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IRRUPTIVE MIGRATION OF COMMON REDPOLLS[1]

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Abstract. We do not know whether the movements of irruptive migrants are fundamentally different from more conventional migration of birds to their wintering areas because irruptive migration has never been thoroughly described for any species on a continent-wide scale. We use data from a citizen-based monitoring program, Project FeederWatch, to describe the patterns of movements of redpolls (principally *Carduelis flammea*) across North America in 1993–1994, the winter of a major irruptive migration. Although redpolls moved into new areas during this irruptive migration, the normal wintering range was not completely abandoned. In fact, redpolls were more prevalent in the southern part of their normal wintering range in an irruption year than was typical in non-irruption years. There also was no indication that the majority of the North American population of redpolls moved continuously through the winter: although redpolls peaked in prevalence at different times across the continent, their spring departure was relatively synchronous across the entire continent. Group sizes were typically smaller the later redpolls arrived in a region, also suggesting that the entire redpoll population did not move continuously. In contrast to a non-irruptive migrant, the American Tree Sparrow (*Spizella arborea*), redpolls arrived at feeders in a given region later but reached peak densities more quickly. Our results suggest that the irruptive migration of redpolls is more allied to conventional winter migration than to nomadism.

Key words: American Tree Sparrow, Carduelis flammea, *Common Redpoll, irruptive migration, Project FeederWatch,* Spizella arborea.

INTRODUCTION

Birds follow many strategies when moving from breeding to nonbreeding areas (Alerstam 1990, Berthold 1993). Many species move repeatedly between the same breeding and wintering grounds, in some cases holding territories at both ends of their migration (Moreau 1972, Sherry and Holmes 1996). Other species, which have specialized food resources (crossbills, genus *Loxia*), are constrained to a nomadic existence, moving across entire continents in response to the presence of their principal food (Newton 1973, Benkman 1992, Adkisson 1996). Between these extremes are species that show regular seasonal movements, but with the extent of their winter movements varying among years; such species are often termed "irruptive."

The phenomenon of irruptive migration has proven difficult to study, constrained by both the unpredictability and the large spatial scale over which movements occur. Most published studies on irruptive species either are restricted to a fraction of the area over which species move (Lensink et al. 1989), attempt to piece together movements from anecdotal information (Svärdson 1957), or reconstruct movements from returns of banded birds (Troy 1983). The single study with data from the entire width of a continent (Bock and Lepthien 1976) contained data from only a narrow time period of 2 weeks. Given the logistical constraints of studying irruptive migrants, there has never been clear documentation of the pattern of movements of an irrup-

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tive migrant across the entire spatial range and temporal duration of its invasion.

Given our lack of knowledge of movement patterns of irruptive species, we still do not know how similar irruptive migration is to the movements typically associated with migration from breeding to nonbreeding areas. The behavior of irruptive migrants may differ because irruptive species face the problem of finding potentially novel food sources in unfamiliar areas. As a result, irruptive migrants may show no indication of becoming sedentary at any time in the winter or may take longer to reach their maximum densities in an area upon arrival. In this respect, irruptive migration may be more akin to the establishment of a species moving into a new breeding area (Hengeveld 1989) than a winter migrant coming to a known wintering area.

One irruptive migrant that has been widely discussed in the literature (Svärdson 1957, Antikainen et al. 1980, Ernst 1983) is the Common Redpoll (*Carduelis flammea*), a species with a circumboreal distribution (Cramp and Perrins 1994). One suggested cause of redpolls' irruptive movements is dependence on the presence of birch (*Betula*) or alder (*Alnus*) seeds, and shortages of seeds in winter may cause redpolls to regularly travel far from their breeding range in winter (Evans 1969, Kennard 1976), occasionally even nesting south of their normal breeding range (Lister 1975). A related possibility is that summers with high food abundance (Enemar and Nyström 1981) cause high post-breeding densities of redpolls, which in turn trigger irruptive migration (Berndt and Henss 1967). Regardless of whether the ultimate cause of irruptive migration is seed production or lack thereof by boreal tree species, synchrony in seed production across large areas (Koenig and Knops 1998) can result in large-scale irruptive movements of birds such as redpolls. The extent of redpoll invasions has been examined, but as typical for invasive species, patterns of movement have only been documented anecdotally (Svärdson 1957), or within restricted areas (Lensink et al. 1989) or time periods (Bock and Lepthien 1976) during an invasion.

