# CHANGES IN A FOREST BIRD COMMUNITY DURING AN OUTBREAK CYCLE OF THE SPRUCE BUDWORM IN NORTHWESTERN ONTARIO[1]

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*Abstract.* We report here changes in the forest bird community of a 10.4 ha study plot located in boreal mixedwood forest of northern Ontario, Canada, between 1966 and 1998. During this period, the region was subject to a severe outbreak of the spruce budworm (*Choristoneura fumiferana*). Overall, community response to increasing budworm prevalence was positive, although response pattern differed among species. All bird species that increased in population size did so during the increasing phase of the budworm cycle. By the time the budworm outbreak reached its peak in 1989-1990, both in terms of budworm density and defoliation, bird numbers had already been declining for five or more years, suggesting that the advantages conferred by a superabundant food supply were offset by negative effects on habitat.

*Key words:* community composition, competition, forest birds, habitat, numerical response, spruce budworm outbreak.

## CAMBIOS EN UNA COMUNIDAD DE AVES DE BOSQUE DURANTE UN BROTE DEL GUSANO DEL ABETO EN EL NOROESTE DE ONTARIO

*Resumen.* Documentamos cambios en la comunidad de aves en una parcela de estudio de 10.4 ha en bosque boreal mixto del norte de Ontario, Canadá, entre 1966 y 1998. Durante este periodo, la región sufrió un fuerte brote del gusano del abeto *(Choristoneura fumiferana)*. En general, la respuesta a nivel de comunidad al aumento de prevalencia del gusano fue positiva, aunque la respuesta varió entre especies. Todas las especies de aves que aumentaron en tamaño poblacional lo hicieron durante la fase de aumento del ciclo del gusano. Cuando el brote de gusanos alcanzó su pico en 1989-1990, tanto en densidad de gusanos como en defoliación, el número de aves ya había estado en declive cinco o más años, lo cual sugiere que las ventajas que confiere un recurso alimenticio superabundante fueron contrarrestadas por los efectos negativos sobre el hábitat.

*Palabras clave:* composición comunitaria, competición, aves de bosque, hábitat, respuesta numérica, brote de gusano del abeto.

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## INTRODUCTION

Bird population densities in the boreal forest are affected temporally by changes in the character of the forest as it matures, including changes in foliation and tree mortality brought by insect infestation. In eastern North America, a major driving force in forest development is the spruce budworm (*Choristoneura fumiferana*), a native species that periodically multiplies to such high densities that it causes extensive mortality of its host tree species, primarily balsam fir (*Abies balsamea)* and white spruce (*Picea glauca*) (Morris 1963). Outbreaks have occurred at intervals ranging from 20 to 140 years (Blais 1983), with an underlying cycle of about 35 years (Royama 1984, Candau et al. 1998). The relationship between insectivorous birds and budworm was demonstrated during a major outbreak in the 1940s and 1950s in Maine (Hensley and Cope 1951), New Brunswick (Morris et al. 1958) and Ontario (Kendeigh 1947). Populations of canopy-feeding warblers, notably Tennessee Warbler (*Vermivora peregrina*), Cape May Warbler (*Dendroica tigrina*), Blackburnian Warbler (*D. fusca*) and Bay-breasted Warbler (*D. castanea*), increased dramatically, but evidently did not contribute significantly to population regulation of the spruce budworm at high budworm densities (Morris et al. 1958, Mook 1963). Based on stomach contents analyses, Crawford et al. (1983) concluded that bird predation is unlikely to have much effect on high density, epidemic populations of budworm, but could play a major role in the regulation of low density, endemic populations. Torgerson et al. (1985) reached a similar conclusion with respect to western spruce budworm (*C. occidentalis* Freeman).

Two major spruce budworm outbreaks have occurred in northern Ontario in the last 70 years, with the first peaking in 1945 and the second in 1980 (Candau et al. 1998). During the first outbreak, breeding bird censuses were carried out by Kendeigh (1947) to assess the effects of aerial spraying with DDT. In the 1960s, when spruce budworm populations had declined to low densities, additional censuses were conducted in two plots in the same general area (Sanders 1970). These showed that bird densities had declined from 788 to 304 pairs km$^{-2}$, a difference that could be attributed to the virtual absence of the four warbler species named

above. Since that time, breeding bird censuses have continued in one of the plots (Sander's 1970: Plot 2). The other plot became an isolated patch of forest in a large clear-cut when the surrounding area was logged in 1993. This made the value of further data from that plot questionable and censuses were discontinued. Since the 1960s, major changes have taken place in the forest due to natural ageing of the stand and to heavy defoliation by budworm during the 1980s outbreak.

Most studies examining the relationship between forest birds and spruce budworm were conducted over a period of just one or two years near the peak of a regional outbreak, although often in multiple blocks with different local budworm populations (Kendeigh 1947, Hensley and Cope 1951, Stewart and Aldrich 1951, Zack and Falls 1975, Crawford et al. 1983, Crawford and Jennings 1989). While such studies may provide a snapshot of the bird community at various intervals during an outbreak, they are incapable of describing the dynamic, temporal response of birds to changing budworm populations. This is particularly true if the confounding effects of habitat on prey availability are ignored, since both budworm and bird population sizes may be determined as much by forest composition and other local conditions, as by the stage of the outbreak. The alternative is to follow changes in the bird community at one or more sites over time as the budworm infestation proceeds from pre-outbreak to outbreak to post-outbreak levels. In this case, presumably, the bird community would be responding primarily to budworm numbers and the damage they cause. This is the approach taken in bird studies conducted as part of the Green River Watershed project in northern New Brunswick, Canada, from 1947-1968. Morris et al. (1958) presented data from the first 10 years of this project (outbreak years), and Gage and Miller (1978) extended the analysis to include all 22 years (both outbreak and post-outbreak periods).

In this paper, we present the results of bird censuses conducted over a 33-yr period from 1966-1998 on Sander's (1970) Plot 2, together with relevant information on changes in budworm density and defoliation during that period. Our objective is to show how the forest bird community and individual species'

populations change through the different stages (pre-outbreak, outbreak and post-outbreak) of a complete spruce budworm cycle.

# METHODS

## STUDY AREA

The study area is situated on the western shore of Black Sturgeon Lake, Ontario (49°18´N, 88°52´W), in the Superior Forest Section (B9) of the Boreal Forest Region of Canada (Rowe 1972). The forest type is boreal mixedwood, composed primarily of white spruce, balsam fir, white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*), with the addition of black spruce (*P. mariana*) and jack pine (*Pinus banksiana*) on some sites. The forest in the 10.4 ha study plot (BSL plot) originated from a salvage cut following a spruce budworm outbreak in the 1940s. At the start of the study in 1966, the young mixedwood stand had a few older trees surviving from the previous budworm outbreak. A detailed description of the study plot as it appeared in 1985 was published by Lethiecq and Régnière (1988), in conjunction with associated studies on spruce budworm population dynamics. Additional plot descriptions and vegetation surveys were carried out in 1967, 1977, 1980, 1985, 1993 and 1995, during which trees were enumerated by species and diameter-at-breast-height (dbh). Only the summary data from these surveys are included in this paper.

