SEED HANDLING ABILITY, BILL STRUCTURE, AND THE COST OF SPECIALIZATION FOR CROSSBILLS

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ABSTRACT.—Crossbills (*Loxia*) are specialized to extract and handle seeds from conifer cones. I evaluated the ability of crossbills to handle nonconifer seeds by comparing seed handling efficiencies with other cardueline finches. For all seed sizes, crossbills required seed encounter rates or seed abundances 2–3 times greater than other species to meet their daily energy requirements. Consequently, crossbills may suffer high mortality during conifer cone failures. Crossbills are inefficient at meeting their energy demands on nonconifer seeds because of their narrow mandibles, lowered horny palate, and large body size. The narrow mandibles enable crossbills to efficiently extract seeds from conifer cones and the lowered palate enables them to handle small seeds rapidly. Crossbills have evolved larger bills, and associated musculature and body mass, to provide the power necessary to separate cone scales. Some of the increase in body mass, however, may counterbalance the large bills to improve predator evasion. *Received 27 October 1987, accepted 17 June 1988.*

THE cardueline finches (subfamily Carduelinae) are highly specialized seedeating birds (Newton 1967, 1972). Most consume seeds, mainly from dicotyledonous plants, throughout the year (Martin et al. 1951; Newton 1967, 1972; Austin 1968). The crossbills (*Loxia*) eat conifer seeds to the near exclusion of other seeds (Newton 1967, 1972; Austin 1968; Nethersole-Thompson 1975; Benkman 1987a).

Crossbills are clearly more efficient at utilizing seeds in closed conifer cones than other cardueline finches (Newton 1967, 1972). Many characteristics of the crossbill's feeding apparatus are adapted for exploiting conifer seeds (Benkman 1987b). Experimental ablation of the crossed portion of the crossbill's mandibles demonstrated that this portion was essential for crossbills to extract seeds from closed conifer cones (Benkman 1988). Further, no carduelines other than crossbills have been found to extract seed from tightly closed conifer cones (Smith and Balda 1979; pers. obs.).

Crossbills may be limited to foraging on conifer seed because they are relatively inefficient at handling other seed types (e.g. Roberts 1936). The reduced efficiency of crossbills is of particular interest because about every 3–4 years conifer seed crops fail over much of the boreal forests of North America (Bock and Lepthien

1976) and Eurasia (Newton 1970, 1972), and at this time many crossbills feed on nonconifer seed (see Newton 1970, 1972). These periods of conifer seed shortage often coincide with failures of other boreal tree seed crops (Bock and Lepthien 1976). Thus, competition for available seed among cardueline finches would be intensified.

I compared the seed-handling rates, on graded seed sizes, of 3 noncrossbill species of carduelines with the 2 species of crossbills in North America. These data are used to determine the relative seed handling abilities of crossbills in comparison to other carduelines and those features that make crossbills inefficient when feeding on nonconifer seeds. The data on noncrossbill carduelines are compared to those on emberizine sparrows, elsewhere (Benkman and Pulliam 1988).

METHODS

Red Crossbills (*L. curvirostra*), American Goldfinches (*Carduelis tristis*), House Finches (*Carpodacus mexicanus*), and Evening Grosbeaks (*Coccothraustes vespertinus*) were captured in Albany Co., New York. White-winged Crossbills (*L. leucoptera*), were caught in Laurentides Reserve, Quebec. Several days prior to and during the experiments, all species were fed commercial sunflower (*Helianthus* spp.) and niger thistle (*Guizotia abyssinica*) seeds, and vitamin-enriched water. Foraging experiments were conducted on the crossbills after a minimum of 5 months in captivity. The other species were completed within 6 days of capture. Even

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TABLE 1. Body masses and bill dimensions of the 5 species of cardueline finches used in the experiments. Sample size for each bill measurement is 10 birds.

	Body mass (g) $\bar{x}$	Bill size (mm)		
		Depth $\bar{x} \pm$ SD	Width $\bar{x} \pm$ SD	Length $\bar{x} \pm$ SD
Species				
A. Goldfinch	13.0	6.4 ± 0.1	5.0 ± 0.1	8.1 ± 0.3
House Finch	21.0	8.2 ± 0.2	7.2 ± 0.2	8.6 ± 0.4
WW Crossbill	26.4	7.8 ± 0.3	5.6 ± 0.3	13.8 ± 0.6
Red Crossbill	35.9	9.3 ± 0.2	7.4 ± 0.2	15.3 ± 1.0
E. Grosbeak	55.0	14.7 ± 0.5	13.8 ± 0.5	15.4 ± 0.7

though the crossbills were housed for longer periods than the other species, they appeared to remain in excellent physical condition.