This paper describes the pattern of movements observed during a recent irruptive migration of redpolls (principally Common Redpolls *C. flammea* but also Hoary Redpolls *C. hornemanni*) from their boreal nesting areas into more temperate regions of North America. Data from a citizen-based program, Project FeederWatch (Wells et al. 1996, 1998), are used to document the presence and abundance of redpolls across the entire width of North America and over an entire winter. The data provided by Project FeederWatch are the most thorough documentation of an irruptive migration available to date. Our goal is to explore the temporal dynamics of an irruptive migration, and describe whether this irruption can be considered a similar phenomenon to annual migrations to a constant wintering area. We asked the questions: (1) what is the pattern of arrival and departure of redpolls from different regions of the continent over the course of the irruption?, (2) does a southward irruption of redpolls mean that their more normal wintering range is abandoned in irruption years?, and (3) within a given region, do the changes in abundance through the winter differ from those seen for non-irruptive winter migrants? We contrast redpolls with a non-irruptive migratory emberizid, the American Tree Sparrow (*Spizella arborea*), in order to address this third question.

METHODS

DATA COLLECTION

A large-scale invasion of Common Redpolls into eastern North America was observed during the winter of 1993–1994 (Kaufman 1994); describing the movements of redpolls during this winter forms the main part of this paper, although we make comparisons with other years. Our source of data for documenting the irruptive migration of redpolls was Project FeederWatch, an ongoing project jointly managed by the Cornell Laboratory of Ornithology and Bird Studies Canada. Details of the FeederWatch protocol are given in Wells et al. (1998). Briefly, volunteers throughout the United States and Canada who enrolled in the project collected data following a standardized protocol, conducting counts of the maximum number of birds of each species seen at their feeders during 2-day count periods. The first week of counting was the calendar (i.e., Sunday–Saturday) week in November that contained November 15. The timing of Project FeederWatch is such that our data detected the arrival but not the departure of redpolls from much of their wintering grounds. Observers were stratified into two groups by the first letter of their last name so that approximately half of the participants began their counts in the first week of the 20-week observation period, and the other half began in the second week. Consequently, data were collected from each week of the 20-week observation period, although data from a given observer were supposed to come only at biweekly intervals. Most participants followed this protocol, although deviations from the fortnightly counting schedule, including late start and early termination of counting, did occur. We did not exclude data from our analyses if reporting intervals deviated from the pattern outlined in the protocol. Observers were told to select their count days at the beginning of the season to reduce the bias that would be created if observers reported only the most interesting counts, or counts with the highest number of birds. The data for examining redpoll movements came from 2,204 (in 1987–1988) to 3,400 (in 1996–1997) participants, over 54% of all FeederWatch participants in each year.

Data were available from across the entire width of the continent, with the northward limit of the data generally falling on the southern side of redpolls' normal winter range (Fig. 1); FeederWatch sites in the Alaska region provide the only exception. Thus, our data were not able to reveal the dynamics of redpoll abundance in the northern-most parts of the birds' wintering range. For statistical analyses, sites have been grouped into regions (Fig. 1). These regions follow political borders on the continent, and roughly correspond to regions from which birds are reported in *American Birds* and *Audubon Field Notes.* Regions are smaller where the number of observers was large, allowing for finer geographical resolution.

