A review of the interaction between forest birds and eastern spruce budworm

L.A. Venier and S.B. Holmes

Abstract: The eastern spruce budworm, *Choristoneura fumiferana* Clem., (hereafter budworm) is responsible for the largest areas of insect-caused disturbance in North America, and as such, is an important part of spruce–fir forest change and succession. The insectivorous forest bird community shows large and rapid responses to budworm outbreaks. There is good evidence that there are budworm-linked species (bay-breasted, Cape May, and Tennessee warblers) that respond to budworm outbreak much more strongly and consistently than other species, probably through increased productivity of local populations when budworm are abundant. There also appears to be a more widespread positive bird community response to budworm outbreak that involves many more species. The response is evident in local and regional scale studies, but individual species' responses across studies are not always consistent, probably because of the relatively small number of studies conducted in a wide variety of contexts. Budworm outbreaks provide a short-term increase in food supply for birds, but also result in longer-term habitat change due to budworm-induced defoliation and tree mortality. Birds appear to influence budworm cycles, mostly at endemic population levels, through predation of large larvae and pupae. There are good arguments suggesting that bird predation is not the primary cause of budworm oscillations, but may play a role in determining the mean level of oscillations. Climate change is expected to change the bird–budworm relationship through changes in fire regimes, spruce–fir distributions, bird distributions, and budworm and bird phenology.

Key words: forest birds, spruce budworm, *Choristoneura fumiferana* Clem., budworm population regulation, numerical response, functional response.

Résumé : La tordeuse du bourgeon de l'épinette, *Choristoneura fumiferana* Clem., (ci-après nommée tordeuse) est responsable des plus grandes superficies dévastées par des insectes en Amérique du Nord, et comme telle joue un rôle important dans les changements et la succession des forêts de sapin et d'épinette. La communauté des oiseaux forestiers insectivores réagit fortement et rapidement aux invasions par la tordeuse. Il semble évident qu'il existe des relations entre les espèces liées à la tordeuse (parulines à flanc marron, du Cap May et du Tennessee) qui réagissent aux épidémies de tordeuses plus fortement et plus régulièrement que les autres espèces, probablement par une productivité accrue des populations locales lorsque les tordeuses sont abondantes. Il semble également y avoir plus de réactions positives et étendues de la communauté aviaire impliquant plusieurs autres espèces. La réaction est évidente dans les études à l'échelle locale et régionale, mais les réactions des espèces individuelles pour l'ensemble des espèces ne sont pas toujours congrues, probablement liées au nombre relativement faible d'études conduites dans une grande variété de contexte. Les épidémies de tordeuses fournissent une augmentation à court terme de nourriture pour les oiseaux, mais conduisent aussi à des modifications à long terme de l'habitat suite à la défoliation causée par la tordeuse et la mortalité des arbres. Les oiseaux semblent influencer les cycles de la tordeuse, surtout à l'état endémique des populations, par prédation des grosses larves et des pupes. Il y a de bons arguments suggérant que la prédation par les oiseaux ne constitue pas la cause primaire des oscillations de la tordeuse, mais pourrait jouer un rôle déterminant dans le degré moyen d'oscillation. On s'attend à ce que le changement climatique modifie la relation entre les oiseaux et la tordeuse par le changement des régimes des feux, des distributions du sapin et de l'épinette, de la distribution des oiseaux et de la phénologie de la tordeuse et des oiseaux.

Mots-clés : Motys clés: oiseaux forestiers, tordeuse du bourgeon de l'épinette, *Choristoneura fumiferana* Clem., régulation des populations de tordeuse, réaction quantitative, réaction fonctionnelle.

[Traduit par la Rédaction]

1. Introduction

The eastern spruce budworm, *Choristoneura fumiferana* Clem., is North America's most damaging native forest insect pest, measured either by total area affected or by amount of tree mortality (Hardy et al. 1986). Spruce budworm outbreaks have been part of the ecology of spruce–fir forests in North America for centuries (Harvey 1985), and form an important part of the cycle of growth and renewal in eastern forests (Baskerville 1975). Its distribution is vast (Harvey 1985) and its long-term impact on forest composition, succession, and therefore habitat for forest birds is profound. Spruce budworm outbreaks also have a direct and immediate local-scale effect on insectivorous forest birds by providing a periodic superabundant source of food (MacArthur 1958). The large and rapid response of the insectivo-

Received 9 December 2009. Accepted 3 February 2010. Published on the NRC Research Press Web site at er.nrc.ca on 14 July 2010.

L.A. Venier[1] and S.B. Holmes. Great Lakes Forestry Centre; Canadian Forest Service, Natural Resources Canada, 1219 Queen St. E, Sault Ste. Marie, ON P6A 2E5, Canada.

[1] Corresponding author (e-mail: lvenier@nrcan.gc.ca).

doi:10.1139/A10-009

rous forest bird community to spruce budworm outbreak is one of the most striking wildlife phenomena in the boreal forest with overall bird densities increasing 2- to 5-fold within the trajectory of an outbreak (Kendeigh 1947; Morris et al. 1958; Sanders 1970; Holmes et al. 2009; Venier et al. 2009).

There have been relatively few field studies that have directly addressed the relationship between forest birds and budworm. Several projects have focused on the response of birds to budworm in Ontario, at Black Sturgeon Lake (Kendeigh 1947; Sanders 1970; Holmes et al. 2009), Manitouwadge (Venier et al. 2009), and Algonquin Park (Zach and Falls 1975). Bird responses to budworm were also examined in New Brunswick, as part of the Green River Project from 1947 to 1978 (Morris et al. 1958; Gage and Miller 1978), and in Quebec (Blais and Parks 1964). The effectiveness of birds in controlling budworm outbreaks was studied in Maine and New Hampshire in the late 1940s (Hensley and Cope 1951; Mitchell 1952; Stewart and Aldrich 1952; Dowden et al. 1953) and again in the 1980s (Crawford and Jennings 1989; Crawford et al. 1983, 1990).

The local effect of increasing bird densities in response to budworm availability is scaled up by the large geographic extents of budworm outbreaks. We see signals of these outbreaks in long-term, broad-scale bird monitoring programs such as the Breeding Bird Survey (Sleep et al. 2009), migration monitoring (Robbins et al. 1989; Hussell et al. 1992; Patten and Burger 1998), and the Christmas Bird Count (Bolgiano 2004).

In eastern North America, it has been more than a decade since a budworm outbreak of any large extent has occurred, but the cyclical nature of budworm outbreaks would suggest that it will not be long before budworm are once again creating an important disturbance over large areas of eastern spruce and fir forests. Our understanding of the relationship between forest birds and budworm outbreaks currently rests on a relatively small collection of studies spread out over the extensive range of the eastern spruce budworm. A thorough review of the bird–budworm relationship is timely because new data have recently become available to examine the issue (Holmes et al. 2009; Venier et al. 2009), new large-scale analyses of pattern have been published (Bolgiano 2004; Patten and Burger 1998; Sleep et al. 2009), concern over the conservation of forest avifauna is increasing (Blancher et al. 2009; Rich et al. 2004), and our next budworm outbreak is likely just around the corner.

2. The ecology of eastern spruce budworm outbreaks in brief

The eastern spruce budworm is an important defoliator of coniferous forests across North America. In the eastern part of its range, balsam fir (*Abies balsamea* (L.) Mill.) and white (*Picea glauca* (Moench) A. Voss), red (*Picea rubens* Sarg.) and, to a lesser extent, black (*Picea mariana* (Mill.) BSP.) spruces are its principal food (Dowden et al. 1950). Tree mortality begins 4 to 5 years after first defoliation and is completed within 10 years (MacLean 1980). The spruce budworm is univoltine. In July and early August, females lay eggs that hatch 7–14 days later. The insects overwinter as second instars. In late April and early May, before tree buds begin to expand, the second instars emerge and move toward the tips of tree branches. Larvae mine old needles until the vegetative buds begin to expand at which time the larvae bore into the buds. Here they molt into third instars and continue feeding until the sixth instar is reached. Larval development is completed about 8 weeks after emergence (Dowden et al. 1950). By late June larvae cease feeding and metamorphize into pupae. Approximately 10 days later adult moths emerge. The vast majority of budworm consumed by birds are fifth and sixth instars, and pupae (Mook 1963). Large larvae and pupae are susceptible to bird predation for about 34 days (Morris 1963*a*).

Eastern spruce budworm outbreaks occur throughout Canada, and in Minnesota, Wisconsin, Michigan, New York, Vermont, New Hampshire, and Maine in the US (Harvey 1985). Between 1954 and 1980, budworm defoliation occurred most frequently in northern Maine, New Brunswick, and southern Manitoba, but was also common in northern Ontario and southern Quebec (Hardy et al. 1986). Moderate to severe defoliation has been recorded in all Canadian provinces and territories except Nunavut (Canadian Council of Forest Ministers 2008). From 1975 to 2008, the total cumulative area moderately to severely defoliated by spruce budworm in Canada was >421 million ha, with the greatest damage occurring in Ontario, New Brunswick, and Quebec (Table 1).

Periods of high budworm population densities and associated moderate to severe defoliation typically last 5–15 years with the end of most outbreaks attributed to host tree mortality resulting in a depleted food supply (Blais 1985). Between outbreaks budworm populations can remain at low levels for from 20 to 100 years (Blais 1985). During the 20th century, outbreaks have occurred every 25 to 40 years in eastern North America (Candau et al. 1998; Jardon et al. 2003; Royama et al. 2005), but patterns of outbreak occurrence appear to have changed over time. In Quebec, outbreaks in the 20th century were generally more severe than those in the 19th century, possibly due to climate-induced reduction in fire frequency (Morin et al. 2009). The proportion of balsam fir in the forest increases with longer fire return intervals (Bergeron and Leduc 1998) and the severity of budworm outbreaks increases with the proportion of balsam fir (Morin et al. 2009). In Ontario, defoliation can be split into western, central, and eastern zones with outbreaks in the eastern zone occurring 5 to 6 years before outbreaks in the central and western zones (Candau et al. 1998). Although budworm outbreaks are cyclical and spatially extensive, there is a great deal of spatial and temporal heterogeneity in their occurrence at local and regional scales (Nealis and Regniere 2004), resulting in heterogeneity of impact on the forest ecosystem (Bergeron et al. 1995; MacLean 1980).

3. Local-scale bird community abundance

There is good evidence that the total number of forest birds rises sharply in stands within spruce budworm outbreaks. For example, bird densities increased from 200 to 355 pairs/40 ha over the period 1947–56 during a budworm outbreak in New Brunswick (Morris et al. 1958). On plots near Black Sturgeon Lake, Ontario, bird density declined

Table 1. Cumulative area within which moderate to severe defoliation by spruce budworm occurred by Canadian province and territory, 1975–2008.

	Land area[a] ($\times 10^3$ km^2)	Moderate to severe budworm defoliation[b] ($\times 10^3$ ha)	($\mathrm{ha/km^2}$)
Newfoundland and Labrador	373.9	6 129.0	16.4
Prince Edward Island	6.6	353.0	53.5
Nova Scotia	53.3	1 275.0	23.9
New Brunswick	71.4	11 720.0	164.1
Quebec	1 365.1	157 353.6	115.3
Ontario	917.7	226 726.8	247.1
Manitoba	553.6	2 195.4	4.0
Saskatchewan	591.7	4 227.0	7.1
Alberta	642.3	3 389.4	5.3
British Columbia	925.1	4 471.2	4.8
Yukon	474.7	12.0	<0.1
Northwest Territories	1 183.1	3 707.4	3.1
Nunavut	1 936.1	0.0	0.0
Canada	9 093.5	421 559.8	46.4

[a] Data from Statistics Canada; available at http://www40.statcan.ca/l01/cst01/phys01-eng.htm [accessed October 2009].

