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POPULATION DENSITIES OF SPIDERS (ARANEAE) AND SPRUCE BUDWORMS (LEPIDOPTERA, TORTRICIDAE) ON FOLIAGE OF BALSAM FIR AND RED SPRUCE IN EAST-CENTRAL MAINE

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ABSTRACT

Spiders of 10 families, 17 genera, and at least 22 species were collected from crown foliage samples of *Abies balsamea* (L.) Mill. and *Picea rubens* Sarg. in east-central Maine. Species of web spinners were more prevalent (68.2% of total species) among branch samples ($N = 613$ branches) than species of hunters (31.8%). Mean species per site ($N = 8$ sites) was 7.6 ± 1.2. Numbers, life stages, and sex ratios of spiders differed between tree species; sex ratios were biased (*G*-test, $P \leq 0.001$) in favor of females. Spider densities per m^2 of foliage area generally were greater ($P \leq 0.05$) on red spruce ($\bar{X} = 12.0 \pm 1.3$) than on balsam fir ($\bar{X} = 7.2 \pm 0.9$), but sampling intensity was important. For intensely sampled sites, overall mean densities of spruce budworms/m^2 of foliage were not significantly different ($P > 0.05$) between tree species. Spearman's rank correlation coefficients indicated that spider-budworm densities covaried weakly among study sites for each tree species; balsam fir ((rho) = 0.17, $N = 343$), red spruce ((rho) = 0.15, $N = 270$). Enhancement of spider populations through silvicultural treatments designed to favor spruces is proposed.

INTRODUCTION

The spruce budworm, *Choristoneura fumiferana* (Clem.), is the most widely distributed and destructive defoliator of spruce-fir (*Picea-Abies*) forests in North America (Talerico 1984). Conservation and enhancement of natural enemies of the spruce budworm are desirable goals of integrated pest management (IPM) systems directed against this forest pest (Simmons et al. 1984). Because spiders are predators of all life stages of the spruce budworm (Jennings and Crawford 1985), they are receiving increased attention from investigators (Renault and Miller 1972; Jennings and Collins 1987; Jennings and Houseweart 1989). Part of this interest stems from the potential to enhance or increase spider populations through habitat manipulations (Riechert and Lockley 1984; Provencher and Vickery 1988; Jennings et al. 1988; Riechert and Bishop 1990).

Spiders respond to structural features within habitats (Greenquist and Rovner 1976), and vegetation structure, complexity, and diversity are important parameters that influence spider numbers and richness (Lubin 1978; Greenstone 1984; Riechert and Gillespie 1986; Young 1989). Because of these attributes, it might be possible to enhance or increase spider populations in northeastern spruce-fir forests by selecting or favoring tree species that harbor abundant spiders. For example, Stratton et al. (1979) found that white spruce, *Picea glauca*, had more spiders (both numbers of individuals and numbers of species) than red pine, *Pinus resinosa*, or northern white-cedar, *Thuja occidentalis*, in Minnesota. Likewise, Jennings and Dimond (1988) found that spider densities generally were greater on spruces (white spruce and red spruce, *Picea rubens*) than on balsam fir, *Abies balsamea*, in Maine. By increasing the percentage tree-species composition of spruces in forest stands, it may be possible to increase population densities of arboreal spiders in these stands. However, we must first determine the species of spiders associated with northeastern conifers, assess their respective population densities, and determine their population enhancement potential.

In 1987, we collected additional data on the population densities of spiders and spruce budworms associated with tree-crown foliage of red spruce and balsam fir in east-central Maine. These data complement and support our earlier findings in east-central Maine (Jennings and Dimond 1988); they also provide historical records (1985-1987) of spider-budworm densities during the decline phase of a spruce budworm epidemic. In this paper we describe the arboreal spider fauna associated with balsam fir and red spruce, compare spider and spruce budworm population densities among study sites and between host-tree species, explore spider-budworm density relationships, and discuss possible pest management implications of our findings in east-central Maine.

