CONTINENTAL AND REGIONAL DISTRIBUTION AND ABUNDANCE PATTERNS OF BOREAL CARDUELINE FINCHES: INFLUENCES OF CONIFER SEED AVAILABILITY

CENTRE FOR NEWFOUNDLAND STUDIES

TOTAL OF 10 PAGES ONLY
MAY BE XEROXED

(Without Author's Permission)

L. SARAH WREN

INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

ProQuest Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
800-521-0600

UMI®

National Library of Canada
Bibliothèque nationale du Canada

Acquisitions and Bibliographic Services
Acquisitions et services bibliographiques

395 Wellington Street
Ottawa ON K1A 0N4
Canada

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-73461-7

Canada

CONTINENTAL AND REGIONAL DISTRIBUTION AND ABUNDANCE PATTERNS OF BOREAL CARDUELINE FINCHES: INFLUENCES OF CONIFER SEED AVAILABILITY

by

L. Sarah Wren

A thesis submitted to the

School of Graduate Studies

in partial fulfillment of the

requirements for the degree of

Master of Science

Interdisciplinary Programme in Biopsychology
Faculty of Science
Memorial University of Newfoundland

© L. Sarah Wren

July 2001

St. John's Newfoundland

ABSTRACT

The mature boreal forest provides essential resources for conifer seed-eating cardueline finches. These resources are important on regional and stand level scales, and on landscape or continental scales, as cardueline finches move nomadically or irruptively in search of conifer seeds. Regional and temporal changes in conifer seed availability and cardueline finch abundance were examined with seed trap sampling and point counts in three mature conifer forests on insular Newfoundland. Seed rain phenology and finch abundance over time varied among the forests. On a landscape scale, analyses of continent-wide distributions of seed-eating finches using Christmas Bird Counts from 1970 - 1997 illustrated inter-annual fluctuations in abundance of six species of cardueline finches. These data encompass key boreal habitat in Canada that had been omitted from previous map-based studies of finch irruptions. The pattern of fluctuating continental abundance was close to biennial in some species like the common redpoll (*Carduelis flammea*). There was a significant effect of boreal cone crop magnitude on annual boreal finch abundance. Abundances of boreal finches were also examined from CBC counts in varied boreal forest habitats in Newfoundland. On such a regional scale, CBC counts are a useful tool for the analysis of population trends between and within habitats, as illustrated by the CBC data that indicate a recent and precipitous decline of the Newfoundland red crossbill, *Loxia curvirostra percna*. Understanding the relationship between boreal finches and conifer resources on small and large scales is essential for gaining insight into how recent landscape-level changes affect such highly specialized feeders.

ACKNOWLEDGMENTS

I would like to thank my thesis co-supervisors Luise Hermanutz and Bill Montevecchi for their continued support, encouragement and patience throughout this research. I also appreciate the support of my committee members Stephen Flemming and Joe Brazil. Thanks to Rob Sexton and Greg Stroud for helping me with fieldwork, and to Keith Lewis for not only field assistance but for lots of advice. The assistance provided by Gros Morne National Park, Terra Nova National Park, Pippy Park, Western Newfoundland Model Forest, and Lem Mayo and the Newfoundland Forestry and Wildlife Division was very much appreciated. This research was supported by grants from Gros Morne and Terra Nova National Parks, NSERC and the Western Newfoundland Model Forest to W. A. Montevecchi.

Mom, Jason and Brad – thanks.

TABLE OF CONTENTS

Abstract ii

Acknowledgments iii

List of Tables vi

List of Figures vi

List of Appendices viii

Chapter 1 – Introduction 1-1

Chapter 2 – Influence of conifer seed availability on spatial and temporal distributions of cardueline finches in Newfoundland 2-1

Introduction 2-1
Methods 2-9
Study location 2-9
Resource sampling and data analysis 2-10
Forager censuses and data analysis 2-12
Results 2-17
Resource variability 2-17
Forager variability 2-21
Resource/forager interactions 2-26
Discussion 2-28
Resource variability 2-28
Forager variability 2-29
Resource/forager interactions 2-29
Scale of monitoring for finch abundance 2-32
Conclusions and recommendations 2-35
Literature cited 2-37
Appendices 2-44

Chapter 3 – An analysis of continental and regional distribution and abundance patterns of boreal cardueline finches from Christmas Bird Count data 3-1
Introduction 3-1
Methods 3-10
Continental patterns of cardueline finch distribution and abundance 3-10
Finch abundance and boreal cone crop magnitude 3-15
Regional patterns of cardueline finch abundance in Newfoundland 3-17
Results 3-18
Continental patterns of cardueline finch distribution and abundance 3-18
Finch abundance and boreal cone crop magnitude 3-42
Regional patterns of cardueline finch abundance in Newfoundland 3-48
Discussion 3-53
Continental patterns of cardueline finch distribution and abundance 3-53
Finch abundance and boreal cone crop magnitude 3-57
Regional patterns of cardueline finch abundance in Newfoundland 3-59
Conservation priorities for boreal cardueline finches 3-61
Conclusions and recommendations 3-66
Literature cited 3-69
Appendices 3-76

Chapter 4 – Summary and conclusions 4-1

LIST OF TABLES

Table 2-1 – Analysis of variance of effect of sampling site on transformed number of conifer seeds at each study location. 2-17
Table 2-2 – Analysis of variance of effect of month and location on transformed number of conifer seeds 2-20
Table 2-3 – Organic and inorganic composition of species of Newfoundland conifer seeds as a function of percent of wet mass 2-20
Table 2-4 – Total abundance per total sampling effort of cardueline finch species and red squirrels at all point count locations from all census dates at each study site 2-21
Table 2-5 – Analysis of variance of effect of month and location on transformed numbers of cardeuline finches and squirrels 2-25
Table 2-6 – Analysis of variance of effect of location on level of red squirrel feeding evidence 2-25
Table 2-7 – Regression analysis of effect of mean transformed conifer seed availability on mean transformed finch abundance across all locations 2-27

Table 3-1 – Number of red crossbills counted on Newfoundland CBCs, 1990 – 1999 3-52

LIST OF FIGURES

Figure 2-1 – Location of study sites on insular Newfoundland 2-9
Figure 2-2 – Monthly phenology of total conifer seed rain in the balsam fir forest 2-18
Figure 2-3 – Monthly phenology of total conifer seed rain in the black spruce forest 2-18
Figure 2-4 – Monthly phenology of total conifer seed rain in the mixed coniferous forest 2-19
Figure 2-5 – Total count per counting effort of cardueline finches and squirrels in the balsam fir study site, 1998-99 2-23
Figure 2-6 – Total count per counting effort of cardueline finches and squirrels in the black spruce study site, 1998-99 2-23
Figure 2-7 – Total count per counting effort of cardueline finches and squirrels in the mixed coniferous study site, 1998-99 2-24
Figure 2-8 – Relationships between mean transformed number of birds and squirrels per point across all study locations and the mean transformed number of balsam fir, white spruce and black spruce seeds collected per seed trap 2-26

Figure 3-1 – Extent of boreal forest zone of Canada 3-9
Figure 3-2 – Relationship between total annual count of finches per party hour and number of annual CBC count circles across North America 3-13
Figure 3-3 – Annual North American winter distribution and abundance of common redpolls from CBC data, 1970 - 1997 3-20
Figure 3-4 – Annual North American winter distribution and abundance of pine grosbeaks from CBC data, 1970 - 1997 3-23
Figure 3-5 – Annual North American winter distribution and abundance of pine siskins from CBC data, 1970 - 1997 3-26
Figure 3-6 – Annual North American winter distribution and abundance of purple finches from CBC data, 1970 - 1997 3-29
Figure 3-7 – Annual North American winter distribution and abundance of red crossbills from CBC data, 1970 - 1997 3-32
Figure 3-8 – Annual North American winter distribution and abundance of white-winged crossbills from CBC data, 1970 - 1997 3-35
Figure 3-9 – North American winter distribution and abundance of common redpolls in 1970 and 1997 overlaid with locations of CBC counts 3-38
Figure 3-10 – Total annual number of continental CBC circles with at least one finch per party hour, 1970 – 1997 3-40
Figure 3-11 – Total annual number of finches per party hour from CBC data, 1970 – 1997 3-41
Figure 3-12 – Relationship between number of finches per party hour and crop magnitude, and significant differences from multiple comparisons of mean ranks of bird abundance per party hour at varying cone crop indices at boreal CBC count circles, 1974 – 1985 3-44
Figure 3-13 – Canadian and Alaskan cone crop magnitudes from CBC data, 1974 – 1985 3-46
Figure 3-14 – Number of crossbills per party hour counted on the Gros Morne National Park CBC, 1972 – 1999 3-49
Figure 3-15 – Number of non-crossbill finches per party hour counted on the Gros Morne National Park CBC, 1972 – 1999 3-49
Figure 3-16 – Number of crossbills per party hour counted on the Terra Nova National Park CBC, 1970 – 1999 3-50
Figure 3-17 – Number of non-crossbill finches per party hour counted on the Terra Nova National Park CBC, 1970 – 1999 3-50
Figure 3-18 – Number of crossbills per party hour counted on the St. John's CBC, 1970 – 1999 3-51
Figure 3-19 – Number of non-crossbill finches per party hour counted on the St. John's CBC, 1970 – 1999 3-51

LIST OF APPENDICES

Appendix 2-1 – Mean number of seeds for each collecting date at each study site 2-44
Appendix 2-2 – Total abundance per total sampling effort of non-cardueline bird species at all point count locations from all census dates at each study site 2-45

Appendix 3-1 – CBC circles in boreal/coniferous habitat used to examine the relationship between finch abundance and cone crop magnitude..... 3-76
Appendix 3-2 – Locations of North American CBC circles, 1970 – 1997..... 3-81

Chapter 1

INTRODUCTION

The North American boreal forest zone is a broad ecoregion that stretches from Alaska across the continent to insular Newfoundland. The boreal forest zone in Canada comprises 529 million hectares, and represents 53% of Canada's land area (Global Forest Watch Canada 2000).

The boreal zone supports many groups of birds that are uniquely adapted to a boreal lifestyle (Erskine 1977). One such group is the cardueline finches (family Fringillidae, subfamily Carduelinae). These birds forage on the seeds on conifer trees, and possess different levels of morphological and behavioural specialization and dependence on conifer seeds. The boreal cardueline finches move nomadically in response to conifer seed resources that are spatially and temporally variable. During winters with patchy seed resources across a broad scale in the boreal forest, cardueline finches can move extended distances in search of food, a behavioural strategy that may result in large irruptions of birds into local forested regions (Newton 1972).

The response of boreal cardueline finches to changing levels of seed availability is seen on the level of broad ecoregions and local forested landscapes. Foraging decisions and nomadic movements are based on seed availability within forest stands (Benkman 1987; Adkisson 1996; Dawson 1997). Different conifer species have variable phenologies of seed ripening and release (Young and Young 1992), and this influences the temporal distributions of cardueline finches on local levels (Ulfstrand 1963).

This close link to seed resources within the boreal forest is also seen when cardueline finch distributions and abundances are considered across large spatial scales (Bock and Lepthien 1976). Because these birds have distributions that may stretch across the continent, a study of their biogeography across a broad range is essential in understanding the large-scale dynamics of these species (Virkkala 1991). Not only is a study of the relationship between boreal forest resources and cardueline finch distributions and abundances informative on large spatial scales, but these populations must also be studied on a large enough temporal scale to illustrate the species' fluctuations in response to the year-to-year variability in boreal seed availability (Wiens 1981).

The cardueline finches that inhabit the boreal forest are inherently linked to it as a result of their reliance on its seed resources. A study of the distributions and abundances of these species across local, regional and continental scales provides insight into the dynamics of seed availability within the boreal forest. Cardueline finches may respond to seed limitations in the boreal forest that result from competitive effects of other seed predators (Smith and Balda 1979), or from habitat alterations such as fire, insect outbreaks and timber harvesting (Thompson et al. 1999) which limit boreal seed resources.

This study examines patterns of distribution and abundance of boreal cardueline finches in relation to seed availability in the boreal forest on multiple scales. The study includes the results of field research done in insular Newfoundland to test the hypothesis that there is a positive relationship between finch abundance and conifer seed availability

on small spatial and temporal scales. On a continental scale, a map-based analysis of Christmas Bird Count data is used to determine the temporal and spatial variability of North American distributions and abundances of cardueline finches. These data are also used to test the hypothesis that there is a positive relationship between finch abundance and coarse-level assessments of cone crop magnitudes across the continent's boreal forests. The use of Christmas Bird Count data as a monitoring tool for cardueline finch populations on regional levels is discussed in this study, with an example of finch population monitoring in Newfoundland.

LITERATURE CITED

Adkisson, C. S. 1996. Red Crossbill. *In* A. Poole and F. Gill (eds.). The Birds of North America. No. 256. American Ornithologists' Union. Washington, DC.

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

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

Dawson, W. R. 1997. Pine Siskin. *In* A. Poole and F. Gill (eds.). The Birds of North America. No. 280. American Ornithologists' Union. Washington, DC.

Erskine, A. J. 1977. Birds in boreal Canada: communities, densities and adaptations. Canadian Wildlife Service Report Series, No. 41.

Global Forest Watch Canada. 2000. Canada's Forests at a Crossroads: An Assessment in the Year 2000. World Resources Institute, Washington, D.C.

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

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

Thompson, I. D., H. A. Hogan, and W. A. Montevecchi. 1999. Avian communities of mature balsam fir forests in Newfoundland: age-dependence and implications for timber harvesting. Condor 101: 311 - 323.

Ulfstrand, S. 1963. Ecological aspects of irruptive bird migration in northwestern Europe. Proceedings of the 13th International Ornithological Congress 780 - 794.

Virkkala, R. 1991. Spatial and temporal variation in bird communities and populations in north-boreal coniferous forests: a multiscale approach. Oikos 62: 59 - 66.

Wiens, J. A. 1981. Scale problems in avian censusing. Studies in Avian Biology 6: 513 - 521.

Young, J. A. and C. G. Young. 1992. Seeds of Woody Plants in North America. Dioscorides Press, Portland, Oregon.

Chapter 2

INFLUENCE OF CONIFER SEED AVAILABILITY ON SPATIAL AND TEMPORAL DISTRIBUTIONS OF CARDUELINE FINCHES IN NEWFOUNDLAND

INTRODUCTION

The boreal forest is a vegetative and climatic zone that extends around the Northern Hemisphere in the holarctic region (Haila and Järvinen 1990). Boreal forests are dominated by the conifer species pine (*Pinus* spp.), spruce (*Picea* spp.), larch (*Larix* spp.) and fir (*Abies* spp.; Vankat 1979; Larsen 1980). Regional differences in forest composition occur on broad geographic scales, but most boreal forests share a very similar physical structure (Larsen 1980).

Boreal coniferous forests around the world support a diverse bird community. However, avian diversity is generally lower in northern coniferous forests than in deciduous forests at similar latitudes (Willson and Comet 1996), with an estimated 138 bird species inhabiting the global boreal zone (Haila and Järvinen 1990). Greater than 80% of the bird species that breed in or north of the boreal forest migrate to more southerly regions (Erskine 1977). Year-round residents of the boreal forest usually belong to taxa with holarctic ranges, for example herbivores like grouse; predators like owls; and seed-eaters like finches (Erskine 1977).

Cardueline finches, a subfamily of the large finch family Fringillidae, have adapted to a boreal forest existence by subsisting almost entirely on seeds (Newton 1972). While most other boreal forest birds are partly or wholly insectivorous, cardueline finches feed extensively on buds, fruits and seeds of trees (Erskine 1977). Overall, boreal

forest bird species are adaptable and opportunistic (Erskine 1977), and carduelline finches in particular demonstrate a high degree of adaptation to a boreal lifestyle. They are morphologically well suited to grasping branches, have varying degrees of specialized bill structures to efficiently exploit coniferous seeds, and forage in all seasons in loosely formed flocks instead of defending feeding territories (Newton 1972).

Boreal carduelline finches do not follow the typical migratory patterns of many other North American passerines. Instead, in order to exploit conifer seed resources that are temporally and geographically variable, these species exhibit a certain degree of nomadism, with abundances that fluctuate between years on local, regional and continental scales (Newton 1972). As a result, these species are not always regularly found in many portions of their typical ranges (Troy 1983). These nomadic influxes towards the periphery of typical ranges are termed irruptions (Newton 1972).

Some wide-ranging North American species of irruptive boreal seed-eating birds are the red-breasted nuthatch (*Sitta canadensis*), purple finch (*Carpodacus purpureus*), red crossbill (*Loxia curvirostra*), white-winged crossbill (*Loxia leucoptera*), pine grosbeak (*Pinicola enucleator*), pine siskin (*Carduelis pinus*), common redpoll (*Carduelis flammea*), hoary redpoll (*Carduelis hornemanni*) and evening grosbeak (*Coccothraustes vespertinus*; Newton 1972; Bock and Lepthien 1976; Erskine 1977). Of these birds, all are fringillids with the exception of the red-breasted nuthatch (family Sittidae).

In a study of cone crop fluctuations and seed-eating bird irruptions, Bock and Lepthien (1976) demonstrated an overall synchrony in levels of seed production among

conifer tree species, and an inverse correlation between levels of seed production and magnitudes of seed-eating bird irruptions. This correlation between coniferous seed crop level and seed-eating finch abundance had previously been noted for red crossbills in Finland (Reinikainen 1937) and northern Europe (Formozov 1960). Widlechner and Dragula (1984) added support to this finding by demonstrating that the winter abundances of red-breasted nuthatches and pine siskins in California are related to poor cone crops in Washington and Oregon. Conversely, common crossbills (*L. curvirostra*) in Spain foraging on conifer seeds from an inter-annually stable cone crop demonstrate resident, non-irruptive behaviour (Senar et al. 1993), which further supports the view that irruptive behaviour is a response to sporadic food availability.

Coniferous seed availability is variable in the boreal forest because mast cone crops are produced on a minimum 2-year interval in many boreal species of pine, fir, spruce and larch (Silvertown 1980; Young and Young 1992). The cyclic nature of cone production is due to a combination of exogenous factors such as climatic conditions, and endogenous influences such as a tree species' reproductive cycle (Owens and Blake 1985). Multiple theories exist to explain reproductive synchrony in tree seed production (Kelly 1994). A widely supported hypothesis, particularly in dry-fruited tree species such as conifers, is that fluctuating seed crop size provides a selective reproductive advantage to the tree by periodically over-saturating seed predators (Levey and Benkman 1999). This is a particularly effective strategy as many conifer tree species produce regionally and interspecifically synchronous mast crops (Smith and Balda 1979; Silvertown 1980).

Bock and Lepthien (1976) found that winter irruptions of seed-eating birds are interspecifically synchronous and generally occur biennially in conjunction with poor boreal cone crops. Such biennial patterns of southward irruptions have been shown from mark-recapture studies of common and hoary redpolls (Troy 1983) and in common redpolls (Larson and Bock 1986) and red-breasted nuthatches (Bock and Lepthien 1972) from continental-scale Christmas Bird Count data.

Nomadic behaviour in search of food resources occurs among individuals during winter months. A continental feeder monitoring program indicated that common redpolls exhibited neither a population-level nomadism nor a uniform migration, and that traditional wintering grounds were not entirely abandoned during irruption years (Hochachka et al. 1999). In several species of seed-eating finches, e.g. common and hoary redpolls (Troy 1983) and evening grosbeaks (Newton 1972), irruption leads to very low inter-annual wintering and breeding site fidelity. This in turn allows irruptive seed-eaters a more flexible strategy to overcome temporally and geographically variable food supplies (Newton 1972).

Haila and Järvinen (1990), in a study of boreal zone bird richness, identified 49 species as inhabitants of boreal forests of the eastern Canadian mainland. There is a decrease in species richness on insular Newfoundland, which may be attributable to climatic and vegetation differences from mainland forests of the same latitude, and to an island effect of decreased emigration (Thompson et al. 1999). In western Newfoundland balsam fir forests, nine species of sparrows/finches have been identified during the breeding season: fox sparrow (*Passerella iliaca*), Lincoln's sparrow (*Melospiza*

lincolnii), white-throated sparrow (*Zonotrichia albicollis*), purple finch, white-winged crossbill, pine grosbeak, pine siskin, common redpoll and evening grosbeak (Thompson et al. 1999).

The cardueline finches are a highly visible portion of the winter avifauna in insular Newfoundland, but there are few studies of bird assemblages in the coniferous forest during the winter (Erskine 1977; Kreisel and Stein 1999). Finches are better able to survive at northern latitudes during winter than ground-foraging sparrows. The finches are more efficient at handling large seeds, allowing them to maximize their energy intake, and their morphological adaptations for storing seeds allow them to survive on patchy food resources (Benkman and Pulliam 1988).

Some cardueline finches are seed generalists and are not wholly dependent on coniferous seeds. For example, pine grosbeaks utilize seeds of deciduous trees and coniferous buds (Pulliainen 1974). Common redpolls have a diet based largely coniferous seeds but also eat deciduous seeds (Bent 1968). Purple finches consume mostly deciduous seeds but also eat coniferous seeds (Wooton 1996). Pine siskins, with their slender bills, consume a wide variety of plant seeds, but prefer coniferous seeds during migration and winter (Dawson 1997). In contrast, crossbills are highly specialized cardueline finches and are generally limited to foraging only on conifer seeds as a result of their bill morphology (Benkman 1993a).

Conifer seed availability is expected to be the major limiting factor in the distributions and abundances of seed-eating finches in Newfoundland. Seed availability may be limited through seed ripening phenology, habitat limitations or alterations such as

clear-cut logging, or interspecific competition with other seed predators. Although there is little evidence of competition between boreal birds for food resources (Martin 1986; Haila and Järvinen 1990), non-avian seed predators such as squirrels could play important roles in reducing seed availability for cone-dependent finches (Smith and Balda 1979).

A notable conifer seed predator in the boreal forest zone of North America is the red squirrel (*Tamiasciurus hudsonicus*). Red squirrels remove whole cones from trees and cache them in well-defended territories (Smith and Balda 1979). This allows them to subsist on variable conifer seed resources. Red squirrels may have a competitive advantage in the timing of exploitation of conifer seeds over most finches, as squirrels extract seeds from closed cones (Smith and Balda 1979). Carduelline finch species such as the house finch (*Carpodacus mexicanus*), American goldfinch (*Carduelis tristis*), evening grosbeak (Benkman 1988) and pine siskin (Benkman and Lindholm 1991) have generalized bill structures that allow them to handle seeds efficiently, but they are not able to remove them from closed cones. Crossbills, however, are unique among the seed-eating finches because they use their distinctive crossed mandibles to extract seeds from closed cones (Benkman 1992; Adkisson 1996).

Red squirrels were introduced in small numbers on the Northern Peninsula of insular Newfoundland during the 1960s. As such they may present a new and significant impact as seed competitors (Benkman 1993c). By the 1980s red squirrels were considered well established on the Northern Peninsula, in central Newfoundland and on the Avalon Peninsula (Dodds 1983). Red squirrels influence conifer seed availability

particularly in years with small cone crops. West (1989) found that red squirrels removed up to 96% of cones from black spruce (*Picea mariana*) trees in a central Newfoundland plantation in years of low cone production. Similarly, 87% of white pine (*Pinus strobus*) cones were removed during a one-year study of rates of red squirrel seed predation in white pine stands across Newfoundland (English 1998). Benkman (1993c) has suggested that high rates of cone predation by red squirrels on insular Newfoundland have brought about the recent precipitous decline in abundance of the Newfoundland subspecies of red crossbill (*L. curvirostra percna*). Montevecchi et al. (in prep.) however, document that the timing of the squirrel introduction and red crossbill decline are not concordant. They contend that cumulative effects and large-scale habitat loss from forestry practices in Newfoundland, as well as competitive exclusion from red squirrels, have resulted in declines of the Newfoundland red crossbill.

Characteristic boreal zone vegetation is found across insular Newfoundland. Over much of the island, the mature forest stands are either balsam fir (*Abies balsamea*) or black spruce dominated. Black spruce is found inland, in wet or nutrient-poor areas, or in fire regeneration sites (Meades and Moores 1994), while balsam fir is found in coastal, humid sites. Throughout the boreal forest, specific vegetational communities are determined by regional differences in climate (Larsen 1980), and this holds true in Newfoundland. Damman (1983) classified these regional climatic and vegetational differences in Newfoundland into ecoregions. These ecoregions range from the balsam fir dominated, heavily forested areas of western Newfoundland and the Northern Peninsula, to the large black spruce component of central Newfoundland, to the strongly

maritime-influenced barrens and mixed coniferous forests of the Avalon Peninsula (Damman 1983).

It is hypothesized that there will be a positive relationship between the abundance of cardueline finches and red squirrels in relation to coniferous seed availability in these three different forest types in insular Newfoundland. This study was carried out from late summer to late winter, when conifer seeds are the primary food resource available to finches, seed profitability is reduced (Benkman 1987) and changes in food availability result in behavioural adaptations such as irruptive movements and winter breeding (Erskine 1977; Martin 1987; Hahn et al. 1997; Hahn 1998).

METHODS

Study location

The influence of seed availability on boreal seed-eating finch distribution and abundance in Newfoundland was studied in three study sites chosen to illustrate the variation in dominant forest types found over the island. A mature balsam fir forest stand in the Greater Gros Morne Ecosystem Main River area was the study site used to represent the predominant forest type of northwestern Newfoundland. A black spruce dominated forest stand in Terra Nova National Park was used as a study site characteristic of central Newfoundland forests. An eastern study site of mixed black spruce, balsam fir and white spruce (*P. glauca*) was chosen to represent the mixed coniferous stands of the island's Avalon Peninsula (Figure 2-1).

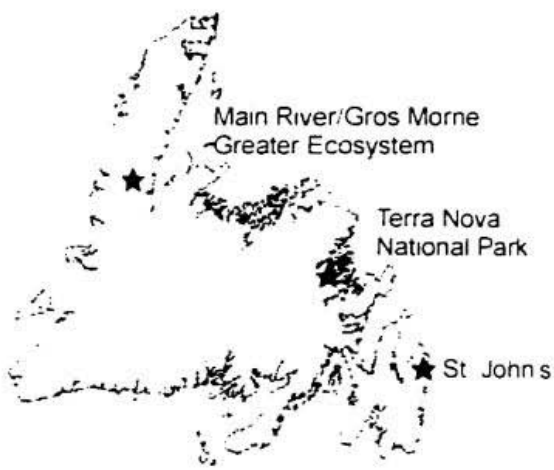


Figure 2-1 – Location of study sites on insular Newfoundland.

Resource sampling and data analysis

Seed traps were used to assess seed rain at each study site in order to determine 1) how cone ripening phenology changed over a season, and 2) how seed availability differed between the three forest stands of different compositions. Following the methodology of Houle and Payette (1991), each trap consisted of a metal cylinder (diameter = 15 cm, height = 20 cm) mounted on a stake approximately 75 cm above ground. Fibreglass mesh (1 mm^2 mesh size) was draped within each cylinder, to an approximate depth of 15 cm, and held in place with an elastic band. This configuration was chosen to allow precipitation to run through the mesh, to separate fine litter from the collected seeds (Kollmann and Goetze 1998), to allow the mesh to be removable so that contents of the traps could be collected on a regular basis, and to prevent losses of collected seed due to wind (Bullock 1996).

Seed traps were placed under the forest canopy in two 20 x 25 m quadrats at each of the three study sites in late August 1998. Each quadrat was divided into twenty 5 x 5 m squares. One seed trap was placed at the centre of each 5 x 5 m square. This resulted in 20 traps in each quadrat, forming a centric systematic area-sample to measure seed rain evenly across each quadrat (Krebs 1989). The sample size of 40 traps per study site was chosen to effectively sample seed rain, which is generally patchy (Bullock 1996). Each quadrat was located a minimum of 100 m from all natural and artificial edges within the forest stands.

Seed traps contents were collected approximately biweekly from all six quadrats and individually stored in small paper bags. Collected seeds were dried, identified to

species, and counted for each seed trap and collection date. Number of seeds in each trap was converted to number of seeds per m^2 based on the surface area of individual seed traps. The total seed rain per species per 500 m^2 for each collecting period was calculated for each quadrat. Seed collection was terminated after November 1998 in the balsam fir study location due to high snow accumulations that made the traps inaccessible, but continued through March 1999 for the mixed coniferous and black spruce study sites.

White birch (*Betula papyrifera*) was the only non-conifer seed collected in the seeds traps. Although some finch populations have been shown to fluctuate with birch crops (Eriksson 1970), coniferous trees were the major component of all study sites and therefore only seed data from conifer trees were examined.

For statistical analyses, numbers of seeds per quadrat were transformed by adding 0.5 and taking the square root of all variates (Greenwood 1996). This allows for typically Poisson-distributed count data to be transformed so that variances are independent of means (Sokal and Rohlf 1995). Analysis of variance (ANOVA) was performed to test whether there was a significant difference in the number of conifer seeds between replicate study quadrats to determine if seed rain data could be grouped by sites at each location. Species type and date were covariates in this analysis to control for their effects on seed rain between quadrats. Not all of the assumptions of ANOVA (residuals normally distributed, independent and variance of residuals homoscedastic) were met with these analyses, therefore probability estimates were obtained from F values calculated from 1000 randomization tests for each comparison. Two-way analysis of variance was performed to test whether there was a significant date effect on number of

seeds of each species at each location, and whether there was a significant location effect on each of the species of seeds collected. The residuals of these analyses met the assumptions of ANOVA therefore no randomization tests were performed for these comparisons. Testing for location effects was warranted in this experiment, as there was independence between the three study locations. In all analyses of variance, probabilities were assessed at an alpha level of 0.05.

Small samples of approximately 100-500 seeds of conifer species collected in the three study areas were chemically analyzed by the Canadian Food Inspection Agency, St. John's, NF, to determine levels of ash, fat, protein, moisture, carbohydrate and calorie content. Nutritional content of whole seeds was compared between black spruce, white spruce and balsam fir seeds to determine differences between the conifer species. Even though foraging finches generally hull seeds from seed coats (Benkman 1988), seed coats were analyzed along with the whole seeds, as red squirrels may consume seed coats when foraging (Grodzinski and Sawicka-Kapusta 1970).

Forager censuses and data analysis

Throughout the period of seed sampling, counts of birds were performed at each study site to determine the relative abundance of cardueline finches (Verner 1985). Multiple counts were performed monthly in order to accurately sample seasonal bird abundance in each habitat (Dettmers et al. 1999). Birds were counted at a total of 12 points, each 200 m apart (Gibbons et al. 1996), along a transect in each habitat. Point counts were chosen over transect sampling to assess bird abundances because they are suitable for conspicuous birds (such as finches) in woody habitats, and because they

provide a higher amount of data per effort than transect sampling (Bibby et al. 1992). Each point count lasted 10 min, a duration that was chosen to maximize counts of low-abundance birds detected during winter, to include a maximum counts in each habitat (Dettmers et al. 1999), and to minimize the increasing standard error associated with longer duration counts (Smith et al. 1998).

Counts of passerines in the coniferous forest may sample species richness more effectively over a period of several hours rather than in the early morning (Verner and Ritter 1986; Patterson et al. 1995). Because of this, counts in this study were generally started near dawn and were continued until 1100 h to maximize the number of counts that could be performed in one morning. Detection probabilities were assumed to be equal over the sampling hours as finches demonstrate fewer negative effects of time of day on detection than do other passerines (Robbins 1981b). As suggested by Dawson (1981), Robbins (1981a) and Verner (1985), counts were not performed on mornings with high wind or heavy rain or snow, to ensure that the probabilities of detecting birds were as equal as possible on all sampling days (Blondel et al. 1981). All visual and auditory encounters with birds within a 100 m radius of each point were recorded, as well as any behavioural observations for seed-eating finches such as flock size and foraging activity. Flocks of finches flying over the area were not counted if they did not land within the radius of each point count.

During each point count in the three forest habitats, all visual and auditory detections of red squirrels were also recorded. The common methodology for assessing squirrel density or abundance, like other small mammals, involves live trapping (Lurz et

al. 1995). This is a time-intensive technique, however, and relative densities of red squirrel have been estimated from acoustic cues in other forest bird studies (Hagan et al. 1996; Bayne and Hobson 2000). Male and female adult red squirrels exhibit highly territorial defence of food resources (Smith and Balda 1979), and their abundance may be estimated by the number of active territories in a habitat (Smith 1968). Territory defence is achieved through advertisement and threat displays, which are primarily vocal (Lair 1990). Thus, just as birds can be censused based on acoustic cues, red squirrels abundances can be estimated from vocal signals. Furthermore, live trapping of red squirrels may not adequately estimate densities when seed crop abundance is high, as squirrels are less attracted to baited traps (Gurnell 1983). This means that trapability of squirrels reaches a low in autumn, when seed crops are high. Trapability may continue to be depressed well into the winter during seed crop mast years (Gurnell 1983). Therefore, estimating red squirrel densities based on acoustic cues is an effective, and possibly more desirable, surrogate for live trapping throughout the autumn and winter.

An index of relative squirrel abundance was also estimated by scoring evidence of feeding activity in each study quadrat (Sutherland 1996). Red squirrels produce characteristic feeding evidence in the form of middens, which are piles of cached cones (Gurnell 1983) and cone scales accumulated from conifer seed consumption (Smith 1968). In late August 1998, the number of food middens visible on the forest floor in each 5 x 5 m quadrat in all study locations was counted. Each midden was scored on a scale of 1 to 5, with 1 representing a single cone, and 5 representing a very large, repeated use midden with a subterranean burrow.