In order to determine if irruptive species differ from non-irruptive migrants in their movements, we compared redpolls to American Tree Sparrows. This species was chosen for comparison because both redpolls and tree sparrows have roughly the same breeding distribution in North America (Godfrey 1986), both species are granivores in winter (Baumgartner 1968, Clement 1968), and the two species have broadly overlapping winter ranges during years of redpoll irruption. However, in many regions of North America covered by Project FeederWatch, tree sparrows are annual winter residents. We identified FeederWatch regions in which both redpolls and tree sparrows were present at more than 20% of feeders in 1993–1994, and only used data from these regions in our comparisons. The FeederWatch regions (Fig. 1) used in comparisons of redpolls and tree sparrows were: Great Lakes (GL), New York and Pennsylvania (NY), Northeastern U.S.A. (NE), Maritimes (MA), mid-Atlantic U.S.A. (AT), and east Central U.S.A. (EC).

In addition to counts of birds, participants were asked to complete a form that provided information on habitat and times of counts. From these more detailed data we used a variable that classified each site on a gradient of urbanization: urban, suburban, sub-rural, or rural. Preliminary analyses showed that much of the variability in habitat descriptions was correlated with the gradient of urbanization, supporting our use of urbanization as a measure of habitat type. Additionally, the degree of urbanization was the habitat variable most consistently provided by participants. The other confounding variable used in our analyses was the number of half days within the 2-week period on which the feeder was watched. This number could vary from a single morning or afternoon, to a full 4 half-days, in integer increments. All of these data were available for the 1988–1989 through 1996–1997 FeederWatch seasons.

In addition to the data collected by Project FeederWatch, we also noted arrival dates of redpolls reported in *American Birds* (Kaufman 1994) during the 1993–1994 irruption. These arrival dates were not tied to observations at feeders, and allowed us to determine whether the appearance of redpolls at feeders was closely tied to their arrival in a given region. Two types of events were noted from the accounts in *American Birds*: first arrivals and dates of peak numbers, both of which could be matched with similar events at individual feeders. All references in *American Birds* that had a specific geographical location and an approximate date (to within a 2-week period, e.g., "mid-December") were used. Most regional reports of redpoll abundance were only general, verbal descriptions of trends through the entire season, which limited the number of data that were obtained. The latitude and longitude of each of the *American Birds* locations was determined, and the closest five FeederWatch sites were found for each location. Within each set of FeederWatch locations, the first date of detection (or peak numbers, as appropriate) was used in comparison with the reports from *American Birds.*