I used 8 size classes of commercial sunflower and niger thistle seeds. Average individual seed wet weights ranged from 2.3–117.5 mg. Sunflower and thistle were chosen because they are composites (Compositae), and are an important natural food for many cardueines (Martin et al. 1951; Newton 1967, 1972; Austin 1968). All 5 species readily ate these seeds and visited feeders, though crossbills do so only infrequently. The shape of thistle and sunflower seeds differs from that of conifers, but the relationships between mass of seed covering (y; mg) and kernel mass (x; mg) were nearly identical for the seeds used in the experiments ($y = 0.46x^{1.01}$, $r^2 = 0.94$, $n = 8$, $P <$ 0.01) and conifer seeds in the Northeast ($y = 0.47x^{1.01}$, $r^2 = 0.93$, $n = 10$, $P < 0.01$). Seed size classes were initially sorted with a sieve. Then seeds most similar in size and shape within size classes and most similar in shape among size classes were individually selected and examined for cracks in the seed hull. I used only seeds with undamaged and uncracked hulls. Seeds were weighed in groups of ten to the nearest 10 mg for sunflower seeds and 0.1 mg for thistle seeds, and reexamined for consistency in size and shape. Variance in seed shape and quality was minimized so that seed handling differences would reflect seed size differences. Two additional size classes of sunflower seeds were given to the goldfinches and White-winged Crossbills to provide finer testing of their seed handling abilities.

During the tests, 10 preweighed seeds of the same size were placed in a partially covered plastic tray attached to a perch 40 cm above the floor of a (60 cm)³ wooden chamber. Because cardueines normally forage within vegetation above the ground (Newton 1967, 1972), the birds were required to handle seeds while perched. The food tray was designed so any kernel (embryo and endosperm) dropped by the birds fell to the floor where recovery was prevented by a screen. A second chamber was connected by a sliding door at the level of the perch. Birds were held overnight without food for >16 h prior to the seed-handling experiments. Each chamber had one perch and a dish

of water. When I was ready to record handling times, the lights were turned off, the door separating the chambers was slid open, and then the lights were turned on. Usually the bird would hop onto the perch in the observation chamber to feed. After feeding, the light on the side the bird was on was turned off, and the bird returned to the other chamber. The door was closed. All seed remains were removed with forceps and weighed.

Initially seed hulls and kernel remains were weighed separately, but it soon became evident that seed hulls were not consumed in any measurable amount. I subtracted total seed remains from initial weight to obtain the average weight of kernel consumed per seed. Wet weights were used because dry weights were over 97% of wet weight. Variation in seed size classes between finch species resulted from seeds selectively consumed. This was especially true for seeds that were relatively difficult to handle.

Handling time began when a seed was picked up and continued until no part of the seed was being mandibulated. Time spent handling seeds that were dropped whole was excluded from analyses. I watched birds through a one-way window and recorded handling times on an Apple II computer, programmed to time and record events to 0.1 s. Data were gathered on 3–5 individuals of each species. Each datum presented represents the mean for one bird handling on average 15.1 seeds (SD = 5.7, range = 3–31).

I estimated the rate at which seeds must be encountered (λ), where $\lambda = 1/T$ and

$$T = \frac{3.6 \times 10^4 \, s(S)}{DEE} - h.$$

I assumed 3.6×10^4 s (10 h) to be the maximum time available to forage during a midwinter day. Midwinter was chosen because this is when diets consist mostly of seeds (Martin et al. 1951) and winter is a period when food is most limiting for cardueines (Newton 1967, Benkman 1987a). S is the product of mass (mg) of kernel consumed per seed, specific energy value (J/mg) of the kernel, and assimilation efficiency. I measured mass of kernel consumed, and I assumed seed kernels commonly consumed by finches have 23 J/mg (Grodzinski and Sawicka-Kapusta 1970) and as-
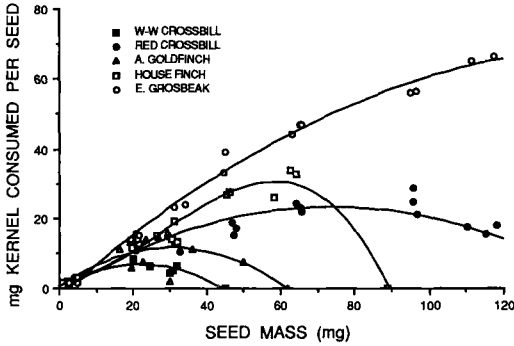
Fig. 1. The amount of seed kernel consumed/seed by 5 species of cardueline finches. Data for each species are indicated by unique symbols that are connected by second or third order polynomial curves. Each point is usually the mean for 20 seeds. For each seed size the different points represent different individuals, but data for the different seed sizes are from the same individuals. Variances are not given because seed remains were weighed in groups, usually of 10.
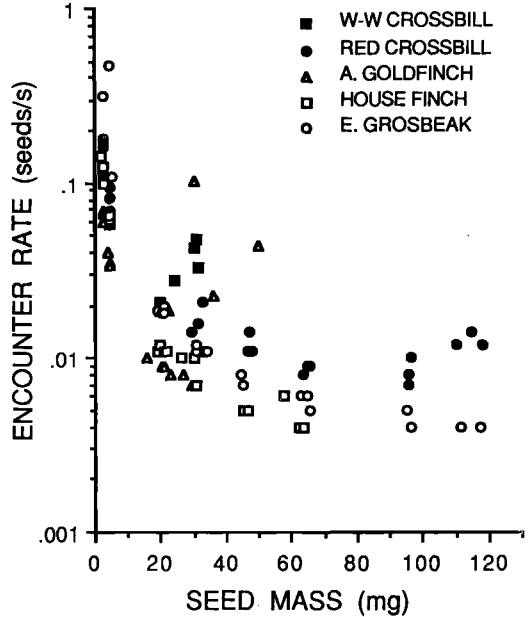

