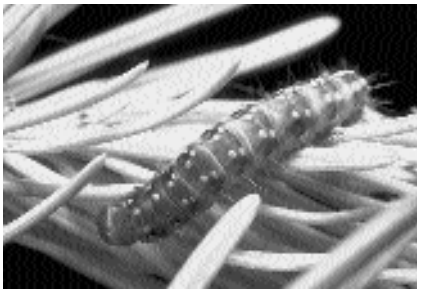
When an outbreak of the eastern spruce budworm *(Choristoneura fumiferana)* (Clem.) began in the boreal forests of eastern Canada and the bordering United States in the late 1960s, changes of immense consequence to the forests and their inhabitants were set in motion. Yet, the vastness and isolation of these forests have hidden the full effects of this infestation—often called the 1970s spruce budworm infestation—on bird populations, containment measures, and consequential changes in forest ecology.



Cause & Effect

Changes in Boreal Bird Irruptions in Eastern North America Relative to the 1970s Spruce Budworm Infestation

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Assessments of the 1970s budworm infestation's impact on birds have included small-scale studies (Zach and Falls 1975; Erskine 1977; Morse 1978; Crawford et al. 1983; Crawford and Jennings 1989), analyses of migration data (Hill and Hagan 1991; Hagan et al. 1992; Hussell et al. 1992; Patten and Burger 1998), and large-scale Breeding Bird Survey trend analyses (Erskine 1978; Robbins et al. 1986; Sauer and Droege 1992). This article adds details about the 1970s infestation and its effect on birds.

A confluence of trends from spruce budworm defoliation data, Christmas Bird Count (CBC) data, and Breeding Bird Survey (BBS) data can only be indicative of the immense scale and impact of this infestation. CBC data show apparent responses of two species to the budworm outbreak and abrupt changes in winter irruptions for five other species near the end of the outbreak. BBS data corroborate the CBC trends. Together, the data suggest that the 1970s spruce budworm infestation and related events had a massive impact upon some boreal species.

Spruce Budworm and the 1970s Infestation

Eastern spruce budworm moths lay their eggs during the summer on needles of conifers, primarily balsam fir *(Abies balsamea),* white spruce *(Picea glauca),* red spruce *(Picea rubens),* and black spruce *(Picea mariana).* Caterpillars overwinter and in the spring feed upon the needles, flowers, buds, and shoots of their host. Large-scale infestations of the eastern boreal forest periodically occur with combinations of consecutive warm, dry springs; expanses of mature forests, especially of balsam fir; and heavy conifer flowering. Over the last century, clear-cutting, replanting with susceptible white spruce, fire suppression, and use of pesticides may have contributed to larger expanses of susceptible forest, thus leading to bigger budworm outbreaks. Twentieth century infestations grew larger over time; those of 1910–1920, 1945–1955, and 1968–1985 defoliated approximately 10, 25, and 55 million hectares, respectively (Blais et al. 1981; Blais 1983, 1985a; Hardy et al. 1983). To put 55 million hectares into perspective, the combined area of New York, Pennsylvania, Maryland, West Virginia, Virginia, and North Carolina is about 57 million hectares.

The 1970s spruce budworm infestation started during the late 1960s in small areas of eastern Ontario, western Quebec, and New Brunswick. In 1974, a spectacular advance coincided with heavy conifer flowering, resulting in the defoliation of large expanses of boreal forest from Lake Superior to the Atlantic by the 1975 peak. By the mid-1980s, the outbreak had collapsed in most areas, except in northwestern Ontario (Figure 1) (Kettela 1981; Figure 1 data from Blais et al. 1981; Armstrong and Ives 1995). Collapse of budworm outbreaks usually occurs when caterpillars starve after eating the available food or die from unfavorable weather, biological agents, or applied pesticides (Blais 1983; Raske 1985).

Host tree species differ in their vulnerability to budworms, which has implications for birds. Balsam fir is a preferred host of spruce budworms and the most likely to die from repeated defolia-

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Eastern spruce budworm *(Choristoneura fumiferana)* larva. Photo/Jerald E. Dewey, USDA Forest Service, www.forestryimages.org

tions. Mortality is typically 70–100 percent in mature balsam fir stands and 30–70 percent in immature stands (MacLean 1980, 1984; Hudak and Raske 1981).

