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SPRUCE BUDWORM AND OTHER LEPIDOPTEROUS PREY OF EUMENID WASPS (HYMENOPTERA: EUMENIDAE) IN SPRUCE-FIR FORESTS OF MAINE

Judith A. Collins¹ and Daniel T. Jennings²

ABSTRACT

Three species of eumenid wasps, *Ancistrocerus adiabatus*, *Ancistrocerus antilope*, and *Euodynerus leucomelas*, accepted and provisioned trap-nesting blocks with lepidopterous larvae. A pyralid, *Nephotyryx* sp., was the most commonly provisioned prey. *A. adiabatus* and *E. leucomelas* preyed on late instars of the spruce budworm, *Choristoneura fumiferana*; however, budworms accounted for only 6% of the provisioned prey. Estimates of budworm population densities before and after wasp predation, and subsamples of provisioned prey indicated no significant reductions ($\bar{x} = 0.065\%$) in budworm populations attributable to trap-nesting wasps.

Natural enemies of the spruce budworm (SBW), *Choristoneura fumiferana* (Clemens), include solitary trap-nesting wasps of the family Eumenidae (Fye 1962, 1965; Jennings and Houseweart 1984; Collins and Jennings, 1987). Jennings and Houseweart (1984) noted that late instars of the spruce budworm constituted 3–38% of the total observed prey of eumenid wasps in strip-clearcut spruce-fir stands in northern Maine. More recently, our studies in Penobscot County, Maine (Collins and Jennings, 1987) indicated that budworm prey were present in 98% of the provisioned blocks and accounted for 94% of the total prey.

In addition to spruce budworm, eumenid wasps provision their nests with a wide variety of other lepidopterous larvae (Krombein 1967 and others). Cooper (1953) found *Ancistrocerus antilope* (Panzer) preying on pyralids and possibly gelechiids. Jennings and Houseweart (1984) observed eumenid wasps preying on lepidopterous larvae of six families in strip-clearcut areas of northern Maine.

The objectives of this study were to determine the species of lepidopterous prey of eumenid wasps in strip-clearcut spruce-fir forests, to determine percentage composition of late instars of the spruce budworm among eumenid prey species, and to estimate the degree of predation by eumenid wasps on late instars of the spruce budworm.

MATERIALS AND METHODS

Study Area. Five strip clearcuts were located on Great Northern Paper Company lands about 60 km northwest of Millinocket, Piscataquis County, Maine. Individual study sites were along the eastern edge of Township 4, Range 12 (WELS), 2.6 km east of Ripogenus

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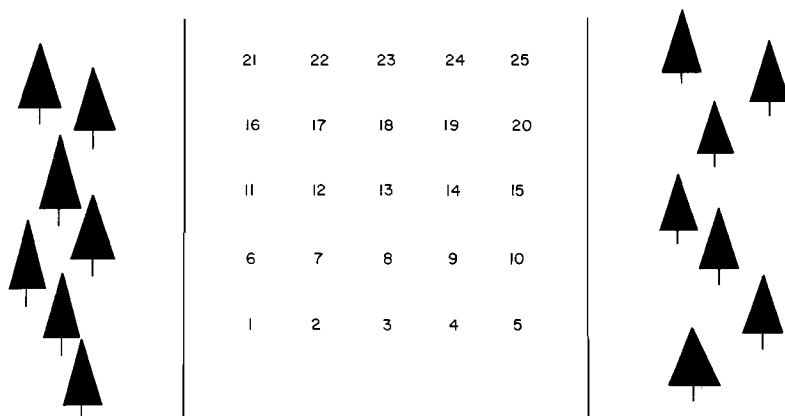


Fig. 1. Plot design in strip clearcut; 5-m spacings between trapping stations, Piscataquis County, Maine, 1984.

Pond, 2.5 km northwest of Soubunge Mountain, and 8.2 km northeast of Weymouth Point (45° 5' N, 69° 13' W). Elevations were about 335 m (USGS Harrington Lake Quadrangle, 1954).