## SPRUCE BUDWORM SAMPLING

Spruce budworm population densities and resulting defoliation were estimated annually from 1961 through 1997. This involved the collection of 45 cm (18 in) branch tips from the upper canopy of the budworm host trees, balsam fir, and white and black spruce. The number of branches sampled each year varied from as few as 20 per tree species to several hundred. Foliage was examined visually for the presence of spruce budworm larvae and numbers were recorded. Visual estimates were also made of the percentage of needles removed from each current-year shoot and these were averaged to get a percent defoliation value for each branch. Details of these sampling methods are provided in Sanders (1980).

## BIRD CENSUSES

We used the same census method as described by Kendeigh (1947) and Sanders (1970). The sample plot measured 16 chains x 16 chains (25.6 acres) or approximately 322 m x 322 m (~10.4 ha). To keep disturbance during censuses to a minimum, trails were cut through the plot at 2 chain (40.2 m) intervals. Stakes were placed along these trails every 2 chains (40.2 m). Censuses were conducted by walking the trails and mapping the locations of all singing male songbirds using the marked stakes as reference points. Other vocalizations and non-vocal sounds, as well as visual observations, were recorded for all species. Early morning censuses (05:30 to 10:30 EDT) were carried out at least three times each year on calm, sunny mornings between 10 and 30 June. One or more evening visits were also made each year. Most of the censuses were conducted by the authors (CS, DF and DW), but other individuals were involved on occasion. Each year, the data for each species were copied onto a single sheet and these were examined to determine the probable number of territories of each species in each plot. In order to standardize the interpretation, this work was done by one person (DF).

## STATISTICAL ANALYSES

We used Non-metric Multidimensional Scaling (NMS) to describe variation in the forest bird community of the BSL plot over the course of the budworm outbreak. The ordination was based on a Bray-Curtis similarity matrix constructed from untransformed species abundance data and was performed using PRIMER 5 for Windows software (PRIMER-E Ltd., Plymouth, UK). NMDS arranges samples in multidimensional species (ordination) space in such a way that the rank order similarity of the samples is maintained. Thus, samples that are closer together on the plot are more similar than samples that are farther apart. Species scores were added to the NMS plot using a weighted averaging approach described by McCune and Grace (2002). Species abundances tend to be greater where species points and sample points are closer together on the plot.

To examine local species' population trends (1966-1998) in their regional contexts, we plotted species abundance data from the BSL plot (pairs per 10.4 ha) and Ontario Breeding Bird Survey

data (annual indices) on the same graphs. The data were first standardized by subtracting the sample mean for each species in each dataset from the raw values (scores) and dividing the differences by the sample standard deviation. This transformation allowed us to compare variables originally measured in different units on the same scale.

# RESULTS

## SPRUCE BUDWORM

Through the 1960s and early 1970s, spruce budworm populations were extremely low in the BSL plot (what we will refer to as the "low" phase of the budworm cycle), with never more than six larvae per 100 branch tips and no larvae at all in some years (Fig. 1a; note the log scale on the y-axis). Beginning in 1974, budworm numbers began to increase (the "increasing" phase of the budworm cycle) and, except for a temporary decline in 1978-1979, continued to increase until 1983 when the density was well over 10 larvae/branch tip. Despite increasing budworm numbers, visible defoliation remained relatively low on the BSL plot and regionally during this period (Fig. 1b). High budworm densities and defoliation were sustained on the BSL plot from 1984 through to the early 1990s (the "high" phase), peaking in 1990 at >60 larvae/branch tip. The population started to decline (the "declining" phase) in 1994. Defoliation also declined during this period, although by this time much of the fir and spruce were already dead (see below).

## STAND DEVELOPMENT

In 1966, the basal area on the BSL plot was dominated by small balsam fir (average dbh 9.3 cm) and trembling aspen (average dbh 9.5 cm). Except for a few large white spruce, survivors of the last spruce budworm outbreak in the 1940s, and white birch, the average stand height was only about 10 m. There were numerous openings in the plot dominated by shrubs, primarily beaked hazel (*Corylus cornuta*). By 1977, the total basal area had increased approximately threefold, with balsam fir (average dbh 10.9 cm) and aspen (average dbh 13.8 cm) still the dominant species (Fig. 2). The canopy was closed and the shrub layer was

suppressed. By 1985, the total basal area had increased only slightly, but the basal area of aspen had almost doubled (Fig. 2). The aspen were larger on average (14.8 cm dbh) and frequently overtopped the balsam fir (11.9 cm dbh and 15 m in height). Total shrub cover was 14%, with 7% in hazel and 5% in alder (Alnus spp. P. Mill.). By 1995, 93% of the balsam fir, 50% of the white spruce and 33% of the black spruce were dead (Fig. 2). Aspen dominated the stand, with some trees up to 50 cm dbh (average dbh 19.6 cm) and over 20m in height. Where groups of balsam fir had died, there were openings in the canopy up to a few hundred square meters in area. Total shrub cover had risen to 37%, with 16% in hazel, 11% in raspberry (*Rubus spp.*) and 3% in dogwood (*Cornus stolonifera*). Although many of the dead trees had fallen, there were still standing dead trees in various states of decay.

## FOREST BIRD COMMUNITY

Through the late 1960s, the number of territories on the 10.4 ha BSL plot remained fairly constant between 32 and 36 (Table 1). From 1977, there was a steady increase in the number of territories to a peak in 1983, followed by a decline back to the starting level in 1998. The most consistently abundant species on the BSL plot over the 33 years of the study was Ovenbird (*Seiurus aurocapillus*), with never less than two territories in any year. Three other species were present in every sample: Golden-crowned Kinglet (*Regulus satrapa*), Red-eyed Vireo (*Vireo olivaceus*) and Swainson's Thrush (*Catharus ustulatus*).

Changes in the bird community of the BSL plot were correlated with the progression of the local spruce budworm outbreak. In the NMS ordination diagram, the sample points (representing bird community composition at varying points in time) progress from left to right across the plot during increasing budworm years, cluster on the right side of the diagram during peak budworm years, and shift back toward the left as budworm numbers begin to decline (Fig. 3a).

