Spruce budworm outbreaks and the incidence of vagrancy in eastern North American wood-warblers

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Abstract: The Tennessee (*Vermivora peregrina*), Cape May (*Dendroica tigrina*), Bay-breasted (*D. castanea*), and Canada (*Wilsonia canadensis*) warblers and the Ovenbird (*Seiurus aurocapillus*) appear to show positive numerical responses to outbreaks of the spruce budworm (*Choristoneura fumiferana*); the Magnolia (*D. magnolia*), Black-throated Green (*D. virens*), and Blackburnian (*D. fusca*) warblers may occur in lower numbers during outbreaks because of increased competition with these budworm specialists. Thus, we predicted that the number of fall vagrant Tennessee, Cape May, and Bay-breasted warblers and Ovenbirds occurring in California are highly positively associated with budworm population density, positively intercorrelated, and negatively associated with numbers of Magnolia, Black-throated Green, and Blackburnian warblers. A 23-year (1972–1994) data set of budworm population densities and vagrant warbler occurrences in California showed that (*i*) budworm population density was an excellent predictor (explaining about 50% of the variance) of numbers of occurrences of the Cape May, Bay-breasted, and Canada warblers; (*ii*) all warbler species tended to co-occur, with numbers of Cape May and Bay-breasted warblers especially highly intercorrelated; and (*iii*) Magnolia Warbler numbers were negatively associated with those of budworm specialists, but Black-throated Green and Blackburnian warblers showed no association.

Résumé : La densité des Parulines obscures (*Vermivora peregrina*), des Parulines tigrées (*Dendroica tigrina*), des Parulines à poitrine baie (*D. castanea*), des Parulines du Canada (*Wilsonia canadensis*) et des Parulines couronnées (*Seiurus aurocapillus*) semble fortement reliée aux épidémies de Tordeuses des bourgeons de l'épinette (*Choristoneura fumiferana*); les Parulines à tête cendrée (*D. magnolia*), les Parulines à gorge noire (*D. virens*) et les Parulines à gorge orangée (*D. fusca*) peuvent être présentes en moins grand nombre lors des épidémies de tordeuses à cause de la compétition accrue que leur font ces consommateurs spécialistes des tordeuses. Nous avons donc posé en hypothèse que les nombres d'individus errants des Parulines obscure, tigrée, à poitrine baie et couronnée présents en Californie en automne sont fortement reliés à la densité des populations de tordeuses, sont fortement interreliés et sont en corrélation négative avec le nombre de Parulines à tête cendrée, à gorge noire et à gorge orangée. Une série de données couvrant 23 ans (1972–1994) de la densité de population des tordeuses et de la présence des parulines errantes en Californie a démontré que (*i*) la densité de population des tordeuses est un excellent indicateur (expliquant environ 50% de la variance) de la présence des Parulines à tête cendrée, à poitrine baie et du Canada; (*ii*) que toutes les espèces de parulines ont tendance à être présentes ensemble, le nombre de Parulines tigrées et le nombre de Parulines à poitrine baie étant particulièrement interreliés; et (*iii*) que le nombre de Parulines à tête cendrée est en en corrélation négative avec le nombre de consommateurs spécialistes de tordeuses, mais que la présence des Parulines à gorge noire et à gorge orangée n'est pas reliée à la présence des espèces consommatrices de tordeuses.
[Traduit par la Rédaction]

Vagrant Cape May Warblers [in northern California] reached a low of three... perhaps illustrative of cyclical populations in Canada. As yet no one has used comparative numbers of vagrants to measure population strength, but this technique may yet show potential.

LeValley and Roberson (1983)

Introduction

The spruce budworm (*Choristoneura fumiferana*), a tortricid moth found in northeastern North America, defoliates fir (*Abies* spp.), spruce (*Picea* spp.), and other boreal conifers. Population levels of this insect are strongly cyclic (Morris 1963; Blais 1983; Sanders 1991), apparently cycle at regular intervals (Royama 1984; Morin et al. 1993), and can reach epidemic levels that can devastate trees in an affected regions if left unchecked by natural predators or other means (Morris 1963; Holling 1988; Sanders 1991). Many insectivorous bird species exhibit functional and numerical responses to such budworm outbreaks (Stewart and Aldrich 1951, 1952; Hensley and Cope 1951; Morris et al. 1958; Crawford and Jennings 1982), especially when large larvae (fifth and sixth instars) and pupae are available (Mook 1963; Jennings and Crawford 1985), leading some authors to suggest biological control of budworms by birds as an important management strategy (Tothill 1923; Dowden et al. 1948, 1950, 1953; Otvos 1979; Takekawa et al. 1982; Wypkema 1982; Jennings and Crawford 1985; Holling 1988). That clear functional responses by birds to increased budworm levels occur is generally not in dispute, and data in support of this view include predation by bird species ranging

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Table 1. Numerical responses by species of wood-warblers (Parulidae) to outbreaks of the spruce budworm reported in, inferred from, or claimed in various studies.