As with the seed rain data, bird and squirrel count data were transformed by adding 0.5 to all variates and taking the square root. This was done to ensure that standard errors would not be proportional to their means, which occurs in non-transformed point count data (Smith et al. 1998). Two-way analysis of variance was performed to test whether there was an effect of study location and sampling date on cardueline finch and red squirrel abundance. All assumptions of analysis of variance were met with this analysis. Single-classification analysis of variance was used to test for differences between the number of food middens in the black spruce and balsam fir study sites. As with seed and finch count data, the counts of numbers of squirrel middens were transformed by adding 0.5 to all variates and taking the square root. Not all assumptions of the ANOVA were met (residuals non-independent and residual variances non-homogeneous), therefore probability estimates for all comparisons between mean transformed number of squirrel middens in the study sites were assessed based on randomization tests with 1000 replicates. All probabilities were assessed at an alpha level of 0.05.

Spearman's Rank Correlation indicated that the mean monthly abundances of balsam fir and white spruce seeds (pooled across all locations) were highly correlated (correlation coefficient = 0.987). To eliminate multicollinearity errors, Principal Component Analysis (PCA) was used to group balsam fir and white spruce seed abundance into one component that explained 98% of the variance in the two seed factors. Regression analysis was then used to examine the relationship between seed availability across all study locations and cardueline finch and squirrel abundances. This

regression analysis was done with black spruce seed abundance, and with the PCA factor representing balsam fir and white spruce seed abundance. Due to the small sample size and non-homogeneity of residual variances for two of the regressions, probability estimates for these two regressions were obtained from randomization tests that involved the generation of 1000 random F-ratios.

RESULTS

Resource variability

No significant differences in the seed rain existed between the two study quadrats at each location (Table 2-1). Based on this, it was decided that grouping the seed rain results from both sites at the three locations was justified.

The variable phenology and composition of coniferous seed rain in the three study locations is illustrated in Figures 2-2, 2-3 and 2-4. These figures illustrate the total number of seeds shed per month in each study location (total area 1000 m^2). Seed rain in the balsam fir forest could only be assessed in October and November due to high snow that made further collections impossible. Seed rain in the black spruce forest was low across the study period, and seed rain in the mixed coniferous forest was much higher than the other two sites, with a maximum of over 70 000 balsam fir seeds/1000m^2 in December 1998. Seed collections did not occur in the mixed coniferous forest in March. Mean values of seed rain for each site, date and study location are presented in Appendix 2-1.

Table 2-1 – Analysis of variance testing for the effect of sampling site on transformed number of conifer seeds at each study location. Species and date were used as covariates in the analysis, but there was no variability in date at the balsam fir location, and no variability in species at the black spruce location. All probability estimates from F-ratios calculated from 1000 randomizations for each test.

Location	n	F	P	Covariate
Balsam fir	80	0.366	0.815	Species
Black spruce	160	1.18	0.578	Date
Mixed conifer	720	1.73	0.624	Species and date

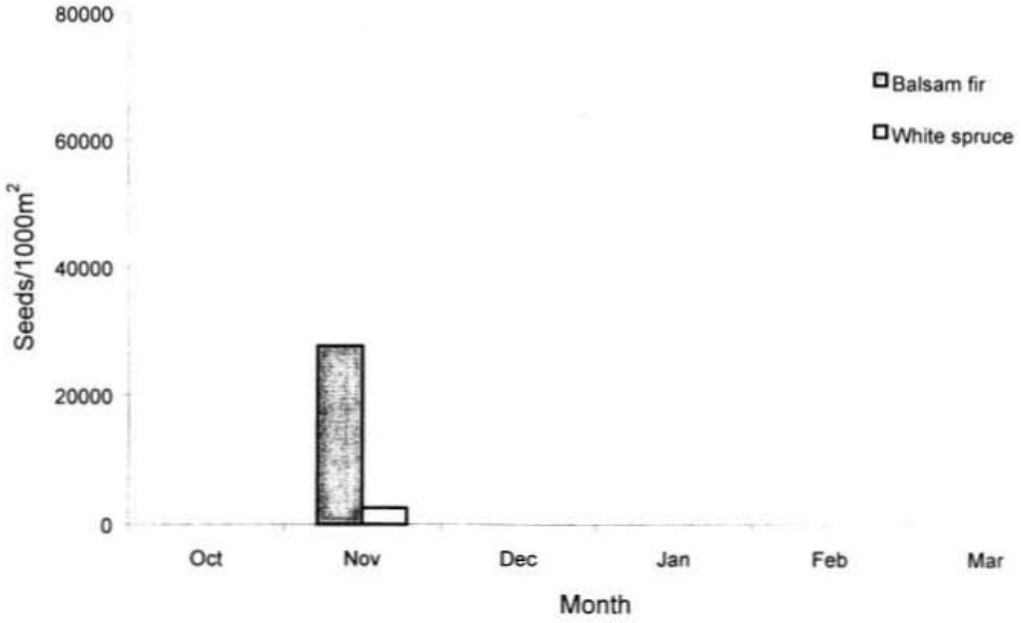


Figure 2-2 – Monthly phenology of total conifer seed rain in the balsam fir forest. Seed collections at this location performed only in October and November 1998.

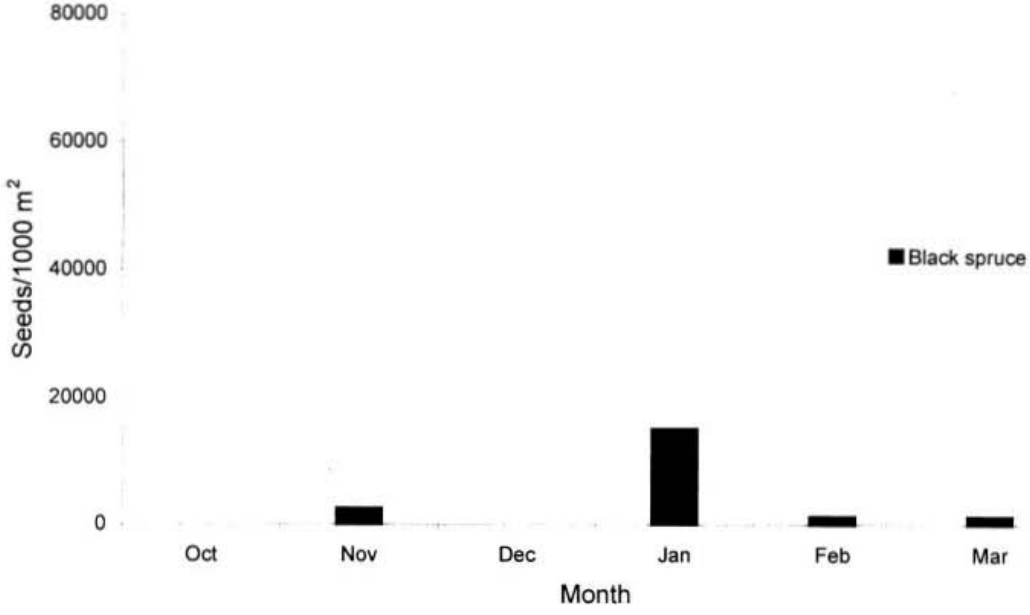


Figure 2-3 – Monthly phenology of total conifer seed rain in the black spruce forest. Seed collections at this location performed from November 1998 to March 1999.

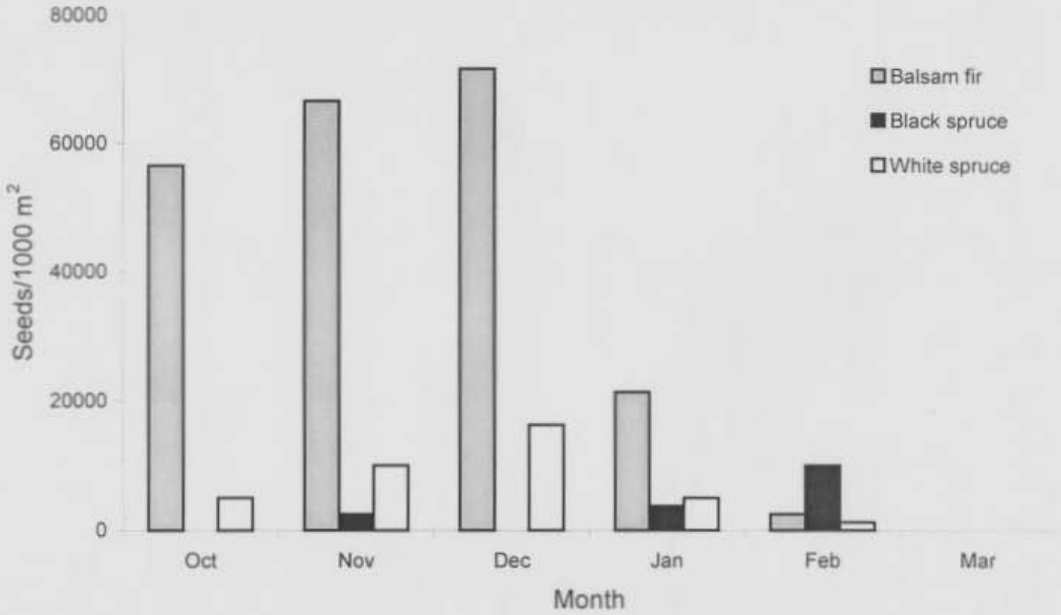


Figure 2-4 – Monthly phenology of total conifer seed rain in the mixed coniferous forest. Seed collections at this location performed from October 1998 to February 1999.

Two-way analysis of variance testing for spatial and temporal effects on coniferous seed rain indicated that abundance of balsam fir and white spruce seeds differed over time between study locations (month*location interaction term). There was no significant difference in black spruce seeds over time between the study locations (Table 2-2).

Table 2-2 – Analysis of variance of effect of month and location on transformed number of conifer seeds. n = 385 for all categories.

Species	Month		Location		Month*Location	
	F	P	F	P	F	P
Balsam fir	23.38	0.000	22.90	0.000	37.96	0.000
Black spruce	1.94	0.165	2.49	0.115	0.69	0.408
White spruce	8.70	0.003	6.36	0.012	10.85	0.001

In analyzing chemical composition of seed samples of white spruce, black spruce and balsam fir from Newfoundland, protein content could not be detected in the balsam fir sample due to the small sample size. As a result, the calorie and carbohydrate contents of the samples were not calculated and only levels of ash, lipid, protein, and moisture were compared among the species of seed. Of the three conifer species, black spruce seeds had the highest lipid, protein and ash contents. Lipid and ash contents were lowest in balsam fir (Table 2-3). Multiple samples of each species of seed were not chemically analyzed therefore no statistical comparisons between the samples could be made.

Table 2-3 – Organic and inorganic composition of species of Newfoundland conifer seeds as a function of percent of wet mass.

Species	% Moisture	Lipid	Protein (N X 6.25)	Ash
Balsam fir	8.1	14	Not detected	1.75
Black spruce	6.5	19	18.2	4.1
White spruce	6.5	16.7	13.5	2.7

Forager variability

The total abundance and diversity of birds counted from all censuses at each location was low. Cardueline finches comprised 14% of all birds and 22% of all passerines counted at the balsam fir site, 19% of all birds and 25% of all passerines at the mixed coniferous site, and 11% of all birds and 13% of all passerines at the black spruce site. The total number of passerine species was 20, with 16 in the mixed coniferous forest, 14 in the balsam fir forest, and 16 in the black spruce forest. The species of cardueline finches counted were pine grosbeak, pine siskin, white-winged crossbill and purple finch, with purple finch counted in only the mixed coniferous forest and only on two occasions. Total abundance per counting effort was low for all species of cardueline finches, but was generally highest in the balsam fir site. Red squirrel abundance was highest in the black spruce forest (Table 2-4). Total abundances per counting effort for all other bird species counted during the study are presented in Appendix 2-2.

Table 2-4 – Total count per total sampling effort of cardueline finch species and red squirrels at all point count locations from all census dates at each study site. Total sampling effort in mixed coniferous forest = 1800 min, balsam fir forest = 1360 min, black spruce forest = 1200 min.

Species	Balsam fir	Black spruce	Mixed conifer
Purple finch (*Carpodacus purpureus*)	0	0	0.0011
White-winged crossbill (*Loxia leucoptera*)	0.17	0	0.0017
Pine grosbeak (*Pinicola enucleator*)	0.033	0.0008	0.0011
Pine siskin (*Carduelis pinus*)	0.13	0.022	0.005
Red squirrel (*Tamiasciurus hudsonicus*)	0.043	0.16	0.013

In the balsam fir study site, a high relative abundance of finches and low relative abundance of squirrels was seen. No squirrels were counted at this site during the spring sampling in March 1999 (Figure 2-5). Finch abundances were low and irregular in the black spruce study site. Pine grosbeaks, pine siskins, and white-winged crossbills were not all seen in every sampling month. In contrast, the relative abundance of red squirrels was consistently high at this study location (Figure 2-6). In the mixed coniferous site pine grosbeaks, pine siskins and white-winged crossbills were regularly present in low abundances across the sampling period. Abundances of white-winged crossbills peaked in December, while pine grosbeak abundances were highest in November and pine siskin abundances were highest from November through January. Red squirrel abundances were generally uniform throughout the counting period at the mixed coniferous location (Figure 2-7).

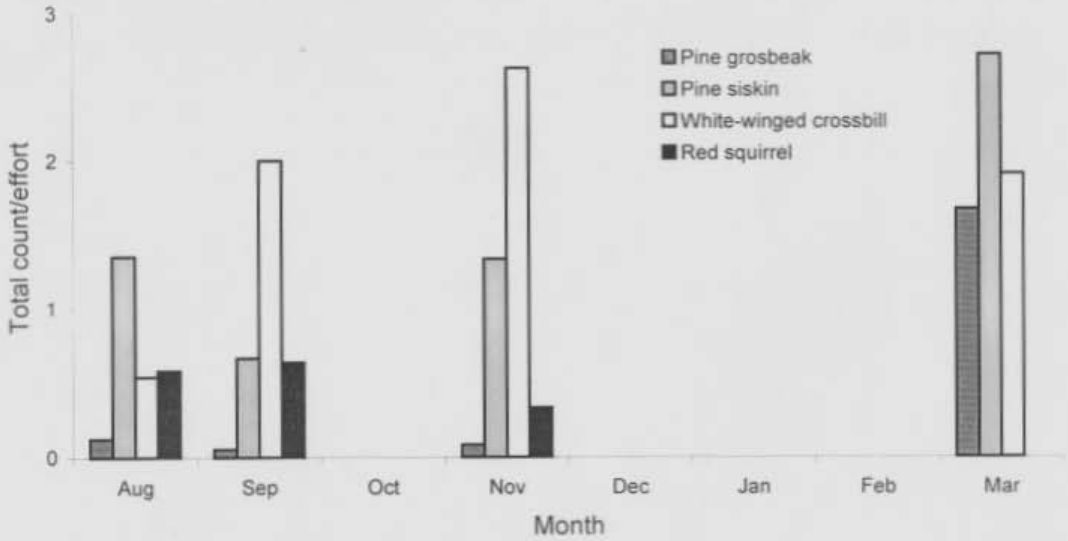


Figure 2-5 – Total count per counting effort of cardueline finches and squirrels in the balsam fir study site, 1998-99. No point count sampling occurred during October, December, January and February.

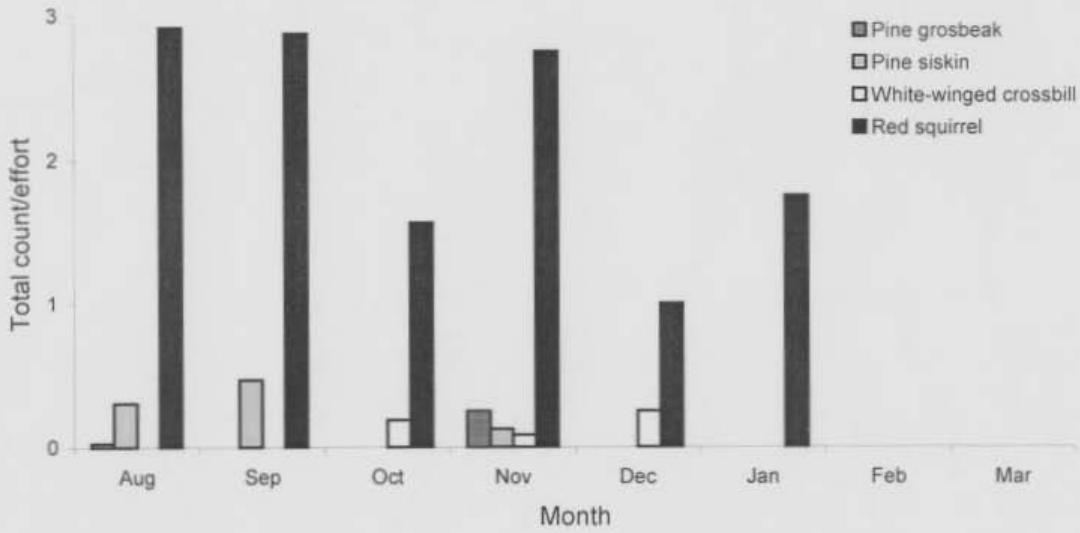


Figure 2-6 – Total count per counting effort of cardueline finches and squirrels in the black spruce study site, 1998-99. No point count sampling occurred during February and March.

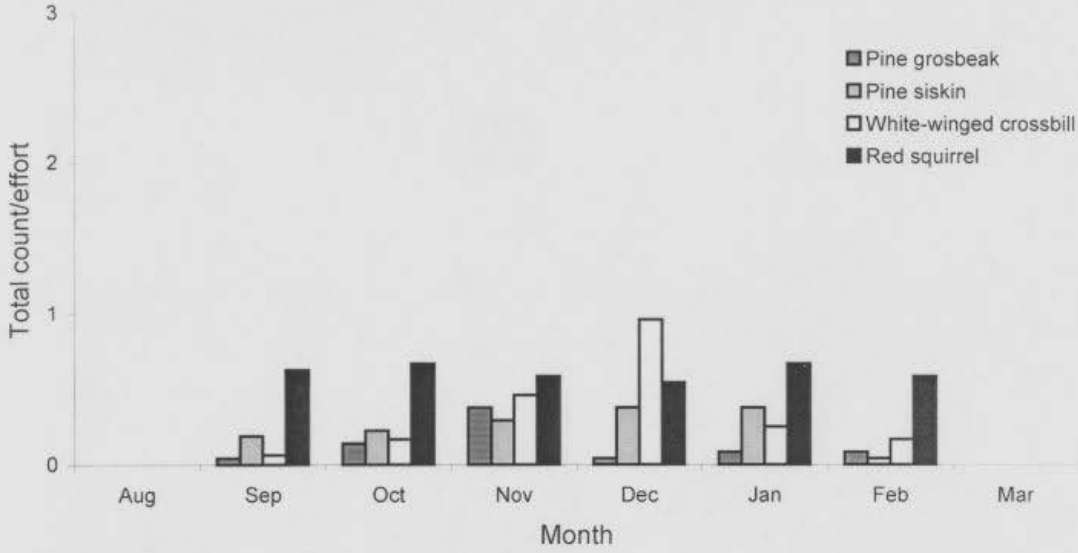


Figure 2-7 – Total count per counting effort of cardueline finches and squirrels in the mixed coniferous study site, 1998-99. No point count sampling occurred during August and March.

Analysis of variance showed a significant difference in the abundance of all three finch species over time between the three locations (month*location interaction effect; Table 2-5).

Evidence of an effect of study location on red squirrel abundance is seen in a comparison of number of middens counted in the balsam fir and black spruce stands (Table 2-6). There were significantly more small feeding middens (categories 1, 2 and 3) in the black spruce forest than the balsam fir forest. Significant differences were not detected between the abundances of the larger feeding middens at the two study sites, possibly due to the very low numbers of these categories of middens at both sites.

As with the patterns seen in the analysis of coniferous seed rain, spatial and temporal patterns exist in the abundances of cardueline finches and red squirrels in

different Newfoundland boreal forest sites. The three species of finches counted at the study sites showed different abundances over time between the three study sites. Red squirrel numbers remained high across the sampling period, with relative abundances much higher in the black spruce forest than in the other forest types.

Table 2-5 – Analysis of variance of effect of month and location on transformed numbers of cardeuline finches and squirrels. n = 432 for all tests.

Species	Month		Location		Month*Location	
	F	P	F	P	F	P
Pine grosbeak	42.818	0.000	6.346	0.012	24.531	0.000
Pine siskin	12.260	0.001	0.088	0.767	12.191	0.001
White-winged crossbill	5.39	0.021	5.63	0.018	4.23	0.040
Red squirrel	0.64	0.423	111.95	0.000	3.05	0.082

Table 2-6 – Analysis of variance of effect of location (balsam fir and black spruce sites only) on level of red squirrel feeding evidence. Midden category 1 = single cone preyed on; 2 = less than 10 cones; 3 = 11 to 25 cones; 4 = more than 25 cones; 5 = large repeated use midden with burrow and cached cones counted in each seed trap quadrat. n = 80 for all tests. All probability estimates from F-ratios calculated from 1000 randomizations for each test.

Feeding evidence category	# of middens (mean ± SD)		F	P
	Balsam fir	Black spruce		
1	0.125 ± 0.4043	5.325 ± 5.516	59.08	< 0.001
2	0.200 ± 0.516	1.700 ± 2.090	26.10	< 0.001
3	0	0.550 ± 0.749	24.70	< 0.001
4	0.025 ± 0.158	0.150 ± 0.362	4.01	0.125
5	0	0.125 ± 0.335	5.57	0.063
Total	0.350 ± 0.802	7.85 ± 6.90	95.92	< 0.001

Resource/forager interactions

The effect of conifer seed availability on cardueline finch and red squirrel abundance was examined by grouping data from all study locations (Figure 2-8). Regression analysis of the effect of mean conifer seed availability on mean abundance of cone-dependent finches revealed significant effects only between black spruce and pine grosbeak abundance, and between black spruce and red squirrel abundance. All other regression analyses were non-significant (Table 2-7).

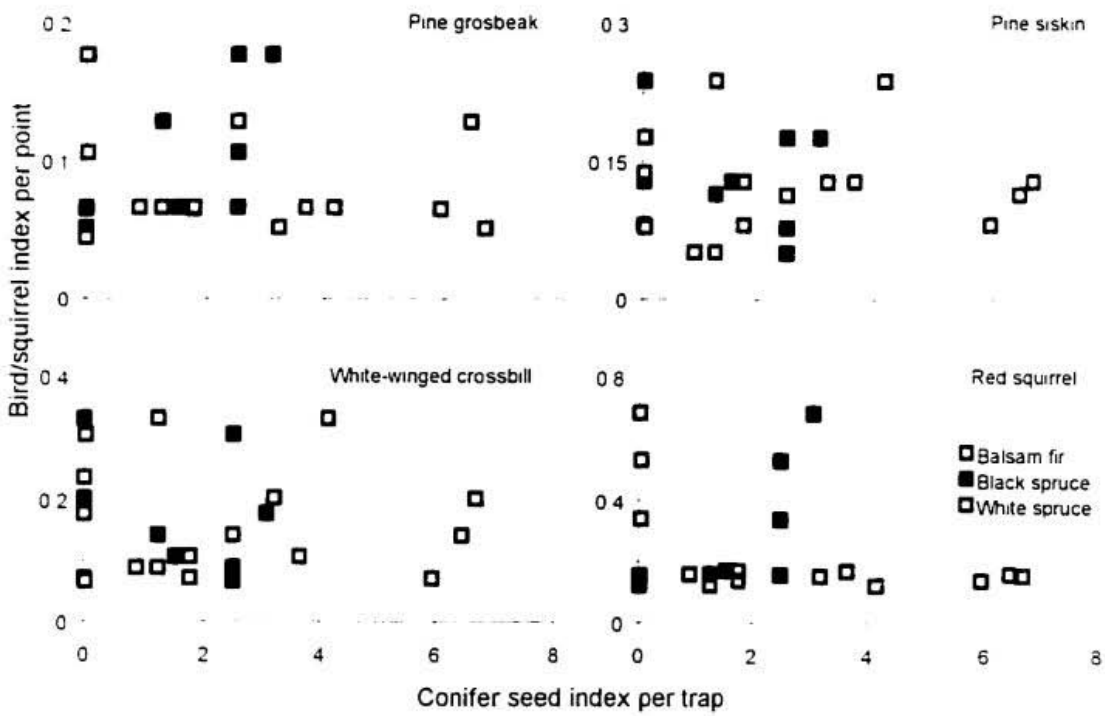


Figure 2-8 – Relationships between mean transformed number of birds and squirrels per point across all study locations and the mean transformed number of balsam fir, white spruce and black spruce seeds collected per seed trap.

Table 2-7 – Regression analysis of effect of mean transformed conifer seed availability on mean transformed finch abundance across all locations. n = 10 for all comparisons. * - P values obtained from distributions of 1000 randomized F-ratios.

Species	Black spruce				PCA (balsam fir, white spruce)			
	b	r^2 (%)	F	P	b	r^2 (%)	F	P
Pine grosbeak	0.0291	53.0	9.02	0.017	0.0143	16.5	1.59	0.642*
Pine siskin	-0.0072	2.2	0.22	0.653	-0.0040	1.0	0.08	0.780
White-winged crossbill	-0.0191	6.2	0.53	0.486	0.0094	1.9	0.16	0.701
Red squirrel	0.118	56.4	10.33	0.012	0.0837	36.5	4.60	0.355*

DISCUSSION

Resource variability

Levels of conifer seed availability differed greatly among the three Newfoundland forest types. Seed availability was highest in the mixed coniferous forest, and was much lower in the black spruce and balsam fir stands. Trends were difficult to examine in the balsam fir site due to the truncated collection period that resulted from the inaccessibility of the site. Overall, however, there were significant differences in seed availability at each of the sites over the collection period. Semi-discrete pulses of conifer seed were released. Seed availability of balsam fir and white spruce seeds differed among the three sites, and is explained by their different stand compositions. The lack of date or location effects on the availability of black spruce seeds may be explained in terms of seed release mechanism. Black spruce cones are semi-serotinous and partially fire-dependent and may be held on the tree for several years with viable seeds inside (Young and Young 1992), which limits the amount of seed that is shed. Thus, conifer seed availability was spatially and temporally variable across the three forest types but levels of black spruce seed were very low in the seed rain. Low levels of black spruce seed within the seed rain do not limit crossbills and squirrels, because both of these seed predators are able to access seeds within closed cones. Squirrels may however have contributed to the low level of black spruce seed rain over the winter by removing cones before their seed could be released.

Forager variability

As expected, bird species richness in the study was low (see Thompson et al. 1999). Finch abundance was very low in the black spruce forest, where seed rain was low. Finch abundance was highest in the balsam fir forest, where seed availability was intermediate, but where seed collections and bird censuses were not complete.

Red squirrel relative abundance was much higher in the black spruce forest than in the other forest types. This trend has also been shown from the results of a red squirrel live trapping study in the same black spruce and balsam fir sites as the present study (K. Lewis, pers. comm.). The significant differences in the number of middens between the black spruce forest and balsam fir forest provide support for the differences in squirrel abundance between these two sites. These results suggest that using acoustic cues in a point count framework is an efficient way to estimate relative abundance of red squirrels in Newfoundland forests.

Resource/forager interactions

Finch abundance and seed rain were low in the black spruce forest. Seed rain sampling may not have accurately measured the seed availability in this location, because much available seed was likely retained in the semi-serotinous cones and not shed as seed rain. The very high relative abundance of red squirrels in this forest type indicates that there must have been sufficient food resources for the squirrels, and many observations were made of squirrels clipping off closed black spruce cones and consuming the seeds within. This could limit seed availability for seed-eating finches, particularly during

periods of low cone abundance, and may explain why finch abundance was lowest at this study location.

The interaction between finch and squirrel seed predation pressure has been studied in England, where Scottish crossbills (*Loxia scotica*) and European red squirrels (*Sciurus vulgaris*) have differing tree preferences for foraging within Scots pine (*Pinus sylvestris*) forests (Summers and Proctor 1999). Spatially variable cone crops allow these irruptive crossbills to escape competitive exclusion from squirrels (Smith and Balda 1979), but this may be harder to achieve in areas such as Newfoundland where squirrel are introduced and their densities are high (Summers and Proctor 1999).

The present study demonstrated positive relationships between conifer seed availability and finch abundance. While the only statistically significant relationship was between black spruce seed availability and abundance of pine grosbeaks and red squirrels, the trend of increasing finch abundance with increasing seed abundance was seen between all other finch species and conifer species. Sample sizes of data demonstrating the inter-relationship between particular finch species and conifer seed species were low. Additional data are required to assess the responses of finch abundance to changes in conifer seed abundance.

It has been hypothesized that black spruce is a key conifer species for cone-dependent finches, especially in times of seed shortages, as some seeds are retained within the cones throughout the winter. In particular, Benkman (1993c) postulates that crossbills rely on black spruce in Newfoundland when other seeds are not available. The findings in the present study indicate, however, that cardueline finch abundances were

higher in both the balsam fir and mixed coniferous forests than the black spruce forest. Finch numbers were still high in the balsam fir forest in March. This is surprising, as balsam fir cones completely disperse their seeds, and seed dispersal generally occurs in October in mainland forests (Young and Young 1992). Observations of finches foraging in the balsam fir forest in March indicated that seed dispersal was not complete by this date, and that many balsam fir trees retained cone scales and seeds at least partially up the cone axis. Pine grosbeaks, pine siskins and white-winged crossbills were all observed consuming these seeds in the balsam fir study site in March. As seed dispersal in coniferous trees is related to wind and moisture levels (Young and Young 1992), winter conditions during the sampling period may have promoted balsam fir seed retention into the spring. It is possible that a significant relationship may have been seen between finch and balsam fir seed abundance if seed rain sampling could have been continued for the entire study period.

Lower finch abundances in the black spruce forest may be attributable to multiple factors. Available seeds for birds may have been limited by the high abundance of red squirrels at that location. Furthermore, differences in energy content and efficiency of procurement between black spruce and balsam fir seeds may make it more profitable for finches to forage on balsam fir seeds when they are available. Although crossbills are morphologically able to extract black spruce seeds from closed cones, it is likely easier for all cone-dependent finches to access the less-tightly held seeds of the balsam fir. Balsam fir seeds offer a greater foraging return from a size perspective than black spruce seeds, with approximately 130 balsam fir seeds/g as compared to 890 black spruce

seeds g (Young and Young 1992). Although conifer seeds in general have a similar nutritive content (Grodzinski and Sawicka-Kapusta 1970), samples of black spruce seeds in Newfoundland had higher lipid content than white spruce or balsam fir, and higher protein content than white spruce seeds (no protein content available for balsam fir seeds).

Despite the higher nutritive content of black spruce seeds, the larger size and easier accessibility of balsam fir seeds may make it more profitable for finches to preferentially forage in balsam fir stands in winters when fir seeds are not completely shed before the winter (Diaz 1996). In contrast, squirrels can more easily access the tightly held seeds of black spruce trees, and may occur in high densities in black spruce stands in Newfoundland because of the nutritional profitability of black spruce seeds. Furthermore, squirrels, like other rodents, may base foraging decisions on taste as well as nutritional content. For example, Grodzinski and Sawicka-Kapusta (1970) demonstrated that mice and voles do not preferentially forage on fir seeds, as they contain a large amount of resin and are not palatable.

Scale of monitoring for finch abundance

Cardueline finches are important subjects for avian monitoring in the boreal forest, as there is the possibility of their use as indicators of boreal forest productivity. Indicator species or groups of species in the boreal forest are important tools that can be used in a monitoring framework to suggest conservation measures (Nilsson and Ericson 1997). Seed-eating finches favour habitat that is non-fragmented (Helle 1985) and productive (Thingstad 1997; Thompson et al. 1999), particularly with respect to cones

(Benkman 1993b; Patterson et al. 1995; Holimon et al. 1998). As a result, these finches as a group may represent a guild that can be used to assess habitat changes in the boreal forest.

Furthermore, some cone-dependent finches have undergone population declines in recent decades. For example, the red crossbill complex in North America consists of morphologically different forms (Griscom 1937) that Knox (1992) separates into pseudospecies, and may even represent distinct species (Groth 1988). The Newfoundland red crossbill (*L. curvirostra percna*) population has declined dramatically on the island since the mid-1970s (Montevecchi et al. in prep.). No red crossbills were seen or heard during any of the point counts in the present study. A monitoring programme is needed to evaluate the status of the Newfoundland red crossbill, to determine whether it is reduced to relict populations on small coastal islands (as suggested by Pimm 1990; Benkman 1993c) or is simply rare across insular Newfoundland (as supported by its occasional, low-abundance presence in recent Newfoundland Christmas Bird Counts), and whether it is found in nearby mainland areas (see Chapter 3 for further discussion).

The foraging strategy of boreal seed-eating finches also necessitates their monitoring on broad geographic scales (see Chapter 3). As shown in the results of this study, finch abundances in Newfoundland varied between forest stands of different composition, and this may have been based on seed availability at the sites. Any monitoring strategy for these finches must therefore incorporate varied coniferous habitats, preferably on a large spatial scale (Willson and Comet 1996). This multi-scale

approach is essential as the effects of spatially patchy and temporally variable seed availability on nomadic seed-eaters are seen both regionally and on much larger scales (Virkkala 1991). This is particularly important in isolated areas with low bird densities (Haila and Järvinen 1990), as is the case in the boreal forests of Newfoundland.

If repeated point counts are to be utilized as a monitoring tool of boreal birds, they must be repeated in all habitats of interest over a sufficiently long period of time. With boreal finches in particular, abundances are inter-annually variable due to temporal changes in seed availability (Haila and Järvinen 1990) and it would be useful to examine how finch abundances respond to changes in seed availability over many seasons.

CONCLUSIONS AND RECOMMENDATIONS

The results of this study suggest two methodological improvements that should be carried out for future studies of the relationship between resource availability and cardueline finch abundance in Newfoundland. Firstly, any further study of seed rain phenology in northern Newfoundland forests should include height adjustments in the seed trap methodology of Houle and Payette (1991) to allow for seed collection even with the high snowfall levels experienced in northern Newfoundland. Secondly, the collection of temporally overlapping data should be refined. In the present study, point count and seed rain data were collected repeatedly from the same locations over the span of multiple visits. This creates the potential problem of pseudoreplication, where non-independent replicates (Sokal and Rohlf 1995) are analyzed with inferential statistics to test for treatment effects (Hurlbert 1984). To correct this potential problem, the effect of date on abundance of finches and seed can be examined by repeated measures analysis of variance. A repeated measures analysis, which accounts for the non-independence of measures that are replicated over time (von Ende 1993), could not be completed with the existing data set as there was insufficient overlap in data for comparisons between all locations and species. This underscores the need for a long-term study design that effectively measures finch abundance and conifer seed rain across a broad temporal scale.