[b] Data from Canadian Council of Forest Ministers (Canadian Council of Forest Ministers 2008).

from 319 pairs/40 ha near the peak of the budworm outbreak in 1947 (Kendeigh 1947), to 123 pairs/40 ha in 1966–1968 during a non-outbreak period (Sanders 1970), and up to 638 pairs/40 ha in 1983 near the peak of the subsequent outbreak (Holmes et al. 2009). About 200 km east in plots near Manitouwadge, Ontario, bird density increased from 156 to 329 pairs/40 ha in the span of 4 years from 1979–83 as a budworm outbreak progressed (Venier et al. 2009).

Morse (1978) suggested that part of the change in insectivorous bird populations during a budworm outbreak is the result of species substitution, whereby some species increase during the outbreak while others decrease due to competition, such that outbreak and non-outbreak densities are similar. Contrary to this suggestion, the vast majority of studies that provide information on overall bird densities indicate large increases. Sanders (1970) found that the overall increase in total bird density between non-outbreak and outbreak years could be accounted for by increases of 4 species of Parulidae that are known to respond numerically to increasing budworm densities (bay-breasted, Cape May, Tennessee, and Blackburnian warblers). Both Holmes et al. (2009) and Venier et al. (2009) found that, even when the most responsive forest bird species were removed from the accounting, the overall territory numbers still showed notable increases with increasing budworm numbers (from 129 to 461 territories/40 ha and from 142 to 227 territories/40 ha, respectively), suggesting that increasing densities are due to more than just increases in a select few responsive species. Number of species (richness) also increases with increasing budworm density (Erskine 1977; Holmes et al. 2009; Venier et al. 2009). Venier et al. (2009) showed an increase in species richness from 50 to 60 species in 4 years as the budworm outbreak developed in their study plots.

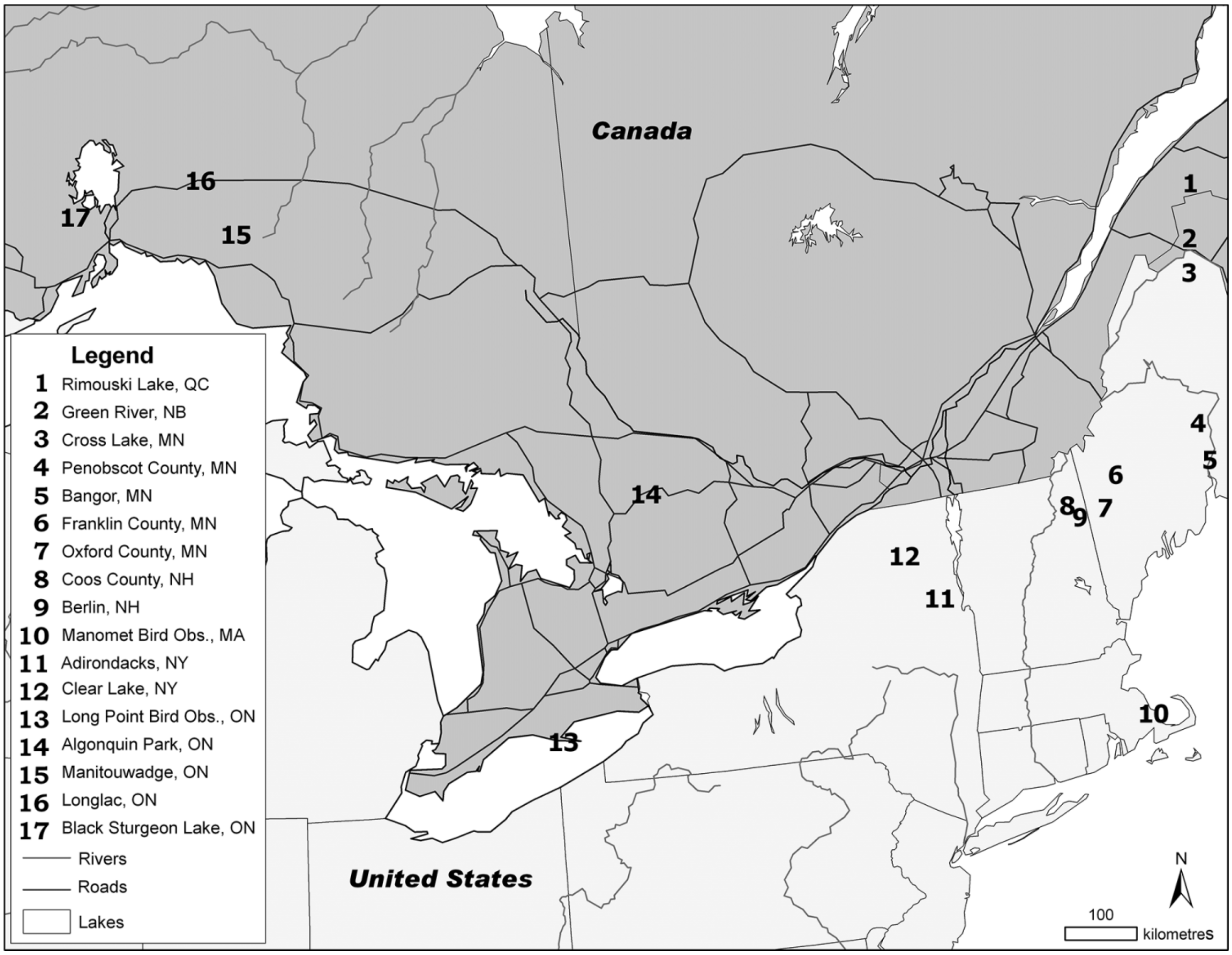
4. Local-scale individual species patterns

Budworm infestations operate at immense spatial scales, with large variations in frequency, extent, duration, and amplitude (Blais 1983; Candau et al. 1998; Nealis and Regniere 2004). It is not surprising, therefore, that there are some inconsistencies in apparent response of individual forest bird species to budworm outbreak, considering that there have been relatively few bird–budworm studies conducted at widely scattered locations across the range of budworm (Fig. 1). Nevertheless, several bird species have been identified as budworm “specialists.” This term could be misleading, however, in that it implies a species that targets only budworm and that would be absent where budworm are not found. This does not appear to be the case for any species. Rather, there are several examples of species that respond more consistently and strongly to the presence of budworm, and are able to take advantage of the additional nutritional resources that the budworm supply during an outbreak by increasing their densities substantially (4 to 12 fold). We will use an alternative term “budworm-linked” in referring to these species. It appears that there are also species which consume significant amounts of budworm when budworm levels are low (e.g., red-breasted nuthatch, white-throated sparrow, Nashville warbler, and black-capped chickadee), but who do not respond strongly to budworm during outbreak conditions (Crawford et al. 1983, 1990).

Although there is not complete agreement as to which species are considered budworm-linked, three species that are most often identified are bay-breasted, Tennessee, and Cape May warblers (Cheshire 1954; Holmes et al. 2009; Kendeigh 1947; Morse 1978; Venier et al. 2009). In Manitouwadge, from 1979 to 1983, these three species showed large numerical responses to the budworm outbreak, including 4 to 10 fold increases in numbers per plot over 4–5 years of increasing budworm numbers (Venier et al. 2009). Likewise, bay-breasted, Tennessee, and Cape May warblers were absent during non-outbreak years at Black Sturgeon Lake, but comprised 25% of the bird population at its peak during the 1980s budworm outbreak (Holmes et al. 2009).

Bay-breasted warbler was the most common bird during the 1950s budworm outbreak at Green River in northern

Fig. 1. Location of bird–budworm studies included in the review. The following are a selection of studies from each location; (1) (Morris et al. 1958), (2) (Blais and Parks 1964), (3) (Mitchell 1952; Dowden et al. 1953), (4) (Morse 1978), (5) (Crawford et al. 1983), (6) (Crawford and Jennings 1989; Crawford et al. 1990), (7) (Crawford and Jennings 1989; Crawford et al. 1990), (8) (Crawford and Jennings 1989; Crawford et al. 1990), (9) (Crawford et al. 1983), (10) (Hagan et al. 1992), (11) (Dowden et al. 1950), (12) (George and Mitchell 1948), (13) (Hussell et al. 1992), (14) (Zach and Falls 1975), (15) (Venier et al. 2009), (16) (McMartin et al. 2002), (17) (Kendeigh 1947; Holmes et al. 2009; Sanders 1970).



New Brunswick, increasing 5 to 7 fold (Cheshire 1954). In the same area, Morris et al. (1958) found a 12 fold increase in bay-breasted warbler numbers as budworm densities increased from moderate to epidemic levels. At Black Sturgeon Lake, bay-breasted warblers were present at densities of <1 pair/40 ha under non-outbreak conditions (Sanders 1970), compared to 92 pairs/40 ha during an earlier spruce budworm outbreak (Kendeigh 1947). Bay-breasted warblers are often the most abundant species during outbreaks, but are relatively rare or absent when no outbreaks are in progress (e.g., Holmes et al. 2009). In removal experiments conducted during a spruce budworm outbreak in northern Maine, more than twice as many bay-breasted warblers (188 in 16.2 ha) were collected as any other species (Hensley and Cope 1951).

Evidence for Cape May warbler as a budworm-linked species is somewhat less consistent, possibly due in part to the species' relative rarity. At Black Sturgeon Lake, the density of Cape May warblers was 28 pairs/40 ha during the 1940s budworm outbreak (Kendeigh 1947), but the species was not found at all in non-budworm years (Sanders 1970). During the next budworm outbreak in the 1980s, Cape May warbler numbers increased from 0 to a peak of 72 pairs/40 ha (Holmes et al. 2009). In Manitouwadge, Cape May warblers increased from 2.8 to 22.8 pairs/40 ha during 4 years of budworm increase (Venier et al. 2009). Forty-four Cape May warblers were removed from a 16.2 ha plot during a budworm outbreak in Maine (Hensley and Cope 1951), a relatively large number of individuals for such a generally uncommon species. However, Morris et al. (1958) found only a few Cape May warblers (<5 pairs/40 ha) in both moderate and epidemic budworm years in New Brunswick, suggesting some variability in response to budworm.

Tennessee warbler response to budworm is convincing, but again not completely consistent. In four study areas where periods of low or moderate budworm numbers were compared to periods of epidemic numbers, large increases in Tennessee warbler were indicated (0 to 59 pairs/40 ha, Kendeigh 1947 and Sanders 1970; 0 to 45 pairs/40 ha, Morris et al. 1958; 0 to 33 pairs/40 ha, Holmes et al. 2009; 9.7

to 58.2 pairs/40 ha, Venier et al. 2009). Interestingly, only 12 Tennessee warblers were collected in the removal experiment in northern Maine, once again suggesting heterogeneity of response.

In a long-term study at Black Sturgeon Lake, the three budworm-linked species had very different patterns of response to the budworm outbreak (Holmes et al. 2009). Compared to Tennessee warbler and Cape May warbler, bay-breasted warbler responded early to increasing budworm numbers, suggesting that bay-breasted warbler may be better adapted for exploiting low budworm numbers. As well, bay-breasted warbler increased more gradually over time in a pattern consistent with increased reproductive success (MacArthur 1958). Cape May warbler and Tennessee warbler peaked more abruptly, possibly reflecting a redistribution of individuals in response to local variability in budworm density (MacArthur 1958; Royama 1984). These patterns of increase are supported by other studies (Morris et al. 1958; Venier et al. 2009). Holmes et al. (2009) also suggest that differences in nesting and foraging locations may contribute to different responses to budworm. Local budworm infestation can result in severe defoliation, especially in upper crowns of spruce and fir trees, where Cape May and Tennessee warblers principally forage. Cape May warbler nests are also usually located near the tops of trees, in contrast with bay-breasted warblers that nest at mid- to lower levels. Thus, foraging and nesting opportunities for Tennessee and Cape May warblers may decline earlier in the budworm cycle.

