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WINTER SURVEY DATA REVEAL RANGEWIDE DECLINE IN EVENING GROSBEAK POPULATIONS

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Abstract. Once one of the most common species seen at bird feeding stations across much of North America in winter, the Evening Grosbeak (*Coccothraustes vespertinus*), appears to be experiencing a population decline. Like other finches associated with the boreal forest or high elevations, Evening Grosbeaks form flocks in winter, often irrupting out of their breeding range and frequenting supplemental feeding stations where populations may be monitored. We sought to quantify the extent of changes in the abundance and distribution of Evening Grosbeak populations using data gathered in winter by Project FeederWatch, a continent-wide monitoring program that began in 1987. Feeder-Watch data gathered between 1988 and 2006 indicated a significant surveywide decline in the mean flock size recorded over time. The proportion of sites reporting Evening Grosbeaks plummeted by 50% in 18 years. At locations where the species continued to be seen, mean flock size declined by 27%. Similarly, analysis of data

from 391 sites reporting data for at least 10 consecutive years indicated significant declines in Evening Grosbeak abundance at 76 sites and increases at no sites. Although the Evening Grosbeak has experienced dramatic rangewide population declines in recent years, the mechanisms contributing to these changes remain unclear. Given the geographic extent and rapid rate of observed population changes, urgent investigation of the mechanisms driving these declines is warranted.

Key words: *Coccothraustes vespertinus*, *Evening Grosbeak*, *population trends*, *Project FeederWatch*.

Datos de Censos de Invierno Revelan una Disminución de la Población de *Coccothraustes vespertinus* en Todo su Rango de Distribución

Resumen. A pesar de ser históricamente considerada una de las especies más frecuentes en los comederos de aves a través de Norteamérica en el invierno, en la actualidad parecería que las poblaciones de *Coccothraustes vespertinus* están disminuyendo.

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Como los otros pinzones asociados al bosque boreal o a las tierras altas, *C. vespertinus* forma grupos en el invierno, a menudo irrumpiendo desde el área de reproducción y frecuentando comederos suplementarios donde es posible monitorear sus poblaciones. Intentamos cuantificar la magnitud de los cambios en la abundancia y la distribución de poblaciones del *C. vespertinus* usando datos obtenidos en el invierno por FeederWatch, un proyecto de monitoreo de todo el continente que comenzó en 1987. Datos de FeederWatch obtenidos entre 1988 y 2006 indican una disminución significativa en el tamaño medio del grupo a lo largo de la región del censo. La proporción de los sitios que registraron *C. vespertinus* disminuyó en un 50% en 18 años. En los lugares donde la especie persistía, el tamaño medio del grupo disminuyó en un 27%. Igualmente, el análisis de 391 sitios que presentaron datos durante por lo menos 10 años consecutivos, indica disminuciones en la abundancia de *C. vespertinus* en 76 sitios, y ningún sitio presentó aumentos. Aunque *C. vespertinus* ha sufrido disminuciones drásticas a través de su rango de distribución en años recientes, los mecanismos que pueden haber contribuido en estos cambios son inciertos. Debido a la extensión geográfica y al ritmo rápido de cambios de la población, es muy importante investigar los mecanismos que están causando las disminuciones.

The Evening Grosbeak (*Coccothraustes vespertinus*) has undergone dramatic distributional changes since first being described in 1825 (Gillihan and Byers 2001). Prior to the middle of the 19th century, Evening Grosbeaks were a species associated with the montane West of North America and were considered rare east of the Mississippi River. In the 1850s, the species began an unprecedented eastward range expansion, colonizing northern forests and reaching the provinces and states along the Atlantic coast by the 1930s (Marble 1926, Gillihan and Byers 2001). More recently, observations indicate that the range of Evening Grosbeaks has contracted (Butcher and Niven 2007).