This regional scale study demonstrated a positive relationship between conifer seed availability and cardueline finch abundance in Newfoundland boreal forests. Cardueline finch numbers were highest in the balsam fir forest, where seed availability in the study period persisted throughout the winter. Red squirrel abundance was highest in

the black spruce forest where finch abundance was much lower. Balsam fir seeds may present an energetic advantage for foraging finches when cone crops are moderate or high, and may allow finches to forage in a different niche than squirrels. Finch abundances must be monitored during poor balsam fir cone years to determine whether black spruce seeds become a more important food source, and whether red squirrels play a role in limiting seed availability during times of cone failures.

Habitat management for seed-eating finches in Newfoundland must include initiatives to preserve forest ecosystems that are productive in terms of seeds/cones, and not just timber. Contrary to current forestry practices in Newfoundland, mature forests must be retained on a landscape level to provide seed resources for cardueline finches. This is an important recommendation in light of the diverse habitat factors that may be affecting cardueline finches in Newfoundland, and in particular the Newfoundland red crossbill. These cumulative effects that result in reduced seed availability within the boreal forest include potential seed-competition impacts of the introduced red squirrel population, historical deforestation which has diminished the extent of pine stands on the island, and routine large-scale clear cutting that is the common logging practice in Newfoundland.

LITERATURE CITED

Adkisson, C. S. 1996. Red Crossbill. *In* A. Poole and F. Gill (eds.). The Birds of North America. No. 256. American Ornithologists' Union, Washington, DC.

Bayne, E. and K. Hobson. 2000. Relative use of contiguous and fragmented boreal forest by red squirrels (*Tamiasciurus hudsonicus*). Canadian Journal of Zoology 78: 359 - 365.

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

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

Benkman, C. W. 1992. White-winged Crossbill. *In* A. Poole and F. Gill (eds.). The Birds of North America. No. 27. American Ornithologists' Union, Washington, DC.

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

Benkman, C. W. 1993b. Logging, conifers, and the conservation of crossbills. Conservation Biology 7: 473 - 479.

Benkman, C. W. 1993c. The evolution, ecology, and decline of the Red Crossbill of Newfoundland. American Birds 47: 225 - 229.

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

Benkman, C. W. and H. R. Pulliam. 1988. The comparative feeding rates of North American sparrows and finches. Ecology 69: 1195 - 1199.

Bent, A. C. 1968. Life Histories of North American Grosbeaks, Buntings, Towhees, Finches, Sparrows and Allies. Dover Publications, New York.

Bibby, C. J., N. D. Burgess, and D. A. Hill. 1992. Bird Census Techniques. Academic Press, London.

Blondel, J., C. Ferry, and B. Frochot. 1981. Point counts with unlimited distance. Studies in Avian Biology 6: 414 - 420.

Bock, C. E. and L. W. Lepthien. 1972. Winter eruptions of Red-breasted Nuthatches in North America, 1950 - 1970. American Birds 26: 558 - 561.

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

Bullock. J. 1996. Plants. Pp. 111 - 137 *in* W. J. Sutherland (ed.). Ecological Census Techniques. Cambridge University Press. Cambridge.

Damman. A. W. H. 1983. An ecological subdivision of the island of Newfoundland. Pp. 163 - 206 *in* G. R. South (ed.). Biogeography and Ecology of the Island of Newfoundland. Dr. W. Junk Publishers. The Hague.

Dawson. D. G. 1981. Counting birds for a relative measure (index) of density. Studies in Avian Biology 6: 12 - 16.

Dawson. W. R. 1997. Pine Siskin. *In* A. Poole and F. Gill (eds.). The Birds of North America. No. 280. American Ornithologists' Union. Washington. DC.

Dettmers. R.. D. A. Buehler. J. G. Bartlett. and N. A. Klaus. 1999. Influence of point count length and repeated visits on habitat model performance. Journal of Wildlife Management 63: 815 - 823.

Diaz. M. 1996. Food choice by seed-eating birds in relation to seed chemistry. Comparative Biochemistry and Physiology 113A: 239 - 246.

Dodds. D. 1983. Terrestrial mammals. Pp. 511 - 550 *in* G. R. South (ed.). Biogeography and Ecology of the Island of Newfoundland. Dr. W. Junk Publishers. The Hague.

English. B. 1998. Impact of squirrel predation on white pine cone collection efforts in Newfoundland. Newfoundland Forest Service Silviculture Notebook. No. 42.

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

Erskine. A. J. 1977. Birds in boreal Canada: communities. densities and adaptations. Canadian Wildlife Service Report Series. No. 41.

Formozov. A. N. 1960. La production de graines dans les forêts de conifères de la taiga de l'U.R.S.S. et l'envahissement de l'Europe occidentale par certaines espèces d'oiseaux. Pp. 216 - 229 *in* G. Bergman. K. O. Donner. and L. V. Haartman (eds.). Proceedings XII Ornithological Congress. vol. 1. Helsinki.

Gibbons. D. W.. D. A. Hill. and W. J. Sutherland. 1996. Birds. Pp. 227 - 255 *in* W. J. Sutherland (ed.). Ecological Census Techniques. Cambridge University Press. Cambridge.

Greenwood, J. J. D. 1996. Basic techniques. Pp. 11 - 109 *in* W. J. Sutherland (ed.). Ecological Census Techniques. Cambridge University Press, Cambridge.

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

Grodzinski, W. and K. Sawicka-Kapusta. 1970. Energy values of tree-seeds eaten by small mammals. Oikos 21: 52 - 58.

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

Gurnell, J. 1983. Squirrel numbers and the abundance of tree seeds. Mammal Review 13: 133 - 148.

Hagan, J. M., W. M. Vander Haegen, and P. S. McKinley. 1996. The early development of forest fragmentation effects on birds. Conservation Biology 10: 188 - 202.

Hahn, T. P. 1998. Reproductive seasonality in an opportunistic breeder, the Red Crossbill, *Loxia curvirostra*. Ecology 79: 2365 - 2375.

Hahn, T. P., T. Boswell, J. C. Wingfield, and G. F. Ball. 1997. Temporal flexibility in avian reproduction. Current Ornithology 14: 39 - 80.

Haila, Y. and O. Järvinen. 1990. Northern conifer forests and their bird species assemblages. Pp. 61 - 85 *in* A. Keast (ed.). Biogeography and Ecology of Forest Bird Communities. SPB Publishing, The Hague.

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

Hochachka, W. M., J. V. Wells, K. V. Rosenberg, D. L. Tessaglia-Hymes, and A. A. Dhondt. 1999. Irruptive migration of Common Redpolls. Condor 101: 195 - 204.

Holimon, W. C., C. W. Benkman, and M. F. Willson. 1998. The importance of mature conifers to red crossbills in southeast Alaska. Forest Ecology and Management 102: 167 - 172.

Houle, G. and S. Payette. 1991. Seed dynamics of *Abies balsamea* and *Acer saccharum* in a deciduous forest of northeastern North America. American Journal of Botany 78: 895 - 905.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187 - 211.

Kelly, D. 1994. The evolutionary ecology of mast seeding. Trends in Ecology and Evolution 9: 465 - 470.

Knox, A. G. 1992. Species and pseudospecies: the structure of crossbill populations. Biological Journal of the Linnean Society 47: 325 - 335.

Kollmann, J. and D. Goetze. 1998. Notes on seed traps in terrestrial plant communities. Flora 193: 31 - 40.

Krebs, C. J. 1989. Ecological Methodology. Harper Collins, New York.

Kreisel, K. J. and S. J. Stein. 1999. Bird use of burned and unburned coniferous forests during winter. Wilson Bulletin 111: 243 - 250.

Lair, H. 1990. The calls of the red squirrel: a contextual analysis of function. Behaviour 115: 254 - 282.

Larsen, J. A. 1980. The Boreal Ecosystem. Academic Press, New York.

Larson, D. L. and C. E. Bock. 1986. Eruptions of some North American boreal seed-eating birds, 1901-1980. Ibis 128: 137 - 140.

Levey, D. J. and C. W. Benkman. 1999. Fruit-seed disperser interactions: timely insights from a long-term perspective. Trends in Ecology and Evolution 14: 41 - 43.

Lurz, P. W. W., P. J. Garson, and S. P. Rushton. 1995. The ecology of squirrels in spruce dominated plantations: implications for forest management. Forest Ecology and Management 79: 79 - 90.

Martin, T. E. 1986. Competition in breeding birds. Current Ornithology 4: 181 - 210.

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

Meades, W. J. and L. Moores. 1994. Forest Site Classification Manual: A Field Guide to the Damman Forest Types of Newfoundland. Edition 2. Newfoundland Department of Forestry and Agriculture.

Montevecchi, W. A., Steele, D. H., Thompson, I. D., and Mosseler, A. In prep. Crossbills, cones and squirrels in Newfoundland: competitive exclusion or boreal forest degradation?

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

Nilsson, S. G. and L. Ericson. 1997. Conservation of plant and animal populations in theory and practice. Ecological Bulletins 46: 117 - 139.

Owens, J. N. and M. D. Blake. 1985. Forest tree seed production. Canadian Forestry Service, Petawawa National Forestry Institute. Report PI-X-53.

Patterson, I. J., J. G. Ollason, and P. Doyle. 1995. Bird populations in upland spruce plantations in northern Britain. Forest Ecology and Management 79: 107 - 131.

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

Pulliainen, E. 1974. Winter nutrition of the common crossbill (*Loxia curvirostra*) and the pine grosbeak (*Pinicola enucleator*) in northeastern Lapland in 1973. Annales Zoologici Fennici 11: 204 - 206.

Reinikainen, A. 1937. The irregular migrations of the crossbill, *Loxia c. curvirostra*, and their relation to the cone-crop of the conifers. Ornis Fennica 14: 55 - 64.

Robbins, C. S. 1981a. Bird activity levels related to weather. Studies in Avian Biology 6: 301 - 310.

Robbins, C. S. 1981b. Effect of time of day on bird activity. Studies in Avian Biology 6: 275 - 286.

Senar, J. C., A. Borras, T. Cabrera, and J. Cabrera. 1993. Testing for the relationship between coniferous crop stability and Common Crossbill residence. Journal of Field Ornithology 64: 464 - 469.

Silvertown, J. W. 1980. The evolutionary ecology of mast seeding in trees. Biological Journal of the Linnean Society 14: 235 - 250.

Smith, C. C. 1968. The adaptive nature of social organization in the genus of three squirrels *Tamiasciurus*. Ecological Monographs 38: 30 - 63.

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

Smith, M. C. 1968. Red squirrel responses to spruce cone failure in interior Alaska. Journal of Wildlife Management 32: 305 - 316.

Smith, W. P., D. J. Twedt, P. B. Hamel, R. P. Ford, D. A. Wiedenfeld, and R. A. Cooper. 1998. Increasing point-count duration increases standard error. Journal of Field Ornithology 69: 450 - 456.

Sokal, R. R. and F. J. Rohlf. 1995. Biometry. Edition 3. W. H. Freeman and Company, New York.

Summers, R. W. and R. Proctor. 1999. Tree and cone selection by crossbills *Loxia* sp. and red squirrels *Sciurus vulgaris* at Abernethy forest, Strathspey. Forest Ecology and Management 118: 173 - 182.

Sutherland, W. J. 1996. Mammals. Pp. 260 - 278 *in* W. J. Sutherland (ed.). Ecological Census Techniques. Cambridge University Press, Cambridge.

Thingstad, P. G. 1997. Challenges to conservation of biological diversity in boreal forestry landscape: a case study using bird guilds as environmental indicators. Fauna Norvegica Series B 20: 49 - 68.

Thompson, I. D., H. A. Hogan, and W. A. Montevecchi. 1999. Avian communities of mature balsam fir forests in Newfoundland: age-dependence and implications for timber harvesting. Condor 101: 311 - 323.

Troy, D. M. 1983. Recaptures of redpolls: movements of an irruptive species. Journal of Field Ornithology 54: 146 - 151.

Vankat, J. L. 1979. The Natural Vegetation of North America. Wiley, New York.

Verner, J. 1985. Assessment of counting techniques. Current Ornithology 2: 247 - 302.

Verner, J. and L. V. Ritter. 1986. Hourly variation in morning point counts of birds. Auk 103: 117 - 124.

Virkkala, R. 1991. Spatial and temporal variation in bird communities and populations in north-boreal coniferous forests: a multiscale approach. Oikos 62: 59 - 66.

von Ende, C. N. 1993. Repeated-measures analysis: Growth and other time-dependent measures. Pp. 113 - 137 *in* S. M. Scheiner and J. Gurevitch (eds.). Design and Analysis of Ecological Experiments. Chapman & Hall, New York.

West, R. J. 1989. Cone depredations by the red squirrel in black spruce stands in Newfoundland: implications for commercial cone collection. Canadian Journal of Forest Research 19: 1207 - 1210.

Widrlechner, M. P. and S. K. Dragula. 1984. Relation of cone-crop size to irruptions of four seed-eating birds in California. American Birds 38: 840 - 846.

Willson, M. F. and T. Comet. 1996. Bird communities of northern forests: patterns of diversity and abundance. Condor 98: 337 - 349.

Wooton, J. T. 1996. Purple Finch. *In* A. Poole and F. Gill (eds.). The Birds of North America, No. 208. American Ornithologists' Union, Washington, DC.

Young. J. A. and C. G. Young. 1992. Seeds of Woody Plants in North America. Dioscorides Press. Portland. Oregon.

Appendix 2-1 – Total contents of seed rain (mean number of seeds per 25 m^2 ± standard error) for each collecting date at each study location and site. n = 20 for all categories.

Forest type	Site	Date	Balsam fir	Black spruce	White spruce	White birch
Mixed conifer	1	04/10/98	691 ± 265	0	125.6 ± 86.5	377 ± 132
Mixed conifer	2	04/10/98	2136 ± 969	0	125.6 ± 86.5	33731 ± 8904
Mixed conifer	1	23/10/98	1131 ± 327	0	691 ± 170	314 ± 155
Mixed conifer	2	23/10/98	1131 ± 272	0	942 ± 339	7726 ± 1213
Mixed conifer	1	15/11/98	440 ± 137	125.6 ± 86.5	188 ± 137	0
Mixed conifer	2	15/11/98	2889 ± 619	0	314 ± 155	13191 ± 1405
Mixed conifer	1	06/12/98	2010 ± 308	0	377 ± 132	377 ± 225
Mixed conifer	2	06/12/98	1570 ± 286	0	440 ± 188	5967 ± 874
Mixed conifer	1	18/01/99	503 ± 168	188 ± 103	251 ± 115	0
Mixed conifer	2	18/01/99	565 ± 170	0	0	1633 ± 409
Mixed conifer	1	10/02/99	62.8 ± 62.8	377 ± 185	62.8 ± 62.8	0
Mixed conifer	2	10/02/99	62.8 ± 62.8	125.6 ± 86.5	0	188 ± 103
Balsam fir	1	01/10/98	0	0	0	503 ± 141
Balsam fir	2	01/10/98	0	0	0	817 ± 262
Balsam fir	1	04/11/98	754 ± 264	0	62.8 ± 62.8	3957 ± 1060
Balsam fir	2	04/11/98	628 ± 281	0	62.8 ± 62.8	7726 ± 995
Black spruce	1	18/11/98	0	125.6 ± 86.5	0	754 ± 212
Black spruce	1	08/12/98	0	125.6 ± 86.5	0	0
Black spruce	1	22/01/99	0	314 ± 155	0	125.6 ± 86.5
Black spruce	2	22/01/99	0	440 ± 188	0	125.6 ± 86.5
Black spruce	1	15/02/99	0	0	0	0
Black spruce	2	15/02/99	0	62.8 ± 62.8	0	0
Black spruce	1	20/03/99	0	62.8 ± 62.8	0	0
Black spruce	2	20/03/99	0	0	0	0

Appendix 2-2 – Total abundance per total sampling effort of non-cardueline bird species at all point count locations from all census dates at each study site. Total sampling effort in mixed coniferous forest = 1800 min, balsam fir forest = 1360 min, black spruce forest = 1200 min.

Species	Balsam fir	Black spruce	Mixed Conifer
Common loon (*Gavia immer*)	0.0037	0.0008	0
Canada goose (*Branta canadensis*)	0.0044	0	0
American black duck (*Anas rubripes*)	0.0015	0	0.001
Sharp-shinned hawk (*Accipiter striatus*)	0	0	0.0006
Spruce grouse (*Falcipennis canadensis*)	0.0007	0	0
Greater yellowlegs (*Tringa melanoleuca*)	0	0	0.0006
Herring gull (*Larus argentatus*)	0.0044	0	0.01
Northern flicker (*Colaptes auratus*)	0	0	0.0017
Three-toed woodpecker (*Picoides tridactylus*)	0.0022	0.0008	0
Black-backed woodpecker (*Picoides arcticus*)	0.0007	0.0008	0
Yellow-bellied flycatcher (*Empidonax flaviventris*)	0.0044	0.0042	0
Blue jay (*Cyanocitta cristata*)	0.0022	0	0.004
Gray jay (*Perisoreus canadensis*)	0.071	0.021	0.0072
American crow (*Corvus brachyrhynchos*)	0.0044	0.033	0.021
Common raven (*Corvus corax*)	0.0059	0.02	0.0006
Black-capped chickadee (*Poecile atricapillus*)	0.011	0.011	0.005
Boreal chickadee (*Poecile hudsonicus*)	0.099	0.0575	0.022
Red-breasted nuthatch (*Sitta canadensis*)	0	0.0017	0.0011
Golden-crowned kinglet (*Regulus satrapa*)	0.0037	0.0092	0
Ruby-crowned kinglet (*Regulus calendula*)	0	0.0058	0
American robin (*Turdus migratorius*)	0	0.0042	0.0039
European starling (*Sturnus vulgaris*)	0	0	0.058
Yellow-rumped warbler (*Dendroica coronata*)	0.0044	0.0058	0.0011
Black-and-white warbler (*Mniotilta varia*)	0	0.0008	0
White-throated sparrow (*Zonotrichia albicollis*)	0.0008	0.0017	0.0017
Dark-eyed junco (*Junco hyemalis*)	0.087	0.013	0.02

Chapter 3

AN ANALYSIS OF CONTINENTAL AND REGIONAL DISTRIBUTION AND ABUNDANCE PATTERNS OF BOREAL CARDUELINE FINCHES FROM CHRISTMAS BIRD COUNT DATA

INTRODUCTION

Many studies of bird populations are conducted on a limited, habitat scale. Variable bird populations between locations can make it difficult or inaccurate to interpret regional bird abundance trends on a broader spatial scale. Understanding population trends across large scales is useful in the study of avian biogeography in general (Verner 1985), and to address specific concerns such as the identification of hotspot areas where high densities of many bird species overlap (Root 1988) or areas where decreases in avian species abundance are seen.

Analysis of continent-wide avian distribution patterns is important to species that have broad ranges. This is the case for the boreal cardueline finches (family Fringillidae, subfamily Carduelinae) in North America, such as the red crossbill (*Loxia curvirostra*), white-winged crossbill (*Loxia leucoptera*), pine siskin (*Carduelis pinus*) and pine grosbeak (*Pinicola enucleator*) that are distributed throughout the entire North American boreal zone (Erskine 1977). Some cardueline finch species, such as the common redpoll (*Carduelis flammea*), pine grosbeak and white-winged crossbill are found circumboreally (Newton 1972).

These finches forage in loosely formed flocks during all seasons rather than defending feeding territories (Newton 1972) and do not follow the typical seasonal migration patterns of many other North American passerines. Their movements are more

nomadic than migratory, with abundances that fluctuate by orders of magnitude between years on local, regional and continental scales (Newton 1972) in order to exploit conifer seed resources that are temporally and spatially variable. As a result, these species are irregularly present in many portions of their ranges (Troy 1983). Furthermore, they exhibit occasional movements beyond the periphery of their typical ranges. These influxes are termed irruptions, and are the direct result of fluctuating conifer food supplies (Ulfstrand 1963). Although the boreal cardueline finches have different levels of dependence on conifer seeds for food (Smith and Balda 1979), all species consume conifer seeds as a primary food source for at least portions of their annual cycle (Bent 1968; Newton 1972).

It is important to examine population trends in birds on appropriate scales. While studies of phenomena such as habitat associations and densities can be informative on a local basis, larger scale spatial and temporal trends must not be overlooked (Wiens 1981). This is essential in order to eliminate uncertainty caused only by stochastic variation and bias from small-scale samples that do not adequately represent population trends on much larger scales. Boreal cardueline finches, as a result of their irruptive behaviour, exhibit population trends on a broad biogeographic scale. These are affected by local-level factors that result in regionally low or high seed crops. They then undergo large-scale nomadic movements, bringing about changes in local community assemblages (Virkkala 1991).

Furthermore, population trends of birds like the conifer seed-eating cardueline finches vary with the temporal scale of the analysis. Patterns in bird distribution and

abundance, which can result from spatial patterns in resources (like spatially variable cone crop resources across the boreal forest), may also be caused by stochastic temporal environmental variation (Ives and Klopper 1997). Boreal cardueline finches are strongly affected by temporal variation in the crop of conifer seeds in the boreal forest because their diet is extensively comprised of seeds (Newton 1972). Bock and Lepthien (1976) demonstrated an inverse correlation between levels of conifer seed production and magnitudes of North American seed-eating bird irruptions. This inverse relationship between conifer seed production and finch abundance across multiple years has also been noted in red crossbills in Finland (Reinikainen 1937) and Northern Europe (Formozov 1960), and in pine siskins in California (Widrlechner and Dragula 1984).

The relationship between conifer seed production and seed-eating finch irruptions is generally cyclical over an extended number of years. This is due to the periodic nature of boreal cone crop mast years, where large cone crops occur at the most frequently every two years (Silvertown 1980) but with very large crops usually separated by several more years and sometimes synchronized between tree species (Owens and Blake 1985). Cyclical, and sometimes interspecifically synchronous, patterns of seed-eating bird irruptions have been shown among redpolls (*Carduelis* spp.; Troy 1983; Larson and Bock 1986), red-breasted nuthatches (*Sitta canadensis*; Bock and Lepthien 1972), and other boreal passerines including pine grosbeaks, pine siskins and crossbills (Bock and Lepthien 1976; Bock 1980).

The inter-annual fluctuations in magnitude of finch irruptions also make it essential to examine their population trends across a large temporal scale (Virkkala

1991). An analysis of trend data over a limited time scale could mask the regular irruptive population fluctuations of these species. Hence, a study of the population changes of widely distributed species like the cardueline finches must be addressed on sufficiently large spatial and temporal scales and must include a consideration of patterns in both distribution and abundance.

Typically, surveys of bird populations are conducted on a regional basis for a limited number of years. This may constrain the extent to which study results can be generalized across broad scales (Wiens 1981). The National Audubon Society Christmas Bird Count, however, is a vast collection of bird count data, which can be used to examine population trends across large spatial and temporal scales. The Christmas Bird Count (CBC) is the largest and oldest running bird census in North America (Bock and Root 1981). It originated in 1900 as an alternative to bird hunting competitions that were common over the Christmas holidays (Root 1988). Since its inception, it has expanded into a continent-wide birding event. Day-long counts are performed annually within a 2-week period of Christmas in hundreds of discrete 24.1 km diameter circles across the continent (Drennan 1981). Numbers of all bird species seen in each count circle are recorded, as well as measures of observer effort, habitat characteristics and weather conditions.

The CBC is an important longitudinal source of ecological data on the winter distributions and spatial abundance patterns of most species of birds across North America (Bock 1980; Drennan 1981). In fact, for some species, CBC counts provide the only large-scale population data available. This is because the North American Breeding

Bird Survey (BBS), a widespread springtime series of more than 3500 roadside surveys across the continent (Link and Sauer 1998), only marginally covers many species that nest in northern latitudes (Dunn and Sauer 1997). This is the case for many irruptive seed-eating species. In particular, the bohemian waxwing (*Bombycilla garrulus*), and carduelline finches such as the common redpoll, hoary redpoll (*Carduelis hornemanni*) and gray-crowned rosy-finch (*Leucosticte tephrocotis*) are all irruptive, breeding species in Canada that are poorly censused by the BBS but are adequately sampled by the CBC (Dunn and Sauer 1997). Overall, there are more than 200 species that are frequently found on CBCs and are found at more than twice as many CBC locations than BBS locations (Butcher et al. 1990).

The use of CBC data to analyze population trends and species densities suffers from several potential drawbacks. The primary criticism of the CBC is that it is an unstandardized data set. Although counting guidelines are consistent between counting circles and across years, there are varied numbers of participants in the counting circles which results in variable levels of observer effort. Thousands of people with varied levels of bird identification experience participate in the counts each year (Root 1988). This may result in higher numbers of birds reported in counting circles with higher effort levels. All analyses of temporal population change, including those using the CBC, must be controlled for temporally-variable effort (Link and Sauer 1997), as even weak correlations between count and level of effort may result in biased population change estimates (Link and Sauer 1999). Generally, the problem of variable levels of effort in

the CBC is overcome by standardizing all count data by the total number of party hours spent counting in each bird count circle (Bock and Root 1981).

Further weaknesses of CBC data, as with some other point count data, include possible confounding effects of poor weather and biased habitat sampling within a count location (Dawson 1981), as well as difficulties associated with counting gregarious birds (Root 1988). Analyzing a large number of counts over an extended number of years generally cancels out the spurious effects of these potential biases (Bock and Root 1981; Dunn and Sauer 1997). The CBC is also criticized because of the distribution of count circle locations across the continent. The nature of the CBC means that count circles are generally clustered around centres of high human population density, and as such do not represent a random sample of avian habitats across the continent (Butcher et al. 1990). Drennan (1981) suggests that this may not be an analytical concern, as non-randomly distributed bird populations are well sampled by the stratified CBC design (where there is a higher probability of counts being held in areas of high species density, and a lower probability of counts being held in areas of low species density).

Even after controlling for differences in observer effort and stochastic events between CBC counting circles, the life-history strategies of many groups of birds makes it difficult to use CBC data to analyze changes in bird abundances and distributions. For example, tracking abundances and population trends of irruptive species using CBC data is confounded by the fact that their nomadic movements result in different winter ranges in different years, where CBC coverage may vary (Dunn and Sauer 1997). It is essential

to examine these trends across large spatial and temporal scales to circumvent this problem.

Overall, the CBC represents a useful source of data on avian distribution and population trends. The data are good descriptors of continental-scale patterns of avian geographic ecology that would otherwise remain undetected (Bock and Root 1981). Population trends estimated from CBC data have been shown to be similar to trends estimated from BBS data (Butcher et al. 1990), which are gathered from rigidly standardized counts. Results of the CBC can be reliably used to estimate bird population and distributional trends because the sample size is large, with an unplanned design and a consistency of results (Drennan 1981).

This study uses CBC data to examine patterns of continental distribution and abundance in six species of conifer seed-eating cardueline finches: common redpoll, pine grosbeak, pine siskin, purple finch (*Carpodacus purpureus*), red crossbill and white-winged crossbill. These species were selected because they range throughout the North American boreal zone (Erskine 1977). They also represent different levels of dependence on conifer seeds for food (Bent 1968). This level of adaptation is most extreme in the crossbills, which possess morphological bill adaptations at the species and subspecies level that make each taxonomic group specialists on key conifer species (Benkman 1993a) and possibly less efficient foragers on non-conifer seeds (Benkman 1988). Other cardueline finches like the pine siskin (Dawson 1997) and pine grosbeak (Newton 1972) are more generalized foragers, supplementing conifer seeds with deciduous seeds, buds, and even insects during summer months.

The objective of this study is to examine spatial and temporal patterns of distribution and abundance of cone-dependent cardueline finches by mapping continental CBC data spanning several decades. The starting point of this work was Bock and Lepthien's (1976) study that demonstrated interspecific synchronicity in boreal seed-eating bird irruptions, but which did not include spatial distribution and abundance patterns for any of the extensive boreal forest zone within Canada (Figure 3-1). To determine how reductions in seed availability by factors such as cone crop failures or loss of cones due to forestry may affect cardueline finches, finch abundance and distribution will be examined in relation to conifer crops across the North American boreal zone. Christmas Bird Counts will also be used to demonstrate how long-term population monitoring can indicate regional changes in distributions and population trends. This will be illustrated by examining changes in boreal cardueline finch abundance from Newfoundland Christmas Bird Counts, with emphasis on the relationship between cardueline finch populations and habitat changes such as increased logging pressure in Newfoundland's boreal forests.

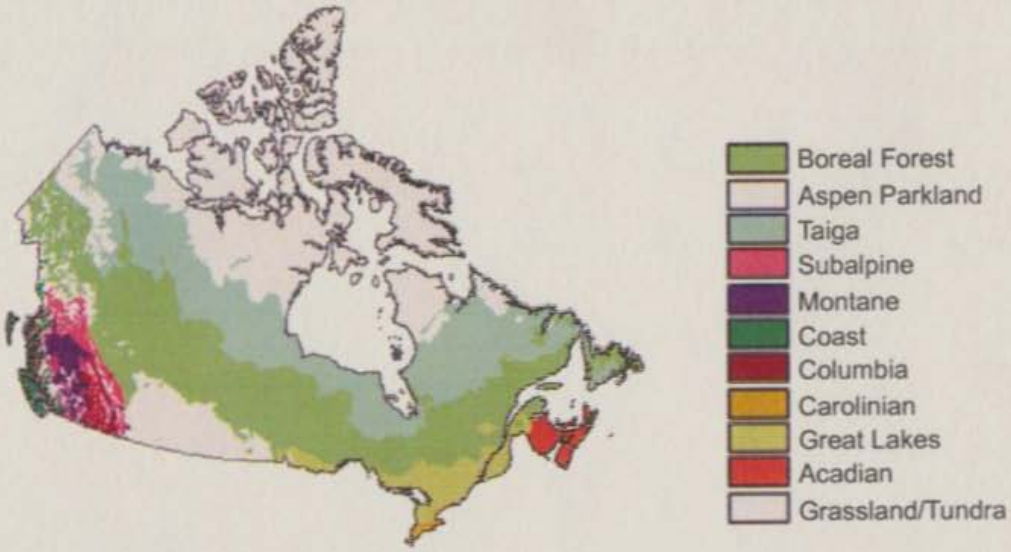


Figure 3-1 – Extent of boreal forest zone of Canada (Global Forest Watch Canada 2000).

METHODS

Continental patterns of cardueline finch distribution and abundance

Finch distribution and abundance data were obtained from Christmas Bird Counts carried out in Canada and the United States from 1969/1970 through 1996/1997. This range of years was chosen to continue the mapping effort of Bock and Lepthien (1976), which illustrated seed-eating bird distributions and abundances in the United States from 1962 to 1972. Furthermore, the time span represents a long enough range of years to illustrate temporal variability in cone-dependent finch distributions. Raw data for each CBC location at each year were obtained from the online Christmas Bird Count Database Project (http://www.nmt.edu/~shipman/z/cbc/homepage.html), which is currently maintained by the Cornell Laboratory of Ornithology. These data were supplemented with additional CBC data from 1970 - 1992, mainly in Canada and Alaska, which were not included in the online database but were published in the annual CBC reports (Audubon Field Notes 1970, American Birds 1971 – 1992). This was done to ensure that all data from within the North American boreal forest zone were included in the mapping effort.

The total number of each species of finch seen at each count circle for each of the study years was standardized by dividing by the total number of observer party hours for each count. One party hour represents one observer in the field for one hour. This is the most accepted method of standardizing CBC raw data (Bock and Root 1981) which acts to eliminate bias associated with unequal numbers of observers and hours of participation in individual count circles (Link and Sauer 1999). No further standardization of counts

was performed (such as controlling for variable weather), as other noise incurred from the non-standardized nature of CBCs is generally cancelled out when data are examined across broad scales (Drennan 1981).

Continental maps of distributions and abundances of each of the six species of carduelline finches were constructed using the GIS program MapInfo Professional 5.0 (1998). The geographic location of every count circle in North America was mapped for each year from 1970 to 1997. Note that the CBC year 1970 represents the count that was conducted in the two week period spanning December 1969 and January 1970. This method of labelling CBC years is used throughout this study. The total count per party hour of each of the study species for all count circles within a year were mapped based on a logarithmic range of values from less than 0.001 birds per party hour up to greater than 100 birds per party hour. Each range of values was assigned a colour, with map areas depicting a very low number of birds per party hour represented in blue, ranging through to map areas with a very high number of birds per party hour represented in red. As the distribution of CBC count circles across North America is non-random, with more counts around population centres (Drennan 1981), the locations of CBC count circles were overlaid on the finch distribution maps. This was done to illustrate that map areas with no birds present are due to lack of CBC sampling and not an absence of birds (for example, in extreme northern boreal regions).

Grid surface interpolation was performed between the data points to represent differences in bird abundances across geographic areas, and to better illustrate bird abundances in areas with high densities of count circles. Grid surface interpolation was

used as an alternative to grid-based mapping of large-scale bird distributions and abundances, which generally present mean abundance values for each grid (see examples in Bock and Lepthien 1972, 1976; Bock 1980), and as such do not accurately reflect maximum and minimum values for specific locations within each grid. Interpolation was done in MapInfo based on an inverse distance weighting of the count per effort values, in which closer cells have a larger influence on the interpolation than those that are further away. The cell size for the interpolations was set at 24.1 km, which is the diameter of each CBC circle. Search radius between cells was set at 96.4 km. With this setting, only counts within 4 diameters of any count circle had an interpolative influence on a cell, and the interpolation was weighted so that closer counts had a larger influence on a given count circle than those that were further away.