Historically, balsam fir has been the second most common conifer in much of the eastern boreal forest, especially in eastern Quebec, western New Brunswick, northern Nova Scotia, and Newfoundland, all areas widely defoliated during the 1970s budworm outbreak (Hudak and Raske 1981; Blais 1985b,c; Kettela 1981). White and red spruces also are vulnerable, while black spruce, the most common conifer of the eastern boreal forest, is less vulnerable. As a result of the 1970s infestation, half or more of the affected forest was dead by the mid-1980s, and many of the weakened and dead trees were felled for salvage (MacLean 1980, 1985; Howse 1995; Hudak and Raske 1981, 1995; Lachance 1995). In recent years, forest managers have utilized these vulnerability differences to try to minimize future budworm outbreaks. The trend has been toward cutting younger trees and replanting with black spruce and jack pine *(Pinus banksiana),* which is not a preferred budworm host. These measures could affect birds as balsam fir forests support some of the highest bird concentrations of Canada's forests, while the same area of jack pine forest supports many fewer birds (Erskine 1977, 1992).

The Irruption Phenomenon

An "irruption" is the movement of an unusually large number of individuals from their usual post-breeding range. Irruptions of birds from Canada and the northern United States southward during fall and early winter were once thought to be irregular events. However, Bagg (1969) noted that large alternate-year movements of Black-capped Chickadees *(Poecile atricapillus)* in Ontario during 1951–1968 coincided with Chapman's observations of low natural food supplies in Maine. Subsequently, Bock and Lepthien (1972; 1976), and later Koenig (2001), in analyses of CBC data, found North American counts of Red-breasted Nuthatches *(Sitta canadensis)* and some of the northern finches synchronized with the Black-capped Chickadee irruptions. Irruptions are apparently related to patterns of tree masting (seed production), which can occur synchronously over vast areas, up to 2500 km (1550 miles) in span (Koenig and Knops 1998, 2000). In winters when there are sufficient seeds, many boreal seed-eating birds remain in northern areas; when seed production is low, they irrupt in search of food (Newton 1973; Bock and Lepthien 1976; Koenig and Knops 2001).

Trends in the Christmas Bird Count

CBC data through the 1996–1997 count were obtained from Shipman (1998), with later data obtained from *American Birds* and www.birdsource.org. For simplicity, I refer to the year as the year in which Christmas occurred.

For seven species, apparent changes in irruption patterns, detected in CBC data, coincide with aspects of the 1970s spruce budworm infestation. The irruption extent of Evening Grosbeaks *(Coccothraustes vespertinus)* and Purple Finches *(Carpodacus purpureus)* follow the trend of the infestation, increasing as the infestation expanded and declining as the infestation collapsed. Irruptions of Black-capped Chickadees, Boreal Chickadees *(Poecile hudsonica),* Pine Grosbeaks *(Pinicola enucleator),* Red Crossbills *(Loxia curvirostra),* and White-winged Crossbills *(Loxia leucoptera)* appear to have abruptly declined in extent near the end of the budworm infestation. Irruption patterns in Red-breasted Nuthatches, Pine Siskins *(Carduelis pinus),* and Common Redpolls *(Carduelis flammea)* did not appear to show similar changes.

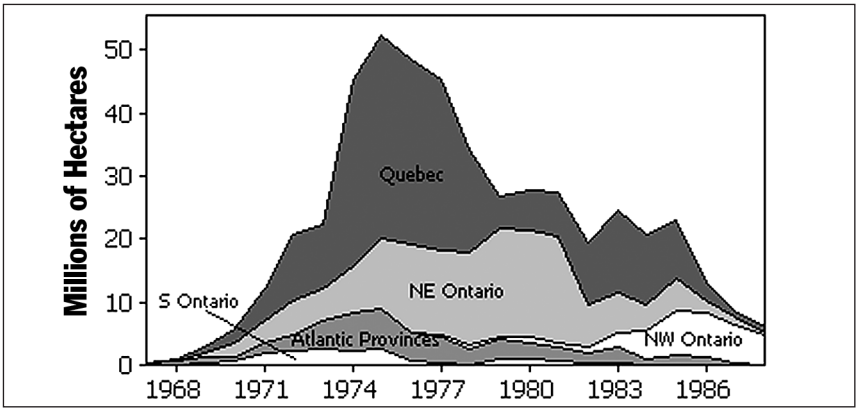

Figure 1. Area, in millions of hectares, defoliated by spruce budworms in eastern Canada, 1967–1988. Atlantic Province data from Newfoundland and the Maritime Provinces.

