population that was formed by a recent bottleneck. Genetics 111:675–689.

NEI, M., T. MARUYAMA, AND R. CHAKRABORTY. 1975. The bottleneck effect and genetic variability in populations. Evolution 29:1–10.

POLANS, N. O., AND R. W. ALLARD. 1985. Inheritance of electrophoretically detectable variants in ryegrass. J. Hered. 76:61–62.

ROBERTSON, A. 1955. Selection in animals: Synthesis. Cold Spr. Harb. Symp. Quant. Biol. 20:225–229.

WATTERSON, G. A. 1984. Allele frequencies after a bottleneck. Theoret. Popul. Biol. 26:387–407.

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

WRIGHT, S., AND W. E. KERR. 1954. Experimental studies of the distribution of gene frequencies in very small populations of Drosophila melanogaster. II. Bar. Evolution 8:225–240.

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ON THE EVOLUTION AND ECOLOGY OF ISLAND POPULATIONS OF CROSSBILLS

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The correlation between bill sizes of different species of Eurasian crossbills (*Loxia*) and the sizes of the conifer cones which crossbills usually exploit is well-known (Lack, 1944; Newton, 1967). In North America, there is a similar correspondence between bill sizes of White-winged Crossbills (*Loxia l. leucoptera*) and Red Crossbills (*L. curvirostra bendirei*) and the sizes of cones on which they feed; this correspondence extends to most subspecies of the Red Crossbill (Griscom, 1937; Benkman 1987a, 1987b). However, the resident Red Crossbill on Newfoundland (*L. c. percna*) (Griscom, 1937; Dickerman, 1986a) is an exception to this general pattern.

The subspecies *percna* has a more massive bill than is characteristic of White-winged Crossbills and a relatively deep bill compared to other Red Crossbills in North America (e.g., *L. c. bendirei*; Fig. 1, Table 1), yet it depends on conifers normally exploited by White-winged Crossbills. White-winged Crossbills also occur on Newfoundland, but have not differentiated into a distinct subspecies, and they apparently move on and off Newfoundland depending on the size of the cone crop. Spruce (*Picea*) has been common on Newfoundland for at least the last 8,000 years (Delcourt and Delcourt, 1987), and black spruce (*P. mariana*), white spruce (*P. glauca*), tamarack (*Larix laricina*), and balsam fir (*Abies balsamea*) are presently the predominant conifers (Damman, 1983). The relatively small- and slender-billed White-winged Crossbill (Fig. 1a) spends most of its time foraging on the relatively small cones

of black spruce (Fig. 1e), white spruce (Fig. 1f), and tamarack on the mainland of North America (Benkman, 1987a, 1987b). Red Crossbills (*L. c. bendirei*; Fig. 1b) are typically associated with the large-coned pines (*Pinus strobus* and *P. resinosa*; Fig. 1g, h; Benkman, 1987a, 1987b), yet pines have been uncommon on Newfoundland for the last 10,000 years, since the glacial retreat (Delcourt and Delcourt, 1987). In general, White-winged Crossbills are more efficient than Red Crossbills when foraging on spruce cones, whereas the converse is true on pine cones (Benkman, 1987b).

Given that *L. c. percna* is adapted for surviving year-round on Newfoundland (Griscom, 1937), two questions need to be addressed. First, why has the Red Crossbill differentiated into a distinct subspecies on Newfoundland? Second, since *L. c. percna* is a resident in the spruce and tamarack forests of Newfoundland, why is *L. c. percna*, or a similarly sized crossbill, not found throughout similar forests on the mainland? No other crossbill species or subspecies in North America is restricted to a small part of the range of a conifer species or group of species on which they forage.

Why Has a Large-billed Crossbill Evolved on an Island with Small Conifer Cones?

Answering this question requires information on conifer-ripening patterns and crossbill ecology (see Benkman, 1987a, 1987b). Cone crops fluctuate tremendously from year to year (Fowells, 1965; Smith, 1970; Janzen, 1971), and during some years, there are few, if any, seeds available over large areas. On the mainland, crossbills are rarely present in a local region for more than a year, and they often remain absent from

