Seed-crop size and eruptions of North American boreal seed-eating birds

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Summary

1. Eruptions occur when a species appears in unusually high densities within and often outside of its normal range. We used 30 years of Christmas Bird Counts combined with cone/seed-crop data on boreal coniferous trees, breeding bird surveys, and weather records to test correlates of winter eruptions by 11 species of primarily boreal North American seed-eating birds.

2. Eruptions of six species in eastern (red-breasted nuthatch Sitta canadensis L., black-capped chickadee Parus atricapillus L., evening grosbeak Hesperiphona vespertina Cooper, pine grosbeak Pinicola enucleator L., red crossbill Loxia curvirostra L. and bohemian waxwing Bombycilla garrulus L.) and five species in western North America (pine grosbeak, pine siskin Carduelis pinus Wilson, evening grosbeak, bohemian waxwing and red-breasted nuthatch) correlated with a combination of large coniferous seed crops in the previous year followed by a poor crop. Breeding population size in the year of the eruption was also correlated positively with the event in two of the species. Eruptions in these species apparently occur when large boreal seed crops resulting in high population densities (via high overwinter survivorship and/or high reproductive success) are confronted with a relatively poor seed crop the next autumn.

3. Eruptions of common redpolls Carduelis flammea L. and black-capped chickadees in the west followed only large seed crops the previous year, suggesting that high density is a more important factor leading to eruptions than seed crop failure. The opposite was true for white-winged crossbills (Loxia leucoptera Gmelin) in the east, where eruptions correlated only with poor current year seed crops. This was the only species supporting the ‘seed-crop failure’ hypothesis as the sole cause of eruptions.

4. Purple finches Carpodacus purpureus Gmelin erupted following years when breeding population densities were high for reasons apparently unrelated to the seed crop. Eruptions of three species in both regions were uncorrelated with any of the variables tested.

5. We conclude that seed crops of boreal trees play a pivotal role in causing eruptions for a majority of boreal species, usually through a combination of a large seed crop resulting in high population densities followed by a poor seed crop rather than seed-crop failure alone. Weather conditions were not a significant factor correlating with eruptions in any of the species.

Key-words: boreal birds, population eruptions, population synchrony, seed production, spatial autocorrelation.

Introduction

Eruptive invasions of boreal seed-eating birds can be dramatic events, with birds appearing in large numbers in areas far outside of their normal range. In North America, eruptions generally occur in the autumn with birds returning in the spring, and appear to be more closely allied to normal winter migration than to nomadism (Hochachka et al. 1999). Unlike normal migratory movements, however, they are irregular in frequency and do not occur every winter.
Two major hypotheses have been proposed to explain eruptions. First, the ‘seed-crop failure’ hypothesis suggests that the widespread failure of conifer and other tree seed crops results in birds moving to sites potentially outside of their normal range in search of food. The alternative, ‘population density’ hypothesis suggests that eruptions occur when populations are unusually large due to high winter survival and/or an unusually successful breeding season.

Numerous authors have proffered support for the seed-crop failure hypothesis for one or more species, including Reinkainen (1937), Formozov (1960), Svardson (1957), Davis & Williams (1957, 1964), Evans (1966), Eriksson (1970) and, most impressively, Bock & Lepthien (1976), who reported evidence that eruptions of boreal seed-eating birds were inversely dependent on what was apparently a circumboreally synchronized pattern of seed crop fluctuations in boreal trees. Support for the population density hypothesis has also been substantial, with several authors concluding that high densities are at least an important predisposing factor for eruption events (Lack 1954; Ulfstrand 1963; Newton 1970, 1972; Van Gasteren et al. 1992).

The critical prediction of the seed-crop failure hypothesis is that there should be a negative correlation between the current seed crop and eruption events. Testing the population density hypothesis is not as straightforward. Because the occurrence of eruptions is generally judged by the presence of relatively large numbers of birds in and beyond their normal wintering range, any direct relationship between eruptions and winter population density will invariably be circular. Consequently, we assume that large seed crops are likely to result in relatively high population densities via increased survivorship and/or reproductive success, and test the indirect prediction that population eruptions should be preceded by a large seed crop the previous year. In some cases, high population densities may be directly detectable by independent estimates obtained during the previous breeding season, and might also be suggested by environmental conditions favourable for breeding.

