Adaptation to Single Resources and the Evolution of Crossbill (Loxia) Diversity

Craig W. Benkman

ADAPTATION TO SINGLE RESOURCES AND THE EVOLUTION OF CROSSBILL (*LOXIA*) DIVERSITY[1]

CRAIG W. BENKMAN[2]

Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada V6T 2A9

Abstract. I quantitatively test the hypothesis that four taxa or "types" (species or subspecies) of Red Crossbills (*Loxia curvirostra*) in the Pacific Northwest have diversified morphologically in bill characters in response to alternative adaptive peaks presented by their food: seeds in conifer cones. Hypothetically, each adaptive peak corresponds to one conifer species whose seeds are (1) produced regularly from year to year, (2) held in cones through late winter when seed is most limiting, and (3) protected from depletion by potential noncrossbill competitors. Four such conifers, termed "key conifers," are present (*Tsuga heterophylla, Pseudotsuga menziesii, Pinus ponderosa,* and *Pinus contorta* var. *latifolia*).

I use data on foraging efficiency for 31 captive crossbills of four types to determine the optimal bill size and palate structure for foraging on the key conifers. As predicted, if each type is adapted for foraging on a key conifer, the observed morphology of a given type is often the predicted optimal morphology for foraging on its respective key conifer. Two of the types have mean bill sizes (bill depth) equalling their predicted optimal size. For one of the remaining types, the observed differs from the optimum by 0.4 mm; I was unable to predict an optimal size for the remaining type. Optimal bill size varies with season. Bill sizes corresponded more closely to the optima for winter (lean period) than for summer. Observed mean width of the palate groove, in which crossbills hold conifer seeds while the seeds are being husked, was consistently close to the estimated optimal groove width. Optimal groove width was correlated ($r^2 = 1.00$, $n = 4$) with seed size (cube root of mass), suggesting optimal groove width is determined by seed size. Overall, each crossbill type has either the optimal bill size or optimal husking groove width, or both, for foraging on their key conifers.

Fitness set analyses indicate that there are substantial trade-offs in foraging efficiency. The best phenotype for foraging on one conifer is often only one-half as efficient on other conifers. All four fitness sets are concave, implying selection against intermediate phenotypes.

I conclude, first, that reliability of seeds on key conifers during periods of food scarcity is a critical feature in the ecology and evolution of crossbills. Second, optimization of morphological traits occurs even in populations in highly variable environments. Third, disruptive selection against intermediate phenotypes is likely. This should maintain, if not reinforce, the distinctiveness of types. Fourth, the diversity of cone structure and seed size among key conifers is ultimately responsible for the diversification of crossbills.

Key words: adaptation; adaptive landscape; conifers; crossbills; diversity, fitness set; foraging efficiency; Loxia; morphology; optimization; Pacific Northwest; trade-offs; specialization.

INTRODUCTION

A central problem in evolutionary biology is how ecological factors might promote morphological diversification in a speciating lineage. One factor figuring prominently in theories of species diversity is resource diversity. The environment of an array of species can be viewed as an "adaptive landscape" with peaks, where fitness is high, and valleys, where fitness is low (Wright 1931, Lande 1976, Rosenzweig 1978). Species diversity results, in part, from different species adapting to different peaks (Hutchinson 1968).

Adaptive peaks may correspond to the alternative resources used when food is scarce (e.g., Liem and Kaufman 1984, Schluter and Grant 1984, Grant and Grant 1990). This is when selection for foraging specializations (e.g., Boag and Grant 1981) and competition for resources promoting divergence among species in resource use should be most intense (Schoener 1982). If resources are sufficiently distinct so that an increase in performance on one resource entails a decline in performance on alternative resources then there should be selection for specialists (Levins 1968, MacArthur 1972, Leigh 1990). If such trade-offs are absent, a generalist can supplant several specialists. Although

[2] Present address: Department of Biology, Box 30001, New Mexico State University, Las Cruces, New Mexico 88003 USA.
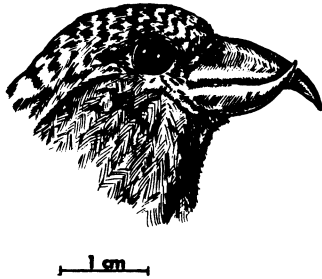
FIG. 1.   A lateral view of the head and bill of a type 3 Red Crossbill.

these ideas have been fundamental to evolutionary biology for >20 yr, adaptive landscapes have been described for few organisms (Schluter and Grant 1984, Kingsolver 1988, Armbruster 1990).

In this study I use both optimality and fitness set (Levins 1968) analyses to test the hypothesis that Red Crossbills (*Loxia curvirostra*; Fig. 1) have undergone morphological diversification in bill characteristics in response to adaptive peaks represented by their main food: seeds in conifer cones. The different bill sizes of crossbill species have long been recognized as adaptations for foraging on cones of different species of conifers (Griscom 1937, Lack 1944*a, b*, 1947, Southern 1945, Newton 1972; see especially Benkman 1987*a, b*). However, the adaptive value of bill size differences among Red Crossbill populations, the focus of this study, remains enigmatic (Griscom 1937, Tordoff 1954, Newton 1972, Nethersole-Thompson 1975, Monson and Phillips 1981, Dickerman 1986, 1987, Massa 1987, Payne 1987, Groth 1988, 1991, Knox 1990).

Although the genetic basis of bill size differences between populations of Red Crossbills also remains incompletely understood, substantial behavioral and morphological differences between sympatric populations have led Groth (1988, 1991; see also Knox 1990) to conclude that Red Crossbills are composed of different species. Groth (1991) recognizes eight different species of Red Crossbill in North America on the basis of several lines of evidence. First, individual Red Crossbills can be categorized into one of eight different call types (Groth 1991; this distinction also applies to other vocalizations including song) that are each cohesive behavioral and reproductive units. That is, individuals associate with the same call type (Groth 1988, 1991; T. P. Hahn, *personal communication*; C. W. Benkman, *personal observation*) and nearly all breeding pairs consist of one call type (Groth 1988, 1991; T. P. Hahn, *personal communication*), even though several different call types can often be found breeding in the same area. Second, call types differ ecologically by tending to associate with different conifers (Groth 1988, 1991; T. P. Hahn, *personal communication*; C. W. Benkman, *personal observation*). Third, multivariate analyses of skeletal and bill measurements show

that call types are morphologically distinct (Groth 1988, 1991).

Genetic data concerning the distinctiveness of the call types are equivocal but not atypical of intrageneric comparisons in birds (Groth 1991). No evidence indicates that the morphological differences among types are induced by the environment. Rather, all evidence indicates bill and body size is highly heritable in crossbills, as in most birds (see Boag and van Noordwijk 1987, Grant and Grant 1990). Offspring produced in captivity, including those from hybrid pairs, resemble their parents in bill and body size (H. B. Tordoff, *personal communication*; T. P. Hahn, *personal communication*; C. W. Benkman, *personal observation*; see also *Discussion*), even though diets during the development of the parents and offspring differed substantially. Although the extent of genetic differentiation between types remains to be determined, it appears almost certain that each call type represents a cohesive group that differs genetically from other call types.

Less certain is the adaptive basis for the difference in bill size between types (but see Benkman 1989*a*). Indeed, Groth (1991, *personal communication*) seems to favor nonadaptive explanations for bill size differences between types. In contrast, based on my studies on the ecology of crossbills relative to the dynamics of their food (Benkman 1987*a*, 1989*a*, 1990), I hypothesize that each taxon of Red Crossbill in North America is adapted to a particular species of conifer, a "key conifer," that can be characterized in three ways. First, the conifer must consistently produce seeds or hold seeds from year to year (see Benkman 1989*a*). Most conifers produce cone crops irregularly (Fowells 1965), yet specialization requires a reliable food resource. Second, seeds must be held in the cones through late winter and early spring when seeds are most limiting (Benkman 1987*a, b*, 1988*a*). Third, the seeds must be encased in cones on which competitors are less efficient at harvesting seeds. That is, the specialized crossbill morphology (Newton 1972, Benkman 1987*b*, 1988*a, b*, Benkman and Lindholm 1991) improves foraging efficiency substantially relative to more generalized morphologies.

Testing this hypothesis requires that I determine whether the different call types have the optimal morphologies for foraging on their key conifers. The optimal crossbill morphology for foraging on a given conifer is related to the size and hardness of cones and seeds. Crossbills use their crossed mandibles to bite between overlapping cone scales, and then laterally abduct the lower mandible (to the side to which it is crossed; see Fig. 1) to spread apart the cone scales and expose the seeds so that they can be extracted from the base of the scales (Tordoff 1954, Newton 1972, Benkman 1987*b*). Bill size is critical because it influences the time required to extract seeds from cones (Benkman 1987*b*). Bill size and associated musculature also influence seed husking ability and set the upper limit

for the largest and hardest seed that can be husked (Newton 1972). Crossbills, however, have larger bills for the sizes of seed they normally consume than other Cardueline finches (Benkman 1988a), presumably because extracting seeds from cones generally demands much greater forces and more exertion than husking them (in contrast to birds that forage on loose seeds). Thus, bill size is not expected to correspond to the optimum size for husking a seed. If there is a correlation between seed size and bill size in crossbills, it is probably due to the fact that among conifers with similar cone ripening phenologies larger seeds are usually protected by larger cones (C. W. Benkman, *personal observation*). The morphological characters that should be most closely related to seed husking ability are those of the horny palate (Fig. 2; see Ziswiler 1965, Newton 1972, Benkman 1988a). Of particular importance is the width of the lateral groove in the palate where crossbills secure seeds (dimension ac in Fig. 2) while the lower mandible is used to apply pressure to crack and remove the seed coat (see description and Fig. 28 in Newton 1972). Based on observations of foraging crossbills and mechanical considerations (C. W. Benkman, *personal observation*), the lateral groove that crossbills use to secure seeds is located on the side opposite to which the lower mandible crosses (hereafter husking groove). The better the fit between seed size and husking groove width, the more securely the seed can be held. If the seed is too large, then the secondary ridge (the ridge between points b and c in Fig. 2) will not touch the seed. If the seed is too small, then only the secondary and not the main ridge (point c in Fig. 2) would secure the seed.

I was able to capture individuals of four call types common in the Pacific Northwest (Groth's types 2, 3, 4, and 5; I will follow Groth's [1991] terminology and classification); types 1 and 6 also occur in western North America, but I was unable to capture them for the experiments. For each of these four call types I predicted a priori its key conifer based on information on both the natural history of the crossbills and the fruiting patterns of the conifers. I provide this information below to justify my choice of conifers.

The smallest crossbill in North America, type 3 (*L. c. minor*; Fig. 1), is most common in western hemlock (*Tsuga heterophylla*; Fig. 3) (T. P. Hahn, *personal communication*; C. W. Benkman, *personal observation*) in the coastal forests from Alaska to northern California (Griscom 1937, Tordoff 1954, Payne 1987). Western hemlock is the most prolific and regular cone producer in this region (Ruth and Berntsen 1955, Fowells 1965). Unlike most conifers, western hemlock produce cone crops virtually every year (Godman 1953, Fowells 1965). Hemlock cones and seeds, like those of all cone-bearing gymnosperms (Pinaceae) in North America, develop during the summer and mature by early fall. Its cones open and seeds are released in autumn, but many seeds are held in the cones through winter and
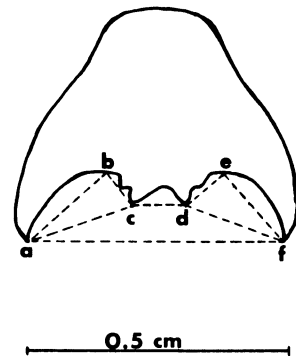

FIG. 2. Cross section of the upper mandible at the distal section (see *Methods*) of a type 2 crossbill. Its lower mandible crossed to the right. Dashed lines represent different palate measurements (see *Methods*).

are shed in spring or early summer (Pickford 1929, Garman 1951, Hetherington 1965, Gashwiler 1969, Harris 1969). Seeds in open cones are exploited more efficiently by Pine Siskins (*Carduelis pinus*) than by crossbills, but seeds in cones that are reclosed by moisture are harvested most efficiently by crossbills (Benkman and Lindholm 1991) and represent the key resource. The super-humid conditions that typify the coastal belt (Burns and Honkala 1990) are probably critical to type 3. Indeed, the absence of such humid conditions in eastern North America may limit the ability of type 3 to survive for extended periods in the eastern hemlock (*T. canadensis*) forests. Type 3 periodically invade these forests (Griscom 1937, Benkman 1987a), but the only area in eastern North America where type 3 remains for extended periods, the Huron Mountains (Payne 1987), is along the south shore of Lake Superior where the climate is "quasi-marine" (Ruffner 1980).