Linear regression analysis was performed to test whether the total annual number of finches censused per party hour by CBCs increases with the number of counts performed each year. There was no significant regression relationship between total annual number of birds per party hour and annual number counts performed each year for any of the six study species (Figure 3-2). Assumptions of normality and independence of residuals and homogeneity of variances were met in these regression analyses. The lack of a significant relationship between total annual number of finches per unit effort and number counts performed each year in this study indicates that there is no confounding effect of increasing counts of these finches through time (Link and Sauer 1999), possibly due to the species' boreal distributions, and the fact that many new CBC counts have been added in southern areas and thus do not sample boreal finches.

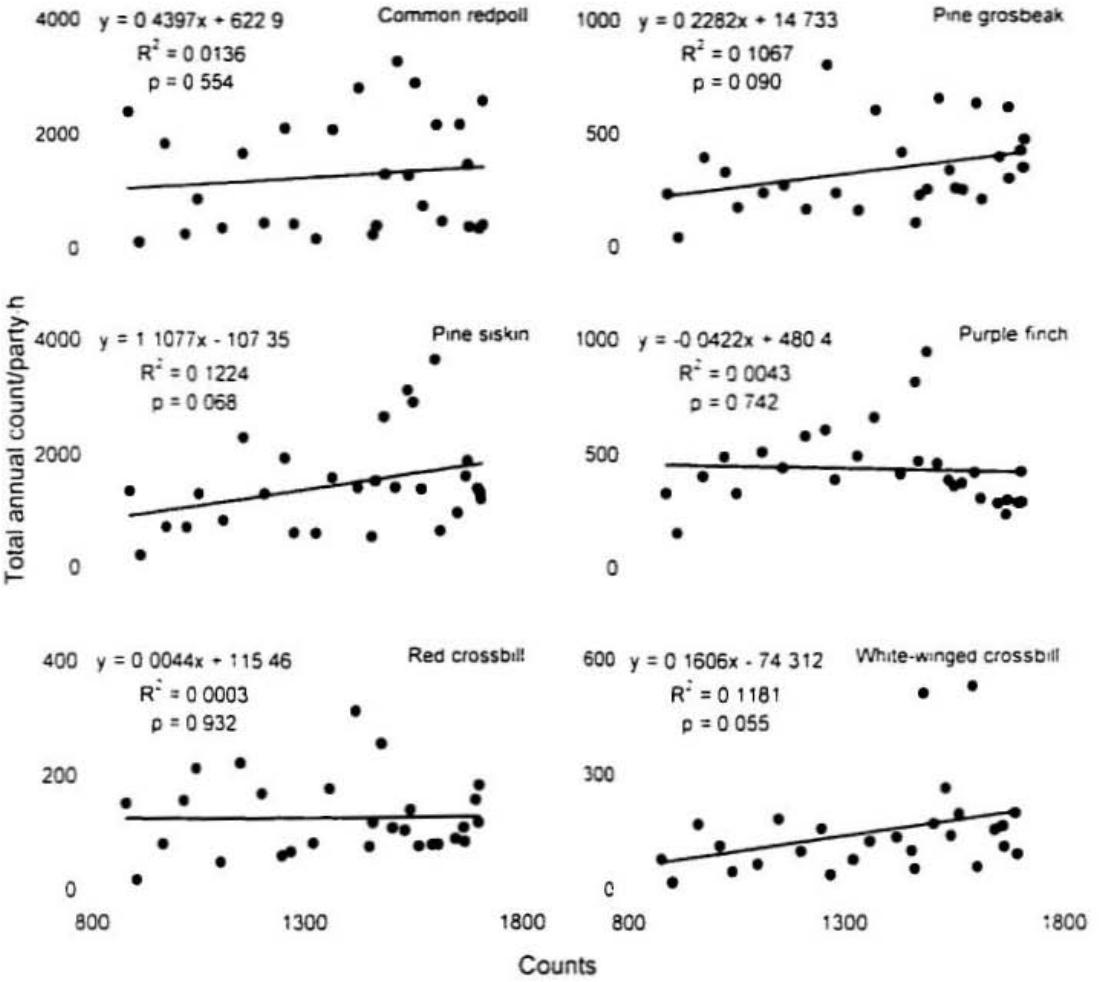


Figure 3-2 – Relationship between total annual count of finches per party hour and number of annual CBC count circles across North America.

Several methods have been used by other authors to evaluate temporal changes in the number of birds censused on annual counts. These methods include time series analysis of the mean number of wading birds in Florida (McCrimmon et al. 1997), and median percent change in numbers of seven diverse species of birds (Butcher et al. 1990). These types of analyses may not be appropriate to illustrate irruptive patterns in cardueline finch abundances, as extreme high and low counts of birds are not portrayed by summary statistics such as means and medians. More appropriate analysis of temporal irruptive patterns includes the total number of birds per unit effort (Bock 1980) or graphical analyses that illustrate spatial as well as temporal trends in abundance (Root 1988).

To demonstrate trends and possible synchrony in irruptions between seed-eating finch species, the total annual number of CBC counts with a count per party hour value equal to or greater than 1.0 were plotted for each species and year. The value of greater than one bird per party hour as a measure of a high count was chosen as an arbitrary indicator of a relatively high number of cardueline finches per party hour. This measure was used instead of mean continental number of birds in order to accurately portray years with many high counts. The fluctuating trends from these graphs were compared to graphs of the total annual continental count per effort for each species, to determine whether the fluctuating trends were similar.

The population trends obtained from these two sets of graphs were analyzed using a runs test for trend data (runs up and down test; Sokal and Rohlf 1995). In this case, runs are groups of years (or single years) with either increasing or decreasing counts. A

runs test can be used to analyze trend data such as periodic finch irruptions, as cyclical data show more than the number of runs expected in a random sequence (Sokal and Rohlf 1995). A runs test on trend data does not compare each observation to the median of the data, as in runs tests for dichotomized data, and is thus more applicable to trend data where successive observations may be autocorrelated and non-independent. The continental response of cardueline finch abundance over time is expected to be cyclic in response to the periodicity of boreal cone crops, which fluctuate between high and low mast years with regularity. Changes in continental abundances of finches (assessed in the present study with runs tests) may be more accurate indicators of variable conifer resources than absolute finch numbers (Summers 1999). Larson and Bock (1986) have performed a similar runs test on common redpoll CBC abundance data.

Finch abundance and boreal cone crop magnitude

Seed crop magnitude throughout Canada was compared to cardueline finch abundance and distribution using assessments of wild seed crop that were included with published CBCs beginning in 1973. Seed crop was assessed by the CBC participants, and was assigned a value of poor, fair, good, or excellent for northern, coniferous, and mountainous count circles (The seventy-second Christmas Bird Count 1972). Similar ratings have been used to illustrate the relationship between irruptive seed-eating birds and cone crops by others (Reinikainen 1937; Formozov 1960; Ulfstrand 1963; Bock and Lepthien 1976; Widrlechner and Dragula 1984). The cone crop index system used in CBCs, while based on subjective volunteer assessments of count circle habitats, is similar to the system used by forestry ecologists to measure cone crops on stand-level and

regional scales (McDonald 1992; Eastham and Jull 1999). It is also the only widespread and multi-year cone crop data sets that include coverage of extensive areas of the North American boreal zone. More quantitative assessments of cone crops on large spatial and temporal scales do not exist.

Seed crop magnitude based on these reports was mapped across Canada from 1974 – 1985 to demonstrate regional trends. A very low number of CBC circles submitted seed crop data in 1973; therefore seed crop data for that year were omitted from the analysis. Maps were not constructed for more recent years because the collection of seed data was not included in the standardized CBC counting methodology after 1985.

Non-parametric analysis of the variation in finch numbers at count circles with different magnitudes of seed crops was performed using the Kruskal-Wallis test (Sokal and Rohlf 1995). For species with a significant effect of cone crop rating on bird abundance, *post hoc* multiple comparisons using Tukey's Honestly Significant Difference test (Matlab 1999) were performed to test where the differences in mean ranks of bird abundance occurred. The analysis was run using only finch and seed crop data from count circles within the boreal forest zone in Canada and Alaska to ensure that the wild food crop assessments made by CBC participants were based primarily on coniferous cone crops, and not on other food sources such as berries and grasses which may have made a contribution to wild food crop assessments at more southerly latitudes. One hundred and two count circles, over the years from 1974 through 1985, were used in the analysis, with a total of 601 counts in the analysis (not all locations had active Christmas

Bird Counts every year, and not all active count circles submitted cone crop information each year). See Appendix 3-1 for a list of boreal count circle locations used in this analysis, and a habitat/land cover description of each circle.

Regional patterns of cardueline finch abundance in Newfoundland

To illustrate the use of CBC data as a long-term monitoring tool for regional bird populations, annual cardueline finch abundance per party hour from CBCs was graphed from 1970 – 1999 for three Newfoundland locations: St. John's, Terra Nova National Park and Gros Morne National Park. These locations were chosen as they are long-running counts within Newfoundland (the St. John's CBC originated in 1967, the Terra Nova CBC in 1969, and the Gros Morne CBC in 1972). Gros Morne National Park is situated within a primarily balsam fir dominated forest region, Terra Nova National Park is within a primarily black spruce dominated forest region, and St. John's is within a mixed coniferous forest region (see Chapter 2). Thus, these CBC locations offer different food crops for wintering cardueline finches. The number of hours spent observing birds at feeder stations was included in the total number of party hours for each count circle. This measure was included to give a more accurate measure of effort as all of the study species may be observed at winter feeders [information from Cornell Laboratory of Ornithology Project FeederWatch (http://birds.cornell.edu/PFW/) – see Hochachka et al. (1999) and Dunn and Sauer (1997)].

RESULTS

Continental patterns of cardueline finch distribution and abundance

Figures 3-3 – 3-8 illustrate the continental distribution and patterns of winter abundance of the six study species of cardueline finches across North America from 1970 through 1997. The maps highlight differences in each species' distributions. Purple finches and pine siskins have the most southerly distributions. Purple finches are not commonly found in much of the western Canadian boreal zone during the winter. In contrast, the distribution maps of common redpolls, pine grosbeaks, red crossbills, and white-winged crossbills show more northerly distributions. These four species also have ranges that generally do not extend as far south as the pine siskins and purple finches. The maps illustrate irruptive movements in these species, with ranges that occasionally extend far south of the species' core range (for example, common redpolls in 1987 and 1990; pine grosbeaks in 1986 and 1990; red crossbills in 1997; and white-winged crossbills in 1986 and 1988).

The continental distribution maps indicate important abundance trends in the cardueline finches. Year-to-year abundances are variable in all of the species. This is perhaps most evident in the common redpoll, where there is a biennial pattern of years with a large concentration of counts with a high number of birds per party hour followed by much lower count years. The inter-annual fluctuations in abundance are also seen in the other five species, although not always following a biennial pattern. For example, some high abundance years seen in pine grosbeaks are 1978, 1981, 1982, 1986 and 1990, with lower abundance years in 1977, 1980, 1983 and 1989.

These maps also illustrate spatial variability in the abundance of cardueline finches. In some cases, there is an east-west asynchrony in high abundance areas of finches, with markedly higher abundances seen in only the west or east for a given year. Examples of this spatial asynchrony occur in 1985 86 in pine grosbeaks, in 1992 93 in white-winged crossbills, and in 1988/89 in pine siskins. When examining trends from the maps, it should be noted that red crossbills, and, to a lesser extent, pine grosbeaks, have winter core ranges that extend farther south in western North America than they do in eastern North America (National Geographic Society 1999).

It is important to note that the number of CBC counts performed in the boreal forest zone has increased throughout the study period. In early study years, an apparent lack of finches in some regions of Canada and Alaska is actually due to the fact that no CBC sampling was done in those locations. The maps of count circle locations overlaid on common redpoll distributions for 1970 and 1997 in Figure 3-9 illustrates this point. From the two maps, it is apparent that the North American boreal zone is much better sampled by CBCs in recent years, with at least some counts performed in the boreal regions of all of the Canadian provinces and territories and Alaska. Despite this, CBC sampling intensity remains highest around highly populated regions of Canada and the United States, and boreal zone sampling intensity is low. See Appendix 3-2 for maps of the locations of all CBC circles from 1970 to 1997.

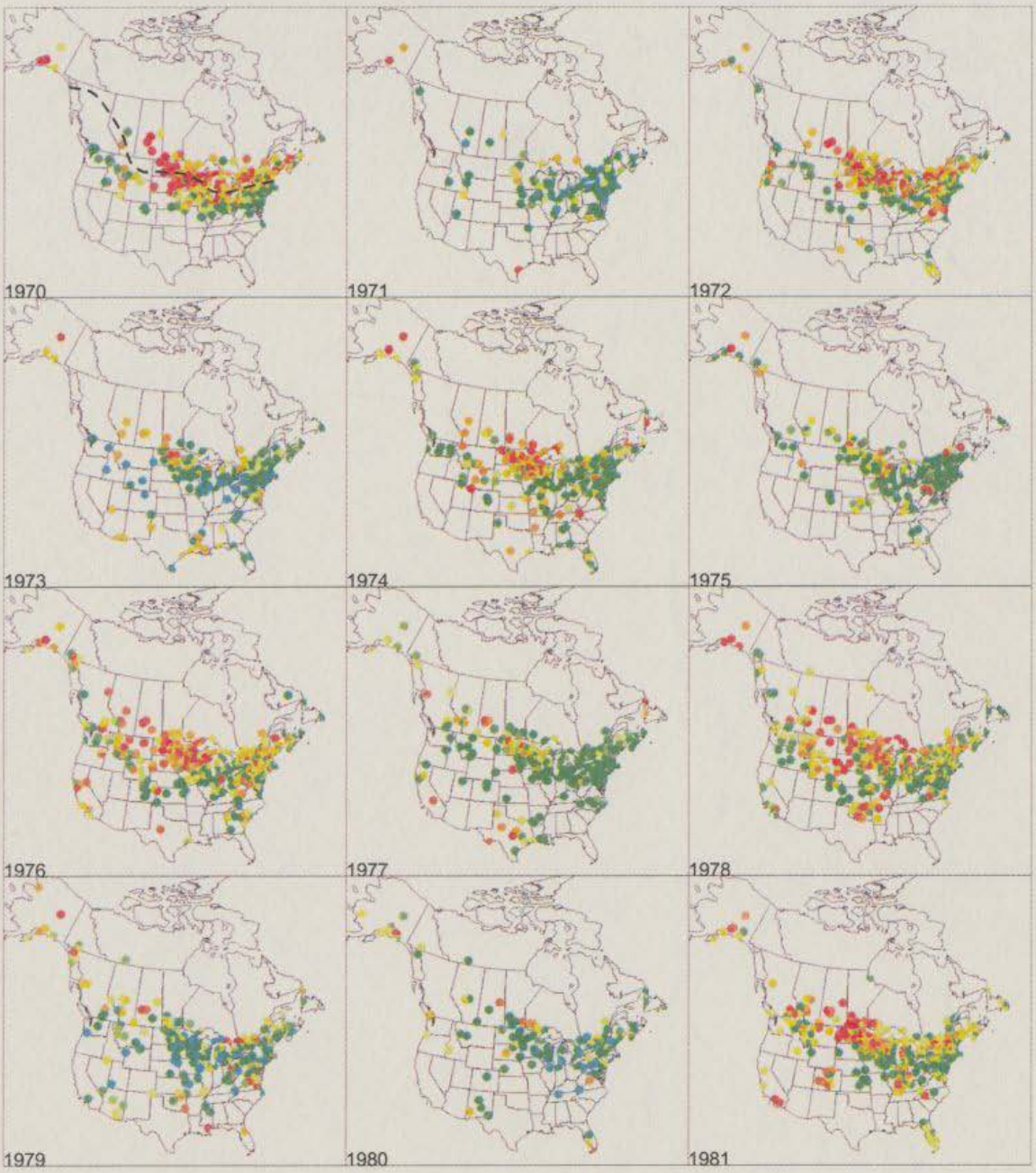


Figure 3-3 – Annual North American winter distribution and abundance of common redpolls from CBC data, 1970 - 1997

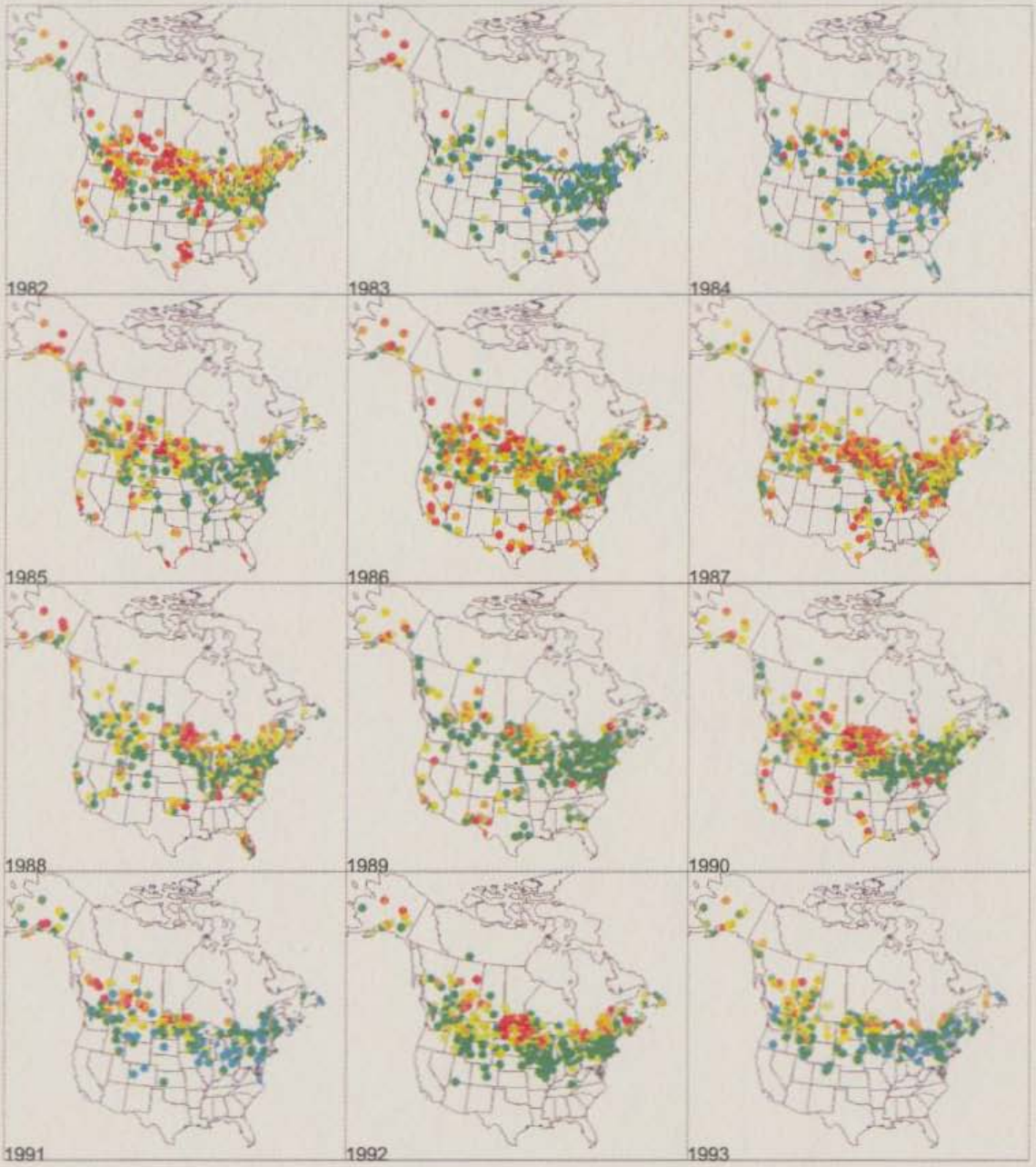


Figure 3-3 (continued) – Annual North American winter distribution and abundance of common redpolls from CBC data, 1970 - 1997

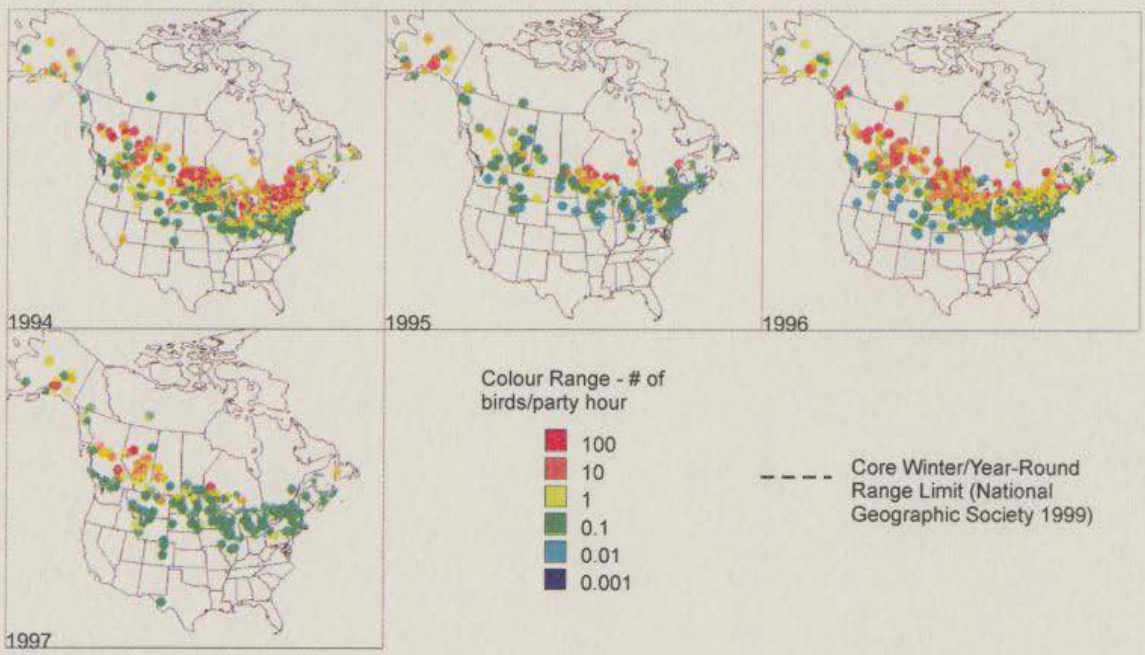


Figure 3-3 (continued) – Annual North American winter distribution and abundance of common redpolls from CBC data, 1970 - 1997

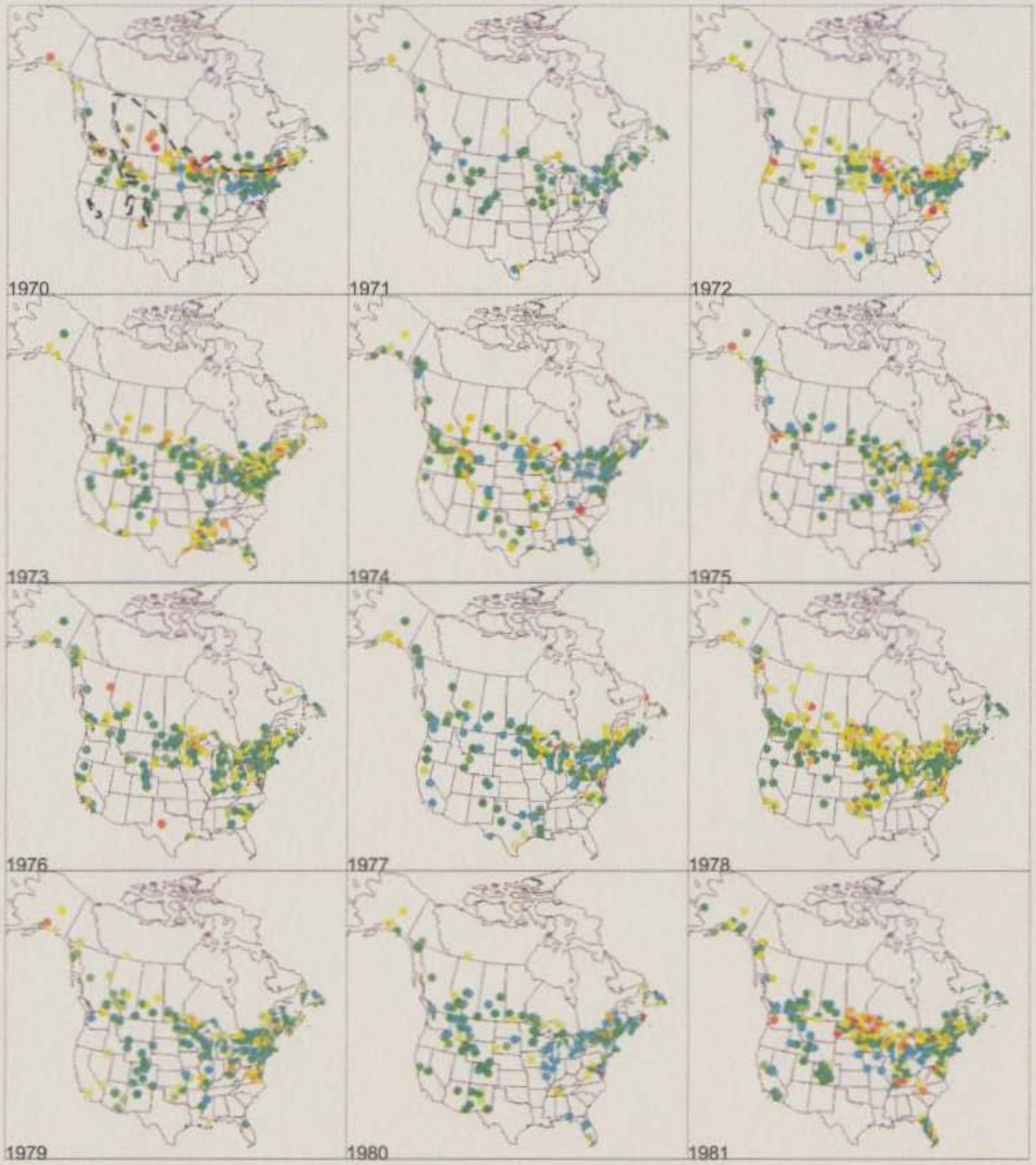


Figure 3-4 – Annual North American winter distribution and abundance of pine grosbeaks from CBC data, 1970 - 1997

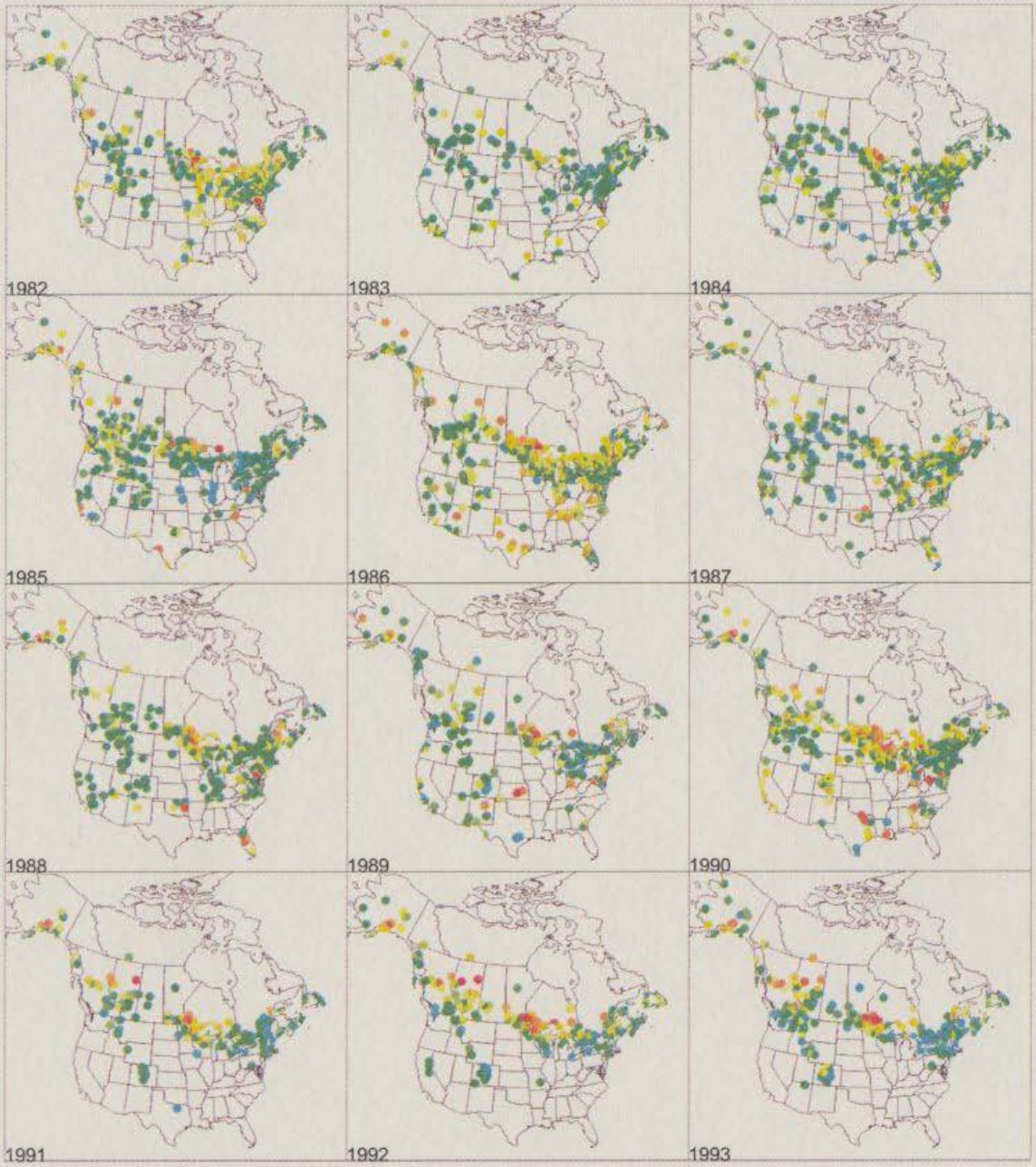


Figure 3-4 (continued) – Annual North American winter distribution and abundance of pine grosbeaks from CBC data, 1970 - 1997

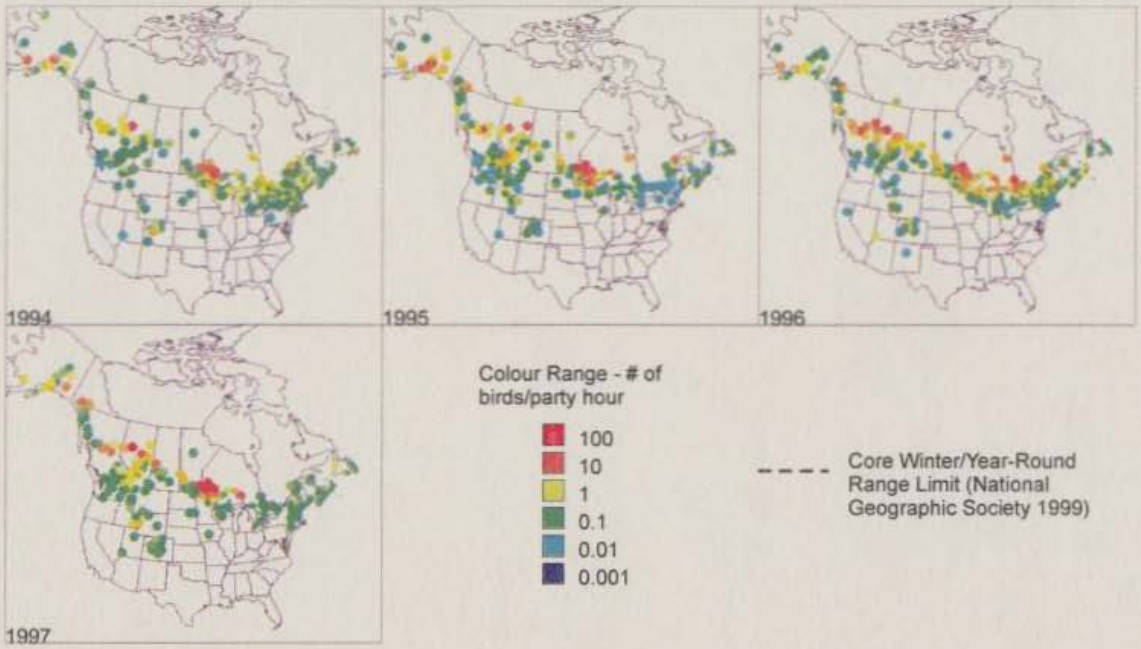


Figure 3-4 (continued) – Annual North American winter distribution and abundance of pine grosbeaks from CBC data, 1970 - 1997