Concern over bird populations that breed in the boreal forests of North America has increased as significant declines have been detected in several species (Blancher 2003, Canadian Boreal Initiative 2005). An irruptive migrant forming gregarious flocks in winter, the Evening Grosbeak occasionally moves out of its boreal and montane breeding areas to winter at lower latitudes and elevations. Individuals readily visit bird-feeding stations during these irruption events and are easily identified. In the 1970s and 1980s, Evening Grosbeaks were frequently reported on Audubon's Christmas Bird Counts (CBC) located as far south as Louisiana and Georgia. By comparison, the species has rarely been recorded by the CBC in areas south of the boreal forest or the mountain west in recent years (Bolgiano 2004).

The extent of recent Evening Grosbeak range and population changes has yet to be quantified. Likewise, the mechanisms contributing to perceived population declines remain poorly understood. Understanding the dynamics of Evening Grosbeak populations requires monitoring programs conducted at the appropriate temporal and spatial (continental) scales. We sought to quantify changes in the distribution and abundance of Evening Grosbeaks across their range using data from a long-term, continental-scale monitoring program.

METHODS

POPULATION TRENDS

Data on Evening Grosbeak populations were collected by Project FeederWatch, a citizen science program operated by the Cornell Lab of Ornithology and Bird Studies Canada since

1987. Wells et al. (1998) report full details of the FeederWatch protocol. In brief, program participants periodically record the maximum number of each species seen in the proximity of a bird-feeding station during two-day count periods. More than 10 000 FeederWatch sites are located across the United States and Canada each year, with data collected between November and April each season. FeederWatch data collected between November 1988 and April 2006 were included in our analyses ($n = 1\,169\,935$ checklists).

Using a mixed model, we tested for changes in the mean flock size of Evening Grosbeaks reported across all sites submitting $n \geq 50$ checklists. The relationship between $\log(\text{maximum number grosbeaks seen} + 1)$ was modeled in relation to winter season and observation effort (fixed effects) and site (random variable). Effort was quantified as a categorical variable that included a count of the number of half-days (range: 1–4) of observation during each two-day count period. Winter season was defined as a categorical variable, with each season including data gathered between November of one calendar year and April of the next calendar year.

Population changes could result in changes in either the number of flocks in an area or in the average flock size, or both. Thus, trends in the abundance of Evening Grosbeaks at FeederWatch locations were calculated by quantifying (1) the proportion of sites reporting the species per season, and (2) estimated mean flock size per season. In calculating the proportion of sites hosting the species, Evening Grosbeaks were considered present at a site if recorded on at least one checklist from that site during a season. To generate biologically meaningful estimates of mean flock size, zero values were not included in calculations of mean flock size (i.e., mean flock size when grosbeaks were present).

As changes in the geographic distribution of FeederWatch participants may potentially influence trends detected in bird populations, we next identified a subset of FeederWatch data recorded from long-term sites for further analysis. A site was identified as long term if data were submitted during at least 10 consecutive seasons from the same location. Counts from long-term sites that reported Evening Grosbeaks in at least three seasons were included in these analyses ($n = 391$ sites).

ABUNDANCE AND DISTRIBUTION MAPS

The irruptive tendencies of Evening Grosbeaks introduced considerable variability in mean and proportion estimates among winters. These irruptive patterns were smoothed by dividing the 18-year dataset into three periods, each including six winter seasons (1989–1994, 1995–2000, and 2001–2006). Maximum grosbeak counts were then averaged to generate mean values for each six-winter period. The average distribution of Evening Grosbeak populations during each six-winter period was mapped using inverse distance weighting to create interpolated surfaces in ArcGIS (Version 9.2, ESRI, Inc., Redlands, California).

To test for geographical patterns in population changes, we calculated the change in the proportion of sites hosting Evening Grosbeaks between 1989–1994 and 2001–2006 within 5° latitude-longitude blocks. Only blocks with $n \geq 20$ sites within each time period were included in the analyses ($n = 47$ blocks). Spatial patterns in the magnitude of change over time were illustrated with an interpolated surface map.