During the late 1960s, when budworm numbers were low, Nashville Warbler (*Vermivora ruficapilla*), Magnolia Warbler (*D. magnolia*), Ovenbird and White-throated Sparrow (*Zonotrichia albicollis*) dominated the BSL bird
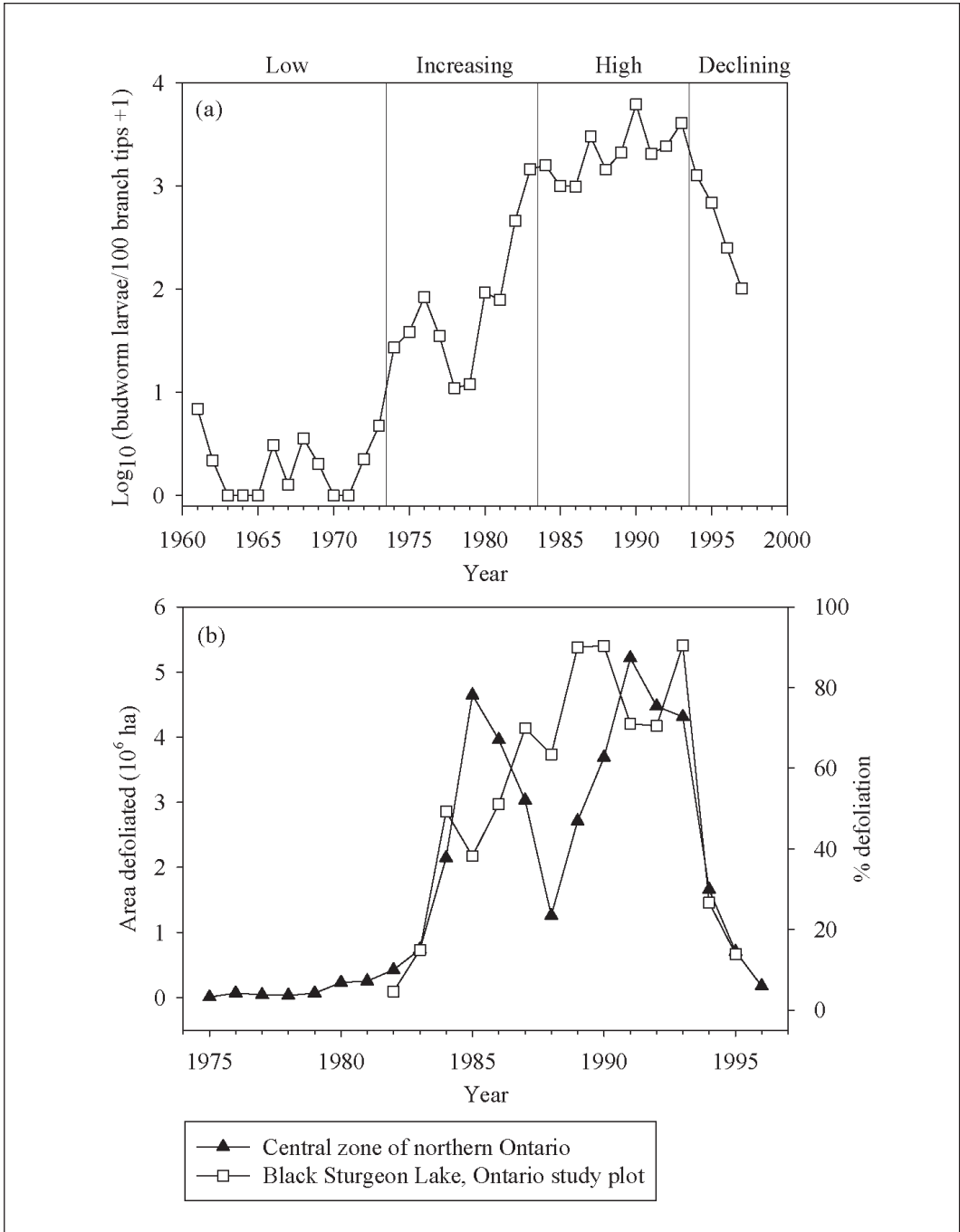
FIGURE 1. Progress of the spruce budworm outbreak locally at Black Sturgeon Lake and regionally in the central zone of northern Ontario: (a) Spruce budworm densities (larvae/100 branch tips) in the Black Sturgeon Lake, Ontario, study plot (1961-1997). Vertical reference lines separate periods of low (1961-1973), increasing (1974-1983), high (1984-1993) and declining (1994-1997) budworm densities; (b) Percent defoliation by budworm in the Black Sturgeon Lake, Ontario, study plot (1982-1995) and area defoliated in the central zone of northern Ontario (1975-1996). Regional data are from Candau et al. (1998).
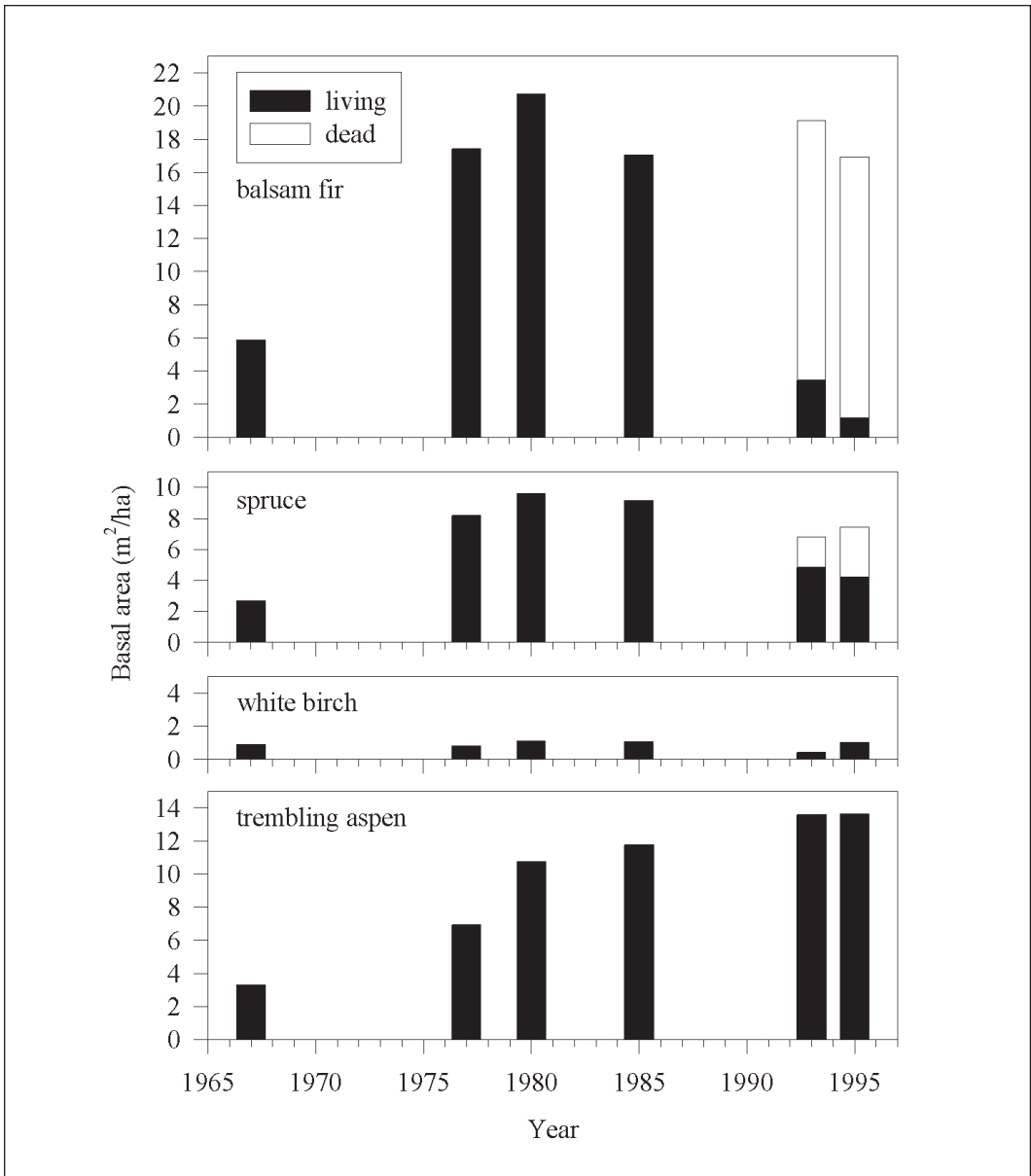
FIGURE 2. Basal areas of dominant tree species (balsam fir, black and white spruce, white birch and trembling aspen) in the Black Sturgeon Lake, Ontario, study plot (1967-1995).