METHODS

Study areas.—Eight forest stands in east-central Maine (Fig. 1) were sampled in 1987. Three of these stands were previously sampled in 1986 (Jennings and Dimond 1988). All sites were in open, spruce-fir stands that had declining populations of the spruce budworm. Study-site abbreviations and their locations by town, township, and county were:

(MA)—Myra I, T32 MD, Hancock County
(MY)—Myra II, T32 MD, Hancock County
(DL)—Deer Lake, T34 MD, south, Hancock County
(MR)—Machias River, T30 MD, Washington County
(HM)—Hermon Mtn., T31 MD, Washington County
(GP)—Georges Pond, Franklin, Hancock County
(SH)—Sugar Hill, Eastbrook, Hancock County
(NL)—Narraguagus Lake, T9 SD, Hancock County

At each location, trees along old logging roads and forest trails were selected for sampling based on tree dominance and accessibility. This resulted in variable-plot sizes with linear transects ranging from 0.5 to 1 km. At most sites, 10 dominant/codominant trees of each species (balsam fir, red spruce) were selected, flagged, and numbered for consecutive sampling on a weekly basis.

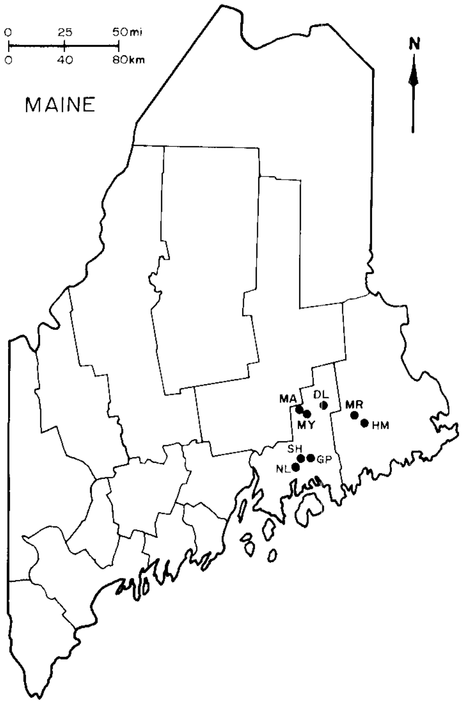

Figure 1.—Study-site locations in east-central Maine for sampling spider and spruce budworm densities, 1987. (See text for detailed descriptions of locations).

Branch samples.—We used a long, sectional pole pruner to cut one 45-cm branch from the upper crown half of each selected tree. The pole pruner was equipped with a cloth-basket attachment for catching any spiders and budworms dislodged when the branch was cut (Jennings and Collins 1987). Once lowered to the ground, severed branches and dislodged arthropods were removed from the basket and placed individually in labeled plastic bags for transport to the laboratory.

In the laboratory, technicians clipped the sample branches into small lengths (8-10 cm) and closely searched all foliage for spiders and spruce budworms. All collected spiders were stored in 2-dram vials containing 75% ethanol. Labels with study-site location, sample date, and branch-tree species were placed inside each vial.

For most study sites, selected trees were sampled at about weekly intervals beginning 27 May and ending 1 July 1987. However, balsam fir and red spruce were sampled only once (11 June 1987) at Georges Pond (GP), Narraguagus Lake (NL), and Sugar Hill (SH).

Spider identifications.—Sexually mature spiders were identified to species; juveniles, including penultimate stages, were identified to genus. However, juveniles of some philodromid spiders were identified to species (i.e., *Philodromus placidus* Banks) or species group (*aureolus, rufus*) based on color patterns of legs, carapace, and abdomen (Dondale and Redner 1978). Representative specimens of all identified species will be deposited in the arachnid collection, U. S. National Museum of Natural History, Washington, DC.

Data analyses.—Branch surface areas of balsam fir and red spruce were calculated by the formula: $A = (L \text{ X } W)/2$, where L is the foliated branch length and W is the maximum foliated width (Sanders 1980). Population densities of both spiders and spruce budworms were expressed as numbers of individuals/m^2 of branch surface area. Because sampling intensities varied among study sites, we grouped the samples into high- and low-intensity sites. The Kruskal-Wallis Test (SAS Institute 1985) was used to compare spider-budworm densities among study sites and between tree species at $P = 0.05$. We used Spearman's rank correlation coefficient (rho) to test for independence between spider and budworm densities. The G-statistic (Sokal and Rohlf 1981) was used to compare sex ratios of collected spiders, where the expected proportions were 0.50 males and 0.50 females. The G-statistic was also used to compare species composition of spiders by foraging strategy, where the expected proportions were: balsam fir—0.57 web spinners, 0.43 hunters; red spruce—0.64 web spinners, 0.36 hunters (Jennings and Dimond 1988).

RESULTS

Forest stands.—The study sites sampled in 1987 were similar to those previously investigated (Jennings and Dimond 1988). Balsam fir and red spruce were the principal softwood components, with occasional eastern white pine, *Pinus strobus*, eastern hemlock, *Tsuga canadensis*, and northern white-cedar. Hardwood components were maples (*Acer* spp.) and birches (*Betula* spp.). Most of the stands were open-grown with mean basal areas < 10 m^2/ha. All stands were infested with the spruce budworm but their populations were declining.