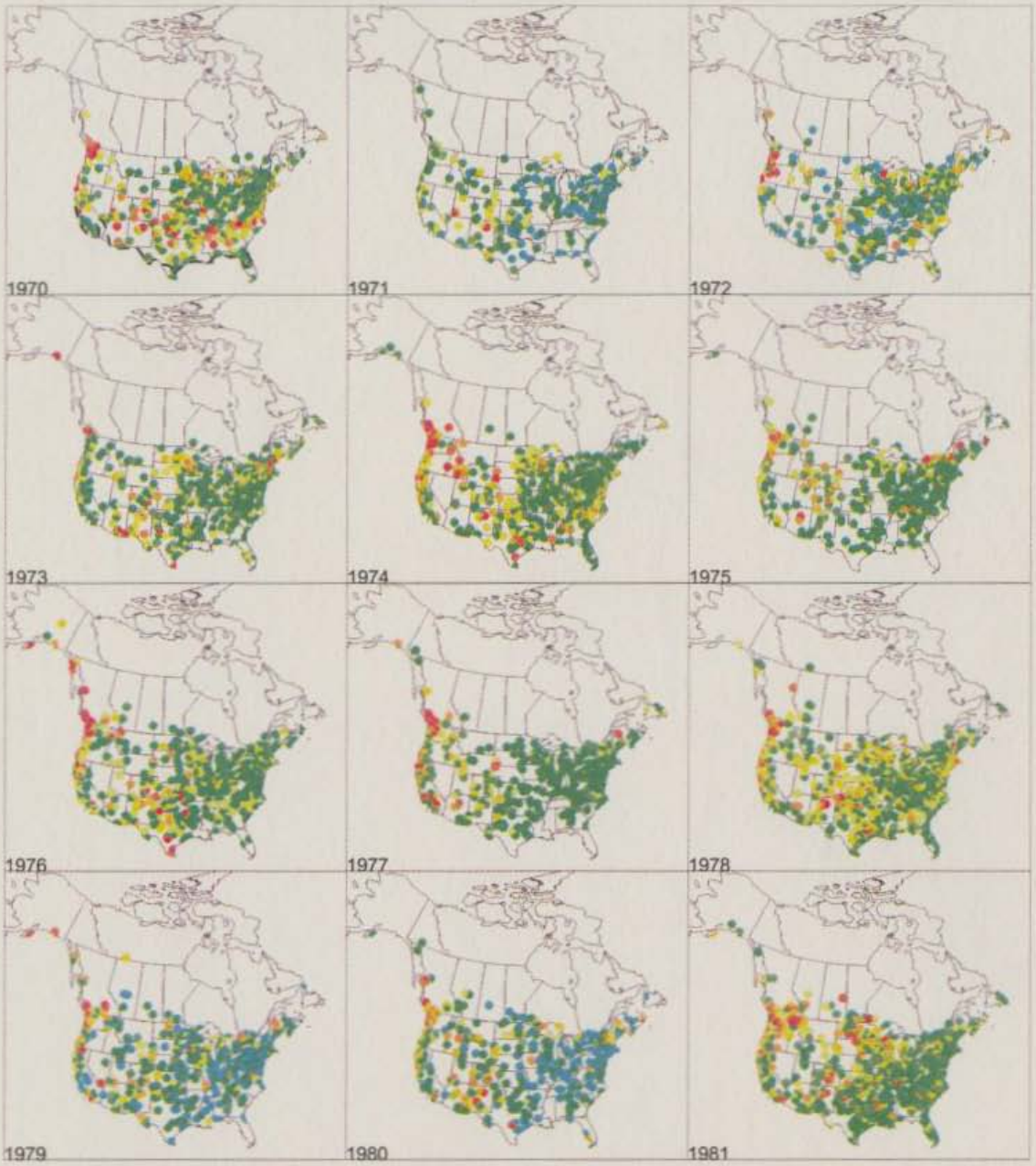


Figure 3-5 – Annual North American winter distribution and abundance of pine siskins from CBC data, 1970 - 1997

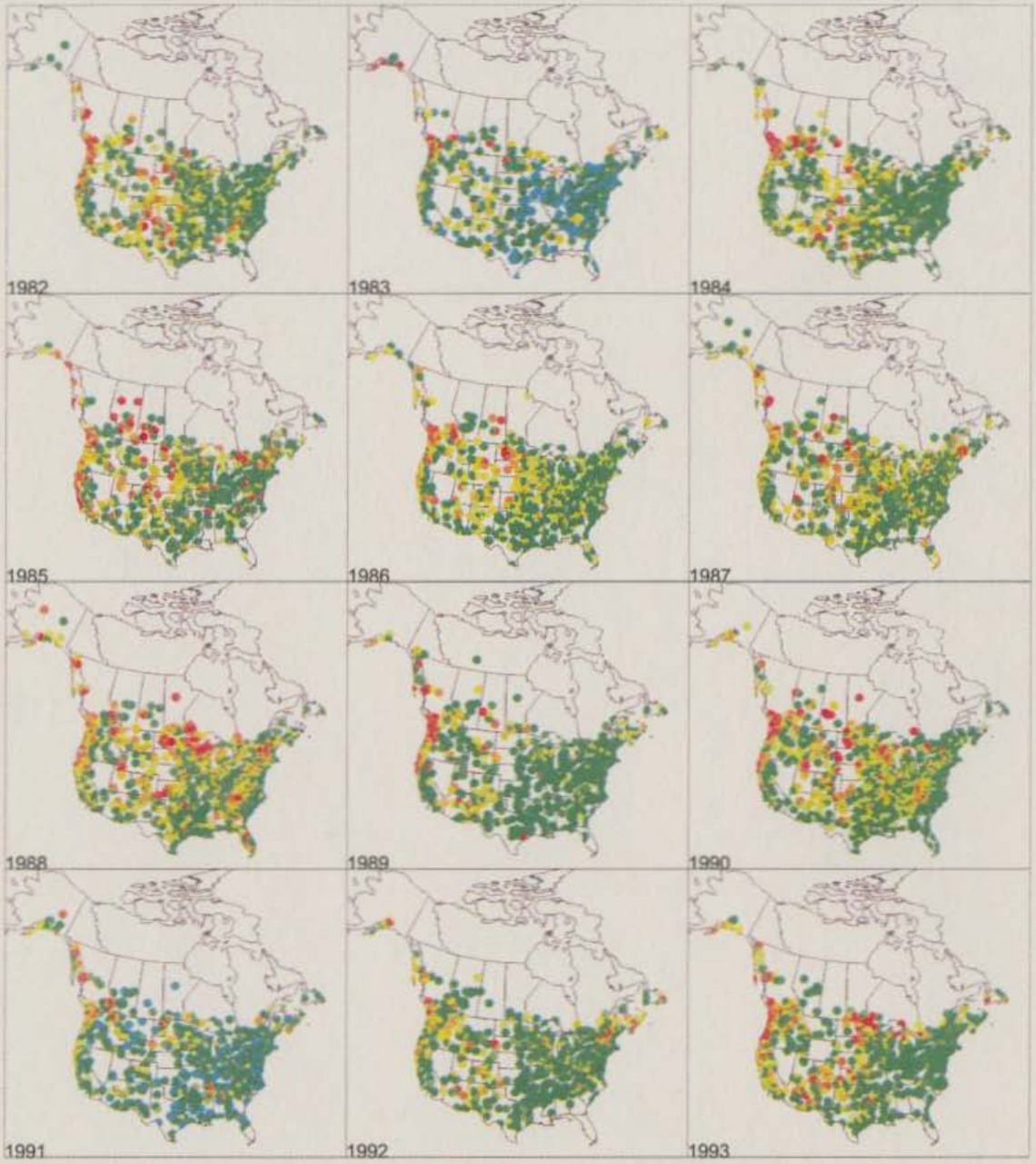


Figure 3-5 (continued) – Annual North American winter distribution and abundance of pine siskins from CBC data, 1970 - 1997

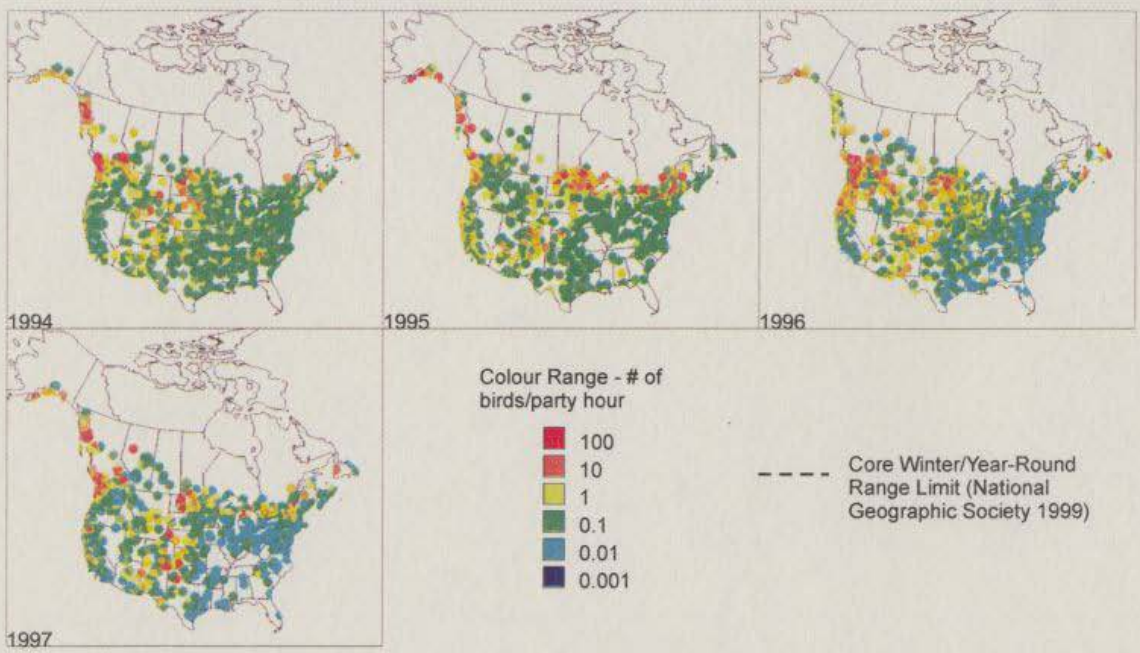


Figure 3-5 (continued) – Annual North American winter distribution and abundance of pine siskins from CBC data, 1970 - 1997

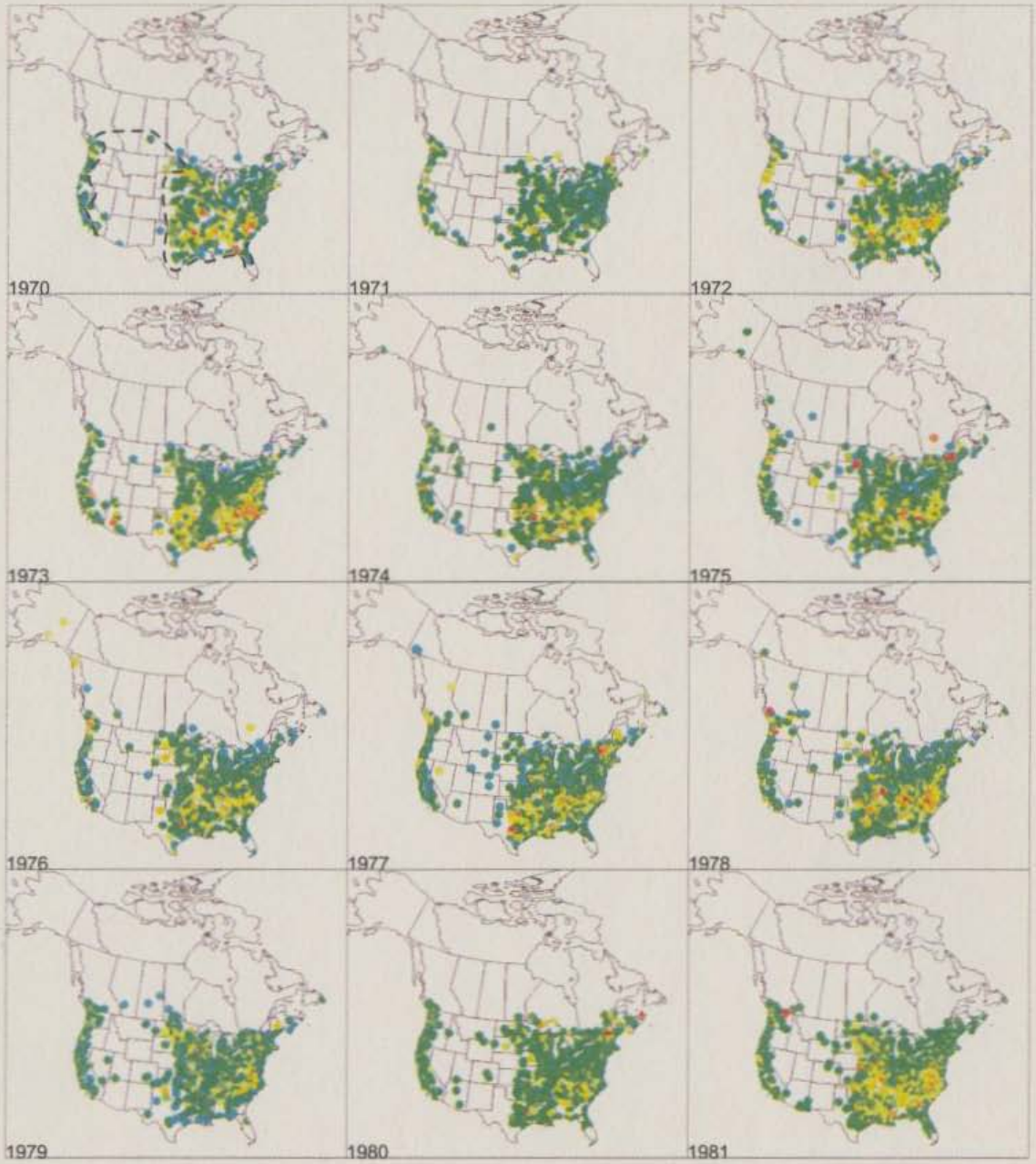


Figure 3-6 – Annual North American winter distribution and abundance of purple finches from CBC data, 1970 - 1997

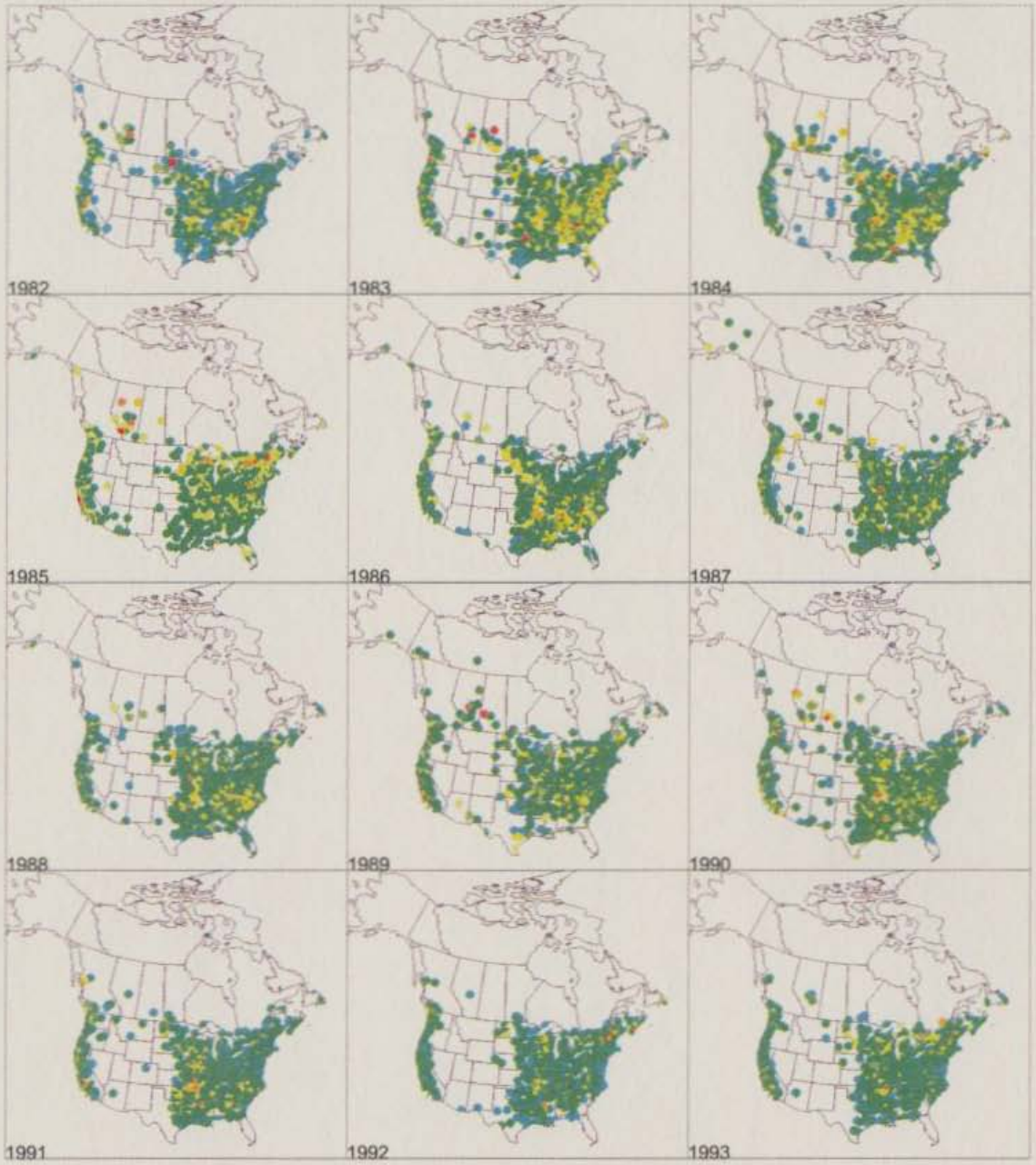


Figure 3-6 (continued) – Annual North American winter distribution and abundance of purple finches from CBC data, 1970 - 1997

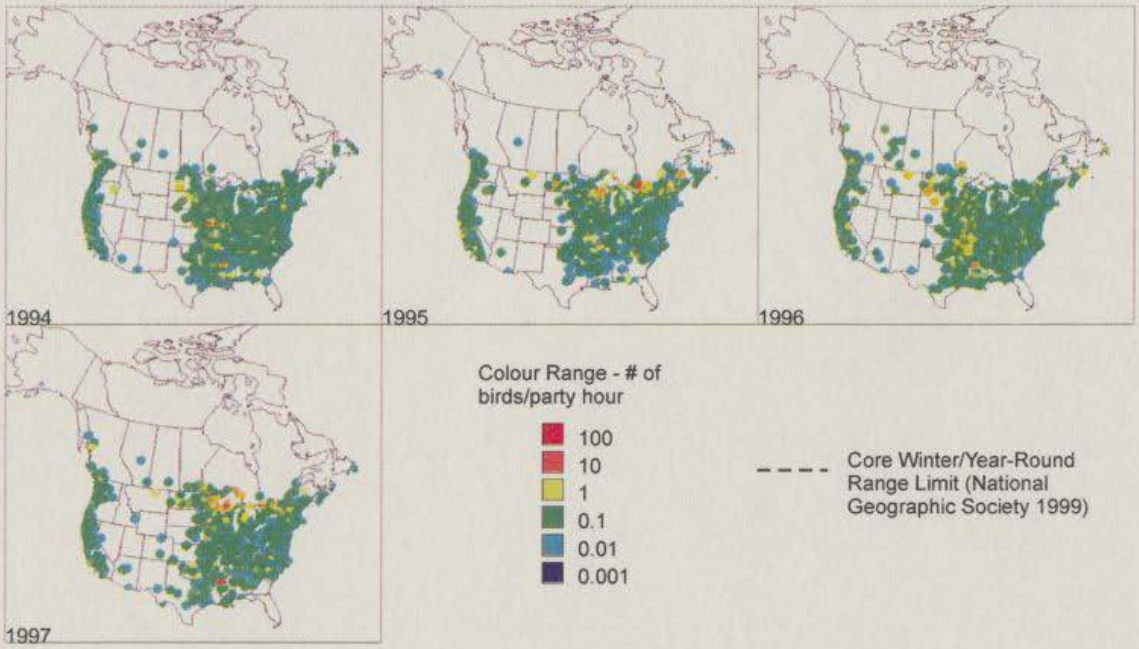


Figure 3-6 (continued) – Annual North American winter distribution and abundance of purple finches from CBC data, 1970 - 1997

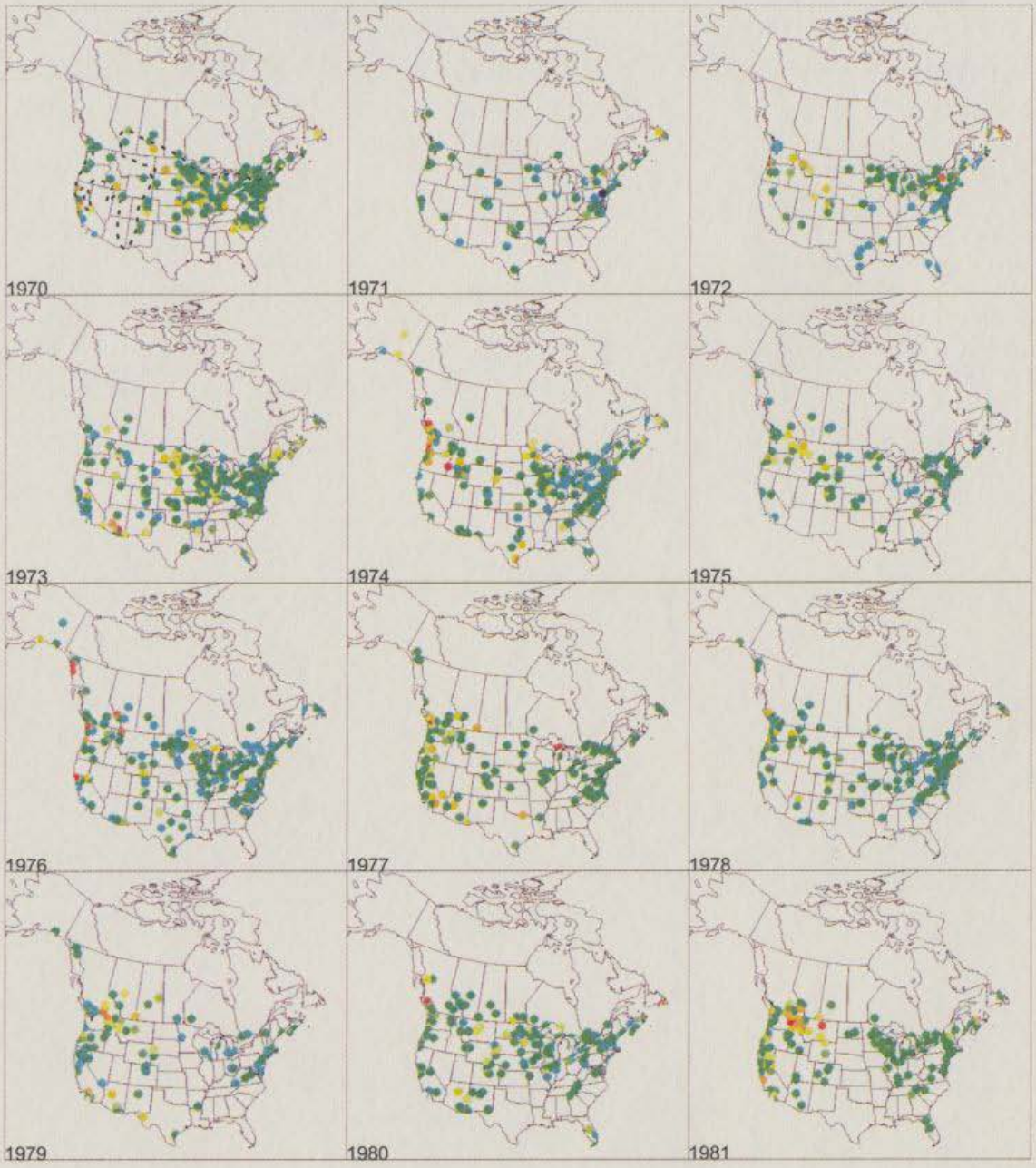


Figure 3-7 – Annual North American winter distribution and abundance of red crossbills from CBC data, 1970 - 1997

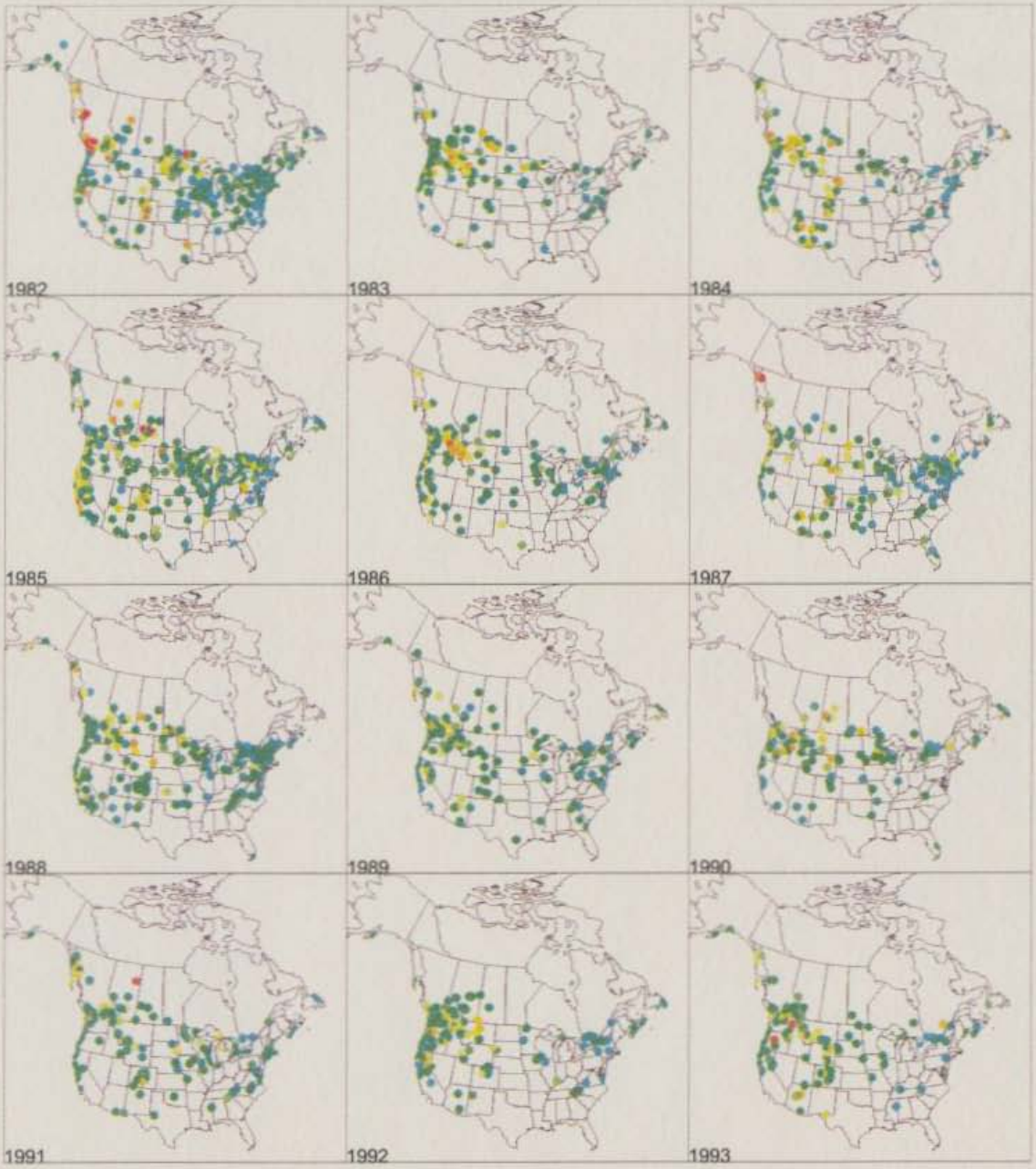


Figure 3-7 (continued) – Annual North American winter distribution and abundance of red crossbills from CBC data, 1970 - 1997

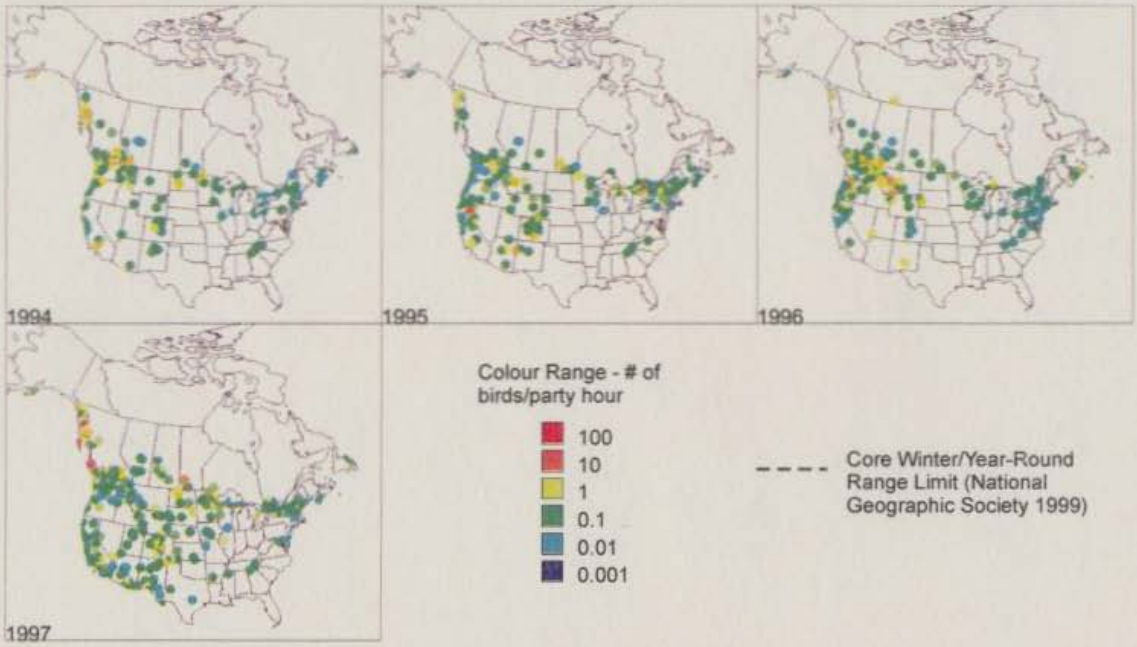


Figure 3-7 (continued) – Annual North American winter distribution and abundance of red crossbills from CBC data, 1970 - 1997

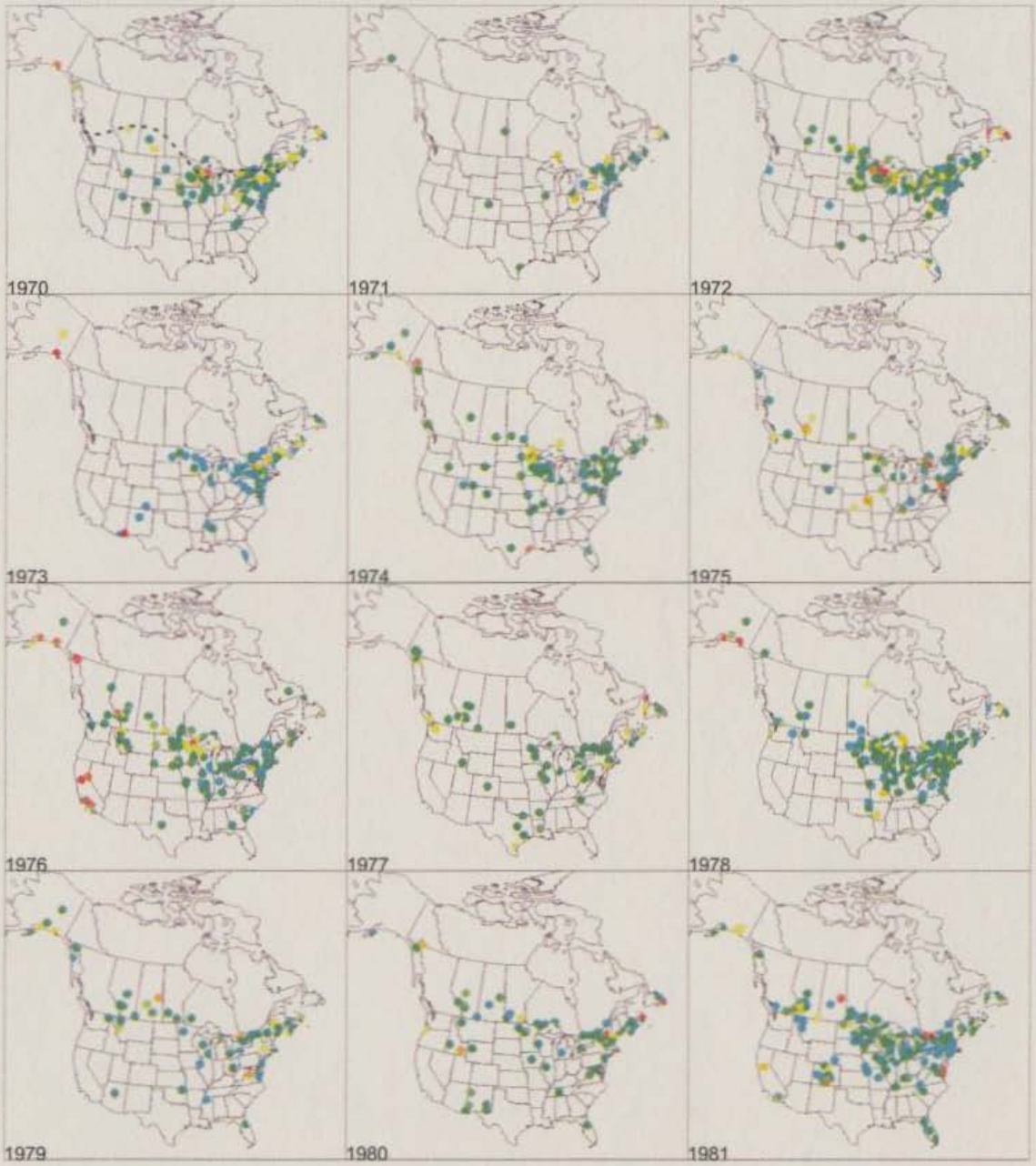


Figure 3-8 – Annual North American winter distribution and abundance of white-winged crossbills from CBC data, 1970 - 1997