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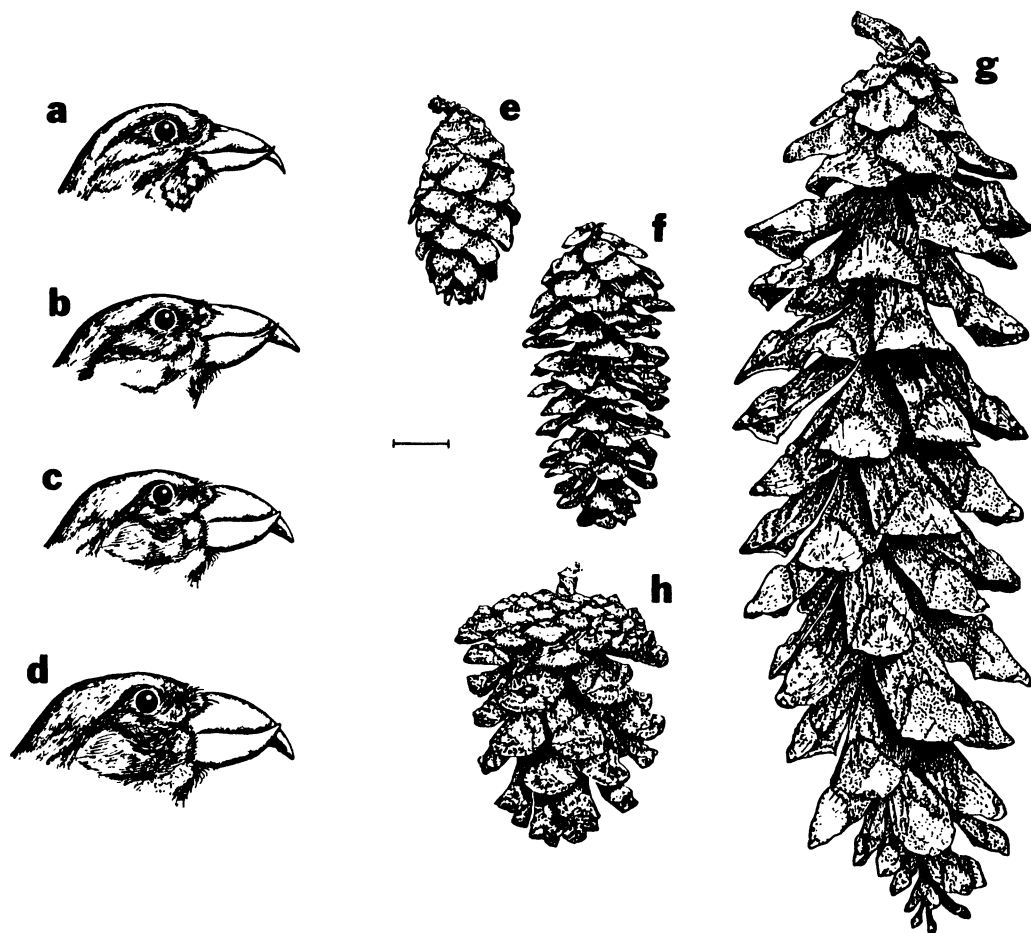
FIG. 1. Head profiles of four subspecies of crossbills (a–d), drawn from a photograph of museum skins, and open conifer cones of four species of conifers (e–h). Crossbills: a = North American White-winged Crossbill (*L. l. leucoptera*), b = North American Red Crossbill (*L. c. bendirei*), c = Newfoundland Red Crossbill (*L. c. percna*), d = European Red Crossbill (*L. c. curvirostra*); conifer cones: e = black spruce (*Picea mariana*), f = white spruce (*P. glauca*), g = white pine (*Pinus strobus*), h = red pine (*P. resinosa*). Scale bar indicates 1 cm.

extensive areas for even greater lengths of time (Benkman, 1987a; also see Lawrence [1949] and Bailey et al. [1953]). Although crossbills may be found in a given area for several years in succession, they are probably just transients in some years. Crossbills escape local or regional cone failures by moving out (Newton, 1972; Smith and Balda, 1979; Benkman, 1987a).

Based on data from the mainland (Benkman, 1987a),

TABLE 1. Bill dimensions ($\bar{x} \pm$ SE) of five crossbill subspecies ($N = 10$ individuals for each, except for bill depth for *megaplaga* where $N = 3$). Measurements were taken as follows: upper mandible length was measured from the tip of upper mandible to the anterior end of the right nares; lower mandible length was measured from the tip of lower mandible to the base where rami meet; bill depth was measured at the nares; and upper mandible width was measured at anterior edge of nares.

