Logging, Conifers, and the Conservation of Crossbills

CRAIG W. BENKMAN*

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

Abstract: *A survey of the forestry literature shows that as the age and area of coniferous forests decline, decreased conifer seed production and increased frequencies of cone failures can be expected. This would, in turn, cause declines in crossbills (Loxia), which specialize on the seeds held in conifer cones. In western North America, at least five different species of Red Crossbills (L. curvirostra) have recently been distinguished (Groth 1990); each specializes on a different species or even a single variety of conifer (Benkman 1993). Measures for conserving this diversity of crossbills include protecting mature and old-growth stands, and increasing rotation ages throughout the range of each of the required conifers. These recommendations are not unique to crossbills, but rather the loss of crossbill diversity is another reason to employ such measures.*

Explotación forestal, coníferas y conservación de piquituertos ("crossbills")

Resumen: *Un estudio de la literatura forestal demostró que cuando la edad y el área de los bosques de coníferas declinan, se puede esperar un decrecimiento en la producción de semillas y un incremento en la frecuencia de fracasos de los conos (piñas). Esto, a su vez, puede causar declinación en piquituertos (Loxia), los cuales se especializan en las semillas que se encuentran en los conos de coníferas. En el oeste de Norte América, por los menos cinco especies diferentes de Piquituertos Rojos (L. curvirostra) han sido reciéntemente identificadas (Groth 1990); cada una está especializada en una especie diferente o incluso en una variedad particular de coníferas (Benkman 1993). Medidas para conservar esta diversidad en piquituertos incluyen protejer rodales maduros y de crecimiento antiguo e incrementar la edad de rotación a lo largo del rango de cada una de las coníferas requeridas. Estas recomendaciones no son únicas para los piquituertos, pero la pérdida de la diversidad de los piquituertos es otra razón para emplear tales medidas.*

Introduction

Specialist species are particularly vulnerable to extinction. Among the most specialized groups of birds are the crossbills (*Loxia*), which are adapted for foraging on seeds in conifer cones (Newton 1972; Benkman 1987b, 1988a, 1988b, 1993; Benkman & Lindholm 1991) and whose survival and reproduction depend on the availability of conifer seeds (Newton 1972; Benkman 1987a, 1988a, 1990, 1992a). Crossbills also are a speciose lin-

eage. What had previously been recognized as a single species, the Red Crossbill (*L. curvirostra*) in North America, consists of at least seven distinct species (Groth 1990). Although the taxonomic basis for recognizing these different crossbills at the species level is still largely unpublished (but see Groth 1988), each species differs in morphology, vocalizations, and ecology, and several species commonly nest syntopically without much interbreeding (Groth 1988, 1980; Benkman 1993). Moreover, most if not all of these species of crossbill are adapted specifically for foraging on single species of conifers, and in some cases just one variety of conifer (Benkman 1989, 1993). For instance, in western North America different species of Red Crossbill are

473

adapted specifically for foraging on each of western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), lodgepole pine (*Pinus contorta* var. *latifolia*), ponderosa pine (*P. ponderosa* var. *scopulorum*), and possibly Sitka spruce (*Picea sitchensis*) (Benkman 1993).

Undisturbed conifer forests were recently widespread but now are among the most intensively exploited habitats (Caufield 1990; McLaren 1990; Norse 1990; also see Rosencranz & Scott 1992). For example, only around 10% of the original old-growth forest in Washington and Oregon may remain (Norse 1990), and most second-growth on federal lands typically has rotation ages of about 80 years (Brown 1985). Many industrial forest lands are managed on a 40 to 60 year rotation (J. F. Franklin, personal communication). Consequently, species dependent on mature conifer forests, such as crossbills, will inevitably decline, with local and possibly global extinctions.