STATISTICAL METHODS

All statistical analyses were conducted in SAS (Version 9.1, SAS Institute, Inc., Cary, North Carolina). We used PROC MIXED for mixed models testing for changes in the abundance of Evening Grosbeaks surveywide. Linear regression (PROC REG)

was used to test for trends in Evening Grosbeak counts at long-term sites over time.

RESULTS

POPULATION TRENDS

Evening Grosbeaks were reported on 58 773 checklists submitted to Project FeederWatch between the winters of 1988–1989 and 2005–2006. Mean flock size when Evening Grosbeaks were present at a site declined from 11.8 in 1989–1994 to 8.6 in 2001–2006, a 27% decrease (Fig. 1A). The proportion of sites reporting

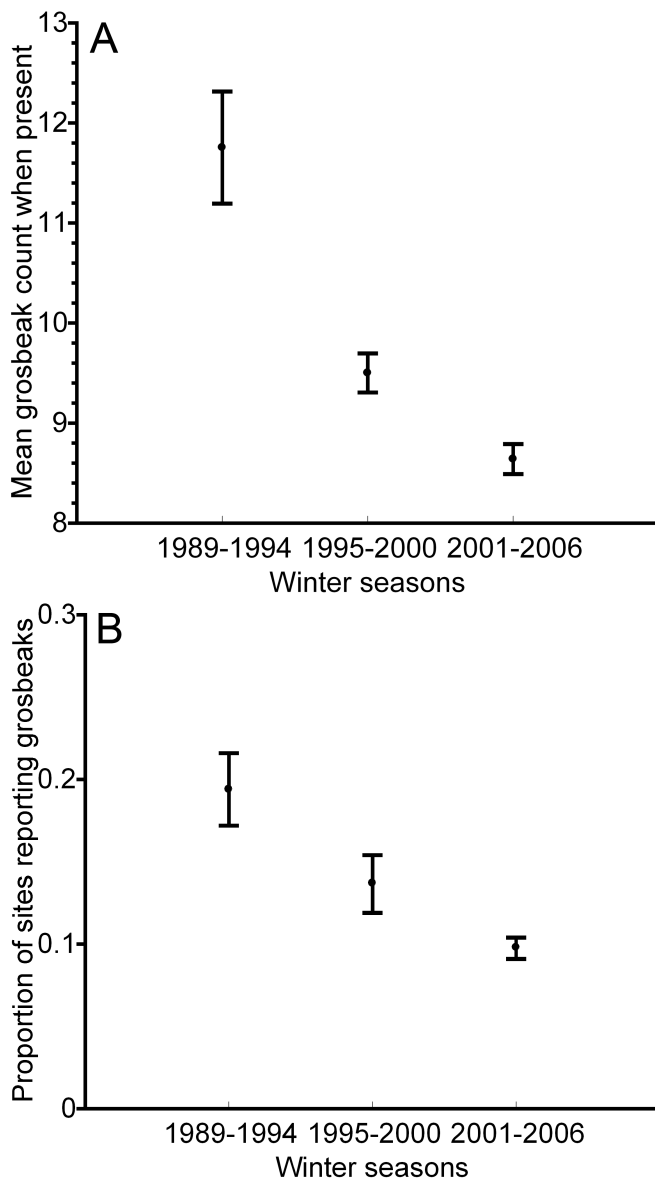


FIGURE 1. (A) Mean Evening Grosbeak flock size when present and (B) average proportion of Project FeederWatch sites in the United States and Canada reporting Evening Grosbeaks at least once during a winter season. Values for individual winters were averaged across six seasons (mean and 95% CI).

Evening Grosbeaks also declined from 0.194 to 0.097, a –50% change (Fig. 1B). The Evening Grosbeak range contracted over the past 18 years, with fewer sites reporting birds in the Rocky Mountain, Great Lakes, Atlantic Canada, and Appalachian regions (Fig. 2). Declines in the proportion of sites reporting Evening Grosbeaks were recorded throughout the species' range, with declines exceeding 50% in areas of the Mountain West, Pacific Northwest, and northeastern North America (Fig. 3).