Fig. 2. The estimated necessary seed encounter rates for 5 species of cardueline finches to meet their estimated daily energy requirements (see Methods).

similation efficiencies of 75% (Willson and Harmeson 1973). *DEE* equals the total daily energy expenditure (kJ) (Walsberg 1983, eq 8). The measured handling time in seconds is *h*.

I used digital calipers to measure bill length, depth, and width, and a Sartorius or Pesola scale to measure body mass. Bill measurements were made on study skins of 10 individuals of each species. Bill depth was the greatest measured depth at the base of the bill. Bill length was measured from the anterior end of the nares to the tip of the upper mandible. Bill width was measured at the anterior end of the nares. Body mass was measured on the captive birds usually within an hour of capture.

RESULTS

The amount of kernel consumed per seed initially increased as seed mass increased but then generally declined for larger sized seeds (Fig. 1). The mass of kernel per seed approximated that consumed by grosbeaks. For all species, both the seed size giving each bird species the maximum amount of kernel consumed per seed and the maximum seed size handled diminished as the body and bill size decreased (Fig. 1, Table 1). Relative to their bill dimensions (Table 1), crossbills consumed proportionately less kernel than did the other finches for all but the smallest seed sizes (Fig. 1). For example, White-winged Crossbills have larger bills than goldfinches, yet they consumed less kernel than

the goldfinch for all but the small (<5 mg) thistle seeds.

Time spent handling the 2 sizes of thistle seeds (<5 mg) differed significantly among species (ANOVA, $F_{4,16} = 10.81, P = 0.0002$; based on the means of individual birds) and both species of crossbills required less time to handle thistle seeds than the other species ($P < 0.05$, Multiple Range test). Seed size had no effect on handling time (ANOVA, $F_{1,16} = 3.26, P = 0.09$). Similar analyses were not conducted on the larger sunflower seeds because there was tremendous variation among species in the amount of kernel dropped (Fig. 1).

To evaluate the seed handling efficiencies, I calculated the necessary seed encounter rates for each species (see Methods). Seed sizes and minimum encounter rates by which each species could meet its energy demands differed (Fig. 2). White-winged Crossbills required seed encounter rates 2–3 times higher and Red Crossbills required seed encounter rates about 2 times higher than the most efficient species at all seed sizes. Goldfinches could exist at lower encounter rates of small seeds (2–23 mg) than the other species. House Finches and grosbeaks each had a range of seed sizes for which they could exist at lower seed encounter rates.
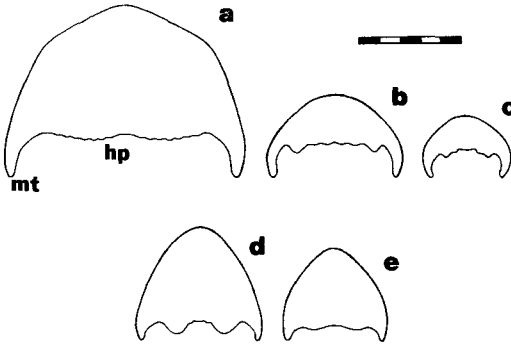
Fig. 3. Diagrammatic cross sections of the upper mandible at the anterior edge of the nares of (a) Evening Grosbeak, (b) House Finch, (c) American Goldfinch, (d) Red Crossbill, and (e) White-winged Crossbill. The maxillary tomia and horny palate are designated by mt and hp, respectively. The bar equals 0.5 cm.