community (Table 1, Fig. 3b). Least Flycatcher (*Empidonax minimus*), Chestnut-sided Warbler (*D. pensylvanica*) and Black-and-white Warbler (*Mniotilta varia*) were also relatively common. As budworm numbers increased through the 1970s and early 1980s, Least Flycatcher, Chestnut-sided Warbler, Black-and-white Warbler and White-throated Sparrow declined in abundance as other species increased, including Red-eyed Vireo, Golden-crowned Kinglet, Ruby-crowned Kinglet (*R. calendula*), Swainson's Thrush, Tennessee Warbler, Nashville Warbler, Magnolia Warbler, Cape May Warbler, Yellow-rumped Warbler (*D. coronata*) , Blackburnian Warbler,

TABLE 1. Number of territories in the 10.4 ha Black Sturgeon Lake, ON, study plot (1966-1998).

| Species | 1966 | 1967 | 1968 | 1977 | 1978 | 1979 | 1980 | 1981 | 1983 | 1984 | 1985 | 1986 | 1988 | 1989 | 1992 | 1995 | 1998 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| OVEN | 2 | 3 | 4 | 7.4 | 7.5 | 13.6 | 13.5 | 11 | 14.3 | 13 | 9 | 8.8 | 8.8 | 6.9 | 11.8 | 6.6 | 5 |
| BBWA | 0 | 0 | 0 | 3 | 2 | 14 | 14 | 14.1 | 18.2 | 11.1 | 9.2 | 12 | 10 | 12 | 7.5 | 6 | 1 |
| GCKI | 1 | 1 | 1 | 2 | 1 | 5 | 5.9 | 8.8 | 37.5 | 15.1 | 5 | 4 | 3 | 5 | 1 | 0.1 | 1 |
| NAWA | 2.5 | 2.5 | 3.5 | 5.9 | 7 | 7.3 | 4.6 | 2.9 | 5.5 | 6.9 | 5.6 | 5 | 1 | 0.1 | 1 | 4.3 | 0 |
| REVI | 1 | 0.5 | 1 | 4 | 1 | 3 | 4.7 | 2 | 8 | 4.2 | 5.5 | 6 | 1.9 | 4.5 | 6.3 | 4.8 | 5.5 |
| CMWA | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 14.8 | 18.8 | 4.5 | 9 | 6 | 2 | 3 | 1 | 0 |
| SWTH | 1 | 0.5 | 0.5 | 6.5 | 4 | 4.5 | 4 | 3.5 | 2.2 | 5 | 1 | 6.3 | 3.9 | 3.8 | 4 | 1.5 | 5 |
| MAWA | 4 | 4 | 3.5 | 5.8 | 6 | 8.2 | 10 | 3.6 | 2.4 | 0.8 | 1 | 0 | 0.6 | 1.8 | 3.3 | 1 | 0.5 |
| BLBW | 0 | 0 | 0 | 1 | 2.9 | 4 | 2 | 6.9 | 4.5 | 6 | 2 | 2 | 4 | 2 | 3 | 3 | 5 |
| YRWA | 1.5 | 1 | 0 | 1 | 2 | 5.8 | 6 | 3.6 | 10.1 | 2 | 2 | 3 | 1 | 1 | 0 | 0.1 | 0 |
| RCKI | 1 | 1.5 | 0 | 1.6 | 1.7 | 3.9 | 6 | 2 | 6 | 1 | 0.1 | 6 | 0 | 0 | 1 | 1 | 0 |
| TEWA | 0 | 0 | 0 | 0 | 0 | 0.1 | 0.1 | 0.1 | 8.5 | 5.2 | 2 | 7.8 | 2 | 1 | 0 | 1 | 0 |
| YBFL | 2 | 2 | 2 | 0 | 0 | 0.1 | 0 | 1 | 2 | 3 | 2 | 1 | 0.1 | 0 | 2 | 4 | 2 |
| WTSP | 4 | 4 | 4.5 | 0 | 0.1 | 0.1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0.1 | 0.5 | 3 | 1.8 |
| RBNU | 0 | 0 | 2 | 0 | 1 | 0 | 3 | 3 | 1 | 2 | 0 | 2 | 1 | 0 | 1 | 2 | 1 |
| LEFL | 3 | 2 | 2 | 0 | 4 | 2 | 1.8 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| AMRO | 0 | 0.1 | 0.5 | 1 | 2 | 1 | 0.8 | 0.5 | 1 | 1 | 0 | 1 | 0 | 0.1 | 1.3 | 0.5 | 0.1 |
| YBSA | 1 | 1 | 1 | 0.1 | 0 | 1 | 1.8 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 |
| BAWW | 2 | 2 | 1 | 0.1 | 0.1 | 0.9 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CSWA | 1.5 | 1 | 1 | 0 | 0.1 | 0 | 0 | 0.9 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Other | 4.7 | 6.7 | 8.1 | 5.1 | 6.3 | 16 | 15.9 | 8.2 | 27.8 | 11.4 | 7.1 | 3.4 | 2.2 | 5 | 9.7 | 5.6 | 6.3 |
| Total | 32.2 | 32.8 | 35.6 | 44.5 | 48.7 | 90.5 | 96.2 | 73.1 | 165.8 | 106.5 | 56.1 | 77.3 | 45.5 | 45.3 | 56.5 | 46.5 | 34.2 |

Note: The 20 most common species (those ranked among the 10 most abundant species on at least three sampling dates) are presented in decreasing order of total abundance. OVEN = ovenbird; BBWA = bay-breasted warbler; GCKI = golden-crowned kinglet; NAWA = Nashville warbler; REVI = red-eyed vireo; CMWA = Cape May warbler; SWTH = Swainson's thrush; MAWA = magnolia warbler; BLBW = Blackburnian warbler; YRWA = yellow-rumped warbler; RCKI = ruby-crowned kinglet; TEWA = Tennessee warbler; YBFL = yellow-bellied flycatcher; WTSP = white-throated sparrow; RBNU = red-breasted nuthatch; LEFL = least flycatcher; AMRO = American robin; YBSA = yellow-bellied sapsucker; BAWW = black-and-white warbler; CSWA = chestnut-sided warbler.