Arguments have been made that the three budworm-linked species are adapted to respond to budworm outbreak by having highly variable and relatively large clutch sizes, which allows them to rapidly increase in numbers in response to a superabundant food supply (MacArthur 1958; Williams 1996; Baltz and Latta 1998; Rimmer and McFarland 1998). MacArthur (1958) examined nest records to reveal that both bay-breasted and Cape May warblers had larger than average clutch sizes (5.4 and 5.8, respectively) and larger standard deviations in clutch size (0.8 and 0.9, respectively) than other related species (average clutch sizes of 4.0–4.1 and standard deviations of 0.4–0.5). He also noted that the only other warbler regularly laying such large clutches is the Tennessee warbler, with a modal clutch size of 6 and range of 3–8 eggs (Rimmer and McFarland 1998). That these species are able to respond rapidly to budworm outbreaks may be because they increase their clutch sizes in response to outbreaks (Baltz and Latta 1998; Morse 1989; Williams 1996). Bay-breasted warbler appear to have smaller clutches when budworm are at endemic population levels than during outbreaks, suggesting such an adaptation (MacArthur 1958).

Data on the timing of warbler nesting within the range of spruce budworm outbreak is relatively sparse. The timing of Tennessee warbler nesting is relatively late in the season and appears to be synchronized with budworm development. For example, the first egg date for Tennessee warbler in a study near Longlac, Ontario was June 17 (Holmes 1998), versus late May or early June for black-throated green warbler (Holmes 1994) and magnolia warbler (Hall 1994), and early June for ovenbird (Van Horn and Donovan 1994). Late nesting results in parents having large budworm larvae and pupae available for feeding young (Holmes 1998). Tennessee warblers also have a relatively short incubation period (7–8 days) compared to other wood warblers, which may be another adaptation that enables this species to take advantage of a pulsed food supply (budworm) for nestling growth and development (Holmes and Nixon 2000).

Other species appear to respond numerically to increasing budworm densities, but not as consistently as the three budworm-linked species. Morris et al. (1958) noted that Blackburnian warblers increased from 5 to 45 pairs/40 ha early in a budworm outbreak, but that their numbers declined again well before budworm numbers returned to endemic levels. Blackburnian warblers showed a local abundance peak at Black Sturgeon Lake 1–2 years earlier than bay-breasted, Cape May, and Tennessee warblers, but there was no regional peak for Blackburnian warblers in Breeding Bird Survey data for the same time period (Holmes et al. 2009). Lack of a regional peak, as well as a small average clutch size relative to the budworm-linked species, suggests that the local peak was more likely the result of immigration (an aggregation response), or possibly increased breeding opportunities for floaters, rather than increased reproduction by the local breeding population (Holmes et al. 2009). Gage and Miller (1978) found Blackburnian warbler abundance to be at least 3 times greater under outbreak than post-outbreak conditions in two plots, one severely infested with budworm and one moderately so. The Blackburnian warbler abundance index pattern in migration monitoring data was similar in direction and size as the 3 budworm-linked species (Hussell et al. 1992).

Magnolia warblers have also increased in abundance at plot scales in response to increasing budworm (Holmes et al. 2009; Venier et al. 2009), but like Blackburnian warblers, no regional peak was observed (Holmes et al. 2009). The strongest evidence for interspecific competition during budworm outbreaks comes from magnolia warbler counts. Kendeigh (1947), Morris et al. (1958), and Holmes et al. (2009) all show some evidence that as bay-breasted warbler numbers increase, magnolia warbler numbers begin to decline. Timing is apparently important in this phenomenon. Holmes et al. (2009) observed a very early peak in magnolia warbler numbers, followed by a decline as bay-breasted warbler and budworm numbers continued to increase. Shorter term studies that only capture a small portion of these trajectories might come to very different conclusions. Thus, a study conducted early in the outbreak cycle might conclude that there is a positive numerical response to budworm by magnolia warblers and no competition with bay-breasted warblers, whereas a study conducted later in the outbreak might conclude an inverse response to budworm and competition with bay-breasted warblers. Venier et al. (2009) found no evidence for an inverse relationship between magnolia and bay-breasted warblers during a five year study early in an outbreak, which is consistent with the early period in the Black Sturgeon Lake results. The results of Gage and Miller (1978) are somewhat contradictory. In a moderately infested plot, magnolia warbler was much more abundant in outbreak than in post-outbreak conditions (22 versus 7.9 birds/40 ha), as were bay-breasted warblers (55.8 versus 16.4 birds/40 ha). However, in a more severely infested plot that experienced severe tree mortality, magnolia warbler was less abundant in outbreak than in post-outbreak years (1.3 versus 14.9 birds/40 ha), although bay-breasted warbler was still more abundant in outbreak years (78.2 versus 2 birds/ 40 ha). Obviously, competition alone cannot provide an explanation for this result. Some consideration of the contribution of habitat change due to tree mortality, both on its own and in combination with competition, is required. The reality is that results from single plots are highly variable for many reasons, including differences in habitat, bird composition and density, budworm density and impact of budworm on foliage availability and tree mortality, and inconsistencies and contradictions should be expected.

In several studies, ovenbird displayed what appeared to be a direct numerical response to increasing budworm numbers (Morris et al. 1958; Zach and Falls 1975; Holmes et al. 2009; Venier et al. 2009). Ovenbird is also the only species, other than bay-breasted warbler, for which increases in clutch size in response to budworm outbreaks have been demonstrated (Zach and Falls 1975). Since second and third nesting attempts are also more common during outbreaks (Zach and Falls 1975), a reproductive response is clearly indicated.

At least 30 species of forest birds have shown evidence of positive numerical responses to budworm at local or regional scales, some more consistently than others (Table 2). The majority of the evidence is correlational, however, so that in at least some studies and for some species the observed relationship may be spurious. Nevertheless, the weight of evidence is overwhelmingly in favour of a broad-based bird community response to budworm outbreaks.

Birds may respond to budworm either directly, as a superabundant food source, or indirectly, through budworm-induced changes in habitat due to defoliation and widespread tree mortality. However, few studies have attempted to separate the effects of habitat change from food supply. Gage and Miller (1978) used a long-term data set (1947–1968) to compare outbreak and post-outbreak bird densities in two plots that differed in their levels of budworm impact. They found much higher post-outbreak densities of least flycatchers and white-throated sparrows in the stand that had severe tree mortality (80% balsam fir and 40% spruce were lost to budworm and windthrow) than in the plot that had little or no tree mortality (15.9 versus 2.8 least flycatchers/40 ha and 19.5 versus 5.0 white-throated sparrows/40 ha). Both of these species prefer more open habitats (Briskie 1994; Falls and Kopachena 1994). In contrast, boreal chickadees were much less common in the severely affected plot during the post-outbreak period than during the outbreak period (<1 bird/40 ha versus 4.7 birds/40 ha), possibly due to a loss of suitable cavity trees. Sixteen other species appeared to respond to the overabundant food supply (Gage and Miller 1978, see Table 2).

5. Who eats spruce budworm

Many forest bird species eat spruce budworm, as is evidenced from both behavioural studies (Kendeigh 1947; Morse 1978; Zach and Falls 1975) and stomach contents analysis (Crawford and Jennings 1989; Crawford et al. 1990; McMartin et al. 2002; Mitchell 1952; Wypkema 1982). During a budworm outbreak near Longlac, Ontario, the mid- to late June diets of Tennessee, Cape May, and bay-breasted warblers consisted of 80.2%, 79.1%, and 57.7% lepidopteran larvae, respectively, the majority of which were most likely spruce budworm (McMartin et al. 2002). Bay-breasted warblers also ate a relatively large number of adult beetles (29.6% of food items). Mitchell (1952) examined the stomach contents of 737 individuals of 45 different bird species during a budworm outbreak in Maine in 1949–50. Budworm remains were found in the stomachs of 37 species. Among the 20 species for which at least 10 individual samples were obtained, 11 had stomach contents that were >30% budworm by volume (red-eyed vireo 31%, Cape May warbler 33%, blue-headed vireo 34%, Swainson’s thrush 37%, red-breasted nuthatch 39%, bay-breasted warbler 42%, magnolia warbler 44%, Nashville warbler 47%, Tennessee warbler 60%, purple finch 73%, and cedar waxwing 85%). Crawford and Jennings (1989) found budworm in the stomachs of 22 of 25 species sampled, with highest budworm counts in purple finch, Cape May warbler, Blackburnian warbler, and black-capped chickadee. Wypkema (1982) sampled stomach contents of 58 species, 44 of which had some budworm in their stomachs and 22 of which had more than 1 budworm per stomach. Of the 14 species that did not have budworm in their stomachs only American robin ($N = 11$) and yellow-bellied flycatcher ($N = 16$) were well sampled. Purple finches, Cape May warblers, Blackburnian warblers, and black-capped chickadees had the highest numbers of budworm per stomach (11.9, 5.7, 3.9, and 3.7, respectively). The wide variety of species that are consuming budworm during outbreaks lends support to the expectation that budworm outbreaks benefit many more species than just the traditional budworm-linked species. Numerical and functional responses can be difficult to detect in less common species and the power of the statistical tests are often low in these kinds of studies, but it is clear that many species are using this resource when it is available. It also appears that even at extremely high budworm densities, birds are still eating other things suggesting that a budworm only diet is not ideal.

6. The role of birds in regulating spruce budworm populations

Predators can limit prey populations, but only if predation is density-dependent; that is, the predators must take a greater proportion of the population as prey density increases (Solomon 1949). There are two forms of density-dependent response: (1) a numerical response, where the number of predators changes in response to increasing prey density (discussed above), and (2) a functional response, where the predator changes its feeding behaviour to include more of the prey in its diet (Solomon 1949).

Kendeigh (1947) describes several examples of birds foraging in unusual ways to exploit an abundant budworm food resource (i.e., a least flycatcher, which normally forages on winged insects, pounding a large budworm larva on a branch so it could be swallowed; a downy woodpecker foraging on a horizontal branch of a balsam fir, instead of on a vertical tree stem; a pair of slate-colored (dark-eyed) juncos foraging 15 ft (5 m) or more up in trees rather than on the

Table 2. List of bird species that have shown a positive numerical response to increasing budworm populations.