Evening Grosbeak

Evening Grosbeaks were infrequently found in eastern North America until the late 1800s, when they began a range expansion from the west. Expansive pulses occurred during 1883–1890, during 1901–1917, and between the early 1940s and the mid-1950s (Forbush 1929; Baillie 1940; Speirs 1968; Shaub 1956; Brunton 1994; Gillihan and Byers 2001).

The classic theory for this range expansion is that the planting of ornamental box-elders *(Acer negundo)* around urban areas attracted irrupting Evening Grosbeaks (Taverner 1921; Forbush 1929; Speirs 1968; Erskine 1992; Gillihan and Byers 2001). However, Ouellet (1974, cited by Gillihan and Byers 2001) thought that spruce budworm caterpillars were the attraction. Evening Grosbeaks are known to congregate in budworm-infested areas to feed upon the caterpillars (Morris et al. 1958; Blais and Parks 1964; Speirs 1968; Erskine 1977; Crawford et al. 1983; Jennings and Crawford 1985; Speirs 1985). Some of the Evening Grosbeak expansions concurred with budworm outbreaks; Blais (1983) documented one budworm outbreak beginning around 1877, and, as previously mentioned, those of 1910–1920 and 1945–1955. Brunton (1994) discounted the classic theory, for in his view, box-elders were too restricted in distribution and too late in becoming

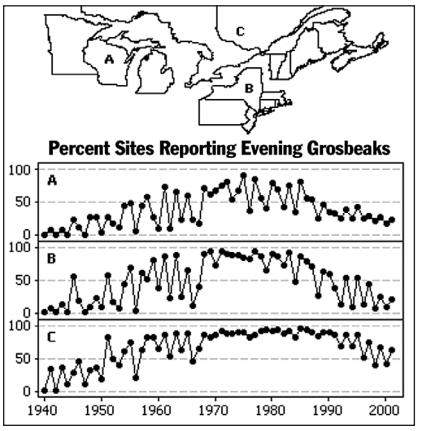

Figure 2. Percent CBC sites reporting Evening Grosbeak, 1940–2001.

established to explain the Evening Grosbeak range expansion. He thought that the grosbeak expansion could only be explained by a major landscape change, the most likely impetus being lumbering and subsequent fires during the early 1900s leading to colonization over large areas by pin cherry *(Prunus pensylvanica),* whose seeds are another favored food of Evening Grosbeaks.

Few Evening Grosbeaks were reported from eastern CBC sites before the winter of 1945–1946, with just 160 reports from sites in Ontario and Minnesota eastward. The percent of sites reporting grosbeaks increased to sustained high values between 1968 and 1985 in Great Lakes states (Figure 2, Region A) and Mid-Atlantic and southern New England states (Figure 2, Region B). In eastern Canada and northern New England (Figure 2, Region C), the peak period lasted longer, until 1991. There was close agreement in report patterns among states and provinces within these three regions. The seesaw pattern indicative of alternate-year irruptions is evident before and after the peak period (Figure 2). The Evening Grosbeak counts adjusted for party-hours increased less rapidly than did the percent of sites reporting grosbeaks, but the peak periods were approximately the same in each region. Regression analysis of both percent sites reporting grosbeaks and effort-adjusted counts showed significant statistical evidence for declines since 1980 in each region. These results, and CBC results for the other species discussed here, were unaffected by data from sites starting up after 1970.