Dependency on a single resource makes crossbills extremely vulnerable to habitat loss and alteration. Because the link between crossbills and their food resources, conifer seeds, is so strong and clear (Newton 1972; Benkman 1987*a*, 1990, 1992*a*), the conservation strategy for crossbills is simplified (see Terborgh 1986). Moreover, because the basic mechanisms influencing crossbill ecology are well understood (Newton 1972; Benkman 1987*a*, 1987*b*, 1988*a*, 1989, 1990, 1992*a*), the general impact on crossbills of habitat alteration, such as that from logging, can be anticipated; this is the subject of this paper. Such predictive analyses are important, in part, because the actual status of nomadic crossbill populations is difficult to assess and large declines may go undetected. For example, during the early 1970s in Newfoundland there appears to have been a severe decline of the formerly abundant and endemic Newfoundland Crossbill (Benkman 1989, 1992*b*; Pimm 1990). This decline was not noted until nearly twenty years later, however, and only after I had predicted such a result from the introduction (in 1963–1964) of red squirrels (*Tamiasciurus hudsonicus*) onto Newfoundland (Benkman 1989, 1992*b*). Although I concentrate on crossbills, the impact may be applicable to populations of numerous other conifer seed-eating animals (see Smith & Balda 1979).

Temporal Variation in Habitat Quality

Logging at short rotation ages increases the domination of forests by younger trees (Harris 1984), which, for at least three reasons, greatly reduces cone and seed production relative to mature or old-growth forests. First, shorter rotation ages reduce the proportion of time a given stand is capable of producing seeds (Fig. 1). Most conifers begin producing cones (seeds) only after they
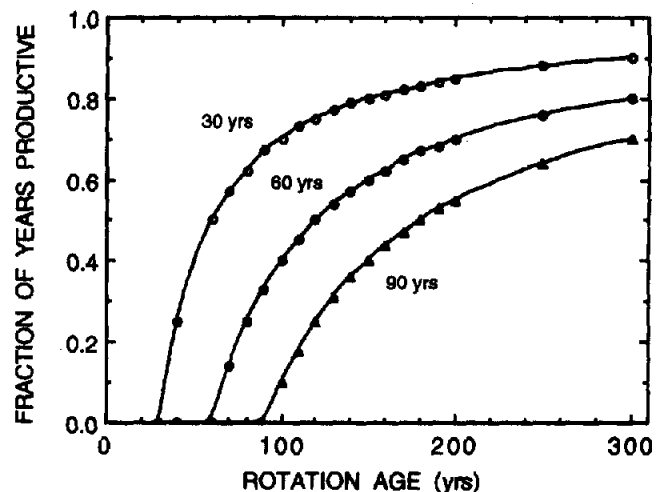

Figure 1. The fraction of years a forest might produce cones in relation to rotation age. The different curves represent different ages (30, 60, and 90 years) after which cones are produced. Although many conifers begin producing cones after 30 years of age (Fowells 1965), the smaller cone crop sizes and the higher frequency of cone failures for younger trees effectively shift the curve down and to the right (toward or below the 90 year curve).

are about 20 to 30 years old (Fowells 1965). Thus, when rotation ages are 80 years and trees produce cones only after 30 years of age, the proportion of time that an area may produce any seed is about five (62%) out of eight years. The intervals between stand-replacing disturbances such as fire or wind in unmanaged stands in western North America are variable, although they usually are greater than 80 years (see Habeck 1988; Peet 1988; Spies & Franklin 1988; Alaback & Juday 1989). For example, west of the Cascade Range many old-growth forests were older than 300 years prior to logging, and many may have been older than 750 years (Spies & Franklin 1988). Assuming that stand-replacing disturbances occur at intervals of 300 years, and that 30 years is the minimum age for cone production, unmanaged stands potentially produce seed at least nine (90%) out of every 10 years. Thus, short rotations increase the proportion of the landscape that is of pre-seed-production age.

Second, younger conifers produce smaller cone crops than do older conifers. For example, an old-growth stand of Douglas fir produces 20 to 30 times more cones than a 50- to 100-year-old second-growth stand (Burns & Honkala 1990). Maximum cone production for some conifers is not reached until trees are 200 years of age (such as the sugar pine [*Pinus lambertiana*; Fowells & Schubert 1956] and Douglas fir [Fowells 1965]). In addition, smaller cone-producing trees in a stand fail to produce cones more often than larger and presumably

older trees (such as ponderosa pine and Douglas fir; Fowells & Schubert 1956, Shearer 1986, Burns & Honkala 1990). This reduces further the proportion of years that harvested forests are productive for seed-eaters. In the above example, a conifer that first begins producing cones at 30 years of age may regularly produce many cones only after 90 or more years of age (see Fig. 1).