Common name	Scientific name	Reference
Yellow-bellied flycatcher	*Empidonax flaviventris*	(Gage and Miller 1978; Hussell et al. 1992)
Least flycatcher	*Empidonax minimus*	(Gage and Miller 1978; Hussell et al. 1992)
Blue-headed vireo	*Vireo solitarius*	(Gage and Miller 1978; Venier et al. 2009)
Red-eyed vireo	*Vireo olivaceus*	(Holmes et al. 2009)
Boreal chickadee	*Poecile hudsonica*	(Gage and Miller 1978)
Brown creeper	*Certhia americana*	(Venier et al. 2009)
Winter wren	*Troglodytes troglodytes*	(Venier et al. 2009)
Golden-crowned kinglet	*Regulus satrapa*	(Crawford and Jennings 1989; Gage and Miller 1978; Holmes et al. 2009; Venier et al. 2009)
Ruby-crowned kinglet	*Regulus calendula*	(Holmes et al. 2009)
Veery	*Catharus fuscescens*	(Venier et al. 2009)
Swainson's thrush	*Catharus ustulatus*	(Gage and Miller 1978, Holmes et al. 2009; Morris et al. 1958)
Tennessee warbler	*Vermivora peregrina*	(Bolgiano 2004; Erskine 1978; Gage and Miller 1978; Hagan et al. 1992; Holmes et al. 2009; Hussell et al. 1992; Morris et al. 1958; Sanders 1970; Venier et al. 2009)
Nashville warbler	*Vermivora ruficapilla*	(Holmes et al. 2009; Hussell et al. 1992)
Magnolia warbler	*Dendroica magnolia*	(Gage and Miller 1978; Holmes et al. 2009; Hussell et al. 1992)
Cape May warbler	*Dendroica tigrina*	(Bolgiano 2004; Hagan et al. 1992; Holmes et al. 2009; Hussell et al. 1992; Morse 1978; Patten and Burger 1998; Sanders 1970)
Black-throated blue warbler	*Dendroica caerulescens*	(Hussell et al. 1992; Venier et al. 2009)
Yellow-rumped warbler	*Dendroica coronata*	(Gage and Miller 1978; Holmes et al. 2009)
Black-throated green warbler	*Dendroica virens*	(Gage and Miller 1978; Hussell et al. 1992)
Blackburnian warbler	*Dendroica fusca*	(Erskine 1978; Gage and Miller 1978; Holmes et al. 2009; Hussell et al. 1992; Morris et al. 1958; Sanders 1970; Venier et al. 2009)
Bay-breasted warbler	*Dendroica castanea*	(Bolgiano 2004; Cheshire 1954; Erskine 1978; Gage and Miller 1978; Hagan et al. 1992; Holmes et al. 2009; Hussell et al. 1992; Morris et al. 1958; Morse 1978; Patten and Burger 1998; Sanders 1970; Venier et al. 2009)
Blackpoll warbler	*Dendroica striata*	(Bolgiano 2004; Hussell et al. 1992)
Black-and-white warbler	*Mniotilta varia*	(Venier et al. 2009)
American redstart	*Setophaga ruticilla*	(Gage and Miller 1978; Hussell et al. 1992; Venier et al. 2009)
Ovenbird	*Seiurus aurocapillus*	(Holmes et al. 2009; Hussell et al. 1992; Morris et al. 1958; Venier et al. 2009; Zach and Falls 1975)
Wilson's warbler	*Wilsonia pusilla*	(Hussell et al. 1992)
Canada warbler	*Wilsonia canadensis*	(Crawford and Jennings 1989; Hussell et al. 1992; Patten and Burger 1998; Sleep et al. 2009)
White-throated sparrow	*Zonotrichia albicollis*	(Gage and Miller 1978; Venier et al. 2009)
Dark-eyed junco	*Junco hyemalis*	(Gage and Miller 1978)
Purple finch	*Carpodacus purpureus*	(Bolgiano 2004; Venier et al. 2009)
Evening grosbeak	*Coccothraustes vespertinus*	(Blais and Parks 1964; Bolgiano 2004; Bonter and Harvey 2008; Morris et al. 1958; Venier et al. 2009)

ground; a red-eyed vireo foraging on coniferous instead of deciduous foliage). Zach and Falls (1975) observed ovenbirds, which normally feed on ground insects, spending more time foraging in trees during a budworm outbreak. Morse (1978) found that bay-breasted warblers spent a considerable amount of time foraging on dead limbs, something they did not do when budworm were not present, to capture budworm larvae as they descended on their threads. In addition, several authors have noted relatively large numbers of budworm larvae in the stomachs of species that do not normally feed on foliage insects (e.g., chipping sparrow, winter wren (Mitchell 1952), white-winged crossbill, downy woodpecker (Wypkema 1982), red-winged blackbird, white-throated sparrow (Crawford et al. 1983), red-breasted nuthatch, and purple finch (Crawford and Jennings 1989)). Finally, even species that commonly feed on foliage insects may greatly increase the proportion of budworm in their diets when populations are higher (Mitchell 1952; Gage 1968;

Crawford et al. 1983; Crawford and Jennings 1989), an example of prey switching (Ludwig et al. 1978; Murdoch 1969).

Vertebrate predators typically display a sigmoidal or S-shaped feeding response to increasing prey density (Holling 1959). The curve displays a positively accelerated rise at low prey densities as a result of learning, followed by a negatively accelerated rise to a plateau at higher prey densities due to decreasing hunger (Holling 1965). Holling (1959) showed that sigmoidal functional responses have regulatory properties, even in the absence of numerical responses, and in fact, a strong functional response may more than counterbalance a weak, random or even negative numerical response (Buckner 1967).

To demonstrate a sigmoidal functional response, it is necessary to measure consumption of prey by predators at a range of prey densities. Mook (1963) collected data on the consumption of spruce budworm by birds by analyzing the stomach contents of birds shot in plots having a range of budworm densities. Using these data, he drew an S-shaped functional response curve for bay-breasted warblers, but cautioned that the shape of the curve at lower densities was only tentative. Using a similar approach, but confining their investigation to low and transitional budworm densities, Crawford and Jennings (1989) demonstrated that consumption of budworm by the entire bird community increased significantly as budworm density increased. This relationship also held true for groups of species that had similar patterns of feeding response to increasing budworm numbers. These included the canopy-feeding warbler–kinglet group, the sparrow–vireo–junco group, and the nuthatch–thrush–purple finch group, but not the chickadee–Nashville warbler group. Only two individual species (solitary vireo and red-breasted nuthatch) showed significant density-dependent feeding responses, however. A visual inspection of the graphs of budworm consumption by budworm density presented in Crawford and Jennings (1989) and Crawford et al. (1990) appear to confirm a positively accelerated rise in feeding response at low to transitional budworm densities. At least in theory then, birds could play some role in regulating budworm densities. The question is, how much of a role?

Most authorities agree that birds have little influence on budworm at high population densities. In western spruce budworm, the combined effects of predaceous birds and ants is greatest when budworm density reaches about 1–2 fourth-instar larvae per m^2 of foliage (Campbell 1993). From this density to about 50 fourth-instar larvae per m^2, average survival from fourth-instar to adults increases with increasing density. Predation on eastern spruce budworm appears to follow a similar pattern. Mook (1963) found that bay-breasted warblers prey with increasing intensity on budworm until the latter reach a density of 2 sixth-instar larvae per 10 ft^2 (0.92 m^2) of foliage. From this density to about 100 larvae per 10 ft^2, large larval survival increases with increasing density (Watt 1963). Morris (1963*c*) suggests that this pattern results from the effect of predators that have a very limited numerical response to budworm density. Thus, there appears to be a plateau in the intensity of budworm consumption by predators at a density of about 2 larvae per 10 ft^2 of foliage, and this plateau is below the level that is required to keep the budworm population in check.

At budworm densities exceeding one million per hectare, birds consume 7% or less of late instar larvae and pupae (Table 3). At lower budworm densities, the proportion of the budworm population consumed is much higher (8%–87%; Table 3). We have little confidence in the high estimate (87%) of Crawford et al. (1983), because it is based on an assumption that cannot be substantiated (i.e., that their low budworm density in Maine in 1976–77 was the same as that reported by Gage (1968) for central New Brunswick 10 years earlier; 1.1 larvae per 100 ft^2 of foliage). Crawford et al. (1983) collected on average 45 moths per pheromone trap in their low budworm density stands. A pheromone trap catch of 45 moths per trap corresponds to a budworm density of about 45 feeding larvae per 100 branch tips (see Fig. 4 in Sanders 1996), or about 20 larvae per 100 ft^2 of foliage (our calculation, assuming an 18 inch (45 cm) branch contains 2.25 ft^2 of foliage). Thus, even allowing for between study differences in trapping efficiency, it appears likely that the population estimate of 6470 budworm per hectare in low density stands in Maine was much too low. The 84% budworm consumption estimate of Crawford and Jennings (1989) has also been criticized. Royama (1992) argued that the statistical model used by Crawford and Jennings (1989) to estimate budworm consumption could grossly inflate predation rates towards the lower end of the budworm density spectrum. Finally, the budworm consumption estimate of Wypkema (1982) is also suspect, since his bird censuses and stomach collections were not conducted in the same plots where his budworm density estimates were made, and he arrived at his L6 budworm population estimate by simply dividing his L3-L4 estimate by 10 (i.e., assumed 90% mortality between these two stages). Leaving these three estimates aside, it is reasonable to conclude that at densities of 100 000 to one million large larvae per hectare, birds consume about 19%–35% of the budworm present. For the reasons discussed above, there are no reliable budworm consumption estimates for budworm densities under 100 000 per hectare. Nevertheless, it is generally accepted that bird predation exerts its greatest influence on budworm at endemic population levels (George and Mitchell 1948; Morris et al. 1958; Morris 1963*c*; Crawford et al. 1983; Crawford and Jennings 1989; Vaidya and Wu 2008).

A number of mathematical models have been developed to simulate the temporal and spatial patterns of spruce budworm outbreaks (e.g., Clark et al. 1979; Holling 1978; Jones 1979; Ludwig et al. 1978; Morris 1963*b*; Mott 1963; Royama et al. 2005; Stedinger 1984; Vaidya and Wu 2008). Most of the data for these models derive from the New Brunswick Green River Project described in Morris (1963*a*). The models of Holling (1978), Ludwig et al. (1978), Clark et al. (1979), and Jones (1979) (collectively the University of British Columbia or UBC model) include bird predation as an important component. As discussed above, the shape of the bird–budworm functional response curve is positively accelerating at low budworm densities. This occurs because vertebrate predators, such as birds, respond rapidly to changes in prey density by switching their feeding to the more abundant species and by aggregating in areas where prey are more common (Berryman et al. 1987).

Table 3. Consumption of spruce budworm by birds.

		Budworm population						
Location	Method	Descriptor	No./ha ($\times 10^3$)	Dev. stage	Bird population (Pairs/ha)	% SBW eaten	No. SBW eaten/ha ($\times 10^3$)	Reference
New Brunswick	Estimate	Declining	—	Egg-Adult	—	13	—	(Tothill 1923)
Maine & New Hampshire	Stomach contents & census	Endemic	6	L5-L6	4.8–12.2	87	6	(Crawford et al. 1983)
Ontario	Stomach contents & census	Endemic	14–76	L6	3.8–6.3	40	9	(Wypkema 1982)
Maine	Stomach contents & census	Low	100	L4	—	84	—	(Crawford and Jennings 1989)
Maine	Shooting	Moderate	72–208	P	7.9- 9.1	19–35	36–90	(Dowden et al. 1953)
Maine & New Hampshire	Stomach contents & census	Transitional	245	L5-L6	4.8–12.2	23	54	(Crawford et al. 1983)
Maine & New Hampshire	Stomach contents & census	Transitional	500	L4	—	22	—	(Crawford and Jennings 1989)
Ontario	Census & calculation	Outbreak	929	L6-P	7.9	4	40	(Kendeigh 1947)
Maine	Census & calculation	—	1442	–	6.6	2.5–6	36–91	(Morse 1978)
New York	Census & calculation	—	1235–2471	–	7.4	3.5–7	85	(George and Mitchell 1948)
Maine & New Hampshire	Stomach contents & census	Epidemic	3640	L5-L6	4.8–12.2	2	89	(Crawford et al. 1983)
Maine	Census & calculation	—	4307	—	8.1	1–3	45–112	(Morse 1978)
New Brunswick	Calculation	Peak	8000	—	—	≤1	49	(Morris et al. 1958)

Note: SBW, spruce budworm.

Thus, when budworm populations are low, most increases will be driven back down by predation, creating a "natural enemy ravine" (Southwood and Comins 1976) or "predator pit" (Holling 1978) in the budworm recruitment curve. In this way, bird predation maintains the budworm population at low levels until foliage volume in the tree crowns increases (as the forest matures) to a point where predation effects are diluted (Holling 1988). This occurs because the greater crown volume represents more foliage to search for the birds, while providing more habitat for the budworm. An outbreak can also occur by "swamping the predator pit" through an influx of budworm moths from other areas, or by the occurrence of warm dry summers, which can raise the budworm population growth rate above the replacement line (Holling 1978). The predator pit is only important in intermediate aged forests, however (Holling 1978). In young forests the recruitment curve never crosses the replacement line, so the population does not increase, whereas in old forests, the recruitment curve is always above the replacement line.