The seed-crop failure and population density hypotheses are not mutually exclusive. Indeed, it is likely that eruptions might be most dramatic when a large seed crop leading to high population densities is followed by a seed crop failure forcing the unusually large numbers of birds present to search for food in areas beyond their normal wintering range, in which case eruptions result from a combination of the two hypotheses (Lack 1954; Newton 1972).

Our analyses extend the previous work of Bock & Lepthien (1976). There are at least two reasons why such a reanalysis is appropriate. First, thanks to efforts by the Laboratory of Ornithology at Cornell University and the National Biological Service, many more years of Christmas Bird Count (CBC) data are now available than those computerized painstakingly by Bock & Lepthien (1976). Similarly, both environmental data and data from the North American Breeding Bird Survey (BBS) are now readily available. Secondly, Bock & Lepthien (1976) did not make a concerted effort to obtain seed production data by boreal trees, and it is thus desirable to re-examine their conclusions in light of a more extensive (and independent) database.

**Methods**

**Winter Bird Data**

We considered 11 species of primarily boreal seed-eating birds including the evening grosbeak, pine grosbeak, purple finch, red crossbill, white-winged crossbill, hoary redpoll (Carduelis hornemanni Holböll), common redpoll, pine siskin, bohemian waxing, red-breasted nuthatch and black-capped chickadee. The most commonly eaten items in the winter diet of these species are summarized in Table 1. Although they vary considerably in their dietary preferences, all are dependent primarily on seeds in the winter, usually but not always of boreal trees, with the exception of black-capped chickadees, which eat a mixture of seed and insects in winter.

CBC data on these species spanning 30 years between the winters of 1959–60 and 1988–89 were downloaded from the database maintained by the National Biological Service. Files were used as given except that counts that did not overlap in time and were within 3 min of both latitude and longitude were assumed to be continuations of the same site and combined. For all species × site combinations, birds per party hour were determined for each year the count was performed. These values (x) were log-transformed (log(x + 1)). This procedure tends to normalize the distributions and makes intuitive sense: the difference between observing 1 and 10 birds per party hour (pph) is more comparable to the difference between observing 10 and 100 birds pph than the difference between observing 91 and 180 birds pph. In all, we analysed data from 31 445 counts conducted at 2250 sites spread out over all but a handful of states and Canadian provinces (Fig. 1). We then removed any long-term trend in numbers at each site by using the residuals from a regression of (log-transformed) birds pph on year (Koenig 1999).

As an index of eruptions, we then determined the proportion of sites in each year at which more than the expected number of birds of each species (after remov- ing the long-term trend) was counted (i.e. the residual of the number of birds pph on year was positive). Data were divided into two geographical regions separated by the eastern edge of the Rocky Mountains (hereafter ‘eastern’ and ‘western’ North America; Fig. 1), because of the distinct differences between eastern North America and the western montane regions found by Bock & Lepthien (1976). Analyses were performed within regions (i.e. western seed crop vs. eruption index in the west) to detect north/south movements. However, at least some boreal species, including common and hoary redpolls (Troy 1983), have been documented making west/east...
movements, and thus we also performed analyses across regions (i.e. western seed crop vs eruption index in the east). In order to focus on years in which relatively large numbers of birds wintered outside their usual more northern range, we restricted the CBC data to sites < 50°N latitude.

**BREEDING BIRD DATA**

As estimates of density in the spring prior to eruptions, we used data collected between 1968 and 1996 for the 11 focal species from the North American Breeding Bird Survey (BBS) programme (ftp://ftp.nbs.gov/pub/data/bbs). Results from 8276 sites, representing the number of birds seen or heard during a standardized census at the site during the spring breeding season, were log-transformed and standardized. The proportion of sites yielding greater than the expected (log-transformed) number of birds of the focal species in a particular year (after removing any long-term trend at the site) determined. This index of relative density was calculated for the two geographical regions of North America and for both < 50°N and > 50°N latitude. Insufficient data were available for either hoary redpolls or bohemian waxwings for analysis.

**BOREAL SEED PRODUCTION DATA**

Data on boreal tree seed and/or cone production were obtained from Koening & Knops (2000). Only sites with at least 5 years of data were used. In all, we used 163 data sets on seven genera of North American coniferous boreal trees from 28 different sources, yielding a total of 1923 years of data between 1900 and 1993 (Fig. 1). Genera used in the analyses included Abies, Larix, Picea, Pinus, Pseudotsuga, Tsuga and Thuja. Analyses were conducted by combining all coniferous genera and for the genus Pinus by itself. Insufficient data were available to separate out any of the other genera of boreal trees.