| Crossbill (locality)	Mandible lengths		Total bill depth (mm)	Upper mandible width (mm)
	Upper (mm)	Lower (mm)		
Loxia l. leucoptera (North America)	13.8 ± 0.21	9.3 ± 0.16	7.8 ± 0.10	5.6 ± 0.09
L. c. bendirei (North America)	15.3 ± 0.33	12.0 ± 0.29	9.3 ± 0.09	7.4 ± 0.08
L. c. percna (Newfoundland)	14.9 ± 0.18	11.0 ± 0.16	10.6 ± 0.10	8.1 ± 0.09
L. c. curvirostra (Eurasia)	15.3 ± 0.18	11.7 ± 0.11	10.7 ± 0.14	8.2 ± 0.06
L. l. megaplaga (Hispaniola)	16.2 ± 0.17	12.2 ± 0.19	9.8 ± 0.28	7.8 ± 0.07
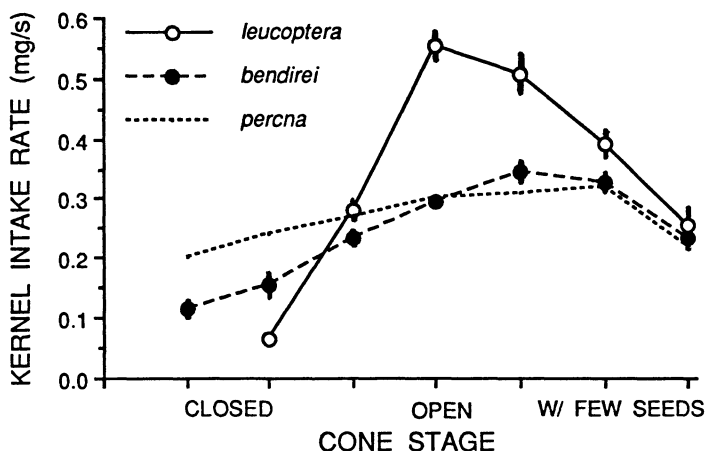
FIG. 2. Kernel intake rates ($\bar{x} \pm$ SE) for two subspecies of crossbills foraging on cones of black spruce. The data are for *L. l. leucoptera* and *L. curvirostra bendirei* foraging on 59 cones (973 seeds) and 87 cones (1,417 seeds), respectively. Predicted intake rates for *L. c. percna* are indicated by the dotted line (see text).

white and black spruce and tamarack are presumably the most important seed trees for crossbills on New-foundland. White spruce and tamarack cone crops fluctuate greatly between years (Fowells, 1965; Benkman, 1987*a*). Furthermore, the cone crops of these three conifers often cycle in synchrony (see Smith and Balda, 1979; pers. observ.); thus, in some years, virtually no seeds are available over extensive areas. For example, in 1987, tamaracks produced few, if any, seeds in New-foundland (pers. observ.), although white spruces did produce some seeds along Newfoundland's west coast (B. Maybank, pers. comm.). Black spruce cone crops, in contrast, rarely fail, and during most (if not all) years, there are at least some seeds available (Fowells, 1965). Moreover, at least some black spruce seeds are held year-round in the cones (Chai and Hansen, 1952). In years of white spruce and tamarack cone failure, a resident crossbill would have to subsist on black spruce seeds throughout the year. Indeed, surveys of birds in Newfoundland from 1957 to 1963 characterized the Red Crossbill as preferring "the old growth, black spruce forest" (H. Deichmann, pers. comm.). On the continent, White-winged Crossbills usually forage on black spruce only from winter to early summer, when the cones are open and seeds are most accessible (Benkman, 1987*a*, 1987*b*). White pine (*Pinus strobus*) is an important seed tree for crossbills but is uncommon on Newfoundland, and by the early 1900's it had been mostly removed by logging (Montevecchi and Tuck, 1987). Furthermore, it also fluctuates in cone-crop production (Fowells, 1965), often in synchrony with spruce and tamarack (pers. observ.).

Cone failures on islands cannot be escaped by nomadic movements. Therefore, crossbills confined to islands should have bills that provide access to seeds over the complete cone-ripening phenology. Large-billed crossbills can extract seeds more rapidly from a wider range of cone sizes and, most importantly, from more stages of cone ripening than can small-billed crossbills (Benkman, 1987*b*). Figure 2 shows the intake rates of mainland Red Crossbills and White-winged Crossbills foraging on black spruce cones at different

cone stages (Benkman, 1987*b* fig. 5c). These data were obtained from captive crossbills foraging on black spruce cones gathered from Maine. Also shown are the predicted intake rates of *L. c. percna*, based on the size of its bill (Table 1). It should be noted that the precise location of the intake rates of *L. c. percna* cannot be assigned, but based on the consistent patterns for the two mainland species, certain relations seem reasonable. For example, as bill depth and width increase, seeds in closed cones become more accessible. The deep-billed *L. c. percna* is predicted to be more efficient on closed cones than are White-winged Crossbills, which have their highest intake rates just after the cones open. Although scales of these cones are only slightly separated, White-winged Crossbills can slide their slender bills easily between the scales. Red Crossbills, with wider bills (Table 1), have their highest intake rates after the cone scales have spread farther apart, even though some seeds have been shed. *L. c. percna* is hypothesized to be less efficient than the other crossbills on open cones because of its wider bill, and its peak intake rate should be on fully open cones (shifted even farther to the right in Fig. 2).