In recent years, Evening Grosbeaks have been consistently found during the CBC only in sites in or near boreal forests, while at many locations to the south, they have become difficult to find. In comparison, during the 1968–1985 period, Evening Grosbeaks were found as far south as Louisiana and Georgia. The CBC data suggest that the 1970s budworm infestation had a direct effect upon Evening Grosbeak numbers, by increasing their food supply and reproduction level.

Purple Finch

Purple Finches are typically found in mature spruce-fir forests and are known for their attraction to and consumption of spruce budworm larvae (Sanders 1970; Erskine 1977). In studies of the stomach contents of boreal birds, Mitchell (1952) and Crawford and Jennings (1989) ranked Purple Finches among the most prolific consumers of spruce budworm larvae. Dowden et al. (1953) noted incursions of Purple Finches to budworm-infested areas, and found that 79–84 percent of the food items in the stomachs of 64 Purple Finches and 32 Cedar Waxwings *(Bombycilla cedrorum)* were budworms. However, Morris et al. (1958) did not find Purple Finches to numerically increase as budworms increased.

In eastern North America, many Purple Finches regularly winter south of their breeding grounds, with some of the highest concentrations from Virginia and the Carolinas to Missouri, Arkansas, and Oklahoma (Root 1988). From sites in or near the central and southern Appalachians, where consistently high reports occurred, the highest effort-adjusted Purple Finch counts occurred between 1972 and 1982. Since 1985, this measure has fallen to very low levels, lower than before the 1970s budworm outbreak (Figure 3). Regression analysis of the 1980–1995 data showed significant statistical evidence for a decline.

Competition with House Finches *(Carpodacus mexicanus),* which can occur at winter feeders (Shedd 1990), has been suggested as the reason for recent Purple Finch declines (Wooton 1987, 1996). However, Purple Finches began declining in New England and elsewhere before House Finches arrived there, suggesting that habitat change was a more likely cause (Dunn and Tessaglia-Hymes 1999). The CBC data suggest that the 1970s budworm infestation and subsequent forest changes may have had a direct effect upon Purple Finch numbers.

Black-capped Chickadee

Large numbers of irrupting Black-capped Chickadees usually disperse by the CBC period, but there are three places in eastern North America where apparently irrupting Black-capped Chickadees have regularly congregated in winter, each near geographical migrant funnels and the contact zone between Black-capped Chickadees and Carolina Chickadees *(Poecile carolinensis):* in southeastern Pennsylvania, along the western end of Lake Erie, and at the

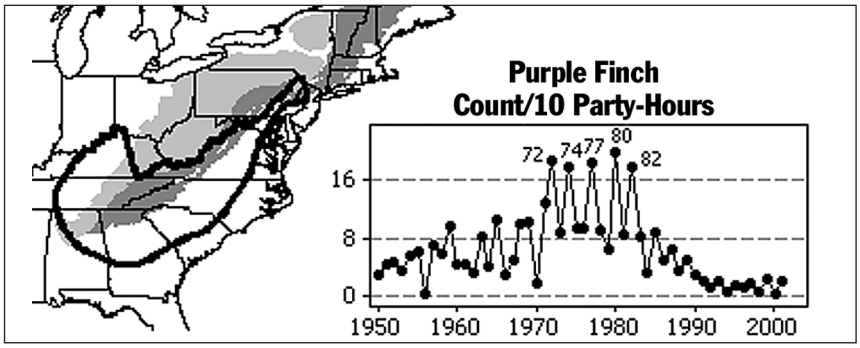

Figure 3. CBC Purple Finch count/10 party-hours, 1950–2001, from sites in the outlined region. Gray shading indicates upland or mountainous physiographic provinces. Numbers above symbols represent year values.

southern end of Lake Michigan. It is from southeastern Pennsylvania where the data have exhibited the strongest signal of regular irruptions (Bolgiano 2004).

CBC counts of Black-capped Chickadees in southeastern Pennsylvania during 1954–1983 showed the seesaw pattern of alternate-year irruptions. However, changes in this pattern occurred after 1983. North of the contact zone (Figure 4, Region A), the oscillating pattern appears to have dampened, as the year-to-year variability, measured by the standard deviation, decreased by half (14.3 during 1950–1983 and 6.9 during 1984–2002). South of the contact zone (Figure 4, Region B), large numbers of Black-capped Chickadees were not observed after 1983.