A significant decline in mean Evening Grosbeak counts over time was detected by the mixed model ($F_{17,812.478} = 818$, $P < 0.001$). We identified 391 long-term sites that reported Evening Grosbeaks in at least three seasons (50 714 checklists). Significant declines were recorded at 76 sites (linear regression of year by \ln [average maximum grosbeak count], all $t > 3.0$, all $P < 0.01$). No significant increases in Evening Grosbeak counts were detected.

DISCUSSION

We documented a widespread contraction of the range and decrease in the abundance of Evening Grosbeaks visiting feeding stations in winter across North America. Counts of birds at feeding stations have proven reliable for monitoring population trends, with widespread agreement between trends detected in feeder-based monitoring programs and other large-scale monitoring efforts such as the Breeding Bird Survey and the Christmas Bird Count (LePage and Francis 2002, Chamberlain et al. 2005, Butcher and Niven 2007).

The mechanisms contributing to these changes have not yet been conclusively identified, and understanding the causes of the observed declines is hampered by a lack of basic life-history information. More information is needed about the breeding biology and reproductive success of Evening Grosbeaks—information that may prove critical to understanding the current population trends. In contrast to their gregarious nature during the nonbreeding season, Evening Grosbeaks become elusive and quiet during the breeding season (Gillihan and Byers 2001). Few studies of the species during the nesting season have been conducted (but see Bekoff et al. 1989, Scott and Bekoff 1991).

Studies of breeding bird communities in western and northern forests point to the potentially negative influence on Evening Grosbeak populations of anthropogenic changes to the environment such as habitat destruction and forest management practices. Large-scale forestry operations are increasingly affecting the age-class composition of stands in the boreal forest. In a study of breeding bird communities in forests of different age classes in Saskatchewan, Cumming and Diamond (2002) surveyed young stands (50–60 years old), rotation-age stands (80–90 years), old stands (100–110 years), and stands older than 140 years. Evening Grosbeaks were significantly more abundant in the two oldest age classes and were not detected in forests <100 years old (Cumming and Diamond 2002).

Three Oregon-based studies help to further elucidate the importance of mature, diverse forests for Evening Grosbeaks. In a large-scale study conducted across various habitat types, McGarigal and McComb (1995) investigated the relationship between landscape structure and breeding bird abundance in the Coast Range of Oregon. Evening Grosbeaks were most often detected in the most mature forest classes (95% of 417 detections at 1046 sampling locations; McGarigal and McComb 1995). In a series of experimentally manipulated stands in western Oregon, Hayes et al. (2003) detected a threefold increase in Evening Grosbeak populations in thinned forests versus unmanaged, even-aged stands of young, regenerating forest. Similarly, in another study

