

THE EVOLUTION, ECOLOGY, AND DECLINE OF THE RED CROSSBILL OF NEWFOUNDLAND

by Craig W. Benkman

The correlation between bill sizes of different species of Eurasian crossbills (*Loxia*) and the sizes of the conifer cones they 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, Benkman 1993a). However, the resident Red Crossbill on Newfoundland, *L. c. percna* (Griscom 1937, Dickerman 1986), is an exception to this general pattern (Benkman 1989, 1992a).

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; 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 8000 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, 1992b). In the Northeast, Red Crossbills (*L. c. bendirei*; Fig. 1b) are typically associated with the large-coned Eastern White and Red 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 with pine cones (Benkman 1987b).

Given that *percna* is adapted for surviving year-round on Newfoundland (Griscom 1937), two questions must be addressed. First, why has the Red Crossbill differentiated into a distinct subspecies on Newfoundland? Second, since *percna* is a resident in the spruce and Tamarack forests of Newfoundland, why is *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.

Each of these questions will be addressed in turn. Background information is given first, and then methods, results, and discussion are briefly combined.

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 (Benkman 1987a, 1987b, 1992b, 1993a). 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 extensive areas for even greater lengths of time (Benkman 1987a; also Lawrence 1949, 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, 1992b).

Based on data from the mainland (Benkman 1987a, 1992b), White and Black spruce and Tamarack are presumably the most important seed trees for crossbills on Newfoundland. White Spruce and Tamarack cone crops fluctuate greatly between years (Fowells 1965, Benkman 1987a). Furthermore, the cone crops of these three conifers often cycle in synchrony (Smith and Balda 1979; pers. obs.). Thus, in some years virtually no seeds are available

over extensive areas. For example, in 1987, Tamarack produced few if any seeds in Newfoundland (pers. obs.), although White Spruce did produce some seeds along Newfoundland's west coast (B. Maybank, pers. comm.). Black Spruce cone crops, in contrast, rarely fail, and during most years at least some seeds are 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. 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 1987a, 1987b, 1992b). Eastern White Pine is an important seed tree for crossbills, but is uncommon on Newfoundland and by the early 1900s had been mostly removed by logging (Montevicchi and Tuck 1987). Furthermore, it also fluctuates in

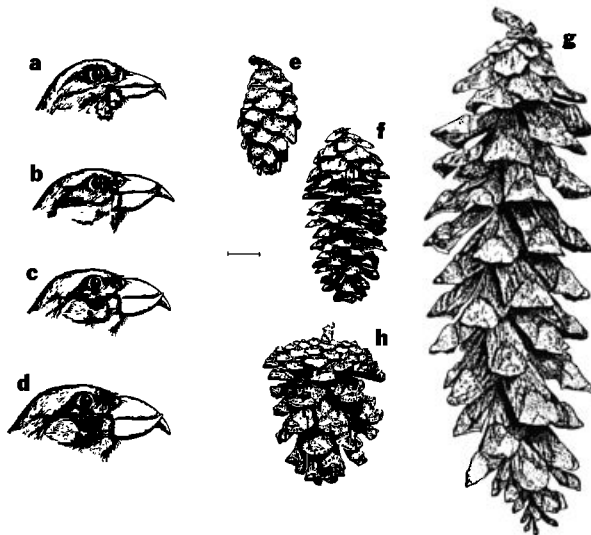


Fig. 1. Head profiles of four subspecies of crossbills (a–d), drawn from a photograph of museum skins, and open conifer cones of four species of conifers (e–h). Crossbills: a=North American White-winged Crossbill (*L. l. leucoptera*), b=North American Red Crossbill (*L. c. bendirei*), c=Newfoundland 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=Eastern White Pine (*Pinus strobus*), h=Red Pine (*P. resinosa*). Scale indicates 1 cm.

cone-crop production (Fowells 1965), often in synchrony with spruce and Tamarack (pers. obs.).