Tennessee Warbler	Magnolia Warbler	Cape May Warbler	Black-throated Green Warbler	Blackburnian Warbler	Bay-breasted Warbler	Ovenbird	Canada Warbler	Reference
P	—	P	—	—	P	—	—	Griscom 1938
P	N	P	—	—	P	—	—	Kendeigh 1947
P	N	0	N	P	P	P	—	Morris et al. 1958
—	—	P	0	0	P	—	—	MacArthur 1958
P	—	P	—	P	P	—	—	Sanders 1970
—	—	—	—	—	—	P	—	Zach and Falls 1975
P	P and N	0	P	P	P	—	—	Gage and Miller 1978
—	—	P	—	—	P	—	—	Morse 1978
P	—	P	N	N	P	—	—	Morse 1989
—	0	0	0	0	0	0	P	Crawford and Jennings 1989

Note: "P" indicates a positive numerical response, "N" a negative numerical response, and "0" no response; a dash indicates that no data were reported.

from woodpeckers (Picidae), chickadees (*Parus* spp.), and Red-breasted Nuthatches (*Sitta canadensis*) to thrushes (Turdidae), vireos (Vireonidae), wood-warblers (Parulidae), and various members of the Fringillidae (Hope 1945; George and Mitchell 1948; Mitchell 1952; Shaub 1956; Morris et al. 1958; Morris 1963; Blais and Parks 1964; Crawford et al. 1983, 1990; Crawford and Jennings 1989).

Whether or not any bird species exhibit a clear numerical response is more contentious (Crawford and Jennings 1989). Some authors suggest that any concomitant increase in bird numbers during a spruce budworm outbreak may be nothing more than coincidental or may be only a local phenomenon (Royama 1984). Nevertheless, various species of American wood-warblers, in particular, apparently undergo dramatic, rather immediate, numerical responses to outbreaks of the spruce budworm, although there is some disagreement as to which species show such a response (Table 1). Even so, there is general agreement (and good evidence) that three species, the Tennessee Warbler (*Vermivora peregrina*), Cape May Warbler (*Dendroica tigrina*), and Bay-breasted Warbler (*D. castanea*), show a positive numerical reponse to spruce budworm outbreaks (Kendeigh 1947; Morris et al. 1958; Morse 1978, 1989). Indeed, these three species, referred to as spruce budworm specialists (Welsh 1985; Morse 1989), can be absent from, or in low densities in, vast regions when budworms are at endemic levels (Griscom 1938; Kendeigh 1947; Sanders 1970). Both the Cape May Warbler and the Bay-breasted Warbler are also said to lay larger clutches during a budworm outbreak (MacArthur 1958). Conversely, there is good evidence that the Magnolia Warbler (*D. magnolia*) shows a negative numerical response (Kendeigh 1947; Morris et al. 1958) either to budworm outbreaks themselves or to increased interspecific competition with those species showing a positive numerical response. The evidence for a positive numerical response by the Ovenbird (*Seiurus aurocapillus*) and Canada Warbler (*Wilsonia canadensis*) is weaker (Morris et al. 1958; Zach and Falls 1975; Crawford and Jennings 1989), as is the evidence for a negative numerical response by the Black-throated Green Warbler (*D. virens*; Morse 1989). Reports on population responses of the Blackburnian Warbler (*D. fusca*) are contradictory, some authors claiming a positive reponse (Morris et al. 1958; Graham 1967; Sanders 1970), oth-

ers claiming a negative one (Morse 1989), and still others saying that there is no response at all (MacArthur 1958; Crawford and Jennings 1989).