Bay-breasted Warbler and Ovenbird. By 1983, when songbird numbers were at their peak, more than half of the BSL bird community was composed of just four species (Golden-crowned Kinglet, Cape May Warbler, Bay-breasted Warbler and Ovenbird). Golden-crowned Kinglet alone accounted for >22% of the territories on the BSL plot. Through the peak years of budworm abundance (1984-1992), populations of these four species and several others, including Tennessee and Yellow-rumped warblers, declined. By 1995-1998, White-throated Sparrows were starting to return to the plot, but not Least Flycatchers nor Chestnut-sided or Black-and-white warblers.

The timing of bird population responses to the budworm outbreak was not consistent among species (Fig. 4). Nashville and Magnolia warblers and Ovenbird all responded to increasing budworm numbers relatively early in the outbreak. However, Magnolia Warbler numbers declined again before budworm numbers peaked. Tennessee and Cape May warblers were the latest to respond, and Golden-crowned Kinglet and Yellow-rumped, Blackburnian and Bay-breasted warblers were intermediate. Golden-crowned Kinglet and Tennessee, Cape May and Yellow-rumped warbler numbers were elevated for only a relatively short period (4-5 yr), whereas Bay-breasted Warbler and Ovenbird maintained high population levels for most of the outbreak.

For many species, such as Yellow-bellied Flycatcher (*E. flaviventris*), Red-breasted Nuthatch (*Sitta canadensis*), Golden-crowned Kinglet, Ruby-crowned Kinglet, Swainson's Thrush, Tennessee Warbler, Nashville Warbler, Yellow-rumped Warbler, Ovenbird and White-
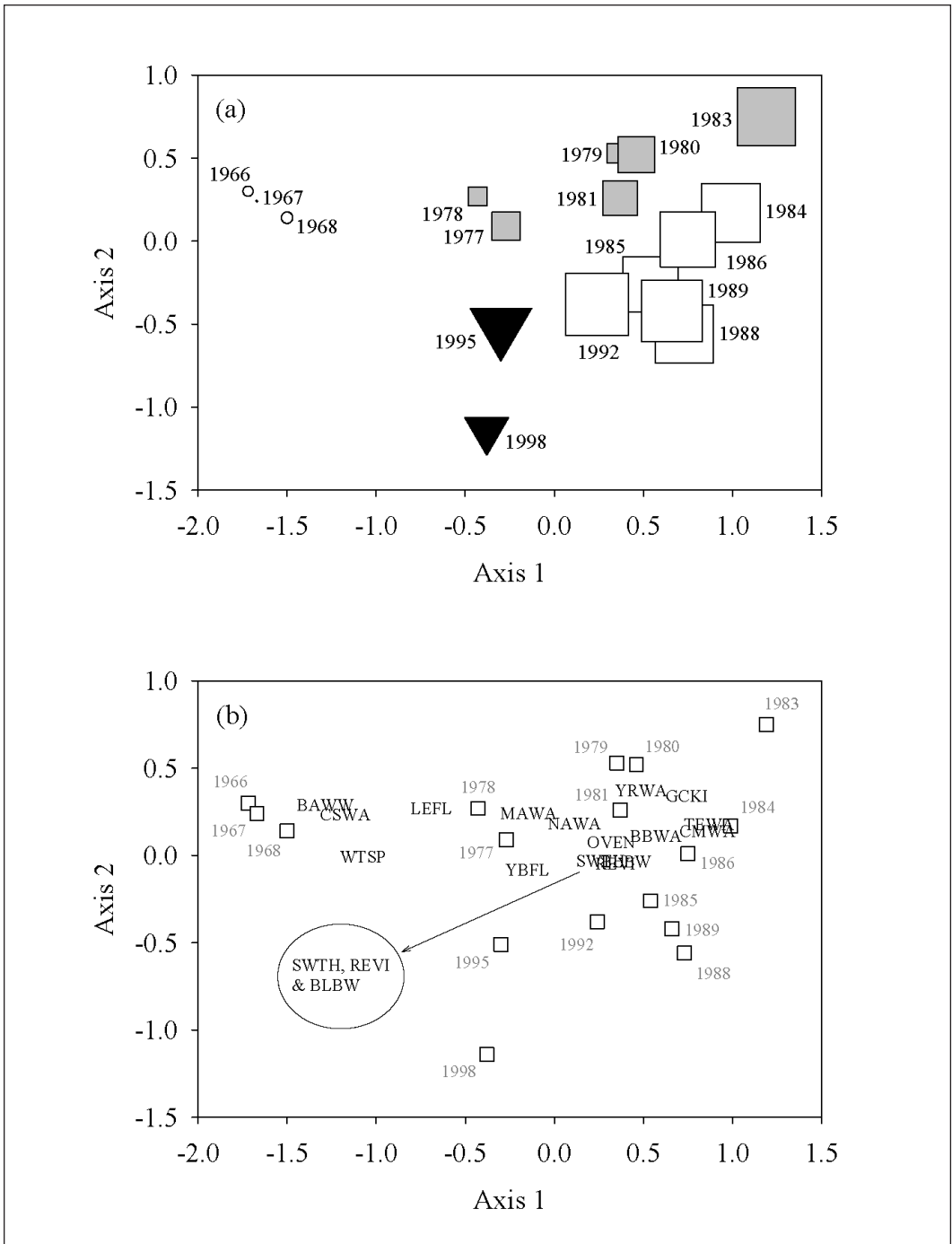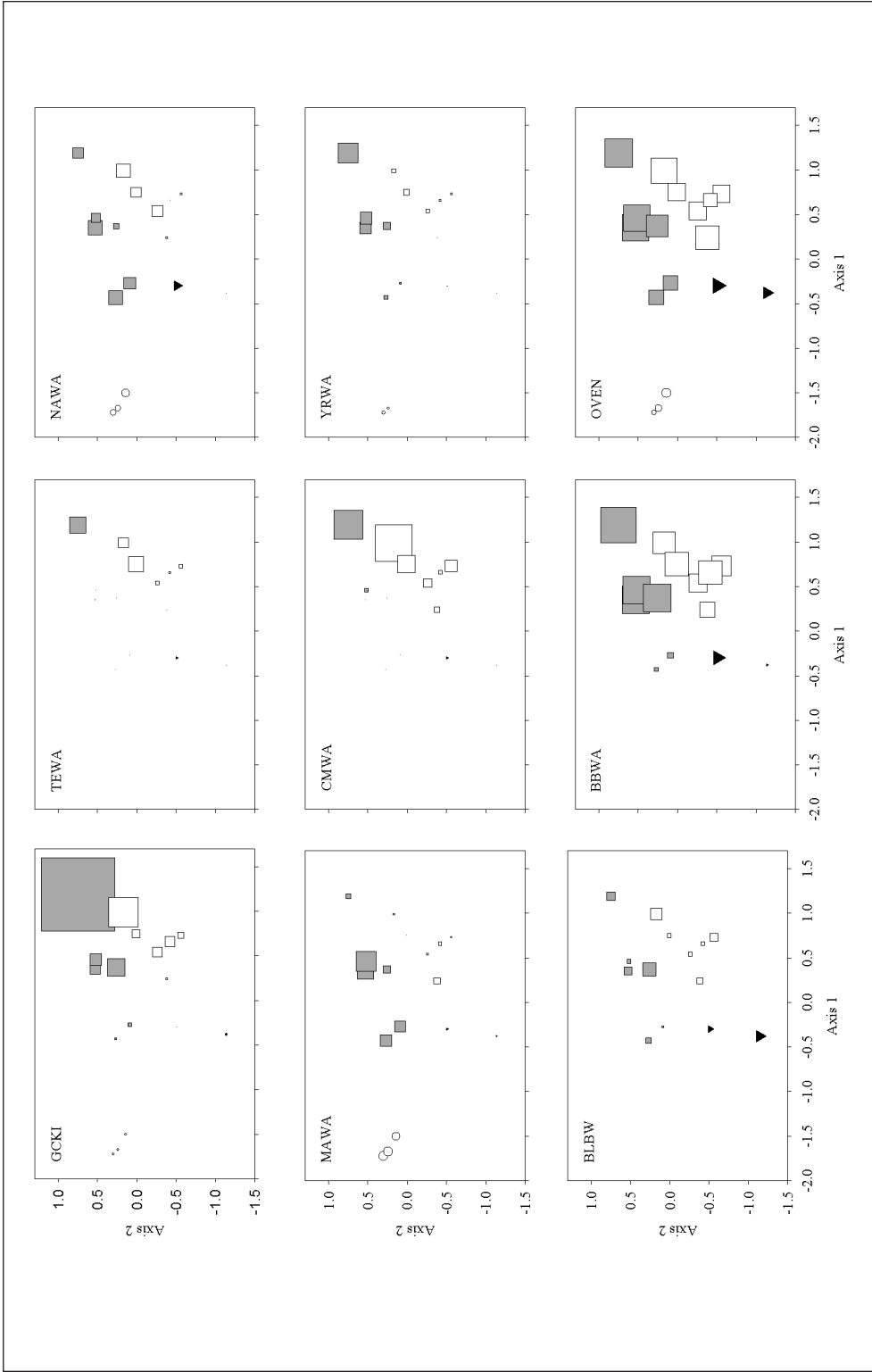
FIGURE 3. Non-metric multidimensional scaling of the Black Sturgeon Lake, ON, bird community on 17 sampling dates between 1966 and 1998: (a) Symbol sizes for sample units (years) are scaled proportionally to spruce budworm abundance, O = low budworm densities, ■ = increasing budworm densities, □ = high budworm densities, ▼ = declining budworm densities; (b) Symbols denote location of samples (in species space) only. Species scores are derived by weighted averaging of the abundances of each species in each sample unit.