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 1987b). Figure 2 shows the intake rates of mainland Red and White-winged crossbills foraging on Black Spruce cones at different cone stages.

These data were obtained from captive crossbills foraging on Black Spruce cones gathered from Maine (Benkman 1987b). Also shown are the predicted intake rates of *percna*, based on the size of its bill (Table 1). It should be noted that the precise location of the intake rates of *percna* cannot be assigned, but based on the consistent patterns for the two mainland species and among different subspecies of Red Crossbills, certain relations seem reasonable. For example, as bill depth and width increase, seeds in closed cones become more accessible (Benkman 1993a). The deep-billed *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 between the scales easily. 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. *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 *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 seeds 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

Table 1. Bill dimensions ($\bar{x} \pm SE$) of four crossbill subspecies (N=10 individuals for each). 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 (Upper Mandible) | |
|---|------------------|-----------|-----------------------------|-----------|
| | upper(mm) | lower(mm) | depth(mm) | width(mm) |
| <i>L. l. leucoptera</i> (North America) | 13.8±0.21 | 9.3±0.16 | 7.8±0.10 | 5.6±0.09 |
| <i>L. c. bendirei</i> (North America) | 15.3±0.33 | 12.0±0.29 | 9.3±0.09 | 7.4±0.08 |
| <i>L. c. percna</i> (Newfoundland) | 14.9±0.18 | 11.0±0.16 | 10.6±0.10 | 8.1±0.09 |
| <i>L. c. curvirostra</i> (Eurasia) | 15.3±0.18 | 11.7±0.11 | 10.7±0.14 | 8.2±0.06 |

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 (Griscom 1937). Alternatively, *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, *percna*'s persistence on Newfoundland and its absence from the boreal forests of the mainland needs explanation.

Why is *percna* confined to Newfoundland?

The absence of Red Squirrels (*Tamiasciurus hudsonicus*) from Newfoundland may have been essential for the evolution of *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). 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 (Benkman 1987b, Benkman 1993a).

To determine whether Black Spruce cones differ between the mainland and Newfoundland, I gathered Black Spruce cones from Riding Mountain National Park, Manitoba, from western and eastern Ontario, and from Newfoundland. Cone-scale thickness was measured with digital calipers at the anterior edge of the seed scars of

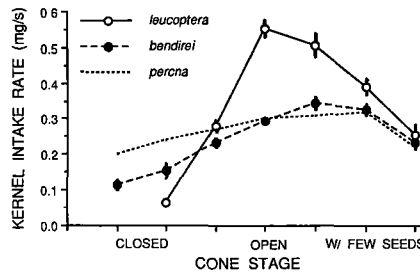


Fig. 2. Kernel intake rates ($\bar{X} \pm \text{SE}$) for two subspecies of crossbills foraging on cones of black spruce. The data are for *L. l. leucoptera* and *L. c. bendirei* foraging on a total of 59 cones (973 seeds) and 87 cones (1417 seeds), respectively. Predicted intake rates for *percna* are indicated by the dotted line.

five scales from the lower half of each of five to ten cones, from five or six 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 by 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, $P \leq 0.05$), 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. obs.). For example, the average spring density for four 3.0 to 6.25 hectare plots in northwest Newfoundland in 1985 was 3.5 individuals per hectare (West 1989). 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 (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, squirrel densities in Black Spruce forests are probably considerably more than twice as high 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 *percna*-type crossbill on the mainland. Even though *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). There is no indication that *percna* moves regularly between Newfoundland and the mainland (contra Dickerman 1987), nor is there evidence that *percna* has persisted on the mainland for extended periods.

Alternatively, White-winged Crossbills may competitively exclude *percna* from the mainland. This alone, however, is not a sufficient explanation, because White-winged Cross-

bills do not seem any less common on Newfoundland than in comparable forests on the mainland (but see below).