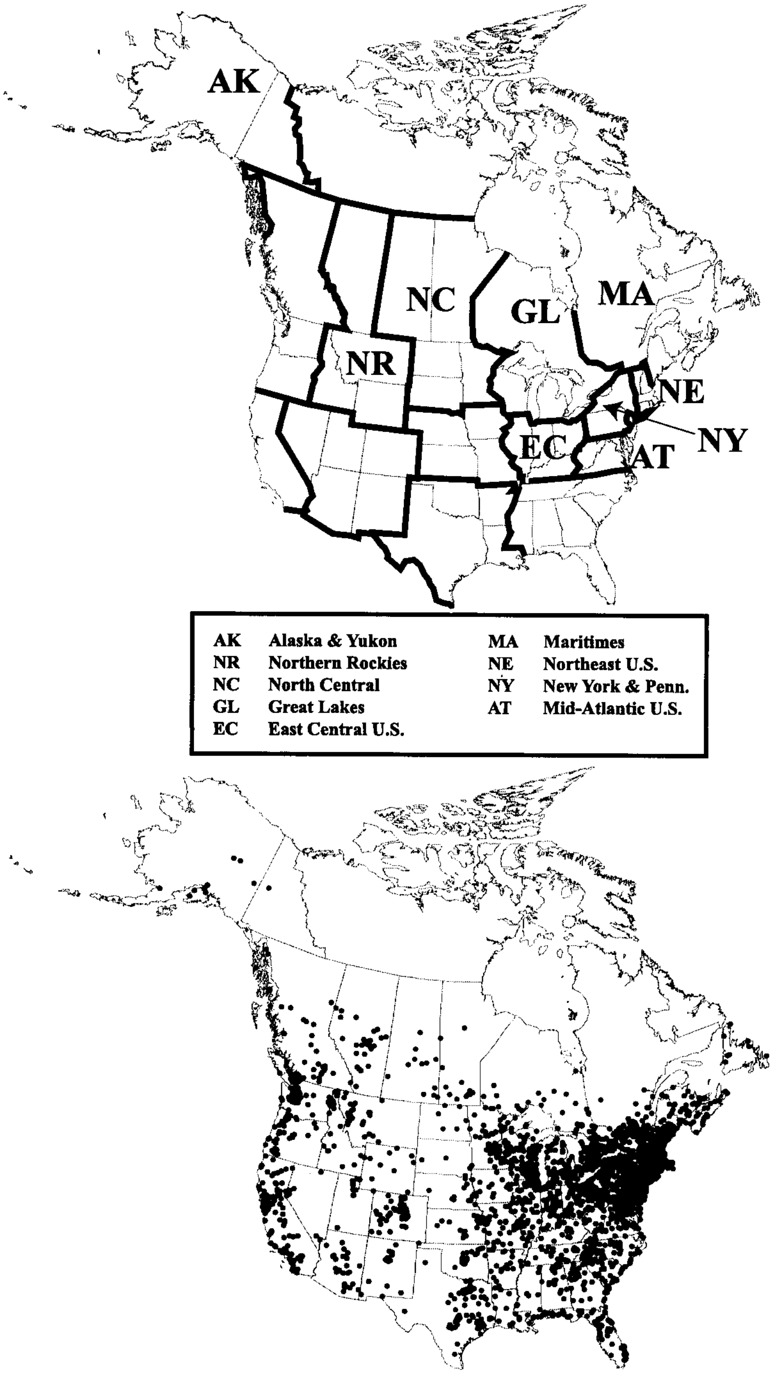

FIGURE 1. FeederWatch regions and the distribution of FeederWatch participants in the 1993–1994 irruption year of redpolls. Regional names are provided for FeederWatch regions in which redpolls visited at least 10% of feeders.

STATISTICAL ANALYSES

Dates noted in *American Birds* were compared to dates for the same events from nearby FeederWatch sites using linear regression.

Two measures of redpoll abundance were available from our data: group sizes and the proportions of feeders in an area that reported at least one redpoll. The data on group size were problematic for statistical analyses due to highly skewed distributions of group sizes (most groups were of one bird), which precluded transforming the data to a normal distribution. Furthermore, the shapes of the group-size distributions were not constant through space or time, in violation of assumptions of nonparametric statistics. Even measuring changes in typical group size was difficult because both mean and median group sizes showed little variation through time because of the heavily skewed data. Maximum group sizes were extreme outliers in distributions, and thus not consistently representative of the sizes of large groups in a region. Therefore, as a compromise between median and maximum group size, we used the 75th quantile of a group size distribution (i.e., the group size for which 25% of groups were larger) as our measure of group size within a region. In contrast to group sizes, presence and absence of redpolls was a statistically more tractable form of data, given its binomial error distribution. We tested whether presence/absence data also contained information on sizes of redpoll groups by regressing our weekly indices of group size against the proportion of feeders with redpolls. A higher probability of sighting any redpolls was significantly related to the presence of larger groups of redpolls ($P < 0.001$ in multiple regression including date of invasion as a significant confounding variable). Thus, most of our questions were addressed only with the more statistically tractable presence/absence data. However, a greater probability of redpolls' presence should be interpreted also to indicate larger groups of redpolls being present in a region.

