Grant 1986). Diet overlap between crossbills is often 100% in late summer when both species forage on white spruce, food abundance is high, and increasing and when crossbills nest. Diet overlap declines in early autumn, and it is virtually nonexistent by late winter (Benkman, in press).

Black spruce is the one conifer in habitats occupied by White-winged Crossbills that consistently holds seeds in its cones during winter (see Fowells 1965). Most of the seeds, however, are in closed cones and are inaccessible to White-winged Crossbills (Fig. 5C). Although a more robust bill and more massive jaw musculature, as found in the Red Crossbill, would improve foraging efficiency on closed black spruce cones, intake rates would still be inadequate to meet energy demands; to survive in winter a White-winged Crossbill requires an estimated minimum intake rate of 0.2 mg/sec (Benkman, in press; compare this estimate to the rates in Fig. 5C). This would be especially true if body mass was increased to provide more power. Instead, White-winged Crossbills have apparently evolved to harvest the more accessible, but less abundant seeds in the slightly open to open black spruce cones. The slender bill is particularly efficient at sliding into the narrow gaps between black spruce cone scales (Fig. 5C; note also the narrow gaps in the open black spruce cone in Fig. 2). Red Crossbills, on the other hand, rely on the few remaining well-secured seeds in the cones of pines such as those of red pine (*P. resinosa*; see Fig. 2). The powerful bill of Red Crossbills is required to efficiently extract these seeds. For example, in January 1985 in Algonquin Provincial Park, Ontario, Red Crossbills had an intake rate on red pine ($\bar{x} = 0.73 \pm 0.06$ mg/sec [SE], $N = 66$ bouts) that was 10 times greater than that for White-winged Crossbills ($\bar{x} = 0.07 \pm 0.03$ mg/sec, $N = 8$ bouts).

A corollary to this argument is that, because natural selection on foraging efficiency is greatest in late winter when White-winged Crossbills forage

on black spruce and Red Crossbills forage on red pine, the variation in foraging efficiency among individuals foraging on these conifers should be less than on other conifers. There are no differences among individual White-winged Crossbills when foraging on black spruce or among Red Crossbills foraging on jack pine (Table 4); jack pine has the most similar cone to red pine (Fig. 2). Individuals within both species of crossbills, however, do differ when foraging on some of the conifers they use infrequently or during periods of high food abundance, and that differ substantially in structure from the cones used in late winter (e.g., jack pine for White-winged Crossbills, hemlock and white spruce for Red Crossbills). Although the number of individual birds studied was quite small, the pattern of individual variation is provocative. A careful laboratory study on many individuals combined with detailed field work could provide a method to indirectly investigate patterns of selection even when individuals cannot be followed over long periods of time in the field.

Extrapolation from laboratory to field. — The different cone stages given to crossbills represent most of the range of conifer cone stages that crossbills may forage on in northeastern North America. The one exception is during late June, July, and August, when crossbills forage on immature seeds in closed cones of red and white spruce and hemlock (Benkman, in press). In these cases, seed accessibilities differ little from those on closed cones in late August and September (pers. obs.), when the cones I used were gathered, although seed mass (and nutritive and caloric value) is less (e.g., Dickmann and Kozlowski 1969).

Other than for the closed-cone stages, specific dates cannot be assigned to most cone stages because ripening phenologies and seed release vary annually (Cayford 1964, Graber 1971), and even geographically (Benkman, in press). Furthermore, cone-crop size can vary by orders of magnitude from year to year (Fowells 1965), and during years of good cone crops seed profitability is usually greater and remains higher for longer periods than during poor cone crop years (Benkman, in press). Because of this variation, quantitative predictions of conifer seed profitability are tenuous.