Presumably, Red Squirrels are now exerting a strong selective force on the structure of Black Spruce cones on Newfoundland. If cone-scale thickness increases among Black Spruce, then intake rates for *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 *percna* (Austin 1968 for comments on *percna*'s former abundance). In fact, there are tremendous differences in the percentage of Black Spruce cones removed by Red Squirrels between Newfoundland and the mainland. For example, during years of poor cone crops, when Red Squirrels most intensely harvest Black Spruce and the seed supply is most limiting, Red Squirrels at several Newfoundland sites removed 64–96% of the cones of Black Spruce by early October (West 1989), but removed only 19% of the Black Spruce cones on the mainland (Ontario) (Prévost *et al.* 1988).

There appears to have been a large decline in Red Crossbills on Newfoundland since 1957–1963, when it was characterized as a “fairly 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). It is ironic that this introduction to help one species, the Pine Marten, has the potential to cause the demise of another.

White-winged Crossbills have also declined on Newfoundland Christmas Bird Counts since the late 1960s (W. A. Montevicchi, pers. comm.). White-winged Crossbills still move onto Newfoundland in the summer and fall when there are large Tamarack and White Spruce cone crops (Benkman, pers. obs.). However, the intense cone harvests by Red Squirrels in the fall presumably depletes

Table 2. Black Spruce cone scale thickness for four sites in Canada. There were significant differences between all samples ($P < 0.05$), except between the two Ontario samples

| Site | Scale thickness (mm) ^a | | | |
|-----------------|-----------------------------------|------|----------------|-----------|
| | x | SE | N ^b | Longitude |
| Manitoba | 1.04 | 0.02 | 5 | 110°W |
| Western Ontario | 1.11 | 0.02 | 5 | 91°W |
| Eastern Ontario | 1.15 | 0.02 | 6 | 82°W |
| Newfoundland | 0.96 | 0.02 | 6 | 58°W |

^aMeasured at the middle of the scale at the anterior end of the seed scars

^bN equals the number of trees. For each tree, five scales were measured from each of 5–10 cones.

seed resources so that few White-winged Crossbills can now survive most winters on Newfoundland.

On an encouraging note, *percna* may survive on smaller islands near the main island of Newfoundland, where Black Spruce is present and squirrels are absent. Indeed, *percna* has been collected on Anticosti Island (National Museum of Canada) and I have received photos of a pair of *percna* taken by Philip Bursey on Random Island, Newfoundland, in May, 1988. Although I hold little hope for *percna* where Red Squirrels persist, I am optimistic that islands such as Anticosti and those surrounding the main island of Newfoundland may provide refuge for *percna*. Nevertheless, it is particularly discouraging that such a distinct population, and most likely a distinct species (Groth 1988), has such a precarious existence.

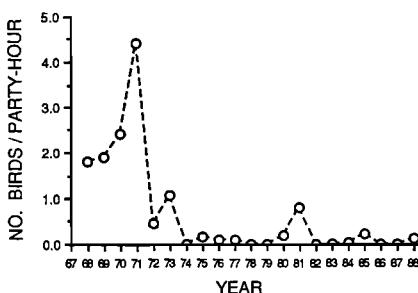


Fig. 3. The number of Red Crossbills observed during the annual Terra Nova National Park, Newfoundland, Christmas Bird Count from 1968 to 1988 (data from Terra Nova National Park records). This trend has continued. For example, in 1991 no Red Crossbills were observed on the Terra Nova Christmas Bird Count. 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. obs.).