Seed and cone production data were originally collected in a wide variety of ways. In order to allow comparisons across studies, they were standardized as follows. If the seed production data were categorical, we ranked the categories in order of increasing crop size, giving the highest category a 10, the lowest category a 0, and making the difference between all intermediate categories equal. For example, if only three categories were used (i.e. good, fair and poor), years when the crop was rated as good were given a 10, those in which the crop was rated as fair were given a 5; and those in which it was rated as poor were given a 0. Categories were divided more finely, but still equally, if more than three categories were used (i.e. excellent, very good, good, fair, poor, very poor), ratings were assigned the values 10, 8, 6, 4, 2 and 0, respectively. If values presented were interval or ratio-level data, such as the actual counts or number of acorns falling in traps, values were log-transformed.

As with the bird census data, we then determined the proportion of sites for which the seed crop in a particular year was above the overall mean, dividing the data into eastern and western North America as above. Analyses were conducted by combining all coniferous genera and for the genus Pinus by itself. Insufficient data were available to separate out any of the other genera of boreal trees.
also included the proportion of sites with above-average seed production in the prior year (current year seed production lagged 1 year).

These data represent a nearly comprehensive synthesis of all published conifer seed or cone production data available for North America (Koenig & Knops 2000). Even so, the data are far more limited in the variety of the weather variables considered. The CV in the proportion of sites reporting greater than the expected number of birds in a particular year. For a comparison with related species not usually considered to erupt, we contrasted these data with annual variability of house finches (Carpodacus mexicanus Müller) (not measured in the east, where numbers increased dramatically over the time period considered), American goldfinches (Carduelis tristis L.), lesser goldfinches (C. psaltria (Müller)) and chestnut-backed chickadees (Parus rufescens Townsend) not present in the area.

Because of limitations of the seed production data, it proved unfeasible to perform multivariate analyses with all the relevant variables considered simultaneously. Consequently, we calculated Spearman rank correlations between the eruption index and the independent variables separately. Because of the limitations of the seed-crop data, we set \( P > 0.05 \) (one-tailed) for tests involving these data. With analyses performed on each species for eastern and western North America both above and below 50°N latitude in the east), a total of 308 tests involving the seed-crop data yielded an expected three significant results at the 0.01 level and an additional 12 at the 0.05 level by chance alone. This complication is considered further below.

For comparative purposes, we also report correlations producing \( P < 0.05 \) for tests involving the BBS data. With 72 such tests (two for each species in eastern and western North America except for hoary redpolls and bohemian waxwings), four of these are expected to be significant by chance alone. Given their more exploratory nature, we set \( \alpha = 0.01 \) for tests involving the weather variables. With a total of 352 correlations, four are again expected to be significant by chance at this level.

Results

Environmental Variables

Monthly rainfall and mean temperature were obtained from the National Oceanic and Atmospheric Administration website (http://tpub.nrc. noaa.gov/pub/data/ghcn).

Two time periods were considered: winter, from 1 October to 31 December of the current year, and summer, from 1 April to 31 July of the current year. Variables considered included total rainfall and mean daily temperature. As with the previous data, values were standardized by using the residuals of a regression on year (within sites) in order to eliminate long-term trends. We then determined the proportion of sites at which the total precipitation or mean temperature was greater than the expected value, dividing the data into eastern and western North America as defined above. We also divided data into sites > 50°N latitude and < 50°N latitude with the goal of including effects potentially attributable to either conditions in the more northern breeding ranges or the more southern wintering ranges of the species considered.

Overall, sample sizes ranged from 870 to 1314 sites in the east and between 472 and 1132 sites in the west, depending on the year. Sample sizes were smaller for sites > 50°N latitude, usually between 40 and 80 sites in the east and 100–300 sites in the west.

Statistical Analyses

As an index of annual variability in numbers, we calculated the coefficient of variation (CV = SD \( \times 100/\text{mean} \) in the proportion of sites reporting greater than the expected number of birds in a particular year.

For comparative purposes, we also report correlations producing \( P < 0.05 \) for tests involving the BBS data. With 72 such tests (two for each species in eastern and western North America except for hoary redpolls and bohemian waxwings), four of these are expected to be significant by chance alone. Given their more exploratory nature, we set \( \alpha = 0.01 \) for tests involving the weather variables. With a total of 352 correlations, four are again expected to be significant by chance at this level.