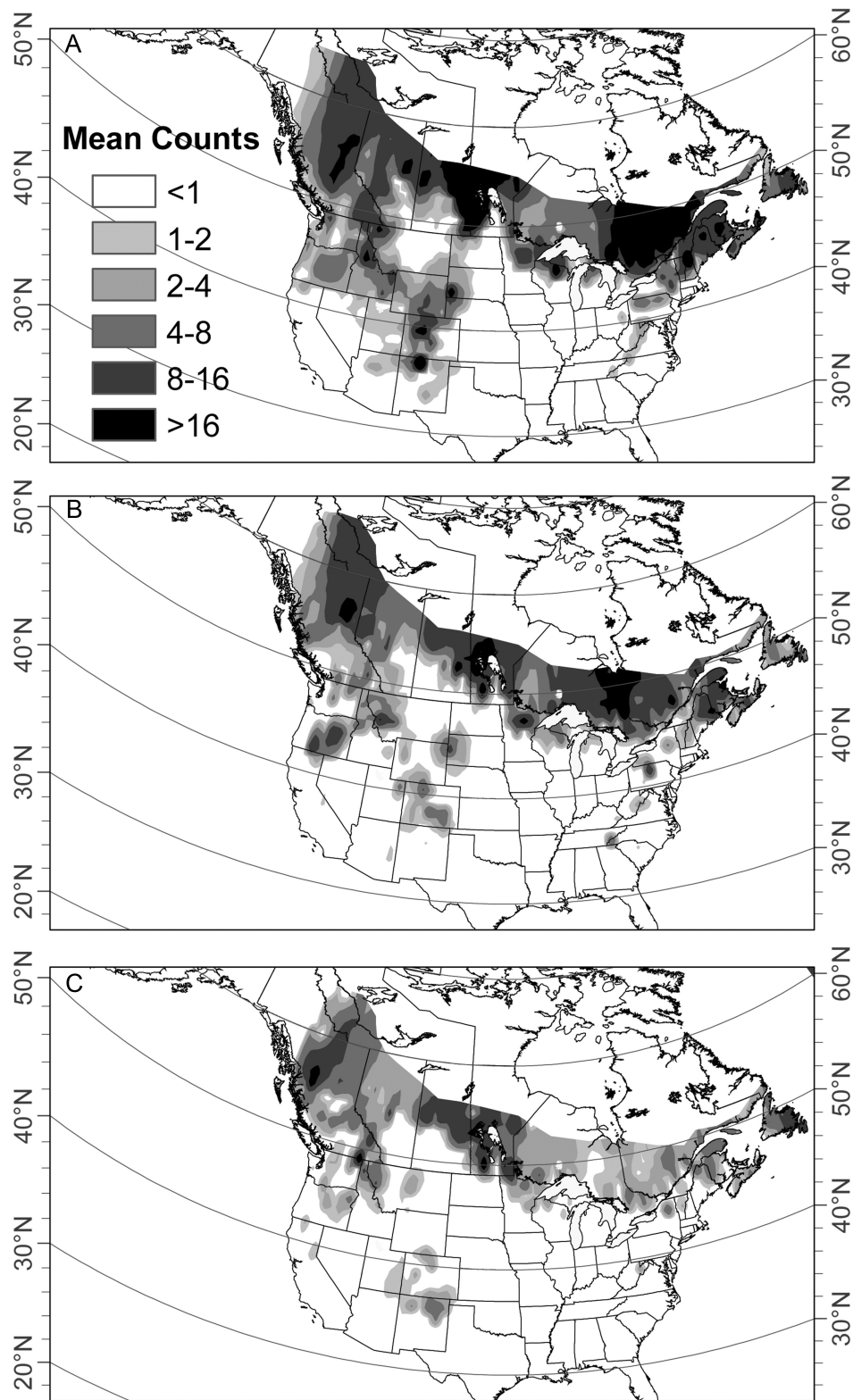


FIGURE 2. Interpolated distribution and mean abundance of Evening Grosbeaks at feeders during winter in (A) 1989–1994, (B) 1995–2000, and (C) 2001–2006. The distribution of Evening Grosbeaks in northern Canada is not shown (white area) due to a lack of data. Evening Grosbeaks were absent from the white areas in the lower 48 states. Maps are based on data submitted from Project FeederWatch locations in the United States and Canada.