FIGURE 4. Non-metric multidimensional scaling of the Black Sturgeon Lake, ON, bird community on 17 sampling dates between 1966 and 1998. Symbol sizes are scaled proportionally to individual bird species' abundances. Species codes are the same as in Table 1, symbols the same as in Figure 3.

throated Sparrow, population trends in the BSL plot resembled regional trends (Fig. 5). For others, there were differences between local and regional trends that can be classified into two main types: 1) species that were virtually eliminated from the BSL plot, but not regionally, over time [Yellow-bellied Sapsucker (*Sphyrapicus varius*), Least Flycatcher, and Chestnut-sided and Black-and-white warblers]; and 2) species with local peaks in abundance during the increasing phase of the budworm cycle that were not seen regionally until several years later [Red-eyed Vireo, American Robin (*Turdus migratorius*) and Magnolia, Cape May, Blackburnian and Bay-breasted warblers].

DISCUSSION

Many bird species clearly responded to the budworm outbreak at Black Sturgeon Lake, but the relationship between bird and budworm numbers was not a simple one. We saw a fivefold increase in the total number of breeding pairs of forest birds in the BSL plot between 1966 and 1983. However, the peak in bird numbers occurred 7 years before the peak in budworm numbers (1983 and 1990, respectively). When budworm numbers were at their highest (>10 larvae per branch tip between 1984 and 1993), populations of many bird species were declining, suggesting that at high budworm densities the advantages of a superabundant food supply may be at least partially offset by negative changes in habitat associated with defoliation. Defoliation jumped from 15% to 49% between 1983 and 1984 and remained high through to 1993.

The reason for the population declines may be related to predation or food supply. Defoliation by gypsy moth has been shown to increase nest predation rates (Thurber et al. 1994). Defoliation may also reduce the abundance of insects other than the pest that require the foliage for food, or as a surface for mating, oviposition, foraging or perching (Pelech and Hannon 1995). Even during budworm outbreaks, the diets of most insectivorous bird species contain substantial numbers of other insects (Mitchell 1952, McMartin et al. 2002). A reduction in food later in the breeding season, when budworm are no longer readily available, could have negative consequences for the survival of recently fledged young (Martin 1987).

Although there has been much written in the scientific and popular literature about the connection between spruce budworm and forest birds, there have been relatively few actual field studies that have directly addressed this relationship. Kendeigh's (1947) work in Ontario in 1945 was the first systematic examination of the numerical and functional responses of some bird species to a budworm outbreak. The effectiveness of birds in controlling budworm populations was studied in Maine in 1949-1950 by comparing an area where much of the bird community was removed by shooting to areas that were undisturbed (Hensley and Cope 1951, Stewart and Aldrich 1951, Dowden et al. 1953). This study also included an analysis of the bird stomach contents (Mitchell 1952). The numerical response of birds to budworm was investigated by Morris et al. (1958) and Gage and Miller (1978), and the functional response by Mook (1963), as part of the New Brunswick Green River Project (1947-1968). The functional and numerical responses of birds to budworm were also investigated in Maine and New Hampshire in two experiments conducted in 1976-1977 (Crawford et al. 1983) and 1982-1983 (Crawford and Jennings 1989, Crawford et al. 1990). Finally, Zach and Falls (1975) compared observations on the feeding and breeding biology of ovenbirds during a spruce budworm outbreak in Ontario in 1973 to historical data collected during a period of low budworm abundance, and Morse (1978) examined the food supply, foraging patterns and densities of Bay-breasted Warbler and Cape May Warbler during a budworm outbreak in Maine in 1976. There are also indirect analyses of monitoring data by Patten and Burger (1998) and Bolgiano (2004).