General Patterns

The CV in the proportion of sites reporting greater than expected numbers of birds in a particular year ranged between 27.8% (purple finches in the east) and 181.3% (hoary redpolls in the west), averaging 62.9% (Table 2). As expected, these values were considerably greater than those for the five non-eruptive species (Mann-Whitney test; \( Z = 3.9; N = 8, 22; P < 0.001 \)), annual CVs for which were all < 32.1% and averaged only 19.4% (data not shown). In general, correlations in the proportion of sites reporting greater than expected values in the east vs. the west were positive but not significant, exceptions being for winter precipitation and five of the 11 species of birds, especially common redpolls, pine siskins, bohemian waxwings and red-breasted nuthatches (Table 2).

Examples of the distribution of sites reporting greater than expected numbers of individuals by year are graphed
for 21 of the years in Fig. 2 for the common redpoll, one of the rarer species, and in Fig. 3 for red-breasted nuthatches, one of the more common species. Although the overall abundance of the latter makes contrasting some of the years difficult, eruption years, including 1969 and 1985, stand out from years in which relatively few birds were counted, such as 1970 and 1988. Graphs of the proportion of sites reporting greater than expected numbers of birds for eight of the species are presented in Fig. 4, while examples of the proportion of sites reporting greater than average seed crops, higher summer temperatures, and greater than average summer rainfall are graphed in Fig. 5.

Significant correlations between the eruption index of the 11 species and the seed crop, BBS data and environmental variables measured within the same geographical region are summarized in Table 3. Only two species (red crossbills and hoary redpolls) failed to correlate with any of the variables. Eruptions of eight of the 11 species correlated with either the previous year’s seed crop, the current year’s seed crop, or (in six of the species) with both in one or both geographical regions. Several of the more northern species, including white-winged crossbills and bohemian waxwings, correlated more strongly with seed crops > 50°N latitude than < 50°N latitude, but this was variable. Two examples of species for which eruptions correlated with both the prior and current year’s seed crop are plotted in Fig. 6.

In contrast to the strong relationships with the seed crop, no significant correlation with any of the environmental variables emerged. Eruptions of five species correlated with breeding density, only one more than expected by chance. With one exception the correlation was positive; that is, eruptions were preceded by greater than average numbers of sites reporting the species in the prior spring.

Unsurprisingly, far fewer significant correlations were found when comparing eruptions in one geographical region with the seed crop, density and weather of the other geographical region (Table 4). However, those few significant correlations that did emerge mainly reinforced the relationships reported in Table 3 (i.e. pine grosbeak, purple finch, white-winged crossbill, bohemian waxwing and red-breasted nuthatch) with two exceptions: eruptions of pine siskins in the west correlated with high breeding densities > 50°N latitude in the east and, more interestingly, eruptions of red crossbills in the east correlated both with large western seed crops in the previous year and poor western seed crops in the current year.

There were no strong differences between species in eastern and western North America. In both regions, eruptions of seven of the 11 species were related to the seed crop. In both the east and the west, five species correlated with both good seed crops in the previous year and poor seed crops in the current year (usually within the same region, except for red crossbills in the east).

### Discussion

As expected, the eruptive species analysed here exhibited greater annual variability in numbers than a small comparison group of closely related noneruptive species. Although synchrony in eruptions usually extends over large geographical areas (W. D. Koenig, unpublished...
Fig. 2. Sites for which the number of common redpolls counted per party hour between winter 1968 and 1988 was greater than the number expected for that site after eliminating long-term trends. The approximate geographical boundary of North America is overlaid on the graph for 1968. Data based on Christmas Bird Counts.

(data), eruptions east of the Rocky Mountains were strongly correlated with those in the west for only four species (common redpoll, pine siskin, bohemian waxwing and red-breasted nuthatch). For the other species, the proportion of sites reporting greater than the expected number of birds in the two regions were usually only weakly positive.

Results of correlations with winter densities are consistent with the hypothesis that eruptions of many boreal seed-eating birds are related to the size of the seed
crop of coniferous trees (Table 5). Despite the large number of tests performed, these relationships are highly unlikely to be due to chance. In all, 30 significant correlations (10 at the 0.01 level) with the seed crop emerged, far more than the 15 (three at the 0.01 level) expected by chance. More convincingly, every one of the 17 significant correlations with the previous seed crop was positive, while all 13 of the significant correlations...
with the current seed crop were negative, values significantly different from the 50:50 ratio expected if these results were due to chance ($\chi^2 > 13$, both $P < 0.001$).