Third, seed production by late successional conifers will be especially reduced by short rotations. In the Cascade Range, western hemlock tends to be a major component only late in succession (Franklin 1988) and is, therefore, often only a minor seed producer except in old-growth forests. For example, in the Douglas fir–western hemlock forest type in the Cascade Range of Washington, western hemlock seed production in a 100-year-old stand (mostly Douglas fir) was less than one two-hundredth of that in a nearby old-growth stand (Isaac 1943).

Crossbills are expected to benefit from mature and old-growth forests because they produce many more cones much more consistently over longer periods than do regularly logged forests. Furthermore, the small cone crops of younger forests may act as cone failures for crossbills because they require a minimum seed abundance to survive, with small cone crops less likely to meet minimum energy requirements (Benkman 1987a, 1992a). Moreover, because the larger the cone crop the more crossbills breed (Benkman 1990), the decline in large cone crops should result in smaller rates of increase after cone failures, and hence slower recovery rates.

Spatial Variation in Habitat Productivity

Geographic Variation

Because cone production can vary so much annually within a given area (Fowells 1965), special considerations need to be made to ensure that areas of abundant cones are available every year. Years of good cone production are usually followed by one to several years of little or no cone production; even the most regular cone-producing conifers have occasional cone failures (Fowells 1965). Moreover, large regions often fail to produce many—or any—conifer seeds during one to several years in succession (see Harris 1962), so that crossbills move out of these areas and concentrate where cone crops are produced (see Benkman 1987a). During many years, only a fraction of the total potential range can support crossbills. Thus, a reserve or system of reserves encompassing only a restricted geographic area would be inadequate to support nomadic populations of crossbills continuously, and most crossbill populations are nomadic. Indeed, bird species whose foods irregularly fail in a given area (such as tropical fru-

givores) tend to be "extinction prone" (Terborgh & Winter 1980; also see Janzen 1986).

Climate influences cone crop production and failures (Roeser 1942; Lowry 1966; Lester 1967; Smith & Balda 1979), hence areas experiencing similar climate are more likely to produce cone crops or fail in synchrony (see Kemp & Keith 1970). In western North America, the mountainous terrain affects local climate so that cone crop production is more likely to vary locally (Bock & Lepthien 1976; Smith & Balda 1979). Nevertheless, cone crops can fail synchronously over large mountainous regions (such as the Cascade Range of Oregon and Washington; Franklin et al. 1974).

The greater the number of distinct climatic regions within a forest reserve, the lower the probability of a complete cone failure. For example, six distinct regions, each with an independent probability of cone failure of one in three years (see, for example, Franklin et al. 1974), have a 0.0014 probability of synchronous cone failure (0.333^6). However, if only three of the regions have mature forest, then the probability of synchronous cone failure increases over 26 times to 0.037 (0.333^3). Compounding this further is that the frequency of small cone crops unable to support crossbills through the winter likely increases in younger stands. If as a result of logging the frequency of failure and of small cone crops doubles, the probability that six distinct regions are synchronously unable to support crossbills increases by over 62 times from 0.0014 to 0.088 (0.666^6). The decrease in distinct regions with mature forest and the decline in forest age from logging both compound the probability of synchronous and widespread cone failures, which are pernicious to crossbills (see Newton 1972 and Benkman 1988a for the effect of cone failures on crossbills).

Local Variation

Even within a given region, only certain areas may be favorable enough to maintain crossbills over many years (source habitat, for example, [Pulliam 1988]). Areas that consistently produce large cone crops and hold seeds for extended periods most likely represent source habitat for crossbills. Large cone crops result in high intake rates for crossbills (Benkman 1987a, 1987b), which improves their reproductive rates (Benkman 1990) and presumably their survival (Benkman 1987a). The value of reserves in protecting crossbills, therefore, depends critically on the amount of productive land or source habitat protected.