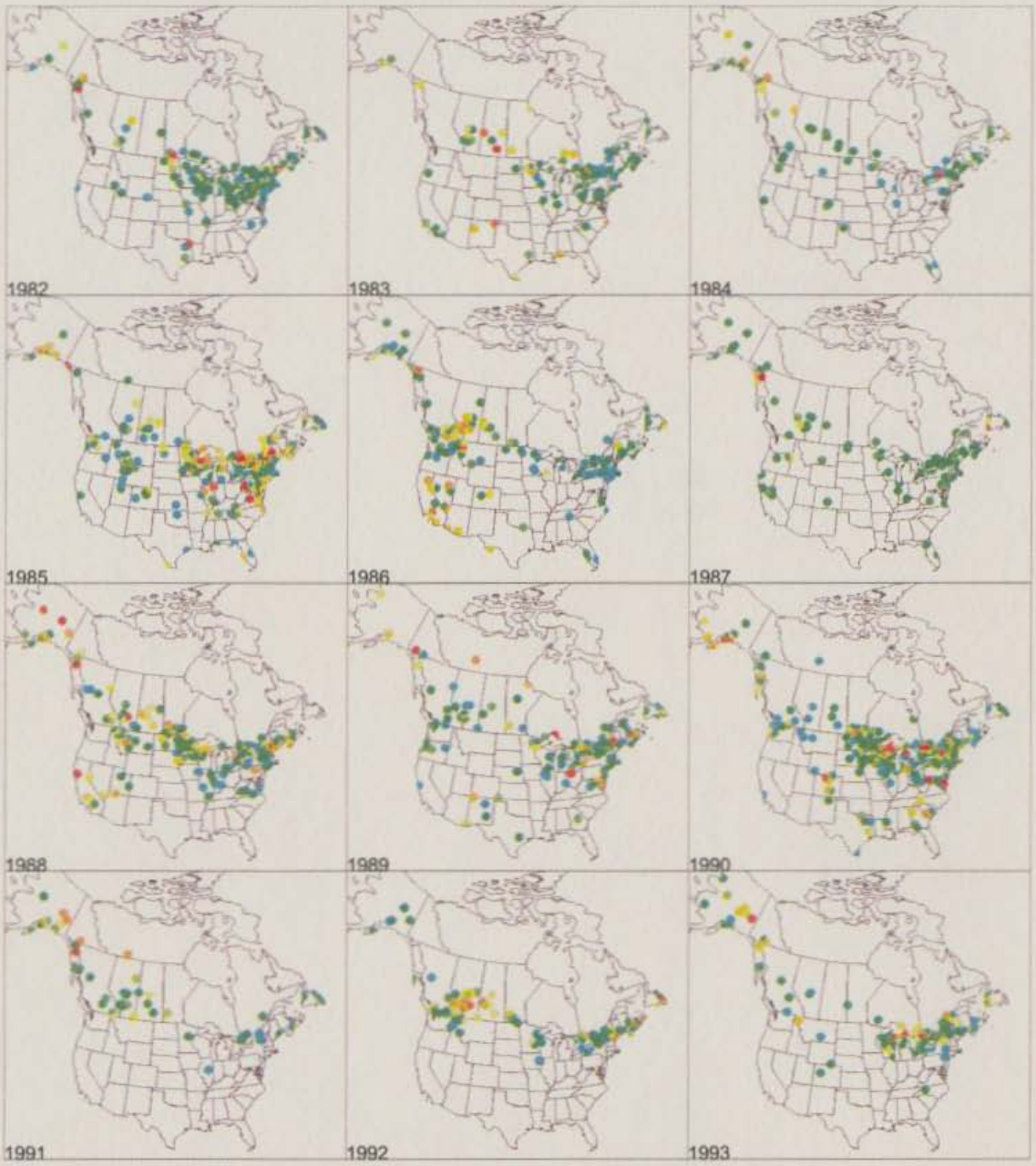


Figure 3-8 (continued) – Annual North American winter distribution and abundance of white-winged crossbills from CBC data, 1970 - 1997

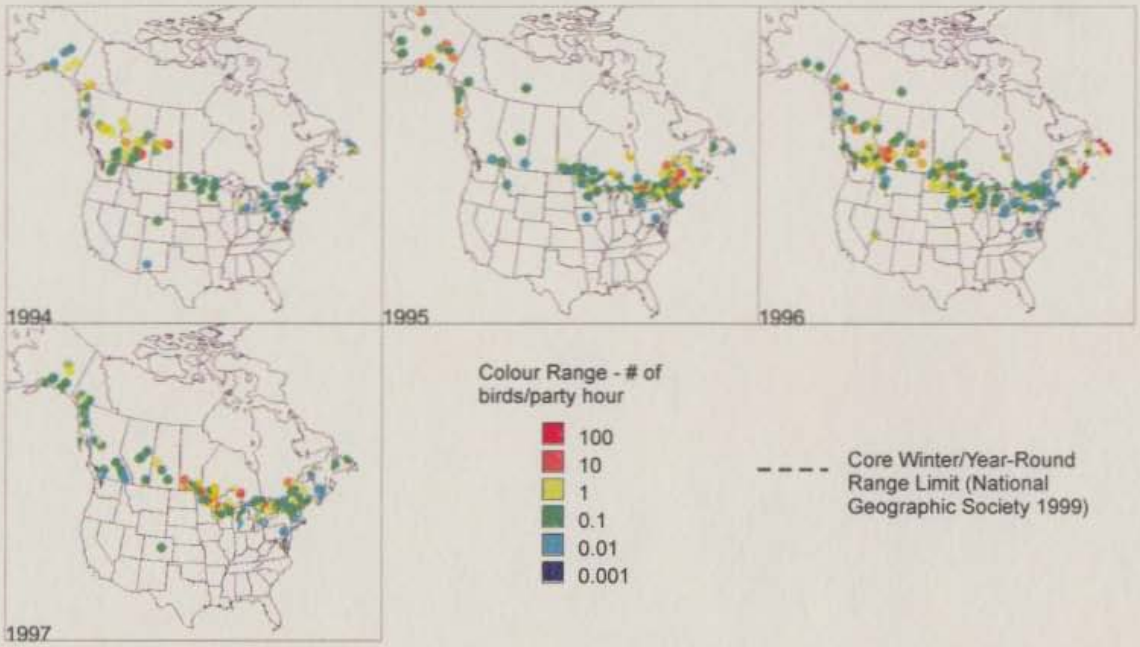


Figure 3-8 (continued) – Annual North American winter distribution and abundance of white-winged crossbills from CBC data, 1970 - 1997

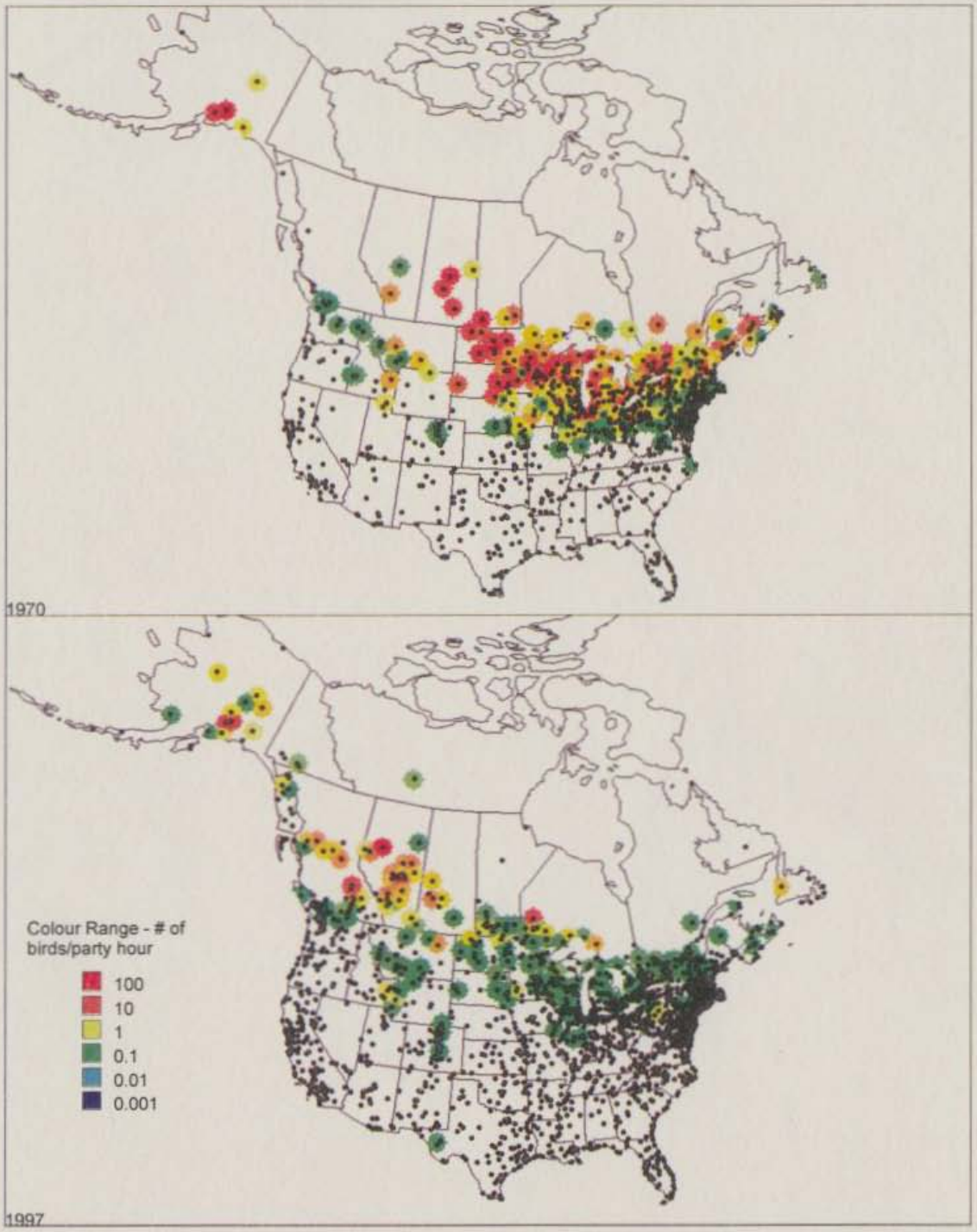


Figure 3-9 – North American winter distribution and abundance of common redpolls in 1970 and 1997 overlaid with locations of CBC counts

Figure 3-10 depicts the total number of North American CBCs with at least one of each of the six species of cardueline finches per party hour. This graph further illustrates the fluctuating nature of finch abundance on a continental scale. In general, the total annual number of counts per party hour greater than or equal to one oscillates between years with high numbers of counts and low numbers of counts. The scale of the total annual number of counts greater than one bird per party hour is variable between the six study species. Pine siskins show the greatest magnitude, with the number of high counts approaching 500 in 1988. The magnitude of oscillations is smallest in red crossbills, with the largest number of high counts of 59 in 1985. The pattern of oscillation is close to biennial in common redpolls, with most high count years being followed by a low count year. The pattern of periodic high count years is also seen in the other species, but with less uniformity than in the common redpolls. The periodic high count years appear to decay from the late 1980s to the late 1990s in purple finches, and, to a lesser degree, red crossbills.

There is some synchrony of high count years between the finch species. The overall trend is for high counts to occur in even-numbered years, although that trend does not hold across all species and years. There are many years that are high count years for some of the species, but the only years that show peaks for all six species are 1970 and 1990. The patterns of generally alternating high and low counts in each species are the same in the graphs of number of annual counts with at least one bird per party hour (Figure 3-10) and the graphs of total annual count per party hour (Figure 3-11).

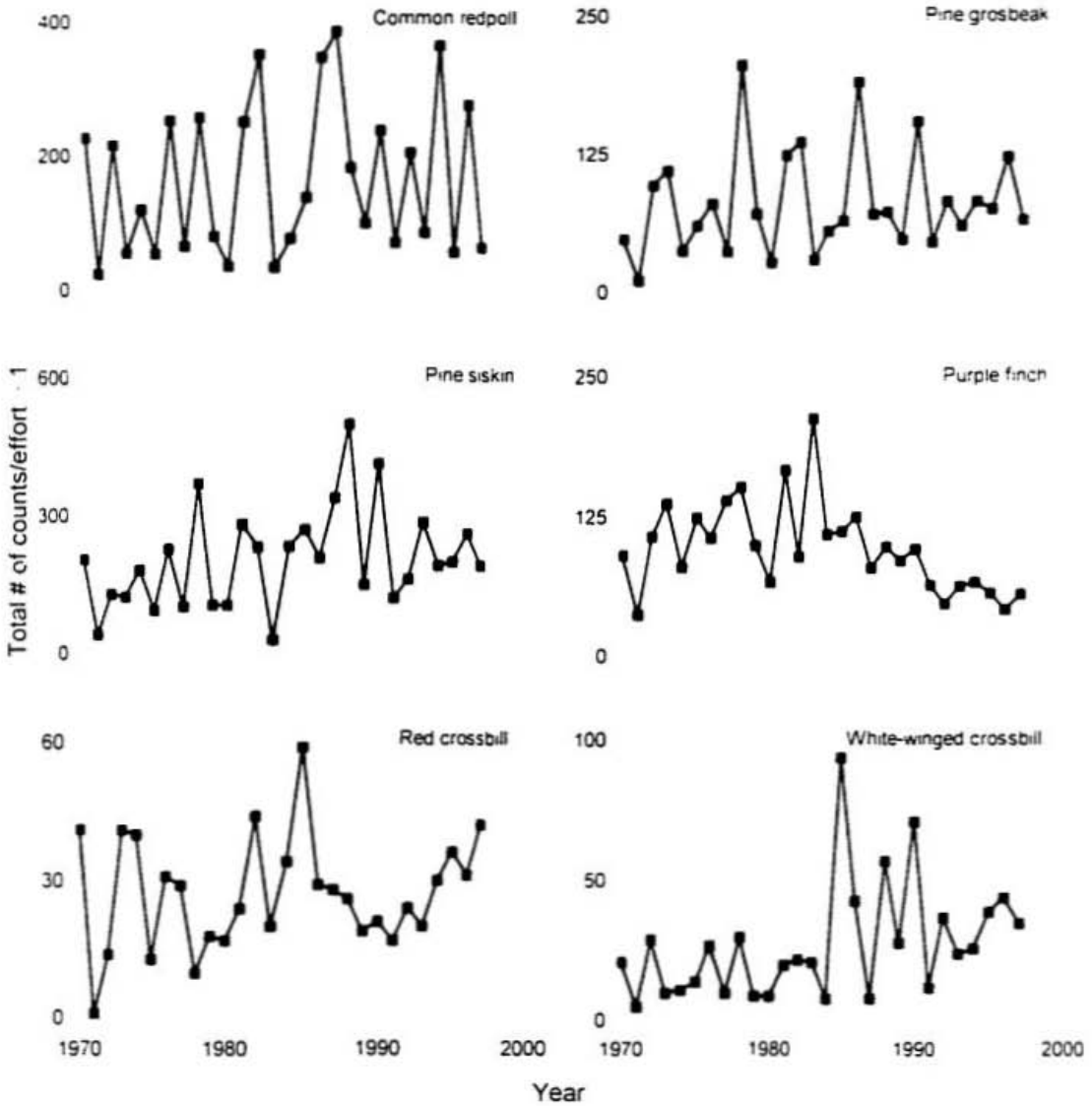


Figure 3-10 – Total annual number of continental CBC circles with at least one finch per party hour, 1970 – 1997.

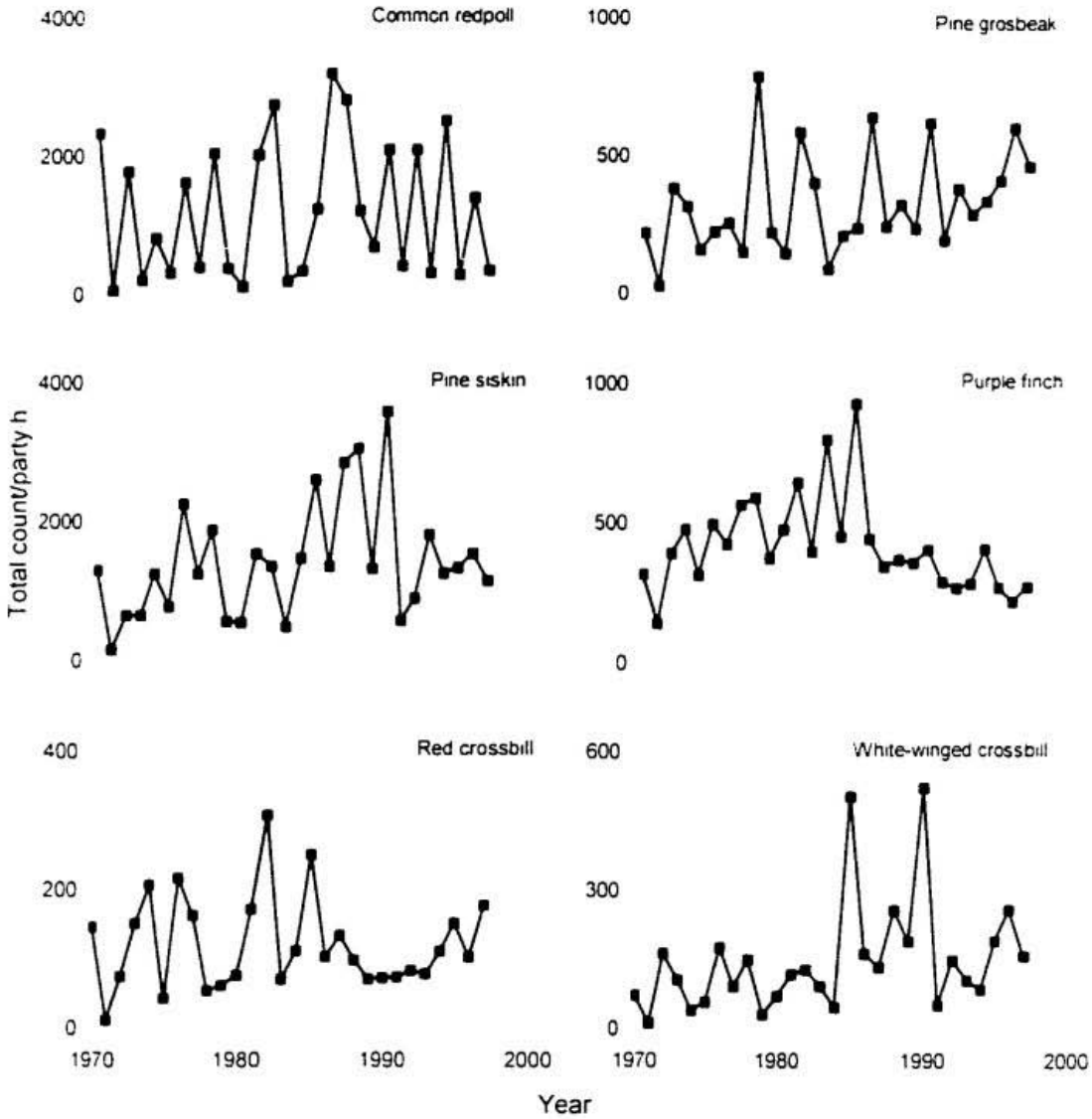


Figure 3-11 – Total annual number of finches per party hour from CBC data, 1970 – 1997.

Runs tests on the trends of total annual number of count circles with more than one bird per party hour show that during the period 1970 – 1997, there are 21 runs for common redpoll, pine grosbeak and pine siskin, 20 runs for purple finch, 19 runs for white-winged crossbill, and 18 runs for red crossbill. The graphs of total annual count effort give runs of 21 for common redpoll and pine siskin, 20 for purple finch, 19 for pine grosbeak, 19 for white-winged crossbill, and 16 for red crossbill. At an alpha level of 5%, only a number of runs greater than 21.8 for these data series would represent an alternation of differences such as would be expected by a cyclical phenomenon (Sokal and Rohlf 1995). Thus, the runs test for trend data does not indicate that the alternation between high and low values occurs more regularly than would be expected from a random sequence of values. It should be noted, however, that runs of 21 in common redpolls, pine grosbeaks and pine siskins are close to the critical value of 21.8 at which point runs can be described as cyclical. The trend data for these three species appear more cyclical than for species with a lower number of runs, like the red crossbill.

Finch abundance and boreal cone crop magnitude

Figure 3-12 illustrates the relationship between finch abundance and magnitude of seed crop in CBC counts from the North American boreal zone. In general, a wider range of finch abundance occurs at higher cone crop magnitudes. The Kruskall-Wallis test of nonparametric analysis of variance (Sokal and Rohlf 1995) was used to test for differences in finch abundance at boreal count circles with differing cone crop indices. There was no significant effect of cone crop index on number of pine grosbeaks ($H = 3.56$, d.f. = 3, $p = 0.314$) or common redpolls ($H = 0.89$, d.f. = 3, $p = 0.828$) per party

hour (all H statistics adjusted for ties in ranks). There was a significant effect of cone crop index on bird abundance per party hour for purple finches ($H = 14.49$, d.f. = 3, $p = 0.002$), pine siskins ($H = 26.42$, d.f. = 3, $p < 0.001$), red crossbills ($H = 17.64$, d.f. = 3, $p = 0.001$) and white-winged crossbills ($H = 16.21$, d.f. = 3, $p = 0.001$).

The results of unplanned comparisons performed on the species with a significant effect of cone crop index on finch abundance per party hour are also presented in Figure 3-12. Most of the differences in mean ranks of bird abundance occur between the poor (1) and excellent (4) cone crop indices.

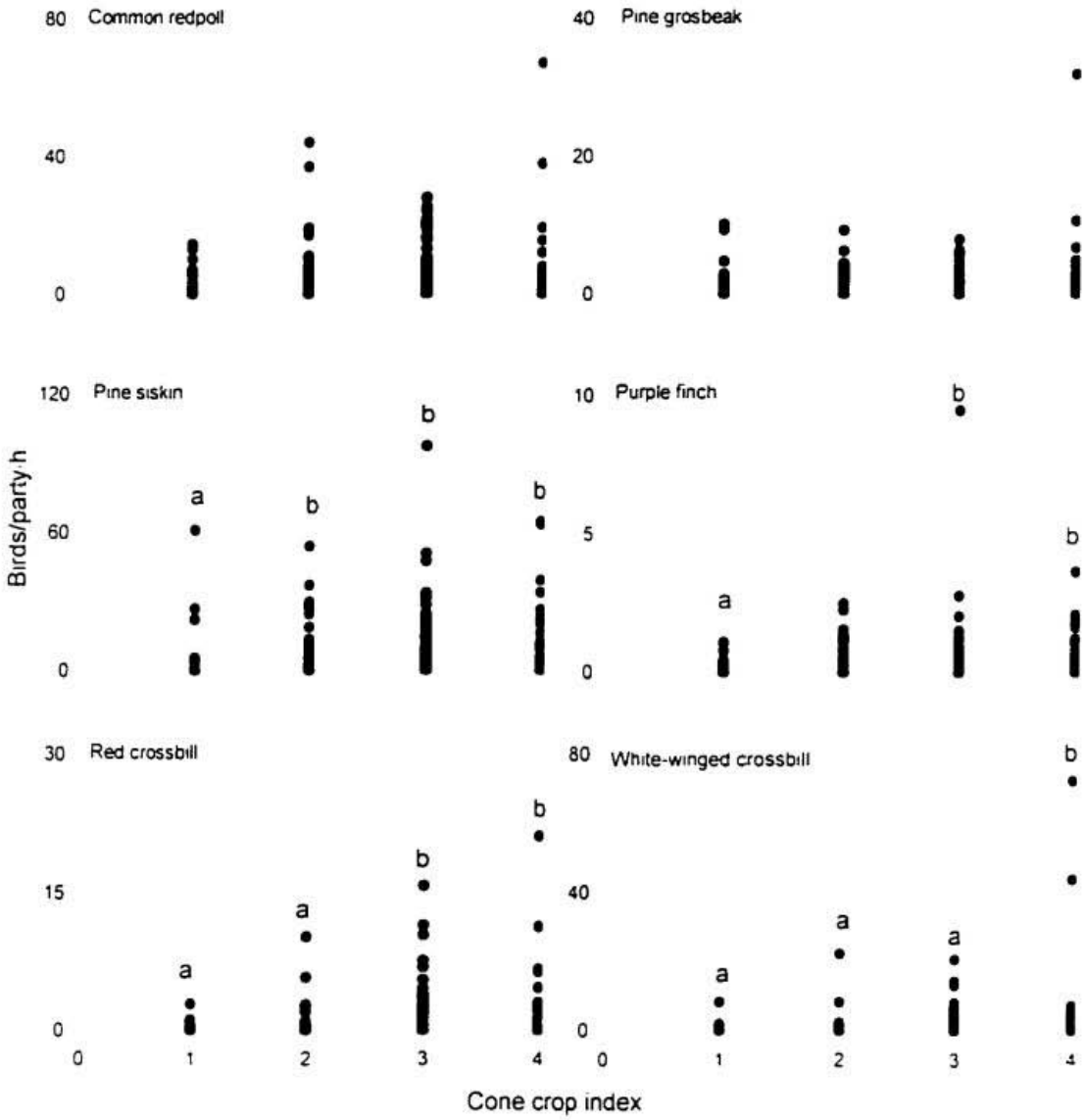


Figure 3-12 – Relationship between number of finches per party hour and crop magnitude, and significant differences from multiple comparisons of mean ranks of bird abundance per party hour at varying cone crop indices at boreal CBC count circles, 1974 – 1985. Cone crop index 1 = poor, 2 = fair, 3 = good, 4 = excellent. Bird abundances at cone crop index a are significantly different (α = 0.05) from bird abundances at cone crop index b.

Maps of cone crop indices across Canada and Alaska for 1974 – 1985 illustrate the distribution of cone crop magnitudes across broad scales (Figure 3-13). There is little continental-scale synchrony in the annual seed crop ratings from CBCs. A regional level of synchrony in cone crop magnitudes does exist across certain areas of Canada and Alaska in some years. This similarity in seed crop ratings particularly holds across regions that support similar types of land covers. For example, the seed crop in the deciduous mixed broadleaf forest of southeastern Ontario was poor/fair in 1974, and good/excellent in 1975, 1979 and 1985. The seed crop in the low/medium density southern evergreen needleleaf forest of southwestern Ontario was good/excellent in 1974, 1980 and 1983, and poor/fair in 1975. The boreal zone of Newfoundland had a uniformly poor seed crop in 1976 and 1982. The seed crop of the mixed intermediate needleleaf forest of Vancouver Island was good/excellent in 1977 and fair/good in 1982.

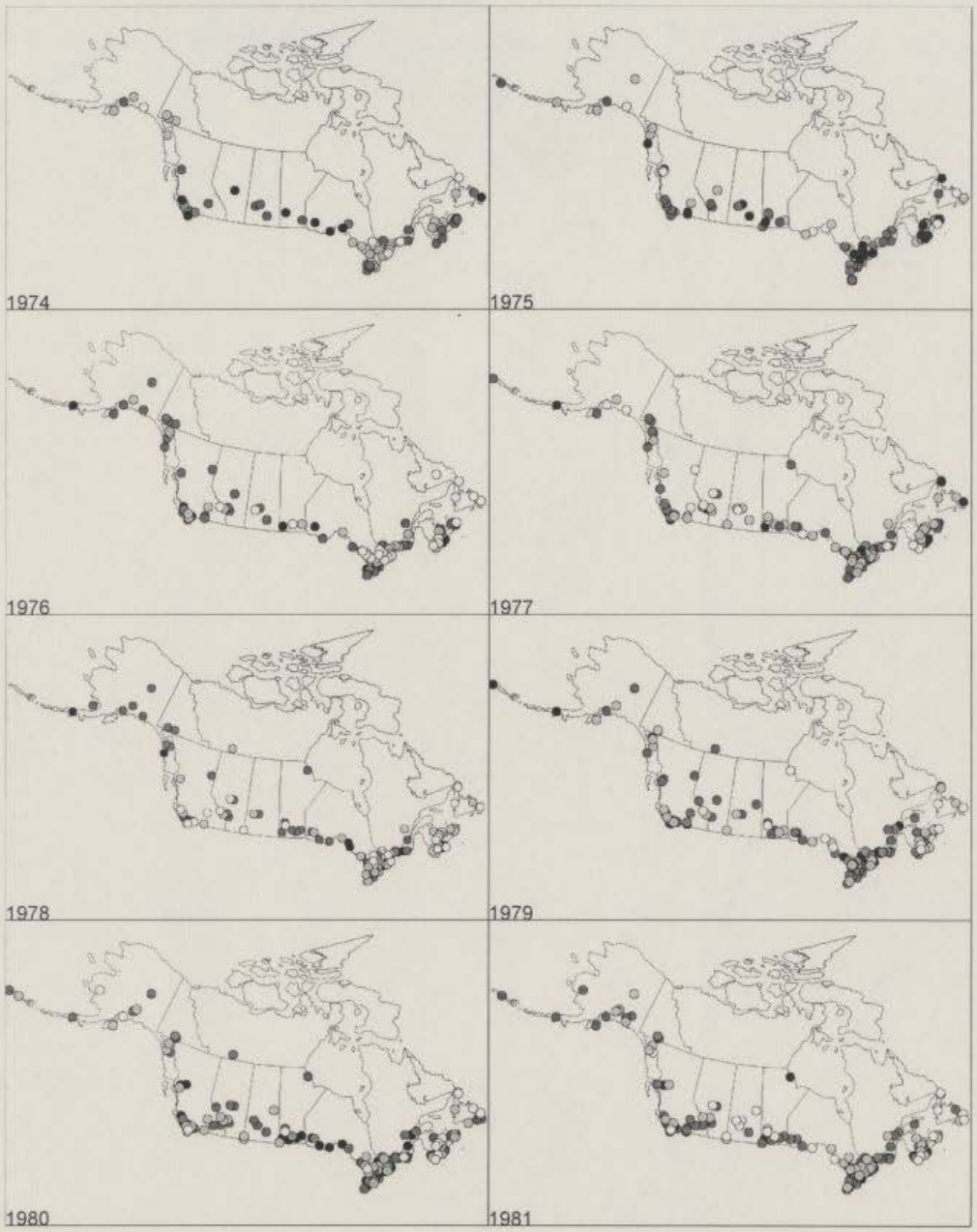


Figure 3-13 – Canadian and Alaskan cone crop magnitudes from CBC data, 1974 - 1985

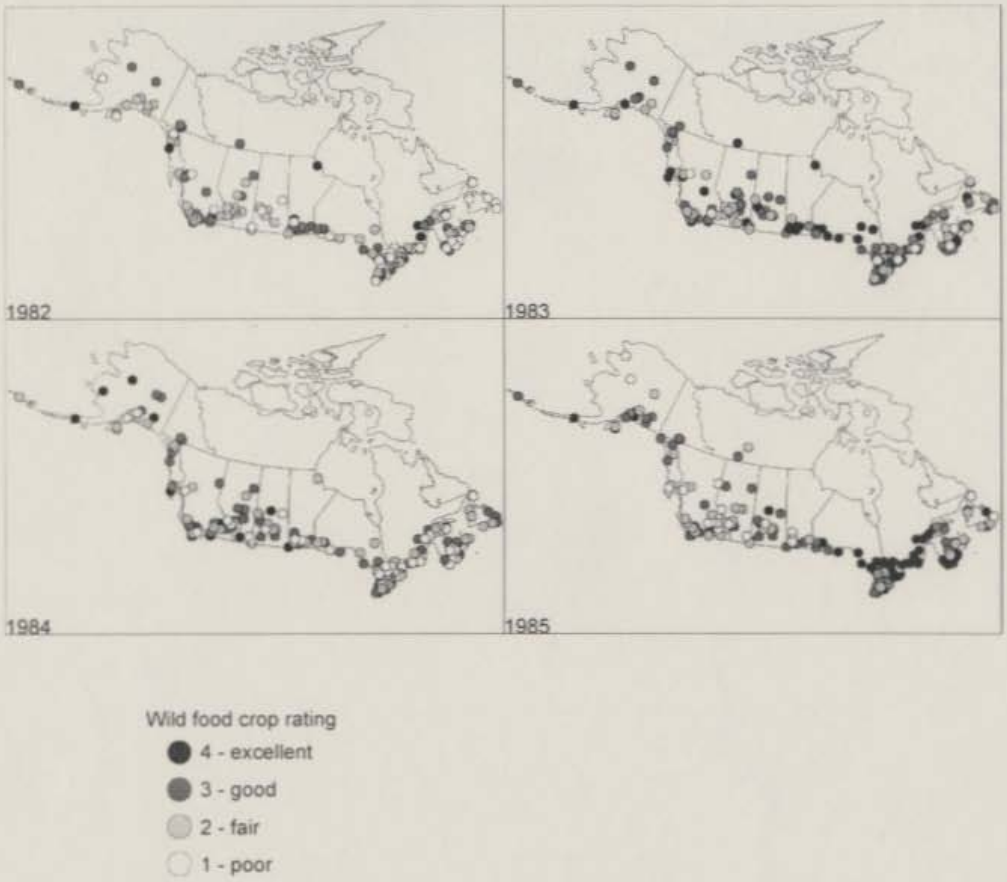


Figure 3-13 (continued) – Canadian and Alaskan cone crop magnitudes from CBC data, 1974 - 1985

Regional patterns of cardueline finch abundance in Newfoundland

Graphs of the annual number of cardueline finches counted on CBCs in three habitats in Newfoundland illustrate variability in abundance, both between and within species (Figures 3-14 – 3-19). Although the three counts are long running, no count summaries were published for Terra Nova National Park for 1986 and 1987, and for Gros Morne National Park for 1988, 1994, 1996 and 1997. No finches were counted on the 1976 and 1989 Gros Morne CBC. The graphs show that cardueline finch abundance is variable and sometimes sporadic on each of these CBCs. Red crossbill abundance has declined on all three counts. There are no red crossbill records from Gros Morne National Park CBCs after 1987, and none from St. John's after 1990. Red crossbills have been recorded on CBCs in Terra Nova National Park in the 1990s, but in numbers much lower than those recorded in the 1970s. While the assemblage of cardueline finches differs slightly between the three count locations in Newfoundland (with respect to presence/absence of purple finches and the relative abundances of pine siskins, pine grosbeaks and common redpolls), only the red crossbill has experienced a decline. Table 3-1 lists all locations in Newfoundland with CBC records of red crossbills from the past decade.