Type 4 are the second largest crossbills found commonly in the Northwest. They are most characteristic of Douglas-fir forests (*Pseudotsuga menziesii*; Fig. 3) (Groth 1991; T. P. Hahn, *personal communication*; C. W. Benkman, *personal observation*; also see Jollie 1953). In many regions Douglas-fir is the most regular cone producer (Fowells 1965), although it does not produce cones as consistently as hemlock (Garman 1951, Gashwiler 1969). Douglas-fir, however, occurs across a large range of climatic conditions and a diversity of regions (Fowells 1965). This is reflected by apparent genetic differentiation among populations of Douglas-fir (Fowells 1965, Schopmeyer 1974), even within a single watershed (Campbell 1979). Because different regions produce cone crops asynchronously (Isaac 1943; C. W. Benkman, *personal observation*; also see Bock and Lepthien 1976), Douglas-fir likely produces a good cone crop somewhere within the Northwest every year. Douglas-fir may hold over a third of its seeds in its cones through winter (Pickford 1929, Isaac 1943, Garman 1951) and crossbills may continue to obtain seeds

Western hemlock   Douglas-fir
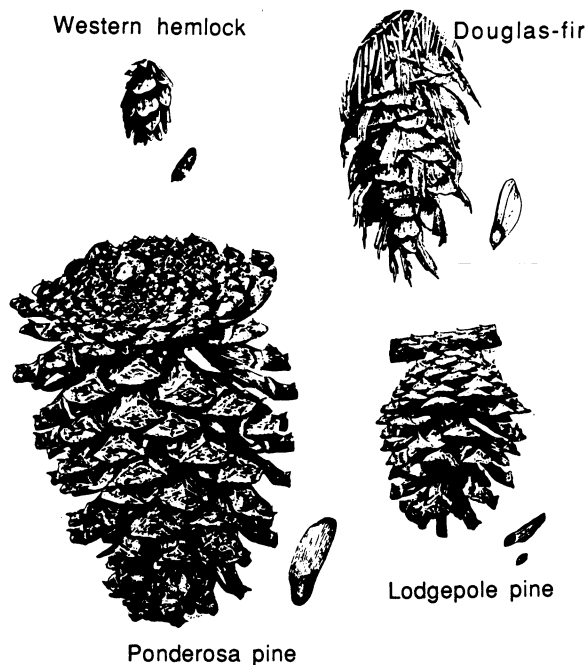
Ponderosa pine   Lodgepole pine

FIG. 3. Cones and seeds (with attached seed wings) of the four key conifers drawn to relative scale (reproduced from Sudworth 1967). The following are the measured dry masses of the seeds (wet mass for ponderosa pine) minus their wings used in the experiments (means ± 1 SE): western hemlock, 1.6 ± 0.08 mg, $n = 5$ trees, 33 seeds; Douglas-fir, 10.7 ± 1.13 mg, $n = 3$ trees, 30 seeds; ponderosa pine, 44.1 ± 0.35 mg, $n = 51$ samples, 225 seeds, 1 tree; lodgepole pine, 2.9 ± 0.14 mg, $n = 10$ trees, 96 seeds.

from cones until at least late May (C. W. Benkman, *personal observation*); the coastal variety of Douglas-fir (*P. m.* var. *menziesii*) better qualifies as the key conifer than the Rocky Mountain variety (*P. m.* var. *glauca*), because it holds seeds in its cones through winter more dependably (Schopmeyer 1974). Pine Siskins forage on seeds in open Douglas-fir cones (Garman 1951; also see Hagar 1960), but rely more on seeds in western redcedar (*Thuja plicata*) cones (Gashwiler and Ward 1966). Red-breasted Nuthatches (*Sitta canadensis*) also forage on seeds in open Douglas-fir cones, but nuthatches are not very efficient at removing seeds that are secured between scales (Smith and Balda 1979).

The largest crossbill in the Northwest, type 2, is most common in ponderosa pine (*Pinus ponderosa*; Fig. 3) (Groth 1991; C. W. Benkman, *personal observation*; T. P. Hahn, *personal communication*; also see Bailey et al. 1953, Jollie 1953). Ponderosa pine does not consistently produce cones in a given region every year (Fowells and Schubert 1956, Fowells 1965, Shearer and Schmidt 1971), but like Douglas-fir, varies geographically (Wells 1964, Schopmeyer 1974) within its extensive range (Fowells 1965) and probably produces large cone crops somewhere every year (also see Smith and Balda 1979). Ponderosa pine sheds most of its

seeds in autumn (Curtis and Foiles 1961, Fowells 1965, Shearer and Schmidt 1971), but holds some seeds through winter (Dahms and Barrett 1975) and even until July (Olson 1932). The Rocky Mountain ponderosa pine (*P. p.* var. *scopulorum*), rather than the western ponderosa pine (*P. p.* var. *ponderosa*), is likely the key conifer, because it holds seeds through winter more consistently (see Schopmeyer 1974) and produces large cone crops more regularly (Burns and Honkala 1990). Although Hairy Woodpeckers (*Picoides villosus*) and White-headed Woodpeckers (*P. albolarvatus*) use their powerful bills to shred cone scales to get to ponderosa pine seeds (Stallcup 1968, 1969, Ligon 1973), woodpeckers mostly confine their foraging on pine seeds to autumn (Otvos and Stark 1985; also see Morrison and With 1987) when seeds are plentiful. Crossbills make more effective competitors for small (<50 mg) conifer seeds because woodpeckers are less efficient at removing and husking pine seeds than crossbills (based on descriptions of woodpecker foraging behavior in Stallcup 1969; C. W. Benkman, *personal observation*) and woodpeckers have higher energy requirements (body masses twice that of crossbills [Dunning 1984]). Squirrels rarely harvest ponderosa pine seeds when few seeds remain secured between the scales (Smith and Balda 1979).

Type 5 is distinguishable mainly by its call since it overlaps with type 2 crossbills nearly completely in size (Groth 1991; see Fig. 4). This crossbill occupies lodgepole pine (*P. contorta* var. *latifolia*; Fig. 3) forests in the Rockies (Groth 1991; T. P. Hahn, *personal communication*; C. W. Benkman, *personal observation*). This pine produces fair to good cone crops nearly every year (Crossley 1956, Smith and Balda 1979, Lotan and Perry 1983) and is characterized by serotinous cones (Lotan and Perry 1983) that remain closed until fire causes the scales to separate. Seeds in closed serotinous cones are inaccessible to crossbills (C. W. Benkman, *personal observation*), but many cones open in autumn (Lotan and Perry 1983) and seeds are shed all year (Crossley 1955). Seeds between scales that have reclosed from moisture or have opened incompletely are the hypothesized key resource and are probably inaccessible to noncrossbill seed-eaters. In contrast to lodgepole pine, the morphologically similar and widespread jack pine (*P. banksiana*; Fowells 1965) sheds its seeds rapidly once its cones open (Critchfield 1984) and does not support a resident crossbill.

METHODS

Crossbills and aviary

Crossbills were captured in Washington, Oregon, Montana, and British Columbia between 22 June and 5 October 1989. They were housed in two indoor rooms that were each partitioned with 1.2-cm mesh screen into two 1.3 × 3.8 × 2.6 m aviaries. Each of the four crossbill types was held separately in one aviary. Cross-

bills were provided with grit, salt, and water containing vitamins and calcium supplement. Fresh cones, usually lodgepole pine, were provided nearly daily, supplemented by sunflower seeds. Fresh conifer branches were provided every 4–7 d. A total of 31 crossbills (7 type 3, 11 type 4, 9 type 2, 2 type 5, 2 possible hybrids) were used in the experiments. The sex ratios for each type were near to or at one to one. The calls of each crossbill were recorded and their identity as to call type verified by T. P. Hahn.

The crossbills remained in excellent condition. No crossbills died during the experiments (16 October 1989–27 February 1990). Mandible lengths were on average 0.19 mm shorter during the experiments than when captured (18 of 30 birds had shorter mandibles during the experiments than when captured). This occurred from wear while foraging on cones and implies, if anything, that foraging in captivity required greater exertion than in the field.

Morphology

Bill size.—I made four external bill measurements (see Fig. 1 for reference). They were taken as follows: upper mandible length was measured from the tip of upper mandible to the anterior end of the right naris; lower mandible length was measured from the tip of lower mandible to the base where rami meet; bill depth was measured at the anterior end of the nares; and upper mandible depth was measured at anterior edge of the nares. Bills were measured to the nearest 0.01 mm with digital calipers at least once during every series of experiments for a given conifer. I used mandible lengths at time of capture and the mean measured bill depth over the course of the experiments (based on 2–7, usually 4–6, measurements per bird; mean SE of mean bill depth measurements per bird was 0.03 mm); there was no evidence of change in bill depth. To increase the sample size of bill measurements of type 5, I measured an additional seven type 5 crossbills captured in Wyoming in September 1991. For comparison, in the *Results* I give the mean bill depths as measured by Groth (1991: Table 10; he presents the means of each sex, but I average the two) for a larger sample of birds.

I conducted a principal components analysis on the ln-transformed bill measurements to characterize size and shape variation among the crossbills (Fig. 4). PC1 accounts for 91% of the variance and reflects overall size, with all four measurements loading positively. Types 3, 4, and 2 separate along PC1. PC2 accounts for an additional 6% of the variance and is a measure of bill shape, with mandible length loading positively and depths loading negatively. Types 3 and 2 tend to have relatively shorter and deeper bills than type 4. Types 2 and 5 are similar in both PC1 and PC2 (Fig. 4). Some of the scatter in PC2 is likely due to variation in lengths caused by wear.

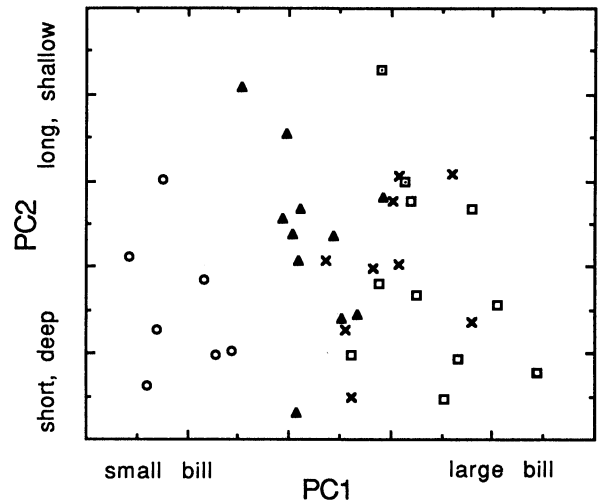*Palate structure.*—I used vinyl polysiloxane, ob-

FIG. 4. The first two principal components of the four external bill measurements. PC1 and PC2 account for 91 and 6% of the total variance, respectively. Each symbol represents an individual bird and the different symbol types represent call types: O = type 3, ▲ = type 4, □ = type 2, × = type 5, ⊡ = type U (see text).

tained from Dental Health Sciences at the University of British Columbia, to make molds of the horny palate of each crossbill. Palate molds were also made of five of the seven type 5 crossbills captured in 1991. Vinyl polysiloxane hardens in ≈5 min once its two putty-like components are combined. I made molds (see Robinson 1989) by first placing a smooth and flattened ball of vinyl polysiloxane on a wooden tongue depressor. Then I forced the mandibles apart and placed the vinyl polysiloxane against the palate by firmly holding the tongue depressor against the underside of the upper mandible, being careful not to impede breathing. The mold and tongue depressor were removed from the mouth after ≈2 min.

I used a razor to make two cross sections of each mold. One cross section was located where the central ridge reaches its highest point near the base of the upper mandible, and the more distal cross section was made where the lateral grooves are widest (see Fig. 4b in Ziswiler 1965). I use the width of the more basal cross section as a measure of mandible width, whereas I present more detailed analyses of the distal section because seeds are husked while being held in this region of the bill (C. W. Benkman, *personal observation*; see Ziswiler 1965).

The cross sections were magnified and I used a digitizer to measure dimensions of the palate to the nearest 0.001 mm (Fig. 2). Points a, c, d, and f correspond to edges, whereas points b and e (Fig. 2) represent the locations judged most distant from the line connecting af. Point f represents the side to which the lower mandible crosses for all crossbills. Measurements involving points b and e have the most measurement error. Also, the shape of the grooves differs among individuals (e.g.,

TABLE 1. Measurements of the horny palate of birds of the different crossbill types (mean ± 1 SE). Measurements are rounded to nearest 0.05 mm.

Dimension[†]		Mean (± SE) length, mm						Factor weightings	
		Crossbill type							
		3 $n = 7$	4 $n = 11$	2 $n = 9$	5 $n = 7$	U $n = 2$	F[‡]	PC1	PC2
		Length of horny palate (mm)							
ab	Mean ± 1 SE	1.15 ± 0.05	1.35 ± 0.03	1.60 ± 0.02	1.25 ± 0.02	1.45 ± 0.08	20.9‖	0.21	0.01
	Type	2,4,5,U	2,3,5	3,4,5,U	2,3,4,U	2,3,5			
bc	Mean ± 1 SE	0.75 ± 0.03	0.75 ± 0.02	0.85 ± 0.03	0.80 ± 0.04	0.75 ± 0.01	2.7	0.00	0.31
ac	Mean ± 1 SE	1.55 ± 0.06	1.75 ± 0.04	2.05 ± 0.03	1.70 ± 0.03	1.80 ± 0.03	20.1‖	0.19	0.08
	Type	2,4,5,U	2,3	3,4,5,U	2,3	2,3			
ef	Mean ± 1 SE	1.30 ± 0.04	1.45 ± 0.05	1.70 ± 0.06	1.30 ± 0.06	1.55 ± 0.10	9.8‖	0.25	−0.13
	Type	2,4,U	2,3,5	3,4,5	2,4,U	3,5			
de	Mean ± 1 SE	0.65 ± 0.03	0.70 ± 0.02	0.80 ± 0.04	0.85 ± 0.04	0.75 ± 0.01	5.5§	−0.11	0.45
	Type	2,5	2,5	3,4	3,4				
df	Mean ± 1 SE	1.60 ± 0.05	1.75 ± 0.03	2.10 ± 0.05	1.70 ± 0.02	1.90 ± 0.03	24.5‖	0.19	0.07
	Type	2,4,5,U	2,3,U	3,4,5,U	2,3,U	2,3,4,5			
cd	Mean ± 1 SE	1.25 ± 0.06	1.30 ± 0.08	1.05 ± 0.04	1.10 ± 0.11	1.15 ± 0.07	2.1	0.12	−0.46
af	Mean ± 1 SE	4.20 ± 0.10	4.55 ± 0.08	4.95 ± 0.06	4.30 ± 0.13	4.75 ± 0.09	10.3‖	0.28	−0.19
	Type	2,4,U	2,3,5	3,4,5	2,4,U	3,5			
g	Mean ± 1 SE	5.30 ± 0.06	5.95 ± 0.11	6.40 ± 0.07	6.45 ± 0.09	6.45 ± 0.16	22.1‖		
	Type	2,4,5,U	2,3,5,U	3,4	3,4	3,4			
h	Mean ± 1 SE	2.40 ± 0.06	2.60 ± 0.08	2.75 ± 0.10	3.15 ± 0.20	2.85 ± 0.15			

† The pairs of letters represent the distances between the letter points in Fig. 2. The width of the palate at the proximal cross-section is represented by g, and the distance between the two cross-sections of the palate mold is h.