Stedinger (1984) criticized the UBC model as overestimating the impact of bird predation at low budworm densities. Specifically, he contended that the density of ground feeding birds, and the density and feeding rate of woodpeckers are exaggerated in the model. Citing data provided by Holling (personal communication), Stedinger (1984) calculated a consumption rate of 92 941 larvae per season per hectare, which does indeed appear to be an overestimate (see Table 3 and discussion above). Using Stedinger's (Stedinger 1984) "more realistic" numbers, the consumption rate drops to 28 327 larvae per season per hectare.

The contention that predation is a primary cause of budworm population oscillations has been forcefully argued against by Royama (1984, 1992). Reviewing the work of Mitchell (1952) and Miller and Renault (1981), Royama (1984) concluded that birds take a substantial number of budworm larvae and pupae when prey density is high, but essentially ignore this food source when the insect is scarce. Under this mechanism, predation is probably a first-order density-dependent process (dependent on prey density in the current generation only), whereas a second-order density-dependent process (dependent on prey density in both the current and previous generations) is required to generate an oscillation in a predator–prey interaction system (Royama 1981). Since birds do not multiply effectively in numbers from one year to the next, as do budworm, a second-order density-dependent process is unlikely (Royama 1984). Near the beginning of a spruce budworm outbreak at Black Sturgeon Lake in Ontario (1978–83), bird densities increased on average by about 33% per year, whereas budworm densities increased by about 358% per year (Holmes et al. 2009 and unpublished data). However, although it may not be the primary cause of budworm oscillations, bird predation probably does play a role in determining the mean level of those oscillations (Royama 1984; Vaidya and Wu 2008).

If bird predation does influence either the periodicity or magnitude of spruce budworm outbreaks, it may be possible to reduce budworm damage by implementing silvicultural practices that support large and diverse bird populations (Crawford and Jennings 1989). Pure balsam fir stands are most susceptible to budworm attack and damage (Needham et al. 1999). These stands also contain a relatively impoverished avifauna compared to mixed spruce–fir stands and mixed conifer–hardwood stands (Crawford and Titterington 1979). Crawford (1985) recommended that managing to produce a mature conifer forest, with a mixture of overstory species and small openings containing different ages of regeneration, should provide habitat for avian predators of budworm and reduce stand susceptibility. These objectives could be achieved either through group selection (the removal of groups of trees in a partial cut to create openings in the forest to allow the regeneration of shade-intolerant tree species) or three-stage shelterwood (the removal of all trees in a series of cuts to achieve a new even-aged stand structure) cutting on a small (10 ha) scale. The alternative view is that the periodic recycling of "over mature" stands of spruce–fir through the actions of budworm is a natural process and that any attempt to budworm-proof the forest, through silviculture, would not make ecological sense, and could introduce instability into the system (Baskerville in Miller 1999, p. 94), potentially exacerbating the problem.

During the last spruce budworm outbreak large areas of forest were treated with various insecticides to protect fir and spruce trees from defoliation; to 1985, about 118 million ha in total, including 64 million ha with fenitrothion, 19 million ha with aminocarb, 15 million ha with DDT, 8 million ha with phosphamidon and lesser amounts of 6 other insecticides (Ennis and Caldwell 1991). Many of these spray programs resulted in direct mortality or sublethal effects on birds (Freedman 1995, pp. 254–59). For example, Pearce et al. (1976) estimated that several million birds were killed, mostly by phosphamidon and to a lesser extent by fenitrothion, during the 1975 spruce budworm control program in New Brunswick. The use of phosphamidon was discontinued in 1978 (Ennis and Caldwell 1991) and severe restrictions were placed on the use of fenitrothion in 1995 (Agriculture and Agri-Food Canada 1995). Aminocarb application had much less of an impact on birds, but did cause a low level of cholinesterase inhibition (Busby et al. 1982, 1983). To our knowledge, the implications of forest spraying with acutely toxic chemical insecticides on bird predation of spruce budworm have not been considered in this context.

The broadscale use of acutely toxic chemical insecticides to control spruce budworm outbreaks is no longer a viable political option (Ennis and Caldwell 1991). The more environmentally acceptable alternatives (e.g., the Lepidoptera-specific bacterial insecticide, *Bacillus thuringiensis* (Bt) and the insect growth regulator, tebufenozide), are now widely used for budworm control (e.g., Cadogan et al. 2005; van Frankenhuyzen 1995). Although these products are not directly toxic to birds, their use could have secondary effects resulting from reduced invertebrate prey availability (Burgess et al. 1995; Holmes 1998; Nagy and Smith 1997; Norton et al. 2001). Holling (1978) suggests that a relaxation of predation pressure through insecticide effects on avian predators, either directly through mortality or indirectly by reducing food availability, can have significant effects on forest condition, budworm densities and periodicity. Although this might not necessarily be a problem during budworm outbreaks when predation intensity is already low, it could be if an early intervention strategy for controlling budworm, by suppressing rising populations, was implemented (Regniere et al. 2001).

7. Habitat change

Spruce budworm is a major disturbance agent over extensive areas of conifer and mixed-conifer forest in northeastern North America (Table 1, Irland 1980). In light or moderate infestations, partial loss of foliage occurs, but trees recover if the infestation collapses after a year or two (Prebble 1975). If the infestation persists and intensifies, the new foliage is fully consumed in successive years, vegetative buds and new shoots are destroyed, twigs are killed, and top-killing occurs (Prebble 1975). Balsam fir mortality usually begins after about 5 successive years of defoliation and may be complete by years 6–8. Red spruce is as susceptible as balsam fir. White spruce and black spruce are less susceptible, but may still sustain significant volume losses when growing in association with balsam fir (Prebble 1975).

Very few studies have examined the impact of budworm caused habitat change on forest birds. In their long-term local-scale study, Holmes et al. (2009) noted early declines in Cape May warblers and Tennessee warblers that could be attributed to defoliation of potential nesting and foraging locations. The result was decreasing population trajectories that occurred well before the peak of the budworm outbreak (Holmes et al. 2009; see also Venier et al. 2009). In addition, ovenbird population trajectories followed suppression and release of the shrub layer, in response to forest maturation and defoliation by spruce budworm (Holmes et al. 2009). Bolgiano (2004) identified trends in the Quebec BBS that were consistent with habitat changes related to the 1970s budworm outbreak. For example, olive-sided flycatchers peaked in abundance in the 1980s when much of the fir dominated forest was dying in the area. Olive-sided flycatchers prefer forest openings with dead snags (Altman and Sallabanks 2000), a more common habitat type in the years following a prolonged spruce budworm outbreak with high tree mortality. Dark-eyed juncos showed a similar pattern of increase in the late 1980s to early 1990s, consistent with an increase in the prevalence of early successional forests (Bolgiano 2004). Gage and Miller (1978) found that least flycatchers, white-throated sparrows, and magnolia warblers all increased in abundance in a post-outbreak stand exhibiting severe tree mortality, but were less abundant in a post-outbreak stand with no tree mortality. Although the information is not specific to budworm, defoliation may also increase nest predation rates (Thurber et al. 1994), and may reduce the abundance of other insects that require the foliage for food, as a surface for mating, oviposition, foraging or perching (Pelech and Hannon 1995). Even during budworm outbreaks, the stomach contents of most insectivorous birds contain less than 50% budworm (Mitchell 1952; McMartin et al. 2002), so potential changes in the availability of other insect food could be important. If budworm defoliation results in reduced populations of insects later in the breeding season, when budworm are no longer readily available, the survival of recently fledged young could be affected (Martin 1987).

Management strategies have been proposed to convert vulnerable balsam fir stands to more resistant black spruce or jack pine (*Pinus banksiana* Lamb.) stands to minimize susceptibility to spruce budworm infestation (e.g., Street et al. 1994). Any large-scale conversion of forest type will necessarily have an impact on bird communities. For example, balsam fir forest supports more species and individuals than the same area of jack pine forest (Erskine 1977).

Any large-scale disturbance, such as spruce budworm outbreak, will necessarily impact the current and future availability of habitat for forest birds. An understanding of natural and anthropogenic disturbance regimes and how they interact at large spatial and temporal scales is necessary to anticipate potential impacts on forest bird habitats and populations.

8. Regional-scale patterns

Several studies have examined the bird–budworm relationship through analyses of large-scale data sets including migration monitoring (Patten and Burger 1998), the Breeding Bird Survey (BBS) (Bolgiano 2004; Sleep et al. 2009), and the Christmas Bird Count (CBC) (Bolgiano 2004). Others have examined trends more generally and interpreted patterns in the data as signals of large-scale budworm outbreaks (Robbins et al. 1989; Hill and Hagan 1991; Hussell et al. 1992). Because of the spatial and temporal variability in budworm abundance during and between outbreaks, it is difficult to examine the relationship between birds and budworm in a precise manner at a regional scale. Most studies derive an abundance index for individual species over large areas and correlate that with periods of extensive budworm outbreak. However, due to the spatial heterogeneity of outbreaks, local bird sampling does not always capture the regional trend so relationships can appear very noisy. This issue is more problematic for BBS data than for migration monitoring or CBC data that, in theory, gather information from a much larger proportion of the area in question thereby generating a more representative sample. Noisy data can reduce the capacity to identify signals of the bird–budworm relationship.

The CBC data show apparent irruptions of two species (evening grosbeak and purple finch) in response to the budworm outbreak of the 1970s (Bolgiano 2004). In this context, an irruption is defined as the movement of unusually large numbers of individuals from their usual post-breeding range. The irruption extent of evening grosbeaks and purple finches followed the trend of infestation, increasing as the infestation expanded and decreasing as the infestation collapsed. Consistent with this, purple finches consume large numbers of budworm according to some studies (Mitchell 1952; Crawford and Jennings 1989) and evening grosbeaks respond numerically to budworm at local scales (Blais and Parks 1964; Morris et al. 1958; Venier et al. 2009). The BBS data corroborated the CBC trends for evening grosbeak and purple finch, and further indicated that the 1970s budworm outbreak and related events had a major impact upon boreal bird species, including Tennessee, Cape May, bay-breasted, and blackpoll warblers (Bolgiano 2004).

Winter irruptions of black-capped chickadee, boreal chickadee, pine grosbeak, red crossbill, and white-winged crossbill appear to have abruptly declined in extent near the end of the 1970s budworm infestation. Bolgiano (2004) attributes this change to a loss of mature boreal forest habitat to budworm, rather than directly to declining budworm populations. Irruption patterns in red-breasted nuthatch, pine siskin, and common redpolls did not show similar changes.

Patten and Burger (1998) found that budworm population density in eastern Canada from 1972 through 1994 was a good predictor of vagrant Cape May, bay-breasted, and Canada warbler occurrences in California. Assuming that level of vagrancy is directly related to the size of the source population, it is suggested that these three warbler species exhibited a direct numerical response to budworm population densities. Contrary to their prediction, however, another budworm-linked species, Tennessee warbler, did not show the same relationship. This may be because the range of the Tennessee warbler is much larger than the other two budworm-linked species, so many of the Tennessee warbler vagrants may have come from outside the core budworm infested areas. Another anomaly in this study is the link between Canada warbler and budworm. Although we believe that for many of the forest bird species that consume spruce budworm an outbreak likely benefits local survival and reproduction, there is little evidence at the local scale that Canada warbler responds strongly to budworm infestation. Only a single local scale study (Crawford and Jennings 1989) has ever shown any relationship between budworm and Canada warbler numbers, and in this case the relationship was at low to moderate budworm population levels where none of the budworm-linked species showed a response. The relationship between budworm and Canada warbler was further examined in a regional-scale study (Sleep et al. 2009). This study examined BBS and budworm defoliation data from 1975 to 2005, a period during which both the survey of budworm infestation and the total occurrences of Canada warbler in the BBS data recorded an overall decline. Based on the correspondence between these two population trajectories, and a similarity to the relationships for bay-breasted and Cape May warblers, the authors concluded that Canada warbler and spruce budworm declines may be linked. However, other analyses of eastern North American BBS data have shown a somewhat different pattern. Robbins et al. (1989) examined BBS trends for two periods: 1966–1978 during which budworm populations were increasing, and 1978–1987 during which budworm populations were decreasing. In their analysis, bay-breasted, Tennessee, and Cape May warblers all had positive trends for the first period and negative trends for the second period. Canada warbler on the other hand had negative trends for both periods. Given the lack of local-scale data linking Canada warbler to budworm and the weakness of the correlational analysis due to the short time frame representing only a decline in budworm defoliation, we would caution against the conclusion that Canada warbler populations are tightly linked to regional budworm levels. To the extent that Canada warbler declines may be related to habitat loss rather than budworm abundance, we suggest that this species is a good candidate for management action to arrest or reverse population decline.