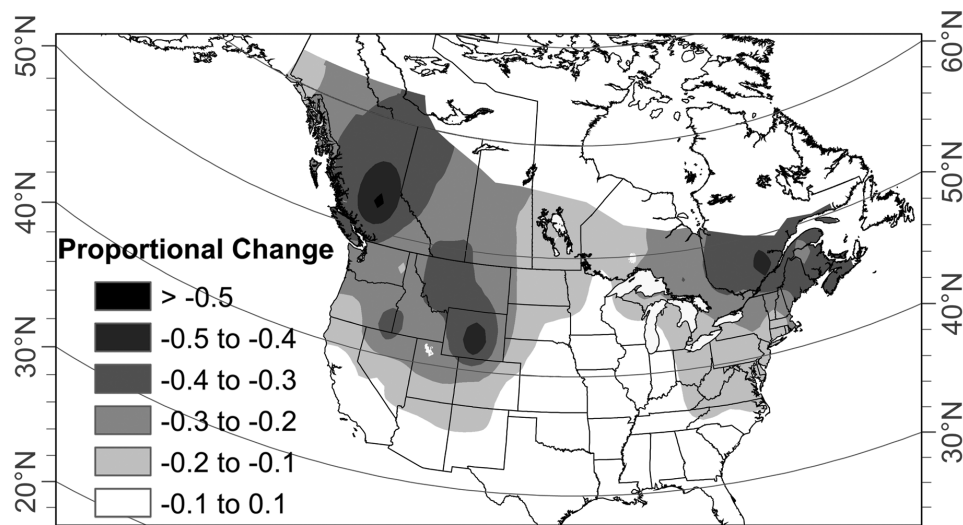


FIGURE 3. Interpolated distribution of changes in the proportion of sites reporting Evening Grosbeaks between 1989–1994 and 2001–2006. Maps are based on data submitted from Project FeederWatch locations in the United States and Canada.

conducted in the Coast Range of Oregon, Hagar et al. (1996) detected significantly fewer Evening Grosbeaks in even-aged tree plantations that lacked structural diversity than in similar stands that had been commercially thinned. Thus, the decreasing structural diversity that results from even-aged forestry management practices may be contributing to the observed decline in Evening Grosbeak populations.

Alteration of Canada's boreal forest is proceeding rapidly with greater than 1 million ha of forest harvested in Canada in 2006 (Natural Resources Canada 2008a). Although forests are widely replanted (>418 000 ha in 2005; Natural Resources Canada 2008b), even-aged stands growing on harvested lands may not provide suitable habitat for Evening Grosbeaks for upwards of 100 years (Hagar et al. 1996, Cumming and Diamond 2002, Hayes et al. 2003). In addition to the potential impacts of the forestry industry, oil and gas development, precious metal and mineral mining, agriculture, and hydroelectric power development are all contributing to alteration of habitat within the Evening Grosbeak's breeding range (Canadian Boreal Initiative 2005).

Although large-scale habitat changes are likely contributing to the observed changes in Evening Grosbeak populations, additional factors including disease or changes in food availability may play a role at smaller scales. Disease has substantially affected populations of some North American birds in recent years and may be partially responsible for the recent trends in Evening Grosbeak populations. House Finch (*Carpodacus mexicanus*) populations have been significantly reduced in the past 15 years as a result of a novel strain of the bacterium *Mycoplasma gallisepticum* (MG; Dhondt et al. 1998). An apparently widespread outbreak of conjunctivitis caused by MG was recorded in Evening Grosbeaks in Quebec in 1999 (Mikaelian et al. 2001). The extent to which Evening Grosbeaks are susceptible to MG and the population consequences to grosbeaks of infection by the bacterium remain unknown.

Other diseases such as salmonellosis and West Nile virus (WNV) may also be influencing Evening Grosbeak populations. Salmonellosis (*Salmonella enterica* serotype Typhimurium) has been recognized as a common cause of mortality in various species of songbirds (Daoust et al. 2000). An outbreak of salmonellosis in

Evening Grosbeaks was recorded during the winter of 1992–1993 along the Pacific coast from British Columbia to California (Tizard 2004). In another outbreak in West Virginia, more than 100 Evening Grosbeaks were found dead in a single yard (Locke et al. 1973). West Nile virus has also significantly affected some bird populations (LaDeau et al. 2007) and has caused mortality in Evening Grosbeaks (Komar 2003). However, widespread mortality in Evening Grosbeaks related to WNV has not been reported. As with MG, the population consequences of salmonellosis and WNV remain unknown.