The size and shape of *L. c. percna*'s bill is similar to that of the Red Crossbill in Eurasia (*L. c. curvirostra*) (Fig. 1, Table 1). This similarity in bill shape may be a result of the importance of seed in closed cones for both subspecies. Seeds in closed pine cones are probably more critical, on average, to Old World Red Crossbills, because Old World pines usually hold mature seeds in closed cones from fall to early spring (Newton, 1972), whereas most New World pines have cones that open in the fall (Fowells, 1965). Presumably, this is why Old World populations of Red Crossbills that forage on pine have much deeper bills than those populations in the New World (see Griscom, 1937). Alternatively, *L. c. percna* may be a recent colonist from the Old World (J. Groth, pers. comm.), and the similarity of its bill size and shape to that of *L. c. curvirostra* may result from lack of divergence. This cannot be confirmed without genetic analysis. Nevertheless, *L. c. percna*'s persistence on Newfoundland and its absence

form the boreal forests of the mainland needs explanation.

Why is L. c. percna Confined to Newfoundland?

The absence of red squirrels (*Tamiasciurus hudsonicus*) from Newfoundland may have been essential for the evolution of *L. c. percna*. Red squirrels have been a major selective force on cone structure, particularly on conifers that produce regular cone crops and hold their seeds for extended periods (Smith, 1970; Elliott, 1974). For example, in western North America, lodgepole pine (*P. contorta*) has thicker cone scales where cone crops are more regular and red squirrel populations are more stable (Smith, 1970). Consequently, the presence of squirrels as a selective agent can have indirect effects on other seed consumers (Benkman et al., 1984). If black spruce cone scales are thinner on Newfoundland because of the absence of red squirrels, then seeds in closed cones may be more accessible to crossbills on Newfoundland than on the mainland (see Benkman, 1987b).

To determine whether black spruce cones differ between the mainland and Newfoundland, I gathered black spruce cones from Riding Mountain National Park, Manitoba, western and eastern Ontario, and Newfoundland. Cone-scale thickness was measured with digital calipers at the anterior edge of the seed scars of five scales from the lower half of each of 5–10 cones from 5–6 trees from each of the above four locations (Table 2). Scale thickness was measured because it is the one scale characteristic of spruce in eastern North America that is uniformly correlated with the time required for crossbills to remove seeds from closed cones (Benkman, 1987b).

Scale thickness was significantly less for cones from Newfoundland than for those from the other sites (Table 2; LSD [least significant difference] multiple-range test, $P < 0.05$), as predicted. Cones from Riding Mountain had significantly thinner scales than did those from the two Ontario sites, and scale thickness decreased to the west in the three mainland samples. The significance of these last two results is unknown.

Red squirrels were introduced to Newfoundland in 1963 and 1964 (Dodds, 1983). The latter introduction, by the Newfoundland Wildlife Service, was apparently done to provide prey for the pine marten (*Martes americana*), which had been overtrapped. Red squirrels are now quite common on Newfoundland (Dodds, 1983; pers. observ.). For example, the average spring density for two three-hectare plots in northwest Newfoundland in 1985 was 3.4 individuals per hectare (R. West, pers. comm.). If black spruce on the mainland has more defenses against vertebrate seed predators, then lower densities of red squirrels are to be expected there. The spring densities of red squirrels in spruce forests on the mainland range from 2.0 to 2.5 individuals per hectare (six studies summarized in Rusch and Reeder [1978]). These values probably overestimate red squirrel densities in black spruce habitat on the mainland, because they include red squirrels in species other than black spruce and black spruce is not a preferred conifer (see Rusch and Reeder, 1978). Red squirrels were found to lose body mass when given only cones from black spruce from the mainland (Alaska), but not when given only cones of white spruce (Brink and Dean, 1966). In sum,

TABLE 2. Black spruce cone-scale thickness for four sites in Canada. Scale thickness was measured at the middle of the scale at the anterior end of the seed scars. N equals the number of trees. For each tree, five scales were measured from each of 5–10 cones. Significant differences between means, as indicated by the LSD multiple-range test ($P < 0.05$), are indicated by different lowercase letters.

| Site | Scale thickness (mm) | | | LSD multiple-range test | Longitude |
	$\bar{x}$	SE	N		
Manitoba	1.04	0.02	5	b	100°W
W. Ontario	1.11	0.02	5	c	91°W
E. Ontario	1.15	0.02	6	c	82°W
Newfoundland	0.96	0.02	6	a	58°W

squirrel densities in black spruce forests are probably considerably more than twice as great on Newfoundland as in comparable forests on the mainland.