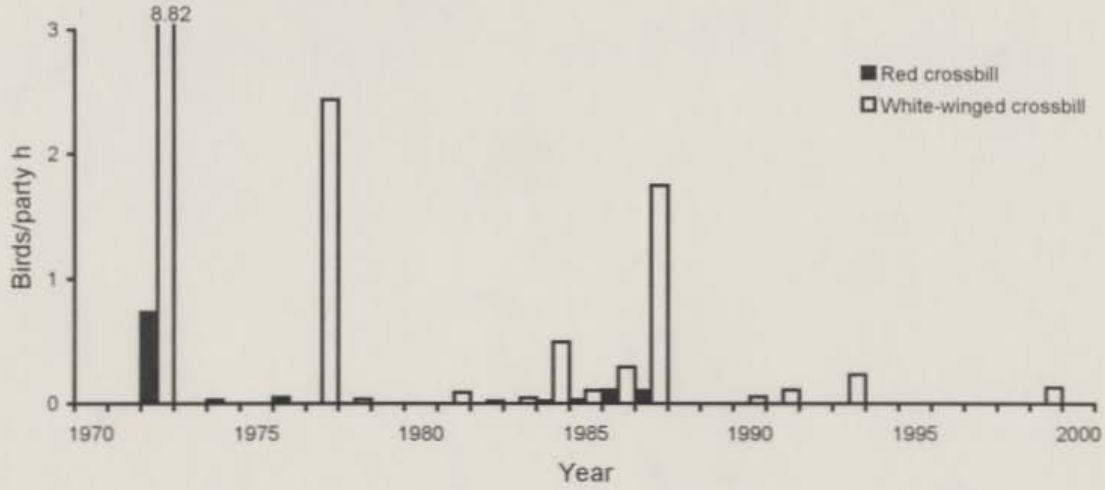


Figure 3-14 – Number of crossbills per party hour counted on the Gros Morne National Park CBC, 1972 – 1999.

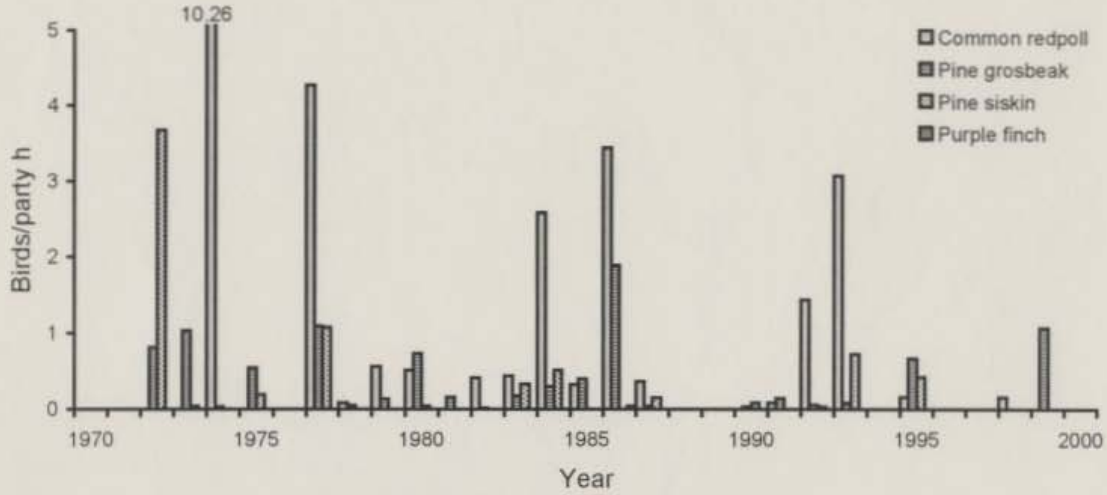


Figure 3-15 – Number of non-crossbill finches per party hour counted on the Gros Morne National Park CBC, 1972 – 1999.

*** This count started in 1972. No counts published for 1988, 1994, 1996, and 1997.**

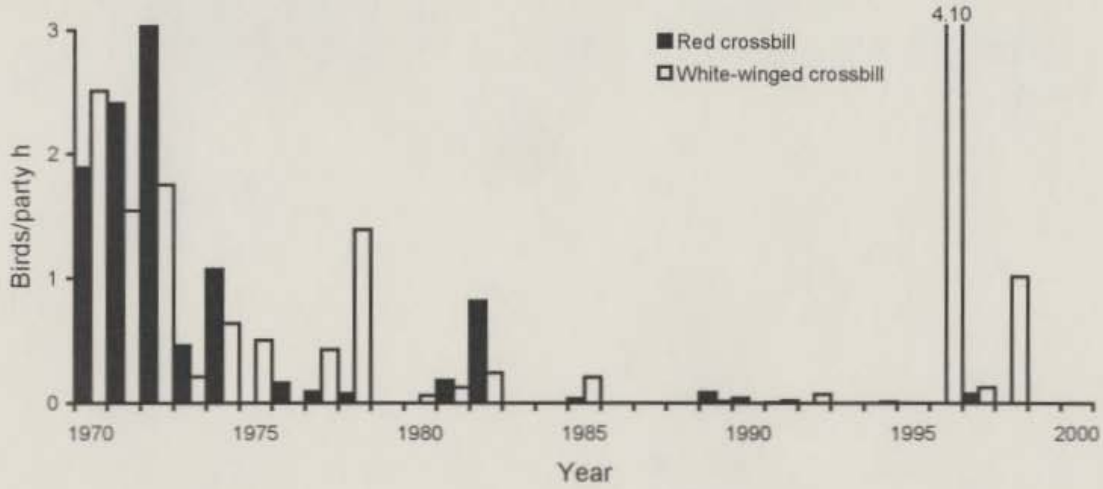


Figure 3-16 – Number of crossbills per party hour counted on the Terra Nova National Park CBC, 1970 – 1999.

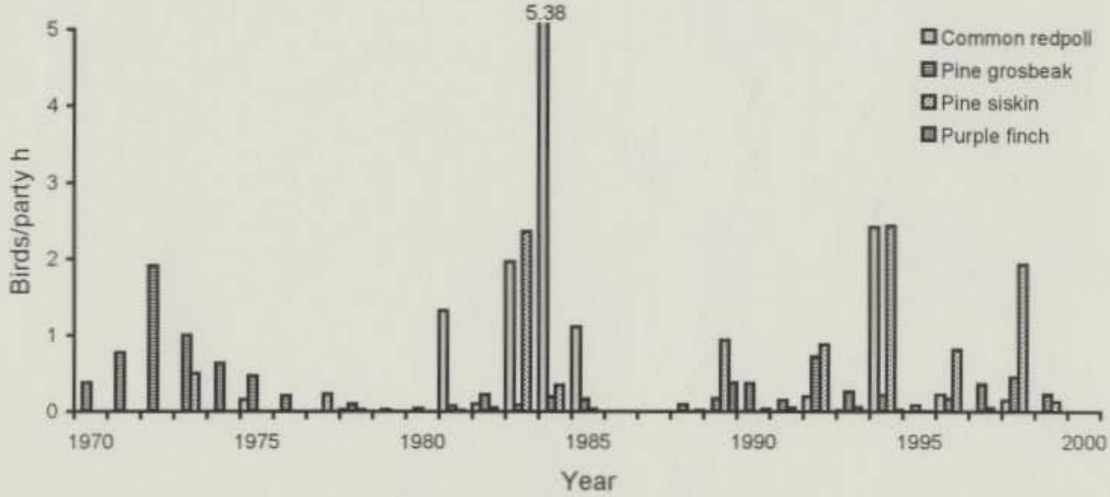


Figure 3-17 – Number of non-crossbill finches per party hour counted on the Terra Nova National Park CBC, 1970 – 1999.

*** No counts published for 1986 and 1987.**

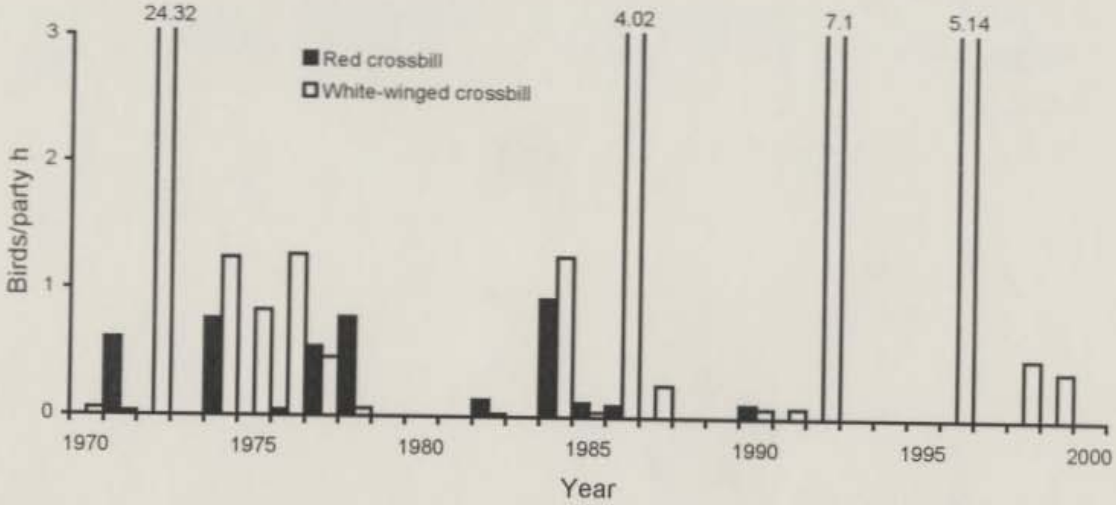


Figure 3-18 – Number of crossbills per party hour counted on the St. John's CBC, 1970 – 1999.

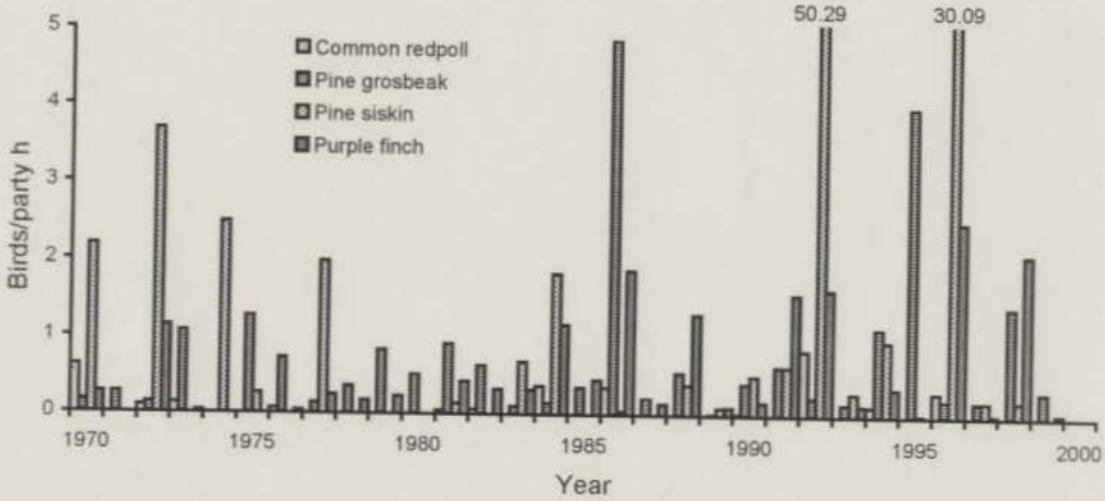


Figure 3-19 – Number of non-crossbill finches per party hour counted on the St. John's CBC, 1970 – 1999.

Table 3-1 – Number of red crossbills counted on Newfoundland CBCs, 1990 – 1999. CW = count week record – species was present during the week of the CBC count, but was not counted during the 24 hour CBC period.

Year	Location	Count
1990	Cape St. Mary's	CW
1990	St. John's	9
1990	Terra Nova National Park	5
1991	Terra Nova National Park	1
1992	Cape St. Mary's	1
1992	Conception Bay North	1
1992	Ferryland	1
1993	Stephenville	20
1994	Cape St. Mary's	3
1994	Ferryland	2
1997	Terra Nova National Park	14
1998	Terra Nova National Park	CW

Discussion

Continental patterns of cardueline finch distribution and abundance

The maps presented here represent the only large temporal and spatial scale analysis of distribution and abundance trends in cardueline finches that includes coverage of the North American boreal zone. A pattern of highly variable winter distributions is illustrated in the CBC abundance maps. From the maps, core winter distribution regions are discernable for each species. Common redpolls, pine grosbeaks and white-winged crossbills have distributions that follow the boreal forest zone, while pine siskins, purple finches, and, to a lesser extent, red crossbills, have more southerly winter distributions. It is apparent that in some winters, distributions extend beyond the limits of each species' core range. This inter-annual variability in distribution is likely due to variations in nomadic behaviour at the individual level. Common redpolls travel varying distances in different winters, are not pre-programmed to follow any set migration (Hochachka et al. 1999) and show little breeding or wintering site fidelity (Troy 1983). This may also be the strategy employed by the other boreal cardueline finches, although breeding site fidelity is generally considered to be stronger than winter site fidelity in irruptive finches (Ulfstrand 1963).

These abundance maps are based on CBC data that are collected in the early winter, non-breeding season for most species. The spatial patterns in abundance of cardueline finches are of particular interest during the winter, as limitations in the winter food supply are the major driving force in the irruptive movements of these species (Ulfstrand 1963; Newton 1972). Some cardueline finches such as redpolls, siskins and

crossbills may breed in autumn and winter months (Newton 1972) and may spend up to 5 months in their winter ranges (Erskine 1977). This strategy of opportunistic breeding is at least partially modulated by the supplementary cue of food availability in an area (Hahn et al. 1997) but is also influenced by proximate environmental factors such as photoperiod in red (Benkman 1990) and white-winged crossbills (Hahn 1995; Deviche 1997). Furthermore, many of the irruptive finches do not return to the same areas in successive years (Newton 1972) so annual variations in winter distributions may be extreme.

The spatial asynchrony seen in the annual winter distribution abundance maps illustrates the importance of analyzing biogeographic trends in irruptive species. The degree of east/west asynchrony in high abundance years varies between the species. These trends are not depicted by continental summary data such as the total annual count per party hour for each species. This asynchrony may be explained by the partial regional synchrony in cone crop magnitude that is seen in Canada and Alaska (Figure 3-13). Similar east/west movements between successive winters have been shown from continental banding recoveries for common redpolls (Troy 1983).

Graphs of the total number of counts with greater than one cardueline finch per party hour across North America illustrate a rough pattern of biennially high years. This pattern is most striking in the common redpoll, with high count years in most even years. Biennial high count years in common redpolls have also been described in even years from feeder monitoring and banding in Saskatchewan and Manitoba (Houston and Smith 2000). Fluctuations between high count years and low count years are also seen in the

other study species, with high count years generally occurring in even years in red crossbills, pine grosbeaks, pine siskins and white-winged crossbills. This high count – even year trend in cardueline finches is supported by Bock and Lepthien's (1976) study of seed-eating bird irruptions. Other studies on the periodicity of seed-eating bird abundances have failed to discriminate whether count years represent late fall (December) or early winter (January) and thus it is unknown if 1970 represents the count that occurred in 1969/1970 or 1970/1971 (Bock 1980; Larson and Bock 1986). Because of this, it is impossible to tell if the trend of high counts in even years is supported by these studies.

The trend of large-magnitude, generally biennial high count years appears to decay in the past decade in purple finches and red crossbills. The low number of runs counted in red crossbills as compared to the other study species supports this decay in periodicity. Patterns of periodic irruptions were found by Larson and Bock (1986) to decay and reform over a period of decades in common redpolls, pine siskins and red-breasted nuthatches. It is difficult to postulate a reason for the decaying trend seen in the present study. Bent (1968) theorized that the introduction of the house sparrow (*Passer domesticus*) to North America in the late 19th century displaced breeding purple finches up until the middle of the 1900s in the American northeast. However, the timing of this introduction and subsequent displacement does not adequately explain why large magnitude periodic irruptions have not been present in recent years in the purple finch. In fact, Bent (1968) recognizes that the loss of nesting trees likely presents a bigger impact to purple finch ecology than does displacement by house sparrows, but

displacement in Eastern North America by introduced house finches (*Carpodacus mexicanus*; Veit and Lewis 1996) may also be affecting purple finch populations. This illustrates why it is essential to examine long-term population data in irruptive species.

The continental fluctuating pattern of high cardueline finch abundance is also seen in the graphs of total annual count per party hour. The similarities in abundance trends from the graphs of total annual number of high counts, the graphs of total annual count per party hour, and the more detailed distribution/abundance maps indicate that the two sets of graphs of continental data are likely adequate summaries of annual cardueline finch abundance. While these two types of data do not portray the spatial differences in abundance that are seen in the maps, they do indicate which years are high abundance years across the continent. They also illustrate the differences in magnitudes of abundance between the finch species. The largest abundances occur in pine siskins and common redpolls. Pine siskins are widespread during the winter across the southern United States, and although common redpolls are more northerly in distribution, they are seen in many annual count circles with a very high number of birds per party hour, which explains these high magnitudes of abundance as compared to the other study species. Red crossbills, with low abundance, have a much more restricted distribution and are recorded with a very high number of birds per party hour in many fewer count circles. The higher abundances of common redpolls and the widespread American distribution of pine siskins and purple finches are likely a result of their more generalized foraging strategy as compared to crossbills. Common redpolls, pine siskins and purple finches feed preferentially on conifer seeds throughout the winter, but will consume many other

types of seeds, particularly during a southern irruption (Bent 1968). In contrast, crossbills are conifer specialists, and likely have restricted distributions and lower abundances as a result of their year-round preference for conifer seeds.

Finch abundance and boreal cone crop magnitude

Maps of wild food crop ratings reported by CBC participants in count circles across Canada and Alaska for 1974 – 1985 indicate that seed crop magnitude is not synchronous on a continental scale. Regional level synchrony does exist in many cases, however, and particularly in areas that support similar forest types. This synchrony is thought to occur as a result of exogenous factors (such as favourable weather conditions) and endogenous factors (such as the species-specific time span required for reproductive bud differentiation and cone growth) in conifers (Silvertown 1980).

While based on a limited number of cone crop ratings from high boreal zone CBCs, this finding does not support the supposition that 'widespread, synchronous, conifer cone crop failures in northern forests' (Bock and Lepthien 1972) occur on a continental scale (Koenig and Knops 1998). A more likely scenario of North American cone crop failures supported by these data is one similar to that described by Ulfstrand (1963), where cone failures in Sweden occur in a patchwork pattern on small scales, and birds can usually access some form of seed within a region. Even such regional level cone crop failures, however, can impact specialized conifer feeders. Crossbill taxa, adapted to foraging on cones to the point of being morphologically and behaviourally adapted to exploit key conifer species (Benkman 1993a), may not find alternate food sources during a regional cone crop failure without wandering large distances. This

patchwork pattern of cone failure may be compared to the pattern of decreased seed availability across a logged boreal forest landscape in North America.

Interestingly, the maps of food crop assessments made during CBCs show that many regions have crops that are either poor/fair or good/excellent. This may be a result of CBC participants failing to consistently discriminate ratings during generally bad or generally good cone years. Visual seed crop ratings are most effective when assessing heavy and very heavy cone crops (McDonald 1992), and the maps presented here are probably most informative and reliable when examining patterns of extreme cone crop ratings.

It was expected that there would be a positive relationship between cone crop magnitude and finch abundance within the boreal forest for all six of the study species. However, this relationship was not found for common redpolls or pine grosbeaks. In a study of finch abundance and cone crop size in California, Widrlechner and Dragula (1984) suggested that a lack of significant relationship between purple finch abundance and cone crop size was due to the fact that purple finches are less dependent on conifer seeds for food than the pine siskins and red-breasted nuthatches which did show a significant relationship with cone crop magnitude in their study. This does not explain the findings in the present study, however, as purple finches found in the boreal zone did show a significant relationship with cone crop magnitude, whereas the more winter conifer-dependent species, common redpoll and pine grosbeak, did not. A more likely explanation in this study is that the data collected by volunteers from the boreal zone were not precise or widespread enough to demonstrate the expected relationship between

abundance and cone crop magnitude for common redpolls and pine grosbeaks, which have northerly year-round distributions. These finches may also respond to changing conifer crop abundance with a lag of more than one year (Summers 1999).

Comparisons of the differences between mean ranks of bird abundance per party hour at varying cone crop indices for pine siskins, purple finches, red crossbills and white-winged crossbills indicated that most differences in finch abundance occurred between extremes of cone crop ratings. This finding further supports the notion that CBC cone crop ratings may be most informative for examining qualitative, binary trends at either very high or very low cone crop magnitudes. This positive relationship between finch abundance and cone crop magnitude provides support for the hypothesis that the level of available conifer seed influences winter abundances of cardueline finches across boreal landscapes. This relationship has clear implications in Canada's boreal forests, where logging can greatly limit conifer seed availability across wide regions. Logging cuts performed on a scale greater than that of the natural disturbance regime of the boreal forest have impacts on a scale above the stand level, and therefore will impact the foraging of finches.

Regional patterns of cardueline finch abundance in Newfoundland

The applicability of Christmas Bird Count data extends beyond the broad-scale mapping effort presented here. CBCs are also an invaluable tool for the long-term monitoring of regional or local populations that demonstrate population trends across long time scales. Short-term field based monitoring (see Chapter 2) is not always

sufficient to demonstrate population fluctuations (Haila and Järvinen 1990; Kirk et al. 1996; Willson and Comet 1996), especially in species such as cone-dependent carduelline finches that undergo irregular irruptive movements (Virkkala 1991; Patterson et al. 1995). Furthermore, a regional scale analysis of CBC data provides measures of bird abundance, and not just the range limits that are found in bird atlases (Bock 1980).

There are large inter-annual fluctuations in the number of carduelline finches counted per party hour on Newfoundland Christmas Bird Counts. In some years, a very high number of some species of finches were reported, while in other years in the same circle, none of that species was reported. Breeding productivity alone cannot explain this local level variation in abundance between years (Ulfstrand 1963). Instead, the fluctuations are attributed to the finches' irruptive movements.

As with all CBC data, an examination of population abundance trends on a small geographic area is more powerful when it is based on large sample sizes (Bock and Root 1981). Trends from single circle CBCs are more reliable when based on a large number of years (in this analysis, 28 – 30 years) and a large number of party hours (in this analysis, 1053.5 for Gros Morne National Park, 2207.75 for Terra Nova National Park, and 1889.25 for St. John's, including feeder watching effort). These three count circles are also representative of the three primary forest types that stretch across Newfoundland: balsam fir dominated, black spruce dominated, and mixed coniferous composition. Trends from these count circles could reasonably be more broadly interpreted to apply to the boreal forest that stretches across insular Newfoundland.

It is considerably difficult to monitor population abundance trends in species that have such variable numbers from year to year as do the boreal cardueline finches. What is clear from the graphs of the finches censused on Newfoundland Christmas Bird Counts is that finch numbers are inter-annually variable. Furthermore, red crossbills appear more common on counts before the mid-1980s than they do in recent counts. This trend is apparent despite the irruptive and periodic presence of cardueline finches on the Newfoundland counts. Although there are years when some of the other finch species do not appear on the counts, no other finch species has declined (and not recovered) in the manner of the Newfoundland red crossbill. This is a trend that was first highlighted by Benkman (1989) from the Terra Nova National Park CBC.

This decline is cause for concern due to the unique ecology, morphology and taxonomy of the Newfoundland red crossbill. North American red crossbills have long been recognized as a complex of distinct forms (Griscom 1937). The red crossbill found in Newfoundland is a unique subspecies, *Loxia curvirostra percna* (Bent 1912), which is considered to be endemic to the island.

Conservation priorities for boreal cardueline finches

The continental abundance maps for these six species of cardueline finches show that all of the species have widespread distributions across North America. None of the study species show clear decreasing population trends on a broad geographic scale. The important information to be gained from these maps, however, is that these six finch species show highly variable distributions and abundances between winters. Finch abundance in boreal regions of Canada and Alaska was shown to be significantly higher

in purple finches, pine siskins, red crossbills and white-winged crossbills in areas with high cone crop abundance. It is this close dependence on conifer seed availability that determines the inter-annual variability in cardueline finch abundance across North America.

This intrinsic link between cone availability and cardueline finch abundance must be considered from a conservation perspective. Although the winter distribution/abundance maps depict species that are reasonably ubiquitous across large tracts of coniferous forests in Canada and the United States, their fluctuating abundances indicate that they are sensitive to food supply limitations. Irruptive finch species have been shown to be most abundant in mature (at least 80 year-old) stands in the Canadian boreal forest (Kirk et al. 1996), presumably because seed availability is lower and cone failures increase in younger age stands (Benkman 1993b; Holimon et al. 1998). Irruptive finches are also vulnerable to forest fragmentation (Helle 1985), as fragments are usually young stands with low cone production. Cardueline finches employ the strategy of nomadism to escape local-level cone shortages, but when conifer seed availability is limited across larger areas, these irruptive movements may not suffice. By adopting a younger rotation age in the boreal forest (Thompson et al. 1999), forestry practices in Canada that are increasingly fragmenting the boreal forest and drastically limiting stands of mature conifers (Imbeau et al. 1999) will negatively impact cardueline finches. A lesson in finch conservation may be gained from Britain, where extensive conifer afforestation over the past century has resulted in increased diversity and abundance of

conifer seed (Marquiss and Rae 1994) and has benefited the formerly rare resident common crossbill (*L. curvirostra*; Avery and Leslie 1990).

The recent decline of the Newfoundland red crossbill provides an example of how loss of conifer seed availability across a region has impacted a taxon of carduelline finch. Although the current population status of *L. c. percna* is unresolved, with Benkman (1989; 1993c) and Pimm (1990) contending that the subspecies has declined to the point of possible extirpation and may only exist on small offshore islands in the absence of competitive exclusion from red squirrels (*Tamiasciurus hudsonicus*), the scenario is not entirely supported by recent Newfoundland CBCs. Table 3-1 lists the locations within Newfoundland that have reported Red Crossbills on CBCs in the past decade. Clearly, there has not been a complete extirpation of the red crossbill on insular Newfoundland. Of the 12 recent Newfoundland CBC red crossbill records, only one (Stephenville) is from the west coast of the island, which suggests that these records may not represent mainland vagrants. Many sightings are from CBCs in central Newfoundland where there are large stands of black spruce and remnant stands of red pine (*Pinus resinosa*; Roberts and Bajzak 1996) and white pine (*Pinus strobus*; English 1998). As with large-billed mainland red crossbill subspecies (Dickerman 1987), the large-billed red crossbill *percna* is expected to be associated with pine stands (Montevecchi et al. in prep.). Presently, there is no direct evidence that mainland red crossbill forms are seen on Newfoundland (J. Groth, pers. comm.).

The decline of the Newfoundland red crossbill cannot be attributed to competitive pressure from introduced red squirrels alone. There is a temporal mismatch in the arrival

of red squirrels and the decline of red crossbills, with red crossbills declining in number before squirrels had reached areas such as Terra Nova National Park (Montevecchi et al. in prep.). Two centuries of logging in Newfoundland have resulted in very restricted stands of pine on the island, which is likely a key conifer seed resource for the large-billed *percna*. Many other stands of mature coniferous forest on the island are becoming increasingly fragmented and exploited by logging (Thompson et al. 1999). These multiple factors, and not solely competitive pressure from red squirrels (cf. Benkman 1993c), are limiting available seed for cardueline finches in Newfoundland.

Another crossbill, the Hispaniolan white-winged crossbill [*Loxia megaplaga* – argued by Smith (1997) to be a distinct species] is endemic to Hispaniola. Its beak is uniquely adapted to foraging on the island's sole native pine, the West Indian pine (*Pinus occidentalis*). Unchecked harvesting and forest clearing has greatly diminished the pine population, and the Hispaniolan crossbill is now presumed to be critically endangered (Benkman 1994; Smith 1997). The declines of the Newfoundland red crossbill and the Hispaniolan crossbill can both be attributed to limitations in conifer seed availability due to habitat alterations. These two species of crossbills are extremely specialized foragers among the cardueline finches, and both are considered to be restricted to living on islands (Benkman 1989), which may make refuge from cone shortages impossible (cf. Dickerman 1987).

These population trends offer an important lesson on how conifer seed limitations can have extreme ecological implications for all boreal cardueline finches, not just crossbills. Despite the widespread continental ranges and the variable responses to seed

resources of the six species examined in this study, their general dependence on conifer seeds and their irruptive ecology makes them sensitive to habitat alterations within the boreal forest.

CONCLUSIONS AND RECOMMENDATIONS

The National Audubon Society Christmas Bird Count provides an invaluable source of long-term and broad-scale bird abundance data for species such as the boreal cardueline finches. Hopefully, the continued use of CBC data will allow researchers to monitor regional and continental population trends in these species. The close link between these cardueline finch species and the availability of conifer seeds means that a declining population trend may be an indication of a decline in the overall health of boreal ecosystems.

The number of CBC counts expands every year, despite the fact that coverage of the continent is generally limited by accessibility and proximity to population centres. Although coverage of boreal regions has improved since 1970, there are still vast tracts of boreal forest that are not censused by bird counts. Additional winter bird count circles in non-fragmented, non-urbanized north boreal regions would further help to illustrate core winter distribution regions in the northern boreal forest, the extent of irruptive movements by cardueline finches, and how cardueline finches may be affected by habitat fragmentation due to forestry pressure in the boreal forest. While the impact of logging in the boreal forest is variable in Canada, 50% of the boreal forest region is under logging tenure, and 30% of it is within a kilometre of a road or access route (Global Forest Watch Canada 2000). In Newfoundland, only 5-10% of the mature boreal forest remains intact (L. Hermanutz, pers. comm.).

The inclusion of wild seed crop ratings with the 1973 – 1985 CBCs was an ambitious undertaking. There are few, if any, other sources of seed crop ratings that exist

on such a scale. Unfortunately, more current CBCs have not included wild seed crop ratings, possibly due to the fact that, in many regions of Canada and the United States, it was difficult to determine exactly what the wild seed crop ratings represented (i.e., grasses, berries, cones, deciduous tree seeds). If CBC participants on counts within the boreal zone were to return to assessing strictly cone crop magnitudes, this would provide a critically important, easily accessible source of data on the periodicity of conifer mast crops and allow researchers to continue to examine the large scale relationship between cardueline finch distributions and abundances and the availability of conifer seeds. This type of data is not available from other sources such as forestry databases; therefore cone assessments done by CBC participants would provide invaluable data.

The continental scale CBC data examined in this study demonstrated a generally biennial pattern of abundance fluctuations in the cardueline finches. The possible decay in the periodic irruptions of purple finches and red crossbills should be further monitored in upcoming years to determine whether it indicates large-scale population decline.

The use of CBC data as a regional monitoring tool in Newfoundland also suggests further conservation initiatives for cardueline finches. When a species such as the Newfoundland red crossbill is in ecological crisis, it is important to make conservation and recovery decisions based on rigorous scientific information. North American red crossbills have been separated into distinct phylogenetic and biological types based on morphology, genetic differentiation, and call note variability. That *L. c. percna* should be considered a distinct species provides an even more compelling reason to prevent the endemic island form from disappearing from Newfoundland. It is important to determine

what subspecies of red crossbill presently occur in Newfoundland to end speculation of its status on the island. This could be accomplished by an analysis of call notes of red crossbills found in Newfoundland, possibly coupled with morphological and genetic studies of individual birds such as has been done by Groth (1993) for the other 7 types of North American red crossbills.

This large temporal and spatial scale study of the distribution and abundance of cardueline finches throughout the North American boreal zone has illustrated the highly variable nature of their winter populations. The correlations between finch abundance and cone crop magnitude shown in this study highlight the need for additional and continued data collection on bird abundance and seed availability within the boreal forest. The Christmas Bird Count is also an effective source of data for long-term monitoring of winter population trends of avian species on a regional level, as illustrated by the population trends of Newfoundland boreal cardueline finches and the evidence of the recent decline of the Newfoundland red crossbill.

LITERATURE CITED

Avery, M. and R. Leslie. 1990. Birds and Forestry. Poyser, London.

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

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

Benkman, C. W. 1990. Intake rates and the timing of crossbill reproduction. Auk 17: 376 - 386.

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

Benkman, C. W. 1993b. Logging, conifers, and the conservation of crossbills. Conservation Biology 7: 473 - 479.

Benkman, C. W. 1993c. The evolution, ecology, and decline of the Red Crossbill of Newfoundland. American Birds 47: 225 - 229.

Benkman, C. W. 1994. Comments on the ecology and status of the Hispaniolan crossbill (*Loxia leucoptera megaplaga*), with recommendations for its conservation. Caribbean Journal of Science 30: 250 - 254.

Bent, A. C. 1912. A new subspecies of crossbill from Newfoundland. Smithsonian Miscellaneous Collections 60: 1 - 3.

Bent, A. C. 1968. Life Histories of North American Grosbeaks, Buntings, Towhees, Finches, Sparrows and Allies. Dover Publications, New York.

Bock, C. E. 1980. Winter bird population trends: scientific evaluation of Christmas Bird Count Data. Atlantic Naturalist 28 - 31.

Bock, C. E. and L. W. Lepthien. 1972. Winter eruptions of Red-breasted Nuthatches in North America, 1950 - 1970. American Birds 26: 558 - 561.

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

Bock, C. E. and T. L. Root. 1981. The Christmas Bird Count and avian ecology. Studies in Avian Biology 6: 17 - 23.

Butcher, G. S., M. R. Fuller, L. S. McAllister, and P. H. Geissler. 1990. An evaluation of the Christmas Bird Count for monitoring population trends of selected species. Wildlife Society Bulletin 18: 129 - 134.

Dawson, D. G. 1981. Counting birds for a relative measure (index) of density. Studies in Avian Biology 6: 12 - 16.

