

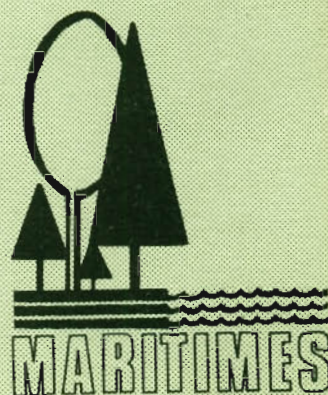


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HABITATS IN
NORTHWESTERN
NEW BRUNSWICK**

by **S.H. GAGE** and **C.A. MILLER**



MARITIMES FOREST RESEARCH CENTRE

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ABSTRACT

A long-term bird census was conducted in five plots located in largely balsam fir stands of northwestern New Brunswick. During part of the 22-year census, two of the plots were heavily infested with spruce budworm *Choristoneura fumiferana* (Clem.), and suffered extensive tree mortality. Nineteen bird species were common to all plots; differences in their densities, relative to forest cover and presence of budworm as a food supply, are presented.

RESUME

Les auteurs effectuèrent un relevé à long terme des Oiseaux dans cinq placettes sises en des peuplements formés surtout de Sapin baumier dans le nord-ouest du Nouveau-Brunswick. Au cours de la période de 22 ans, deux des placettes furent infestées fortement par la Tordeuse, *Choristoneura fumiferana* (Clem.) et la mortalité des arbres fut élevée. Dix-neuf espèces d'oiseaux habitaient toutes les placettes; les auteurs donnent les différences de densité de chaque espèce par rapport au couvert forestier et à la présence des Tordeuses en tant que nourriture.

INTRODUCTION

Tothill (1923) and other observers recognized bird predation as a potentially important process in the natural control of spruce budworm, *Choristoneura fumiferana* (Clem.). Consequently, an annual bird census was conducted and the feeding behavior of some species was observed as part of a research program at Green River in northwestern New Brunswick, initiated in the 1940's. The program was designed to explain the forest-budworm interaction and to identify potential methods of control through forest management (Morris 1963).

Bird abundance and diversity were recorded for 22 years beginning in 1947. Some of these data have been published: Morris et al. (1958) analyzed the census data for the first 10 years when the budworm was at outbreak levels and found that six species increased in abundance; the classic numerical response. Mook (1963) discussed budworm mortality caused by birds, and changes in predation pressure by one species relative to changes in budworm density. Gage et al. (1970) analyzed the feeding response of nine species to a defoliator, *Acleris variana* Fern., a close ally of the spruce budworm in the fir-spruce habitat.

The objectives of this paper are; (a) to compare bird abundance in the outbreak and postoutbreak

phases of a spruce budworm epidemic, (b) to supplement evidence on the numerical response of some bird species to the budworm, and (c) to discuss changes in bird density relative to forest types that are highly susceptible to budworm attack.

METHODS

The population of small birds was measured each spring between 1947-1968 by a song census of territorial males, based on the general assumption that each territorial male represents a breeding pair of birds. Marked, parallel lines through a 5-ha plot were traversed on five or more successive mornings and the positions of singing males were recorded. This technique has been discussed by Kendeigh (1947) and has been further elaborated and standardized in Audubon Field Notes 4: 185-187 (1950). At Green River, the census was started in the latter half of June, after all migratory species had arrived and established nesting territories. Five plots, designated as K1, K2, G4, G5, G17 and representative of forest stands found in the Restigouche-Bras d'Or Ecoregion of the Maritime Provinces (Loucks 1962), were sampled during the 22-year study, two on a continuing basis, the others for shorter times (Table 1).

