Spiders in a fir-spruce biotype: abundance, diversity, and influence on spruce budworm densities

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Results of an intensive 9-year census of the arboreal spider fauna in a fir-spruce forest in northwestern New Brunswick and of a 3-year census in similar biotypes in other parts of the province are reported. A total of 129 species were collected, although only 14, mostly web-spinning species make up the bulk of the spider population. Spider density over the years is remarkably stable in any one biotype. Considerable variation in species composition occurs between biotypes, but the density of the total spider complex in each varies little.

Field experiments with a web-spinning Dictynid and "planted" populations of second-instar budworm larvae show a high level of predation but the wide prey selectivity, population stability, and other traits of the arboreal spiders suggest that, despite their high consumption rate, these predators are unlikely to respond to sudden outbreaks of a particular food item. It is assumed, therefore, that spiders have little influence in moderating the periodic population explosions of the spruce budworm.

Introduction

Spiders occupy many diverse habitats in temperate forests and occur in such numbers that one would expect them to play an important role in the dynamics of many of their prey species. In the Maritime region of eastern Canada, many species are found in association with a major forest pest, the spruce budworm, *Choristoneura fumiferana* (Clem.). The dynamics of this pest have been investigated in the Green River area in northwestern New Brunswick since 1945 (Morris 1963) and a number of workers have investigated the ecological role of spiders. Some aspects of the spider studies have been reported; the taxonomic phase in an unpublished report by the senior author, the predatory behavior of two species (Haynes and Sisojevic 1966, and an unpublished report), and the role of spiders during a budworm outbreak (Loughton et al. 1963; Watt 1963).

Budworm populations collapsed in the Green River area in 1959, and since then we have been investigating the abundance of spiders and their predatory influence on sparse budworm populations. Furthermore, since 1968, we have compared spider abundance and diversity in areas of New Brunswick where chemical sprays have been used to control epidemic budworm populations. These topics are the subject of this paper.

Methods

Plot Description
Sampling was carried out in four areas in New Brunswick (Table 1) and these are briefly described below. Greenbank's (1970) bioclimatic regions are used in the description.

(1) The Green River area is located in northwestern New Brunswick and has a continental climate with relatively cool summers. The plot on which the spiders were studied intensively was in a young, dense, balsam fir stand that originated from a clear-cutting operation. Budworm density on this plot was very low throughout...
the study period but significant increases did occur in the late 1960's. Spider counts were also obtained on four other plots in the Green River area in conjunction with spruce budworm sampling but only brief mention is made of these data.

(2) The Lincoln area is located in central New Brunswick. It has a continental climate with the warmest summers in the region (temperature index, Table 1). The study plot was located in a relatively open, maturing, balsam fir stand and budworm density was very low until a moth flight in 1968 produced a 500-fold increase in 1969. Current shoots were severely defoliated in 1969 and again in 1970.

(3) The Priceville area is also located in central New Brunswick and has a continental climate with moderately warm summers. It has been under severe budworm attack for about a decade, even though insecticides, DDT or fenitrothion, have been applied almost every year for tree protection. The study plot was located in a young balsam fir stand with a relatively high hardwood component and an overstory of scattered mature spruce (Table 1).

(4) The Fundy National Park area is located on the Bay of Fundy and has a cool, maritime climate and a high incidence of fog. The study plot was in a relatively young stand with a high proportion of balsam fir and was under severe attack during the study period.