The purpose of our analyses of presence/absence data was to model variation in the abundance of redpolls through space and time. In these analyses, each FeederWatch site was treated as a separate data point, with repeated measurements of the numbers of birds being made at each site. Thus, the appropriate statistical analyses to be used are repeated-measures. Within these analyses, the measure of time over which repeated measurements were made was the FeederWatch week (1–20), which was treated both as a linear and a squared (quadratic) variable. The quadratic effect was used in order to allow for numbers of birds to increase and then decrease over the season. We had to include two potential confounding variables in our analyses: the time expended watching feeders, and urbanization around feeder sites. Preliminary analyses indicated that the number of count periods could be treated as a continuous variable, with the probability of sighting redpolls increasing with increasing observer effort. Preliminary analyses also indicated that the degree of urbanization could be treated as a continuous variable (integer values 1–4), with the abundance of redpolls typically declining with greater urbanization around a given site. We were interested in describing geographical variation in the distribution of invading redpolls, and thus included not only time but also region (Fig. 1) in our analyses. In all of our analyses, the statistical effects of particular interest were those interaction terms that indicated different patterns of redpoll abundance occurred in different regions. Biologically relevant interactions are noted and interpreted in the Results. Only interactions at least approaching statistical significance ($P < 0.10$) are discussed in this paper. At times, interaction terms were mutually exclusive, either one or the other but not both being statistically significant. When this occurred, we used Akaike's Information Criterion (Lebreton et al. 1992) to judge between the potential interactions. The probability of redpolls' occurrence was tested using a repeated-measures logistic regression (PROC GENMOD; SAS Institute Inc. 1997) with the "exchangeable" correlation among time periods. This SAS procedure uses maximum-likelihood to fit models, allows covariates to vary among time periods in a repeated-measures analysis, and also allows missing values within a time series.

Because the biological meanings of statistical interactions are difficult to interpret, we have plotted the predicted prevalence of redpolls from our analyses and interpreted patterns from these figures. In all cases we have plotted results from semi-rural sites for which feeders were watched both morning and afternoon for both days of a count period; patterns were qualitatively similar for other degrees of urbanization and durations

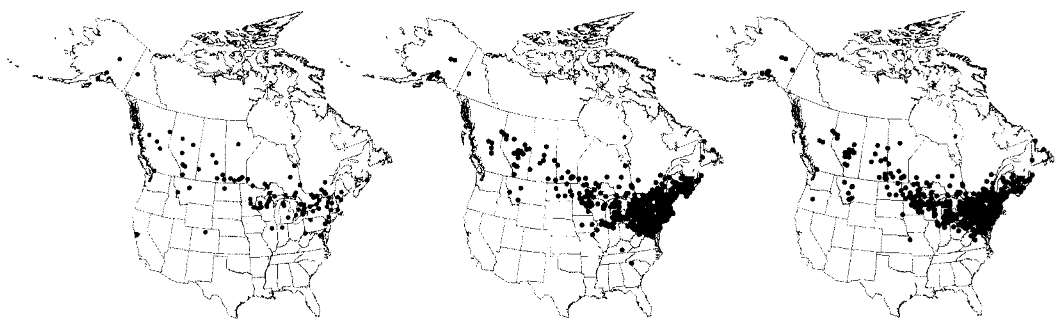

FIGURE 2. Seasonal variation in the location of redpolls in the 1993–1994 winter. Plotted data are the locations of feeders visited by at least one redpoll during a 2-week period for three periods of the winter (beginning, middle, and end of data collection by FeederWatch).

of observation. The semi-rural sites were not chosen for presentation for any biologically relevant reason, but because these sites consistently contained the most complete time series of records, easing our calculation of predicted values.

Three types of repeated-measures analyses were used in this paper. The first type was used to describe the pattern of arrival and departure of redpolls during the 1993–1994 invasion. For this analysis we used data from all FeederWatch regions from which at least 10% of participants reported redpolls in that winter. The second type of repeated-measures analysis addressed whether irruptions produced major changes in the abundance of redpolls in those parts of their normal range that were covered by FeederWatch. For this second analysis, we examined inter-annual variation within redpolls' normal wintering range. We identified the FeederWatch regions in which redpolls were counted at more than 10% of feeders in every winter for which data were available, and used data from only these regions in this second analysis. The FeederWatch regions used were: Alaska (AK), Northern Rockies (NR), and North Central (NC) (Fig. 1). The final repeated-measures analyses contrasted redpolls with a non-irruptive migrant, the American Tree Sparrow, by treating redpoll and tree sparrow sightings at each site as paired data (a "within" effect in a repeated-measures ANOVA). The comparison of species only was done in the 1993–1994 winter, and was restricted to FeederWatch regions in which at least 20% of the sites reported both redpolls and tree sparrows.