Unfortunately, for the same reasons habitats are most productive for crossbills (edaphic characteristics and climate favorable for cone production) they are likely to be most productive for commercial interests and to be intensively managed. In the Pacific Northwest, for example, lowland forests are the most productive, and

they have been largely logged (Norse 1990). Most of the remaining old growth in the Pacific Northwest is at higher elevations on steep slopes (Norse 1990). Here, cone production is less than at lower elevations because it often declines with increases in elevation (as in Douglas fir and ponderosa pine [Jacobsen 1986]). In fact, most protected areas (such as wilderness areas) are confined to higher elevations (Harris 1984), where conifers likely produce fewer seeds than at lower elevations where logging is permitted.

Habitat Fragmentation

As remnant forest patches become smaller and more isolated and fragmented, many forest species decline disproportionately relative to forest loss (Wilcove et al. 1986). Crossbills have been found to decline as forests are fragmented (Helle 1985). However, their decline is more likely in response to the concurrent decline in forest age as a result of logging rather than to habitat fragmentation per se (Helle & Järvinen 1986). Forest fragmentation is likely not as detrimental for crossbills, which regularly may fly distances for greater than 1 km (Benkman, personal observation), as it is for other old-growth species (Norse 1990). Thus, local management policies that account for more area-sensitive species (such as the Northern Spotted Owl Strix occidentalis caurian and Northern Goshawk [Accipiter gentilis]) would be adequate for crossbills.

Habitat fragmentation, nevertheless, may make crossbills more vulnerable to extinction by reducing the rate at which suitable patches of habitat (those containing a good cone crop)—are colonized. Levins (1969, 1970) has shown that when extinction rates of local individual populations exceed colonization rates, the species or metapopulation may go extinct. Crossbills can be thought of as being composed of many populations repeatedly colonizing patches of habitat containing good cone crops, and then going extinct locally when the cone crop fails. As patches become smaller and more isolated, their rate of colonization by crossbills may decline. Because a nomadic crossbill may need to colonize many patches during its lifetime, even slight declines in colonization rates can be important.

Evidence of Adverse Effects on Crossbills

As expected from much greater seed production in old than young forests, Red Crossbills were more abundant in older than in younger forests in Finland (Helle & Järvinen 1986) and in northern California (Raphael et al. 1988). In another study, Red Crossbills were 30 times more abundant in old-growth (325 to >500 years old) than in younger (65 to 140 years old) forests during two years of poor seed crops in the Cascade Range of south-

ern Washington (Huff et al. 1991). Such a pronounced difference occurred because the only conifer to produce seeds was the late-seral (at least in this forest type) western hemlock, and it was of cone-producing size and age only in the old-growth forests (Manual & Huff 1987; Huff et al. 1991; see previous discussion).

Although this system has not been modeled, diminished cone production and the increased isolation of productive habitats as a result of logging will likely result in declines of crossbills even within mature forests (see Fahrig 1992). Consequently, crossbill abundance should decline disproportionately to forest loss. Evidence of declines in crossbills that are disproportionate to the loss of habitat has been found in northern Finland: as the proportion of land containing older forests (>121 years old) diminished by 27% between the early 1950s and 1970s because of clear-cutting, Red Crossbills declined by 75% (Väisänen et al. 1986). Väisänen et al. (1986) also present evidence that crossbills declined even within an unaltered forest.

In sum, older forests tend to support more crossbills than do younger forests, and as the proportion of the landscape containing older forests declines, crossbills decrease disproportionately in abundance. This could have been anticipated from our knowledge of the natural history of crossbills and of conifer seed production. We should anticipate that if the extent and frequency of logging increases, crossbills will continue to decline and will become increasingly vulnerable to environmental and demographic stochasticity and to losses to genetic variability (see Lande 1988).

Conclusions and Recommendations

Protecting nomadic populations of crossbills presents some of the same challenges confronted in the conservation of migratory species (Myers et al. 1987), where species often concentrate in small areas during their annual cycle. However, protecting nomadic species such as crossbills represents a more formidable challenge because critical habitats are more difficult to recognize since they may be used only once every several years, with different areas crucial during different years. Nonetheless, several practices would aid crossbills and other conifer seed–eating animals.