ACKNOWLEDGMENTS

R. Pulliam provided materials and space to conduct this research. NSF Grants DEB-13017 and DEB-8206936 to Dr. Pulliam and grants from the Frank M. Chapman Memorial Fund and a NSF Postdoctoral Research Fellowship in Environmental Biology to the author provided financial support. K. Able, K. Bildstein, P. Boag, W. Bock, J. Brown, C. del Rio, J. Gilliam, K. Johnson, D. Levey, S. Mountainspring, R. Pulliam, and L. Wolf, and two anonymous reviewers, read and made constructive comments on several versions of this

manuscript. Many people cared for my crossbills while I was in the field. These people include: J. Beacham, C. Staicer, B. Holberton, R. Bakerian, S. Terrill, K. Johnson, S. Weissmann, C. Frank, U. Grafe, and D. Tieman. C. Staicer was especially helpful during early stages of my experiments. I am most grateful to all those mentioned above and to the patient and cooperative crossbills.

LITERATURE CITED

- BENKMAN, C. W. 1985. The foraging ecology of crossbills in eastern North America. Ph.D. diss., State Univ. New York at Albany, Albany, New York.
- . Food profitability and the foraging ecology of crossbills. Ecol. Monogr. In press.
- BOAG, P. T. AND P. R. GRANT. 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galápagos. Science 214:82-85.
- BOCK, W. J. 1966. An approach to the functional analysis of bill shape. Auk 83:10-51.
- CAYFORD, J. H. 1964. Red pine seedfall in southeastern Manitoba. Forest. Chron. 40:78-85.
- DICKERMAN, R. W. 1986. A review of the Red Crossbill in New York state. Part 2. Identification of specimens from New York. Kingbird 36:127-134.
- DICKMANN, D. I. AND T. T. KOZLOWSKI. 1969. Seasonal changes in the macro- and micro-nutrient composition of ovulate strobili and seeds of *Pinus resinosa*. Can. J. Bot. 47: 1547-1554.
- FOWELLS, H. A. 1965. Silvics of forest trees in the United States. U.S.D.A. Agric. Handb. 271.
- GRABER, R. E. 1971. Natural seed fall in white pine (*Pinus strobus* L.) stands of varying density. U.S.D.A. For. Serv. Res. Note NE-119.
- GRANT, P. R. 1981. The feeding of Darwin's finches on *Tribulus cistoides* (L.) seeds. Anim. Behav. 29:785-793.
- . 1986. Ecology and evolution of Darwin's finches. Princeton University Press, Princeton, New Jersey.
- GRISCOM, L. 1937. A monographic study of the Red Crossbill. Proc. Boston Soc. Nat. Hist. 41:77-210.
- HADDON, B. D. 1982. A list of seed in the Canadian Forestry Service seed bank. Information Report PI-X-13. Canadian Forestry Service, Environment Canada, Chalk River, Ontario.
- LACK, D. 1944a. Ecological aspects of species formation in passerine birds. Ibis 86:260-286.
- . 1944b. Correlation between beak and food in the crossbill (*L. curvirostra*). Ibis 86:552-553.
- . 1947. Darwin's finches. Cambridge Univ. Press, Cambridge, England.
- LYONS, L. A. 1956. The seed production capacity and efficiency of red pine cones (*Pinus resinosa* Ait.). Can. J. Bot. 34:27-36.
- NEWTON, I. 1967. The adaptive radiation and feeding ecology of some British finches. Ibis 109:33-98.
- . 1972. Finches. Collins, London, England.
- PRICE, T. D., P. R. GRANT, H. L. GIBBS, AND P. T. BOAG. 1984. Recurrent patterns of natural selection in a population of Darwin's finches. Nature 309:787-789.
- PULLIAM, H. R. 1980. Do Chipping Sparrows forage optimally? Ardea 68:75-82.
- PYKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. 52:137-154.

- SMITH, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecol. Monogr. 40:349–371.
- SOUTHERN, H. N. 1945. Correlation between beak and food in the crossbills. Ibis 87:287.
- TORDOFF, H. B. 1954. Social organization and behavior in a flock of captive, nonbreeding Red Crossbills. Condor 56:346–358.
- ZISWILER, V. 1965. Zur Kenntnis des Samenöffnens und der Struktur des hörnernen Gaumens bei körnerfressenden Oscines. J. Ornithol. 106:1–48.

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