All analyses were conducted using SAS/STAT (SAS Institute Inc. 1989). Results from statistical tests were considered significant at a critical value of alpha = 0.05.

RESULTS

Before describing patterns of abundance of redpolls, we tested whether data from Project FeederWatch describe patterns of arrival per se, or a combination of arrival of redpolls in a region followed by a lag period in which the redpolls found feeders. In a comparison between sight records from *American Birds* and FeederWatch data, early sightings of redpolls in a region did not necessarily mean early detection at nearby feeders ($r^2 = 0.04$, $n = 9$). Furthermore, first arrivals or peak numbers occurred at feeders on average over 7 weeks later than was the case for sight records ($P = 0.03$). Thus, times shown in all subsequent analyses indicate not just the times of arrival of redpolls in a region, but a combination of arrival and discovery of feeders by redpolls.

The observed pattern of movement (Fig. 2) was for redpolls to be sparsely distributed but present in most of their wintering range from the beginning of the FeederWatch period, but with prevalence increasing through the middle of the winter, most noticeably in the northeastern United States. Regional differences in the pattern of movement of redpolls were borne out in our statistical analyses, as indicated by the significant interactions of FeederWatch week and region ($P < 0.001$ in multiple regressions). The only changes in prevalence that were consistent with an west-to-east movement came from the Maritime region, where numbers increased as

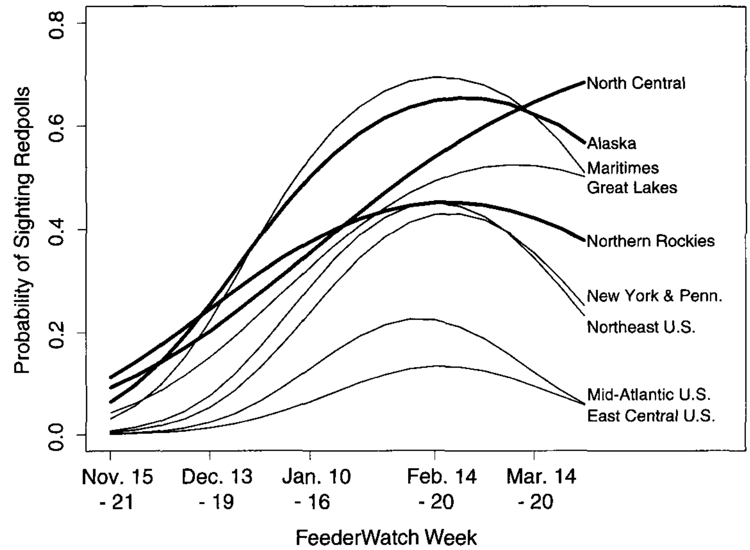

FIGURE 3. Seasonal variation in the probability of sighting redpolls in different geographic regions in the 1993–1994 winter. The lines are predicted probabilities of redpoll occurrence from repeated-measures logistic regression. Predictions are for semi-rural areas for observers watching feeders for 2 days (both morning and afternoon). The regions in which redpolls winter annually are highlighted with broader lines.

though birds were arriving from farther south after encountering the continent's edge (Fig. 2).