First, as a general rule, the amount of old-growth forest should be maximized simply because it is consistently the most productive for crossbills. In areas where little old growth remains (such as Siuslaw National Forest in coastal Oregon [Harris 1984]), second-growth should be protected and allowed to mature. Especially beneficial to the crossbills specialized on Douglas fir and western hemlock is the recent proposal to protect an additional 2.4 million ha of U.S. Forest Service and Bureau of Land Management lands in northern California,

western Oregon, and western Washington to protect the Northern Spotted Owl (Thomas et al. 1990).

Second, rotation ages of managed forests need to be lengthened. In western North America, the proportion of lands logged and the rotation ages set by the U.S. Forest Service and Bureau of Land Management will have a profound impact on crossbill populations, because these two agencies control most of the federal forests required by crossbills (see Crumpacker et al. 1988). A similar arrangement exists in Canada, where even less old-growth forest is protected from logging than in the United States (for example, only about 17,600 ha of old-growth Sitka spruce–western hemlock forest were protected in British Columbia as of 1987 [Roemer et al. 1988; see also Beebe 1991]).

Third, mature trees should be left in cutover areas (as in partial cuts; see Franklin & Spies 1991). This will act to increase the proportion of the landscape containing trees of cone-bearing age. Furthermore, the remaining trees, released from competition, may then produce larger cone crops (see Fowells 1965). However, because cross-pollination and the number of full seeds per cone declines as mature tree density decreases (Smith et al. 1988), there will be a lower limit to tree density below which crossbills cannot be supported in the long term.

Fourth, because geographically separated areas often produce cone crops asynchronously, a geographically limited reserve of each forest type, (such as spruce-hemlock forest) will be inadequate for protecting nomadic populations of crossbills. Forest reserves should be located among as many distinct climatological regions as possible to avoid synchronous cone failures among all areas, and to minimize the risk from catastrophes (see, for example, Walters 1991). Tree seed zones, each of which represent different climates and elevations, represent such distinct regions (Schopmeyer 1974). Information on geographic variation (morphological or phenological) in conifers can also be used in determining favorable distributions of forests, because morphological variation is correlated with climate (such as ponderosa pine [Fowells 1965] and Douglas fir [Sorensen & Miles 1978]). The policy to protect forest tracts throughout the Northern Spotted Owl's range (Thomas et al. 1990) will reduce the likelihood of a complete cone failure in the Pacific Northwest.

Fifth, reserves should encompass productive forests. This will be difficult where commercial interests are powerful. For example, in the Cascade Range the most productive areas are low-lying valleys, of which few are protected (Norse 1990).

Last, aiding seed-eating animals will seem heretical to silviculturalists, who have invested a considerable amount of energy eradicating these animals (see Fowells 1965). However, by increasing rotation intervals, we enhance seed production and especially the occurrence of large cone crops. Because the greatest fraction and by far the greatest number of seeds remain uneaten during large cone crops (see Fowells & Schubert 1956), they are the most critical for natural regeneration. By increasing rotation ages (and the amount of old growth) we can increase the occurrence and extent of large cone crops and thereby protect the great diversity of conifer seed–eating animals (see Smith & Balda 1979).

Literature Cited

Alaback, P. B., and G. P. Juday. 1989. Structure and composition of low elevation old-growth forests in Research Natural Areas of southeast Alaska. Natural Areas Journal 9:27–39.

Beebe, S. B. 1991. Conservation in temperate and tropical rain forests: The search for an ecosystem approach to sustainability. Transactions of the North American Wildlife and Natural Resources Conference 56:595–603.

Benkman, C. W. 1987a. Food profitability and foraging ecology of crossbills. Ecological Monographs 57:251–267.

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

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

Benkman, C. W. 1988b. On the advantages of crossed mandibles: An experimental approach. Ibis 129:288–293.

Benkman, C. W. 1989. On the evolution and ecology of island populations of crossbills. Evolution 43:1324–1330.

Benkman, C. W. 1990. Foraging rates and the timing of crossbill reproduction. Auk 107:376–386.

Benkman, C. W. 1992a. White-winged Crossbills. In A. Poole, P. Stattenheim, and F. Gill, editors. The birds of North America. Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania.

Benkman, C. W. 1992b. Newfoundland Crossbill's Twist of Fate. Natural History. 101(12): 39–42.