‡ ANOVA; crossbill types that differ significantly (LSD Multiple Range test, $P < .05$) are shown below the mean. * $P < .05$, § $P < .005$, ‖ $P < .0005$.

the grooves of some individuals peaked relatively closer to the middle than others). This increases the variation in measurements among individuals, especially for dimensions ab, bc, de, and df.

Principal components analysis was conducted on ln-transformed palate measurements to characterize size and shape variation. Most measurements loaded positively on PC1, and they tended to increase from types 3 to 4 to 2 (Table 1). However, two measurements, bc and de, had factor score weightings near or less than zero. These two measurements roughly measure how far the central region (between and above c and d; see Fig. 2) extends down from the top of the lateral grooves. As these two measurements increase, buccal volume, or the overall area between and above points a and f (see Fig. 2), tends to decline, whereas increases in the other dimensions result in increases in buccal volume. PC1 is interpreted as a measure of buccal volume. PC1 accounts for 57% of the variation and it separates types 3, 4, and 2, whereas type 5 overlaps types 3 and 4 (Fig. 5a). PC2 accounted for an additional 17% of the variation, and it tended to separate type 5 from types 3 and 4 (not shown).

Plotting husking groove width relative to bill depth (Fig. 5b) results in similar patterns among the types as a plot of PC1 of palate structure relative to PC1 of bill size (Fig. 5a). Palate dimensions and bill size are generally related except for type 5, which have relatively small buccal volumes and narrow husking grooves for their bill size.

Scatter in both PC1 and PC2 of palate structure may reflect, in part, measurement error. Measurement error also arises because of inaccuracies in determining by eye where the distal cross section should be located. Moreover, the distance from the base of the bill to where the lateral grooves are widest (measurement h) tends to be relatively greater for type 5 than for the other types (measurement h, Table 1). This is another dimension in which palates differ, and it results in type 5 having a narrower overall cross section (measurement af) relative to their basal cross section (measurement g) as compared to the other types (Table 1).

Two individual crossbills initially listed as possible hybrids require comment because their calls and morphology were not concordant. They gave calls unlike any described type as well as type 2 calls (T. P. Hahn, *personal communication*). Based on morphology it is unclear that they represent type 2 (Fig. 5) and they are designated by unique symbols in the figures. These two birds were captured one morning in an extensive lodgepole pine forest in the Rocky Mountains with the two type 5. Because these two birds may represent hybrids (see *Discussion*), they are analyzed separately and referred to as type "U."

Foraging data

I measured crossbill foraging rates on cones of the four hypothetical key conifer species (Fig. 3). I used western hemlock cones of three stages of ripeness: closed cones (summer and early fall food, $n = 35$ cones per

bird); open cones moistened so that scales were re-closed (winter food, usual conditions along coast in Pacific Northwest, $n = 10$ cones per bird); and open cones (fall and winter food, dry conditions, $n = 10$ cones per bird). Hemlock cones were gathered from two recently felled trees on the University of British Columbia campus on 11–12 September 1989. I used Douglas-fir (*Pseudotsuga m.* var. *menziesii*) cones with scales beginning to separate (early fall food, $n = 10$ cones per bird) from one tree in the Saanich Seed Orchard near Victoria, British Columbia on 25 August 1989. The cones scales were probably less easily separated than those from cones in winter that had dried more thoroughly (C. W. Benkman, *personal observation*). I used ponderosa pine cones representing two stages of ripeness: closed cones (summer food, $n = 2$ cones per bird) and opening cones with slight gaps between the scales (winter food, $n = 1$–2 cones per bird). I gathered ponderosa pine (*Pinus p.* var. *ponderosa*) cones from >50 trees ≈20 miles east of Tonasket, Washington, on 1 September 1989. I should have used cones from Rocky mountain ponderosa pines (*P.p.* var *scopulorum*; see *Introduction*), but I did not realize the substantial differences between varieties until after the experiments. The effect of this is mentioned in the *Results*. I used serotinous cones of lodgepole pine (*P. c.* var. *latifolia*), gathered from >10 trees near Lac La Jeune, British Columbia on 29 October 1989. Cones collected near Lac La Jeune are representative of cones from much of the range of *P. c.* var. *latifolia* (Critchfield 1957). To represent cones that had opened but reclosed from moisture (winter food), I opened the scales by placing cones in an oven at 180°C for 5 min, and then I briefly soaked the cones in water to reclose the scales ($n = 10$–15 cones per bird). I selected cones from each conifer that were of similar size and shape, to minimize variation in feeding rates on a given cone type, and these cones were also selected to represent an average-sized cone. For example, I used western hemlock cones that were mostly between 1.95 and 2.25 cm long, whereas the species range is 1.5–2.5 cm (Hitchcock and Cronquist 1973). When it was necessary to stop cone opening, cones were stored in plastic bags at −20°C.

During foraging experiments only one bird occupied an aviary to eliminate interference between birds. Between 4 and 11 other crossbills were in the adjacent aviary. The experiments were usually conducted between 0900 and 1300. Birds were deprived of seeds for ≈15 h before the experiments.

I recorded the time required to extract and to husk 5 or 10 seeds (5 seeds for open ponderosa pine cones and 10 seeds for all other cones) beginning after the first seed was eaten (see Benkman 1987b). Crossbills did not drop pieces of seed kernel except when husking ponderosa pine seeds. For ponderosa pine, I gave pre-weighed groups of five seeds to individual crossbills and weighed the remains of kernel and seed coat that fell onto a screen-covered tray to determine the average
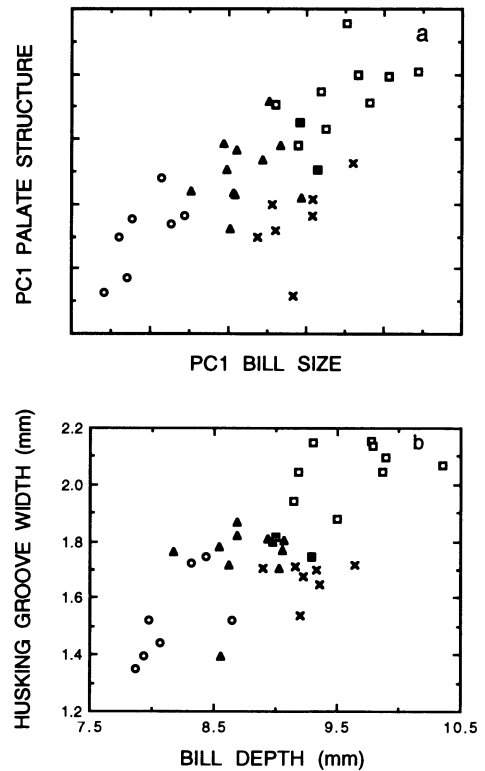

FIG. 5.   (a) A plot of PC1 measurements of palate structure and bill sizes and (b) husking groove width vs. bill depth for the different individual crossbills. Symbols as in Fig. 4.

amount of kernel consumed and dropped per seed per trial (see Benkman 1988a). Seed and kernel masses were measured to the nearest 0.001 mg. All times were recorded to the nearest 0.1 s.

I attempted to gather data from types 2, 3, and 4 foraging on all four conifers. Because of the small number of types 5 and U, and because I expected them to take the same time to extract seeds from cones as type 2 (their bills are similar in size [Fig. 4]), I did not include type 5 and U in all the experiments. Instead, I focused on the use of types 5 and U for comparing their seed husking abilities to those of type 2. I expected that seed husking abilities (and palate structure) would differ between types 5 and 2 because the seed size of their predicted key conifers differs by an order of magnitude. The predicted key conifer for type 5, lodgepole pine, has seeds that weigh only ≈3 mg, whereas the predicted key conifer for type 2, ponderosa pine, has seeds that weigh ≈40 mg (Wells 1964). I also timed type 5 (and type U) foraging on lodgepole pine cones (its predicted key conifer).

Data analyses

I conducted ANOVA and LSD multiple range tests to determine if each type spent less time extracting seeds (hereafter prying time) from its respective hypothesized key conifer than did other types. I then used

TABLE 2. Prying times (in seconds) for the different crossbill types on the four key conifers. Sample sizes (*n*) are the numbers of crossbills. ANOVAs were conducted on ln-transformed means of individual crossbills.

Type	Hemlock			Douglas-fir			Ponderosa pine			Lodgepole pine		
	$\bar{X}$	SE	*n*	$\bar{X}$	SE	*n*	$\bar{X}$	SE	*n*	$\bar{X}$	SE	*n*
3	2.01	0.06	7	12.20	1.15	7	...	...	...	5.55	0.72	7
4	3.06	0.10	11	5.77	0.41	11	29.43	2.34	10	3.65	0.16	11
2	3.61	0.13	9	6.27	0.40	9	16.92	1.62	9	3.32	0.14	9
5	...	...	...	...	...	...	...	...	...	2.36	0.15	2
U	...	...	...	...	...	...	...	...	...	2.32	0.10	2

Hemlock: ANOVA, $F_{2,24} = 64.9$, $P < .0001$; significant differences among all three types (LSD Multiple Range test, $P < .05$).
Douglas-fir: ANOVA, $F_{2,24} = 27.9$, $P < .0001$; significant differences among all but types 4 and 2 (LSD Multiple Range test, $P < .05$).
Ponderosa pine: ANOVA, $F_{1,17} = 18.9$, $P < .0005$.
Lodgepole pine: ANOVA, $F_{4,26} = 13.3$, $P < .0001$; significant differences among all but types 4 and 2, and between types 5 and U (LSD Multiple Range test, $P < .05$).

regression analyses on the type or types with the smallest prying times to estimate the bill size that minimizes prying time. I used bill depth as a measure of bill size because it (1) is not subject to wear, (2) had the largest weighting on PC1, and (3) should be proportional to the maximum force a crossbill can exert when biting between the cone scales (Benkman 1987b). I used quadratic equations to fit the data if the quadratic term was significant and if a cubic spline (Schluter 1988) confirmed that there was a peak or valley in the function fitting the data rather than asymptote. Otherwise I used linear regression.

I define optimal bill size as that yielding daily energy demands (*E*) in the minimum time. The optimum was estimated as that minimizing the product of *E* and prying time. Optimal bill depth can be smaller than that which minimizes prying time because smaller billed (and bodied) finches have lower daily energy requirements than larger billed finches; bill depth is positively correlated with body mass in seed-eating finches (see Benkman 1991). *E* was estimated as (body mass in grams)$^{0.6052}$ (Walsberg 1983). I used the following equation to estimate body mass for an individual of a given bill depth: $Y = -7.770 + 4.214X$ ($r^2 = 0.84$, df = 12, $P < .01$), where *Y* is body mass (in grams) at time of capture of crossbills lacking much fat and *X* is bill depth (in millimetres). Prying time was estimated from the regressions for each conifer.

As a measure of palate structure, I use husking groove width because it is easy to interpret. The husking groove width that minimizes seed husking time is the optimum because husking groove width can vary independently of bill (or body) size (Fig. 5b). I used similar analyses to determine the optimal husking groove width as to determine the bill depth that minimized prying time. Analyses were conducted on measurements made to the nearest 0.01 mm and 0.001 mm for bill and palate dimensions, respectively, but I present mean measurements and estimates of the optima rounded to the nearest 0.05 mm.

Using data from different individuals of different types together in a regression analysis violates the as-

sumption of independence of data. However, foraging time changes continuously and appears to be little influenced by type per se within the range of bill depths considered in each analysis. Individuals, therefore, can be considered independent regardless of type so that combined regressions were justified. Nevertheless, when individuals from more than one type are included in a regression I do not present probabilities and let the reader judge its significance.

Last, I determined the extent of selection for specialization by constructing fitness sets (Levins 1968). Fitness was estimated as the inverse of the product of daily energy demands (*E*) and total time foraging per seed. *E* was estimated as above, and total time foraging per seed was the mean measured value for each bird. This assumes that fitness is related to foraging efficiency. Such an assumption is consistent with the demonstration that crossbills maximize feeding intake rates while foraging (Benkman 1987a, 1989b) and that breeding behavior depends on seasonal intake rates (Benkman 1989c, 1990).

RESULTS

Are mean bill sizes optimal for extracting seeds from key conifer cones?

Western hemlock.—Each crossbill type differed significantly from the others in its mean time to extract a seed (prying time) from a cone (Table 2), with type 3 being the fastest. Among type 3 individuals prying time was curvilinearly related to bill depth (Fig. 6; $Y = 172.10 - 41.22X + 2.49X^2$, $r^2 = 0.82$, df = 4, $P = .03$). Prying time for type 3 was also curvilinearly related to bill depth on both moisture-reclosed cones ($Y = 153.28 - 36.98X + 2.25X^2$, $r^2 = 0.67$, df = 4, $P = .11$) and open cones ($Y = 282.94 - 68.91X + 4.21X^2$, $r^2 = 0.83$, df = 4, $P = .03$). Based on these quadratic equations, the bill depth that minimizes prying time for foraging on hemlock cones decreases from 8.25 mm on closed cones to 8.20 mm on moisture-reclosed and open cones. Type 3 bill depth was 8.20 ± 0.07 mm (mean ± 1 SE; *n* = 10, including the seven used in the experiments; mean type 3 bill depth from Groth [1991],
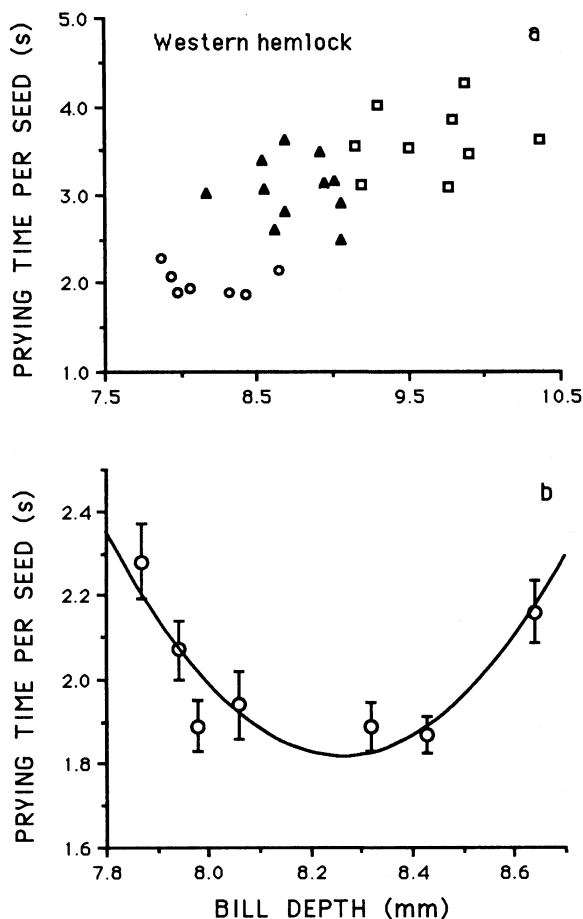
FIG. 6. Mean prying time per western hemlock seed in relation to bill depth for (a) crossbill types 3, 4, and 2, and (b) for crossbill type 3 alone (±1 SE). Cones were green and closed (n = 35 cones per bird). Curve represents quadratic equation. Symbols as in Fig. 4.