Strip clearcuts consisted of alternating uncut residual spruce-fir stands and clearcut strips from which trees had been harvested and removed in 1977. The strips were oriented east-west (\bar{x} = 94° E; range = 90–96°). The study area was sprayed with Sevin-4-oil³ for spruce budworm suppression in 1981.

Species composition by percentage basal area showed that the study area had a softwood component of red spruce, *Picea rubens* Sargent (69.5%); northern white cedar, *Thuja occidentalis* L. (11.6%); white spruce, *Picea glauca* (Moench) Voss (10.2%); balsam fir, *Abies balsamea* (L.) Miller (4.1%); and white pine, *Pinus strobus* L. (2.7%). Two hardwoods, white birch, *Betula papyrifera* Marsh., and red maple, *Acer rubrum* L., combined, accounted for less than 2% of the total basal area. Tree heights, diameters, and ages of the dominant or codominant softwoods were about equal over all plots; mean height = 12.4 ± 0.4 m, mean dbh = 13.9 ± 1.8 cm, mean age = 62.1 ± 1.5 years.

Experimental Design. At each site, 25 trap-nesting bundles (16 blocks/bundle) (Collins and Jennings 1984) were placed in a 5 × 5-grid with 5-m spacings between bundles (Fig. 1). Each grid was centered in the strip clearcut at least 5 m from forested edges. All traps were hung at a uniform height (0.25 m) from cedar stakes with nesting holes (8 mm diam.) oriented south.

Traps were deployed on 10 June 1984 and examined every 7 or 8 days thereafter for 6 weeks. At each examination, a 30% subsample was taken of recently provisioned blocks; the remaining 70% were left in the field to allow wasp emergence and reproduction. Blocks with emergence holes were also noted and, if subsequently reprovisioned, counted as new nests. Blocks provisioned by trap-nesting bees (pollen and leaf plugs) were removed and replaced with new, unused blocks.

Laboratory Examinations. In the laboratory, provisioned blocks were split longitudinally with the grain using a wood chisel and rubber mallet. Laboratory observations

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included cells per block, wasp developmental stage (egg, larva, pupa), and provisioned prey larvae per cell. Prey larvae were preserved in 75% ethanol and sent to specialists for identification.

Eumenid eggs, larvae, or pupae were removed from provisioned cells and reared individually in 4-dram shell vials at room temperature (ca. 20°C). Moistened tissue paper was placed in the bottom of each vial. When wasp eggs or larvae were reared, several prey larvae including spruce budworms were provided. Vials were closed with cotton plugs and checked periodically for emergence of adult wasps. Diapausing wasp larvae were stored at 5–6°C for 4 mo., then reared at 30°C. Associated Diptera and Hymenoptera were reared by the same methods.

Budworm Population Estimates. Spruce budworm populations were estimated before and after predation by eumenid wasps. The first sample (7–8 June 1984) corresponded with the budworm's L₃-L₄ stages; the second (24–25 July 1984) with the budworm's pupal stage. Ten dominant or codominant red spruce were chosen for sampling from the uncut areas immediately adjacent to each study site. Trees were flagged and numbered (10 trees plot × 2 plots/site × 8 sites = 160 trees/sample). The same trees were used for both population estimates. For each estimate, two midcrown branches (≥ 45 cm) were pruned from each tree (320 branches). Foliated branch lengths and widths were measured (cm) and foliage areas (A) calculated by the formula $A = \text{length} \times \text{width}/2$ (Sanders 1980).

Budworm population densities were calculated as mean larvae and pupae/m² foliage area. Only live larvae and pupae and successfully emerged pupal cases were included in the population estimates. Budworm larval and pupal densities were converted to absolute populations per hectare by the method of Morris (1955). Branch surface area (BSA) per spruce tree was calculated by the formula $BSA = 2.64 + 3.34 \text{ diam. (cm) at breast height (dbh) after Dimond (Jennings et al. 1983)}$.

Based on the 30% subsample of provisioned blocks, we estimated total numbers of spruce budworms in all nesting blocks. We then calculated and converted budworms per nesting block to budworms per meter² of plot area and budworms per hectare. Percent reduction in the budworm population per hectare due to trap-nesting wasps was determined by the formula: provisioned SBW larvae/(initial population density of larvae-pupae) × 100. Although foraging ranges of eumenid wasps generally are unknown, we assumed that most budworm prey came from nearby trees.