Benkman, C. W. 1993. Adaptation to a single resource and the evolution of crossbill (*Loxia*) diversity. Ecological Monographs. 63:305–325.

Benkman, C. W., and A. K. Lindholm. 1991. The advantages and evolution of a morphological novelty. Nature 349:519–520.

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

Brown, E. R. 1985. Management of wildlife and fish habitat in forests in western Oregon and Washington. Technical Report, No. RG-FGWL-192-1985. U.S. Forest Service, Portland, Oregon.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America, vol. 1. Handbook 654. U.S. Department of Agriculture, Washington, D.C.

Caufield, C. 1990. The ancient forest. The New Yorker, May 14.

Crumpacker, D. W., S. W. Hodge, D. Friedley, and W. P. Gregg, Jr. 1988. A preliminary assessment of the status of major terrestrial and wetland ecosystems on federal and Indian lands in the United States. Conservation Biology 2:103–115.

Fahrig, L. 1992. Relative importance of spatial and temporal scales in a patchy environment. Theoretical Population Biology 41:300–314.

Fowells, H. A. 1965. Silvics of forest trees in the United States. Number 271. Agricultural handbook, U.S. Department of Agriculture, Washington, D.C.

Fowells, H. A., and G. H. Schubert. 1956. Seed crops of forest trees in the pine region of California. U.S. Department of Agriculture Technical Bulletin 1150:1–48.

Franklin, J. F. 1988. Pacific Northwest forests. Pages 104–130 in M. G. Barbour and W. D. Billings, editors. North American terrestrial vegetation. Cambridge University Press, New York, New York.

Franklin, J. F., and T. A. Spies. 1991. Composition, function, and structure of old-growth Douglas-fir forests. Pages 71–80 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical editors. Wildlife and vegetation of unmanaged Douglas-fir forests. General Technical Report PNW-GTR-285. U.S. Department of Agriculture, Forest Service, Portland, Oregon.

Franklin, J. F., R. Carkin, and J. Booth. 1974. Seeding habits of upper-slope tree species. I. A 12-year record of cone production. Research Note PNW-213. United States Department of Agriculture, Washington, D.C.

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

Groth, J. G. 1990. Cryptic species of nomadic birds in the Red Crossbill (*Loxia curvirostra*) complex of North America. Dissertation. University of California, Berkeley, California.

Habeck, J. R. 1988. Old-growth forests in the northern Rocky Mountains. Natural Areas Journal 8:202–211.

Harris, A. S. 1962. Cone crops in coastal Alaska—1960 and 1961. Technical Note No. 53. Northern Forest Experiment Station, U.S. Department of Agriculture, Forest Service, Juneau, Alaska.

Harris, L. D. 1984. The fragmented forest: Island biogeography theory and the preservation of biotic diversity. University of Chicago Press, Chicago, Illinois.

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

Helle, P., and O. Järvinen. 1986. Population changes of north Finnish land birds in relation to their habitat selection and changes in forest structure. Oikos 46:107–115.

Huff, M. H., D. A. Manuwal, and J. A. Putera. 1991. Winter bird communities in the southern Washington Cascade Range. Pages 207–218 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. General Technical Report PNW-GTR-285. U.S. Department of Agriculture, Forest Service, PNRS, Portland, Oregon.

Isaac, L. A. 1943. Reproductive habits of Douglas-fir. Charles Lathrop Park Forestry Foundation, United States Forest Service.

Jacobsen, G. L. 1986. Are you getting ponderosa pine and Douglas-fir cone crops at high elevations? Pages 47–49 in R. C. Shearer, Proceedings—conifer tree seed in the Inland Mountain West Symposium. General Technical Report INT-203. United States Department of Agriculture, Washington, D.C.

Janzen, D. H. 1986. The eternal external threat. Pages 286–303 in M. E. Soulé, editor. Conservation biology: The science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.

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

Lande, R. 1988. Genetics and demography in biological conservation. Science 241:1455–1460.

Lester, D. T. 1967. Variation in cone production of red pine in relation to weather. Canadian Journal of Botany 45:1683–1691.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237–240.

Levins, R. 1970. Extinction. Lectures in Mathematics and Life Sciences 2:75–107.