The size of the source population explains between 30% (DeSante 1983) and 60% (DeBenedictis 1971) of the variance in number of occurrences of vagrant wood-warblers in California. Assuming that these wood-warbler species do indeed exhibit a numerical response to higher spruce budworm population densities, this response ought to be evident from the number of migrant wood-warblers detected, including the number of vagrants recorded far outside their normal migratory pathways. Thus, it has been hypothesized that species which show a strong positive numerical response to outbreaks of the spruce budworm, particularly the Cape May and Bay-breasted warblers, ought to be recorded with increased frequency in California during periods when budworm population are at high levels, and at lower frequencies when budworms are at endemic levels (Roberson 1980; LeValley and Roberson 1983; Patten and Marantz 1996). This idea is supported by the observation that there is a sharp increase in the number of migrant Cape May and Bay-breasted warblers along the Atlantic coast during a spruce budworm outbreak (Griscom 1950; Stewart and Aldrich 1952).

We used a long-term data set (1972 through 1994 inclusive) to determine whether or not the size of the spruce budworm population was a good predictor of the number of occurrences of vagrant wood-warblers in California. We also examined (*i*) the spatial autocorrelation in budworm population densities, (*ii*) the association between geographic region and vagrant numbers to determine if vagrants originated from locations closest geographically to where they were detected, (*iii*) the intercorrelations of vagrant wood-warbler occurrences, and (*iv*) the potential effects of interspecific competition manifested by elevated population levels of budworm followers supressing population numbers of other wood-warbler species. Because the wood-warbler data we use are not affected by local population shifts, any positive results should be indicative of true numerical responses in these species.

Materials and methods

California records for the Tennessee, Magnolia, Cape May, Black-throated Green, Blackburnian, Bay-breasted, and Canada warblers

Table 2. Spearman's rank autocorrelations for the size of the spruce budworm population in eastern Canada from 1972 to 1994.

	Newfoundland	Nova Scotia	New Brunswick	Quebec
Nova Scotia	0.831 (0.0001)			
New Brunswick	0.571 (0.004)	0.648 (0.0008)		
Quebec	0.904 (0.0001)	0.908 (0.0001)	0.734 (0.0001)	
Ontario	0.676 (0.0004)	0.819 (0.0001)	0.334 (0.119)	0.667 (0.0005)

Note: Values in parentheses are probabilities under the null hypothesis of no association ($n = 23$ years).

and the Ovenbird were obtained from regional reports from the middle Pacific Coast (northern California) and southern Pacific Coast (southern California) published in *American Birds/National Audubon Society Field Notes* and from Roberson (1980). Only records from the fall migration period (mid-August through November) in 1972 through 1994 inclusive were used. Some additional unpublished information was obtained from data files maintained by the editors of the above-mentioned regional reports (G. McCaskie, D. Roberson, and D. Singer, personal communication in a letter). Because the number of Tennessee Warblers recorded in southern California during the fall of 1985 was not published, and no data on these records were kept (G. McCaskie, personal communication), the number of records from northern California was doubled to provide a total for that year.

Sizes of the spruce budworm population in eastern Canada from 1972 through 1994 inclusive were supplied by the Canadian Forest Service (C.J. Sanders, personal communication in a letter). These population data are for Newfoundland, Nova Scotia, New Brunswick, Quebec, and Ontario.

A canonical correlation analysis between wood-warbler numbers and budworm numbers was conducted, with a redundancy analysis (Tabachnick and Fidell 1983; Rotenberry et al. 1996) to examine the proportion of variance in the wood-warbler data set associated with the budworm data set.

Spearman's rank correlations were calculated to determine (*i*) the degree to which the numbers of vagrant wood-warbler occurrences were intercorrelated, (*ii*) the level of spatial autocorrelation in the spruce budworm population size in eastern Canada, (*iii*) the strength of association between vagrant wood-warbler numbers and budworm population size, and (*iv*) the potential effects of interspecific competition from increased numbers of the Tennessee, Cape May, and Bay-breasted warblers and Ovenbirds on numbers of Magnolia, Black-throated Green, and Blackburnian warblers. For this last analysis, a 1-year lag was introduced into the data under the assumption that numbers of the Magnolia, Black-throated Green, and Blackburnian warblers would be depressed in the year following increases in the numbers of the other species.

A full-model multiple regression was conducted, with spruce budworm population size in eastern Canada as the predictor and the number of vagrants in California of each wood-warbler species as the criterion. Each of these multiple-regression analyses was also performed using a correction for temporal autocorrelation in budworm population densities and wood-warbler occurrences.