The higher squirrel density on Newfoundland may be because there are fewer predators. However, food supply, and not predators, generally limits densities of squirrels in the genus *Tamiasciurus* (Smith, 1968, 1970; Kemp and Keith, 1970; Rusch and Reeder, 1978; Sullivan and Sullivan, 1982).

The presence of red squirrels may have precluded a resident *L. c. percna*-type crossbill on the mainland. Even though *L. c. percna* is presumably more efficient on closed black spruce cones than are other subspecies of Red Crossbills in North America, it may not be able to survive for extended periods on mainland black spruce, which have thicker cone scales. There are no records of Red Crossbills on the Labrador Peninsula adjacent to Newfoundland, where black spruce is abundant (Todd, 1963). *L. c. percna* has been collected on Anticosti Island (National Museum of Canada). These birds, however, probably represent eruptive birds (birds that emigrate when their densities are high relative to the available food supply in their usual habitat) and although eruptive birds may return to previously occupied habitat (Newton, 1972), there is no indication that they move regularly between Newfoundland and the mainland (contra Dickerman, 1986b). Moreover, there is no evidence that *L. c. percna* has persisted on the mainland for extended periods.

Alternatively, White-winged Crossbills may competitively exclude *L. c. percna* from the mainland. This alone, however, is not a sufficient explanation, because White-winged Crossbills do not seem any less common on Newfoundland than in comparable forests on the mainland.

Presumably, red squirrels are now exerting a strong selective force on black spruce cone structure on Newfoundland. If cone-scale thickness increases among black spruce, then intake rates for *L. c. percna* will decline. This, in combination with cone removal by squirrels, a competitive effect, may cause the decline, and possible extinction, of the once plentiful *L. c. percna* (see Austin [1968] for comments on *L. c. percna*'s former abundance). In fact, there appears to have been a large decline in Red Crossbills on Newfoundland since 1957–1963, when it was characterized as a "fairly

TABLE 3. Summary of the seven species/subspecies of crossbills restricted to islands. Conifer distribution is based on Critchfield and Little (1966) and Mirov (1967); all are species of *Pinus* except *Picea mariana*. Fire-adapted status is based on the known adaptations to fire, fire frequency (see text), and whether the pines occur in savanna-type habitats perpetuated by fire (Mirov, 1967). Squirrel presence is based on Walker (1975) and Brink (1977). Bill size is based on Griscom (1937), Knox (1975; pers. comm.), Massa (1987), and Table 1 (see text).

Crossbill	Island	Conifer	Conifer fire-adapted?	Squirrel present?	Bill size relative to mainland counterpart
L. c. percna	Newfoundland	*Picea mariana*	yes	yes[a]	large
L. l. megaplaga	Hispaniola	*Pinus occidentalis*	yes	no	large
L. c. balearica	Majorca	*P. halepensis*	yes	no	small
L. c. corsicana	Corsica	*P. halepensis, P. nigra, P. pinaster*	yes	no	large
L. c. guillemardi	Cyprus	*P. nigra*	yes	no	large
L. c. luzoniensis	Luzon	*P. insularis*	yes	no	small
L. scotia	Great Britain	*P. sylvestris*	?	yes	small

[a] Recent introduction (1963–1964).

regular resident" (H. Deichmann, pers. comm.). Such a decline is confirmed by data from annual Christmas bird counts in Terra Nova National Park, Newfoundland (Fig. 3). In contrast, the status of the White-winged Crossbill, which relies more on the fluctuating cone crops of tamarack and white spruce, appears to have remained unchanged (H. Deichmann, pers. comm.). It is ironic that this introduction to help one species, the marten, has the potential to cause the demise of another.

Does the Pattern Found for the Newfoundland Crossbill Represent an Isolated Case, or Are the Principles General to Other Island Populations of Crossbills?

