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Research Papers

Effects of Spruce Budworm (*Choristoneura fumiferana* (Clem.)) Outbreaks on Boreal Mixed-Wood Bird Communities

Effets des épidémies de Tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clem.)) sur les communautés d'oiseaux de la forêt boréale mixte

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ABSTRACT. This study examined the influence of a spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreak on a boreal mixed-wood bird community in forest stands ranging in age from 0 to 223 yr. We asked if (1) patterns of species response were consistent with the existence of spruce budworm specialists, i.e., species that respond in a stronger quantitative or qualitative way than other species; (2) the superabundance of food made it possible for species to expand their habitat use in age classes that were normally less used; and (3) the response to budworm was limited to specialists or was it more widespread. Results here indicated that three species, specifically the Bay-breasted Warbler (*Dendroica castanea*), Tennessee Warbler (*Vermivora peregrina*), and Cape May Warbler (*Dendroica tigrina*), had a larger numerical response to the budworm outbreak. They responded with increases in density of up to tenfold over 4 or 5 yr. No other species responded with more than a twofold increase in the same time period. These species also showed a functional response by breeding more frequently in young stands aged 1–21 yr and intermediate stands aged 22–36 yr as budworm numbers increased. Our data also suggested that many species profited to a lesser extent from budworm outbreaks, but that this effect may be too subtle to detect in most studies. We found evidence of a positive numerical effect in at least 18 additional species in one or two stand-age categories but never in all three for any one species. Given the numerical response in many species and the potential influence of budworm on bird populations because of the vast extent of outbreaks, we believe that the population cycle of spruce budworm should be considered in any evaluation of population trends in eastern boreal birds.

RÉSUMÉ. Cette recherche a pour but d'évaluer l'influence d'une épidémie de Tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clem.)) sur une communauté d'oiseaux en forêt boréale mixte, dans des peuplements âgés de 0 à 223 ans. Nous nous sommes demandés si : 1) les profils de réponse des oiseaux concordaient avec l'existence de spécialistes de la tordeuse, c.-à-d. les espèces qui répondent de façon plus marquée – tant sur le plan quantitatif que sur le plan qualitatif – que les autres espèces; 2) la surabondance de nourriture permettait aux espèces de fréquenter des types de peuplements habituellement moins utilisés en raison de leur classe d'âge; et 3) la réponse à la tordeuse était limitée aux spécialistes ou si elle s'étendait à d'autres espèces. Nos résultats indiquent que trois espèces, soit la Paruline à poitrine baie (*Dendroica castanea*), la Paruline obscure (*Vermivora peregrina*) et la Paruline tigrée (*Dendroica tigrina*), ont eu des augmentations importantes d'effectifs qui coïncidaient avec l'épidémie de tordeuse. La densité de ces espèces a augmenté par un facteur de 10 en 4 à 5 ans. La densité des autres espèces n'a pas augmenté de plus du double pendant la même période. Les trois espèces de paruline ont aussi montré une réponse fonctionnelle en nichant plus souvent que d'habitude dans les jeunes peuplements (1–21 ans) et dans les peuplements d'âge intermédiaire (22–36 ans) à mesure que le nombre de tordeuses augmentait. Nos données

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laissent aussi croire qu'un grand nombre d'espèces a profité, dans une moindre mesure, des épidémies de tordeuse, mais que cet effet est peut-être souvent trop faible pour être détecté. Nous avons également observé une augmentation des effectifs chez au moins 18 autres espèces dans une ou deux catégories de classe d'âge, mais jamais dans les trois catégories. Étant donné l'augmentation des effectifs chez de nombreuses espèces et l'influence potentielle de la tordeuse sur les populations d'oiseaux en raison de la vaste étendue des épidémies, nous croyons que le cycle des populations de Tordeuse des bourgeons de l'épinette devrait être pris en considération dans toute évaluation de la tendance des populations d'oiseaux boréaux de l'Est.

Key Words: *boreal forest birds; spruce budworm; succession; boreal mixed woods; mapping census; Choristoneura fumiferana (Clem.)*

INTRODUCTION

Forest landbirds are an integral part of the boreal ecosystem and play an important role in forest integrity and sustainability (Niemi et al. 1998). Thirty-seven of the 138 species of landbirds that regularly breed or winter in Ontario's Boreal Shield ecozone have been identified as priority species by Ontario Partners in Flight (2006). Most of the priority species are common boreal forest landbirds for which the Ontario Boreal Shield has a high conservation responsibility because a large proportion of these populations live in the region. Some high-priority species such as the Bay-breasted Warbler (*Dendroica castanea*) and the Canada Warbler (*Wilsonia canadensis*) have high vulnerability and have experienced population declines. The ecology of forest birds in the eastern boreal forest has not been well studied relative to other North American ecosystems, but assessing the status of and trends affecting forest landbirds in this region has become an important priority (Environment Canada 1995, Ontario Ministry of Natural Resources 2005). As well, forest landbirds have been proposed and used as an important tool in assessing the sustainability of forest management (Voigt et al. 2000, Holloway et al. 2004, Venier and Pearce 2004, Venier et al. 2007). For these reasons it is important to understand the ecological processes of the boreal forest that affect the population levels of this taxon.

In this paper we examine the effects of a spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreak on a boreal mixed-wood bird community in stands representing a range of successional stages. Spruce budworm are a major driver of ecosystem dynamics, and their outbreaks have profound effects on forest composition and structure over very large areas (Blais 1983, Bergeron et al. 1995, Candau and Fleming 2005, MacLean and Andersen 2008). For example, 41 million ha of Ontario forest have been defoliated by spruce budworm at least once since 1941. Outbreaks occur with a basic oscillation of approximately 36 yr (Candau et al. 1998). Forest disturbances such as spruce budworm outbreaks, fires, and harvesting all have a significant influence on forest age-class distribution, which in turn is an extremely important predictor of bird community composition (Welsh 1987, Helle and Mönkkönen 1990, Hobson and Schieck 1999, Venier and Pearce 2005). As well, a budworm outbreak has the direct effect of increasing food availability for many forest landbirds (Mitchell 1952, Dowden et al. 1953, Crawford and Jennings 1989). The interaction of forest stand age and response to spruce budworm outbreak can provide additional insight into the relationship between the bird community and budworm.

Several studies have documented the numerical response of individual bird species to outbreak levels of spruce budworm (Kendeigh 1947, Hensley and Cope 1951, Morris et al. 1958, Erskine1977, Morse 1978, Crawford et al. 1983); please see Appendix 1 for a summary. Several species have been called spruce budworm "specialists," including the Bay-breasted Warbler (*Dendroica castanea*), the Tennessee Warbler (*Vermivora peregrina*), and the Cape May Warbler (*Dendroica tigrina*), because of their large and consistent response (Welsh 1985, Morse 1989, Patten and Burger 1998). Some species have shown responses in some but not all studies, e.g., the Blue-headed Vireo (*Vireo solitarius*). In separate studies, the

Blackburnian Warbler (*Dendroica fusca*) and the Yellow-rumped Warbler (*Dendroica coronata*) showed both positive and negative responses (Appendix 1); the negative response are attributed to competition with more abundant species (Morris et al. 1958, Morse 1989).

This study examined 18 9-ha plots ranging in age from 1 yr since disturbance to 223 yr since disturbance over the five years between 1979 and 1983, when spruce budworm levels transitioned from endemic to epidemic in this region. Data were collected intensively using mapping census techniques (IBCC 1970), with the result that this study provides one of the most in-depth examinations of the bird community response to spruce budworm of those currently in the literature. The intensive nature of the data collection and the relatively large number of plots allowed us to document the presence of a numerical response in a large number of species with greater confidence than was possible in previous studies, which commonly used low-intensity methods or lower replication. We were interested in three principal questions in relation to these data. First, were patterns of species response consistent with the existence of spruce budworm specialists, i.e., species that respond in a stronger quantitative or qualitative way than other species? Second, did the superabundance of food allow bird species to expand their habitat use into stand ages that were normally lesser used? Third, was the bird response to budworm limited to specialists, or was it more widespread?