8.15 mm [n = 45], is similar to what I measured). Taking into account reductions in energy requirements as bill size decreases (see *Methods*), optimal bill depth is not altered from that predicted by the prying time relationships. All of these predicted optima are within 1 SE of the mean for type 3, and the predicted optimum for moisture reclosed cones (the predicted critical stage) is identical to the observed.

Douglas-fir. —Prying time differed significantly among the three types (Table 2), although type 4, the hypothesized specialist on Douglas-fir, did not differ significantly from type 2 (Table 2, Fig. 7). A quadratic equation fit the data for types 2 and 4 (Fig. 7; $Y = 196.06 - 41.23X + 2.23X^2$, $r^2 = 0.38$, df = 17). Based on this equation, the bill depth that minimized prying time is 9.25 mm and the optimal bill depth is 9.15 mm. Type 4 was predicted to be adapted for foraging on Douglas-fir cones and its mean measured bill depth was 8.75 ± 0.08 mm (mean ± SE, n = 11; mean type 4 bill depth from Groth [1991, n = 47] was identical

to what I measured), which differs from the optimum by 0.40 mm.

Ponderosa pine. —Closed ponderosa pine cones were given only to type 2 because the smaller type 4, and especially type 3, had extreme difficulty removing seeds from these cones and would not consistently forage on them. Prying time on closed cones decreased linearly as bill depth increased within type 2 (Fig. 8a; $Y = 146.80 - 11.63X$, $r^2 = 0.73$, df = 7, $P < .005$), suggesting that the optimal bill depth for foraging on closed cones is greater than the mean bill depth of type 2 ($\bar{X} \pm 1$ SE = 9.70 ± 0.13 mm, n = 8; mean type 2 bill depth from Groth [1991], 9.55 mm [n = 307], is even smaller than what I measured). In support of this hypothesis (see also Benkman 1989a), the crossbill found in the Sierra Madre of Mexico (*L. c. stricklandi*; Griscom 1937; type 6), where most pine cones remain closed through winter (Olesen 1972), has a relatively large bill (bill depth: $\bar{X} \pm 1$ SE = 11.07 ± 0.11 mm, n = 13 study skins).

Both types 2 and 4 could consistently remove seeds from opening ponderosa pine cones, but the larger type 2 spent significantly less time prying per seed than did type 4 (Table 2, Fig. 8b). In contrast to that on closed cones, the decline in prying time with increasing bill depth within type 2 was not significant (Fig. 8b; $Y = 56.80 - 4.13X$, $r^2 = 0.11$, df = 7, $P = .37$). The lack of a significant slope (m) in this regression ($m = -4.13$, SE = 4.35) suggests that type 2 individuals have bill depths that are closer to the optimum for foraging on opening cones than on closed cones. Nevertheless, large-billed type 2 tended to spend less time prying seeds from opening cones than those with smaller bills (Fig. 8b), implying that a bill larger than that of the average type 2 would be optimal. Conversely, the average type
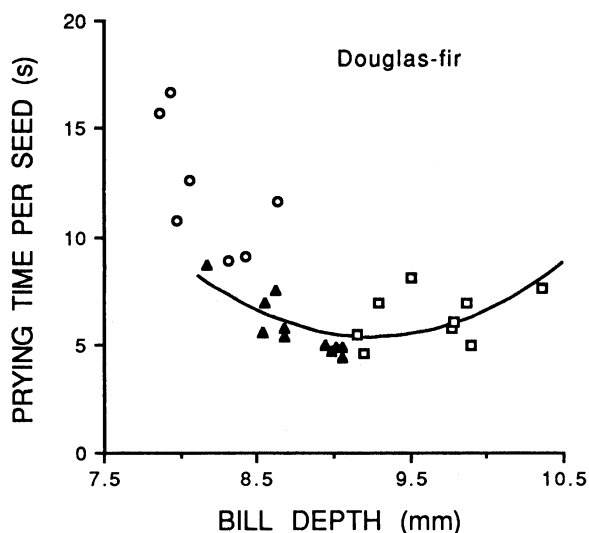

FIG. 7. Mean prying time per Douglas-fir seed in relation to bill depth (n = 10 cones per bird). Curve represents a quadratic equation fitted to the data from crossbill types 4 and 2 (see text). Symbols as in Fig. 4.
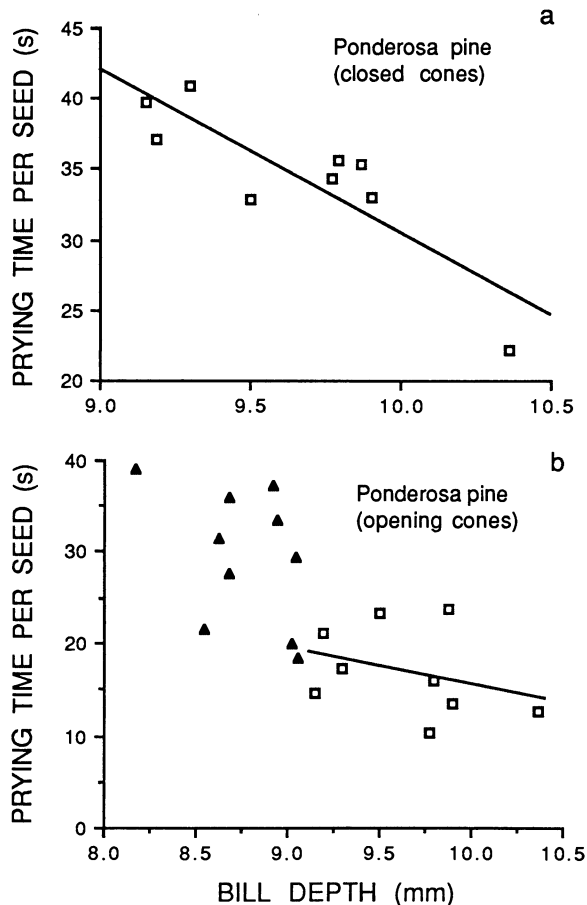
FIG. 8. Mean prying time per ponderosa pine seed in relation to crossbill bill depth. (a) Closed cones: line represents least squares regression (n = 2 cones per bird). (b) Partly open cones: line represents least squares regression for crossbill type 2 (n = 1–2 cones per bird). Symbols as in Fig. 4.

2 is probably optimal for foraging on smaller cones than those used in the experiments. In fact, the Rocky Mountain ponderosa pine (*P. p.* var. *scopulorum*) has a smaller cone than those used in the experiments (*P. p.* var. *ponderosa*), and as mentioned in the *Introduction,* is more likely to represent the key conifer.

Lodgepole pine.—Prying time differed significantly among types, with type 5 (and U) being the fastest (Table 2). Type 5 individuals tend to spend less time prying per seed than other crossbills of similar bill depths (Fig. 9), implying that unmeasured differences between species also influenced prying time. One character that may enable type 5 (and U) individuals to extract seeds so quickly from lodgepole pine cones is their relatively slender upper mandible. The width of the upper mandible narrows more rapidly for type 5 than for type 2 (0.68 mm vs. 0.53 mm decrease in width, respectively, for every millimetre from the base) (type U is intermediate at 0.60 mm: computed as [g − af]/h; symbols as in Table 1). A more slender upper mandible could enable a type 5 to extract the small

lodgepole pine seeds from a narrower gap than could a type 2, and thus reduce the time and energy to extract seeds (see Benkman 1987*b*).

To estimate the bill depth that minimizes prying time, I fit a quadratic equation to the data for types 4 and 2 (Fig. 9; $Y = 85.71 - 17.52X + 0.93X^2$, $r^2 = 0.54$, df = 17). I included only types 4 and 2 because they spent significantly less time prying per seed than type 3 individuals, but did not differ from each other (Table 2). I excluded type 5 from the regression because differences in bill shape, other than bill depth, between type 5 and other similarly sized crossbills affected prying time. Based on this equation, the bill depth minimizing prying time is 9.45 mm. The optimal bill depth is 9.30 mm. The mean bill depth of type 5 ($\bar{X} = 9.30$, SE = 0.09, n = 9 birds; mean type 5 bill depth from Groth [1991], 9.40 mm [n = 55] was slightly larger than what I measured) is the same as the optimum.

Are mean palate dimensions optimal for husking seeds?

Western hemlock.—Type 3 individuals have the narrowest husking grooves (Table 1, Fig. 5b) and husked the small hemlock seeds (Fig. 3) significantly faster than either types 2 or 4 (Table 3). Within type 3 a curvilinear relationship is suggested between husking time and husking groove width (Fig. 10; $Y = 11.42 - 13.60X + 4.43X^2$, $r^2 = 0.52$, df = 4, $P = .23$). Although not significant, this equation predicts an optimal groove width of 1.55 mm, which is identical to the mean for type 3 (Table 1).

Douglas-fir.—Type 4 spent significantly less time husking Douglas-fir seeds (Fig. 3) than did either the smaller type 3 or the larger type 2 (Table 3). Types 2 and 3 did not differ (Table 3). There was no pattern
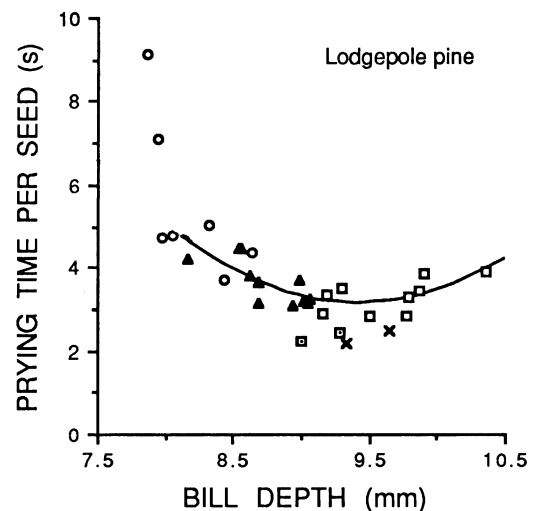

FIG. 9. Mean prying time per lodgepole pine seed in relation to bill depth of crossbills (n = 10–15 cones per bird). Curve represents quadratic equation fit to data from crossbill types 4 and 2. Symbols as in Fig. 4.

TABLE 3.   Seed husking times (in seconds) for the different crossbill types. Sample sizes are the numbers of crossbills. ANOVAs were conducted on ln-tranformed means of individual crossbills.

Type	Hemlock			Douglas-fir			Ponderosa pine			Lodgepole pine		
	$\bar{X}$	SE	n	$\bar{X}$	SE	n	$\bar{X}$	SE	n	$\bar{X}$	SE	n
3	1.08	0.04	7	1.90	0.11	7	...	...	...	1.22	0.03	7
4	1.80	0.08	11	1.54	0.05	11	27.38	6.22	11	1.25	0.02	11
2	2.17	0.11	9	1.93	0.08	9	5.96	0.27	9	1.40	0.05	9
5	...	...	...	...	...	...	14.72	3.60	2	1.13	0.02	2
U	...	...	...	...	...	...	9.31	1.56	2	1.11	0.02	2

Hemlock: ANOVA, $F_{2,24}$ = 41.2, $P < .0001$; there are significant differences among all three types (LSD Multiple Range test, $P < .05$). The means for each bird are based on an average of 68 seeds husked.

Douglas-fir: ANOVA, $F_{2,24}$ = 9.1, $P < .005$; types 3 and 2 differ significantly from type 4, but not from each other (LSD Multiple Range test, $P < .05$). The means for each bird are based on an average of 42 seeds husked.

Ponderosa pine: ANOVA, $F_{3,30}$ = 15.4, $P < .0001$; there are significant differences between type 4 and types 2 and U, and between types 2 and 5 (LSD Multiple Range test, $P < .05$). Types 5 and U combined differed significantly from type 2 (LSD Multiple Range test, $P < .05$). The means for each bird are based on an average of 14 seeds husked.

Lodgepole pine: ANOVA, $F_{4,26}$ = 7.2, $P < .0005$; type 2 differs significantly from all other types, and types 4 and U differ significantly (LSD Multiple Range test, $P < .05$). The means for each bird are based on an average of 54 seeds husked.

between seed husking time and husking groove width within type 4 (Fig. 11). However, for all three types combined a quadratic equation provides a fairly good fit to the data (Fig. 11; $Y = 8.08 - 7.38X + 2.12X^2$, $r^2 = 0.21$, df = 24). Based on this equation, the predicted optimal groove width for handling Douglas-fir seeds is 1.75 mm, the same as the mean for type 4 (Table 1).

Ponderosa pine. —Crossbills dropped pieces of kernel while husking the large ponderosa pine seeds (Fig. 3). I did not quantify kernel consumption rates (in milligrams per second) for type 3 individuals, because they often could not husk these seeds. Type 4 spent more time husking ponderosa pine seeds than types 2, 5, and U (Table 3), but I did not measure the amount of kernel dropped by type 4 individuals; they rarely husked seeds over the seed tray, and, instead, flew until they found a solid surface from which they could retrieve dropped seed pieces.