In order to consider the effects of observer bias in reporting vagrant numbers in California, simple statistics (mean and range) for the numbers of vagrant wood-warbler occurrences in California were computed, and trends in occurrence were examined using Spearman's rank correlations, with the null hypothesis of no association between the number of annual records and the year of occurrence.

Most statistical analyses were conducted using SAS (SAS Institute Inc. 1996), although some statistics were computed by hand using

procedures described by Tabachnick and Fidell (1983) and Sokal and Rohlf (1995).

Results

The first two canonical variates in the canonical correlation analysis showed a significant amount of shared variance between the budworm and wood-warbler data sets ($R_c^2 = 0.889$, Wilks' $\Lambda = 0.02$, $P < 0.05$). The first canonical variate for the budworm data set was loaded highly with those regions showing the highest spatial autocorrelation in budworm population densities (Table 2), namely Newfoundland ($r = 0.97$), Nova Scotia ($r = 0.91$), and Quebec ($r = 0.93$). The first canonical variate for the warbler data set was associated with those species considered to show a numerical response to budworm population densities, with the Cape May Warbler ($r = 0.58$) and Bay-breasted Warbler ($r = 0.54$) having the highest positive loadings and the Magnolia Warbler showing a large negative loading ($r = -0.41$). Scores for these species on the first canonical variate of the budworm data set are similar, suggesting that the Cape May ($r = 0.55$) and Bay-breasted ($r = 0.51$) warblers do show a strong positive numerical response (the loading for the Black-throated Green Warbler, $r = 0.44$, was also fairly high), whereas the Magnolia Warbler ($r = -0.38$) shows a strong negative response. Redundancy analyses with the canonical variates indicated that the budworm data set extracted 57.8% of the variance in the wood-warbler data set, but that the wood-warbler data extracted only 14.0% from the budworm set. Thus, whereas much of the variance in overall wood-warbler occurrence can be accounted for by budworm population size, little about the budworm populations can be accounted for by wood-warbler numbers.

Occurrences of vagrant Cape May and Bay-breasted warblers were significantly positively correlated with spruce budworm population densities (Table 3, Fig. 1). Tennessee Warbler occurrences showed only mild associations with spruce budworm population densities, none of which were significant. Associations between budworm population density and frequency of occurrence of Cape May and Bay-breasted warblers was strongest with budworm population densities in Ontario (Table 3). Occurrences of the Magnolia Warbler, a potential competitor of the budworm specialists, showed a significant negative association with budworm densities (Table 3, Fig. 1). With a lag introduced, the Magnolia Warbler showed a marginally significant negative association with the Bay-breasted Warbler (Table 4). By contrast, Black-throated Green and Blackburnian warbler occurrences showed no association with Cape May and Bay-breasted warbler occurrences once a lag was introduced.

Spruce budworm population size was a good predictor of vagrant numbers in both the Cape May Warbler ($R^2 = 0.49$, $F_{[5,17]} = 3.27$, $P = 0.03$) and Bay-breasted Warbler ($R^2 = 0.40$, $F_{[5,17]} = 2.32$, $P < 0.09$), but was not a good predictor of vagrant occurrences in any other wood-warbler species ($R^2 < 0.40$, $P > 0.10$ for each of the other five species). With corrections made for temporal autocorrelation, spruce budworm population size explained roughly 50% of the variance in the numbers of vagrant Cape May ($R^2 = 0.49$, $F_{[4,16]} = 3.87$, $P < 0.03$), Bay-breasted ($R^2 = 0.52$, $F_{[4,16]} = 4.38$, $P < 0.02$), and Canada warblers ($R^2 = 0.51$, $F_{[4,16]} = 4.15$, $P < 0.03$) recorded in California, compared with less than 40% for the Black-throated