Parasitic infection by a mite, *Knemidokoptes jamaicensis*, has also affected some Evening Grosbeak populations (Carothers 1974, Alberta Fish & Wildlife 2004). Birds with advanced infections may lose digits or entire feet, negatively affecting their ability to perch, walk, and feed (Pence et al. 1999).

Some observers have suggested that the decline in Evening Grosbeak populations may be related to a decline in the abundance of spruce budworms (*Choristoneura fumiferana*), an insect that is exploited as a food source by grosbeaks and other birds (Patten and Burger 1998, Bolgiano 2004). Aerial applications of budworm-control chemicals by the U.S. and Canadian Forest Services have likely limited budworm outbreaks since the 1970s. Budworm populations have been recorded at only background levels in Atlantic Canada since the late 1980s (Natural Resources Canada 2007). The current decline in Evening Grosbeak populations has coincided with a low point in the budworm cycle. However, the link between bird and budworm populations remains correlative.

With continued habitat loss due to anthropogenic activities and predicted habitat changes due to climate change likely placing further pressure on Evening Grosbeak populations, the future of the species may be tenuous in eastern North America. Near extirpation of the Evening Grosbeak in the northeastern United States is predicted by two climate change models as balsam fir (*Abies balsamea*) forests are projected to retreat into Canada (Matthews et al. 2004). The mechanisms that facilitated the initial range expansion of Evening Grosbeak populations across North America remain poorly understood. Likewise, determining the causes of the current range contraction and population decline presents a challenge. Understanding the factors influencing

Evening Grosbeak populations is critical to developing conservation plans and reversing current population trends.