To reiterate the main points: 1) conifers that produce at least some cones every year and hold seeds throughout the year are critical for island populations of crossbills; 2) there is selection for larger bills to open closed
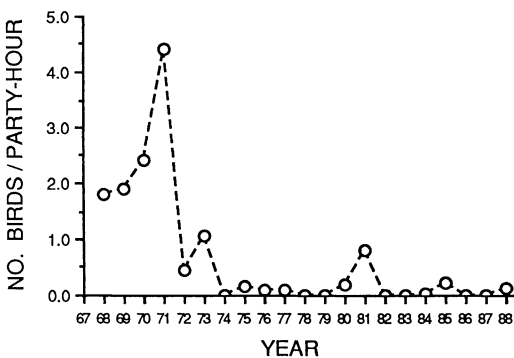

FIG. 3. The number of Red Crossbills observed during the annual Terra Nova National Park, Newfoundland, Christmas bird count from 1968 to 1988 (data from Terra Nova National Park records). A "party-hour" is one hour of observation by an independent group of observers. The number of party-hours ranged from 12 (in 1971) to 88 (in 1984). The census area encompasses extensive areas of undisturbed black spruce forest (pers. observ.).

cones, but these cones often have thick cone scales (Smith, 1970) that are difficult for crossbills to open; and 3) it is easier to open closed cones on Newfoundland, where squirrels have not selected for thick cone scales, than on the mainland. Thus, it is predicted that 1) crossbills are more likely to establish themselves and evolve on islands where conifers produce cone crops every year and squirrels are absent and 2) island crossbill populations should have larger bills than their mainland counterparts foraging on cones of the same species or on cones of similar size.

There are seven species or subspecies of crossbills restricted to islands (Table 3). Although detailed ecological information is not known for most of these islands, some general comments can be made concerning the conifers on the islands, the presence of squirrels, and the size of the bills of the island populations of crossbills.

First, most of the habitats in which island populations of crossbills occur experience frequent fires (Table 3). For instance, black spruce is most common on Newfoundland where fires are frequent (Damman, 1983). Fires are frequent and critical in maintaining *P. occidentalis* as the dominant tree in the mountains of Hispaniola (Fisher-Meero, 1983). On the Mediterranean islands of Majorca, Corsica, and Cyprus, fire is frequent and has been a critical influence in the evolution of the vegetation (Mooney and Parsons, 1973). Fire-adapted conifers are characterized by little annual variation in cone-crop size and by the fact that they hold seeds in their cones for extended periods (Fowells, 1965; Smith, 1970).

Second, tree squirrels (*Tamiasciurus* and *Sciurus*) and other squirrels that eat conifer seeds are absent from all the islands except Newfoundland (where they were introduced only about 25 years ago) and Great Britain (Table 3; Walker, 1975; Brink, 1977). On Great Britain, squirrels (*Sciurus vulgaris*) feed on *Pinus sylvestris* cones (Nethersole-Thompson, 1975; Gurnell, 1987) and appear to have a negative impact on the abundance of *L. scotia*. This is suggested by the decline in *L. scotia*'s abundance between 1930 and the 1970's (Nethersole-Thompson, 1975), when the abundance of squirrels (*S. vulgaris*) in Scotland was increasing (Gurnell, 1987). What is probably essential for the crossbills

to survive on Great Britain is sufficient geographic variation in cone production so that during any given year crossbills can find some areas with good cone crops (see Nethersole-Thompson, 1975; Knox, 1987). This is critical, because in any one area in Great Britain, *P. sylvestris* cone crops vary greatly in size from year to year (Nethersole-Thompson, 1975). In effect, spatial variation provides a key ingredient more characteristic of continents and often missing from (or at least more limited on) islands.

The few islands that commonly support crossbills but lack endemic populations either are very wet and lack fire-adapted conifers or have squirrels. These islands include the Queen Charlotte Islands, which lack squirrels but are quite mesic, and Japan, which has squirrels.

Third, four island populations have relatively large or stout bills as compared to their mainland counterparts, but three do not (Table 3). For most of the crossbill populations, there is no simple mainland counterpart, because conifers on the islands differ in specific or subspecific status from those on the mainland and may differ in terms of cone size. For example, the pine on Hispaniola, *P. occidentalis,* is not found on the continent. However, the cones of *P. occidentalis* are similar in appearance to those of *P. ponderosa,* although they are smaller (*P. occidentalis* cone length: $\bar{x} \pm SD = 5.6 \pm 0.6$ cm, range 4.6–6.6 cm, $N = 20$ cones; *P. ponderosa* cones are usually between 7 and 15 cm in length [Munz, 1959]). Consistent with the idea that island populations have relatively large bills, the crossbill subspecies on Hispaniola, *L. l. megaplaga,* has a similar although slightly larger bill than the crossbill that normally occupies *P. ponderosa* forests (*L. c. bendirei*; Table 1) (see Benkman, 1987*a*; Dickerman, 1986*a*).