That the spikes in southeastern Pennsylvania CBC Black-capped Chickadee counts represent irrupting chickadees is corroborated by the fall reports of observers to *Audubon Field Notes, American Birds,* and *North American Birds,* reports previously summarized by James (1958) and Bock and Lepthien (1976). There was close agreement between CBC data and observers' reports for all years but two (Bolgiano 2004). The consistency of irruptions throughout 1954–1983 with an abrupt change near the onset of widespread boreal forest destruction suggests this destruction as a possible cause for the dampening of chickadee irruptions.

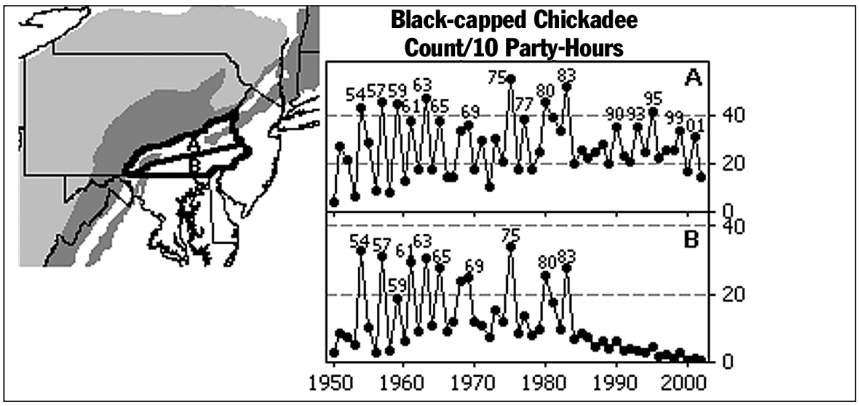

Figure 4. CBC Black-capped Chickadee count/10 party-hours from southeastern Pennsylvania sites, above (A) and below (B) the contact zone between chickadee species, 1950–2002. Gray shading indicates upland or mountainous physiographic provinces.

Boreal Chickadee

Boreal Chickadee irruptions often occur during the same season as Black-capped Chickadee irruptions (Bull 1985; Ficken et al. 1996; Peterjohn 2001), though Boreal flights may lag behind Black-capped flights by a few weeks to a month (Carleton 1966; Finch 1970). For the Boreal Chickadee, as for the Pine Grosbeak and the two crossbills, New York and southern New England (Massachusetts, Connecticut, Rhode Island) are where large irruptions are periodically observed (Yunick 1984; Veit and Petersen 1993; Levine 1998). CBC data from this region indicate major Boreal Chickadee irruptions in 1954, 1961, 1969, and 1975, and much less extensive irruptions in other years. Since 1983, only a few Boreal Chickadees have been tallied on CBCs within this region, with most being found in the Adirondacks (Figure 5).

Mature conifer stands appear to be essential for Boreal Chickadees. They tend to be more abundant during budworm outbreaks than otherwise, and timber salvage cuts following budworm outbreaks apparently can reduce available habitat (Erskine 1992; Smith 1994; Ficken et al. 1996). The loss of mature forests suggests that a population decline in Boreal Chickadees accompanied the change in irruptions.

Pine Grosbeak

Like the Boreal Chickadee, the Pine Grosbeak is uncommon south of the boreal forest except during major irruptions (Austin 1968; Levine 1998). The CBC data from New York and southern New England since 1940 show widespread irruptions at regular intervals of three to five years. Since 1985, irruptions have been much smaller in extent (Figure 5). When counts were adjusted for party-hours, the minor post-1985 irruptions represented very few grosbeaks.