METHODS

Study area

The study area is located north of Manitouwadge, Ontario, Canada, at 49° 30’ N, 86 ° W, in the Boreal Shield ecozone (Fig. 1) in mixed coniferous and deciduous stands of the Central Plateau Region of the boreal forest (Rowe 1972). Plots of 9 ha were established in 18 upland mixed-wood stands that had a similar topography, similar soils and moisture regimes, and predisturbance vegetation that was a mixture of black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), and aspen (*Populus balsamifera* or *P. tremuloides*). These stands represented an age gradient of natural regeneration from harvesting (1945–1979) and fire. The six oldest stands were of fire origin and varied in age from 60 to 223 yr. The 12 youngest stands (0–33 yr) had been harvested for merchantable conifer and aspen. One stand, aged 109 yr in 1979, was harvested but not sampled in 1981 and then became a 1-yr-old stand in 1982. Stands were identified by their approximate age since disturbance. Sampling plots had one of two configurations: squares of 300 x 300 m and rectangles of 500 x 200 m with an area of 100 x 100 m removed from one corner. We classified the plots into three stand age categories, i.e., young, intermediate, and mature, based on time since disturbance in years. In 1979, the young stands were aged 1, 4, 6, 8, 9, 11, 15, 17, and 21 yr. Intermediate-aged stands were 24, 26, 30, and 36 yr. The mature plots were 60, 109, 150, 151, 179, and 223 yr. Plot 109 (1979 and 1980) became plot 1 in 1982 and 1983 after it was logged in 1981.

Bird sampling

A mapping census technique (IBCC 1970) was used to identify species-specific territories in each of five years (1979 through 1983). Experienced observers visited plots seven to 10 times each year between 23 May and 7 July. Visits were made between dawn and 1000 Eastern Daylight Time. Visits lasted approximately 1–2 hr. Transects were walked in alternate directions on successive visits, and visit times alternated between dawn and mid-morning. Visits were made by 10 different observers over the 5-yr period. Each observer was assigned four or five plots depending on difficulty and traveling distance between plots. A single supervisor censused all plots at least once during each census season to confirm procedures, species identification, and territory boundaries.

Plots were gridded with 50 m spacing to help bird observers map the locations of observations. All birds seen or heard were indicated on a territory map. Simultaneous observations of more than one individual of a species were recorded to differentiate multiple individuals of the same species. Clusters were identified as a group of records of a species that, on final analysis of a species map, appeared to be associated with a territory held by one male. The minimum number of records required before a cluster was accepted as a territory was related to the number of valid visits and the migratory status of the species. For eight to 10 valid visits, three records were required, and for five to seven valid visits, two records were required. The number of valid visits is

Fig. 1. Map of the study location.

the number of visits on which the given species could have been observed; for example, early visits for a late migrant are not valid. The assignment of territories for resident species required only two records because of their secretive nature and earlier breeding habits. At least two records needed to be of high territorial significance for any territory, e.g., song. Territories that overlapped the plot edge were counted as fractional territories based on the amount of the territory contained in the plot. Plot maps from each visit were synthesized at the end of the season to generate a territory map for each species. If the observations for a particular individual did not meet the requirements for territory acceptance, that individual was recorded as a visitor on that plot. Birds were not sampled in plot 151 in 1979 and in plot 109 in 1981. Otherwise, all plot-year combinations were sampled.

Budworm sampling

Spruce budworm were sampled in 1982 and 1983 using standard techniques (Morris 1955). Extendable pole pruners were used to remove one 45-cm branch tip from the mid-crown of each of three co-dominant balsam fir trees selected at random on each sample date. Branches were bagged in the field and returned to the laboratory, where they were examined, and all stages of all insect species were removed, identified, and enumerated. Budworm density was expressed as the number of insects per 45-cm branch tip. Budworm were sampled on 17 June 1982 (n = 342 branch tips), and on 15, 16, 17, 21, and 23 June 1983 (n = 342 branch tips).

Data analysis

Bird community analysis

To assess the overall changes in the bird community as a function of increasing budworm through time, we calculated the total number of species and the total number of territories for each of the five study years. We also calculated the mean number of territories per plot for all species combined as a function of year for each of three stand-age categories. Using S-PLUS Version 7.0 software (Insightful Corporation, Seattle, Washington, USA), we developed a linear mixed regression model to examine the relationship between the number of territories per plot and the year and stand-age category. Year acted as a surrogate for the number of budworm and was identified as the fixed effect; plot , which was measured over five years, served as the random effect; and stand-age category provided an outer co-variate. We conducted this test with and without budworm specialists as part of the total.

Budworm counts

We compared the number of budworm per branch tip in three stand-age categories and in two years, 1982 and 1983, using a two-way ANOVA with replication and multiple comparisons with a simulation-based method. Data were transformed using a square root + 0.5 transformation to improve the distribution of the residuals (Zar 1984).

Bird response to budworm

We examined the number of bird territories per plot as a function of mean budworm count per branch tip in balsam fir with year (1982, 1983) as a co-variate using an analysis of co-variance.

Individual species analysis

Data were insufficient to allow for rigorous statistical analysis of the change in territories over time on an individual species basis. We examined plots of all species and stand-age category combinations to assess evidence of a response. We also compared the number of territories at the beginning of the study (1979 + 1980) to the number of territories at the end of the study (1982 + 1983) for the 30 most abundant species. Statistical comparisons were made using the Wilcoxon signed-ranks test for paired nonparametric data. *P*-values were used to indicate relative effect size but not to indicate statistical significance.

RESULTS

Bird territory changes through time

Sixty-six forest bird species had territories in the 18 study plots (Appendix 2). The total number of bird territories more than doubled from 1979 (598 territories) to 1982 (1259 territories), then dropped in 1983 to 1082 territories (Fig. 2). The number of species showed a similar pattern, increasing from 1979 to 1982 and then declining in 1983 (Fig. 2). The results from the linear mixed regression model indicated that there was a significant positive relationship between the number of territories per plot and the year (estimate = 0.137, df = 66, t-value = 5.15, $p < 0.0001$). The response variable was transformed with a square root plus 0.5 transformation to improve the distribution of the residuals of the fit. We included the stand-age category as an outer co-variate and saw no evidence of an interaction between stand-age category and the relationship between territories per plot and year (year * intermediate, estimate = 0.034, df = 66, t-value 0.739, $p > 0.463$: year * mature, estimate = 0.036, df = 66, t-value = 0.817, $p > 0.417$), although the sample sizes were small within stand-age categories and the power to detect differences was probably low. Visually, the pattern of increase in territories appeared different in mature vs. intermediate and young plots (Fig. 3), which appeared to respond more slowly at first, with only moderate increases in territory density in 1980 and 1981, and then more rapidly in 1982 (Fig. 3).

Budworm counts

Budworm counts per balsam fir branch tip increased from 1982 (mean= 5.56, $n = 396$) to 1983 (mean= 9.17, $n = 384$; two-way ANOVA: $F = 20.38$; $p < 0.001$, df = 1), suggesting that the outbreak was still occurring in 1983. Budworm counts differed among age classes ($F = 13.23$, $p < 0.001$, df = 2). However, there was no evidence of an interaction between year and age class ($F = 1.83$, $p > 0.160$, df = 2). Multiple comparisons based on simulations indicated that budworm counts in young stands (mean= 5.91, $n = 290$) were less than in both intermediate stands (mean= 6.94, $n = 153$; estimate = -0.32, SE = 0.09) and mature stands (mean= 8.44, $n = 243$; estimate = -0.44, SE = 0.08), but that counts in intermediate stands did not differ from counts in mature stands (estimate = -0.13, SE = 0.09), although a trend is evident.

Bird response to budworm

Overall, there was a significant positive relationship between number of bird territories and mean budworm count per balsam fir branch tip ($F = 4.278$ on 3 and 28 df, $p < 0.013$, multiple $R^2 = 0.314$). Budworm count was a significant predictor of the number of bird territories in 1982 (t-value = 2.814, $p < 0.008$), but not in 1983 (t-value = 1.42, $p = 0.168$), although a trend was still apparent in 1983.