Although patterns of changing prevalence of redpolls differed among regions, there was no evidence of continuous and systematic movement of the entire population throughout the irruption. A systematic movement of the entire

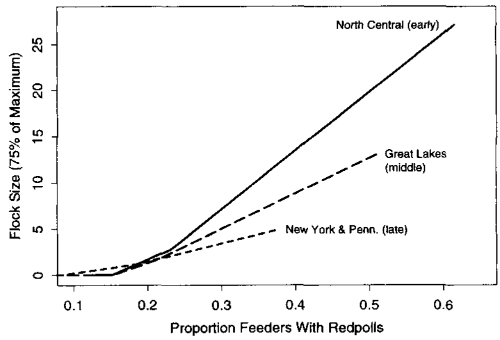

FIGURE 4. Relationship between group size and the proportion of feeders visited by redpolls in a region. Results were dependent on the arrival date of redpolls in a region, and results from regions of early, middle, and late arrival are presented. Group sizes were indexed as the 75th quartile of the distribution of group sizes, and the period of arrival of redpolls in a region was judged as the period in which at least 10% of feeders were visited by redpolls. Plotted lines are predicted values from a multiple regression.

population of redpolls would have resulted in numbers of redpolls peaking earlier in their normal wintering range, followed by a mid-winter decline as redpolls appeared in large numbers farther south. This pattern was not found (Fig. 3). The prevalence of redpolls increased throughout all regions as the winter progressed, with numbers starting to decline again in most regions at roughly the same time. Simply plotting the locations reporting redpolls also shows that birds were present in the northern part of their winter range throughout the irruption (Fig. 2).

A final suggestion that redpolls did not move continuously through the winter comes from examination of the manner in which group size systematically changed as redpolls invaded new regions over the winter (Fig. 4). Continuous movement by all redpolls would mean that flocks of redpolls would constantly travel to new areas; as long as flocks were relatively cohesive, the result would be that observed group sizes should be relatively constant regardless of how late in the winter redpolls invaded a region in large numbers. However, we found regional differences in the sizes of groups associated with the same percentage of feeders reporting redpolls (Fig. 4). This variation appears related to

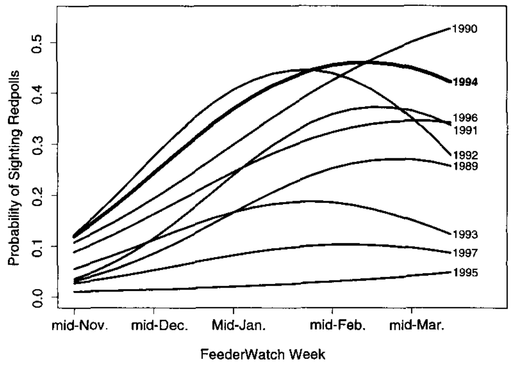

FIGURE 5. Annual variation in the probability of sighting redpolls in part of their normal wintering range. Note that redpolls were present in all years, including the irruption year (labeled 1994). Data are presented from FeederWatch participants in semi-rural areas of the Northern Rockies region; results were similar from the Alaska and North Central regions, and for different degrees of urbanization. The plotted lines are predicted probabilities from repeated-measures logistic regression.

regional differences in the time of arrival of redpolls: region per se (a categorical variable) and the timing of the major influx of redpolls into a region (a continuous variable) could be interchanged without appreciably affecting the goodness-of-fit (r^2 varied by only 0.03) of the analysis. Regions invaded later in the winter contained smaller groups of redpolls.

FeederWatch participants were only present in the southern part of the redpolls' normal winter range, but in those parts of the normal wintering range that were monitored redpolls did not leave during the 1993–1994 irruption. There were significant annual differences in the pattern of occurrence of redpolls, as indicated by statistical interactions involving year and time period ($P < 0.001$ in multiple regressions). If redpolls were to completely leave their normal wintering range during an irruption, we would expect to find lower numbers of redpolls in their normal winter range in the year of the irruption. However, redpolls were more prevalent in the 1993–1994 irruption year than in most other years of the study (Fig. 5). These results indicate that redpolls do not entirely vacate their normal wintering range in years of irruptive migration.