Data Analyses. Means and standard errors were calculated for prey per block and per cell, blocks provisioned per week, spruce budworm larval-pupal populations per meter² of foliage area, and percent reduction in spruce budworm population.

Before analyses, all data were subjected to Hartley's Test for homogeneity of variance (Sokal & Rohlf 1981) and appropriate transformations made (natural log). Analysis of variance (ANOVA) ($P = 0.05$) (SAS Institute 1982: 113) and Duncan's multiple range test (var. 0.05) (SAS Institute 1982: 122) were used to compare mean blocks provisioned per week and mean budworm populations (larvae and pupae) among sites.

RESULTS AND DISCUSSION

Nesting-Block Acceptance and Provisioning. Eumenid wasps accepted and provisioned nesting blocks on all sites (Table 1); there was no significant difference in mean blocks provisioned per week among the five sites. Mean blocks per week was lowest on site H, but not significantly.

Predator-Prey Species. Generally, the same kinds of lepidopterous prey were provisioned by eumenid wasps among all sites (Table 2). Some sites had only five prey species; others ranged from six to nine species. Some nesting blocks and cells were provisioned with more than one prey species. Mean prey per block ranged from 1.4 (± 0.1) to 54.5 (± 29.5). *Nephoteryx* group—sp. #1 was the most commonly provisioned prey; 83% of the provisioned blocks had larvae of this pyralid. Only 13 blocks (7.7%) contained spruce budworm larvae; most were fifth and sixth instars.

Table 1. Nesting blocks provisioned (30%) subsample, and mean (\pm SE) blocks provisioned per week, each site.

Site	Total blocks prov.	Mean blocks prov. per week ^a
A	34	5.7 (\pm 2.3)
D	32	5.3 (\pm 2.6)
E	40	6.7 (\pm 2.8)
F	37	6.2 (\pm 2.7)
H	26	4.3 (\pm 1.5)
All	169	5.6 (\pm 1.9)

^aNatural log transformations [$\ln(x + 1)$] before analyses. Weekly means are not significantly different among sites at the $P = 0.05$ level (ANOVA and Duncan's multiple range test [SAS Institute 1982]).

Table 2. Distribution of lepidopterous prey among eumenid nesting blocks by site over all weeks (30% subsample).

Prey species	Blocks/site					Total blocks	Total prey	Mean prey (\pm SE)/blk
	A	D	E	F	H			
<i>Coleotechnites</i> sp.	1				1	2	109	54.5 (\pm 29.5)
<i>Acleris</i> sp. #1					1	1	3	3.0 (\pm 0.0)
<i>Archips rosana</i> (L.)	1				5	6	30	5.0 (\pm 1.3)
<i>Spilonota ocellana</i> (Dennis and Schiffermuller)	1		1	2	1	5	27	5.4 (\pm 2.7)
<i>Nephoteryx</i> group—sp. #1	30	27	33	31	19	140	1316	9.4 (\pm 0.6)
<i>Nephoteryx</i> group—sp. #2	3	2	1	2	1	9	14	1.6 (\pm 0.4)
<i>Nephoteryx</i> group—sp. #3	3	4	8	3	4	22	32	1.4 (\pm 0.1)
<i>Argyrotaenia</i> sp.	1	1	1		3	6	32	5.3 (\pm 2.2)
<i>Choristoneura fumiferana</i>	1	2	2	3	5	13	66	5.1 (\pm 0.9)

Three species of eumenid wasps and nine species of lepidopterous prey were recovered from nesting blocks (Table 3). Two of the eumenid species, *Ancistrocerus adiabatus* (Saussure) and *Euodynerus leucomelas* (Saussure), preyed on larvae of the spruce budworm; however, budworm larvae constituted only 7.2 and 4.7% ($\bar{x} = 6.0\%$) of their total cell provisions, respectively. *E. leucomelas* was our most abundantly reared wasp ($n = 169$) and showed the greatest diversity of lepidopterous prey species ($n = 7$). *A. adiabatus* was next ($n = 9$) with five prey species; *A. antilope* was reared from only one trap provisioned with *Nephoteryx* group—sp. #1.