**Sampling Methods**

The sampling plan developed for the spruce budworm (Morris 1955) was used largely because we wanted to make spider and spruce budworm counts on the same

**TABLE 1**

<table>
<thead>
<tr>
<th>Plots</th>
<th>Temperature index in 1968</th>
<th>% Fir</th>
<th>% Spruce</th>
<th>Stems/acre</th>
<th>% Fir</th>
<th>% Spruce</th>
<th>1-3</th>
<th>4-7</th>
<th>8+</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lincoln</td>
<td>738</td>
<td>90</td>
<td>0</td>
<td>740</td>
<td>0</td>
<td>0</td>
<td>21</td>
<td>68</td>
<td>11</td>
</tr>
<tr>
<td>Fundy</td>
<td>525</td>
<td>86</td>
<td>13</td>
<td>805</td>
<td>122</td>
<td>62</td>
<td>62</td>
<td>34</td>
<td>4</td>
</tr>
<tr>
<td>Priceville</td>
<td>627</td>
<td>70</td>
<td>7</td>
<td>648</td>
<td>62</td>
<td>51</td>
<td>47</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Green River</td>
<td>543</td>
<td>81</td>
<td>9</td>
<td>1838</td>
<td>208</td>
<td>85</td>
<td>15</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

*Cumulative degree-days above 42°F from April 1 to June 21.

Diameter (inches) at breast height.

Fig. 1. Seasonal population density of *C. atriceps* in five crown levels of balsam fir in the Green River area. Level F refers to the base of deep-crowned trees.
affected the sampling method: the foliage. Briefly, the plan consisted of arbitrarily partitioning the living tree crown into four levels, A, B, C, and D from top to bottom, and clipping a set number of branches from the midpoint of each level. In the basic sampling scheme, six branches were taken from each tree in the ratio of two from the A level, two from the B, one from the C, and one D. All six branches, or collection units, were then combined into one sample unit for the tree. There were two variations of this plan: one (Miller, unpublished report) in which one branch only was collected from each tree, from the B level, to permit the sampling of a larger number of trees; the other in which a seventh branch was collected from the bottom branches of deep-crowned trees in order to detect the migration of some species to and from the forest floor. In all cases, the length and mean width of each branch was measured and the area of the branch computed in square feet to standardize the collection unit. The usual sample size was 20 trees for the four-level sample, and 40 trees for the single-level sample. Sample trees of balsam fir were selected from the codominant strata and the branches were carefully clipped from the tree and dropped to a canvas mat. Each branch was beaten vigorously, and the dislodged spiders were collected from the mat with small aspirators and placed in 70% alcohol. In special study plots, samples were drawn weekly throughout the season in order to assess seasonal changes in spider abundance as well as changes in the proportions of immature and mature forms. On other plots, spiders were counted in conjunction with spruce budworm sampling, and this usually meant one population fix per year.

Despite careful collecting techniques, several factors were responsible for reducing sampling accuracy: (1) webs spun between two branches were broken and spiders dropped as single branches were clipped from the tree; (2) the necessity of clipping and dropping foliage from 50-ft standing trees in some plots obviously resulted in the loss of spiders; and (3) the random occurrence of cool, damp weather on some collection dates reduced spider activity and made them more difficult to dislodge from the foliage.

There were two major sources of variation in spider counts that had direct bearing on the sampling method: variation within trees and between trees. Branches were collected from the four crown levels of the tree and these data permitted an analysis of density in different strata of the crown canopy. Furthermore, such samples were collected at intervals between May and September and determine seasonal trends in each level. Figure 1 shows the density of the sheet-spinner, Ceraticelus atriceps (O.P.-Cambridge), in four crown levels during this period. The figure suggests that early in the season this spider, while migrating from overwintering shelters in the litter (Kaston 1948) into the tree canopy, is found only in the lower portions of the crown. Throughout most of the summer, its favorite habitat appears to be the B and C, or midcrown, levels. In the fall, there is a progressive downward migration with individuals first leaving the A level, then the B, the C, and finally the D. Not all species behave in this manner and some prefer the lower rather than the upper crown levels throughout most of the summer. Such spatial gradients in density create sampling problems particularly when, to minimize sampling effort, we selected and sampled only the B crown level in some years. Because we used two sampling schemes, we required a conversion from the B-level density to whole-tree density, and conversion statistics for the whole spider complex and for two important species are shown in Table 2. The $r^2$ values indicate that the B-level density approximates whole-tree density with varying precision according to species and the lower value for Dictyna phylax Gertsch and Ivie doubtless results from its preference for the D- rather than the B-crown level.

