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### Patterns of Consumption and Diet Differentiation for Three Breeding Warbler Species During a Spruce Budworm Outbreak

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**ABSTRACT.**—Diets of three warbler species were analyzed during a spruce budworm outbreak in the boreal forest of northern Ontario. Beetles constituted a large portion of the food items consumed by Cape May (*Dendroica tigrina*), Bay-breasted (*Dendroica castanea*), and Tennessee (*Vermivora peregrina*) warblers early in the breeding season (7–11 June), and caterpillars were the most frequently used food category shortly later (18–24 June). Differences in diet served to differentiate the warbler species in the earlier period when Bay-breasted Warblers consumed more beetles, Tennessee Warblers consumed more caterpillars, and Cape May Warblers consumed more flies than the other species. Only Bay-breasted Warblers' continuing preference for beetles differentiated the warblers' diets in the later period. Food-niche overlaps increased for two of the three warbler species pairs between the two periods in June, but there was no change in the overlap between Bay-breasted and Cape May warbler diets.

**RESUMEN.**—Se analizaron las dietas de tres especies de parúlidos insectívoros durante la erupción del gusano del abeto en los bosques boreales del nor-

te de Ontario, Canadá. Durante el primer período de la época reproductiva (7–11 junio), una gran proporción de los ítems alimenticios consumidos por *Dendroica tigrina*, *D. castanea* y *Vermivora peregrina* consistió en escarabajos, mientras que más tarde (18–24 junio) el ítem alimenticio consumido con mayor frecuencia fue orugas. Las diferencias en la dieta sirvieron para diferenciar las tres especies de parúlidos durante el periodo inicial, cuando *D. castanea* consumió más escarabajos, *V. peregrina* consumió más orugas y *D. tigrina* consumió más moscas con relación a las otras especies. Durante el periodo más tardío, la dieta sólo se diferenció entre las tres especies por la continuación de la preferencia de escarabajos por parte de *D. castanea*. La superposición de los nichos alimenticios aumentó para dos de los tres pares de especies entre los dos períodos en junio, pero no hubo cambios en la superposición de la dieta entre *D. castanea* y *D. tigrina*.

There have been few systematic studies of warblers' diets during their breeding season. Historical reports were anecdotal, based on collection of a limited number of individual birds and generating a simple list of food items found in gizzards (e.g. Bent 1963). Busby and Sealey (1979), Holmes and Robinson (1988), and Cooper et al. (1990) performed quan-

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titative studies of Neotropical migrants' diets during the breeding season, but none included the boreal forest warblers that were the focus of this study. Current knowledge of the diets of Cape May (*Dendroica tigrina*; Baltz and Latta 1998) and Bay-breasted (*D. castanea*; Williams 1996) warblers during the breeding season comes from descriptive reports identifying primarily lepidopteran larvae and other invertebrates. Quantitative analysis of the diets of these two warbler species relies almost exclusively on research by Crawford and Jennings (1989) and Mitchell (1952) which provide little data on consumption of food items other than spruce budworm larvae. Quantitative accounts of the Tennessee Warbler's (*Vermivora peregrina*) diet (Rimmer and McFarland 1998) are largely based on data from McMartin (1996). Little further information exists regarding the diets of these three warbler species.

Efforts to define the ecological niches of warbler species have traditionally focused on foraging behavior and habitat use (MacArthur 1958), in part because of difficulties associated with diet studies. Coarse-scale habitat measures, such as forest structure or tree species composition, can be considered static during a breeding season, whereas abundance of food resources for birds may change over time so that there is little reason to assume that extent of food niche overlap is static. Thus, we do not know if diets of warbler species are differentiated during the breeding season or if diets change within that brief time. Existence of diet differentiation among boreal forest warblers would provide an important new insight into coexistence of ecologically similar species. We therefore examined the composition of Tennessee, Cape May, and Bay-breasted warblers' diets, measured food-niche overlap among the warbler species, and determined if diets changed within the breeding season. We tested the hypothesis that the diets of the three warbler species are differentiated by the type of prey items they consume during the breeding season.