Four neotropical migrants (Tennessee, Cape May, Blackburnian, and bay-breasted warblers) showed significant double-digit percentage increases in Ontario migration-based abundance indices in the 1970s during widespread spruce budworm outbreaks (Hussell et al. 1992). All of these species have responded strongly to outbreaks of spruce budworm at local scales (Kendeigh 1947; Morris et al. 1958; Erskine 1978; Gage and Miller 1978; Holmes et al. 2009). Other warblers showed similar, but much less pronounced, increases in the same time period, including Nashville, magnolia, black-throated blue, black-throated green, Wilson's and Canada warblers, American redstart and ovenbird (Hussell et al. 1992), supporting the idea that the impact of budworm on forest birds is widespread. Data from Manomet Bird Observatory confirms the regional signal for the three budworm-linked species. Yearly migration counts of Cape May, Tennessee, and bay-breasted warblers in eastern Massachusetts were significantly positively correlated with spruce budworm densities, estimated from area of defoliation in eastern North America from 1970 to 1980 and from light trap moth counts in Maine from 1970 to 1988 (Hagan et al. 1992).

9. Climate change

Climate change will likely result in changes in the spatial and temporal pattern of spruce budworm outbreak (Williams and Liebhold 1997; Fleming 2000) and the breeding phenology of birds (Hughes 2000). This may lead to changes in the impact of budworm on bird population trajectories and conversely the impact of bird predation on budworm cycles. Climate is considered a major driver in restricting the extent and intensity of outbreaks (Volney and Fleming 2007). Generally, outbreaks are expected to be more frequent (Mattson and Haack 1987) and last longer (Greenbank 1963) in boreal forests with a warmer climate. Budworm outbreaks in the 20th century were generally more severe than those in the 19th century, possibly due to climate-induced reduction in fire frequency (Morin et al. 2009), since the proportion of balsam fir in the forest increases with longer fire return intervals (Bergeron and Leduc 1998) and the severity of budworm outbreaks increases with the proportion of balsam fir (Morin et al. 2009). However, others have suggested that spruce budworm disturbances may promote wildfire in warmer, drier climates (Fleming 2000). The interaction between climate, fire, and budworm outbreak will complicate any attempts to understand the potential impact of climate change on budworm. Also, impacts are likely to vary geographically in response to the local and regional realities of forest composition and climate. Thus, contrary to predictions for the boreal, the southern edge of the budworm's range is expected to have smaller areas of defoliation with increasing temperature, due to a northward shift of both budworm and spruce–fir forests (Williams and Liebhold 1997). Both of these shifts should have significant impacts on bird communities in the region.

Reproduction and population dynamics of birds are also expected to be influenced by climate. Bird ranges have changed (Thomas and Lennon 1999) and breeding phenologies have shifted in response to climate change. Long-term trends of earlier laying dates (8.8 days on average) have been demonstrated in the UK (Crick and Sparks 1999; Crick et al. 1997; McCleery and Perrins 1998) and in North America (Brown et al. 1999; Winkler et al. 2002). There is also evidence of a decoupling of breeding phenology with the timing of highest food availability (Visser et al. 1998; Both and Visser 2005; Both et al. 2006). A decoupling of bird and budworm phenolgies could lead to less budworm available at times critical for feeding nestlings and therefore a significant reduction in the benefit of budworm outbreaks to birds. In addition, birds may be less able to regulate endemic budworm populations if the timing of their food requirements is not synchronized with large larval and pupal availability. It is the large larval period that mainly determines generation survival for the spruce budworm (Morris 1963*c*). A complete analysis of the impact of climate change on the bird–budworm interaction is beyond the scope of this paper, but would be necessary to fully understand the dynamics of forest bird populations and their potential role in regulating spruce budworm populations in a changing climate.

10. Conclusions

There is good evidence that there are 3 budworm-linked species (bay-breasted, Cape May, and Tennessee warblers) that respond to budworm outbreak much more strongly and consistently than other species, probably through increased productivity of local populations when budworm are abundant and movement into budworm infested areas. Beyond that, there appears to be a widespread positive bird community response to budworm outbreak that involves many species in the community. Several species have been shown to respond numerically and functionally to budworm at local scales, likely through some combination of increased reproductive success, increased opportunities to breed, movement of individuals to budworm infested areas, and behavioural adaptations for foraging on budworm. The strength of the response of individual species is not consistent, as would be expected given the limited number of studies conducted in a wide variety of contexts. Responses of budworm-linked species and others have also been demonstrated at more regional scales, with evidence coming from large-scale monitoring programs such as the Breeding Bird Survey, the Christmas Bird Count, and migration monitoring. Long-term trends in forest bird populations show distinct signals of large-scale budworm infestations and interpretation of these trends for conservation and land management should include consideration of the budworm outbreak cycle. Birds are directly and immediately impacted by the superabundance of food provided by spruce budworm, but there are clear indications that the longer-term effects of habitat change resulting from defoliation and tree mortality also have significant impacts on forest birds. The budworm cycle along with fire, logging, and succession dictate the availability of forest bird habitat over the long-term and large spatial scales.

Evidence is strong that birds have little influence on budworm populations at densities exceeding one million per hectare, consuming 7% or less of late instar larvae and pupae when budworm are at these levels. However, birds likely play a regulatory role at endemic population levels, although estimating consumption by birds when budworm are at low levels is more problematic. Based on a synthesis of existing studies, we estimate that birds consume roughly 19 to 35% of the budworm at densities of 100 000 to one million large larvae per hectare. Below these levels there are no reliable estimates for budworm consumption. There are good arguments suggesting that bird predation is not the primary cause of budworm oscillations, but some evidence that it does play a role in determining the mean level of oscillations.

The relationship between budworm and forest birds is likely to be affected by climate change, both in terms of how budworm influence bird populations over time and how birds influence budworm cycles. However, the complex interactions between climate change, tree distributions, fire regimes, budworm outbreaks, and bird populations will make it very difficult to anticipate the direction and magnitude of these changes.

Acknowledgements

We thank Kees van Frankenhuyzen and Carl Nystrom for their assistance with questions related to spruce budworm. Two anonymous reviewers provided helpful comments. Kerrie Wainio-Keizer provided assistance with figures.

References

Agriculture and Agri-Food Canada. 1995. Registration status of fenitrothion insecticide. Decision Document E95-01. Agriculture and Agri-Food Canada, Information Division, Ottawa, Ont.

Altman, B., and Sallabanks, R. 2000. Olive-sided flycatcher (*Contopus cooperi*). *In* The Birds of North America. *Edited by* A. Poole and F. Gill. Academy of Natural Sciences, Philadelphia, PA and American Ornithologists' Union, Wash.

Baltz, M.E., and Latta, S.C. 1998. Cape May warbler (*Dendroica tigrina*). *In* The Birds of North America. *Edited by* A. Poole and F. Gill. Academy of Natural Sciences, Philadelphia, PA and American Ornithologists' Union, Wash.

Baskerville, G.L. 1975. Spruce budworm: super silviculturalist. For. Chron. **51**: 138–140.

Bergeron, Y., and Leduc, A. 1998. Relationships between change in fire frequency and mortality due to spruce budworm outbreak in the southeastern Canadian boreal forest. J. Veg. Sci. **9**(4): 492–500. doi:10.2307/3237264.

Bergeron, Y., Leduc, A., Joyal, C., and Morin, H. 1995. Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. Can. J. For. Res. **25**(8): 1375–1384. doi:10.1139/x95-150.

Berryman, A.A., Stenseth, N.C., and Isaev, A.S. 1987. Natural regulation of herbivorous forest insect populations. Oecologia (Berl.), **71**(2): 174–184. doi:10.1007/BF00377282.

Blais, J.R. 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Can. J. For. Res. **13**(4): 539–547. doi:10.1139/x83-079.

Blais, J.R. 1985. The ecology of the eastern spruce budworm: a review and discussion. *In* Proceedings of the CANUSA Research Symposium on Recent Advances in Spruce Budworms Research, Bangor, ME, 16–20 September 1984. *Edited by* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy. United States Department of Agriculture, Forest Service, Bangor, Maine. pp. 49–59.

Blais, J.R., and Parks, G.R. 1964. Interaction of evening grosbeak (*Hesperiphona vespertina*) and spruce budworm (*Choristoneura fumiferana* (Clem.)) in a localized budworm outbreak treated with DDT in Quebec. Can. J. Zool. **42**(6): 1017–1024. doi:10.1139/z64-099.

Blancher, P.J., Phoenix, R.D., Badzinski, D.S., Cadman, M.D., Crewe, T.L., Downes, C.M., Fillman, D., Francis, C.M., Hughes, J., Hussell, D.J.T., Lepage, D., McCracken, J.D., McNicol, D.K., Pond, B.A., Ross, R.K., Russell, R., Venier, L.A., and Weeber, R.C. 2009. Population trend status of Ontario's forest birds. For. Chron. **85**: 184–201.

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.

Bonter, D.N., and Harvey, M.G. 2008. Winter survey data reveal rangewide decline in Evening Grosbeak populations. Condor, **110**(2): 376–381. doi:10.1525/cond.2008.8463.

Both, C., and Visser, M.E. 2005. The effect of climate change on the correlation between avian life- history traits. Glob. Change Biol. **11**(10): 1606–1613. doi:10.1111/j.1365-2486.2005.01038.x.

Both, C., Bouwhuis, S., Lessells, C.M., and Visser, M.E. 2006. Climate change and population declines in a long-distance migratory bird. Nature, **441**(7089): 81–83. doi:10.1038/nature04539. PMID:16672969.

Briskie, J.V. 1994. Least flycatcher (*Empidonax minimus*). *In* The Birds of North America. *Edited by* A. Poole and F. Gill. Academy of Natural Sciences, Philadelphia, PA and American Ornithologists; Union, Wash.

Brown, J.L., Li, S.H., and Bhagabati, N. 1999. Long-term trend toward earlier breeding in an American bird: a response to global warming? Proc. Natl. Acad. Sci. U.S.A. **96**: 5565–5569.

Buckner, C.H. 1967. Avian and mammalian predators of forest insects. Entomophaga, **12**(4): 491–501. doi:10.1007/BF02376935.

Burgess, N.M., Holmes, S.B., Pauli, B.D., and Millikin, R.L. 1995. Potential indirect impacts of *Btk* on insectivorous birds: Canadian concerns and research response. I*n Bacillus thuringiensis* Biotechnology and Environmental Benefits. *Edited by* T.-Y. Feng, K.-F. Chak, R. Smith, T. Yamamoto, J. Margalit, C. Chilcott, and R. Rose. Hua Shiang Yuan Publishing Co., Taipei, Taiwan. Pp. 505–519.

Busby, D.G., Pearce, P.A., and Garrity, N.R. 1982. Brain cholinesterase inhibition in forest passerines exposed to experimental aminocarb spraying. Bull. Environ. Contam. Toxicol. **28**(2): 225–229. doi:10.1007/BF01608580. PMID:7066566.