Variation between trees was measured only for the more common species such as C. atriceps. The inter-tree variance of this species on balsam fir was determined for three different sizes of sample unit: (1) a sample unit of one branch from the B-crown level; (2) a unit of two branches from the B-level; and (3) a unit of six branches from four crown levels. As expected, the smallest unit had the highest variance and doubling the unit size halved the inter-tree variance. When six branches were collected per tree, the relationship between the inter-tree variance and the mean density of C. atriceps is described by the equation:

$$\text{inter-tree variance} = (1.07) \cdot \overline{x}^{0.762}$$

Sample size, or the required number of trees, can be computed from this equation and Table 3 shows computations for densities ranging from 1.0 to 4.0 C. atriceps per 10 ft$^2$ of foliage. A rule of thumb is that 30 trees would be required to determine the mean density of the more common species of spiders on balsam fir where the sample unit equals six branches per tree drawn from four crown levels. Thus, our sample unit of 20 trees did not produce a high degree of precision even for the more common species of spider and was certainly inadequate for the rare ones.

**Table 2**

<table>
<thead>
<tr>
<th>Spider species</th>
<th>Number of observations</th>
<th>Intercept</th>
<th>Slope</th>
<th>$r^2$ (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. atriceps</td>
<td>18</td>
<td>1.16</td>
<td>0.46</td>
<td>59</td>
</tr>
<tr>
<td>D. phylax</td>
<td>21</td>
<td>0.39</td>
<td>0.79</td>
<td>35</td>
</tr>
<tr>
<td>Total spider complex</td>
<td>20</td>
<td>2.02</td>
<td>0.65</td>
<td>71</td>
</tr>
</tbody>
</table>

*Each observation represents the mean of a 20-tree sample.*

**Table 3**

<table>
<thead>
<tr>
<th>Mean density per 10 ft$^2$</th>
<th>Precision, $%$</th>
<th>Required trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.0</td>
<td>15</td>
<td>48</td>
</tr>
<tr>
<td>2.0</td>
<td>15</td>
<td>20</td>
</tr>
<tr>
<td>4.0</td>
<td>15</td>
<td>9</td>
</tr>
</tbody>
</table>

*$^a$Standard error as percent of the mean.

Note: Sample unit consists of six branches from four crown levels per tree.
Predation Studies

Investigations on spider predation have focused on D. phylax, a small, quite sedentary, web-building spider, averaging 3.0 mm in length. The web of this spider is spun near the periphery of fir and spruce branches, an ideal site to capture migrating second-instar budworm in the spring or wandering first-instar hatchlings during July. It consists generally of a framework of dry lines to which viscid silk is added to form a highly effective adhesive trap. The typical web covers about 2 in. along the length of a shoot or may be placed at the juncture of three peripheral shoots and virtually every needle is in contact with the web. Field experiments were designed and conducted in 1968, 1969, and 1970 to assess the predatory behavior of D. phylax on spruce budworm emerging in the spring. In these experiments, second-instar larvae, just out of hibernacula, were "planted" on fir tree branches, some of which harbored D. phylax (including juveniles and adults) and others which were spider-free. Laboratory experiments on predation were also conducted in which second-instar larvae were dropped directly into the web of partially starved D. phylax.

Results and Discussion

A synopsis of the sampling program in the four study areas is given in Table 4. Some 129 species of spiders in 17 families were identified in the fir-spruce forest and most of these have been listed and keyed elsewhere (Renault, unpublished report). However, the great bulk of the 20,000 spiders examined belonged to nine families and a further taxonomic breakdown shows that 90% or more of these specimens could be grouped into the 14 species listed in Table 5. Nine of the listed species are web-spinners; the remainder are hunting spiders.