Individual species

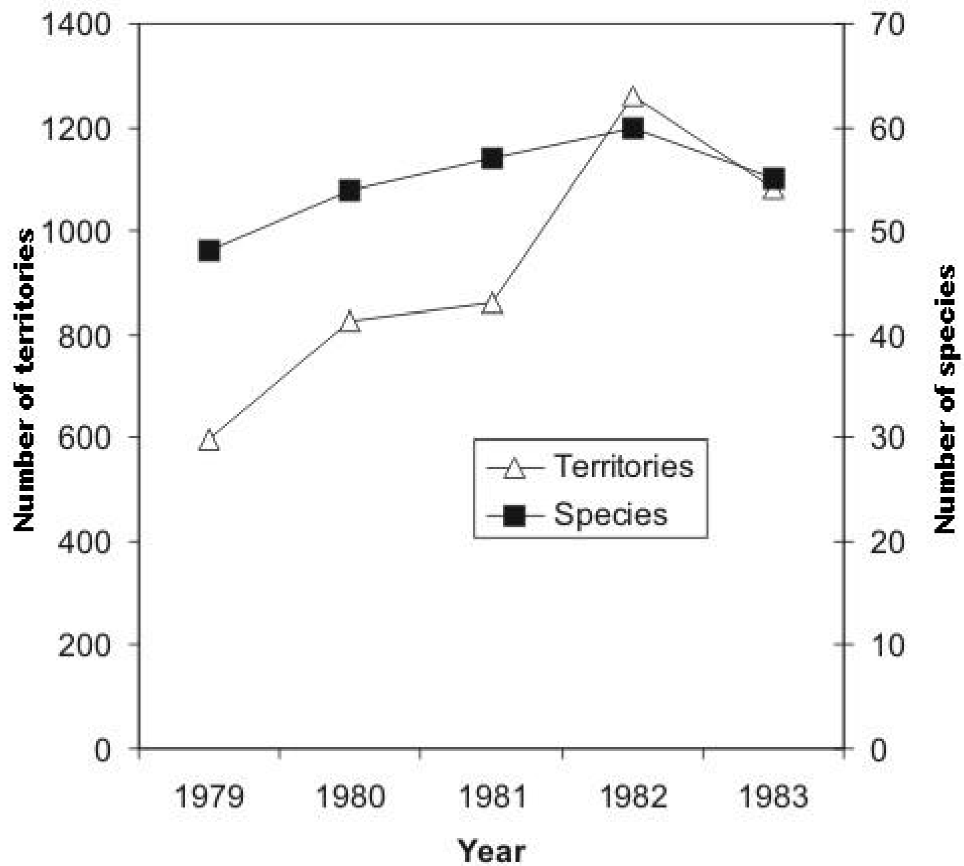
Enormous increases in territory densities from 1979 to 1982 and in 1983 were shown by three species: the Bay-breasted Warbler, the Tennessee Warbler, and the Cape May Warbler (Fig. 4A-C). The largest absolute increase in territory number was observed for the Bay-breasted Warbler, which increased from approximately four territories per plot to more than 17 territories per plot in mature forest stands (a 4.7-fold increase in 5 yr). Cape May Warblers were less abundant overall, but their mean number of territories increased from less than one territory per plot in 1979 to more than five territories per plot (a 10.4-fold increase in 4 yr). Tennessee Warblers increased 9.1-fold over 4 yr.

A positive increase in the numbers of territories for the Bay-breasted Warbler, Tennessee Warbler, and Cape May Warbler was observed in all three stand-age categories of plots (Fig. 4A-C). Cape May Warblers did not occur in the young and intermediate-aged plots from 1979 to 1981, but appeared in 1982 (7.7 territories) and 1983 (four territories). Their abundance in 1982 in young and intermediate-aged plots was greater than in mature plots in 1979 (3.2). The number of Bay-breasted Warbler territories was low from 1979 to 1981 in the young and intermediate-aged plots and significantly higher in 1982 and 1983. Again, the number of territories in intermediate-aged plots in 1982 and 1983 (35.4, 54.9) exceeded the number of Bay-breasted Warbler territories in mature plots in 1979 (21.8). The response of these species in young and intermediate-aged stands was different than the response observed in mature stands. In young and intermediate-aged stands, the response occurred later in the progression of the outbreak, although, proportionally, the response was as strong or stronger (Fig. 4A,C) than observed in mature stands. Although Tennessee Warblers were more abundant in mature plots than in intermediate or young plots (Fig. 4B), they showed a proportionally higher response in younger plots than did Bay-breasted Warblers and Cape May Warblers.

When these three species were removed from the combined species data, the general pattern of increase in territory density remained (Fig. 5), and the statistically positive relationship between the square-root transformed number of territories per plot and the year continued (Fig. 5; linear mixed model, estimate = 0.296, df = 68, t-value = 5.20, $p < 0.0001$).

We examined plots of the relationship between the number of territories and the year for all species and stand-age category combinations, and included plots here for a selection of species that were indicated in the literature to have responded to budworm outbreaks (Appendix 1) or that appeared to show an effect in our data. We found subtle patterns of territory increase for several species, e.g., the White-throated Sparrow (*Zonotrichia albicollis*) and the Ovenbird (*Seiurus aurocapillus*), although these patterns were generally evident in only one or two stand-age categories rather than all

Fig. 2. Number of bird territories and the number of species in all 18 plots from 1979 to 1983.

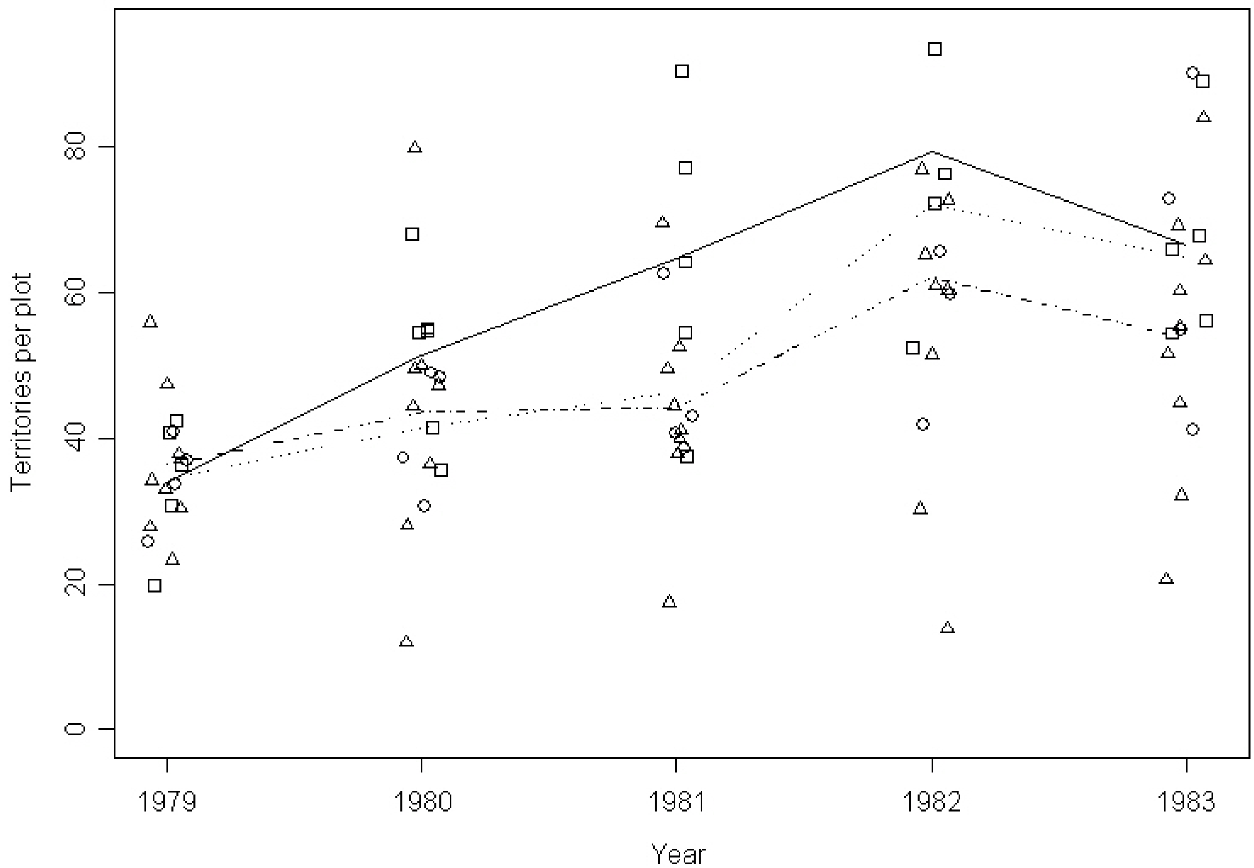


three (Fig. 6). In our results, many species showed a subtle response to the budworm outbreak. Cumulatively, the effect was quite strong (Fig. 5), although individual species responses were not always evident or measurable (Fig. 6, Table 1).