Busby, D.G., Pearce, P.A., and Garrity, N.R. 1983. Brain ChE response in forest songbirds exposed to aerial spraying of aminocarb and possible influence of application methodology and insecticide formulation. Bull. Environ. Contam. Toxicol. **31**(2): 125–131. doi:10.1007/BF01607882. PMID:6616082.

Cadogan, B.L., Scharbach, R.D., Knowles, K.R., and Krause, R.E. 2005. Efficacy evaluation of a reduced dosage of tebufenozide applied aerially to control spruce budworm (*Choristoneura fumiferana*). Crop Prot. **24**(6): 557–563. doi:10.1016/j.cropro.2004.10.008.

Campbell, R.W. 1993. Population Dynamics of the Major North American Needle-eating Budworms. Research Paper PNW-RP-463. USDA Forest Service, Pacific Northwest Research Station, Portland, OR. 222 pp.

Canadian Council of Forest Ministers. 2008. National Forestry Database. Canadian Council of Forest Ministers. Available from http://nfdp.ccfm.org/copy_e.php [accessed October 2009].

Candau, J.-N., Fleming, R.A., and Hopkin, A.A. 1998. Spatiotemporal patterns of large-scale defoliation caused by the spruce budworm in Ontario since 1941. Can. J. For. Res. **28**(11): 1733–1741. doi:10.1139/cjfr-28-11-1733.

Cheshire, W.P. 1954. Bird populations and potential predation on the spruce budworm. Section 14, Green River Project, 1953, Annual Technical Report. Canada Department of Agriculture, Science Service.

Clark, W.C., Jones, D.D., and Holling, C.S. 1979. Lessons for ecological policy design: a case study of ecosystem management. Ecol. Model. **7**(1): 1–53. doi:10.1016/0304-3800(79)90008-5.

Crawford, H.S. 1985. Effects of silvicultural practice on bird predation. *In* Spruce-Fir Management and Spruce Budworm. Society of American Foresters Region VI Technical Committee, Report SAF 84-07. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Broomall, Pa. pp. 173–175.

Crawford, H.S., and Jennings, D.T. 1989. Predation by birds on spruce budworm *Choristoneura fumiferana*: functional, numerical, and total responses. Ecology, **70**(1): 152–163. doi:10.2307/1938422.

Crawford, H.S., and Titterington, R.W. 1979. Effects of silvicultural practice on bird communities in upland spruce-fir stands. in Management of North Central and Northeastern Forests for Nongame birds. General Technical Report NC-51. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn.

Crawford, H.S., Titterington, R.W., and Jennings, D.T. 1983. Bird predation and spruce budworm populations. J. For. **81**: 433–435.

Crawford, H.S., Jennings, D.T., and Stone, T.L. 1990. Red-breasted nuthatches detect early increase in spruce budworm populations. North. J. Appl. For. **7**: 81–83.

Crick, H.Q.P., and Sparks, T.H. 1999. Climate change related to egg-laying trends. Nature, **399**(6735): 423–424. doi:10.1038/20839.

Crick, H.Q.P., Dudley, C., Glue, D.E., and Thomson, D.L. 1997. UK birds are laying eggs earlier. Nature, **388**: 526. doi:10.1038/41453.

Dowden, P.B., Carolin, V.M., and Dirks, C.O. 1950. Natural control factors affecting the spruce budworm in the Adirondacks during 1946–1948. J. Econ. Entomol. **43**: 774–783.

Dowden, P.B., Jaynes, H.A., and Carolin, V.M. 1953. The role of birds in a spruce budworm outbreak in Maine. J. Econ. Entomol. **46**: 307–312.

Ennis, T., and Caldwell, E.T.N. 1991. Spruce budworm, chemical and biological control. *In* Tortricid Pests, Their Biology, Natural Enemies and Control. *Edited by* L.P.S. van der Geest, and H.H. Evenhuis. Elsevier Science Publishers B.V., Amersterdam, The Netherlands. pp. 621–641.

Erskine, A.J. 1977. Birds in boreal Canada. Report Series Number 41. Fisheries and Environment Canada, Canadian Wildlife Service. 73 pp.

Erskine, A.J. 1978. The first ten years of the co-operative breeding bird survey in Canada. Report Series Number 42. Fisheries and Environment Canada, Canadian Wildlife Service. 61 pp.

Falls, J.B., and Kopachena, J.G. 1994. White-throated sparrow (*Zonotrichia albicollis*). *In* The Birds of North America. *Edited by* A. Poole and F. Gill. Academy of Natural Sciences, Philadelphia, Pa., and American Ornithologists' Union, Wash.

Fleming, R.A. 2000. Climate change and insect disturbance regimes in Canada's boreal forests. World Resour. Rev. **12**: 520–554.

Freedman, B. 1995. Environmental ecology: The ecological effects of pollution, disturbance, and other stresses. Academic Press, Toronto, ON, Canada. 606 pp.

Gage, S.H. 1968. Consumption by adult birds of the spruce budworm at different larval densities. Internal Report M-36. Department of Forestry and Rural Development, Forestry Branch, Maritimes Region, Forest Research Laboratory, Fredericton, NB. 5 pp. + tables.

Gage, S.H., and Miller, C.A. 1978. A long-term bird census in spruce-budworm-prone balsam fir habitats in northwestern New

Burnswick. Information Report M-X-84. Canadian Forest Service, Maritimes Forest Research Centre, Fredericton, NB. 6 pp.

George, J.L., and Mitchell, R.T. 1948. Calculations on the extent of spruce budworm control by insectivorous birds. J. For. **46**: 454–455.

Greenbank, D.O. 1963. Climate and the spruce budworm. Mem. Entomol. Soc. Can. **31**: 174–180.

Hagan, J.M.I., Lloyd-Evans, T.L., Atwood, J.L., and Wood, D.S. 1992. Long-term changes in migratory landbirds in the northeastern United States: evidence from migration capture data. *In* Ecology and Conservation of Neotropical Migrant Landbirds. *Edited by* J.M.I. Hagan and D.W. Johnston. Smithsonian Institution Press, Wash. pp. 115–130.

Hall, G.A. 1994. Magnolia warbler (*Dendroica magnolia*). *In* The Birds of North America. *Edited by* A. Poole and F. Gill. Academy of Natural Sciences, Philadelphia, Pa., and American Ornithologists' Union, Wash.

Hardy, Y., Mainville, M., and Schmitt, D.M. 1986. A cartographic history of spruce budworm defoliation in eastern North America, 1938–1980. Miscellaneous Publication No. 1449. USDA Forest Service. 52 pp.

Harvey, G.T. 1985. The taxonomy of the coniferophagous *Choristoneura* (Lepidoptera: Tortricidae): a review. *In* Proceedings of the CANUSA Research Symposium on Recent Advances in Spruce Budworms Research, Bangor, ME, 16–20 September 1984. *Edited by* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy. United States Department of Agriculture, Forest Service, Bangor, ME. pp. 16–48.

Hensley, M.M., and Cope, J.B. 1951. Further data on removal and repopulation of the breeding birds in a spruce-fir forest community. Auk, **68**: 483–493.

Hill, N.P., and Hagan, J.M.I. 1991. Population trends of some northeastern North America landbirds: a half-century of data. Wilson Bull. **103**: 165–182.

Holling, C.S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Can. Entomol. **91**(5): 293–320. doi:10.4039/Ent91293-5.

Holling, C.S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Entomol. Soc. Can. **45**: 1–60.

Holling, C.C. 1978. The spruce-budworm/forest-management problem. *In* Adaptive Environmental Assessment and Management. *Edited by* C.S. Holling. John Wiley & Sons, Toronto, Ont. pp. 143–192.

Holling, C.S. 1988. Temperate forest insect outbreaks, tropical deforestation and migratory birds. Mem. Entomol. Soc. Can. **146**: 21–32.

Holmes, R.T. 1994. Black-throated Blue Warbler (*Dedroica caerulescens*). *In* The Birds of North America. *Edited by* A. Poole and F. Gill. Academy of Natural Sciences, Philadelphia, PA and American Ornithologists' Union, Wash.

Holmes, S.B. 1998. Reproduction and nest behaviour of Tennessee warblers, *Vermivora peregrina*, in forests treated with Lepidoptera-specific insecticides. J. Appl. Ecol. **35**(2): 185–194. doi:10.1046/j.1365-2664.1998.00298.x.

Holmes, S.B., and Nixon, E.A. 2000. Nesting biology of the Tennessee warbler, *Vermivora peregrina*, in northern Ontario. Can. Field Nat. **114**: 34–44.

Holmes, S.B., Sanders, C.J., Fillman, D., and Welsh, D.A. 2009. Changes in a forest bird community during an outbreak cycle of the spruce budworm in northwestern Ontario. Bird Populations, **9**: 13–28. Available at http://birdpop.net/pubs/birdpopv9.php [accessed October 2009].

Hughes, I., I. 2000. Biological consequences of global warming: is the signal already apparent? Trends Ecol. Evol. **15**(2): 56–61. doi:10.1016/S0169-5347(99)01764-4. PMID:10652556.

Hussell, D.J.T., Mather, M.H., and Sinclair, P.H. 1992. Trends in numbers of tropical- and temperate-wintering migrant landbirds in migration at Long Point, Ontario, 1961–1988. *In* Ecology and Conservation of Neotropical Migrant Landbirds. *Edited by* J.M.I. Hagan and D.W. Johnston. Smithsonian Institution Press, Wash. pp. 101–114.

Irland, L.C. 1980. Pulpwood, pesticides, and people. Controlling spruce budworm in northeastern North America. Environ. Manage. **4**(5): 381–389. doi:10.1007/BF01869650.

Jardon, Y., Morin, H., and Dutilleul, P. 2003. Périodicité et synchronisme des épidémies de la tordeuse des bourgeons de l'épinette au Québec. Can. J. For. Res. **33**(10): 1947–1961. doi:10.1139/x03-108.

Jones, D.D. 1979. The budworm site model. *In* Proceedings of an International Conference, Pest Management. *Edited by* G.A. Norton, and C.S. Holling. Pergamon Press, Oxford, UK. pp. 91–150.

Kendeigh, S.C. 1947. Bird population studies in the coniferous forest biome during a spruce budworm outbreak. Biological Bulletin No. 1. Ontario Department of Lands and Forests, Division of Research. 100 pp.

Ludwig, D., Jones, D.D., and Holling, C.S. 1978. Qualitative analysis of insect outbreak systems: the spruce budworm and forest. J. Anim. Ecol. **47**(1): 315–332. doi:10.2307/3939.

MacArthur, R.H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology, **39**(4): 599–619. doi:10.2307/1931600.

MacLean, D.A. 1980. Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. For. Chron. **56**: 213–221.

Martin, T.E. 1987. Food as a limit on breeding birds: a life history perspective. Annu. Rev. Ecol. Syst. **18**(1): 453–487. doi:10.1146/annurev.es.18.110187.002321.

Mattson, W.J., and Haack, R.A. 1987. The role of drought in outbreaks of plant-eating insects. Bioscience, **37**(2): 110–118. doi:10.2307/1310365.

McCleery, R.H., and Perrins, C.M. 1998. Temperature and egg-laying trends. Nature, **391**(6662): 30–31. doi:10.1038/34073.

McMartin, B., Bellocq, I., and Smith, S.M. 2002. Patterns of consumption and diet differentiation for three breeding warbler species during a spruce budworm outbreak. Auk, **119**(1): 216–220. doi:10.1642/0004-8038(2002)119[0216:POCADD]2.0.CO;2.

Miller, A. 1999. Environmental problem solving: Psychosocial barriers to adaptive change. Springer-Verlag, New York, NY.

Miller, C.A., and Renault, T.R. 1981. The use of experimental populations to assess budworm larval mortality at low densities. Information Report M-X-115. Environment Canada, Canadian Forestry Service, Maritimes Forest Research Centre, Fredericton, NB.

Mitchell, R.T. 1952. Consumption of spruce budworms by birds in a Maine spruce-fir forest. J. For. **50**: 387–389.