Lowry, W. P. 1966. Apparent meterological requirements for abundant cone crop in Douglas-fir. Forest Sciences 12:185–192.

Manual, D. A., and M. H. Huff. 1987. Spring and winter bird populations in a Douglas-fir forest sere. Journal of Wildlife Management 51:586–595.

McLaren, C. 1990. Heartwood. Equinox 53(9):43–55.

Myers, J. P., R. I. G. Morrison, P. Z. Antas, B. A. Harrington, T. E. Lovejoy, M. Sallaberry, S. E. Senner, and A. Tarak. 1987. Conservation strategy for migratory species. American Scientist 75:19–26.

Newton, I. 1972. Finches. Collins, London, England.

Norse, E. A. 1990. Ancient forests of the Pacific Northwest. Island Press, Washington, D.C.

Peet, R. K. 1988. Forests of the Rocky Mountains. Pages 64–101 in M. G. Barbour and W. D. Billings, editors. North America terrestrial vegetation. Cambridge University Press, New York, New York.

Pimm, S. L. 1990. The decline of the Newfoundland crossbill. Trends in Ecology and Evolution 5:350–351.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

Raphael, M. G., K. V. Rosenberg, and B. G. Marcot. 1988. Large-scale changes in bird populations of Douglas-fir forests, north-western California. Pages 63–83 in Bird Conservation 3. J. A. Jackson, editor. International Council for Bird Preservation, U.S. Section, University of Wisconsin Press, Madison, Wisconsin.

Roemer, H. L., J. Pojar, and K. R. Joy. 1988. Protected old-growth forests in coastal British Columbia. Natural Areas Journal 8:146–159.

Roeser, J. 1942. The influence of climate on seed production in Douglas fir. Journal of Forestry 40:304–307.

Rosencranz, A., and A. Scott. 1992. Siberia's threatened forests. Nature 355:293–294.

Schopmeyer, C. S. 1974. Seeds of woody plants in the United States. Agriculture Handbook No. 450. U.S. Department of Agriculture, Washington, D.C.

Shearer, R. C. 1986. Cone production on Douglas-fir and western larch in Montana. Pages 63–67 in R. C. Shearer, compiler. Proceedings—conifer tree seed in the Inland Mountain West symposium. General Technical Report INT-203. U.S. Department of Agriculture, Washington, D.C.

Smith, C. C., and R. P. Balda. 1979. Competition among insects, birds and mammals for conifer seeds. American Zoologist 19:1065–1083.

Smith, C. C., J. L. Hamrick, and C. L. Kramer. 1988. The effects of stand density on frequency of filled seeds and fecundity of lodgepole pine (*Pinus contorta* Dougl.). Canadian Journal of Forest Research 18:453–460.

Sorensen, F. C., and R. S. Miles. 1978. Cone and seed weight relationships in Douglas-fir from western and central Oregon. Ecology 59:641–644.

Spies, T. A., and J. F. Franklin. 1988. Old growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. Natural Areas Journal 8:190–201.

Terborgh, J. 1986. Keystone plant resources in the tropical forest. Pages 330–344 in M. E. Soulé, editor. Conservation biology: The science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.

Terborgh, J., and B. Winter. 1980. Some causes of extinction. Pages 119–133 in M. E. Soulé and B. A. Wilcox, editors. Conservation biology: An evolutionary-ecological perspective. Sinauer Associates, Sunderland, Masschusetts.

Thomas, J. W., E. D. Forsman, J. B. Lint, E. C. Meslow, B. R. Noon, and J. Verner. 1990. A conservation strategy for the Northern Spotted Owl: Report of the Interagency Scientific Committee to address the conservation of the Northern Spotted Owl, United States Forest Service. Portland, Oregon.

Väisänen, R. A., O. Järvinen, and P. Rauhala. 1986. How are extensive, human-caused habitat alterations expressed on the scale of local bird populations in boreal forests? Ornis Scandinavica 17:282–292.

Walters, J. R. 1991. Application of ecological principles to the management of endangered species: The case of the Red-Cockaded Woodpecker. Annual Review of Ecology and Systematics 22:505–523.

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

Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237–256 in M. E. Soulé, editor. Conservation biology: The science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.