We found that 25 of 30 abundant species had more territories in 1982 + 1983 compared with 1979 + 1980; of these, nine species, including the Bay-breasted Warbler, Tennessee Warbler, and Cape May Warbler, had Wilcoxon-based *p*-values of less than 0.05 (Table 1). Because mature and intermediate age classes contained only four plots each, we combined young and intermediate plots, and intermediate and mature aged plots for comparisons. Only Bay-breasted Warbler, Tennessee Warbler, and Cape May Warbler had *p*-values below 0.05 for all young + intermediate + mature, young + intermediate, and intermediate + mature stand-age categories. All three species had *p*-values of 0.1 or less for the young stand-age category. As seen in Table 1 and Fig. 6, other species that showed some evidence of a positive response in young or intermediate-aged stands included the White-throated Sparrow, Ovenbird, Golden-crowned Kinglet (*Regulus satrapa*), American Redstart (*Setophaga ruticilla*), Black-and-white Warbler (*Mniotilta varia*), Veery (*Catharus fuscescens*), and Purple Finch (*Carpodacus purpureus*).

Because of the small sample sizes of mature plots, species that increased in mature plots alone were

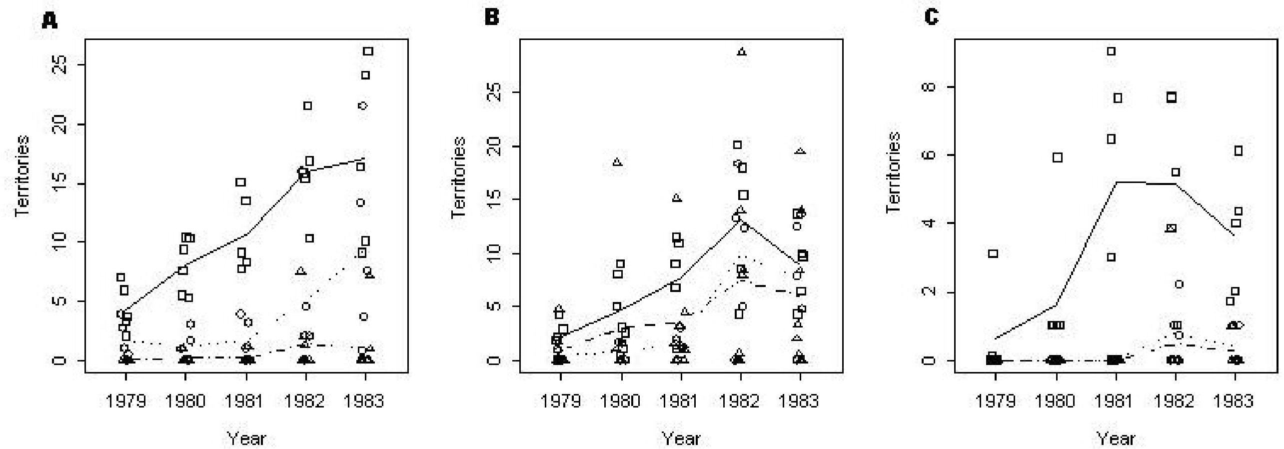
Fig. 3. Number of bird territories in each plot in young (triangle), intermediate (circle), and mature (square) stand-age classes. Lines indicate the mean in mature plots (solid), intermediate plots (dotted), and young plots (dashed).



difficult to identify. Several species showed large increases in territories from 1979+1980 to 1982+1983 in mature plots, including the Blackburnian Warbler, which increased from 14.6 to 20.85; the Brown Creeper (*Certhia americana*), 4 to 8.15; the Black-throated Blue Warbler (*Dendroica caerulescens*), 0.35 to 3.7; the Blue-headed Vireo (*Vireo solitarius*), 3.7 to 7.75; the Winter Wren (*Troglodytes troglodytes*), 5.3 to 12.95; and the Evening Grosbeak (*Coccothraustes vespertinus*), 0 to 7.75 (Fig. 6).

In the young stand-age category, 147 of 231 (65%) comparisons of species and stand-age category demonstrated a positive change from 1979 + 1980 to 1982 + 1983. In the intermediate stand-age category, 75 of 115 (64%) comparisons showed positive changes, and in the mature stand-age category, 78 of 117 (67%) comparisons showed positive changes. Although it is difficult to draw strong conclusions about individual species based on these analyses, it is clear that the large increase in the numbers of territories observed over the study

Fig. 4. Number of territories of (A) Bay-breasted Warbler (*Dendroica castanea*), (B) Tennessee Warbler (*Vermivora peregrina*), and (C) Cape May Warbler (*Dendroica tigrina*) in young stands (triangles represent plots , dashed line represents mean), intermediate-aged stands (circles represent plots, dotted line represents mean), and mature stands (squares represent plots, solid line represents mean).



period was a consequence of a positive response by multiple species and not just a few strong responders. Although we expected that the number of territories for some species would be reduced because of competition from other increasing species, no species was notably less abundant in 1982 + 1983 than in 1979 + 1980 (Table 1).