Dawson, W. R. 1997. Pine Siskin. *In* A. Poole and F. Gill (eds.). The Birds of North America, No. 280. American Ornithologists' Union, Washington, DC.

Deviche, P. 1997. Seasonal reproductive pattern of White-winged Crossbills in interior Alaska. Journal of Field Ornithology 68: 613 - 621.

Dickerman, R. W. 1987. The "Old Northeastern" subspecies of Red Crossbill. American Birds 41: 189 - 194.

Drennan, S. R. 1981. The Christmas Bird Count: an overlooked and underused sample. Studies in Avian Biology 6: 24 - 29.

Dunn, E. H. and J. R. Sauer. 1997. Monitoring Canadian bird populations with winter counts. Pp. 49 - 55 *in* Monitoring Bird Populations: The Canadian Experience. Canadian Wildlife Service, Occasional Paper Number 95.

Eastham, A. M. and M. J. Jull. 1999. Factors affecting natural regeneration of *Abies lasiocarpa* and *Picea engelmannii* in a subalpine silvicultural systems trial. Canadian Journal of Forest Research 29: 1847 - 1855.

English, B. 1998. Impact of squirrel predation on white pine cone collection efforts in Newfoundland. Newfoundland Forest Service Silviculture Notebook, No. 42.

Erskine, A. J. 1977. Birds in boreal Canada: communities, densities and adaptations. Canadian Wildlife Service Report Series, No. 41.

Formozov, A. N. 1960. La production de graines dans les forêts de conifères de la taiga de l'U.R.S.S. et l'envahissement de l'Europe occidentale par certaines espèces d'oiseaux. Pp. 216 - 229 *in* G. Bergman, K. O. Donner, and L. V. Haartman (eds.). Proceedings XII Ornithological Congress, vol. 1, Helsinki.

Global Forest Watch Canada. 2000. Canada's Forests at a Crossroads: An Assessment in the Year 2000. World Resources Institute, Washington, D.C.

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

Groth. J. G. 1993. Evolutionary differentiation in morphology. vocalizations. and allozymes among nomadic sibling species in the North American Red Crossbill (*Loxia curvirostra*) complex. University of California Publications in Zoology 127: 1 - 143.

Hahn. T. P. 1995. Integration of photoperiodic and food cues to time changes in reproductive physiology by an opportunistic breeder. the Red Crossbill. *Loxia curvirostra* (Aves: Carduelinae). Journal of Experimental Zoology 272: 213 - 226.

Hahn. T. P.. T. Boswell. J. C. Wingfield. and G. F. Ball. 1997. Temporal flexibility in avian reproduction. Current Ornithology 14: 39 - 80.

Haila. Y. and O. Järvinen. 1990. Northern conifer forests and their bird species assemblages. Pp. 61 - 85 *in* A. Keast (ed.). Biogeography and Ecology of Forest Bird Communities. SPB Publishing. The Hague.

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

Hochachka. W. M.. J. V. Wells. K. V. Rosenberg. D. L. Tessaglia-Hymes. and A. A. Dhondt. 1999. Irruptive migration of Common Redpolls. Condor 101: 195 - 204.

Holimon. W. C.. C. W. Benkman. and M. F. Willson. 1998. The importance of mature conifers to red crossbills in southeast Alaska. Forest Ecology and Management 102: 167 - 172.

Houston. C. S. and Smith. A. R. 2000. Biennial redpoll invasions of Saskatchewan and Manitoba. Abstract. 118th Meeting of the American Ornithologists' Union. St. John's. Newfoundland.

Imbeau. L.. J.-P. L. Savard. and R. Gagnon. 1999. Comparing bird assemblages in successional black spruce stands originating from fire and logging. Canadian Journal of Zoology 77: 1850 - 1860.

Ives. A. R. and E. D. Klopper. 1997. Spatial variation in abundance created by stochastic temporal variation. Ecology 78: 1907 - 1913.

Kirk. D. A.. A. W. Diamond. K. A. Hobson. and A. R. Smith. 1996. Breeding bird communities of the western and northern Canadian boreal forest: relationship to forest type. Canadian Journal of Zoology 74: 1749 - 1770.

Koenig. W. D. and J. M. H. Knops. 1998. Scale of mast-seeding and tree-ring growth. Nature 396: 225 - 226.

Land Cover of Canada. 1999. Canada Centre for Remote Sensing. Geomatics Canada. Earth Sciences Sector. Natural Resources Canada. National Atlas of Canada Reference Map Series.

Larson. D. L. and C. E. Bock. 1986. Eruptions of some North American boreal seed-eating birds. 1901-1980. Ibis 128: 137 - 140.

Link. W. A. and J. R. Sauer. 1997. New approaches to the analysis of population trends in land birds: comment. Ecology 78: 2632 - 2634.

Link. W. A. and J. R. Sauer. 1998. Estimating population change from count data: application to the North American Breeding Bird Survey. Ecological Applications 8: 258 - 268.

Link. W. A. and J. R. Sauer. 1999. Controlling for varying effort in count surveys - an analysis of Christmas Bird Count data. Journal of Agricultural. Biological. and Environmental Statistics 4: 116 - 125.

MapInfo Professional 5.0. 1998. MapInfo Corporation. New York.

Marquiss. M. and R. Rae. 1994. Seasonal trends in abundance. diet and breeding of Common Crossbills (*Loxia curvirostra*) in an area of mixed species conifer plantation following the 1990 crossbill 'irruption'. Forestry 67: 31 - 47.

Matlab 5.3. 1999. Mathworks Inc.. Natick. MA.

McCrimmon. D. A.. Jr.. S. T. Fryska. J. C. Ogden. and G. S. Butcher. 1997. Nonlinear population dynamics of six species of Florida Ciconiiformes assessed by Christmas Bird Counts. Ecological Applications 7: 581 - 592.

McDonald. P. M. 1992. Estimating seed crops of conifer and hardwood species. Canadian Journal of Forest Research 22: 832 - 838.

Montevecchi. W. A.. Steele. D. H.. Thompson. I. D.. and Mosseler. A. In prep. Crossbills. cones and squirrels in Newfoundland: competitive exclusion or boreal forest degradation?

National Geographic Society. 1999. Field Guide to the Birds of North America. Edition 3. National Geographic Society. Washington. D.C.

Newton. I. 1972. Finches. Collins. London.

Owens. J. N. and M. D. Blake. 1985. Forest tree seed production. Canadian Forestry Service. Petawawa National Forestry Institute. Report PI-X-53.

Patterson. I. J., J. G. Ollason. and P. Doyle. 1995. Bird populations in upland spruce plantations in northern Britain. Forest Ecology and Management 79: 107 - 131.

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

Reinikainen. A. 1937. The irregular migrations of the crossbill. *Loxia c. curvirostra*. and their relation to the cone-crop of the conifers. Ornis Fennica 14: 55 - 64.

Roberts. B. A. and D. Bajzak. 1996. Site characteristics. growth and nutrition of natural red pine stands in Newfoundland. Environmental Monitoring and Assessment 39: 509 - 530.

Root. T. 1988. Atlas of Wintering North American Birds: An Analysis of Christmas Bird Count Data. University of Chicago Press. Chicago.

Silvertown. J. W. 1980. The evolutionary ecology of mast seeding in trees. Biological Journal of the Linnean Society 14: 235 - 250.

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

Smith. P. W. 1997. The history and taxonomic status of the Hispaniolan Crossbill *Loxia megaplaga*. Bulletin of the British Ornithologists' Club 117: 264 - 271.

Sokal. R. R. and F. J. Rohlf. 1995. Biometry. Edition 3. W. H. Freeman and Company. New York.

Summers. R. W. 1999. Numerical responses by crossbills *Loxia* spp. to annual fluctuations in cone crops. Ornis Fennica 76: 141 - 144.

The 87th Christmas Bird Count. 1987. American Birds 41: 583 - 1321.

The 88th Christmas Bird Count. 1988. American Birds 42: 567 - 1162.

The 89th Christmas Bird Count. 1989. American Birds 43: 607 - 1201.

The 90th Christmas Bird Count. 1990. American Birds 44: 547 - 1037.

The eightieth Audubon Christmas Bird Count. 1980. American Birds 34: 355 - 681.

The eighty-fifth Christmas Bird Count. 1985. American Birds 39: 427 - 823.

The eighty-first Audubon Christmas Bird Count. 1981. American Birds 35: 382 - 749.

The eighty-fourth Audubon Christmas Bird Count. 1984. American Birds 38: 433 - 830.

The eighty-second Audubon Christmas Bird Count. 1982. American Birds 36: 404 - 778.

The eighty-sixth Christmas Bird Count. 1986. American Birds 40: 607 - 1032.

The eighty-third Audubon Christmas Bird Count. 1983. American Birds 37: 409 - 792.

The ninety-first Christmas Bird Count. 1991. American Birds 45: 551 - 1022.

The ninety-second Christmas Bird Count. 1992. American Birds 46: 539 - 1047.

The seventieth Christmas Bird Count. 1970. Audubon Field Notes 24: 101 - 464.

The seventy-eighth Audubon Christmas Bird Count. 1978. American Birds 32: 447 - 911.

The seventy-fifth Audubon Christmas Bird Count. 1975. American Birds 29: 178 - 602.

The seventy-first Christmas Bird Count. 1971. American Birds 25: 131 - 514.

The seventy-fourth Christmas Bird Count. 1974. American Birds 28: 165 - 556.

The seventy-ninth Audubon Christmas Bird Count. 1979. American Birds 33: 353 - 687.

The seventy-second Christmas Bird Count. 1972. American Birds 26: 147 - 530.

The seventy-seventh Audubon Christmas Bird Count. 1977. American Birds 31: 428 - 909.

The seventy-sixth Audubon Christmas Bird Count. 1976. American Birds 30: 182 - 633.

The seventy-third Christmas Bird Count. 1973. American Birds 27: 155 - 540.

Thompson. I. D., H. A. Hogan. and W. A. Montevecchi. 1999. Avian communities of mature balsam fir forests in Newfoundland: age-dependence and implications for timber harvesting. Condor 101: 311 - 323.

Troy. D. M. 1983. Recaptures of redpolls: movements of an irruptive species. Journal of Field Ornithology 54: 146 - 151.

Ulfstrand. S. 1963. Ecological aspects of irruptive bird migration in northwestern Europe. Proceedings of the 13th International Ornithological Congress: 780 - 794.

Veit. R. R. and M. A. Lewis. 1996. Dispersal. population growth. and the Allee effect: Dynamics of the house finch invasion of eastern North America. American Naturalist 148: 255 - 274.

Verner, J. 1985. Assessment of counting techniques. Current Ornithology 2: 247 - 302.

Virkkala, R. 1991. Spatial and temporal variation in bird communities and populations in north-boreal coniferous forests: a multiscale approach. Oikos 62: 59 - 66.

Widrlechner, M. P. and S. K. Dragula. 1984. Relation of cone-crop size to irruptions of four seed-eating birds in California. American Birds 38: 840 - 846.

Wiens, J. A. 1981. Scale problems in avian censusing. Studies in Avian Biology 6: 513 - 521.

Willson, M. F. and T. Comet. 1996. Bird communities of northern forests: patterns of diversity and abundance. Condor 98: 337 - 349.

APPENDICES

Appendix 3-1 – CBC circles in boreal/coniferous habitat used to examine the relationship between finch abundance and cone crop magnitude. Land cover classifications for Canadian points from Land Cover of Canada Map (1999): evergreen needleleaf forest: forest containing more than 80% needleleaf trees; mixed intermediate forest: forest containing 40 – 60% evergreen needleleaf trees: mixed broadleaf forest: forest containing more than 60% deciduous broadleaf trees; transition treed shrubland: land with tree crown density below 10%, found primarily in northern boreal forests; wetland/shrubland: land covered mainly by low to intermediate woody shrubs; shrub and lichen dominated: barren land with shrubs and lichen as dominant cover type.

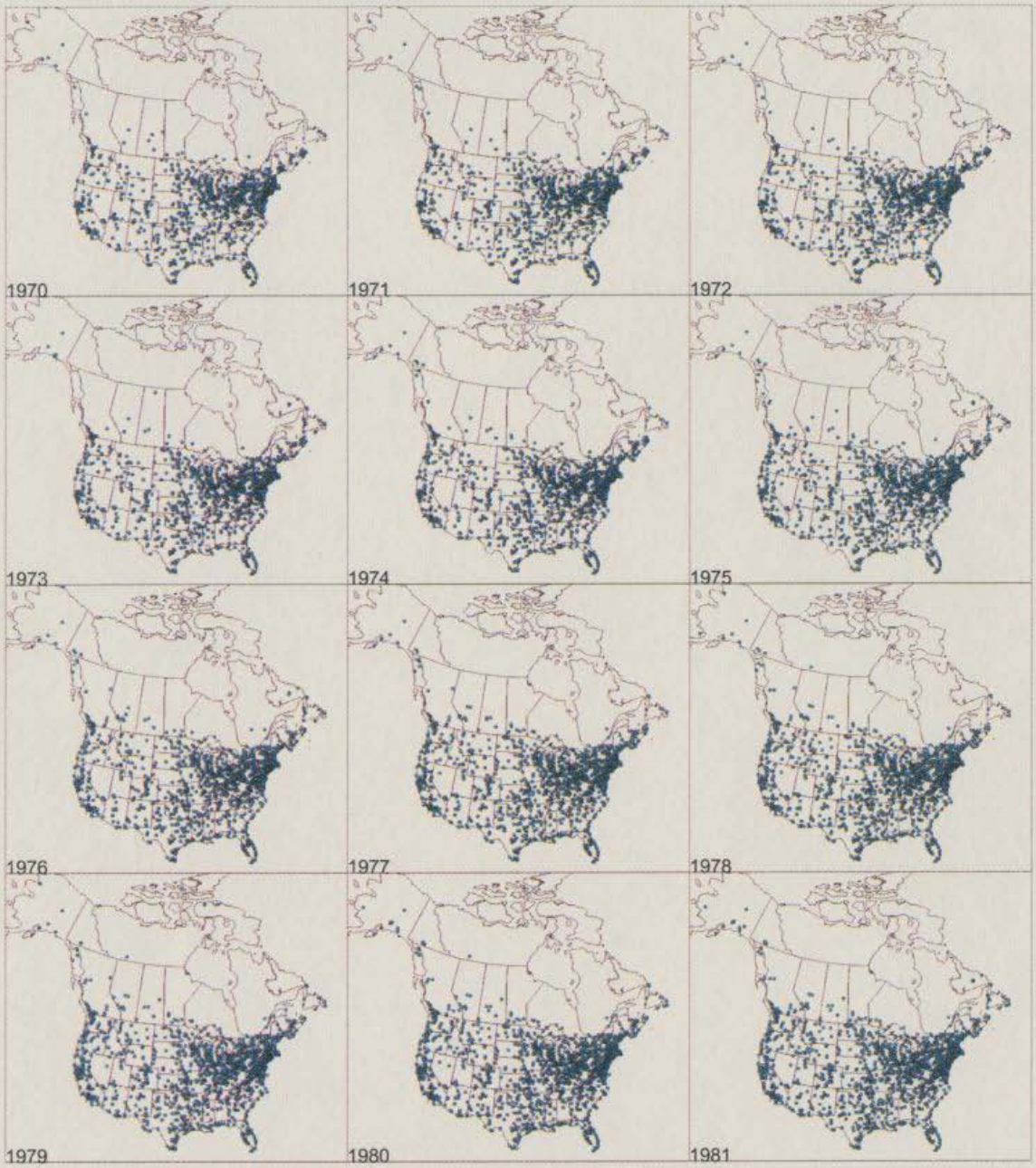
Location	Habitat Description 1. CBC 2. Land Cover of Canada Classification
Cape St. Mary's, NF	1. 5% boreal forest 2. Medium density wetland shrubland
Corner Brook, NF	1. 22% coniferous forest 2. Mixed intermediate forest
Gros Morne National Park, NF	1. 35% mixed boreal forest 2. Mixed intermediate/low density evergreen needleleaf forest
Happy Valley-Goose Bay, LAB	1. 25% spruce woodland 2. Medium density evergreen needleleaf forest
Cartwright, LAB	1. 8% forest 2. Medium density evergreen needleleaf forest/wetland/shrubland
L'Anse aux Meadows, NF	1. 10% forest 2. Low density evergreen needleleaf forest/wetland shrubland
St. Anthony, NF	1. 15% coniferous woodland 2. Low density evergreen needleleaf forest/wetland shrubland
St. John's, NF	1. 28% coniferous woodlands and barrens 2. Mixed intermediate low density evergreen needleleaf forest/wetland/shrubland
St. Paul's/Cow Head, NF	1. 30% boreal forest 2. Mixed intermediate evergreen needleleaf /wetland/shrubland
Terra Nova National Park, NF	1. 25% coniferous forest 2. Medium/low density southern evergreen needleleaf forest
Baie-Comeau, PQ	1. 40% coniferous forest 2. Mixed intermediate/low density southern evergreen needleleaf forest

Cap-Chat - Ste. Anne des Monts, PQ	1. 10% coniferous forest 2. Mixed intermediate low density southern evergreen needleleaf forest
Forillon National Park, PQ	1. 8% evergreen forest 2. Mixed intermediate/broadleaf forest
Tadoussac, PQ	1. 25% mixed boreal forest 2. Mixed intermediate forest
Algonquin Provincial Park, ON	1. 40% coniferous woodland 2. Mixed intermediate/broadleaf forest
Atikokan, ON	1. 50% forested 2. Evergreen needleleaf southern/mixed intermediate forest
Cochrane, ON	1. 30% forested 2. Low density evergreen needleleaf southern mixed intermediate forest
Dryden, ON	1. 35% woodland 2. Southern evergreen needleleaf mixed intermediate forest
Hearst, ON	1. 50% forested 2. Mixed intermediate forest
Ignace, ON	1. 60% upland boreal forest, 5% lowland boreal forest 2. Southern evergreen needleleaf mixed intermediate forest
Kenora, ON	1. 20% forested 2. Southern evergreen needleleaf forest
Morson, ON	1. 79% woodlands 2. Mixed intermediate forest
North Bay, ON	1. 15% coniferous forest 2. Mixed intermediate/broadleaf forest
Sudbury, ON	1. 19% forested 2. Low density southern evergreen needleleaf/mixed intermediate forest
Thunder Bay, ON	1. 46% woodlands 2. Mixed broadleaf/intermediate forest
Vermillion Bay, ON	1. 35% forested 2. Medium density southern evergreen needleleaf mixed intermediate forest
Churchill, MB	1. 40% boreal forest 2. Transition treed shrubland/northern evergreen needleleaf forest
Pinawa – Lac du Bonnet, MB	1. 60% mixed boreal forest, 15% spruce forest 2. Low density southern evergreen needleleaf/mixed intermediate forest
Prince Albert National Park, SK	1. 25% coniferous forest 2. Medium/low density southern evergreen needleleaf/mixed intermediate forest
Squaw Rapids, SK	1. 80% mixedwood forest 2. Low density southern evergreen needleleaf forest
Banff – Canmore, AB	1. 75% woodland 2. Southern evergreen needleleaf forest/wetland/shrubland/heather

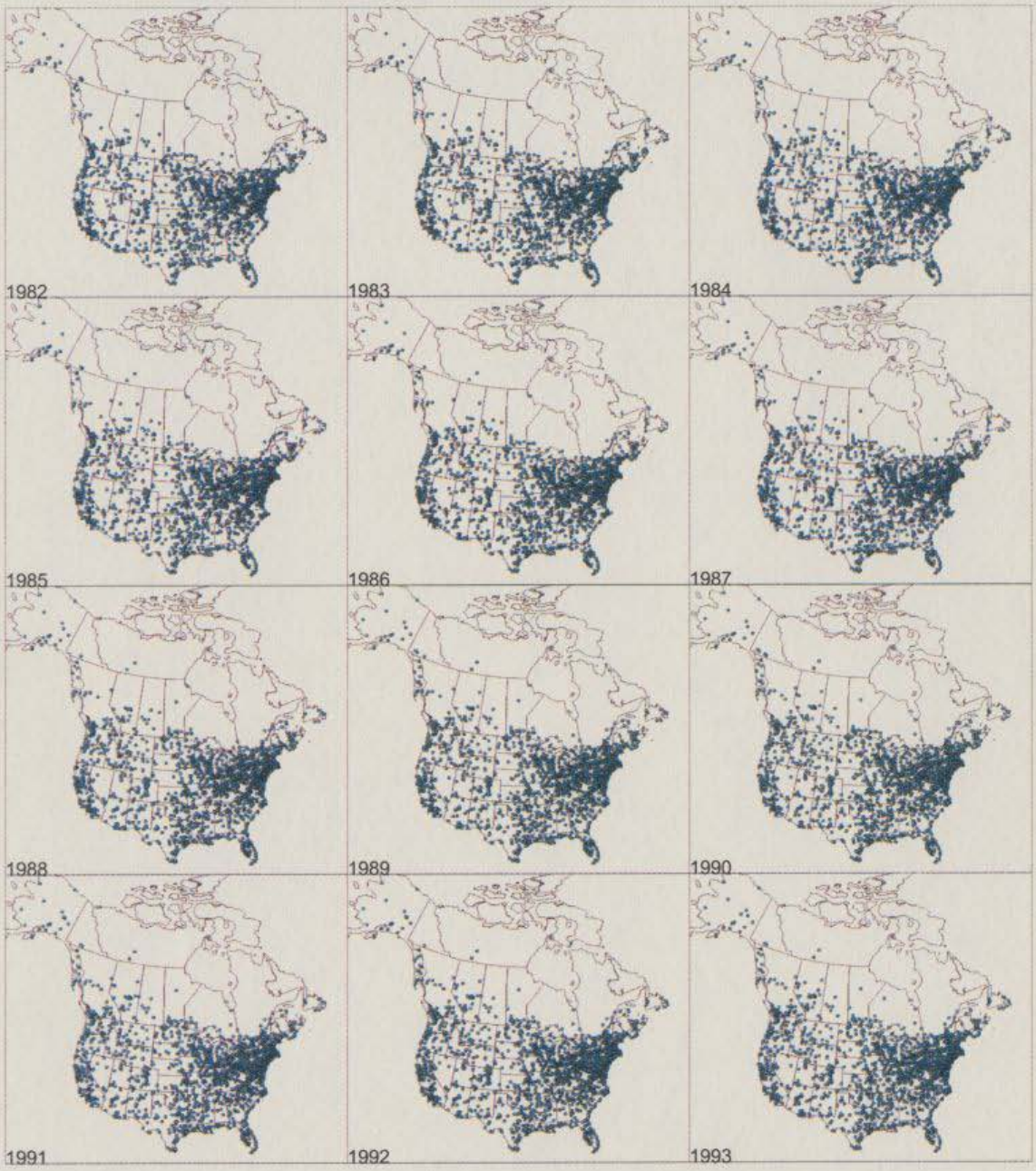
Bow Summit, AB	1. 63% coniferous woodland 2. Southern evergreen needleleaf forest/heather
Fort McMurray, AB	1. 45% forested 2. Mixed broadleaf/intermediate/southern evergreen needleleaf forest
Jasper, AB	1. 75% montane forest 2. Southern evergreen needleleaf forest/wetland/shrubland/heather
Kananaskis Valley, AB	1. 80% lodgepole pine-spruce-fir forest 2. Southern evergreen needleleaf/mixed intermediate forest
Wildlife Reserve of Western Canada, AB	2. Southern evergreen needleleaf/mixed intermediate forest
Hay River, NWT	1. 65% coniferous forest 2. Northern evergreen needleleaf forest
Yellowknife, NWT	1. 30% black spruce-tamarack forest 2. Northern evergreen needleleaf forest
Marsh Lake – Yukon River, YT	1. 50 % forested 2. Medium density evergreen needleleaf forest/wetland/shrubland
Whitehorse (north), YT	1. 40 % woodland 2. Shrubland/wetland/lichen/low density evergreen needleleaf forest
Whitehorse (south), YT	1. 60 % boreal forest 2. Shrubland/wetland/lichen/low density evergreen needleleaf forest
Campbell River, BC	1. 9% coniferous forests 2. Mixed needleleaf/intermediate forest
Chilliwack, BC	1. 20% wooded 2. Mixed intermediate deciduous broadleaf forest
Comox, BC	1. 10% mixed woods 2. Mixed needleleaf/intermediate forest
Cranbrook, BC	1. 20% woodland 2. Southern evergreen needleleaf/mixed intermediate forest
Deep Bay, BC	1. 25% forested 2. Mixed needleleaf/intermediate forest
Duncan, BC	1. 45% coniferous mountains 2. Mixed/medium density evergreen needleleaf forest
Fauquier, BC	1. 30% woodland 2. Medium density southern evergreen needleleaf forest
Kamloops, BC	1. 35% ponderosa pine-Douglas fir forest 2. Southern evergreen needleleaf/mixed intermediate forest
Kelowna, BC	1. 30% woodland 2. Southern evergreen needleleaf forest
Kitimat, BC	1. 20% forested 2. Mixed intermediate forest/wetland/shrubland
Lake Windermere, BC	1. 50% woodland 2. Southern evergreen needleleaf forest/wetland/shrubland/heather
Mackenzie, BC	1. 60% spruce-aspen woodlands 2. Mixed intermediate heterogeneous/low density evergreen needleleaf forest
Masset, BC	1. 2.5% coniferous forest 2. Mixed intermediate/broadleaf forest

Nakusp, BC	1. 60% woodland 2. Mixed intermediate forest
Nanaimo, BC	1. 10% coniferous woods 2. Mixed intermediated/medium density evergreen needleleaf forest
North Pine, BC	1. 5% coniferous forest 2. Mixed intermediate forest
Oliver, BC	1. 21% pine-fir forest 2. Southern evergreen needleleaf/mixed intermediate forest
Pender Islands, BC	1. 45% coniferous mountains 2. Medium density southern evergreen/mixed needleleaf forest
Penticton, BC	1. 25% ponderosa pine, 7% Douglas fir forests 2. Low/medium density southern evergreen needleleaf forest
Pitt Meadows, BC	1. 20% woodland 2. Mixed intermediate broadleaf forest
Port Clements, BC	1. 20% coniferous forest 2. Mixed needleleaf/intermediate forest
Prince Rupert, BC	1. 10% forested 2. Mixed intermediate southern evergreen needleleaf forest
Quesnel, BC	1. 60% Douglas fir – white spruce – lodgepole pine hills 2. Mixed needleleaf intermediate forest
Revelstoke, BC	1. 50% woodland 2. Mixed intermediate heterogeneous forest/wetland shrubland
Sayward, BC	1. 25% mixed wood, 5% coniferous wood 2. Mixed intermediate heterogeneous forest
Skidegate Inlet, BC	1. 5% coniferous forest 2. Mixed intermediate/needleleaf forest
Shuswap Lake Provincial Park, BC	1. 35% woodland 2. Mixed intermediate/deciduous broadleaf forest
Smithers, BC	1. 30% mixed forest, 5% closed coniferous forest 2. Medium density southern evergreen needleleaf/mixed intermediate forest
Sooke, BC	1. 36% woodland 2. Mixed intermediate southern evergreen needleleaf forest
Squamish, BC	1. 37% mainly coniferous forest 2. Mixed intermediate broadleaf forest
Sunshine Coast, BC	1. 32% mainly coniferous forest 2. Mixed intermediate forest
Terrace, BC	1. 35% coniferous forest 2. Mixed intermediate/deciduous broadleaf forest
Vancouver, BC	1. 11% coniferous forest 2. Mixed intermediate medium density evergreen needleleaf forest
Vaseux Lake, BC	1. 35% ponderosa pine – Douglas fir forest 2. Medium/low density southern evergreen needleleaf forest
Vernon, BC	1. 30% montane and subalpine forest 2. Southern evergreen needleleaf/mixed intermediate forest
Victoria, BC	1. 15% coniferous forest 2. Mixed/medium density evergreen needleleaf forest

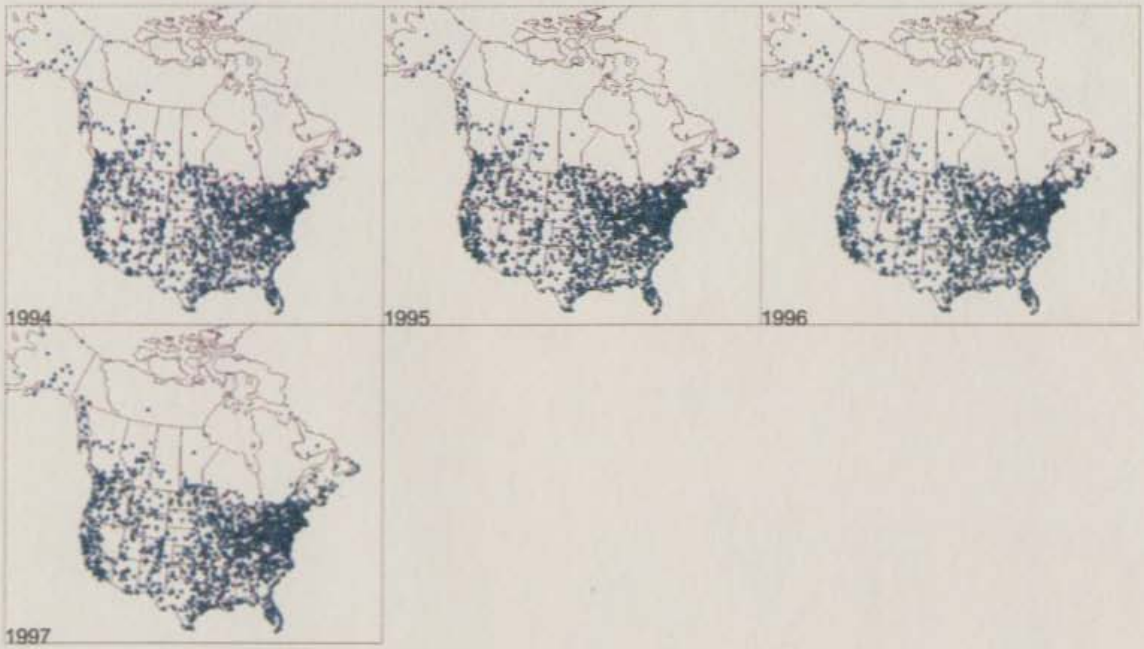
Wells Gray Provincial Park, BC	1. 80% mixed montane forest 2. Mixed intermediate/southern evergreen needleleaf forest
Yoho National Park, BC	1. 70% valley bottom, 30% subalpine forest 2. Southern evergreen needleleaf forest/wetland/shrubland/heather
Anchorage, AK	1. 20% spruce-birch-alder forest, 4% black spruce bog
Cordova AK	1. 20% forests and brushlands
Craig, AK	1. 15% coniferous forest
Eagle River, AK	1. 50% mixed woodlands
Fairbanks, AK	1. 40% mixed spruce-birch-aspen forests
Galena, AK	1. 20% spruce forest
Glacier Bay, AK	1. 20% spruce forest
Haines, AK	1. 15% hillside forest
Homer, AK	1. 15% mixed woodlands
Izembek National Wildlife Refuge, AK	
Juneau, AK	1. 10% mixed woodlands
Kenny Lake, AK	1. 26% spruce woods
Klukwan, AK	1. 30% forested
Kodiak, AK	1. 15% spruce – alder forest
Matanuska Valley, AK	1. 36% forested
Moose Pass, AK	1. 80% deciduous – spruce lowlands, 10% spruce – hemlock forest
Narrow Cape – Kalsin Bay, AK	1. 7% spruce forest
Sanningaruq, AK	1. 50% white spruce-willow forest
Seward, AK	1. 15% spruce – hemlock forest, 5% deciduous – spruce lowlands
Sitka, AK	1. 25% woodlands
Soldotna, AK	1. 50% mixed woodlands
Tok, AK	1. 60% spruce forest
Yakutat, AK	1. 35% old growth forest



Appendix 3-2 – Locations of North American CBC circles, 1970 - 1997



Appendix 3-2 (continued) – Locations of North American CBC circles, 1970 - 1997



Appendix 3-2 (continued) – Locations of North American CBC circles, 1970 - 1997

Chapter 4

SUMMARY AND CONCLUSIONS

The biogeography of boreal cardueline finches is linked to conifer seed resources at the scale of local forest stands, regional landscapes, and continental expanses. At the stand level in insular Newfoundland, the abundance of pine grosbeaks, pine siskins and white-winged crossbills was variable between forests of differing conifer composition. Seed availability and phenology, assessed by measuring seed rain, were also variable between the different stands. The distribution and abundance of the non-native red squirrels in Newfoundland forest stands was closely linked to black spruce forests. Cardueline finch abundance was high in the balsam fir forest, where possible competitive effects from red squirrels were lower than the black spruce or mixed coniferous forest. This is an important finding, as large tracts of Newfoundland's mature balsam fir forest are under pressure from extensive clear-cut logging activity.

On a continental scale, abundances of cardueline finches from Christmas Bird Count data were spatially and temporally variable. Common redpoll, pine grosbeak, pine siskin, purple finch, red crossbill and white-winged crossbill abundances fluctuated between years, with some interspecific synchrony in high counts, many of which occurred in even numbered years. A trend of increasing finch abundance at Christmas Bird Count locations that reported a high cone crop magnitude was significant for four of the finches studied.

Long time-scale studies of boreal cardueline finches at Newfoundland Christmas Bird Count locations revealed that finch abundance is variable and sporadic in boreal

habitats across the island. These large temporal scale data provide an effective tool for monitoring the regional population status of boreal cardueline finches. An example of this is the recent decline of the Newfoundland subspecies of red crossbill, which is evident in examining long-term population trends from Newfoundland Christmas Bird Counts.

The small and large scale relationships between cardueline finches and boreal conifer seed availability renders these finches significant indicators of the general health of boreal landscapes. This study, which incorporated both field-based assessments of avian abundance on local scales and population studies from long-term data on regional and continental scales, illustrates an effective framework for monitoring the biogeography of cardueline finches, and, more broadly, their response to habitat changes within the boreal ecosystem.