Complete seed husking data (kernel dropped and husking time) were obtained from types 2, 5, and U ($n = 13$ birds, 16 seeds per bird). Type 2 individuals have significantly wider grooves than those of types 5 and U (Table 1; see Fig. 5b) and also had significantly higher kernel consumption rates when husking ponderosa pine seeds (Fig. 12; $F_{1,11} = 42.60$, df = 1,11, $P < .0001$). The difference in intake rate is attributable to two factors. Types 5 and U dropped over 11 times more kernel per seed ($\bar{X} = 32.7\%$ dropped of each seed husked, $n = 4$ birds) than did type 2 ($\bar{X} = 2.8\%$, $n = 9$ birds; Kruskal–Wallis test, $H_2 = 7.74, P < .01$); crossbills did not drop any kernel while husking the smaller seeds of the other conifers. Second, type 2 spent less time husking ponderosa pine seeds than did type 5 (Table 3; although type U tended to spend less time husking the seeds than type 5, type U tended to drop a greater percentage of kernel per seed [36.1%] than type 5 [29.3%]).
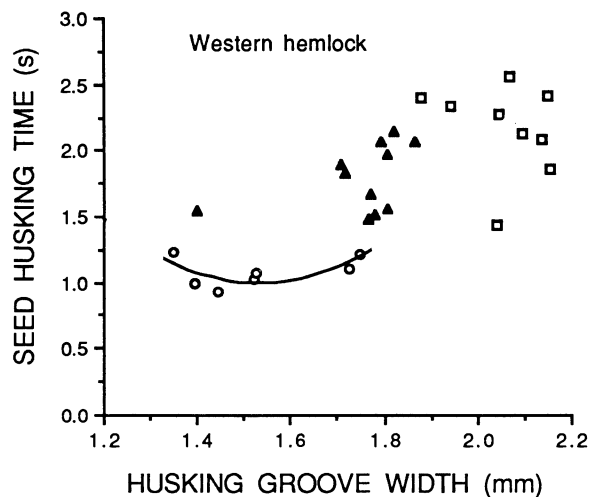

FIG. 10.   Mean western hemlock seed husking times for crossbill types 3, 4, and 2 in relation to husking groove width. Curve represents a quadratic equation fit to data from type 3. Symbols as in Fig. 4.
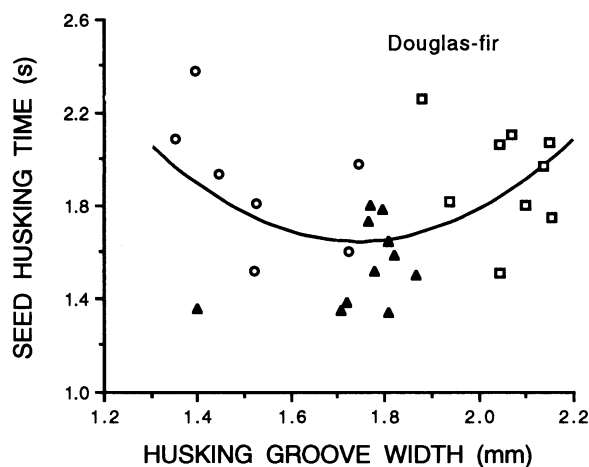

FIG. 11.   Mean Douglas-fir seed husking times for crossbill types 3, 4, and 2 in relation to husking groove width. Curve represents a quadratic equation fit to all the data. Symbols as in Fig. 4.
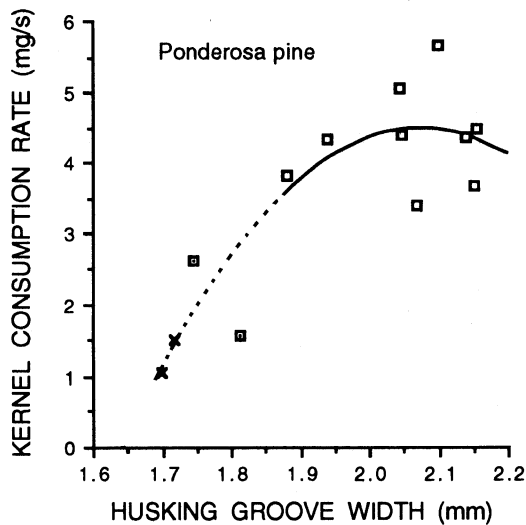
FIG. 12. (a) Mass of ponderosa pine seed kernel consumed per second in relation to husking groove width for crossbill types 2, 5, and U. Curve represents quadratic equation fit to data from type 2 (see text). The dashed line extends the curve to types 5 and U. The quadratic equation fit to all the data produces a virtually identical curve. Symbols as in Fig. 4.

The amount of kernel consumed per second was not significantly related to husking groove width for type 2 (Fig. 12; $Y = -116.80 + 118.86X - 29.09X^2$, $r^2 = 0.13$, df = 6, $P = .66$). However, a virtually identical regression line results if I combine types 2, 5, and U in the analysis ($Y = -98.61 + 99.40X - 23.96X^2$, $r^2 = 0.77$, df = 10). Based on the quadratic equation for type 2 alone (Fig. 12), the optimal groove width for husking ponderosa pine seeds is 2.05 mm, which is the same as that measured for type 2 (Table 1).

Lodgepole pine. — Type 5 spent significantly less time husking the small lodgepole pine seeds (Fig. 3) than did either types 4 or 2, but type 5 did not differ from type 3 (Table 3). As for Douglas-fir, seed husking time was not obviously related to husking groove width when only individuals from one or two types were analyzed (Fig. 13). Among all crossbill types seed husking time is curvilinearly related to husking groove width, and a
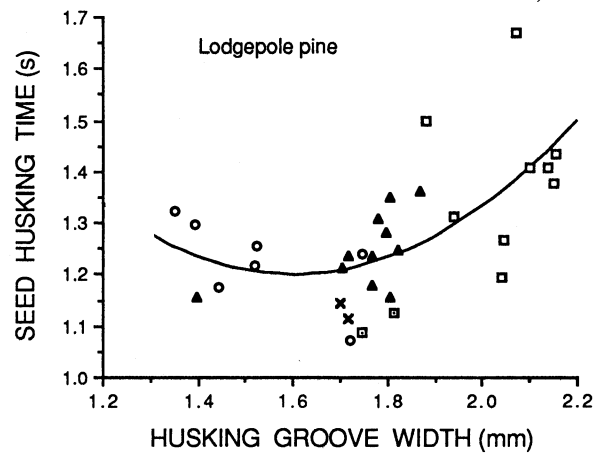

FIG. 13. Mean lodgepole pine seed husking times for all the crossbill types in relation to husking groove width. Curve represents a quadratic equation fit to all the data. Symbols as in Fig. 4.

quadratic equation fits the data well (Fig. 13; $Y = 3.38 - 2.71X + 0.85X^2$, $r^2 = 0.39$, df = 28). Based on this equation, the optimal groove width for husking lodgepole pine seeds is 1.60, which is 0.10 mm less than that measured for type 5 (Table 1).

General relationships and seed size variation. — All of the predicted optimal husking groove widths were remarkably close to the mean measurements for the respective types (Table 4). These results would gain credence if there were a consistent relationship between optimal husking groove width and seed size, such as seed width, as argued in the *Methods*. Because the different conifer seeds have similar shape (C. W. Benkman, *personal observation*; see Schopmeyer 1974), a good proportional measure of seed width is the cube root of seed mass. The linear and significant relationship (Fig. 14; $Y = 1.28 + 0.21X$, $r^2 = 0.998$, df = 2, $P < .002$) between the predicted optimal husking groove width for husking a given conifer seed (Y) and the cube root of the seed's mass (X) indicates that the individual results are not spurious and that the optimal husking groove width is directly proportional to seed size.

TABLE 4. Time minimizing, optimal and observed bill depths and husking groove widths. Mean estimates are rounded to nearest 0.05 mm.

	Bill depth (mm)			Husking groove width (mm)		
Conifer	Time minimizer	Optimal	Observed* ($\bar{X} \pm$ SE)	Optimal†	Optimal‡ for average seed	Observed* ($\bar{X} \pm$ SE)
Western hemlock	8.20	8.20	8.20 ± 0.07	1.55	1.55	1.55 ± 0.06
Douglas-fir	9.25	9.15	8.75 ± 0.08	1.75	1.75	1.75 ± 0.04
Ponderosa pine	···	···	9.70 ± 0.14	2.05	2.00	2.05 ± 0.04
Lodgepole pine	9.45	9.30	9.30 ± 0.09	1.60	1.65	1.70 ± 0.03

* Measurements for call type predicted to be adapted to respective key conifer.
† Optimal based on regressions for each conifer (*Results*).
‡ Optimal groove width (Y) was estimated from the regression $Y = 1.28 + 0.21X$ (*Results: General relationships and seed size variation*), where X equals the cube root of the average seed mass from the literature (Schopmeyer 1974: *Tsuga heterophylla*, 1.7 mg; *Pseudotsuga menziesii* var. *menziesii*, 11.5 mg; *Pinus contorta* var. *latifolia*, 4.8 mg; and Wells 1964: *Pinus ponderosa* var. *scopulorum*, 40.3 mg).
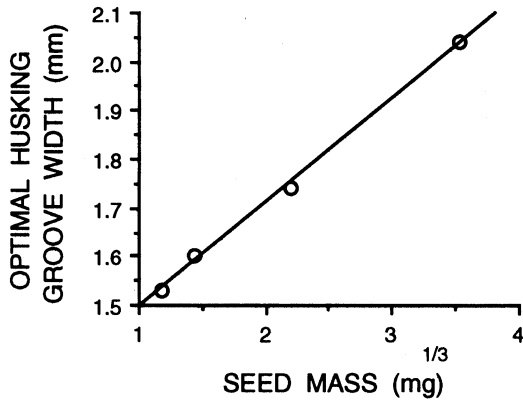
FIG. 14. Predicted optimal groove width of crossbills (to nearest 0.01 mm; Table 4) in relation to cube root of dry seed mass (Fig. 3). Each open circle represents the respective values for a given key conifer. Line represents least squares regression.

Moreover, this relationship enables us to predict the optimal groove width for a given seed size.

I was careful to select cones judged to be representative of an average cone for each conifer, but I was less careful with seed mass. The above relationship (Fig. 14), however, enables me to determine whether the mean observed husking groove widths correspond to the optima predicted for the average-sized seed of each key conifer, as given in the literature (Wells 1964, Schopmeyer 1974), rather than just to the seeds I used. The predicted optimal husking groove widths for husking the average-sized seed of each key conifer are also close to the observed for each type (Table 4).

Should there be selection for specialization?

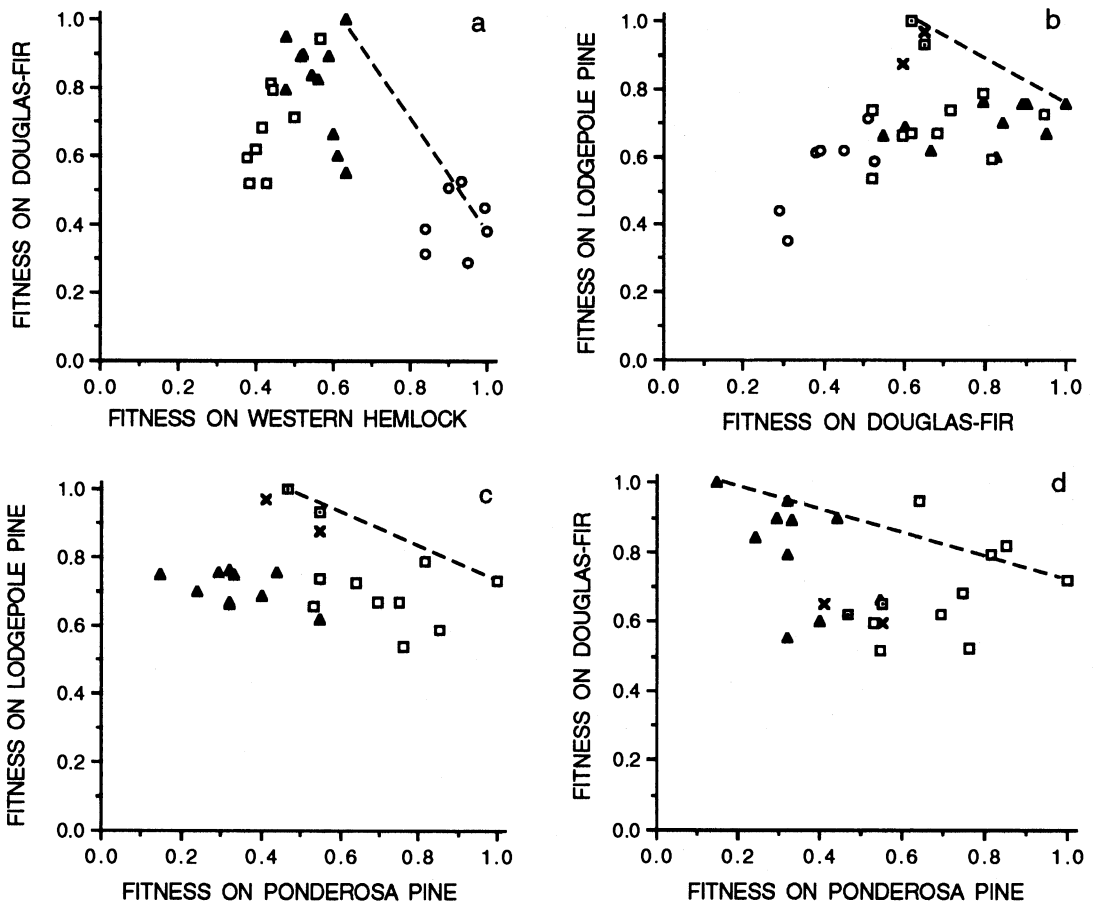Fig. 15 presents four fitness sets, with each point representing the estimated relative fitness (see *Meth-*