Given the immense spatial scale and temporal variability of budworm infestations (Blais 1983, Candau et al. 1998), and the relatively few bird/budworm studies that have been conducted at widely scattered locations across the budworm's range (see above), the inconsistency in the literature regarding individual species' responses is not surprising. Nevertheless, it is generally agreed that Tennessee, Cape May and Bay-breasted warblers, the so-called 'budworm specialists' of Morse (1989), respond strongly and positively to budworm outbreaks, and our data would support this conclusion. Other species that
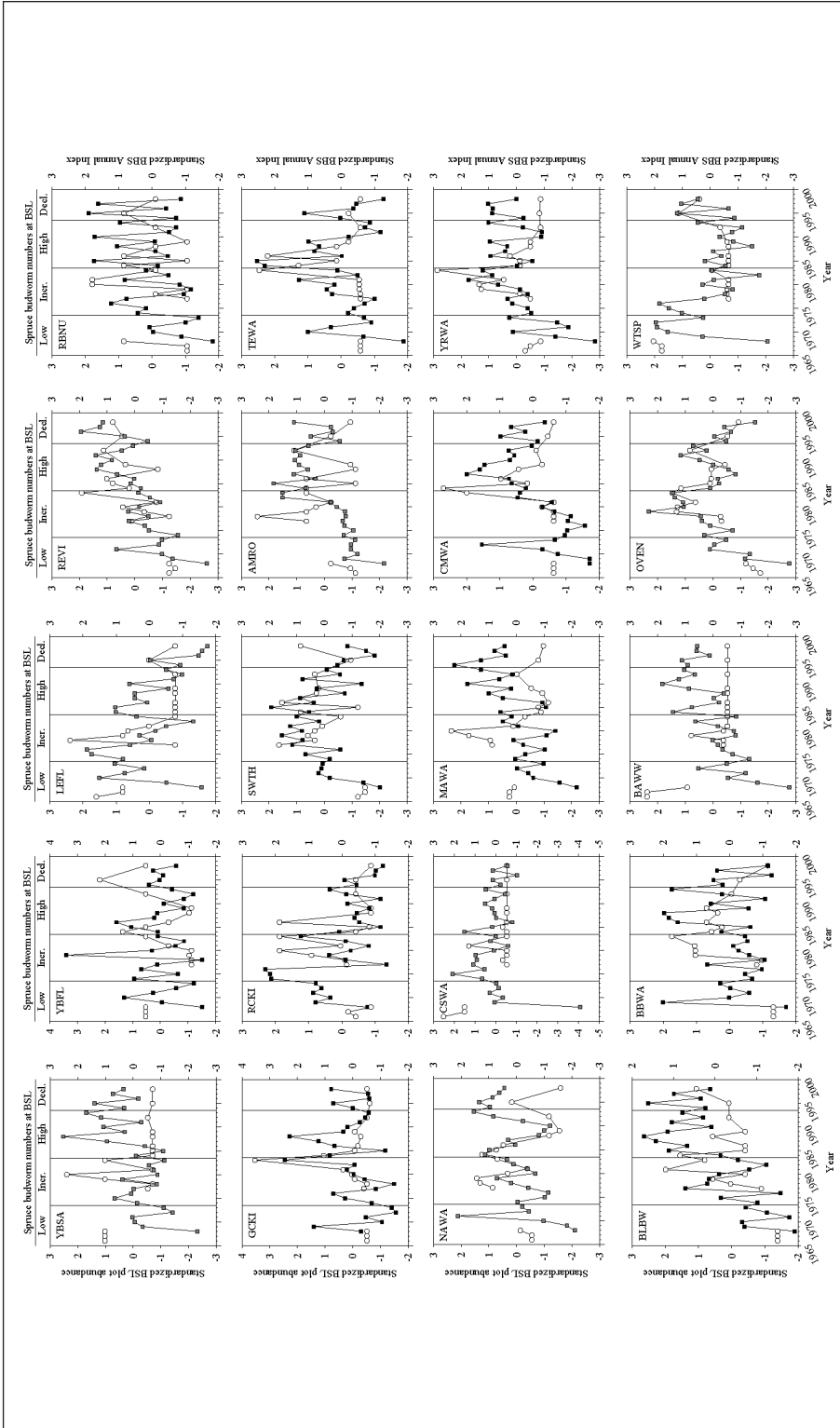
FIGURE 5. Population trends for selected bird species in the Black Sturgeon Lake, ON, study plot and the province of Ontario (1966-1998). Ontario data are from the Ontario Breeding Bird Survey (available from http://www.cws-scf.ec.gc.ca/mgbc/trends/index.cfm [accessed 15 September 2008]). Data were standardized to allow comparisons on the same scale. For BBS data, grey symbols denote species with a distribution that includes a significant portion of southern Ontario, whereas black symbols denote species that are primarily northern (the portion of the province affected by budworm). Vertical reference lines divide the plots into periods of low (1961-1973), increasing (1974-1983), high (1984-1993) and declining (1994-1997) budworm populations at Black Sturgeon Lake. Species codes are the same as in Table 1.

responded positively to budworm in our study area, and that have been shown to do the same elsewhere, include Golden-crowned Kinglet (Gage and Miller 1978, Morse 1978, Crawford and Jennings 1989), Swainson's Thrush (Hensley and Cope 1951, Morris et al. 1958, Gage and Miller 1978), Magnolia Warbler (Hensley and Cope 1951, Stewart and Aldrich 1951, Gage and Miller 1978), Yellow-rumped Warbler (Gage and Miller 1978), Blackburnian Warbler (Hensley and Cope 1951, Morris et al. 1958, Gage and Miller 1978) and Ovenbird (Kendeigh 1947, Morris et al. 1958, Zak and Falls 1975).

The three 'budworm specialists' (Tennessee Warbler, Cape May Warbler and Bay-breasted Warbler) had very different patterns of response to the budworm outbreak on the BSL study plot. None of the three was present in the 1960s when the budworm population was at an endemic (low) level. Bay-breasted Warbler responded relatively early to increasing budworm numbers (late 1970s) compared to Cape May and Tennessee warblers (1983), suggesting that the Bay-breasted Warbler may be better adapted for exploiting low budworm densities. Bay-breasted Warbler numbers also built up gradually over time, presumably as a result of increased reproductive success (MacArthur 1958), whereas Cape May and Tennessee warbler numbers peaked abruptly, possibly reflecting a redistribution of individuals across the landscape in response to local differences in budworm density (MacArthur 1958, Royama 1984), rather than increased local reproduction. Finally, declines in Cape May and Tennessee warbler numbers occurred sooner than for Bay-breasted Warbler. This disparity may be related to differences in nesting and/or foraging location. Cape May and Tennessee warbler forage primarily on the outer branches and foliage near the tops of trees, whereas Bay-breasted Warbler forages mostly at mid-level close to the trunk (MacArthur 1958, Morse 1978, Rimmer and McFarland 1998). Cape May Warbler nests are also usually located near the tops of trees, as opposed to mid- to lower level for Bay-breasted Warbler and ground level for Tennessee Warbler (Harrison 1978). Since budworm damage tends to be most severe in the upper crowns of spruce and fir trees, with top killing becoming common after a few successive years of defoliation (Prebble 1975), it is possible

that degradation of habitat due to defoliation may have been an early limiting factor for Cape May and Tennessee warblers.

Cape May and Bay-breasted warblers had local peaks in abundance in 1983-1984 that preceded their regional peaks in 1987-1988. It appears that, while degradation of habitat may have limited populations of these two species at the local level, the process was operating differently at the regional scale. Spruce budworm outbreaks are not spatially homogeneous. Rather, there is considerable variation in the frequency, duration and amplitude of local and regional outbreaks (Nealis and Régnière 2004). Although there was a general increase in the severity of the budworm outbreak locally on the BSL block between 1983 and 1990, the area of moderate to severe defoliation in the Lake Nipigon zone of the budworm outbreak temporarily declined between 1986 and 1988. Thus, the life history requirements of the Cape May and the Bay-breasted warblers may have been maintained at a regional level through the mid to late 1980s, even though local populations on the BSL block were declining.