Fig. 1. Relationship between the density of the spruce budworm population, averaged across five provinces, and occurrences of three wood-warbler species in California. Note the tendency for the Cape May and Bay-breasted warblers to track budworm density and the inverse tendency in the Magnolia Warbler.
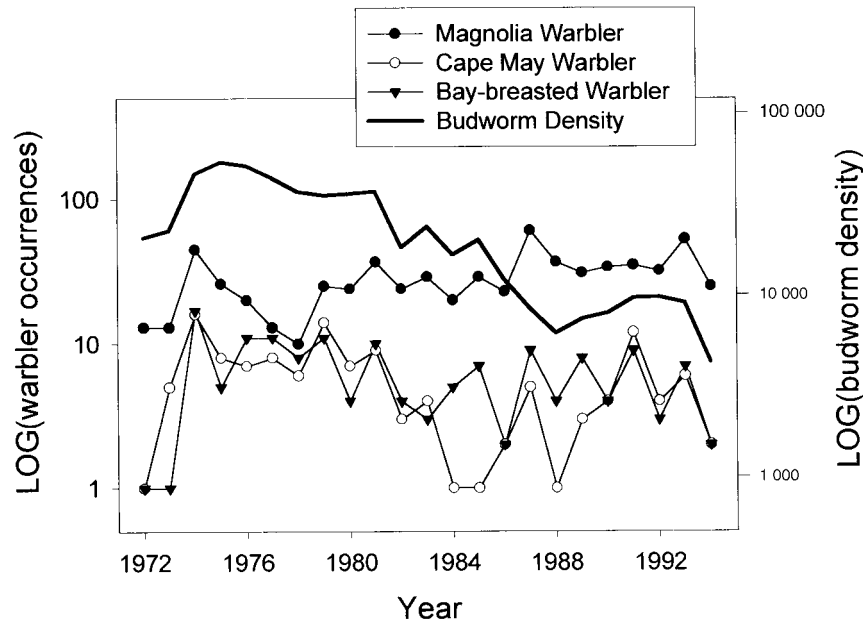

Table 3. Spearman's rank correlations for vagrant occurrences of seven species of wood-warblers in California from 1972 to 1994 against the size of the spruce budworm population in eastern Canada.

	Newfoundland	Nova Scotia	New Brunswick	Quebec	Ontario
Tennessee Warbler	0.236	0.292	0.063	0.293	0.275
	(0.277)	(0.177)	(0.774)	(0.175)	(0.204)
Magnolia Warbler	–0.450	–0.451	–0.294	–0.436	–0.195
	(0.031)	(0.031)	(0.174)	(0.038)	(0.374)
Cape May Warbler	0.598	0.505	0.194	0.517	0.673
	(0.003)	(0.014)	(0.376)	(0.012)	(0.0004)
Black-throated Green Warbler	0.574	0.403	0.283	0.441	0.327
	(0.004)	(0.057)	(0.191)	(0.035)	(0.128)
Blackburnian Warbler	0.111	0.084	–0.151	0.014	0.295
	(0.613)	(0.702)	(0.492)	(0.950)	(0.172)
Bay-breasted Warbler	0.409	0.402	0.014	0.383	0.517
	(0.053)	(0.058)	(0.949)	(0.071)	(0.012)
Ovenbird	0.058	0.088	–0.156	0.072	0.181
	(0.794)	(0.688)	(0.479)	(0.743)	(0.409)
Canada Warbler	0.126	0.016	–0.137	0.056	–0.006
	(0.567)	(0.940)	(0.532)	(0.801)	(0.978)

Note: Values in parentheses are probabilities under the null hypothesis of no association ($n = 23$ years).

Green Warbler ($R^2 = 0.39$, $F_{[4,16]} = 2.54$, $0.05 < P < 0.10$) and less than 25% for the Tennessee, Magnolia, and Blackburnian warblers and the Ovenbird.

Although most vireos and wood-warblers from the south-eastern United States have been recorded in California with significantly increasing frequency (Patten and Marantz 1996), such is not the case for all but one of the northeastern wood-warbler species considered herein (Table 5). However, as with the southeastern vireos and wood-warblers (Patten and Marantz 1996), vagrant occurrences of these wood-warbler species from northeastern North America tend to be highly intercorrelated

(Table 6), even among species said to show a negative response to budworm followers.

Discussion

If any of the wood-warbler species we considered showed a positive numerical response to spruce budworm outbreaks, then we predicted (*i*) significant positive correlations between wood-warbler occurrences and budworm population densities, this effect becoming apparent in the first fall following the beginning of a budworm outbreak, (*ii*) that budworm

Table 4. Spearman's rank correlations for occurrences in California of vagrants of seven species of wood-warblers that breed in spruce forest in northeastern North America.