FIG. 15. Fitness sets for crossbills where the two seed resources are (a) Douglas-fir and western hemlock, (b) lodgepole pine and Douglas-fir, (c) lodgepole and ponderosa pines, and (d) Douglas-fir and ponderosa pine. Each point represents the estimated relative fitness for an individual (see text). Symbols as in Fig. 4. – – – connect the individuals with relative fitnesses of one on a conifer. Because I did not gather data on types 5 and U foraging on Douglas-fir or prying time on ponderosa pine (see *Methods*), I estimated these data based on relationships for the other types. Total foraging time per Douglas-fir seed was estimated with the equation fitted to the data for types 3, 4, and 2 ($Y = 398.8 - 84.0X + 4.5X^2$, $r^2 = 0.71$, df = 24; where Y is total time per seed and X is bill depth). Prying time per ponderosa pine seed was estimated from data on types 4 and 2 (see Fig. 9b: $Y = 129.8 - 11.6X$, $r^2 = 0.53$, df = 15; where Y is prying time per seed and X is bill depth). I did not incorporate data on kernel droppage of ponderosa pine seeds because I lacked such data for type 4. I used only time spent per ponderosa pine seed, which underestimates the differences in fitness between types because the type that spent the least amount of time per seed (type 2) also dropped the least amount of kernel. This, however, does not alter the results qualitatively.
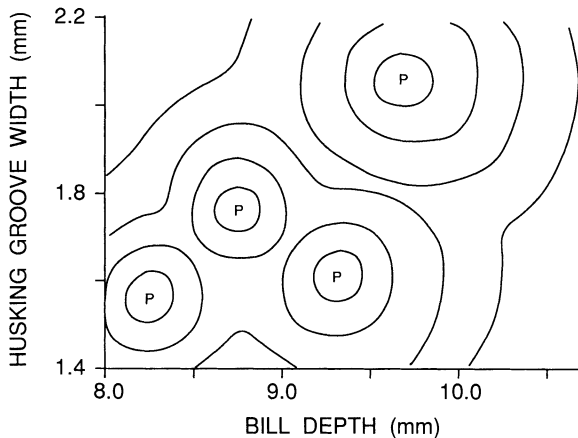
FIG. 16. A schematic of an adaptive landscape where the contours represent different fitnesses. Each "P" corresponds to an adaptive peak based on the predicted optimal bill depths and husking groove widths for foraging on a given conifer (see Table 4), except for the bill depths predicted for foraging on Douglas-fir and ponderosa pine. For Douglas-fir, I used the mean bill depth of type 4, because this probably better reflects the optimum than that predicted from the experiments (see *Methods*). For ponderosa pine, I used the mean bill depth of type 2, because I was unable to predict an optimal bill depth for foraging on ponderosa pine. All peaks are assumed of equal height and the depths of the valleys were approximated from the fitness sets (Fig. 15).

ods) of a single bird on each of two conifers. The shape of the outer boundary of points determines whether there will be selection for generalists or specialists (Levins 1968; also see Roughgarden 1979, Ricklefs 1990). A convex fitness set implies selection for a generalist, whereas a concave fitness set implies selection for one or two specialists (intermediate or generalist morphologies are selected against). Selection should favor specialists for each resource rather than a single specialist if crossbills forage selectively on the most profitable conifers (see Levins 1968), which they do (Benkman 1987*a*). The fitness set is concave if data points fall below and to the left of the dashed line that connects the two points with the maximum fitness on each of the conifers (Fig. 15). If away from either end of the dashed line points lie above and to the right of this line, then the fitness set is convex.

In three of the cases (Fig. 15a–c) the fitness sets are strongly concave, with most of the data points between the two maxima lying well below and to the left of the dashed lines. In the fourth case (Fig. 15d), the fitness set is concave with the exception of one bird, which lies above the middle of the dashed line. This individual was the closest of any individual to a Jack-of-all trades because it handled all seed types well: this bird had a wide husking groove like other type 2, but its overall palate structure was more like that of a type 4 (the type 2 most similar to type 4 in PC1 of palate structure in Fig. 5a). Nevertheless, it was still relatively inefficient on ponderosa pine compared to most type 2 individuals (Fig. 15d).

The two fitness sets contrasting fitnesses on the conifers with the most dissimilar cones, western hemlock and either pine, are not shown, in part, because they should be even more strongly concave than those contrasting more similar cones. The fitness set for western hemlock and lodgepole pine is strongly concave and similar to Fig. 15a (with lodgepole pine replacing Douglas-fir), whereas I have insufficient data to produce a fitness set for western hemlock and ponderosa pine. Nevertheless, this fitness set is likely to be more strongly concave than that for Douglas-fir and ponderosa pine (Fig. 15d), because type 3 is much more efficient on hemlock and much less efficient on ponderosa pine than type 4 (or type 2).

Concave fitness sets indicate that intermediate morphologies should be selected against and there should be selection for crossbills to specialize on single conifer species. The most fit individuals on one conifer are usually one-half to three-fourths as fit on other conifers, and each type is much more efficient on a different conifer, its key conifer.

These figures also lend insight into general patterns of conifer use. For example, it has been noted that type 2 use both ponderosa and lodgepole pines, whereas type 5 use lodgepole pine but not ponderosa pine (Groth 1991; T. P. Hahn, *personal communication*). This asymmetry is consistent with the fact that type 5 have a relatively low estimated fitness on ponderosa pine relative to that on lodgepole pine or compared to type 2 on either pine (Fig. 15c).

Adaptive landscape

Fig. 16 is an adaptive landscape showing relative fitness for crossbills in relation to bill depth and palate groove width. The four peaks correspond to the morphologies with the highest fitnesses on the respective key conifers. This presentation makes clear that the combination of bill and palate structures is critical in separating the best morphologies for foraging on each key conifer. Adaptive peaks tend to lie on a diagonal because large seeds are protected by robust cones. Peaks should also lie to the right and below the diagonal, representing conifers whose cones remain closed for extended periods (e.g., *Pinus c.* var. *latifolia*) and, hence, have evolved tougher scales (for a given seed size) to deter seed predators (see Smith 1970).

DISCUSSION

Because populations can differ from the optimum for many reasons (Gould and Lewontin 1979), the close match between crossbill bill structure and the optimum (Table 4) may surprise some, especially because crossbills are noted for their irruptions and large fluctuations in abundance (Newton 1972, Bock and Lepthien 1976, Benkman 1987*a*). These are characteristics that have led some to believe that populations should rarely conform to any optimum (e.g., Wiens 1977). Clearly, such a belief is unwarranted. Nevertheless, the close match

between the predicted optima and observed might be considered exceptional because few species are as specialized as crossbills. I would argue, instead, that specialization made it relatively easy to document such a match, not that the results are atypical. Rather, the match between the optimum and observed morphologies, especially structures involved in the securing and processing of foods, may often be close (e.g., Schluter and Grant 1984). Nevertheless, determining the optimum will be difficult when several distinct resources represent what I call a key resource. Not only will each resource select for a different optimum, but each resource may differ in importance.

The close match between the predicted optimum and the mean of each type implies, first, that I have correctly identified the critical factors influencing the ecology and evolution of crossbills in North America. These factors make the seeds of key conifers (see *Introduction*), rather than those of other conifers, a reliable resource for crossbills during winter and early spring year after year. Second, each crossbill type is specialized for foraging on a single key conifer species. Such specialization has arisen because specialists on single key conifers can presumably outcompete a generalist. This is implied by concave fitness sets.

Third, the close match between the optimum predicted for a single conifer and the observed indicates that competition has been important in selecting for the extreme specialization found in crossbills. Each specialist in the absence of competitors should have a morphology tending toward generalization, whereas in the presence of a competitor (another specialist) a more specialized morphology is expected (Lawlor and Smith 1976). Selection for specialization is particularly likely if all key conifers simultaneously limit the size of different crossbill populations so that the best option for individuals of any given type is to use the conifer on which it is most competitive (i.e., its key conifer). Such is probably the case. Late winter is the time when conifer seeds are generally most limiting to crossbills (Benkman 1987a, 1992).

Competitors can also shift the optimum by differentially depleting a given key resource (see Schluter et al. 1985). For example, if type 3 in addition to foraging on western hemlock harvest the softest Douglas-fir cones, then the optimal bill size for crossbills specializing on Douglas-fir would be larger than in the absence of type 3. Although crossbills may prefer cones with thinner cone scales, other traits, including the number of seeds per cone, influence cone choice (Benkman 1992). Because these traits may vary independently, or even inversely, and may change through time as cones open and seeds are shed, it is unclear whether potential competitors consistently shift the optimum bill size for foraging on a given conifer. (For the same reasons crossbills may have a relatively minor selective impact on many conifer cone traits compared to animals that concentrate their harvest over a brief interval, such as

before the cones open [e.g., *Tamiasciurus* spp.].) One exception may occur on Newfoundland where White-winged Crossbills (*L. leucoptera*) specialize on the black spruce (*Picea mariana*) cones that open in the autumn, and Newfoundland Crossbills (*L. c. percna*) specialize on black spruce cones that remain closed until spring (Benkman 1989a). This is a situation where depletion by one crossbill species might have shifted the adaptive peak for another species and resulted in character displacement.

Seasonality and adaptation

Adaptive peaks may shift between seasons, because crossbills forage on different species of conifers during different seasons (Newton 1972, Benkman 1987a). For instance, types 2 and 5 often forage on the thin-scaled and small-seeded Engelmann spruce (*Picea engelmannii*) in summer, but by autumn they forage usually on the much tougher cones of ponderosa and lodgepole pines, respectively (C. W. Benkman, *personal observation*). Such seasonal switches are common (Newton 1972, Benkman 1987a). However, the fact that the bill size and palate structure of each type are so close to the optima for foraging on its key conifer indicates that each crossbill type is adapted specifically for foraging on a single conifer species, which is also their usual winter food. Of course, a given morphology might also be optimal for foraging on a conifer other than the ones used in the experiments; however, I know of no likely candidates.

Selection for foraging efficiently on key conifers may occur during most winters because intake rates are often near the estimated minimum rate required to survive (see Benkman 1987a). Moreover, selection for foraging on key conifers is undoubtedly intense every 3–4 yr, because this is the rate at which cone crops of many conifers fail over large areas (Bock and Lepthien 1976; also see Fowells 1965). Key conifers are particularly critical at these times, because although less abundant than during most years, they are the most reliable seed sources. Erupting crossbills may experience selection for foraging on alternative foods (see, e.g., Newton 1972). However, this may have little impact on the subsequent population, because erupting crossbills likely suffer high mortality (Newton 1972, Benkman 1988a; also see Eriksson 1970), and, therefore, would contribute relatively little to subsequent generations (see Holt and Gaines 1992).

In contrast, crossbill intake rates are high relative to demands in summer (Benkman 1987a, 1990), and fitness differentials for bill size are probably small. In fact, different species of crossbills can have complete diet overlap during summer (Pulliainen 1972, Benkman 1987a; C. W. Benkman, *personal observation*) and breed successfully (Benkman 1985; C. W. Benkman, *personal observation*). When food is abundant, factors other than bill size or shape, such as age or experience, may be more critical to fitness (see Dunning 1986,

Martin 1987, Grant and Grant 1990), and the lack of correspondence between morphology and breeding season diet (e.g., Wiens and Rotenberry 1980), therefore, is not surprising (Baker and Baker 1973, Schoener 1982, Grant and Schluter 1984, Dunning 1986).

Specialization on one or several resources during lean times may be general to many species besides crossbills. Although few studies have determined resource dynamics, those that have (e.g., Leighton and Leighton 1983, Terborgh 1983, 1986a, b, Grant 1986a, Grant and Grant 1990) find species relying on several or just a single food type during periods of food scarcity. In the case of Darwin's finches (Geospiza), bill sizes approximate the optima for foraging on certain seed species eaten during lean times (Schluter and Grant 1984). In general morphology is more strongly correlated with lean season diet than with diets at other times (e.g., Newton 1967, 1972, Baker and Baker 1973, Schoener 1982, Grant 1986a). Presumably such a pattern arises because selection on bill structure is greater when food is scarce than when abundant; fitness differentials should be inversely proportional to the extent food availability is greater than individual demands (Sih 1982, Price 1987).

Phenotypic plasticity and hybridization

The two type U birds might represent type 2 birds whose palates were modified epigenetically. Several lines of evidence, however, indicate environmental effects have little effect on palate structure. First, it is doubtful that palates of adult crossbills undergo much change because all captive crossbills ate mostly lodgepole pine and sunflower seeds during the 6–9 mo between capture and when I measured palates, yet the different types maintained distinct (and optimal for their key conifer) palate structure. Second, a pair of Red Crossbills (a type 1 male with husking groove width of 1.45 mm and a type 3 female with husking groove width of 1.50 mm) bred in captivity (T. P. Hahn, personal communication), producing two offspring with 1.50 and 1.55 mm husking groove widths. These crossbills ate mostly shelled sunflower seeds, yet the offspring had groove widths that were similar to their parents. Moreover, epigenetic variation would be maladaptive because cues (i.e., conifer seeds eaten) encountered during ontogeny do not reliably indicate future conditions (see Levins 1963) or key conifers. For example, a given type of crossbill may breed foraging on seeds from different species of conifers with a wide range of seed sizes: in the summer of 1990 I found breeding type 2 foraging on P. ponderosa var. scopulorum (33.0 mg per seed [Wells 1964]) in one location and in another location Picea engelmannii (3.4 mg per seed [Schopmeyer 1974]), and in two other locations probably breeding while foraging on P. contorta var. murrayana (≈8.3 mg per seed [Critchfield 1980]) and Pinus longaeva (25.1 mg per seed for the closely related P. aristata [Schopmeyer 1974]).