Seasonal Trend in Density

We have already referred to C. atriceps (Fig. 1) to exemplify seasonal trend in spider density in different crown levels. Except for very early or very late seasonal counts, its density as well as that of some common species remained relatively constant. For example, Fig. 2 shows the seasonal density of D. phylax for 4 years and the mid-season counts illustrate relative population stability. A wide spectrum of prey, and therefore a steady food supply, probably contributes to this stability. As a result of this phenomenon, we have grouped successive midseason counts into one mean-estimate of density for each year in the following analyses.

Time-Space Trends in Spider Density

The main objective of the spider population study was to detect annual changes in abundance and, if significant, to determine if the changes were related to changes in budworm density. As noted above, this entailed a major sampling

### Table 4

Summary of sampling program at Green River, Lincoln, Fundy, and Priceville, 1962-1970

<table>
<thead>
<tr>
<th>Samples</th>
<th>Total trees sampled</th>
<th>Total spiders collected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plot and year</td>
<td>Number examined per sample</td>
<td></td>
</tr>
<tr>
<td>Green River</td>
<td>1962</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>1963</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>1964</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>1965</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>1966*</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>1967*</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>1968</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>1969</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>1970</td>
<td>3</td>
</tr>
<tr>
<td>Lincoln</td>
<td>1968</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>1969</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>1970</td>
<td>3</td>
</tr>
<tr>
<td>Fundy</td>
<td>1968</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>1969</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>1970</td>
<td>2</td>
</tr>
<tr>
<td>Priceville</td>
<td>1968</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>1969</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>1970</td>
<td>3</td>
</tr>
</tbody>
</table>

*Samples from B-crown level only.

**Note:** Samples taken from all crown levels except where noted.

### Table 5

The most common species of arboreal spiders found in fir-spruce forests in New Brunswick

<table>
<thead>
<tr>
<th>Family</th>
<th>Species Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Araneidae</td>
<td>Araneidae dilata (Hentz)</td>
</tr>
<tr>
<td>Clubionidae</td>
<td>Clubiona canadensis Emerton</td>
</tr>
<tr>
<td>Dictynidae</td>
<td>Dictyna breviflora Emerton</td>
</tr>
<tr>
<td>Dictyna phylax Gertsch &amp; Ivy</td>
<td></td>
</tr>
<tr>
<td>Ergonidae</td>
<td>Ceraticius atriceps (O.P.-Cambridge)</td>
</tr>
<tr>
<td>Grammomota angusta Dondale</td>
<td></td>
</tr>
<tr>
<td>Linophoridae</td>
<td>Pityohyphantes costatus (Hentz)</td>
</tr>
<tr>
<td>Salticidae</td>
<td>Metaphidippus flavipes (Peckham)</td>
</tr>
<tr>
<td>Tetragnathidae</td>
<td>Tetragnatha versicolor Walckenaer</td>
</tr>
<tr>
<td>Theridiidae</td>
<td>Theridion montanum Emerton</td>
</tr>
<tr>
<td>Theridion marium Emerton</td>
<td></td>
</tr>
<tr>
<td>Thomisidae</td>
<td>Philodromus placidus Banks</td>
</tr>
<tr>
<td>Philodromus rufus Walckenaer</td>
<td></td>
</tr>
</tbody>
</table>
effort over a number of years in four sampling plots. The spider population data revealed two interesting results. The first was that the proportion of each species to the total spider complex remained extremely constant within a particular habitat. This is illustrated in Table 6 which shows that, from 1962 to 1970, *C. atriceps* was the most common species in the Green River area and it constituted 30 to 43% of the total spider population over a 9-year span. Table 6 also shows that *D. phylax*, *Theridion montanum* Emerton, and *Grammonota angusta* Dondale demonstrated remarkable constancy within the total spider complex. Shorter term data for the other sampling areas gave similar results. This is not to say that species composition was constant from place to place. Striking differences were recorded between the four sampling plots in New Brunswick even though they could all be classed as fir-spruce biotypes. Table 7 shows that, in 1969, *C. atriceps* was the most common species at Green River (32%) but constituted only 2% of the population at Lincoln. *Dictyna phylax* was the most common species at Lincoln (29%) but