	Tennessee Warbler	Cape May Warbler	Bay-breasted Warbler	Ovenbird
Magnolia Warbler	−0.257	−0.218	−0.375	−0.133
	(0.248)	(0.330)	(0.086)	(0.554)
Black-throated Green Warbler	0.116	0.271	0.188	−0.142
	(0.609)	(0.222)	(0.403)	(0.527)
Blackburnian Warbler	−0.092	0.219	0.023	0.139
	(0.682)	(0.328)	(0.919)	(0.538)

Note: Data for the Magnolia, Black-throated Green, and Blackburnian warblers were shifted forward by 1 year (1973–1994 data were used), allowing a time lag for responding to larger populations of the Tennessee, Cape May, and Bay-breasted warblers and the Ovenbird (1972–1993 data were used). Values in parentheses are probabilities under the null hypothesis of no association ($n = 22$ years).

Table 5. Fall occurrences in California from 1972 to 1994 of vagrants of seven species of wood-warblers (Aves: Parulidae) that breed in spruce forest in northeastern North America.

	Mean	Range	Trend (r_s)	P
Tennessee Warbler	57.3	21–107	−0.06	>0.75
Magnolia Warbler	28.6	10–61	0.54	<0.01
Cape May Warbler	5.6	0–16	−0.34	>0.10
Black-throated Green Warbler	8.6	2–17	−0.38	0.07
Blackburnian Warbler	16.9	8–30	0.12	>0.55
Bay-breasted Warbler	6.3	0–17	−0.16	>0.45
Ovenbird	14.3	4–26	0.16	>0.45
Canada Warbler	8.5	2–17	0.03	>0.95

population size would be a good predictor of the number of vagrant wood-warbler occurrences, and (*iii*) significant positive correlations among the numbers of occurrences of vagrants of these species. We further predicted that (*iv*) competing wood-warbler species that are not budworm specialists would be recorded with decreasing frequency, and (*v*) vagrant occurrences of budworm specialists in California would be mostly highly correlated with budworm population densities in Ontario and least with those in the Maritime Provinces. Because various studies have demonstrated that the Tennessee, Cape May, and Bay-breasted warblers show a strong positive numerical response (Table 1), we predicted that relationships would be strongest with these three species, particularly the last two, given their much greater percentage range overlap with the spruce budworm. We found at least partial support for all of these predictions.

Our findings support the hypothesis that vagrant numbers of two of these three budworm specialists (Morse 1989), the Cape May Warbler and the Bay-breasted Warbler, are strongly associated with spruce budworm population density (Roberson 1980; LeValley and Roberson 1983). Because the numbers of fall vagrants reported over the 23-year period have remained fairly constant, we are confident that this conclusion is not the result of observer bias. When corrected for temporal autocorrelation, spruce budworm population size was also a good predictor of the number of Canada Warbler occurrences in California, lending some support to the finding that this species also shows a numerical response to outbreaks (Crawford and Jennings 1989). Although occurrences of the Tennessee

Warbler were significantly positively correlated with occurrences of the Cape May and Bay-breasted warblers, their occurrences were independent of spruce budworm population densities. The Tennessee Warbler occupies a geographic range substantially larger than that of the spruce budworm; thus, such a finding is not surprising, as budworm numbers can affect only a portion of the warbler's population dynamics.

The eight wood-warbler species we considered tended to co-occur, although correlations in occurrences within the budworm specialists and within the non-budworm followers were strongest. Some associations that were particularly strong would be predicted from the hypotheses presented, e.g., between Cape May and Bay-breasted warbler occurrences and between Black-throated Green and Blackburnian warbler occurrences, but others of equal magnitude ran counter to predictions, e.g., between Cape May and Black-throated Green warbler occurrences. There are two, non-mutually exclusive explanations for this result. Firstly, there is probably a substantial geographic and climatic component to vagrancy patterns and numbers of occurrences (DeSante 1983), so species that occupy a given geographic region tend to co-occur as vagrants (Patten and Marantz 1996).

Secondly, it has been found that many bird species, not just budworm specialists, show some level of functional response to outbreaks of the spruce budworm (Hope 1945; Kendeigh 1947; George and Mitchell 1948; Mitchell 1952; Gage and Miller 1978; Crawford and Jennings 1982, 1989), which could result in somewhat higher reproductive success during outbreak years (i.e., a weak numerical response). Thus, although Cape May and Bay-breasted warblers apparently show a strong numerical response to spruce budworm outbreaks in terms of increased clutch size (MacArthur 1958), each of the other wood-warbler species may have slightly higher fledging success during outbreaks, resulting in an elevated migrant pool that fall. Because most fall vagrants are birds attempting their first southward migration (DeSante 1973), such an increase in the migrant pool should lead to an increased number of vagrant occurrences.