Alternatively, the two type U may be hybrids between types 2 and 5. Hybridization is probably most likely when females (generally the rarer sex) of one type occur uncommonly among another type that is abundant. Indeed, this is the type of situation during which nesting hybrid pairs have been found in the wild (C. W. Benkman, personal observation; T. P. Hahn, personal observation); types also interbreed in captivity (Groth 1991; T. P. Hahn, personal communication). The summer and fall a year before I captured the crossbills, type 5 were abundant and type 2 much less common in the lodgepole pine forests in and around Yellowstone National Park (T. P. Hahn, personal communication). These crossbills probably bred following the extensive fires in 1988, which would have caused the serotinous cones to open and make their seeds abundantly available to crossbills. This tremendous abundance of seed should have enabled many crossbills, nearly regardless of bill size, to breed and might have resulted in mixed pairs. Nevertheless, in spite of occasional hybridization, concave fitness sets imply the potential for strong disruptive selection that would maintain or reinforce differences between types.

Evidence of such reinforcement promoting species isolation may occur in vocalizations. For example, types 5 and 6 have similar vocalizations, and they are allopatric (Groth 1991). Such similarity in vocalizations could represent convergence or lack of divergence. In support of the latter view, type 6 may be more closely related to type 5 than to any other North American crossbill (see Groth 1991). In contrast, types 2 and 5 are among the most similar of all types in allozyme variation, yet they differ substantially in vocalizations (Groth 1991). Because types 2 and 5 often co-occur and may regularly breed concurrently while foraging on the same species of conifer (e.g., Picea engelmannii) (C. W. Benkman, personal observation), their pronounced differences in vocalizations may represent character displacement. Similarly, types 3 and 4 overlap greatly in distributions, are the most similar of all types in allozyme variation, yet they differ much in vocalizations (see Groth 1991).

The origin of specialization and crossbill diversity

Specialization might have arisen in the last glacial period if the distributions of the key conifers were more isolated so that only a single key conifer was encountered by a crossbill population. For example, the Rocky Mountain ponderosa pine (P. p. var. scopulorum), a hypothesized key conifer, had a very restricted distribution throughout the last glacial relative to its current widespread distribution (Thompson 1988). Indeed, the temporary composition of terrestrial plant and animal assemblages over geologic time (e.g., Graham 1986, Jacobson et al. 1987, Thompson 1988) may have forced many species to specialize on either a single or narrow subset of species that were tracked over time.

On the other hand, during the last glacial the ranges of many conifer species might have been too small to support specialists on all but the most reliable cone-producing conifers. In fact, it is doubtful crossbills specialized on any one conifer confined to eastern North America during the last glacial, because the distributions of eastern conifers were severely restricted (Jacobson et al. 1987; also see Critchfield 1984) and seed crop failures are apparently more widespread in eastern than western North America (James 1958, Bock and Lepthien 1976). The present diversity of crossbills in North America, therefore, might largely reflect the recent postglacial expansion of conifers. Such recent diversification is consistent with the similarity of allozymes among crossbill types (see Groth 1991) and with the origin of the Newfoundland Crossbill (Benkman 1989a).

Some types might have differentiated in sympatry, because some key conifers have not been geographically isolated (see Barnosky et al. 1987). Concave fitness sets suggest an explanation for why crossbills specialize on the different key conifers, and how morphs, each specialized on different conifers, might have arisen (Levins 1968; see Wilson 1989 for a scenario of sympatric differentiation involving both density- and frequency-dependent selection that could apply to crossbills; also see Rosenzweig 1978, Pimm 1979, Wilson and Turelli 1986). However, why the different crossbill types represent distinct populations rather than different morphs within a population (e.g., African seedcracker finches *Pyrenestes ostrinus* [Smith 1987, 1990]) requires, in addition, positive assortative mating between types. Positive assortative mating could follow as a correlated character to habitat selection (Slatkin 1982, Rice 1984, 1987), thereby circumventing the formidable requirement of linkage disequilibrium between habitat use and positive assortative mating for speciation (Felsenstein 1981). Because crossbills specialize on the most profitable conifer and differ in conifer/habitat use depending on morphology (Benkman 1987a), different morphs should tend to occur in different habitats promoting reproductive isolation between specialists even in sympatry.

Are there other conifers in the Northwest that could support crossbills?

Only one other conifer in the Northwest, Sitka spruce (*Picea sitchensis*), likely represents a key conifer. It is a prolific seed producer (Fowells 1965), consistently holds seeds in its cones through winter (Ruth and Berntsen 1955, Harris 1969) and may occur over a large enough geographic area so that cones are likely to be produced every year. Sitka spruce cones have perhaps slightly thinner scales, but are comparable in size to Douglas-fir cones. However, Sitka spruce seeds ($\bar{X} = 2.1$ mg per seed, SE = 0.09, $n = 5$ trees, 50 seeds) are only one-fifth as large as those of Douglas-fir (10.7 mg per seed). Thus, a crossbill adapted specifically to Sitka spruce should have a bill of similar or slightly smaller size as type 4, but with narrower husking groove widths (≈ 1.55 mm instead of 1.75 mm, see Fig. 14). Another call type, type 1, has been found recently in the coastal forests during the last two large Sitka spruce cone crops (T. P. Hahn, *personal communication*). This call type has a bill of comparable size to that of type 4 (Groth 1991) and the husking groove width of the one type 1 I have measured was 1.45 mm. More research is required on this type, especially considering the rapid loss of Sitka spruce forests in the Pacific Northwest.

Although there are many other conifers in the Northwest, species that could represent key conifers, other than those previously mentioned, are doubtful. However, geographic variation within the key conifers that regularly produce cone crops within a local area may result in selection for different phenotypes in different areas. For example, on the mainland of North America the key conifer for White-winged Crossbills is partly open black spruce cones (Benkman 1987a, b). On Newfoundland black spruce cones differ from the mainland because of the absence of red squirrels (*Tamiasciurus hudsonicus*), and crossbills have evolved a much deeper bill for harvesting seeds from the closed black spruce cones (Benkman 1989a). A similar situation may be occurring in lodgepole pine. Within lodgepole pine (*L. c.* var. *latifolia*) there is an isolated population in the Cypress Hills (on the border of Alberta and Saskatchewan) that has substantially larger cones and seeds than other populations (Wheeler and Guries 1982). As on Newfoundland, the distinct structure of these cones might have evolved because of the absence of red squirrels. A large bill would be adaptive for foraging on the relatively large lodgepole pine cones. In fact, Red Crossbills collected in the Cypress Hills possess a distinctly deeper bill (mean depth = 10.04 mm, SE = 0.05, $n = 10$ study skins; also see Godfrey 1950) than type 5 (or type 2).

Geographic variation in other key conifers, such as Douglas-fir and ponderosa pine, which fluctuate more in annual cone crop production than the other key conifers and where individual crossbills may regularly move between geographic areas, should select for a crossbill morphology intermediate between the optima for the different geographic variants. This latter explanation could account, in part, for type 4 having a bill depth smaller than optimal for foraging on the relatively large cones of the coastal variety of Douglas-fir. On the other hand, the Douglas-fir cones I used in the experiments may not have represented winter cones very well (see *Methods*).

CONCLUSIONS

The mean bill depth or palate structure, or both, of each of four crossbill taxa closely correspond to the predicted optima or adaptive peaks. This indicates, first, I have correctly identified the key food resources,

which are characterized as foods that are consistently available during lean periods (late winter). Key conifers on the mainland of North America are those that hold seeds in partly closed cones through winter; crossbills are particularly effective consumers of seeds secured between partly closed scales (Benkman and Lindholm 1991), especially when few seeds remain in the cone. This ability to out-compete competitors delimits the conifers that can serve as key resources for crossbills. Most of the potential competitors of crossbills (e.g., *Carduelis* finches, woodpeckers, nuthatches) are limited by foods other than conifer seeds (Smith and Balda 1979). These species opportunistically exploit large cone crops.

Second, although crossbills may undergo large fluctuations in population numbers, such fluctuations have not impeded adaptation to critical periods. Indeed, during much of the year seed resources are extremely abundant (Benkman 1990) and selection for foraging efficiency is probably relaxed. But during most winters some to most of the crossbill populations likely experience optimizing selection that is consistent in form from year to year. This is apparently sufficient for the optimal phenotype to be maintained (also see Grant 1986*b*).

Third, the diversity in cone structure and seed size and trade-offs in foraging efficiency experienced by crossbills are responsible for the diversity of crossbill types. Resource diversity depends on conifer taxonomic diversity, variation in structure and phenology resulting from selective predation by seed predators such as squirrels (especially *Tamiasciurus*) (Smith 1970, Elliott 1974, Benkman 1989*a*), and abiotic factors influencing seed size (Baker 1972, Turner 1985). The steepness of the trade-offs indicates that deviation from the optimum greatly reduces fitness, which implies that the slight absolute size differences between types is of ecological importance strengthening the case for recognizing types as species (see Groth 1991).

Finally, key resources or key conifers are merely what MacArthur and Levins (1964) refer to as resources in their theories of species diversity. In addition to qualifying what is a key resource for crossbills and testing this quantitatively, this study reaffirms the value of the MacArthur-Levins approach (also see Leigh 1990). However, determining what is a resource, or what I call a key resource, for most populations is not an easy matter, and such determination remains a major obstacle to ecology. Moreover, this study reinforces the point that determining the period(s) of food limitation is critical for testing ecological and evolutionary hypotheses (e.g., Tilman 1982). I would further stress that trade-offs need to be examined in the context of limiting resources (e.g., Benkman 1988*a*). Studies examining trade-offs in the absence of such information on resource dynamics (e.g., Huey and Hertz 1984) may have limited value, much like competition studies conducted during periods when food is abundant.

LITERATURE CITED

Armbruster, W. S. 1990. Estimating and testing the shapes of adaptive surfaces: the morphology and pollination of *Dalechampia* blossoms. American Naturalist **135**:14–31.

Bailey, A. M., R. J. Niedrach, and A. L. Baily. 1953. The Red Crossbills of Colorado. Publication of the Denver Museum of Natural History **9**:1–64.

Baker, H. G. 1972. Seed weight in relation to environmental conditions in California. Ecology **53**:997–1010.

Baker, M. C., and A. E. M. Baker. 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. Ecological Monographs **43**:193–212.

Barnosky, C. W., P. M. Anderson, and P. J. Bartlein. 1987. The northwestern U.S. during deglaciation; vegetational history and paleoclimatic implications. Pages 289–321 *in* W. F. Ruddiman and H. E. Wright, Jr., editors. North America and adjacent oceans during the last deglaciation. The geology of North America. Volume K-3. Geological Society of America, Boulder, Colorado, USA.

Benkman, C. W. 1985. The foraging ecology of crossbills in eastern North America. Dissertation. State University of New York, Albany, New York, USA.

———. 1987*a*. Food profitability and the foraging ecology of crossbills. Ecological Monographs **57**:251–267.

———. 1987*b*. Crossbill foraging behavior, bill structure, and patterns of food profitability. Wilson Bulletin **99**:351–368.

———. 1988*a*. Seed handling efficiency, bill structure, and the cost of specialization for crossbills. Auk **105**:715–719.

———. 1988*b*. On the advantages of crossed mandibles: an experimental approach. Ibis **129**:288–293.

———. 1989*a*. On the evolution and ecology of island populations of crossbills. Evolution **43**:1324–1330.

———. 1989*b*. Intake rate maximization and the foraging behaviour of crossbills. Ornis Scandinavica **20**:65–68.

———. 1989*c*. Breeding opportunities, foraging rates, and parental care in White-winged Crossbills. Auk **106**:483–485.

———. 1990. Foraging rates and the timing of crossbill reproduction. Auk **107**:376–386.

———. 1991. Predation, seed size partitioning, and the evolution of body size in seed-eating finches. Evolutionary Ecology **5**:118–127.

———. 1992. White-winged Crossbills. *In* A Poole, P. Stettenheim, and S. Gill, editors. The birds of North America. Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA.

Benkman, C. W., and A. K. Lindholm. 1991. An experi-

mental analysis of the advantages and evolution of a mor-
phological novelty. Nature **349**:519–520.

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.

Boag, P. T., and A. van Noordwijk. 1987. Quantitative
genetics. Pages 45–78 in F. Cooke and P. A. Buckley, ed-
itors. Avian genetics: a population and ecological approach.
Academic Press, New York, New York, USA.

Bock, C. E., and L. W. Lepthien. 1976. Synchronous erup-
tions of boreal seed-eating birds. American Naturalist **110**:
559–571.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North
America. Volume 1. United States Department of Agri-
culture, Agricultural Handbook **654**.

Campbell, R. K. 1979. Genecology of Douglas-fir in a wa-
tershed in the Oregon Cascades. Ecology **60**:1036–1050.

Critchfield, W. B. 1957. Geographic variation in *Pinus con-
torta*. Publication 3, Maria Moors Cabot Foundation, Cam-
bridge, Massachusetts, USA.

———. 1980. Genetics of lodgepole pine. United States
Forest Service Research Paper **WO-37**.

———. 1984. Impact of the Pleistocene on the genetic struc-
ture of North American conifers. Pages 70–118 in R. M.
Lanner, editor. Proceedings of the Eighth North American
Forest Biology Workshop. Utah State University, Logan,
Utah, USA.

Crossley, D. I. 1955. The production and dispersal of lodge-
pole pine seed. Forest Research Division, Canada Depart-
ment Northern Affairs and Natural Resources, Technical
Note **25**.

———. 1956. Fruiting habits of lodgepole pine. Forest Re-
search Division, Canadian Forestry Branch, Technical Note
Number **35**.

Curtis, J. D., and M. W. Foiles. 1961. Ponderosa pine seed
dissemination into group clearcuttings. Journal of Forestry
59:766–767.

Dahms, W. G., and J. W. Barrett. 1975. Seed production
of central Oregon ponderosa and lodgepole pine. Pacific
Northwest Forest and Range Experiment Station, Research
Paper **PNW-191**.

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.

———. 1987. The "old northeastern" subspecies of Red
Crossbill. American Birds **41**:188–194.

Dunning, J. B., Jr. 1984. Body weights of 686 species of
North American birds. Western Bird Banding Association
Monographs Number **1**.

———. 1986. Shrub-steppe bird assemblages revisited: im-
plications for community theory. American Naturalist **128**:
82–98.

Elliott, P. F. 1974. Evolutionary response of plants to seed-
eaters: pine squirrel predation on lodgepole pine. Evolution
28:221–231.