**Study Area and Methods.**—The diets of Tennessee, Cape May, and Bay-breasted warblers were examined during a spruce budworm outbreak near Longlac, Ontario (49°47'N, 86°32'W). Those warbler species were selected because they were common at the study site, and because they are important predators of large spruce budworm larvae (Morris et al. 1958, Jennings and Crawford 1985). The boreal forest in that area is predominantly balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*) with extensive aspen stands (*Populus* spp.), and smaller numbers of jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), and tamarack (*Larix laricina*). This study was conducted on three 300 ha forest blocks that consisted of at least 50% balsam fir and white spruce—primary host trees of spruce budworm. It was also part of a larger project that concluded no changes in diets, foraging heights or locations, or foraging maneuvers by

Tennessee and Bay-breasted warblers were attributable to insecticide applications (McMartin 1996). Data from both treated and control blocks were combined and are used here.

Territorial males were collected under a Canadian Wildlife Service permit with the help of recorded songs of conspecific males. Selecting only males eliminated possible biases from diet differences based on sex. The first sample from 7–11 June 1994 corresponded to the early breeding season when pair formation and nest building were occurring. The second sample from 18–24 June 1994 corresponded to the mid-breeding season when egg-laying and incubation were underway. The study concluded before most adults began feeding young because insecticide-induced reductions in caterpillar populations were expected to have the greatest effect on warblers during the second sampling period. One milliliter of 70% ethanol was injected into the digestive tract of each bird through the esophagus to prevent continued digestion of the gizzard contents. The carcasses were stored in portable coolers in the field, and gizzards were removed and stored in alcohol later the same day. After completion of field work, gizzard contents were flushed out, and individual food items were counted and identified to order. Even though gizzard contents were generally fragmented, it was possible to estimate minimum number of each type of food item present by counting heads, head capsules and whole bodies, and by matching pairs of wings, elytra, and mandibles. Food items were assumed to represent prey taken sometime during the last 2 h a bird lived because gizzards of small insectivorous birds are almost empty 2 h after feeding if no further food is taken (Mook and Marshall 1965, Custer and Pitelka 1974). Counts of food category items were highly skewed, and could not be normalized, so a Kruskal-Wallis test was used to determine if the diet of each warbler species changed between the early and midbreeding season periods.

Food-niche breadth was calculated for each warbler species during the early and midbreeding season periods using Levin's standardized measure,  $B_A$ . Morisita's index of similarity ( $C$ ) was used to provide an unbiased measure of food-niche overlaps between pairs of species (Krebs 1989). Jack-knife estimates of standard deviation were used to determine if changes in niche overlap between the two collection periods were significant. We used logistic regression to determine if diets of the three warbler species could be differentiated by their consumption of items from different food categories during the 7–11 June and 18–24 June periods. SAS proc CATMOD (SAS Institute 1985) provided a distribution-free statistical test of diet differentiation for highly skewed data that made distribution-sensitive tests inappropriate.

**Results.**—Over 2,000 food items were classified to order from 283 warbler gizzards that were collected

TABLE 1. Diet differentiation among Bay-breasted, Cape May, and Tennessee warblers during early (7–11 June) and mid-breeding season (18–24 June) in northern Ontario, based on maximum-likelihood analysis of variance. Mean number of food items per gizzard are shown, with percentages in parentheses constituting each food category for each species.

	$\chi^2$	<i>P</i>	Mean number of food items per gizzard (% of total)		
			Bay-breasted	Cape May	Tennessee
<b>Early breeding season</b>					
Number of gizzards			49	25	45
Coleopteran adults	12.22	0.0022	5.3 (75.7%)	3.9 (52.7%)	2.7 (41.5%)
Lepidopteran larvae	12.96	0.0015	0.4 (5.7%)	1.3 (17.6%)	3.1 (47.7%)
Diptera	8.76	0.0125	0.6 (8.6%)	1.4 (18.9%)	0.3 (4.6%)
Araneae	0.97	NS	0.2 (2.9%)	0.2 (2.7%)	0.1 (1.5%)
Other <sup>a</sup>	1.52	NS	0.5 (7.1%)	0.6 (8.1%)	0.3 (4.6%)
<b>Mid-breeding season</b>					
Number of gizzards			59	45	60
Coleopteran adults	15.11	0.0005	2.1 (29.6%)	0.8 (8.8%)	0.5 (5.8%)
Lepidopteran larvae	5.47	NS	4.1 (57.7%)	7.2 (79.1%)	6.9 (80.2%)
Diptera	3.30	NS	0.4 (5.6%)	0.4 (4.4%)	0.2 (2.3%)
Araneae	3.67	NS	0.2 (2.8%)	0.5 (5.5%)	0.3 (3.5%)
Other	2.51	NS	0.3 (4.2%)	0.2 (2.2%)	0.7 (8.1%)