Whichever the case may be, the level of increase in budworm followers can be detected over and above whatever factors affect all of these species in common. Thus, we concur that "an increase in the population of bay-breasted, Tennessee, and Cape May warblers has some value as an indicator of spruce budworm outbreaks" (Kendeigh 1947, p. 94). Furthermore, fluctuations in the numbers of migrant budworm

Table 6. Spearman's rank correlations for fall occurrences in California from 1972 to 1994 of vagrants of seven species of wood-warblers that breed in spruce forest in northeastern North America.

	Tennessee Warbler	Magnolia Warbler	Cape May Warbler	Black-throated Green Warbler	Blackburnian Warbler	Bay-breasted Warbler	Ovenbird
Magnolia Warbler	0.381 (0.073)						
Cape May Warbler	0.472 (0.023)	0.159 (0.469)					
Black-throated Green Warbler	0.242 (0.266)	0.100 (0.649)	0.612 (0.002)				
Blackburnian Warbler	0.464 (0.026)	0.472 (0.023)	0.527 (0.010)	0.608 (0.002)			
Bay-breasted Warbler	0.492 (0.017)	0.272 (0.208)	0.676 (0.0004)	0.397 (0.060)	0.575 (0.004)		
Ovenbird	0.418 (0.047)	0.476 (0.022)	0.283 (0.190)	0.357 (0.095)	0.472 (0.023)	0.192 (0.381)	
Canada Warbler	0.346 (0.105)	0.213 (0.330)	0.101 (0.646)	0.139 (0.526)	0.191 (0.383)	0.370 (0.082)	-0.043 (0.847)

Note: Values in parentheses are probabilities under the null hypothesis of no association ($n = 23$ years).

specialists may actually be a better predictor of numerical response to budworm population density than would local breeding bird surveys, as these fluctuations are not affected by smaller scale functional responses to budworms.

Our evidence for interspecific competition is circumstantial, although results for the Magnolia Warbler are in agreement with the findings of Kendeigh (1947, p. 97), who noted: "During the development of these unusually dense bird populations, the bay-breasted, Tennessee, and Cape May warblers increase in abundance at the expense of several other species of warblers, of which the magnolia warbler may actually decrease." We did not detect negative associations between increased numbers of budworm specialists and the occurrences of the Black-throated Green and Blackburnian warblers, even when these two species were allowed a 1-year lag during which to respond. Indeed, spruce budworm population levels were actually a marginally good predictor of Black-throated Green Warbler numbers in California, despite the fact that this species is supposed to show a negative numerical response to outbreaks (Morris et al. 1958; Morse 1989). Because a competitive reaction requires that some resources be in short supply and because food during a budworm outbreak could not be that limiting a resource (Graham 1967; Royama 1984), the factors leading to the reduction in the numbers of Magnolia Warblers or any other species are not clear. Possibilities include differences in functional responses to high budworm population densities, in nesting and foraging strata, and (or) in nesting season (Graham 1967); furthermore, budworms may have a strong effect on other foliage-eating prey, and some wood-warbler species may subsist better on a monotonous diet.

In conclusion, we found spruce budworm population density in eastern Canada to be an excellent predictor of numbers of fall vagrant Cape May and Bay-breasted warblers in California. The Magnolia Warbler appeared to respond negatively to budworms, whereas trends were less clear or nonexistent for the Tennessee, Black-throated Green, and Blackburnian warbers and the Ovenbird. We propose that censuses of vagrant or migrant birds rather than of breeding birds provide a more direct measure of the true population-level effects of budworms. Because the vast majority of vagrants are first-year birds, and a true numerical response should be initially reflected in an increase in reproductive output, numbers of vagrant budworm specialists should accurately reflect increases in reproductive success as a result of increases in their food source during budworm outbreaks. Similarly, fall migrant (or vagrant) bird counts should provide better estimates of numerical responses than breeding bird surveys because (*i*) bias in estimates of bird numbers resulting from local movement to areas of high budworm density (i.e., functional responses) is eliminated and (*ii*) birds are sampled after their exposure to budworms for a summer, rather than during breeding, when populations show the effects of mortality in winter and during spring migration.

Acknowledgements

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