<table>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. atriceps</em></td>
<td>43</td>
<td>35</td>
<td>34</td>
<td>32</td>
<td>36</td>
<td>40</td>
<td>35</td>
<td>32</td>
<td>30</td>
</tr>
<tr>
<td><em>D. phylax</em></td>
<td>12</td>
<td>18</td>
<td>18</td>
<td>20</td>
<td>14</td>
<td>16</td>
<td>22</td>
<td>18</td>
<td>21</td>
</tr>
<tr>
<td><em>T. montanum</em></td>
<td>12</td>
<td>11</td>
<td>11</td>
<td>14</td>
<td>14</td>
<td>11</td>
<td>15</td>
<td>15</td>
<td>12</td>
</tr>
<tr>
<td><em>G. angusta</em></td>
<td>9</td>
<td>9</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>8</td>
<td>9</td>
<td>7</td>
</tr>
</tbody>
</table>

**Fig. 2.** Trend in seasonal density of *D. phylax* in each of 4 years in the Green River area.
constituted only 9% at Fundy and has never been collected at Priceville. Theridion montanum was common at Fundy (35%) but was rarely found at Priceville (1%). We have no clear explanation for these differences in species composition; they are not related to budworm density nor, as far as we can determine, to the side-effects of the spray program in the Priceville area.

The second noteworthy point in the spider population data was that, excluding Priceville, there were no sudden changes in the density of a particular species in a particular habitat, for example at Green River (Table 8). Furthermore, the Green River data show that the difference between the lowest and highest densities of the more common species over a 9-year span was rarely greater than three-fold. Table 8 shows that the density of C. atriceps ranged from 1.83 per 10 ft² in 1964 to 3.77 in 1969.

The constancy of spider abundance raises the question of their potential to regulate a dynamic prey such as the spruce budworm. Turnbull (1956) found salticids to be aggressive hunters, readily attacking all larval instars and capable of capturing gravid female moths. He also recorded moths in the webs of araneids and theridiids but discounted the significance of these observations on the assumption that only females which had already deposited a large proportion of their eggs were susceptible to capture by web-spinners.

Laughton et al. (1963) were able to demonstrate by precipitin tests that 20% of the spiders collected throughout the season in a spruce budworm epidemic had fed on budworm, with theridiids appearing as the most effective group. Unfortunately, the data could not be quantified.

### TABLE 7

Percent contribution of 11 species to the total spider complex on balsam fir in the four study areas in 1969

<table>
<thead>
<tr>
<th>Species</th>
<th>Green River</th>
<th>Lincoln</th>
<th>Fundy</th>
<th>Priceville</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. atriceps</td>
<td>32</td>
<td>2</td>
<td>3</td>
<td>28</td>
</tr>
<tr>
<td>D. phylax</td>
<td>18</td>
<td>29</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td>T. montanum</td>
<td>15</td>
<td>2</td>
<td>35</td>
<td>1</td>
</tr>
<tr>
<td>G. angusta</td>
<td>9</td>
<td>9</td>
<td>30</td>
<td>7</td>
</tr>
<tr>
<td>P. costatus</td>
<td>5</td>
<td>5</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>P. placentis</td>
<td>2</td>
<td>6</td>
<td>Tr</td>
<td>30</td>
</tr>
<tr>
<td>M. flavipesd</td>
<td>2</td>
<td>12</td>
<td>1</td>
<td>17</td>
</tr>
<tr>
<td>T. murarium</td>
<td>Tr</td>
<td>8</td>
<td>1</td>
<td>9</td>
</tr>
<tr>
<td>D. brevitarsus</td>
<td>2</td>
<td>4</td>
<td>6</td>
<td>Tr</td>
</tr>
<tr>
<td>P. rufa vibrans</td>
<td>1</td>
<td>5</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>A. displicata</td>
<td>2</td>
<td>4</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>

*Trace.