The crossbill on Majorca (*L. c. balearica*) has a smaller bill than its mainland counterpart in northern Africa (*L. c. poliogyna*) (Massa, 1987). Both subspecies of crossbills forage mostly on *Pinus halepensis,* which is the predominant pine on Majorca and the only pine in the crossbill's range in northern Africa. *Pinus halepensis* has a restricted distribution in Africa (Critchfield and Little, 1966), however, so *L. c. poliogyna* might be effectively an island population; *L. c. poliogyna,* like the Mediterranean island populations, is thought to be sedentary (Massa, 1987). Moreover, there are probably more seed predators, especially mammals, in northern Africa than on Majorca. As a result, *P. halepensis* may have thicker cone scales in north Africa than on Majorca. If this is true, then a larger-billed crossbill is expected in northern Africa than on Majorca.

The crossbill confined to Luzon (*L. c. luzoniensis*) also has a smaller bill than its mainland counterpart (*L. c. meridionalis*) (Griscom, 1937; A. Knox, pers. comm.; Table 3). However, like *L. c. poliogyna, L. c. meridionalis* can be considered to be effectively an island population (see Critchfield and Little [1966] for the distribution of pines), and thus, similar arguments as given above for *L. c. balearica* and *L. c. poliogyna* apply to *L. c. luzoniensis* and *L. c. meridionalis.*

The Scottish crossbill (*L. scotia*) is confined to *Pinus sylvestris* in Scotland (Nethersole-Thompson, 1975), and it has a smaller bill (Table 3) than its mainland counterpart, the Parrot Crossbill (*L. pytyopsittacus*) in northern Europe (Newton, 1972). This is the one clear exception to the rule of island populations having relatively large bills compared to their mainland counterparts that rely on cones of similar size.

In summary, there are rather specific requirements for the evolution of island populations of crossbills, including the presence of fire-adapted conifers and the absence of squirrels. This implies that squirrels, as a selective agent on cone structure, have had a strong impact on both island and continental crossbill populations. The extent of current competition between squirrels and crossbills for conifer seeds is unknown, although on Newfoundland it is now likely to be intense. On the other hand, the long-term effect of squirrels on crossbills may have been to increase the diversity of cone structures and, hence, of crossbill species and subspecies. The selective feeding of squirrels on conifers has caused a greater variety of defense mechanisms among conifer species (Smith, 1970), and possibly as a result, different bill structures are required for foraging efficiently on the more distinct cone structures (Benkman, 1987*b*). Moreover, the increase in cone defenses brought about from selective feeding by squirrels (Smith, 1970) may ultimately be responsible for the evolution of crossbills from less specialized *Carduelis* finches.

LITERATURE CITED

AUSTIN, O. L. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows and allies, Part I. U.S. Nat. Mus. Bull. 237:498–500.

BAILEY, A. M., R. J. NIEDRACH, AND A. L. BAILY. 1953. The Red Crossbills of Colorado. Publ. Denver Mus. Nat. Hist. 9:1–64.

BENKMAN, C. W. 1987*a*. Food profitability and the foraging ecology of crossbills. Ecol. Monogr. 57: 251–267.

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

BENKMAN, C. W., R. P. BALDA, AND C. C. SMITH. 1984. Adaptations for seed dispersal and the compromises due to seed predation in limber pine. Ecology 65:632–642.

BRINK, C. H ., AND F. C. DEAN. 1966. Spruce seed as a food of red squirrels and flying squirrels in interior Alaska. J. Wildl. Manag. 30:503–512.

BRINK, F. H. VAN DEN. 1977. A Field Guide to the Mammals of Britain and Europe. Collins, London, U.K.

CHAI, T. S., AND H. L. HANSEN. 1952. Characteristics

of Black Spruce Seed from Cones of Different Ages. School of Forestry, Univ. Minnesota, St. Paul.

CRITCHFIELD, W. B., AND E. L. LITTLE, JR. 1966. Geographic Distribution of the Pines of the World. Miscellaneous Publication 991. U.S. Department of Agriculture, Wash., DC.