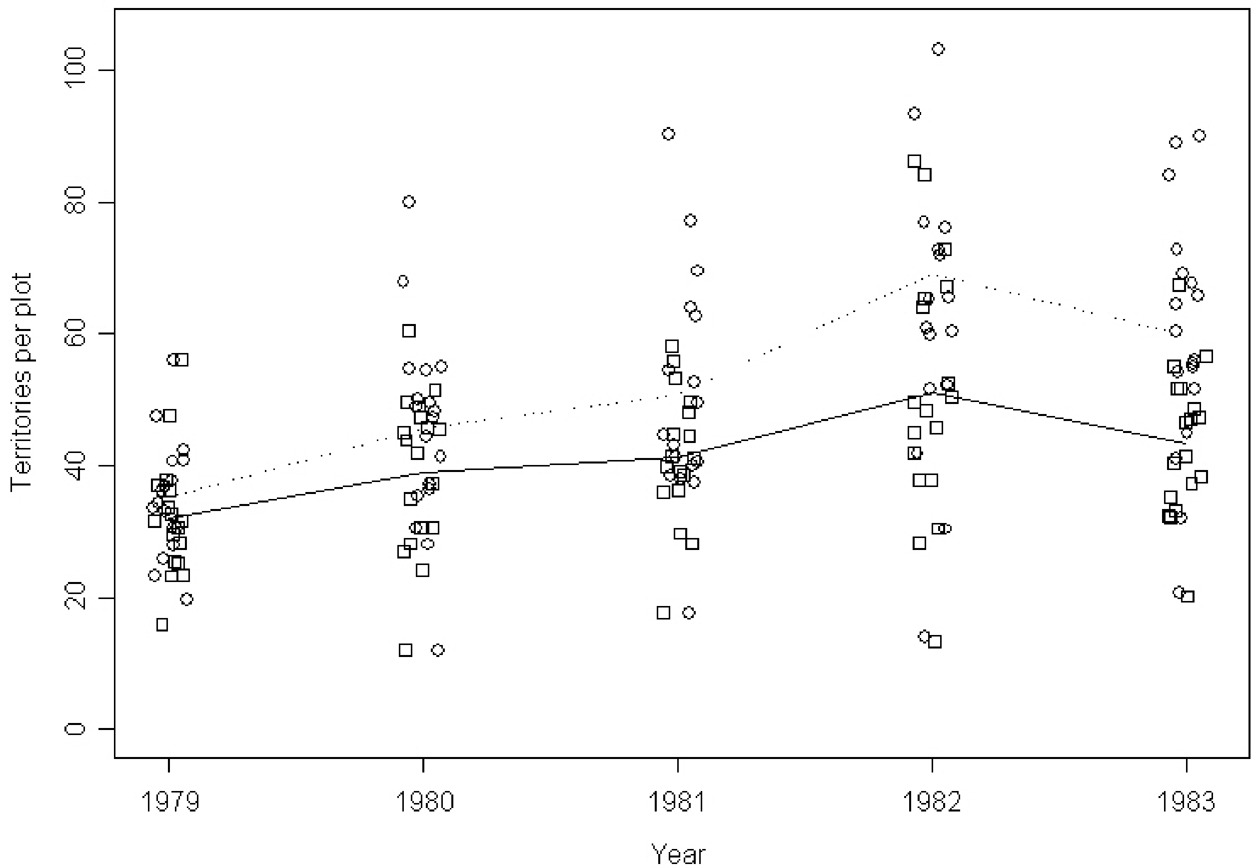
DISCUSSION

The budworm specialists

A wide variety of bird species has been shown to respond numerically to spruce budworm outbreaks (Appendix 1). Three species that have been consistently identified as spruce budworm specialists are the Bay-breasted Warbler, the Tennessee Warbler, and the Cape May Warbler (Kendeigh 1947, MacArthur 1958, Morris et al. 1958). For example, Bay-breasted Warblers showed a 12-fold increase over 12 yr in the 1958 study by Morris et al. Tennessee Warblers increased from no pairs to 122 pairs/100 ha in the same study. Morse (1978) found a 12-fold increase in Cape May Warblers from 1974 to 1976. These results are consistent with our findings, in which these species increased 4.7- to 10.4-fold or more over four years; no other species increased more than twofold over the same time period. These three species are relatively uncommon in years in which there are no budworm outbreaks (Sanders 1970). Even in this study area, in which we believe that budworm populations were already on the rise in 1979, Bay-breasted Warbler, Tennessee Warbler, and Cape May Warbler moved from the ranks of 6th, 11th, and 35th most common species that year to 2nd, 1st, and 10th, respectively, in 1982.

It is possible that these species respond rapidly to budworm outbreaks because they are able to increase their clutch sizes in response to outbreaks (Morse 1989, Williams 1996, Baltz and Latta 1998). MacArthur (1958) observed that Bay-breasted Warbler clutches were smaller during endemic budworm levels than during epidemic levels. The clutch sizes of Bay-breasted Warblers, Tennessee Warblers, and Cape May Warblers all have larger ranges relative to those of most other wood warblers (Ehrlich et al. 1988). Even though these three species are able to consistently respond numerically to budworm outbreaks, it is unlikely that they can

Fig. 5. Mean number of territories per plot for all species (circles, dotted line represents means), and for all species except Bay-breasted Warbler (*Dendroica castanea*), Tennessee Warbler (*Vermivora peregrina*), and Cape May Warbler (*Dendroica tigrina*; squares, solid line represents means).



control budworm effectively. Crawford et al. (1983) note that the most important bird predators are those that maintain high population densities and high feeding rates over the lower ranges of the insect's density and found that this was most true of the Blackburnian Warbler and Golden-crowned Kinglet and not of the three budworm specialists.

Budworm defoliation in Ontario peaked in 1980 at 18,850,000 ha and has declined steadily since then to 280,000 ha in 2004 (Cadman et al 2007). In a recent synthesis of the status and trends of birds in Ontario, Blancher et al. (2009) reviewed evidence for long-term trends in Ontario birds. Analysis of migration monitoring data from Long Point Bird Observatory indicated good evidence for population declines in all three budworm specialists from the 1981–1986 period to the 2001–2006 period. All three species showed statistically significant annual declines in spring and fall migration numbers: for Cape May Warblers, 4.4% ($p < 0.000$) and 3.2% ($p < 0.000$); for Bay-breasted Warblers, 3.4% ($p <$

Fig. 6. Number of territories per plot for mature plots (squares represent plots, solid line represents means), intermediate-aged plots (circles represent plots, dotted line represents means), and young plots (triangles represent plots, dashed line represents means) for 20 individual species.