Conclusions are identical, although less extreme, considering each species as a single datum. Thus, despite the problem of multiple comparisons, these analyses provide good evidence that the seed crop has a strong effect on eruptions of most boreal seed-eating birds.

For two species in the east and two different species in the west, eruptions correlated with a combination of large seed crops followed by poor seed crops, with additional independent evidence for relatively large densities of breeding birds prior to the eruption. For these species, eruptions apparently occur when good seed crops in the autumn result in relatively high survivorship and thus high densities of birds the following spring (with potentially high reproductive success as well), that then experience a poor seed crop during the subsequent autumn. Given that good seed crops of boreal trees are generally followed by relatively poor seed crops (Koenig & Knops 2000), this pattern of seed-crop production is likely to be fairly common.
For four species in the east and three in the west, we detected correlations between eruptions and both large seed crops followed by poor seed crops, but with no independent evidence for high population densities prior to the eruption. In these populations it is possible that the critical effect of the good seed crop was not on overwinter survivorship, but rather on reproductive success the following spring. Once again, relatively large numbers of birds would then erupt when faced with a poor seed crop the next autumn. Indirect evidence for this scenario would include the presence of large proportions of immatures during eruption events, a finding for which there is considerable evidence, particularly in European species (Lack 1954; Van Gasteren et al. 1992; Riddington & Ward 1998).

Eruptions of two species in the west correlated only with large seed crops the previous year, suggesting that for these species high densities alone may be a more important predisposing factor leading to eruptions than seed-crop failures. The opposite was true for white-winged crossbills in the east, whose eruptions correlated only with seed-crop failures during the year of the eruption.

Eruptions of purple finches in both the east and the west correlated with high breeding densities that were apparently unrelated to the seed crop. No significant correlation with any relevant variable was found for three species in the east and three in the west, only one of which (hoary redpoll) was common to both regions.

Thus, the only population for which the seed-crop failure hypothesis by itself was supported was the white-winged crossbill in the east. The population density hypothesis by itself was also supported in only three species, including purple finches, whose population densities were apparently unrelated to the seed crop, and common redpolls and black-capped chickadees in the west, for which eruptions were correlated with a large seed crop in the previous year. The majority of species (six in the east, five in the west) support the combination of these factors being critical to eruption events, more or less as envisioned by Lack (1954) and Newton (1970). Our results provide no support for hypotheses relating eruptions directly to environmental conditions, such as relatively mild winters leading to high overwinter survivorship (Van Gasteren et al. 1992), severe winters resulting in abandonment of normal winter ranges or warm conditions during the breeding season resulting in high reproductive success.

These results explain the variability in conclusions reached by previous workers studying one or more of these species usually on a smaller geographical scale. For about half the populations and more than half the species considered here, eruptions appear to result from what amounts to a combination of both the seed-crop failure and population density hypotheses.
Eruptions of one of the species (purple finches) appear to be due to high density unrelated to the seed crop, while we were unsuccessful at determining any correlate of eruptions in three species in eastern and three species in western North America.

At least generally, results match expectations based on the winter diet of the species considered. Major consumers of conifer seeds include evening and pine grosbeaks, red and white-winged crossbills, pine siskins and red-breasted nuthatches (Table 1), eruptions of all of which are related to the coniferous seed crop either in the east, west, or both (Table 5). Of the seven species for which pine seeds make up a substantial portion of the diet (Table 1), three (evening and pine grosbeaks and red-breasted nuthatches) correlate with the seed crop of pines alone either in the same (Table 3) or the opposite (Table 4) geographical region. Conversely, conifer seeds do not make up a major portion of the diets of either
eruptions are generally attributable to a combination of boreal seed-eating birds and, in particular, such factors such as weather may play an important role in synchronizing eruptions. Our failure to detect any significant relationships between weather and eruptions fails to support the latter of these alternatives.