Table 1. Mean tree age and budworm abundance on the bird-census plots under outbreak and postoutbreak conditions

Parameters	K1		G4		K2		G5		G17
	Outbreak 1950's	Post- outbreak 1960's	Outbreak 1950's	Post- outbreak 1960's	Outbreak 1950's	Post- outbreak 1960's	Outbreak 1950's	Post- outbreak 1960's	Post- outbreak 1960's
Mean age of balsam fir (yr)	80+	<10	120+	120+	45	55	45	55	15
Budworm per tree ¹	20,000	<5	2,500	<10	6,000	<10	1,000	<10	5
Bird-census years ²	1953-1966 (1959, 1965)		1947-1966 (1959)		1956-1966 (1959, 1965)		1957-1968 (1959)		1961-1966

¹ Large larvae plus pupae.

² Years in brackets, no census taken.

Budworm Abundance and Stand Description

All plots were dominated (76% of total stems) by balsam fir, *Abies balsamea* L. Mill. Initially, the trees on plots K1 and G4 were overmature (80 years plus), K2 and G5 middle-aged, having developed after the 1912-1920 budworm outbreak in the region, and G17, advanced reproduction resulting from a clear cut in 1945 (Table 1). Structural changes occurred on plots K1 and K2 as a result of budworm attack as noted below.

A spruce budworm outbreak swept through New Brunswick in the 1950's. In the study area, this outbreak collapsed in 1958-1959 and populations reverted to low density in the postoutbreak period, 1960-1967. The pattern of outbreak and collapse of the 1950's-1960's occurred on plots K1 and K2. The trees were severely infested in the 1950's with budworm at a very high density on K1 and moderate density on K2. Both plots suffered budworm-induced tree mortality. On K1, dieback began in dominant balsam fir crowns in 1953, and understory trees were dead by 1956. By 1958, 80% of the balsam fir in plot K1 was dead, as expected in an overmature fir stand subject to uncontrolled infestation. Fewer white spruce, *Picea glauca* (Moench) Voss, died from attack but a 40% loss of both white and black spruce, *Picea mariana* (Mill.) B.S.P., resulted from windblow. By 1961, many of the dead trees had fallen and openings were covered by a dense mat of raspberry; the general structure of the forest was patches of young balsam fir 2.0-5.0 m in height, interspersed with hardwood reproduction, and overtopped by scattered +80-year-old spruce. On plot K2, 50% of the trees died; severe mortality occurred among the larger diameter classes (Baskerville 1960).

Budworm damage was far less severe in plots G4 and G5 which had been isolated by cutting operations from the heavily infested zones during the 1949-1959 outbreak. Budworm density increased in these plots in the mid-1950's but the destruction of needles on current shoots never reached the 100% level and there was no budworm-induced tree mortality.

When the bird census was extended in 1961, plot G17 was stocked at 5,000 balsam fir per hectare, averaging 3 m height.

Bird Density as a Function of Budworm Density

A total of 67 bird species was recorded on the five plots; 18 species were common to all plots and 19 were common to all but one plot. The 19 species

comprised at least 86% of the total bird population on any plot. Discussion is limited to those species in the following analysis.

Two of the five plots, K1 and G4, were sampled at both high budworm densities in the 1950's and low budworm densities in the 1960's, thus providing a sequence of bird abundance relative to changes in budworm abundance and a means of evaluating numerical responses. However, the data for K1 have to be interpreted with caution because of the catastrophic change in the habitat (Table 1). No such change occurred on plot G4. To determine the occurrence of a numerical response, mean bird densities in budworm-outbreak years, 1950-1957, were compared to mean densities in postoutbreak years, 1961-1966 (Table 2). The above comparison did not include the period 1958 to 1960 because no census was conducted in 1959 and all 3 years were considered to be a transition between outbreak and postoutbreak conditions. The comparison of mean densities showed that 12 of the 19 species on plot K1 and 14 of the 19 species on G4 had higher densities under outbreak than under postoutbreak conditions. Thus, densities of many species apparently responded to the overabundant food supply in their habitat (Table 2).