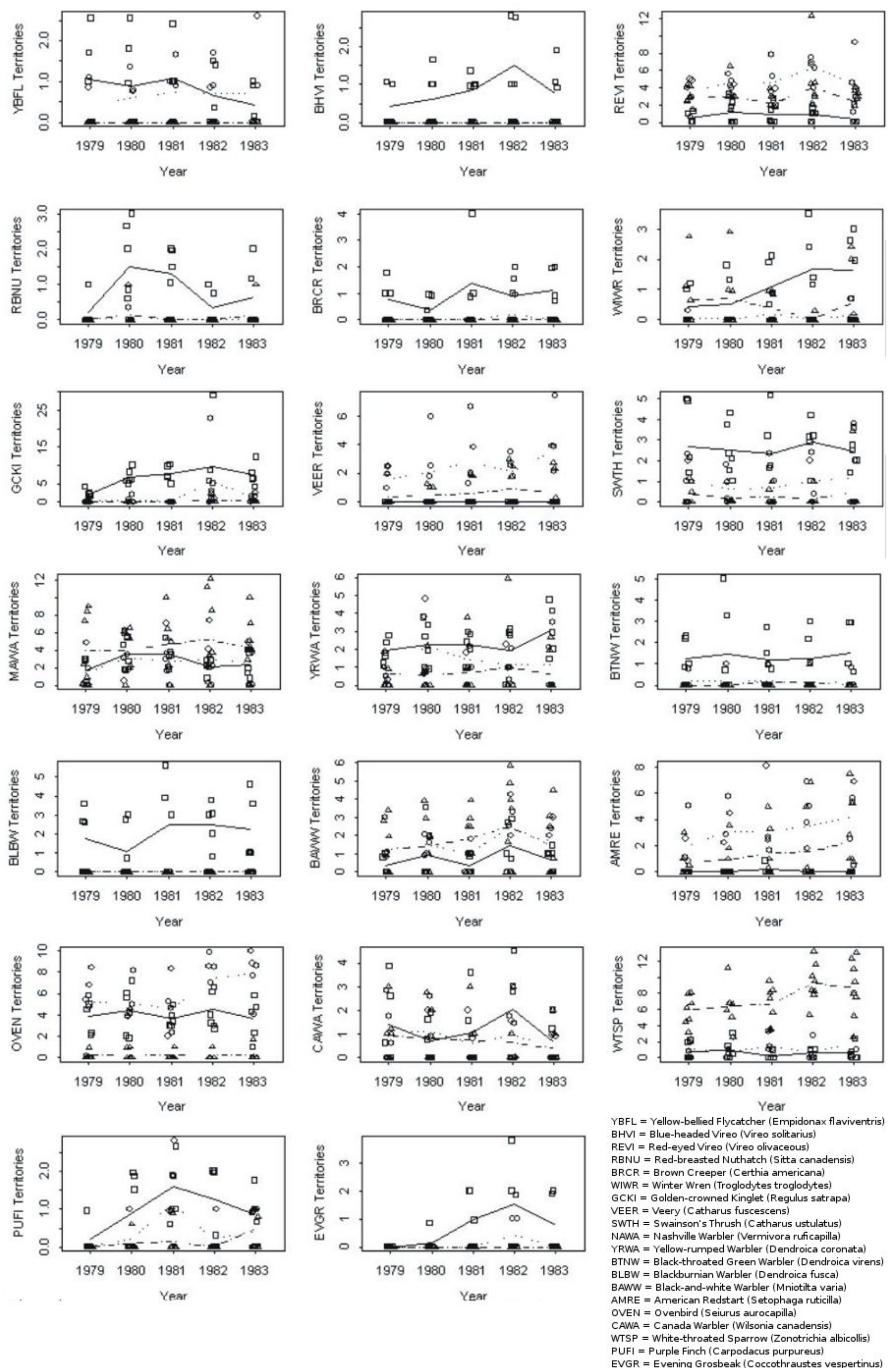


Table 1. Change in number of territories from 1979 + 1980 to 1982 + 1983, and results of Wilcoxon signed-ranks test for paired data for the 30 most common species in the study plots. *P*-values less than 0.05 are highlighted in gray along with their associated species. For n > 25 or when there are ties, the normal approximation (*z*) of the test statistic is provided, otherwise the Wilcoxon signed-ranks test statistic *V* is provided. RUGR = Ruffled Grouse (*Bonasa umbellus*), YBFL = Yellow-bellied Flycatcher (*Empidonax flaviventris*), ALFL = Alder Flycatcher (*Empidonax alnorum*), LEFL = Least Flycatcher (*Empidonax minimus*), REVI = Red-eyed Vireo (*Vireo olivaceus*), PHVI = Philadephia Vireo (*Vireo philadelphicus*), BCCH = Black-capped Chickadee (*Poecile hudsonia*), WIWR = Winter Wren (*Troglodytes troglodytes*), GCKI = Golden-crowned Kinglet (*Regulus satrapa*), VEER = Veery (*Catharus fuscenscens*), SWTH = Swainson's Thrush (*Catharus ustulatus*), HETH = Hermit Thrush (*Catharus guttatus*), TEWA = Tennessee Warbler (*Vermivora peregrina*), NAWA = Nashville Warbler (*Vermivora ruficapilla*), CSWA = Chestnut-sided Warbler (*Dendroica pensylvanica*), MAWA = Magnolia Warbler (*Dendroica magnolia*), CMWA = Cape May Warbler (*Dendroica tigrina*), YRWA = Yellow-rumped Warbler (*Dendroica coronata*), BTNW = Black-throated Green Warbler (*Dendroica virens*), BLBW = Blackburnian Warbler (*Dendroica fusca*), BBWA = Bay-breasted Warbler (*Dendroica castanea*), BAWW = Black-and-white Warbler (*Mniotilta varia*), AMRE = American Redstart (*Setophaga ruticilla*), OVEN = Ovenbird (*Seiurus aurocapilla*), MOWA = Mourning Warbler (*Oporonis philadelphia*), CAWA = Canada Warbler (*Wilsonia canadensis*), LISP = Lincoln's Sparrow (*Melospiza lincolnii*), WTSP = White-throated Sparrow (*Zonotrichia albicollis*), RBGR = Rose-breasted Grosbeak (*Pheucticus ludovicianus*), and PUFI = Purple Finch (*Carpodacus purpureus*).

Species	Plots of all ages			Youngs plots			Mature and intermediate plots			Intermediate and young plots		
	Change	*z*	*p*	Change	*z* (*V*)	*p*	Change	*z* (*V*)	*p*	Change	*z* (*V*)	*p*
RUGR	-3.95	0.52	0.6031	-6.35	1.8454	0.0650	2.4	-0.8422	0.3997	-1.65	0.3944	0.693
YBFL	-3.75	0.977	0.3286	-0.75	0.875	0.3816	-3	0.5671	0.5706	2.1	-0.1421	0.887
ALFL	18.7	-0.4173	0.6765	18.7	(10)	0.3125		NA	NA	18.7	-0.6024	0.547
LEFL	15.35	-0.738	0.4608	-3.05	0.2836	0.7768	18.4	-1.233	0.2175	15.15	-0.5512	0.582
REVI	22.1	-1.009	0.3131	13	(14)	0.6406	9.1	-0.773	0.4395	22.8	-1.2556	0.209
PHVI	13.15	-1.5476	0.1217	3	-1.5255	0.1271	10.15	-0.798	0.4249	11.15	-1.808	0.071
BCCH	12.75	-1.0973	0.2725	5.65	0.1418	0.8873	7.1	-1.6325	0.1026	10.85	-0.4363	0.663
WIWR	3.6	-0.3688	0.7123	-3.75	0.7019	0.4828	7.35	-1.1371	0.2555	-4.05	0.8434	0.399
GCKI	44.15	-2.308	0.021	4.1	-1.317	0.1878	40.05	-1.8248	0.0680	33.6	-2.1698	0.03
VEER	17.15	-2.1422	0.0322	7.35	-0.9855	0.3244	9.8	-1.8952	0.0581	17.15	-2.1285	0.033
SWTH	4.55	0.1306	0.8961	-2.55	0.8339	0.4043	7.1	(14)	0.6406	3.1	-0.2008	0.841
HETH	5.25	-1.2647	0.206	3.15	-1.1356	0.2561	2.1	-0.3627	0.7168	6	-1.3393	0.181
TEWA	219.35	-3.14	0.0017	102.95	-1.8843	0.0653	116.4	-2.3863	0.017	160.45	-2.4981	0.013
NAWA	8.2	-0.6476	0.5173	13.7	(6)	0.1094	-5.5	1.1342	0.2567	6.4	-0.3139	0.754
CSWA	23.15	-0.601	0.548	25.35	(13)	0.5469	-2.2	0.0758	0.9396	23.1	-0.5495	0.583

(con'd)

MAWA	21.55	-1.19	0.234	19.85	-1.6845	0.0921	1.7	(18)	1	23.45	-1.6486	0.099
CMWA	44.45	-2.9057	0.0037	7.8	-1.6385	0.1013	36.65	-2.2684	0.0233	11.7	-2.1698	0.03
YRWA	4.95	-0.1036	0.9175	6.05	-0.4253	0.6706	-1.1	(24)	0.4609	3.25	0.1575	0.875
BTNW	-1.25	-0.3496	0.7266	1	-0.875	0.3816	-2.25	0.0758	0.9396	0.1		1
BLBW	6.25	-1.0658	0.2865		NA	NA	6.25	-1.1371	0.2555		NA	NA
BBWA	162.1	-3.35	0.0008	23.85	-2.1039	0.0354	138.25	(0)	0.0078	75.6	-2.8153	0.005
BAWW	22.6	-2.9528	0.0031	14.75	-2.3863	0.017	7.85	-1.4037	0.1604	20.9	-2.7477	0.006
AMRE	33	-2.134	0.0328	20.05	-1.5595	0.1189	12.95	-1.1371	0.2555	33	-2.205	0.028
OVEN	27.55	-1.9066	0.0566	2.9	-0.8339	0.4043	24.65	(5)	0.0781	25	-2.1285	0.033
MOWA	-1.7	0.0261	0.9792	-2.25	(20)	0.8438	0.55		1	-1.7	(40)	0.97
CAWA	-5.65	0.5006	0.6166	-3.75	0.5811	0.5611	-1.9	0.1418	0.8873	-7.85	1.0446	0.296
LISP	0.05	0.66	0.5092	0.05	0.4253	0.6706		NA	NA	0.05	0.5921	0.554
WTSP	49.35	-2.28	0.0228	50.2	-2.4535	0.0141	-0.85	0.2807	0.7789	47.75	-2.2776	0.023
RBGR	2.85	-0.3448	0.7302	4.55		1	-1.7		1	1.95		1
PUFI	8.8	-2.0619	0.0392	4.2	-1.8667	0.0619	4.6	-0.798	0.4249	5.15	-1.822	0.685

0.000) and 6.0% (p < 0.000); and for Tennessee Warblers, 5.6% (p < 0.000) and 3.2% (p < 0.000), respectively. Results here and elsewhere suggest that population levels of spruce budworm may have an important effect on the population levels of these three species. Consequently, the status of spruce budworm should be considered when monitoring and interpreting the status of these budworm specialists. Similarly, factors that may alter the severity and extent of spruce budworm outbreaks, such as climate change, changing forest composition because of forestry, the suppression of forest fires, and the active suppression of budworm with insecticides such as Bt (*Bacillus thuringiensis*), have the potential to alter the long-term fate of spruce budworm bird specialists.

Our results confirmed the status of the Cape May Warbler, Tennessee Warbler, and Bay-breasted Warbler as budworm specialists. Each species showed a dramatic numerical response in all three stand-age classes, their habitat choices became more generalized with increasing abundance of budworm, and their responses were notably larger than those of any other species. Although Bay-breasted Warbler and Cape May Warbler are considered mature-forest species (Williams 1996, Baltz and Latta 1998), they clearly alter their habitat choices in the face of superabundant food. Cape May Warblers, which sing, feed, and nest high in the spruce canopy (Baltz and Latta 1998), did not occur in the young and intermediate plots in 1979–1981 but increased dramatically in numbers in these plots later in the spruce budworm outbreak. Bay-breasted Warblers tell a similar story, with relatively low territory numbers in 1979–1981 in the young and intermediate plots and significant increases in 1982 and 1983, with higher territory numbers than were present in mature plots in 1979. The response of these species in young and intermediate stands differed in mature stands. In younger stands, the response came later in the outbreak progression, although proportionally the response was as strong or stronger. Budworm density was higher in older stands and increased from 1982 to 1983 in all three stand-age categories. New territories were still being established in mature and younger stands in 1982 and 1983, suggesting that the younger stands were improving in their capacity to provide desirable habitat for individuals, and not that individuals were moving from mature habitat to younger habitat because mature habitat was becoming less suitable.