No single factor is apparently behind all eruptions of boreal seed-eating birds throughout the Northern Hemisphere, or even within eastern or western North America. Even within a species, the relative importance of prior and current seed crops may apparently vary from region to region (Table 5) and possibly from one time period to another (Larson & Bock 1986). However, our results confirm that the seed crop of boreal trees (or the seed crops of other boreal plants that mast-fruit synchronously with the trees) are the primary ultimate factor determining population eruptions of the majority of boreal seed-eating birds and, in particular, such eruptions are generally attributable to a combination of a good seed crop (presumably resulting in high survivorship and/or high reproductive success) followed by a poor seed crop the next autumn, forcing the relatively high densities of birds to search for food beyond their normal range. For four species (red-breasted nuthatches and black-capped chickadees in the east and pine grosbeaks and pine siskins in the west), nearly all components of this hypothesis are detectable: eruptions correlate with good seed crops in the previous year, high densities of breeding birds in the previous spring, and poor seed crops in the year of the event. For four additional species in the east and three in the west, no direct evidence of high densities was found but otherwise the patterns appear similar, with the caveat that for red crossbills in the east eruptions are correlated with western, rather than eastern, seed crops (Table 4).

For several remaining species we were able to garner support for only a portion of this scenario. However, for purple finches, eruptions are preceded by high densities that are apparently unrelated to the seed crop, while no relationship between eruptions and any of the variables examined was found for three species in both the east and the west (Table 5).

Thus, although our results suggest that the seed crops of boreal trees are a major ultimate factor determining population eruptions of boreal seed-eating birds they are apparently not the only factor, at least for some species in some geographical regions. Future studies, incorporating large networks of seed crop reports comparable to CBC counts or the kind of large-scale volunteer efforts mobilized by Hochachka et al. (1999), will be needed to further elucidate the specific causes of boreal bird eruptions in these cases.

Acknowledgements

We thank Sam Droege and Brett Hoover for assistance with the Christmas Bird Count database and the referees for their comments. Financial support was provided by the University of California’s Integrated Hardwood Range Management Program and the National Science Foundation.

Table 5. Summary of the hypotheses for the causes of winter eruptions by boreal seed-eating birds supported by the results

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>East</th>
<th>West</th>
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<tr>
<td>Eruptions occur when a combination of large</td>
<td>Red-breasted nuthatch</td>
<td>Pine grosbeak</td>
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<td>seed crops resulting in high densities of birds</td>
<td>Black-capped chickadee</td>
<td>Pine siskin</td>
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<td>is followed by a poor seed crop, forcing</td>
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<td>relatively large numbers of birds to wander</td>
<td>daytime</td>
<td></td>
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<td>in search of food</td>
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<td></td>
</tr>
<tr>
<td>Eruptions occur when a combination of large</td>
<td>Evening grosbeak</td>
<td>Evening grosbeak</td>
</tr>
<tr>
<td>seed crops is followed by a poor seed crop,</td>
<td>Pine grosbeak</td>
<td>Bohemian waxwing</td>
</tr>
<tr>
<td>forcing birds to wander in search of food,</td>
<td>Red crossbill</td>
<td>Red-breasted nuthatch</td>
</tr>
<tr>
<td>but no direct evidence that densities are high</td>
<td>Bohemian waxing</td>
<td></td>
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<tr>
<td>Eruptions occur when the prior year’s seed</td>
<td>White-winged crossbill</td>
<td></td>
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<tr>
<td>crop was unusually large; no direct evidence</td>
<td>Purple finch</td>
<td>Purple finch</td>
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<td>that densities are high</td>
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<tr>
<td>Eruptions occur when the current year’s seed</td>
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<td>crop is unusually poor</td>
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<td>Eruptions occur when breeding densities are</td>
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<td>relatively high; cause not determined</td>
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</tr>
<tr>
<td>No correlate of eruptions</td>
<td>Hoary redpoll</td>
<td>White-winged crossbill</td>
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<tr>
<td></td>
<td>Common redpoll</td>
<td>Red crossbill</td>
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<tr>
<td></td>
<td>Pine siskin</td>
<td>Hoary redpoll</td>
</tr>
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</table>

Purple finches or hoary redpolls, for which eruptions were not found to vary in conjunction with the coniferous seed crop. The two exceptions were common redpolls and bohemian waxwings, eruptions of which were both related in some way to coniferous seed crops even though conifer seeds do not make up a significant fraction of the diet of either species. This discrepancy between eruptions and diet is also evident in the weak relationship found between patterns of interspecific synchrony of eruptions and diet (Lack 1954), particularly in western North America (W. D. Koenig, unpublished data).

Two potential explanations for the discordance between eruptions and diet are that synchrony among food resources may encompass a much larger taxonomic range of species than currently realized, or that other factors such as weather may play an important role in synchronizing eruptions. Our failure to detect any significant relationships between weather and eruptions warn that further study is needed to further elucidate the specific causes of boreal bird eruptions in these cases.
References


Received 20 January 2001; revision received 27 February 2001