To interpret these data, we have arbitrarily selected a three-fold difference in density as a strong positive (++) or a strong inverse (---) response to changes in budworm density (Table 2). Our analysis agrees with Morris et al. (1958) and shows that the Tennessee, Blackburnian, and Bay-breasted Warblers were much more abundant under outbreak than under postoutbreak conditions. We also found that they were more abundant in densely-infested K1 than in lightly-infested G4 (Table 3). The Yellow-bellied Flycatcher¹ and the Solitary Vireo, although not abundant, also showed a marked increase in density under outbreak conditions (Table 2). Neither of these birds was shown to increase with budworm outbreak by Kendeigh (1947), Hensley and Cope (1951), or by Morris et al. (1958). On the other hand, we found that the Cape May Warbler was scarce under outbreak conditions which is not in agreement with observations by Kendeigh (1947) and Hensley and Cope (1951). The Evening Grosbeak, an opportunistic forager, was not observed as a breeding resident. Large flocks were

¹ Vocal separation of the Yellow-bellied and Least Flycatchers is often difficult (P.A. Pearce, Canadian Wildlife Service, Fredericton, N.B. Personal communication).

Table 2. Mean densities of 19 species of birds/40 ha under budworm outbreak (1950-1957) and postoutbreak conditions in two budworm susceptible stands

Bird species	Plot G4			Plot K1		
	Outbreak	Postoutbreak	Response	Outbreak	Postoutbreak	Response
Number of consecutive census years	8	6		5	5	
Yellow-bellied Flycatcher	4.6	P ¹	++	5.1	0	++
Least Flycatcher	3.9	2.8	+	2.1	15.9	—
Boreal Chickadee	2.0	4.7	—	2.0	P	++
Winter Wren	5.9	8.2	—	2.2	3.3	—
Swainson's Thrush	15.1	11.9	+	14.0	8.7	+
Golden-crowned Kinglet	8.9	3.0	+	2.3	0	++
Ruby-crowned Kinglet	P	10.1	—	1.1	2.7	—
Solitary Vireo	8.3	P	++	7.7	0	++
Tennessee Warbler	9.9	0	++	25.7	0	++
Nashville Warbler	P	3.0	—	0	P	—
Magnolia Warbler	22.0	7.9	+	1.3	14.9	—
Yellow-rumped Warbler	7.1	1.6	++	5.1	2.1	+
Black-throated Green Warbler	11.9	4.2	+	11.8	4.2	+
Blackburnian Warbler	17.1	5.3	++	19.5	1.5	++
Bay-breasted Warbler	55.8	16.4	++	78.2	2.0	++
Blackpoll Warbler	P	4.9	—	1.1	5.1	—
American Redstart	3.9	2.3	+	2.1	P	++
Dark-eyed Junco	5.9	3.5	+	8.4	4.1	+
White-throated Sparrow	9.3	5.0	+	11.4	19.5	—

¹ P denotes present at <1.0/40 ha.

Table 3. Mean densities of three warblers at moderate (plot G4) and high (plot K1) budworm densities (1950-1957)

Plot	Peak budworm density ¹	Warblers/40 ha		
		Tennessee	Blackburnian	Bay-breasted
K1	400	25.7	19.5	78.2
G4	50	9.9	17.1	35.8

¹ Fourth-instar larvae/m² of foliage.

Table 4. Mean densities of 19 species of birds/40 ha in three balsam fir stands under postoutbreak conditions (1960's)

Bird species	Middle-aged stand		Young stand
	K2	G5	G17
Number of consecutive census years	5	8	6
Yellow-bellied Flycatcher	0	1.2	3.5
Least Flycatcher	8.1	4.5	5.0
Boreal Chickadee	2.1	2.5	P ¹
Winter Wren	4.0	5.1	5.6
Swainson's Thrush	15.0	12.0	15.0
Golden-crowned Kinglet	P	4.8	P
Ruby-crowned Kinglet	P	10.4	7.6
Solitary Vireo	2.1	P	P
Tennessee Warbler	P	P	2.9
Nashville Warbler	P	2.5	15.0
Magnolia Warbler	9.0	6.1	25.0
Yellow-rumped Warbler	2.7	4.8	4.6
Black-throated Green Warbler	13.0	5.6	P
Blackburnian Warbler	2.0	2.0	0
Bay-breasted Warbler	8.5	13.6	16.3
Blackpoll Warbler	18.5	6.7	26.7
American Redstart	3.0	P	4.3
Dark-eyed Junco	5.6	7.5	9.6
White-throated Sparrow	13.5	7.5	11.7