Although Tennessee Warblers are known to use a wide range of habitat ages (Rimmer and McFarland 1998), they showed a clear preference for mature plots in our study area. Their response was slower in the younger plots than in the mature plots but more immediate than those of the other two species. They also showed a proportionally higher response in the younger plots than did Bay-breasted Warbler and Cape May Warbler.

Budworm-bird interactions

Overall, birds had a positive numerical response to the spruce budworm outbreak; numbers of birds and species increased through time, and the total number of individuals was positively related to budworm density in 1982 and 1983. The decline in total number of individuals and species in 1983 suggests that a significant event affected bird abundance in that year. Because we do not have good quantitative information on the change in spruce budworm abundance throughout the study period, we cannot reliably relate these changes in bird abundance to spruce budworm density. However, it was observed that the budworm outbreak increased in intensity throughout the 5-yr study period (D. R. Fillman, *unpublished data*). Budworm counts from 1982 and 1983 are consistent with this position, but, it is unclear if the total abundance of budworm available for bird foraging was greater in 1983 than 1982 because we have no measures of the total foliage available for foraging. It is possible that there were fewer spruce budworm available for foraging by 1983. Alternatively, an abiotic factor such as a weather event may have reduced territory numbers. We examined the annual weather data for the period of the study and found no anomalies in the 1983 breeding season relative to long-term normals.

An overall increase in number of territories for all species combined, even when the three budworm specialists were excluded, suggests that many, if not most, species enjoyed a positive benefit from the budworm outbreak. Many of the species considered here reportedly consume budworm (Mitchell 1952, Dowden et al. 1953, Crawford and Jennings 1989). Although we cannot demonstrate a statistically significant numerical response for individual species because of the large number of comparisons made, positive responses in the young and intermediate stand-age categories are suggested for Golden-crowned Kinglet, Veery, Black-and-white Warbler, American Redstart, Ovenbird, White-throated Sparrow, and Purple Finch. Positive responses in the mature stand-age category include Blackburnian Warbler, Brown Creeper, Black-throated Blue Warbler, Blue-headed Vireo, Winter Wren, and Evening Grosbeak. Of the 13 species with positive responses, seven showed positive responses in at least one previous study. No response has been reported previously for five species: Brown Creeper, Veery, Black-throated Blue Warbler, Black-and-white Warbler, and American Redstart. One species, Winter Wren, had previously shown only a negative response to budworm (Appendix 1).

We did not find a decline in abundance through the study period for any species. Magnolia Warbler (*Dendroica magnolia*), Black-throated Green Warbler (*Dendroica virens*), Blackburnian Warbler, Yellow-rumped Warbler, and Winter Wren have all reportedly had negative responses to spurce budworm elsewhere, which were attributed to competition with increasing species (Appendix 1). Based on stomach content analysis, all five of these species appear to eat budworm (Mitchell 1952, Dowden et al. 1953, Crawford and Jennings 1989). We found some evidence for a positive response in Blackburnian Warbler and Winter Wren and possibly Magnolia Warbler (Table 1), but no evidence of a response in Black-throated Green Warbler or Yellow-rumped Warbler. In most cases, the evidence in the literature for competition comes from one or only a few locations and may not describe a general response to budworm or a response to budworm at all. Conditions specific to each location and time may play enough of a role in the response of species that it is difficult to generalize based on only a few observations.

CONCLUSION

Spruce budworm exert a major influence on the boreal ecosystems of eastern Canada (Blais 1983, Candau et al. 1998) by causing tree mortality over large areas. The last outbreak in eastern Canada resulted in the defoliation of more than 55 million ha of forest (Blais 1983). Budworm outbreaks also have a direct effect on forest bird populations by providing superabundant food for many species. Our data suggest that many bird species profit from the increased abundance of food, but only three species, specifically the Bay-breasted Warbler, the Tennessee Warbler, and the Cape May Warbler, respond with large population increases of up to tenfold over four to five years. These species appear to alter their usual habitat selection by establishing their territories in young and intermediate-aged stands as budworm numbers increase. Although the number of territories in young and intermediate-aged stands grew more slowly in response to the outbreaks, there were still very important increases in bird numbers with higher budworm counts. Contrary to some previous studies, we found no species with a negative numerical response. The cyclical nature of budworm outbreaks makes it difficult to assess the status of populations of the three specialists unless these outbreaks are taken into consideration. These outbreaks may also be important in the long-term population trajectories of nonspecialist species.

Responses to this article can be read online at:
http://www.ace-eco.org/vol4/iss1/art3/responses/

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APPENDIX 1

Table A1-1. Summary of species response to spruce budworm (*Choristoneura fumiferana* (Clem.)) from the literature. A numerical response indicates a change in the number of individuals in conjunction with a change in budworm abundance. A functional response indicates a change in behavior in conjunction with a change in budworm abundance.

Species name	Response	Budworm status	References
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	Positive numerical	Epidemic	Gage and Miller (1978)
	None	Epidemic	Kendeigh (1947) Morris et al. (1958)
	None	Moderate	Hensley and Cope (1951)
Blue-headed Vireo (*Vireo solitarius*)	Positive functional	Moderate	Crawford and Jennings (1989)
	Positive numerical	Epidemic	Gage and Miller (1978)
	None	Moderate	Hensley and Cope (1951)
	None	Epidemic	Kendeigh (1947) Morris et al. (1958)
Red-breasted Nuthatch (*Sitta canadensis*)	Positive functional	Moderate	Crawford and Jennings (1989)
	None	Epidemic	Morris et al. (1958)
Winter Wren (*Troglodytes troglodytes*)	Negative numerical	Epidemic	Morris et al. (1958)
Golden-crowned Kinglet (*Regulus satrapa*)	Positive numerical	Epidemic	Morse (1978)
	Positive numerical	Moderate	Crawford and Jennings (1989)
	None	Epidemic	Morris et al. (1958)
Ruby-crowned Kinglet (*Regulus calendula*)	Positive functional	Epidemic	Crawford et al. (1983)
	None	Epidemic	Morris et al. (1958)
Swainson’s Thrush (*Catharus ustulatus*)	Positive numerical	Epidemic	Morris et al. (1958) Morse (1978) Gage and Miller (1978)
	Positive numerical	Moderate	Dowden et al. (1953) Hensley and Cope (1951)
Tennessee Warbler (*Vermivora peregrina*)	Positive numerical	Epidemic	Morris et al. (1958) Kendeigh (1947) Sanders (1970) Crawford et al. (1983) Bolgiano (2004) Gage and Miller (1978)
	Positive numerical	Moderate	Stewart and Aldrich (1952)

(con'd)

Magnolia Warbler (*Dendroica magnolia*)	Negative numerical	Epidemic	Morris et al. (1958)
	Negative numerical	Moderate	Dowden et al. (1953) Hensley and Cope (1951) (same data)
Cape May Warbler (*Dendroica tigrina*)	Positive numerical	Epidemic	Kendeigh (1947) Sanders (1970) Crawford et al. (1983) Bolgiano (2004) Morse (1978)
	Positive numerical	Moderate	Stewart and Aldrich (1952)
	None	Epidemic	Morris et al. (1958) Gage and Miller (1978)
Yellow-rumped Warbler (*Dendroica coronata*)	Positive numerical	Epidemic	Gage and Miller (1978)
	Positive numerical	Moderate	Stewart and Aldrich (1952)
	Negative numerical	Epidemic	Morris et al. (1958)
Black-throated Green Warbler (*Dendroica virens*)	Negative numerical	Epidemic	Morris et al. (1958)
	Positive numerical		Gage and Miller (1978)
Blackburnian Warbler (*Dendroica fusca*)	Positive numerical	Epidemic	Morris et al. (1958) Sanders (1970) Morse (1978) Gage and Miller (1978)
	Positive numerical	Moderate	Stewart and Aldrich (1952)
	Negative numerical	Epidemic	Morris et al. (1958)
Bay-breasted Warbler (*Dendroica castanea*)	Positive numerical	Epidemic	Morris et al. (1958) Kendeigh (1947) Sanders (1970) Crawford et al. (1983) Bolgiano (2004) Morse (1978) Gage and Miller (1978)
	Positive numerical	Moderate	Stewart and Aldrich (1952)
Blackpoll Warbler (*Dendroica striata*)	Positive numerical	Epidemic	Bolgiano (2004)
	None	Epidemic	Morris et al. (1958)
Ovenbird (*Sieurus aurocapillus*)	Positive numerical	Epidemic	Morris et al. (1958) Morse (1978)
	Positive numerical	Moderate	Zach and Falls (1975)
	Positive functional	Moderate	Zach and Falls (1975)