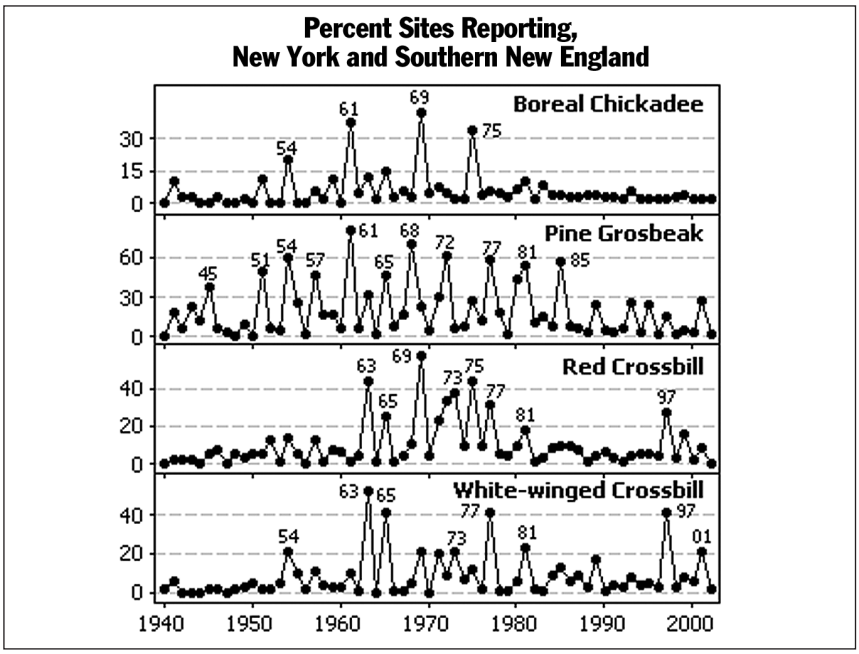

Figure 5. Percent of New York and southern New England CBC sites reporting Boreal Chickadee, Pine Grosbeak, and the two crossbills, 1940–2002. Numbers next to symbols are year values.

The presence of Pine Grosbeaks has been linked to forestry practices. Clear-cutting has been blamed for the decline of Pine Grosbeaks in Finland. In Newfoundland and the Queen Charlotte Islands of British Columbia, Pine Grosbeaks were difficult to find except in small regenerating clear-cuts or clear-cuts surrounded by undisturbed forest (Adkisson 1999). Although Pine Grosbeaks feed upon budworms (Mitchell 1952; Jennings and Crawford 1985; Erskine 1992), the abrupt change in Pine Grosbeak irruptions suggests that, as for the chickadees, it may have been caused by the boreal forest destruction near the end of the budworm infestation.

Red Crossbill and White-winged Crossbill

The irruption patterns of the Red Crossbill and White-winged Crossbill in eastern North American share common features, although the breeding range of White-winged Crossbills tends to be more northerly than the breeding range of Red Crossbills, and the latter species is classified into multiple "call types" (Benkman 1992; Groth 1993; Adkisson 1996). CBC data from New York and southern New England since 1940 show irruptions of both crossbill species at two- to four-year intervals between 1963 and 1981, then a break of 15 years during which crossbills were seldom found, and then more recent irruptions beginning in 1997 (Figure 5). When counts were adjusted for party-hours, the 1989 White-winged Crossbill numbers were comparatively high, but they were concentrated at two sites in the Adirondacks. Red Crossbill irruptions in New York occurred after the CBC count period during the winters of 1960–1961 and 1984-1985 (Levine 1998).

Crossbill population numbers and irruptions are closely tied to the size of conifer cone crops (Benkman 1992, 1993; Adkisson 1996). Crossbills have historically disappeared from large regions after logging, as happened for Red Crossbills in Nova Scotia after 1922 (Erskine 1992) and in New York and other northeastern states after 1910 (Dickerman 1987). Red Crossbills returned to Nova Scotia during the 1960s and 1970s as the forest matured. White-winged Crossbills appeared in large numbers in the Maritime Provinces during 1988, coinciding with the heaviest cone crop in many years (Erskine 1992). The trend toward lumbering younger trees is thought to be detrimental to crossbill populations, as mature trees produce the heaviest cone crops (Benkman 1992, 1993). The gap in irruptions after 1981 suggests that the large-scale forest destruction by budworms may have caused crossbill population declines.