DISCUSSION

Crossbills require seed encounter rates 2–3 times higher than required by other carduelines. Because seed encounter rates decrease as seed abundance declines, particularly at low seed densities (Schluter 1984, Benkman 1987a), other carduelines out-compete crossbills by lowering seed abundances below those necessary for crossbills to survive. When conifer cone crops fail over large areas, crossbills probably suffer high mortality (see Eriksson 1970). This will result in strong natural selection on crossbills for increases in foraging efficiency on those conifers that produce seeds during cone failures, but, as a consequence, further reduce their ability to survive on nonconifer seeds. This is the cost of specialization for crossbills.

Three characteristics of crossbills reduce their efficiency on nonconifer seeds. First, crossbills have long narrow bills that enable them to be slid efficiently between conifer cone scales (Benkman 1987b). Narrow bills, however, reduce the efficiency with which large seeds can be handled. For example, as bill width decreases in either noncrossbill finches or crossbills, the consumed proportion of large-sized seed kernels decreased. This relationship probably results from the ability of finches with different sized bills to surround and secure the kernel when it is broken into pieces prior to swallowing.

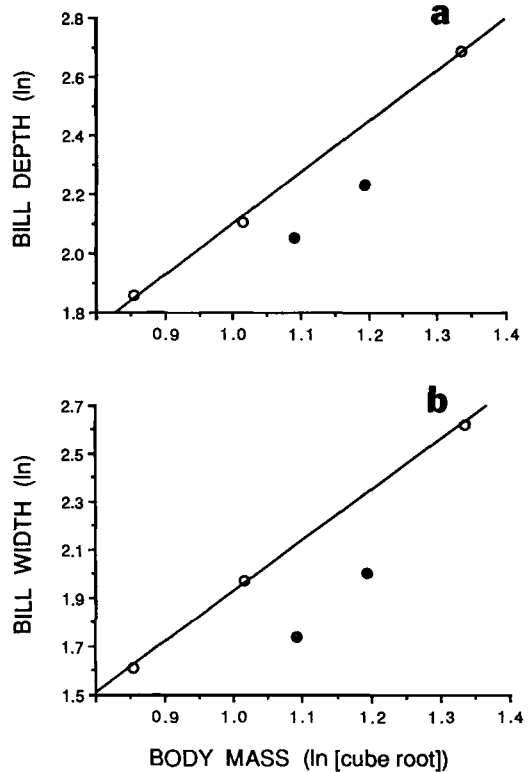Bill size was also correlated with the size of the largest seeds handled. The wide range of

Fig. 4. The relationships of bill depth (a) and bill width (b) (mm) to body mass (gm) for crossbills (solid circles) and noncrossbill carduelines (open circles). The fitted linear regression line among the noncrossbills is shown. Data are from Table 1.

seed sizes handled was apparently a consequence of the Red Crossbill requiring a powerful bite to obtain seed in closed, thick-scaled conifer cones (Benkman 1987b).

A second reason crossbills were less efficient at meeting energy demands when foraging on large seeds is because of differences in the structure of the horny palate. The noncrossbill finches have a high palate relative to the maxillary tomia, whereas the crossbill's palate is more flush with the maxillary tomia (Fig. 3; see also Ziswiler 1965). The low palate may facilitate handling small seeds; crossbills usually consume seeds weighing less than 20 mg (Benkman 1987a, b). For a given bill width, noncrossbill finches have a larger buccal volume. Presumably this will reduce the amount of kernel dropped while kernels are being broken and swallowed. This may explain why goldfinches dropped less kernel than did White-winged Crossbills, even

though goldfinches have narrower bills than White-winged Crossbills.

Crossbills have larger bills and bodies than birds in the genus *Carduelis,* yet crossbills typically eat smaller seeds (Newton 1967, 1972; Benkman 1987a, b). The large bills of crossbills are required to extract seeds from conifer cones. Most of the variation in bill size and shape increases the efficiency of extracting seeds (Benkman 1987b). In contrast, the general bill characteristics of noncrossbill carduelines may be adapted most for handling seed and not securing them from the plant. Indeed, when seeds are readily accessible in open conifer cones, *Carduelis* finches and crossbills have similar feeding rates (pers. obs.).

A large body mass, however, increases metabolic costs and is the third reason crossbills are relatively inefficient on nonconifer seeds. Moreover, crossbills have proportionately larger bodies in relation to their bill depth and width than other carduelines (Fig. 4). Large body mass may be important for predator evasion because a large body and wings may counterbalance a large bill so that flight is less awkward (Schluter 1988). Crossbills eat small seeds, and must spend relatively more time feeding, and they often forage out on the distal end of limbs exposed to predators. Hence, crossbills may be more vulnerable to predators and their relatively large bodies compared to the other carduelines (Fig. 4a) may be important for predator evasion.

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