At least some of the population change we saw in Ovenbird may have been due only indirectly to budworm. In the 1960s, defoliation and tree mortality resulting from the previous budworm outbreak had created a relatively open stand with a well developed shrub layer. Through the 1970s, when Ovenbird numbers were increasing, tree basal area was higher, the canopy was closed and the shrub layer was suppressed, all parameters that have been shown to be important in determining the placement of ovenbird territories (Van Horn and Donovan 1994). This pattern was reversed in the 1990s, by which point several years of continuous defoliation had resulted in significant mortality of spruce and fir, an opening up of the canopy and a re-emergence of the shrub layer. The fact that the local Ovenbird trend very closely tracked the provincial trend also suggests that other regional factors may have had a predominant influence on the BSL population.

We saw a distinct early peak in Magnolia Warbler numbers at the BSL study site, apparently in response to a low, but increasing, budworm population in the late 1970s. During

the previous budworm outbreak at Black Sturgeon Lake, Magnolia Warbler showed a strong negative response to budworm, although this study was conducted relatively late in the outbreak, "just preceding the killing of many trees" (Kendeigh 1947). Morris et al. (1958) also suggested an inverse relationship between budworm and Magnolia Warbler. The early decrease in Magnolia Warbler numbers on the BSL plot occurred when budworm numbers were still increasing and there had yet to be any significant change in habitat due to defoliation or tree mortality. It was also coincident with a peak in Bay-breasted Warbler numbers. These observations provide some support for Kendeigh's (1947) suggestion that Magnolia Warbler numbers decrease during budworm outbreaks as a result of interspecific competition with the more aggressive Bay-breasted Warbler.

Both Magnolia and Blackburnian warbler showed distinct peaks in abundance on the BSL plot, but no such peaks were seen regionally. Unlike the "budworm specialists", neither species has a particularly high reproductive potential (average clutch size of 4 for Magnolia and Blackburnian warbler versus 5 for Tennessee, 6.5 for Cape May and 5.5 for Bay-breasted warbler; data available from http://wildspace.ec.gc.ca/ [accessed 18 June 2007]). This suggests that the local peaks in abundance on the BSL plot were more likely the result of immigration (an aggregational response), or possibly increased breeding opportunities for floaters, than the classic numerical response described by Morris et al. (1958).

We saw a strong, but relatively short-lived, response to budworm by the Yellow-rumped Warbler. In other studies, this species has been variously reported to respond positively (Hensley and Cope 1951, Gage and Miller 1978) and negatively (Kendeigh 1947, Morris et al. 1958) to budworm outbreaks. The reasons for this discrepancy are unclear, but may also be related to interspecific competition, since the sharp decline in Yellow-rumped Warbler numbers takes place at a time when other *Dendroica* species are still peaking. Like Magnolia Warbler, the Yellow-rumped has a low level of interspecific dominance (Morse 1976) and thus may have been excluded from the BSL plot by the socially dominant Bay-

breasted Warbler.

Although not generally considered to be a budworm specialist, the species that showed the greatest response to budworm in our study was the Golden-crowned Kinglet. We believe the large peak in Golden-crowned Kinglet numbers in 1983 (14 times as many as in the 1970s) is a special case and can be attributed to a unique combination of factors. The Golden-crowned Kinglet is a short distance migrant/resident, with some central North American populations wintering as far north as the southern portions of Minnesota, Wisconsin, Michigan and Ontario (Ingold and Galati 1997). Populations wintering near the northern limits of the winter range may suffer high (up to 100% local) mortality during severe winters, which could affect breeding densities during the next breeding season (Ingold and Galati 1997). This susceptibility to winter mortality may explain why the Golden-crowned Kinglet has evolved a relatively high reproductive potential [frequently double brooded, average clutch size 8.6 (range 5-11) for *R. s. satrapa* (Ingold and Galati 1997)]. MacArthur (1958) suggests that a large and variable clutch size may also be beneficial in taking advantage of a periodically abundant, but unpredictable, food source like spruce budworm. Over the 20-yr period from December 1976 to February 1996, the winter preceding the peak in Golden-crowned Kinglet numbers was the warmest winter on record in southern Ontario and lower Michigan (based on mean daily temperatures and mean daily minimum temperatures for December, January and February at London, ON (data available from http://climate.weatheroffice.ec.gc.ca/ [accessed 25 June 2007]) and Lansing, MI (data available from http://www.wunderground.com/history/airport/KLAN/ [accessed 25 June 2007]) weather stations. As an example, the mean daily minimum temperature for the winter of 1982-1983 at London, ON (-5° C) was 4.1° C above the 20-yr normal. We believe that a high survival of broods during the 1982 breeding season (due to the presence of an abundant food source) combined with a low mortality during the winter of 1982-1983 (due to an unusually warm winter) resulted in an extremely high breeding density of Golden-crowned Kinglets in 1983. If such were the case, one would expect to see the same trend both regionally and locally, although not

necessarily of the same magnitude due to spatial variability in budworm densities, and indeed we did. Following two colder winters in 1983-1984 [mean daily minimum temperature at London, ON (-9.7º C) was 0.7º C below normal] and 1984-1985 [(-8.8º C) 0.3º C above normal], Golden-crowned Kinglet densities dropped to 1970s levels.

Previous studies have shown that many species of birds consume large numbers of budworm when budworm populations are high, but that this represents only a small fraction (1-7%) of the total budworm population (Kendeigh 1947, George and Mitchell 1948, Morse 1978, Crawford et al. 1983). At low budworm densities, the proportion of the budworm population consumed is much higher, however, leading several authors to suggest that birds may play a significant role in regulating budworm numbers at endemic population levels (Morris et al. 1958, Gage and Miller 1978, Crawford et al. 1983, Crawford and Jennings 1989). The avian species most effective in suppressing budworm populations during the endemic period of the budworm cycle, or during the early years of population release, should be those that respond quickly to changes in the insect's density (Crawford et al. 1983). In our study, this would include Swainson's Thrush and Nashville, Magnolia, Blackburnian and Bay-breasted warblers. There is some suggestion that birds may play a role in suppressing residual budworm populations after the major outbreak has run its course (Blais and Parks 1964, Buckner 1971). However, we found that populations of most bird species started to decline well before the collapse of the budworm outbreak, presumably in response to the deteriorating condition of the stand, which probably limited their effectiveness in suppressing the already declining budworm population.

In conclusion, for most bird species, budworm outbreaks tend to be positive events, but only during the increasing phase of the budworm cycle. When budworm numbers are high and defoliation is severe, the negative effects of habitat change tend to outweigh the advantages of a superabundant food supply. While the overall response of the bird community to increasing budworm numbers was positive, the pattern of response differed among species.

Factors that appeared to influence individual species' responses to budworm included habitat, weather, competition and reproductive biology.

## ACKNOWLEDGEMENTS

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