Corroborative Trends in the Breeding Bird Survey

BBS trends corroborate the CBC trends for the Evening Grosbeak and Purple Finch and add context to the irruption changes for the Black-capped Chickadee, Boreal Chickadee, Pine Grosbeak, Red Crossbill, and White-winged Crossbill. BBS data were obtained from www.mp2-pwrc.usgs.gov/bbs. Data from eastern Quebec routes showed the most consistent response of birds to the budworm infestation, specifically those routes near Quebec City and on both sides of the St. Lawrence River as it widens east of Quebec City (north of 46.8 degrees latitude, east of 73 degrees longitude). These routes were within balsam fir's core range (Blais 1985b) and an expansive region of the budworm infestation (Kettela 1981). The BBS started in 1967 in eastern Quebec, but I omitted data from that year, as there were only two routes. During subsequent years, the number of routes ranged from four to 20, representing 19–44 percent of the Quebec routes.

BBS counts of the Tennessee Warbler *(Vermivora peregrina),* Cape May Warbler *(Dendroica tigrina),* Bay-breasted Warbler *(Dendroica castanea),* Blackpoll Warbler *(Dendroica striata),* Evening Grosbeak, and Purple Finch showed a close correspondence to the budworm infestation. Tennessee, Cape May, and Bay-breasted warblers are often called "spruce budworm warblers" because of their consistent positive responses to budworm outbreaks (Kendeigh 1947; Hensley and Cope 1951; Stewart and Aldrich 1951; Mitchell 1952; Dowden et al. 1953; MacArthur 1958; Morris et al. 1958; Mook 1963; Morse 1978; Crawford et al. 1983; Welsh 1987a,b; Erskine 1992). Blackpoll Warblers have sometimes increased during budworm infestations (Morris et al. 1958; Robbins et al. 1986; Hill and Hagan 1991; Hagan et al. 1992; Hussell et al. 1992; Hunt and Eliason

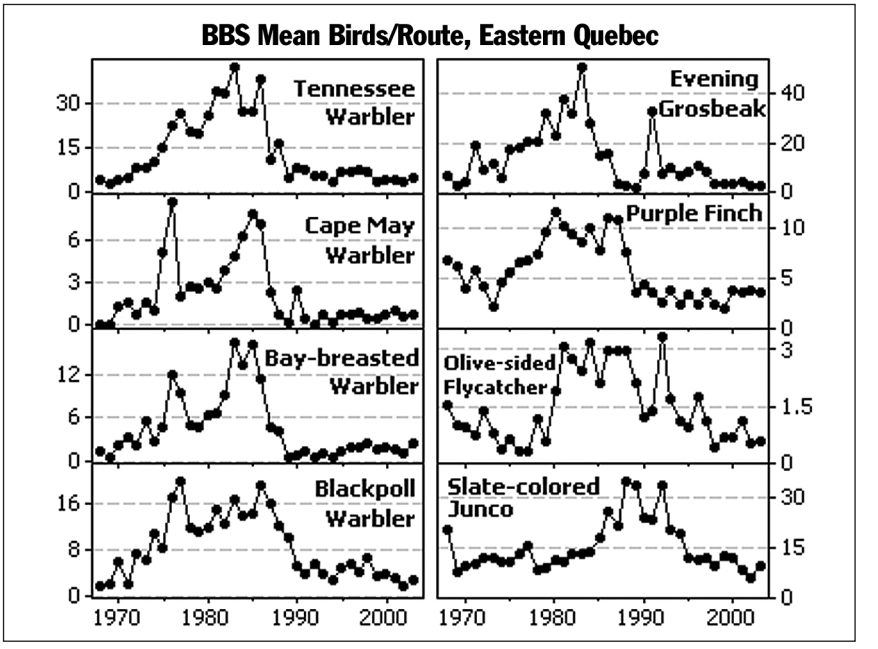

Figure 6. BBS mean birds/route from eastern Quebec, 1968–2003, for eight species.

1999). Blackpolls may be unable to coexist with the dominant Bay-breasted Warblers in many places (Morse 1979, 1989), but are able to coexist with Bay-breasteds with many budworms present (Erskine 1977). In eastern Quebec, the trend of Blackpoll Warblers was very similar to those of the budworm warblers.