Mook, L.J. 1963. Birds and the spruce budworm. *In* The Dynamics of Epidemic Spruce Budworm Populations. *Edited by* R.F. Morris. Memoirs of the Entomological Society of Canada No. 31, pp. 268–271

Morin, H., Laprise, D., Simard, A.-A., and Amouch, S. 2009. Spruce budworm outbreak regimes in eastern North America. *In* Ecosystem Management in the Boreal Forest. *Edited by* S. Gauthier, M.-A. Vaillancourt, A. Leduc, L. De Grandpré, D. Kneeshaw, H. Morin, P. Drapeau, and Y. Bergeron. Presse de l'Université du Québec, Québec, QC. pp. 155–182.

Morris, R.F. 1963*a*. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. **31**: 1–332.

Morris, R.F. 1963*b*. The development of predictive equations for the spruce budworm based on key-factor analysis. *In* The Dynamics of Epidemic Spruce Budworm Populations. *Edited by* R.F. Morris. Memoirs of the Entomological Society of Canada No. 31, pp. 116–129

Morris, R.F. 1963*c*. Predation and the spruce budworm. *In* The Dynamics of Epidemic Spruce Budworm Populations. *Edited by* R.F. Morris. Memoirs of the Entomological Society of Canada No. 31, pp. 244–248.

Morris, R.F., Cheshire, W.F., Miller, C.A., and Mott, D.G. 1958. The numerical response of avian and mammalian predators during a gradation of the spruce budworm. Ecology, **39**(3): 487–494. doi:10.2307/1931758.

Morse, D.H. 1978. Populations of bay-breasted and Cape May warblers during an outbreak of the spruce budworm. Wilson Bull. **90**: 404–413.

Morse, D.H. 1989. American warblers: An ecological and behavioral perspective. Harvard University Press, Cambridge, Mass.

Mott, D.G. 1963. The population model for the unsprayed area. *In* The Dynamics of Epidemic Spruce Budworm Populations. *Edited by* R.F. Morris. Memoirs of the Entomological Society of Canada No. 31, pp. 99–109

Murdoch, W.W. 1969. Switching in generalist predators: experiments on prey specificity and stability of prey populations. Ecol. Monogr. **39**(4): 335–354. doi:10.2307/1942352.

Nagy, L.R., and Smith, K.G. 1997. Effects of insecticide-induced reduction in lepidopteran larvae on reproductive success of hooded warblers. Auk, **114**: 619–627.

Nealis, V.G., and Regniere, J. 2004. Insect-host relationships influencing disturbance by the spruce budworm in a boreal mixedwood forest. Can. J. For. Res. **34**(9): 1870–1882. doi:10.1139/x04-061.

Needham, T., Kershaw, J.A., Jr., and McLean, D.A. 1999. Effects of mixed stand management to reduce impacts of spruce budworm defoliation on balsam fir stand-level growth and yield. North. J. Appl. For. **16**: 19–24.

Norton, M.L., Bendell, J.F., Bendell-Young, L.I., and LeBlanc, C.W. 2001. Secondary effects of the pesticide *Bacillus thuringiensis kurstaki* on chicks of spruce grouse (*Dendragapus canadensis*). Arch. Environ. Contam. Toxicol. **41**(3): 369–373. doi:10.1007/s002440010261. PMID:11503075.

Patten, M.A., and Burger, J.C. 1998. Spruce budworm outbreaks and the incidence of vagrancy in eastern North American wood-warblers. Can. J. Zool. **76**(3): 433–439. doi:10.1139/cjz-76-3-433.

Pearce, P.A., Peakall, D.B., and Erskine, A.J. 1976. Impact on forest birds of the 1975 spruce budworm spray operation in New Brunswick. Progress Note No. 62. Canadian Wildlife Service. 7 pp.

Pelech, S., and Hannon, S.J. 1995. Impact of tent caterpillar defoliation on the reproductive success of black-capped chickadees. Condor, **97**(4): 1071–1074. doi:10.2307/1369549.

Prebble, M.L. 1975. Aerial control projects. Spruce budworm. Introduction. *In* Aerial Control of Forest Insects in Canada. *Edited by* M.L. Prebble. Department of the Environment, Ottawa, Ont. pp. 77–84.

Regniere, J., Delisle, J., Bauce, É., Dupont, A., Therrien, P., Kettela, E., Cadogan, L., Retnakaran, A., and van Frankenhuyzen, K. 2001. Applying current understanding of spruce budworm population dynamics: development of early intervention strategies. Research Note. Canadian Forest Service, Laurentian Forestry Centre, Quebec, QC. 11 pp.

Rich, T.D., Beardmore, C.J., Berlanga, H., Blancher, P.J., Bradstreet, M.S.W., Butcher, G.S., Demarest, D.W., Dunn, E.H., Hunter, W.C., Inigo-Elias, E.E., Kennedy, J.A., Martell, A.M., Panjabi, A.O., Pashley, D.N., Rosenberg, K.V., Rustay, C.M., Wendt, J.S., and Will, T.C. 2004. Partners in flight north american landbird conservation plan. Cornell Lab. of Ornithology, Ithaca, NY. 84 pp.

Rimmer, C.C., and McFarland, K.P. 1998. Tennessee warbler (*Vermivora peregrina*). *In* The Birds of North America. *Edited by* A. Poole and F. Gill. Academy of Natural Sciences, Philadelphia, Pa., and American Ornithologists' Union, Wash.

Robbins, C.S., Sauer, J.R., Greenberg, R.S., and Droege, S. 1989. Population declines in North American birds that migrate to the neotropics. Proc. Natl. Acad. Sci. U.S.A. **86**(19): 7658–7662. doi:10.1073/pnas.86.19.7658. PMID:2798430.

Royama, T. 1981. Fundamental concepts and methodology for the analysis of animal population dynamics, with particular reference to univoltine species. Ecol. Monogr. **51**(4): 473–493. doi:10.2307/2937325.

Royama, T. 1984. Population dynamics of the spruce budworm *Choristoneura fumiferana.* Ecol. Monogr. **54**(4): 429–462. doi:10.2307/1942595.

Royama, T. 1992. Analytical population dynamics. Chapman & Hall, New York.

Royama, T., MacKinnon, W.E., Kettela, E.G., Carter, N.E., and Harting, L.K. 2005. Analysis of spruce budworm outbreak cycles in New Brunswick, Canada, since 1952. Ecology, **86**(5): 1212–1224. doi:10.1890/03-4077.

Sanders, C.J. 1970. Populations of breeding birds in the spruce- fir forests of northwestern Ontario. Can. Field Nat. **84**: 131–135.

Sanders, C.J. 1996. Pheromone traps for detecting incipient outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.). NODA/NFP Technical Report TR-32. Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre, Sault Ste. Marie, Ont. 8 pp. + appendices.

Sleep, D.J.H., Drever, M.C., and Szuba, K.J. 2009. Potential role of spruce budworm in range-wide decline of Canada Warbler. J. Wildl. Manage. **73**(4): 546–555. doi:10.2193/2008-216.

Solomon, M.E. 1949. The natural control of animal populations. J. Anim. Ecol. **18**(1): 1–35. doi:10.2307/1578.

Southwood, T.R.E., and Comins, H.N. 1976. A synoptic population model. J. Anim. Ecol. **45**(3): 949–965. doi:10.2307/3591.

Stedinger, J.R. 1984. A spruce budworm-forest model and its implications for suppression programs. For. Sci. **30**: 597–615.

Stewart, R.E., and Aldrich, J.W. 1952. Ecological studies of breeding bird populations in northern Maine. Ecology, **33**(2): 226–238. doi:10.2307/1930641.

Street, P.W., Arlidgel, C.J., Hollstedt, C., Bell, F.W., and Towill, W.D. 1994. Development of silvicultural keys to support integrated vegetation management decision making in forest renewal. Technical Note TN-28. Ontario Ministry of Natural Resources, NWR Science and Technology. 16 pp. Available from www.mnr.gov.on.ca/MNR_E005384.pdf [accessed November 2009].

Thomas, C.D., and Lennon, J.J. 1999. Birds extend their ranges northwards. Nature, **399**: 213. doi:10.1038/20335.

Thurber, D.K., McClain, W.R., and Whitmore, R.C. 1994. Indirect effects of gypsy moth defoliation on nest predation. J. Wildl. Manage. **58**(3): 493–500. doi:10.2307/3809321.

Tothill, J.D. 1923. Notes on the outbreaks of spruce budworm, forest tent caterpillar and larch sawfly. Proc. Acadian Entomol. Soc. **8**: 172–182.

Vaidya, N.K., and Wu, J. 2008. Modeling spruce budworm population revisited: impact of physiological structure on outbreak control. Bull. Math. Biol. **70**(3): 769–784. doi:10.1007/s11538-007-9278-x. PMID:18306004.

van Frankenhuyzen, K. 1995. The development of *Bacillus thuringiensis* for control of the spruce budworm, *Choristoneura fumiferana*, in Canada. *In* Bacillus thuringiensis Biotechnology and Environmental Benefits. *Edited by* T.-Y. Feng, K.-F. Chak, R. Smith, T. Yamamoto, J. Margalit, C. Chilcott, and R. Rose. Hua Shiang Yuan Publishing Co., Taipei, Taiwan. pp. 405–423.

Van Horn, M.A., and Donovan, T. 1994. Ovenbird (*Seiurus aurocapillus*). *In* The Birds of North America. *Edited by* A. Poole and F. Gill. Academy of Natural Sciences, Philadelphia, Pa., and American Ornithologists' Union, Wash.

Venier, L.A., Pearce, J.L., Fillman, D.R., McNicol, D.K., and Welsh, D.A. 2009. Effects of spruce budworm outbreaks on boreal mixedwood bird communities. Avian Conserv. Ecol. **4**: 3. Available from www.ace-eco.org/vol4/iss1/art3 [accessed October 2009].

Visser, M.E., van Noordwijk, A.J., Tinbergen, J.M., and Lessells, C.M. 1998. Warmer springs lead to mistimed reproduction in great tits (Parus major). Proc. Biol. Sci. **265**(1408): 1867–1870. doi:10.1098/rspb.1998.0514.

Volney, W.J.A., and Fleming, R.A. 2007. Spruce budworm (*Choristoneura* spp.) biotype reactions to forest and climate characteristics. Glob. Change Biol. **13**(8): 1630–1643. doi:10.1111/j.1365-2486.2007.01402.x.

Watt, K.E.F. 1963. *In* The Dynamics of Epidemic Spruce Budworm Populations. *Edited by* R.F. Morris. Memoirs of the Entomological Society of Canada No. 31, pp. 52–63.

Williams, J.M. 1996. Bay-breasted warbler (*Dendroica castanea*). *In* The Birds of North America. *Edited by* A. Poole and F. Gill. Academy of Natural Sciences, Philadelphia, Pa., and American Ornithologists' Union, Wash.

Williams, D.W., and Liebhold, A.M. 1997. Latitudinal shifts in spruce budworm (Lepidoptera: Tortricidae) outbreaks and spruce-fir forest distributions with climate change. Acta Phytopathol. Entomol. Hung. **32**: 205–215.

Winkler, D.W., Dunn, P.O., and McCulloch, C.E. 2002. Predicting the effects of climate change on avian life-history traits. Proc. Natl. Acad. Sci. U.S.A. **99**(21): 13595–13599. doi:10.1073/pnas.212251999. PMID:12370441.

Wypkema, R.C.P. 1982. The role of avian predators in the control of spruce budworm at endemic levels. Ph.D. thesis, Queen's University, Kingston, Ont.

Zach, R., and Falls, J.B. 1975. Response of the ovenbird (Aves: Parulidae) to an outbreak of the spruce budworm. Can. J. Zool. **53**(11): 1669–1672. doi:10.1139/z75-201.