### TABLE 8

Spider density per 10 ft² of foliage, Green River area, 1962–1970

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>C. atriceps</td>
<td>3.15</td>
<td>2.17</td>
<td>1.83</td>
<td>2.38</td>
<td>2.90</td>
<td>3.44</td>
<td>3.04</td>
<td>3.77</td>
<td>2.34</td>
</tr>
<tr>
<td>D. phylax</td>
<td>0.70</td>
<td>0.92</td>
<td>1.70</td>
<td>1.05</td>
<td>1.20</td>
<td>1.00</td>
<td>1.32</td>
<td>1.78</td>
<td>0.94</td>
</tr>
<tr>
<td>T. montanum</td>
<td>0.68</td>
<td>0.55</td>
<td>0.58</td>
<td>0.78</td>
<td>0.77</td>
<td>1.06</td>
<td>0.72</td>
<td>1.04</td>
<td>0.54</td>
</tr>
<tr>
<td>G. angusta</td>
<td>0.10</td>
<td>0.20</td>
<td>0.28</td>
<td>0.32</td>
<td>0.09</td>
<td>0.29</td>
<td>0.29</td>
<td>0.54</td>
<td>0.13</td>
</tr>
<tr>
<td>P. costatus</td>
<td>0.20</td>
<td>0.18</td>
<td>0.25</td>
<td>0.27</td>
<td>0.35</td>
<td>0.15</td>
<td>0.20</td>
<td>0.28</td>
<td>0.29</td>
</tr>
<tr>
<td>P. placentis</td>
<td>6.52</td>
<td>5.67</td>
<td>5.22</td>
<td>7.30</td>
<td>6.65</td>
<td>8.65</td>
<td>8.76</td>
<td>11.8</td>
<td>7.79</td>
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</tbody>
</table>
Haynes and Sisojevic (1966) found that, when starved, *Philodromus rufus* Walckenaer showed typical invertebrate feeding response (i.e., decreasing rate of attack) to an increasing prey density; they found that the same was true for *G. angusta* (unpublished). They also found that both species could withstand long starvation periods and then take full advantage of a sudden increase in prey such as hatching first-instar budworm in late summer or emerging postdiapause, second-instar larvae in the spring.

Results of field experiments carried out over a 3-year period with *D. phylax* and “planted” populations of second-instar larvae at Green River are presented in Table 10. They show that about 3% of the larvae survived on foliage with a spider predator while 60% survived on the control foliage. The data leave little doubt that *D. phylax* is extremely efficient in capturing small budworm larvae attempting to establish feeding sites at the tips of branches.

Partially starved *D. phylax* female adults, fed a surplus diet of second-instar larvae, consumed an average of 15 larvae in a 6-h period before significant changes were noted in the attack response, handling time, and utilization of prey. This does not necessarily imply, however, that *D. phylax* would invariably have a significant effect on a field population, particularly at endemic densities. For example, *D. phylax* as a web-spinner captures, and may prefer, a varied diet (Table 11). Furthermore, the endemic density of the spruce budworm is as low as 1.0 larva on every 10 midcrown branches of balsam fir. About 5.0 *D. phylax* would be found on the same 10 branches. Assuming that each spider spins a web at the juncture of three peripheral shoots, then these data can be extrapolated to 5.0 *D. phylax* inhabiting 670 branch tips or sites where one budworm larva might wander to establish a feeding site. The probability of a predator–prey encounter is extremely low even though the larva has the ability to wander almost continuously at 300 cm/h for 40 h. Thus *D. phylax* has the potential to consume a large number of small larvae but its limited numerical response and sedentary habits preclude any real effect on the regulation of budworm populations.