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LITERATURE CITED

- ALBERTA FISH & WILDLIFE. 2004. Scaly-leg mites (*Knemidokoptes* sp.) in Alberta. Alberta Sustainable Resource Development. Pub. No. I/167.
- BEKOFF, M., A. C. SCOTT, AND D. A. CONNER. 1989. Ecological analyses of nesting success in Evening Grosbeaks. *Oecologia* 81:67–74.
- BLANCHER, P. 2003. Importance of Canada's boreal forest to landbirds. Canadian Boreal Initiative, Ottawa, Canada, and the Boreal Songbird Initiative, Seattle, WA.
- BOLGIANO, N. C. 2004. Cause and effect: changes in boreal bird irruptions in Eastern North America relative to the 1970s spruce budworm infestation. *American Birds* 58:26–33.
- BUTCHER, G. S., AND D. K. NIVEN. 2007. Combining data from the Christmas Bird Count and the Breeding Bird Survey to determine the continental status and trends of North American Birds. National Audubon Society, Ivyland, PA.
- CANADIAN BOREAL INITIATIVE. 2005. The boreal in the balance: securing the future of Canada's boreal region: a status report. Canadian Boreal Initiative, Ottawa, Canada.
- CAROTHERS, S. W., N. J. SHARBER, AND G. F. FOSTER. 1974. Scaly-leg (*Knemidokoptiasis*) in a population of Evening Grosbeaks. *Wilson Bulletin* 86:121–124.
- CHAMBERLAIN, D. E., J. A. VICKERY, D. E. GLUE, R. A. ROBINSON, G. J. CONWAY, R. J. W. WOODBURN, AND A. R. CANNON. 2005. Annual and seasonal trends in the use of garden feeders by birds in winter. *Ibis* 147:563–575.
- CUMMING, E. E., AND A. W. DIAMOND. 2002. Songbird community composition versus forest rotation age in Saskatchewan boreal mixedwood forest. *Canadian Field-Naturalist* 116:69–75.
- DAOUST, P. Y., D. G. BUSBY, L. FERNS, J. GOLTZ, S. MCBURNEY, C. POPPE, AND H. WHITNEY. 2000. Salmonellosis in songbirds in the Canadian Atlantic provinces during winter–summer 1997–98. *Canadian Veterinary Journal* 41:54–59.
- DHONDT, A. A., D. L. TESSAGLIA, AND R. L. SLOTHOWER. 1998. Epidemic mycoplasmal conjunctivitis in House Finches from eastern North America. *Journal of Wildlife Diseases* 34:265–280.
- GILLIHAN, S. W., AND B. BYERS. 2001. Evening Grosbeak (*Coccothraustes vespertinus*). In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 599. The Birds of North America, Inc., Philadelphia, PA.
- HAGAR, J. C., W. C. MCCOMB, AND W. H. EMMINGHAM. 1996. Bird communities in commercially thinned and unthinned Douglas-fir stands of western Oregon. *Wildlife Society Bulletin* 24:353–366.
- HAYES, J. P., J. M. WEIKEL, AND M. M. P. HUSO. 2003. Response of birds to thinning young Douglas-fir forests. *Ecological Applications* 13:1222–1232.
- KOMAR, N. 2003. West Nile Virus: epidemiology and ecology in North America. *Advances in Virus Research* 61:185–234.
- LADÉAU, S. L., A. M. KILPATRICK, AND P. P. MARRA. 2007. West Nile virus emergence and large-scale declines of North American bird populations. *Nature* 447:710–714.
- LEPAGE, D., AND C. M. FRANCIS. 2002. Do feeder counts reliably indicate bird population changes? 21 years of winter bird counts in Ontario, Canada. *Condor* 104:255–270.
- LOCKE, L. N., R. B. SHILLINGER, AND T. JAREED. 1973. Salmonellosis in passerine birds in Maryland and West Virginia. *Journal of Wildlife Diseases* 9:144–145.
- MARBLE, R. M. 1926. Nesting of Evening Grosbeak at Woodstock, Vermont. *Auk* 43:549.
- MATTHEWS, S. N., R. J. O'CONNOR, L. R. IVERSON, AND A. M. PRASAD. 2004. Atlas of climate change effects in 150 bird species of the eastern United States. USDA Forest Service General Technical Report NE-318.
- MCGARIGAL, K., AND W. C. MCCOMB. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecological Monographs* 65:235–260.
- MIKAELEIAN, I., D. H. LEY, R. CLAVEAU, M. LEMIEUX, AND J.-P. BÉRUBÉ. 2001. Mycoplasmosis in Evening and Pine Grosbeaks with conjunctivitis in Quebec. *Journal of Wildlife Diseases* 37:826–830.
- NATURAL RESOURCES CANADA. [ONLINE]. 2007. Spruce Budworm. <<http://cfs.nrcan.gc.ca/index/sprucebudworm>> (3 June 2007).
- NATURAL RESOURCES CANADA. [ONLINE]. 2008a. Canada's Forest Statistical Data. <<http://canadaforests.nrcan.gc.ca/statsprofile>> (25 February 2008).
- NATURAL RESOURCES CANADA. [ONLINE]. 2008b. Canada's Forests—Regeneration. <http://canadaforests.nrcan.gc.ca/article/trend/top_suj/28> (4 March 2008).
- PATTEN, M. A., AND J. C. BURGER. 1998. Spruce budworm outbreaks and the incidence of vagrancy in eastern North American wood-warblers. *Canadian Journal of Zoology* 76:433–439.
- PENCE, D. B., R. A. COLE, K. E. BRUGGER, AND J. R. FISCHER. 1999. Epizootic podoknemidokoptiasis in American Robins. *Journal of Wildlife Diseases* 35:1–7.
- SCOTT, A. C., AND M. BEKOFF. 1991. Breeding behavior of Evening Grosbeaks. *Condor* 93:71–81.
- TIZARD, I. 2004. Salmonellosis in wild birds. *Seminars in Avian and Exotic Pet Medicine* 13:50–66.
- WELLS, J. V., K. V. ROSENBERG, E. H. DUNN, D. L. TESSAGLIA-HYMES, AND A. A. DHONDT. 1998. Feeder counts as indicators of spatial and temporal variation in winter abundance of resident birds. *Journal of Field Ornithology* 69:577–586.