Eriksson, K. 1970. Ecology of the irruption and wintering
of Fennoscandian Redpolls (*Carduelis flammea* coll.). An-
nales Zoologici Fennici **7**:273–282.

Felsenstein, J. 1981. Skepticism toward Santa Rosalia, or
why are there so few kinds of animals? Evolution **35**:124–
138.

Fowells, H. A. 1965. Silvics of forest trees in the United
States. United States Department of Agriculture, Agricul-
tural Handbook Number **271**.

Fowells, H. A., and G. H. Schubert. 1956. Seed crops of
forest trees in the pine region of California. United States
Department of Agriculture Technical Bulletin Number **1150**.

Garman, E. H. 1951. Seed production by conifers in the
coastal region of British Columbia related to dissemination

and regeneration. British Columbia Forest Service Tech-
nical Publication Number T. **35**.

Gashwiler, J. S. 1969. Seed fall of three conifers in west-
central Oregon. Forest Science **15**:290–295.

Gashwiler, J. S., and A. L. Ward. 1966. Western redcedar
seed, a food of pine siskins. Murrelet **47**:73–75.

Godfrey, W. E. 1950. Birds of the Cypress Hills and Flotten
Lake regions, Saskatchewan. National Museum of Canada,
Department of Resources and Development, Bulletin
Number **120**.

Godman, R. M. 1953. Seed dispersal in southeast Alaska.
United States Forest Service Alaska Forest Research Center
Technical Note **16**.

Gould, S. J., and R. C. Lewontin. 1979. The spandrels of
San Marco and the Panglossian paradigm: a critique of the
adaptationist programme. Proceedings of the Royal Society
of London B **205**:581–598.

Graham, R. W. 1986. Response of mammalian commu-
nities to environmental changes during the later Quater-
nary. Pages 300–313 in J. Diamond and T. J. Case, editors.
Community ecology. Harper & Row, New York, New York,
USA.

Grant, B. R., and P. R. Grant. 1990. Evolutionary dynamics
of a natural population: the large Cactus Finch of the Ga-
lápagos. University of Chicago Press, Chicago, Illinois, USA.

Grant, P. R. 1986a. Ecology and evolution of Darwin's
Finches. Princeton University Press, Princeton, New Jer-
sey, USA.

———. 1986b. Interspecific competition in fluctuating en-
vironments. Pages 173–191 in J. Diamond and T. J. Case,
editors. Community ecology. Harper & Row, New York,
New York, USA.

Grant, P. R., and D. Schluter. 1984. Interspecific compe-
tition inferred from patterns of guild structure. Pages 201–
223 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, Prince-
ton, New Jersey, USA.

Griscom, L. 1937. A monographic study of the Red Cross-
bill. Proceedings of the Boston Society of Natural History
41:77–210.

Groth, J. G. 1988. Resolution of cryptic species in Appa-
lachian Red Crossbills. Condor **90**:745–760.

———. 1991. Cryptic species of nomadic birds in the Red
Crossbill (*Loxia curvirostra*) complex of North America.
Dissertation. University of California, Berkeley, California,
USA.

Hagar, D. C. 1960. The interrelationships of logging, birds,
and timber regeneration in the Douglas-fir region of north-
western California. Ecology **41**:116–125.

Harris, A. S. 1969. Ripening and dispersal of a bumper
western hemlock–Sitka spruce seed crop in southeast Alas-
ka. United States Department of Agriculture Pacific North-
west Forest and Range Experimental Station Research Note
PNW-105.

Hetherington, J. C. 1965. The dissemination, germination,
and survival of seed on the west coast of Vancouver Island
from western hemlock and associated species. British Co-
lumbia Forest Service Research Note **39**.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pa-
cific Northwest: an illustrated manual. University of Wash-
ington Press, Seattle, Washington, USA.

Holt, R. D., and M. S. Gaines. 1992. Analysis of adaptation
in heterogeneous landscapes: implications for the evolution
of fundamental niches. Evolutionary Ecology **6**:433–447.

Huey, R. B., and P. E. Hertz. 1984. Is a Jack-of-all-tem-
peratures a master of none? Evolution **38**:441–444.

Hutchinson, G. E. 1968. When are species necessary? Pages
177–186 in R. C. Lewontin, editor. Population biology and

evolution. Syracuse University Press, Syracuse, New York, USA.

Isaac, L. A. 1943. Reproductive habits of Douglas-fir. Charles Lathrop Park Forestry Foundation, Washington, D.C., USA.

Jacobson, G. L., T. Webb, and E. C. Grimm. 1987. Patterns and rates of vegetation change during the deglaciation of eastern North America. Pages 277–288 in W. F. Ruddiman and H. E. Wright, Jr., editors. North America and adjacent oceans during the last deglaciation. The geology of North America. Volume K-3. Geological Society of America, Boulder, Colorado, USA.

James, D. 1958. A summary of the winter season. Audubon Field Notes 12:256–260.

Jollie, M. 1953. Plumages, molt, and racial status of Red Crossbills in northern Idaho. Condor 55:193–197.

Kingsolver, J. G. 1988. Thermoregulation, flight, and the evolution of wing pattern in pierid butterflies: the topography of adaptive landscapes. American Zoologist 28:899–912.

Knox, A. 1990. The sympatric breeding of Common and Scottish Crossbills Loxia curvirostra and L. scotia and the evolution of crossbills. Ibis 132:454–466.

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 University Press, Cambridge, England.

Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. Evolution 30:314–334.

Lawlor, L. R., and J. M. Smith. 1976. The coevolution and stability of competing species. American Naturalist 110:79–99.

Leigh, E. G., Jr. 1990. Community diversity and environmental stability: a re-examination. Trends in Ecology and Evolution 5:340–344.

Leighton, M., and D. R. Leighton. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. Pages 181–196 in S. L. Sutton, T. C. Whitmore, and A. C. Chadwick, editors. Tropical rain forest: ecology and management. Blackwell Scientific, London, England.

Levins, R. 1963. Theory of fitness in a heterogeneous environment. II. Developmental flexibility and niche selection. American Naturalist 97:75–90.

———. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey, USA.

Liem, K. F., and L. S. Kaufman. 1984. Intraspecific macroevolution: functional biology of the polymorphic cichlid species Cichlasoma minckleyi. Pages 203–215 in A. A. Echelle and I. Kornfield, editors. Evolution of fish species flocks. University of Maine Press, Orono, Maine, USA.

Ligon, J. D. 1973. Foraging behavior of the White-headed Woodpeckers in Idaho. Auk 90:862–869.

Lotan, J. E., and D. A. Perry. 1983. Ecology and regeneration of lodgepole pine. United States Department of Agriculture, Agricultural Handbook Number 606.

MacArthur, R. H. 1972. Geographical ecology. Harper & Row, New York, New York, USA.

MacArthur, R. H., and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. Proceedings of the National Academy of Sciences (USA) 51:1207–1210.

Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. Annual Review of Ecology and Systematics 18:453–487.

Massa, B. 1987. Variations in Mediterranean crossbills Loxia curvirostra. Bulletin of the British Ornithological Club 107:118–129.

Monson, G., and A. R. Phillips. 1981. Annotated checklist of birds of Arizona. Second edition. University of Arizona Press, Tucson, Arizona, USA.

Morrison, M. L., and K. A. With. 1987. Interseasonal and intersexual resource partitioning in Hairy and White-headed Woodpeckers. Auk 104:225–233.

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.

———. 1972. Finches. Collins, London, England.

Olesen, P. O. 1972. Collection of forest tree seed in Mexico, 1968. Pages 29–37 in J. Burley and D. G. Nikles, editors. Selection and breeding to improve some tropical conifers. Volume 1. Commonwealth Forestry Institute, Oxford University, Oxford, England.

Olson, D. S. 1932. Seed release from western white pine and ponderosa pine cones. Journal of Forestry 30:748–749.

Otvos, I. S., and R. W. Stark. 1985. Arthropod food of some forest-inhabiting birds. Canadian Entomologist 117:971–990.

Payne, R. B. 1987. Populations and type specimens of a nomadic bird: comments on the North American crossbills Loxia pusilla Gloger 1834 and Crucirostra minor Brehm 1845. Occasional Papers of the Museum of Zoology of the University of Michigan, Number 714.

Pickford, A. E. 1929. Studies of seed dissemination in British Columbia. Forestry Chronicle 5:8–16.

Pimm, S. L. 1979. Sympatric speciation: a simulation model. Biological Journal of the Linnean Society 11:131–139.

Price, T. D. 1987. Diet variation in a population of Darwin's finches. Ecology 68:1015–1028.

Pulliainen, E. 1972. Summer nutrition of crossbills (Loxia pytyopsittacus. L. curvirostra and L. leucoptera) in northeast Lapland. Annales Zoologica Fennica 9:28–31.

Rice, W. R. 1984. Disruptive selection on habitat preference and the evolution of reproductive isolation: a simulation study. Evolution 38:1251–1260.

———. 1987. Speciation via habitat specialization. Evolutionary Ecology 1:301–314.

Ricklefs, R. E. 1990. Ecology. Third edition. W. H. Freeman, New York, New York, USA.

Robinson, F. 1989. Dental, palate and tongue imprints of bats: a new field technique. Journal of Zoology (London) 219:681–684.

Rosenzweig, M. L. 1978. Competitive speciation. Biological Journal of the Linnean Society 10:275–289.

Roughgarden, J. 1979. Theory of population genetics and evolutionary ecology: an introduction. MacMillan, New York, New York, USA.

Ruffner, J. A. 1980. Climates of the states. Volume I. Second edition. Gale Research Company, Book Tower, Detroit, Michigan, USA.

Ruth, R. H., and C. M. Berntsen. 1955. A 4-year record of Sitka spruce and western hemlock seed fall. United States Department of Agriculture Pacific Northwest Forest and Range Experimental Station Research Paper Number 12.

Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. Evolution 42:849–861.

Schluter, D., and P. R. Grant. 1984. Determinants of morphological patterns in communities of Darwin's Finches. American Naturalist 123:175–196.

Schluter, D., T. D. Price, and P. R. Grant. 1985. Ecological character displacement in Darwin's finches. Science 227:1056–1059.

Schoener, T. W. 1982. The controversy over interspecific competition. American Scientist 70:586–595.

Schopmeyer, C. S. 1974. Seeds of woody plants in the United States. United States Department of Agriculture, Agricultural Handbook Number 450.

Shearer, R. C., and W. C. Schmidt. 1971. Ponderosa pine cone and seed losses. Journal of Forestry 69:370–372.

Sih, A. 1982. Optimal patch use: variation in selective pres-

sure for efficient foraging. American Naturalist **120**:666–685.

Slatkin, M. 1982. Pleiotropy and parapatric speciation. Evolution **36**:263–270.

Smith, C. C. 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, T. B. 1987. Bill size polymorphism and intraspecific niche utilization in an African finch. Nature **329**:717–719.

——. 1990. Comparative breeding biology of the two bill morphs of the Black-bellied Seedcracker. Auk **107**:153–160.

Southern, H. N. 1945. Correlation between beak and food in the crossbills. Ibis **87**:287.

Stallcup, P. L. 1968. Spatio-temporal relationships of nuthatches and woodpeckers in ponderosa pine forests of Colorado. Ecology **49**:831–843.

——. 1969. Hairy Woodpeckers feeding on pine seeds. Auk **86**:134–135.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey, USA.

Sudworth, G. B. 1967. Forest trees of the Pacific slope. Dover, New York, New York, USA.

Terborgh, J. 1983. Five New World primates: a study in comparative ecology. Princeton University Press, Princeton, New Jersey, USA.

——. 1986a. Community aspects of frugivory in tropical forests. Pages 371–384 *in* A. Estrada and T. H. Flemming, editors. Frugivores and seed dispersal. W. Junk, Dordrecht, The Netherlands.

——. 1986b. Keystone plant resources in the tropical forest. Pages 330–344 *in* M. E. Soulé, editor. Conservation biology. Sinauer, Sunderland, Massachusetts, USA.

Thompson, R. S. 1988. Vegetation dynamics in the western United States: modes of response to climatic fluctuations. Pages 415–458 *in* B. Huntley and T. Webb III, editors. Vegetation history. Kluwer, Boston, Massachusetts, USA.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

Tordoff, H. B. 1954. Social organization and behavior in a flock of captive, nonbreeding Red Crossbills. Condor **56**:346–358.

Turner, D. P. 1985. Successional relationships and a comparison of biological characteristics among six northwestern conifers. Bulletin of the Torrey Botanical Club **112**:421–428.

Walsberg, G. E. 1983. Avian ecological energetics. Pages 161–220 *in* Avian biology. Volume 7. D. S. Farner, J. R. King, and K. C. Parkes, editors. Academic Press, New York, New York, USA.

Wells, O. O. 1964. Geographic variation in ponderosa pine. I. The ecotypes and their distribution. Silvae Genetica **13**:89–103.

Wheeler, N. C., and R. P. Guries. 1982. Population structure, genic diversity, and morphological variation in *Pinus contorta* Dougl. Canadian Journal of Forest Research **12**:595–606.

Wiens, J. A. 1977. On competition and variable environments. American Scientist **65**:590–597.

Wiens, J. A., and J. T. Rotenberry. 1980. Patterns of morphology and ecology in grassland and shrubsteppe bird populations. Ecological Monographs **50**:287–308.

Wilson, D. S. 1989. The diversification of single gene pools by density- and frequency-dependent selection. Pages 366–385 *in* D. Otte and J. A. Endler, editors. Speciation and its consequences. Sinauer, Sunderland, Massachusetts, USA.

Wilson, D. S., and M. Turelli. 1986. Stable underdominance and the evolutionary invasion of empty niches. American Naturalist **127**:835–850.

Wright, S. 1931. Evolution in Mendelian populations. Genetics **16**:97–159.

Ziswiler, V. 1965. Zur Kenntnis des Samenöffnenes und der Struktur des hörnernen Gaumens bei körnerfressenden Oscines. Journal für Ornithologie **106**:1–48.