In order to judge how similar redpolls' irruptive migration is to the movements of a more regular winter migrant, we contrasted the pattern of redpolls' arrival and departure with that of American Tree Sparrows. The two species differed in the patterns with which abundance changed through time, as indicated by significant interactions between species and time period ($P < 0.001$ in multiple regression). The typical pattern was that redpolls arrived later, and their arrival was more synchronous (a steeper curve) than that of tree sparrows. Note however, that these results indicate that either the pattern of arrival or the pattern of discovery of feeders differed between redpolls and tree sparrows.

DISCUSSION

Our first goal was to describe the patterns of movements of an irruptive migrant, placing our observations within the context of the general patterns of movement of birds that have already been described. The types of movements for which we have a better understanding are regular migrations between specific breeding and nonbreeding areas, nomadism, and permanent range expansions. Our analyses indicate that the irruptive migration of redpolls is not a form of population-level nomadism, because redpolls did not display a continually shifting center of abundance during their irruption (Fig. 3), and did not entirely abandon their normal wintering range (Fig. 5). Our data also suggest that irruption does not follow the patterns of movement associated with range expansion, because redpoll numbers built up even more rapidly at feeders than did the number of the regularly migrating American Tree Sparrow, and opposite the pattern found during range expansion (Hengeveld 1989). However, redpolls' rapid increase in numbers at feeders could indicate their rapid discovery of feeders and not a rapid movement into new areas. Thus, the suggestion of rapid buildup of redpolls' numbers is not conclusive. Regular, annual migration was the form of population movement most consistent with our data, not just because redpoll numbers built up rapidly at feeders, as also seen for tree sparrows, but also because the entire population of redpolls did not continuously move throughout the winter (Fig. 3).

Data from FeederWatch indicate that redpolls differed from more conventional migrants primarily in the varying distances that redpolls traveled in different years. This behavior identifies redpolls as irruptive migrants, but also suggests that redpolls are not uniformly "preprogrammed" to follow a set migration once an irruption begins (Berthold 1993). Instead, the numbers of birds that move appears to decrease through time, as shown by the decreasing sizes of redpoll groups with later arrival of birds in a region (Fig. 4). This observation is more consistent with the suggestion that irruptive migrants stop when they encounter sufficient food (Newton 1973) than with a pre-programmed destination. However, we do not know whether the redpolls that continue moving are qualitatively different from those that settle early, for example, in geographic origin, age, or sex (Henning and Karlsson 1997).

Our data also enable us to address the suggestion that irruptions by redpolls are a general northwest to southeast movement of birds across North America (Troy 1983). Figures 3 and 4 provide the clearest indication that redpolls were present in small numbers across the entire width of the continent from the start of observations. The main suggestion of lateral movement comes from the Maritimes, in which redpolls may have been moving northward from the northeastern United States! We suggest that any interpretation of lateral movements of birds across the continent should be tempered by the knowledge that the northern edge of the distribution of ornithologists, both amateur (Fig. 1) and professional, is higher in western than eastern North America. Thus, even a synchronous, purely north-south movement of birds would appear to have an east-west component simply because birds would be detected earlier in the western part of the continent. Indirect methods (such as Dawson et al. 1997, Hobson and Wassenaar 1997) may be required to identify the geographic origins of irruptive migrants.

The great strength of organized data collection by the general public is the documentation of patterns on a geographic and temporal scale otherwise unattainable. Although this paper documents the movement of a single irruptive species, the potential exists to examine the phenomenon of irruptive migration more broadly by contrasting the movements of several species in years in which many irruptive migrants move south simultaneously. Data from FeederWatch, by themselves, are limited in their usefulness for cross-species comparisons because it is unlikely that all species will discover and use feeders at the same rate. Thus, examination of dates of first arrival or peak number, while valid for within-species comparisons, may not provide useful information for among-species comparisons. However, combining data from FeederWatch and independent sources would allow us to explore whether species differ in their abilities to identify and aggregate at novel food sources. To date, the most visible use of data collected by the public has been monitoring of bird populations (e.g., Robbins et al. 1989, Morris et al. 1994). With projects such as FeederWatch, we feel that data collected by the general public can be used to address questions from a wider range of topics.

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