Very few of the four warbler species were found during the early years of the BBS in eastern Quebec (Figure 6). Numbers quickly increased as the budworm infestation expanded, with high counts in the mid-1970s and the mid-1980s. Starting in 1987, rapid declines occurred for Tennessee, Cape May, and Bay-breasted warblers, with a more gradual decline in Blackpolls. Counts have remained low since 1990. BBS counts for Evening Grosbeaks and Purple Finches resembled the trends for the budworm warblers and the CBC trends for these two species. Evening Grosbeak numbers increased during 1975–1983 and subsequently declined, except for 1991, which is probably an anomaly caused by 352 grosbeaks being tallied on one route. Purple Finch numbers peaked during 1979–1987 and have been low since 1989 (Figure 6). Trend analysis over 1980–1995 for the four warblers and two finches in Quebec as a whole indicates significant statistical evidence for declines, with estimated yearly declines of 8.2–19.4 percent (Sauer et al. 2003).

The eastern Quebec BBS trends of other species are consistent with ecological changes related to the 1970s budworm infestation. For example, Olive-sided Flycatchers *(Contopus cooperi),* which prefer forest openings with dead snags, were most commonly found during the 1980s, when much of the forest was dying. Increases in Dark-eyed (Slate-colored) Juncos *(Junco hyemalis hyemalis)* during the late 1980s to early 1990s are consistent with more forest openings and early succession (Figure 6).

Discussion

Changes in irruption patterns in eastern North America, as evident in the CBC data, coincide with the 1970s spruce budworm infestation. The numbers of Evening Grosbeak and Purple Finch, both known to feed heavily upon budworms, appear to have increased as the budworm infestation expanded, and declined as the budworm infestation collapsed. Purple Finch counts appear to have decreased even further as large areas of forest were destroyed. For the Black-capped Chickadee, Boreal Chickadee, Pine Grosbeak, Red Crossbill, and White-winged Crossbill, the number of irrupting birds appears to have abruptly declined after the mid-1980s. That their irruptions continued unabated before and during the 1970s budworm infestation indicates that these irruptions were probably related more to forest conditions than to the presence of budworms. For the Boreal Chickadee, Red Crossbill, and White-winged Crossbill, species associated with mature conifers, evidence suggests population declines; this possibility exists for the Pine Grosbeak as well. Whether the crossbill irruptions that began during the winter of 1997–1998 represented a resumption of regular irruptions remains to be seen.

We have learned much about boreal bird irruptions in the 25 years after Bagg's observations. But if irruptions are related to either budworm infestations or the extent of mature conifers, perhaps there are cyclic patterns to irruptions for some species, as suggested by Larson and Bock (1986). This could help explain observed changes in irruption synchrony (Koenig 2001). There may be a periodicity to budworm infestations; those in New Brunswick have occurred, on average, about every 35 years (Royama 1984). Did a golden age of irruptions end during the mid-1980s; will it recur when the forest matures? We may need to wait until that time, or for another budworm outbreak, before this question can be addressed.

An understanding of population trends of many of eastern North America's boreal birds must include the role of the 1970s spruce budworm infestation. Ironically, though the impact of the 1945–1955 budworm infestation on birds was well studied, it may have been dwarfed by the impact of the lesser-studied 1970s infestation, as suggested by the CBC data. Was the 1970s event large enough to significantly contribute to general declines of neotropical migrants during the 1980s (Hagan and Johnston 1992), and of the concurrent decline of one of their main predators, the Sharp-shinned Hawk *(Accipiter striatus)* (Viverette et al. 1996)? The magnitude and timing of forest changes, and of some bird population changes, suggest that the budworm infestation and related events be considered as contributing factors. If shown to be true, it would be consistent with previous research indicating the importance of breeding- season events to explaining population trends (Holmes and Sherry 1988). As we retrospectively examine this period, the words of Morris et al. (1958, p. 492) about the prior infestation may prove insightful: "An event of such ecological magnitude could hardly fail to have its ramifications throughout the populations of all forest animals." We have yet to decipher all the details of what happened then, but North America's two large-scale bird surveys, the CBC and the BBS, have informed us that the spruce budworm event of the 1970s apparently had a major impact on boreal forest bird populations.

Acknowledgments

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