This is but one example of the impacts of man on crossbills. There are more, some of which are more subtle. A subspecies (species?) of crossbill more appropriately considered a western form (*L. c. bendirei*; Type 2 of Groth 1988) associated mostly with Ponderosa Pine (*P. ponderosa*) (Benkman 1987a, 1993a) has increased in the Northeast (Dickerman 1987). I attribute this increase to the increase in mature Red Pine, which has relatively tough cones similar to (although smaller) than those of Ponderosa Pine. Red pine used to be found in scattered small stands (Cook *et al.* 1952) and may not have been plentiful enough to support a Red Crossbill population. Now Red Pine is planted more extensively, particularly in the Great Lakes region. Indeed, this “western” subspecies is most common in the Great Lakes area. Moreover, there may have been a decrease in bill size in these Red Crossbills in the East relative to those in the West, as one would expect considering the relatively small cones of Red Pine. The mean bill depth of Type 2s in the Appalachians is 9.48 mm (Groth 1988; I averaged the mean of the males [$n = 41$] and females [$n = 23$]), whereas those I measured in the Northwest had a mean bill depth of 9.70 mm (SE = 0.14, $n = 9$).

Other impacts on crossbills are more pronounced and negative (Benkman 1993b). Crossbills have declined because of forest loss and fragmentation in Finland (Helle 1985) and Dickerman (1987) suggests that the “northeastern” subspecies of Red Crossbill declined because of extensive logging near the beginning of this century. Moreover, the tendency for crossbills to concentrate during any given year in areas of large cone crops will potentially result in much greater declines of crossbills than those just proportional to habitat lost. In the fall and winter of 1988–1989, most of the White-winged Crossbills in North America were probably concentrated in the Maritime Prov-

inces of Canada (pers. obs.). Thus, if 50% of the conifer forests in the Maritimes were to be logged, we might expect nearly a 50% decline in the White-winged Crossbill population, even though the decrease in the total area of conifers used by this species represents a much smaller fraction than 50%. Indeed, nomadic behavior makes crossbill populations both more vulnerable to habitat loss and more difficult to assess. Because crossbill abundance is difficult to assess, the decline in the Newfoundland crossbill remained unappreciated until now.

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Literature Cited

AUSTIN, O. L. JR., (Ed.) 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows and allies. Part I. U.S. Natl. Mus. Bull. 237.

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. 1987a. Food profitability and the foraging ecology of crossbills. Ecol. Monogr. 57:251-267.

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

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

———. 1992a. A crossbill's twist of fate. Natural History 101(12):39-42.

———. 1992b. White-winged Crossbill. In The Birds of North, No. 27 (A. Poole, P. Stettenheim, and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences; Washington, DC: The American Ornithologists' Union.

———. 1993a. Adaptation to single re-

sources and the evolution of crossbill (*Loxia*) diversity. Ecol. Monogr., in press.

———. 1993b. Logging, conifers, and the conservation of crossbills. Conservation Biology, in press.

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

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.

CHAI, T. S., and H. L. HANSEN. 1952. Characteristics of black spruce seed from cones of different ages. Minn. Forest. Notes 2, Univ. Minn., St. Paul, Minn.

COOK, D. B., R. H. SMITH, and E. L. STONE. 1952. The natural distribution of red pine in New York. Ecology 33:500-512.

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. 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. 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.

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

FOWELLS, H. A. 1965. Silvics of forest trees in the United States. U.S.D.A. Agric. Handb. 271.

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

GROTH, J. G. 1988. Resolution of cryptic species in Appalachian Red Crossbills. Condor 90:745-760.

HELLE, P. 1985. Effects of forest fragmentation on bird densities in northern boreal forests. Ornis Fennica 62:35-41.

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.

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

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

MONTEVECCHI, W. A., and L. M. TUCK. 1987. Newfoundland birds: exploitation, study, conservation. Publ. Nutt. Ornithol. Club No. 21. Cambridge, Ma.

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

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

PRÉVOST, Y. H., J. E. LAING, and V. F. HAAVISTO. 1988. Seasonal damage by insects and squirrels to female reproductive structures of black spruce, *Picea mariana* (Mill.). B.S.P. Can. Ent. 120:1113-1121.

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.

——— 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.

WEST, R. J. 1989. Cone depredations by the red squirrel in black spruce stands in Newfoundland: implications for commercial cone collection. Can. J. For. Res. 19:1207-1210.

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