<sup>a</sup> Other food includes Homoptera, Hymenopteran adults and larvae, Hemiptera, Coleopteran larvae, Gastropoda, Odonata, Trichoptera, and Neuroptera.

(Table 1). A larger number of prey items may have been present, but the state of fragmentation of arthropods found in the warblers' gizzards made counting and identification of additional prey items unreliable. Of those food items, 85.7% were either coleopteran adults or lepidopteran larvae, and Diptera and Araneae accounted for a further 8.8% of the total. Nine other food categories represented in very low numbers were pooled as "other food" for statistical analysis.

Of the five major food categories, Bay-breasted Warblers consumed predominantly coleopteran adults (75.7%) early in the breeding season, with no other food category constituting more than 10% of the total (Table 1). Just two weeks later, the diet consisted of 29.6% coleopteran adults and 57.7% lepidopteran larvae. The increase in consumption of lepidopteran larvae ( $F = 80.97$ ,  $P = 0.0001$ ) and decrease in consumption of coleopteran adults ( $F = 49.86$ ,  $P = 0.0001$ ) between 7–11 June and 18–24 June were statistically significant, whereas consumption of Diptera also declined significantly ( $F = 4.21$ ,  $P = 0.0426$ ).

Cape May Warblers' diet was less dominated by coleopteran adults early in the breeding season (52.7%) than the diet of Bay-breasted Warblers, but Cape May Warblers shifted to a diet of 79.1% lepidopteran larvae during the midbreeding season (Table 1). There were significant decreases in consumption of coleopteran adults ( $F = 57.90$ ,  $P = 0.0001$ ) and increases for lepidopteran larvae ( $F = 92.45$ ,  $P = 0.0001$ ), whereas consumption of Diptera ( $F = 5.99$ ,  $P = 0.0170$ ) and other food also declined ( $F = 7.42$ ,  $P = 0.0082$ ) between the early and midbreeding season.

Early in the breeding season, coleopteran adults represented 41.5% of the Tennessee Warblers' diet, whereas lepidopteran larvae were 47.7% (Table 1). As with the other two species, use of coleopteran adults dropped significantly ( $F = 58.65$ ,  $P = 0.0001$ ), whereas consumption of lepidopteran larvae increased to 80.2% of the diet in the later period ( $F = 58.11$ ,  $P = 0.0001$ ).

Standardized food-niche breadth for Bay-breasted Warblers doubled from early to midbreeding season, but declined by two-thirds for Cape May and Tennessee warblers over the same period (Table 2a). Cape May and Bay-breasted warblers' diets overlapped more than other warbler pairs in the early breeding season, whereas Cape May and Tennessee warbler diets overlapped most in the midbreeding season (Table 2b). Food-niche overlap between Bay-breasted and Cape May warblers remained static from early to midbreeding season, but overlaps between other pairs of warbler species increased over the two periods. Morisita's *C* rose from 0.43 in the early period to 0.60 in the later period for Bay-breasted and Tennessee warblers, and from 0.44 to 0.78 for Cape May and Tennessee warblers.

The warbler species differed in their consumption of coleopteran adults ( $\chi^2 = 12.22$ ,  $P = 0.0022$ ), lepidopteran larvae ( $\chi^2 = 12.96$ ,  $P = 0.0015$ ) and Diptera ( $\chi^2 = 8.76$ ,  $P = 0.0125$ ), in the early breeding season (Table 1). Bay-breasted Warblers consumed more beetles, Cape May Warblers consumed more flies, and Tennessee Warblers consumed more caterpillars than other warbler species between 7–11 June. Later in the breeding season, from 18–24 June, only cole-

TABLE 2. Food-niche metrics including (a) Levin's standardized niche breadth ( $B_A$ ), and (b) Morisita's measure of overlap ( $C \pm SD$ ) between pairs of warbler species during the early and mid-breeding season.