¹ P denotes present at <1.0/40 ha.

recorded in some years but they did not appear to be reacting directly to budworm abundance, at least in the manner reported by Blais and Parks (1964) in Quebec. Morris et al. (1958) state that Swainson's Thrush showed a weak numerical response. We came to a similar conclusion for both Swainson's Thrush and the Dark-eyed Junco (Table 2).

Not all bird species were more abundant under outbreak than under postoutbreak conditions; some showed an inverse response and this phenomenon has been generally ascribed to interspecific competition. Kendeigh (1947) and Morris et al. (1958) listed the Magnolia, Yellow-rumped, and Black-throated Green Warblers as showing inverse responses. However, our analysis showed more Yellow-rumped and Black-throated Green Warblers under outbreak than under postoutbreak conditions (Table 2). There is one possible explanation for the conflicting conclusions. In the early 1950's, those two species were more abundant on plot G4 (few budworms) than on K1 (heavily infested), which may have led to the inverse response conclusions by Morris et al. (1958). We believe that our long-term observations are a better data source and suggest a positive rather than an inverse response.

The Winter Wren, Ruby-crowned Kinglet, and Blackpoll Warbler were more abundant under postoutbreak than under outbreak conditions. The Least Flycatcher was also very common in plot K1 in the post-outbreak period; a response we have characterized as inverse although we suspect that it is a reaction to the major change in the habitat.

Bird Abundance Relative to Habitat

The density of birds in the five different-aged study plots is of interest because it is generally accepted that birds can play a role in determining budworm abundance, particularly during the preoutbreak period of the population cycle. If birds do, in fact, play a regulating role, our data suggest that in the boreal forests of northern New Brunswick six species form the bulk of the regulating complex; Swainson's Thrush (11.9-15 singing males/40 ha), the Warbler complex of Magnolia (6.1-9/40 ha), Black-throated Green (4.2-13/40 ha), Bay-breasted (8.5-16.4/40 ha), and Blackpoll (4.9-18.5/40 ha), and the White-throated Sparrow (5-13.5/40 ha) (Tables 2 and 4). Of these, Swainson's Thrush and the White-throated Sparrow were relatively common on all plots, while the Black-throated Green and Bay-breasted Warblers were common in the older stands that are most susceptible to budworm attack. In contrast, the Magnolia Warbler was most abundant in

the young stands. The Ruby-crowned Kinglet was also most abundant in the older stands, G5 and G4. The data also suggest that in the preoutbreak period the six common species would range in density from about 40 to 90 singing males/40 ha, while the density of all common insectivorous species would range from 100 to 150/40 ha or about 4.0 pairs/ha. It is difficult to check the generality of these data on bird abundance. Morse (1976) studied four Warbler species (Magnolia, Yellow-rumped, Black-throated Green, and Blackburnian) in spruce-wood habitats in Maine and recorded densities from 3 to 4 pairs/ha. For those species we recorded half that density in the predominately fir forests of our study area (Tables 2 and 4).

Budworm density in the preoutbreak phase of a budworm cycle fluctuates between 1,000 and 10,000 sixth-instar larvae and pupae per hectare. How many of these budworm might be taken by birds is open to speculation. Kendeigh concluded that one nesting pair of warblers could consume 16,000 larvae and pupae and thus four families per hectare might consume 64,000. Estimates based on George and Mitchell (1948) and Mitchell (1952) suggest a total consumption of about 12,000 larvae/ha. In 1968, the senior author analyzed the gizzard contents of birds collected at low and moderate budworm densities in New Brunswick and estimated a consumption of 3,000 to 20,000 budworm/ha. It therefore seems quite apparent that birds are capable of exerting a strong predation pressure on preoutbreak populations of spruce budworm.

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