Budworm Population Reduction. Before predation by eumenid wasps, mean overall budworm population density was 27.2 ± 2.6 larvae/m² of foliage area. After predation, mean overall density was 5.4 ± 0.6 pupae/m² of foliage area. As expected, there was a significant ($P < 0.05$) reduction in budworm population densities between sampling periods over all plots.

Estimates of total spruce budworms provisioned in all blocks ranged from 23 to 77 per site and 575 to 1925 per hectare (Table 4). Absolute populations of spruce budworm

Table 3. Eumenid predator and lepidopterous prey species.

Wasp species	Prey species	Prey (n)	%
<i>A. antilope</i>	<i>Nephoteryx</i> group—sp. #1	8	100.0
<i>A. adiabatus</i>	<i>Choristoneura fumiferana</i>	10	7.2
	<i>Archips rosana</i>	14	10.1
	<i>Spilonota ocellana</i>	2	1.4
	<i>Acleris</i> sp. #1	3	2.2
	<i>Coleotechnites</i> sp.	109	79.0
<i>E. leucomelas</i>	<i>Choristoneura fumiferana</i>	42	4.7
	<i>Argyrotaenia</i> sp.	2	0.2
	<i>Spilonota ocellana</i>	7	0.8
	<i>Archips rosana</i>	10	1.1
	<i>Nephoteryx</i> group—sp. #1	817	90.7
	<i>Nephoteryx</i> group—sp. #2	10	1.1
	<i>Nephoteryx</i> group—sp. #3	13	1.4

Table 4. Estimates of spruce budworm (SBW) provisioned by trap-nesting wasps, and SBW provisioned per meter² of area (400 m²), and per hectare.

Site	Total SBW prov.	SBW/m ²	SBW/ha
A	33	0.082	825
D	30	0.075	750
E	23	0.058	575
F	57	0.142	1425
H	77	0.192	1925

larvae ranged from 1.3 to 2.8 million per hectare (Table 5). Age-interval losses between larval and pupal stages averaged 79.4%.

We estimated that the mean overall reduction in budworm population due to eumenid wasps was only 0.065% (Table 5). Eumenid wasps provisioned < 0.2 spruce budworm prey per meter² of plot area. Watt (1963) estimated that 0.5 spruce budworm larvae per meter² of foliage area must be eaten by predators to account for a decrease in survival rates at low larval densities.

In Maine's strip-clearcut forests, our results indicate that eumenid wasps prey on a variety of lepidopterous species including spruce budworm. The eumenids may be generalist predators that take advantage of whatever larvae are most readily available. In this study, budworm larval populations were low (27.2 larvae/m² of foliage area); predation by eumenid wasps on spruce budworms was similarly low (6% of total prey). Earlier, Jennings and Houseweart (1984) found that spruce budworms comprised 3–38% of the total prey where budworm populations ranged from 74.6 to 100.7 larvae-pupae/m². Likewise, we found that spruce budworms accounted for 94% of total eumenid prey in an area where spruce budworm populations were estimated to be moderately high (Collins and Jennings, 1987).

Table 5. Absolute populations of spruce budworm (SBW) larvae and pupae per hectare, percent age-interval loss (larvae-pupae), estimated SBW provisioned by trap-nesting wasps (TNW) per hectare, and percent reduction SBW by TNW.

Site	Larvae/ha	Pupae/ha	% loss larvae-pupae	TNW prov. (SBW)/ha	% reduction of SBW by TNW
A	1,827,059	385,126	78.9	825	0.057
D	1,355,071	154,994	88.6	750	0.062
E	1,783,791	674,084	62.2	575	0.052
F	2,848,751	515,793	81.9	1425	0.061
H	2,401,345	344,811	85.6	1925	0.094
			$\bar{x} =$ 79.4		$\bar{x} =$ 0.065

Numerous factors need further study, including the extent of eumenid population build-up due to continued availability of trap nests, changes in prey percentages from year to year depending upon host abundance, and foraging ranges of eumenid wasps.

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