	Early breeding season (7–11 June)	Mid-breeding season (18–24 June)
<b>(a) Standardized food niche breadth, Levin's <math>B_A</math></b>		
Bay-breasted Warbler	0.162	0.329
Cape May Warbler	0.447	0.135
Tennessee Warbler	0.369	0.125
<b>(b) Paired comparisons, Morisita's <math>C</math></b>		
Bay-breasted: Cape May	0.604 $\pm$ 0.006	0.604 $\pm$ 0.006
Bay-breasted: Tennessee	0.434 $\pm$ 0.006	0.603 $\pm$ 0.006
Cape May: Tennessee	0.441 $\pm$ 0.010	0.777 $\pm$ 0.008

opteran adults ( $\chi^2 = 15.11$ ,  $P = 0.0005$ ) served to differentiate the warblers' diets with Bay-breasted Warblers again consuming beetles more than the other warbler species (Table 1).

**Discussion.**—Diet differentiation among warblers was extensive early in the breeding season, when there were differences in use of beetles, caterpillars, and flies by the three species. Differences in diet composition reflect to some extent differences in foraging strategies and locations used by the warblers. For example, Tennessee Warblers' consumption of caterpillars in that period can be explained in part by extensive probing of alder (*Alnus* spp.) foliage for leaf-rolling caterpillars (McMartin 1996). That is consistent with Graber and Graber's (1983) record of extensive probing for leafrollers by Tennessee Warblers during spring migration. Bay-breasted Warblers' use of beetles and Cape May Warblers' use of flies from 7–11 June could reflect their tendencies to forage in different locations within the canopy (MacArthur 1958), but additional research would be needed to confirm differences in prey-type abundance among microsites. Relatively limited use of lepidopteran larvae early in June, especially by Cape May and Bay-breasted warblers, may be explained in part by spruce budworm phenology. The smaller instars of spruce budworm that were present during this period are rarely consumed by birds, either because they are hidden within buds, avoided or simply not detected (Jennings and Crawford 1985, Morse 1989) and therefore may not qualify as a potential food resource.

Later in the breeding season, only the use of beetles differed among the three species, with Bay-breasted Warblers maintaining their preference for beetles. That may be attributed to the dominant use of lepidopteran larvae by all three species during that period, and to the superabundance of spruce budworm larvae even after insecticide application reduced the number of lepidopteran larvae by 86% on one treated block (McMartin 1996). Outbreak populations of spruce budworm can be over 70 $\times$  background levels in nonepidemic years (Crawford and Jennings 1989), and the spruce budworm pop-

ulation at Longlac was expected to be at an epidemic level. As a result, large, accessible spruce budworm larvae were probably still abundant in late June, and were not a limiting resource even though the total number of caterpillars had dropped. All three warbler species included caterpillars in their fundamental niches, but did not compete for a resource that was effectively unlimited, so that there was no need to segregate diet among those species while the budworm larvae were still available. The different extent of diet differentiation between the two periods suggests that selection of food categories is less likely to be meaningful as a dimension of niche definition when a major food resource is superabundant.

The changes in food consumption between 7–11 June and 18–24 June were remarkable, with increasing consumption of lepidopteran larvae for all three warbler species. Coleopteran adults formed a large part of the diets of all three warbler species early in the breeding season, but their importance as a food resource was much reduced just two weeks later. Diet overlaps in late June were over the 0.6 level considered to be biologically significant (Zaret and Rand 1971); however, it is not surprising to find high food-niche overlaps at the same trophic level during a brief period when one high-energy food resource, spruce budworm larvae, is readily available in great numbers. These boreal forest warblers all exploited that resource while it was abundant.

An in-depth understanding of use of food resources by coexisting warbler species is only starting to be revealed, and our results show that analysis of warbler diets during the breeding season requires a dynamic approach. Relative use of different food resources changes over a short time, and as a result food-niche overlaps among warblers change, at least in boreal forest habitat where an insect pest has reached unusually high densities. Diet serves as a niche dimension at some times, but can be less meaningful when one food resource is superabundant. Those changes highlight the complexity of diet analysis for the three warbler species.

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