DAMMAN, A. W. H. 1983. An ecological subdivision of the island of Newfoundland, pp. 163–200. In G. R. South (ed.), Biogeography and Ecology of the Island of Newfoundland. Junk, The Hague, Neth.

DELCOURT, P. A., AND H. R. DELCOURT. 1987. Long-term forest dynamics of the temperate zone. Springer-Verlag, N.Y.

DICKERMAN, R. W. 1986a. A review of the Red Crossbill in New York state, Part 2. Identification of specimens from New York. Kingbird 36:127–134.

———. 1986b. The "old northeastern" subspecies of Red Crossbill. Amer. Birds 41:188–194.

DODDS, D. 1983. Terrestrial mammals, pp. 509–550. In G. R. South (ed.), Biogeography and Ecology of the Island of Newfoundland. Junk, The Hague, Neth.

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

FISHER-MEERO, L. L. 1983. Floristics, ecology, phytogeography, and history of botanical exploration of the Sierra de Bahoruco, Dominican Republic. M.S. Thesis. Univ. Florida, Gainesville.

FOWELLS, H. A. 1965. Silvics of Forest Trees in the United States. Agricultural Handbook 271. U.S. Department of Agriculture, Wash., DC.

GRISCOM, L. 1937. A monographic study of the Red Crossbill. Proc. Boston Soc. Nat. Hist. 41:77–210.

GURNELL, J. 1987. The natural history of squirrels. Facts on File, N.Y.

JANZEN, D. H. 1971. Seed predation by animals. Ann. Rev. Ecol. Syst. 2:465–492.

KEMP, G. A., AND L. B. KEITH. 1970. Dynamics and regulation of red squirrel (Tamiasciurus hudsonicus) populations. Ecology 51:763–779.

KNOX, A. 1975. Crossbill taxonomy, pp. 191–201. In D. Nethersole-Thompson (ed.), Pine Crossbills: A Scottish Contribution. Poyser, Berkhamsted, U.K.

———. 1987. Crossbills: Their general biology and some conservation problems, pp. 64–74. In E. Cameron (ed.), Glen Tanar: Its Human and Natural History. [Internal report, Scotland Northeast Region]. Nature Conservancy Council, Aberdeen, U.K.

LACK, D. 1944. Correlation between beak and food in the crossbill (L. curvirostra). Ibis 86:552–553.

LAWRENCE, L. DE K. 1949. The Red Crossbills at Pimisi Bay, Ontario. Can. Field-Natur. 63:147–160.

MASSA, B. 1987. Variation in Mediterranean crossbills Loxia curvirostra. Bull. Brit. Ornithol. Club 107:118–129.

MIROV, N. T. 1967. The genus Pinus. Ronald, N.Y.

MONTEVECCHI, W. A., AND L. M. TUCK. 1987. Newfoundland birds: Exploitation, study, conservation. Nuttall Ornithological Club, Cambridge, MA.

MOONEY, H. A., AND D. J. PARSONS. 1973. Structure and function of the California chaparral—An example from San Dimas, pp. 83–112. In F. di Castri and H. A. Mooney (eds.), Mediterranean Type Ecosystems: Origin and Function. Springer-Verlag, N.Y.

MUNZ, P. A. 1959. A California Flora. Univ. Calif. Press, Berkeley.

NETHERSOLE-THOMPSON, D. 1975. Pine Crossbills: A Scottish Contribution. Poyser, Berkhamsted, U.K.

NEWTON, I. 1967. The adaptive radiation and feeding ecology of some British finches. Ibis 109:33–98.

———. 1972. Finches. Collins, London, U.K.

RUSCH, D. A., AND W. G. REEDER. 1978. Population ecology of Alberta red squirrels. Ecology 59:400–420.

SMITH, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels, Tamiasciurus. Ecol. Monogr. 38:31–63.

———. 1970. The coevolution of pine squirrels (Tamiasciurus) and conifers. Ecol. Monogr. 40:349–371.

SMITH, C. C., AND R. P. BALDA. 1979. Competition among insects, birds and mammals for conifer seeds. Amer. Zool. 19:1065–1083.

SULLIVAN, T. P., AND D. S. SULLIVAN. 1982. Population dynamics and regulation of the Douglas squirrel (Tamiasciurus douglasii) with supplemental food. Oecologia 53:264–270.

TODD, W. E. C. 1963. Birds of the Labrador Peninsula and adjacent areas. Univ. Toronto Press, Toronto, Canada.

WALKER, E. P. 1975. Mammals of the World, Vol. II, 3rd Ed. Johns Hopkins Univ. Press, Baltimore, MD.

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