(con'd)

Canada Warbler (*Wilsonia canadensis*)	Positive numerical	Moderate	Crawford and Jennings (1989)
White-throated Sparrow (*Zonotrichia albicollis*)	Positive numerical	Epidemic	Kendeigh (1947)
	None	Epidemic	Morris et al. (1958)
Dark-eyed Junco (*Junco hyemalis*)	Positive numerical	Epidemic	Morse (1978) Gage and Miller (1978)
	None	Epidemic	Morris et al. (1958)
Purple Finch (*Carpodacus purpureus*)	Positive numerical	Epidemic	Bolgiano (2004)
	None	Epidemic	Morris et al. (1958)
Evening Grosbeak (*Coccothraustas vespertinus*)	Positive numerical	Epidemic	Morris et al. (1958) Bolgiano (2004) Blais and Parks (1964)
	Positive numerical	Moderate	Crawford et al. (1983)
	None	Epidemic	Gage and Miller (1978)

APPENDIX 2

Table A2-1. Species list, total territory count, and territory density for each age group.

Species name	Total territories	Territories/ mature plot	Territories/ intermediate plot	Territories/ young plot
Ruffed Grouse (*Bonasa umbellus*)	88.05	0.694	1.715	0.850
Spruce Grouse (*Falcipennis canadensis*)	0.00	0.000	1.000	0.024
Sharp-shinned Hawk (*Accipiter striatus*)	2.80	0.038	0.000	0.043
Cooper's Hawk (*Accipiter cooperii*)	1.00	0.000	0.050	0.000
American Kestrel (*Falco sparverius*)	5.30	0.000	0.000	0.126
Killdeer (*Charadrius vociferus*)	3.15	0.000	0.000	0.075
Solitary Sandpiper (*Tringa solitaria*)	0.00	0.000	1.000	0.024
Common Snipe (*Gallinago gallinago*)	3.85	0.000	0.000	0.092
American Woodcock (*Scolopax minor*)	1.15	0.000	0.058	0.000
Common Nighthawk (*Chordeiles minor*)	2.95	0.000	0.000	0.070
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	32.65	0.694	1.290	0.276
Downy Woodpecker (*Picoides pubescens*)	30.65	0.346	0.100	0.468
Hairy Woodpecker (*Picoides villosus*)	27.40	0.294	0.145	0.401
Black-backed Woodpecker (*Picoides arcticus*)	1.00	0.038	0.000	0.000
Northern Flicker (*Colaptes auratus*)	29.25	0.037	0.000	0.539
Piliated Woodpecker (*Dryocopus pileatus*)	6.80	0.148	0.098	0.024

(con'd)

Eastern Wood-Pewee (*Contopus virens*)	0.55	0.021	0.000	0.000
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	36.60	0.817	0.150	0.058
Alder Flycatcher (*Empidonax alnorum*)	111.60	0.000	0.000	2.657
Least Flycatcher (*Empidonax minimus*)	149.9	0.092	5.208	1.032
Blue-headed Vireo (*Vireo solitarius*)	20.40	0.785	0.245	0.000
Philadelphia Vireo (*Vireo philadelphicus*)	34.50	0.323	0.865	0.210
Red-eyed Vireo (*Vireo olivaceus*)	244.40	0.827	5.080	2.889
Gray Jay (*Perisoreus canadensis*)	12.35	0.235	0.100	0.101
Blue Jay (*Cyanocitta cristata*)	9.85	0.094	0.100	0.129
Black-capped Chickadee (*Poecile atricapillus*)	78.75	0.752	1.230	0.824
Boreal Chickadee (*Poecile hudsonica*)	14.40	0.415	0.100	0.038
Red-breasted Nuthatch (*Sitta canadensis*)	23.85	0.826	0.000	0.056
Brown Creeper (*Certhia americana*)	23.85	0.881	0.000	0.023
Winter Wren (*Toglodytes troglodytes*)	46.30	1.053	0.510	0.421
Golden-crowned Kinglet (*Rgulus satrapa*)	214.30	6.762	1.720	0.098
Ruby-crowned Kinglet (*Regulus calendula*)	21.25	0.35	0.333	0.131
Veery (*Catharus fuscescens*)	81.20	0.000	0.000	0.511
Swainson's Thrush (*Catharus ustulatus*)	98.85	2.573	3.590	0.311
Hermit Thrush (*Catharus guttatus*)	38.35	0.137	0.685	0.502
American Robin (*Turdus migratorius*)	21.85	0.000	0.525	0.270

(con'd)

Cedar Waxwing (*Bombycilla cedrorum*)	1.85	0.000	0.000	0.068
Tennessee Warbler (*Vermivora peregrina*)	449.10	7.246	2.988	4.497
Orange-crowned Warbler (*Vermivora celata*)	0.90	0.035	0.000	0.000
Nashville Warbler (*Vermivora ruficapilla*)	119.00	0.771	0.283	1.829
Norther Parula (*Parula americana*)	2.20	0.085	0.000	0.000
Chestnut-sided Warbler (*Dendroica pensylvanica*)	271.35	0.002	0.348	6.294
Magnolia Warbler (*Dendroica magnolia*)	296.15	2.715	0.500	4.619
Cape May Warbler (*Dendroica tigrina*)	94.75	3.194	0.195	0.186
Black-throated Blue Warbler (*Dendroica caerulescens*)	5.35	0.162	0.058	0.000
Yellow-rumped Warbler (*Dendroica coronata*)	115.05	2.285	0.000	0.711
Black-throated Green Warbler (*Dendroica virens*)	40.50	1.342	0.180	0.048
Blackburnian Warbler (*Dendroica fusca*)	51.65	1.987	0.000	0.000
Bay-breasted Warbler (*Dendroica castanea*)	403.40	11.123	3.938	0.844
Black-and-white Warbler (*Mniotilta varia*)	121.15	0.767	1.533	1.680
American Redstart (*Setophaga ruticilla*)	129.65	0.033	3.870	1.224
Ovenbird (*Seiurus aurocapilla*)	260.90	4.035	6.798	0.477
Connecticut Warbler (*Oporornis agilis*)	1.00	0.039	0.000	0.000
Mourning Warbler (*Oporornis philadelphia*)	124.80	0.000	1.108	2.733
Common Yellowthroat (*Geothlypis trichas*)	7.45	0.000	0.000	0.177

(con'd)

Wilson's Warbler (*Wilsonia pusilla*)	19.00	0.029	0.060	0.435
Canada Warbler (*Wilsonia canadensis*)	74.85	1.152	1.005	0.590
Scarlet Tanager (*Piranga olivacea*)	5.90	0.245	0.000	0.024
Chipping Sparrow (*Spizella passerina*)	5.95	0.000	0.020	0.132
Lincoln's Sparrow (*Melospiza lincolnii*)	47.00	0.000	0.000	1.119
White-throated Sparrow (*Zonotrichia albicollis*)	318.90	0.633	0.645	6.958
Dark-eyed Junco (*Junco hyemalis*)	4.75	0.071	0.000	0.069
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	33.35	0.035	1.185	0.208
Purple Finch (*Carpodacus purpureus*)	39.75	0.954	0.433	0.150
Pine Siskin (*Carduelis pinus*)	7.75	0.273	0.000	0.016
Evening Grosbeak (*Coccothraustes vespertinus*)	19.35	0.667	0.100	0.000