**Conclusions**

An intensive 9-year census of the spider fauna in one fir–spruce biotype in northwestern New Brunswick and 3 years’ data from similar biotypes in other parts of the province reveal:

1. a remarkable constancy in the species composition in any one location;
2. a marked year-to-year constancy in the total number of spiders per unit area of foliage in any one location;

---

### Table 9

<table>
<thead>
<tr>
<th>Year</th>
<th>Green River</th>
<th>Lincoln</th>
<th>Fundy</th>
<th>Priceville</th>
</tr>
</thead>
<tbody>
<tr>
<td>1968</td>
<td>8.76</td>
<td>6.14</td>
<td>4.29</td>
<td>1.96</td>
</tr>
<tr>
<td>1969</td>
<td>11.8</td>
<td>9.60</td>
<td>5.69</td>
<td>5.73</td>
</tr>
<tr>
<td>1970</td>
<td>7.79</td>
<td>10.3</td>
<td>6.72</td>
<td>5.36</td>
</tr>
</tbody>
</table>

### Table 10

<table>
<thead>
<tr>
<th>Year</th>
<th>With <em>D. phylax</em></th>
<th>Without <em>D. phylax</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. of budworm larvae</td>
<td>Percent survival</td>
</tr>
<tr>
<td>1968</td>
<td>112</td>
<td>5</td>
</tr>
<tr>
<td>1969</td>
<td>123</td>
<td>2</td>
</tr>
<tr>
<td>1970</td>
<td>178</td>
<td>3</td>
</tr>
</tbody>
</table>

### Table 11

<table>
<thead>
<tr>
<th>Taxonomic group</th>
<th>Percentage composition</th>
</tr>
</thead>
<tbody>
<tr>
<td>DIPTERA</td>
<td>74</td>
</tr>
<tr>
<td>Nematocera</td>
<td>72</td>
</tr>
<tr>
<td>Chironomidae</td>
<td>35</td>
</tr>
<tr>
<td>Sciaridae</td>
<td>16</td>
</tr>
<tr>
<td>Cecidomyiidae</td>
<td>10</td>
</tr>
<tr>
<td>Ceratopogonidae</td>
<td>3</td>
</tr>
<tr>
<td>Mycetophilidae</td>
<td>1</td>
</tr>
<tr>
<td>Undetermined</td>
<td>7</td>
</tr>
<tr>
<td>Others</td>
<td>2</td>
</tr>
<tr>
<td>HYMENOPTERA</td>
<td>9</td>
</tr>
<tr>
<td>Platygasteridae</td>
<td>5</td>
</tr>
<tr>
<td>Chalcidoidea</td>
<td>4</td>
</tr>
<tr>
<td>HOMOPTERA</td>
<td>7</td>
</tr>
<tr>
<td>Aphididae</td>
<td>5</td>
</tr>
<tr>
<td>Others</td>
<td>2</td>
</tr>
<tr>
<td>THYSANOPTERA</td>
<td>7</td>
</tr>
</tbody>
</table>
a marked dissimilarity in the species composition in different areas even though all areas could be classed as a fir-spruce biotype;
(4) even though species composition differed between locations, the total numbers of spiders per unit area of foliage was quite constant;
(5) within a fir-spruce biotype, most spiders appear to be well adapted to utilize a wide variety of food but show little tendency to respond to periodic outbreaks of a particular food item, such as the budworm;
(6) the predatory effect on budworm is further limited because most spiders cannot successfully attack large larvae (2.0–3.5 cm in length);
(7) web-spinners prey on beneficial as well as pest species: it is within their capability to capture small adult parasites such as the various species of Apanteles, a common budworm parasite;
(8) the possibility of manipulating spiders as control agents (laboratory propagation and inundative release) is remote because rearing techniques are still prohibitively time-consuming in terms of maintaining live prey and providing individual care for a predator which, besides having an exceptionally long maturation period, displays a strong cannibalistic urge.

It would appear that spiders, like birds and non-specific parasites, might consume or kill a relatively large number of prey, but that the number of prey killed would remain fairly stable. In this way, such general predators might play a significant role in determining the mean endemic density of budworm during the 20–30 years between outbreaks, but have little influence in regulating the explosive outbreaks that periodically occur in an otherwise permissive environment.