Spider taxa.—Spiders of 10 families, 17 genera, and at least 22 species were collected from foliage of balsam fir and red spruce in east-central Maine (Table 1). Despite unequal sample sizes (balsam fir, $N = 343$ branches; red spruce, $N = 270$ branches), the species of spiders were distributed about equally between tree species, i.e., balsam fir, 19 species; red spruce, 20 species. However, web-spinning species were more prevalent among branch samples for both balsam fir (63.2%) and red spruce (70.0%). These observed species compositions did not differ significantly ($P > 0.05$) from the expected proportions (Jennings and Dimond 1988) for either tree species (balsam fir, $G = 0.28$; red spruce, $G = 0.32$).

The number of species per spider family ranged from one (Tetragnathidae) to five (Araneidae); the latter includes species identified only to generic-level (*Araneus* sp., *Neoscona* sp.).

Spider species composition varied among sites; $\bar{X} = 7.6 \pm 1.2$ SE, range 3 (SH) to 12 (DL, MR), where $N = 8$ sites. Only one species, *Grammonota angusta* Dondale, was common to all eight study sites sampled in 1987. *Dictyna brevitarsus* Emerton, *Theridion* sp., *Philodromus* sp. (*rufus* grp.), and *Metaphidippus flaviceps* Kaston were each found on seven sites. Five species represented by adult spiders, *Ceraticelus atriceps* (O. P.-Cambridge), ERIGONIDAE undet. female, *Cyclosa conica* (Pallas), *Mangora placida* (Hentz), and *Eris militaris* (Hentz), were each found on only one study site.

Spider numbers, life stages, sex ratios.—Despite the unequal distribution of branch samples between tree species, over half (55.9%) of the total *sampled* spiders ($N = 315$) were from red spruce. Most of the *collected* spiders (13 lost, $N = 302$, Table 1) were females (47.4%), followed by juveniles (44.0%) and males (8.6%). Distributions of spider life stages for each tree species were: balsam fir—juveniles (41.5%), males (12.6%), females (45.9%); red spruce—juveniles (46.1%),

Table 1.—Spiders on foliage of *Abies balsamea* and *Picea rubens*, east-central Maine, 1987.

FAMILY	Balsam fir			Red spruce		
Species	Male	Female	juv.	Male	Female	juv.
	WEB SPINNERS					
DICTYNIDAE						
Dictyna brevitarsus Emerton	4	8		3	12	
Dictyna phylax Gertsch & Ivie		3			4	
Dictyna sp.			7			4
THERIDIIDAE						
Theridion differens Emerton	1				1	
Theridion murarium Emerton	1	2			1	
Theridion sp.			5			9
LINYPHIIDAE						
Pityohyphantes costatus (Hentz)		3			4	
Pityohyphantes sp.			1			1
ERIGONIDAE						
Ceraticelus atriceps (O. P.-Cambridge)					1	
Grammonota angusta Dondale	3	16		4	22	
Grammonota pictilis (O. P.-Cambridge)		1			1	
Grammonota sp.			1			
Undet. sp.					1	
ARANEIDAE						
Araniella displicata (Hentz)	1	2			3	
Araniella sp.			1			3
Araneus sp.			2			2
Cyclosa conica (Pallas)		1				
Mangora placida (Hentz)					1	
Neoscona sp.			1			1
TETRAGNATHIDAE						
Tetragnatha sp.			1			1
Subtotals	10	36	19	7	51	21
	HUNTERS					
CLUBIONIDAE						
Clubiona trivialis C. L. Koch		3			4	
Clubiona sp.			5			3
PHILODROMIDAE						
Philodromus exilis Banks	1	2			7	
Philodromus pernix Blackwall	1	1				
Philodromus placidus Banks	1	3	7		3	8
Philodromus sp. (*aureolus* grp.)			5			4
Philodromus sp. (*rufus* grp.)			7			16
THOMISIDAE						
Xysticus punctatus Keyserling		1			2	
Xysticus sp.			1			6
SALTICIDAE						
Eris militaris (Hentz)		1				
Eris sp.						1
Metaphidippus flaviceps Kaston	4	15		2	14	
Metaphidippus sp.			12			18
Subtotals	7	26	37	2	30	56
TOTALS	17	62	56	9	81	77

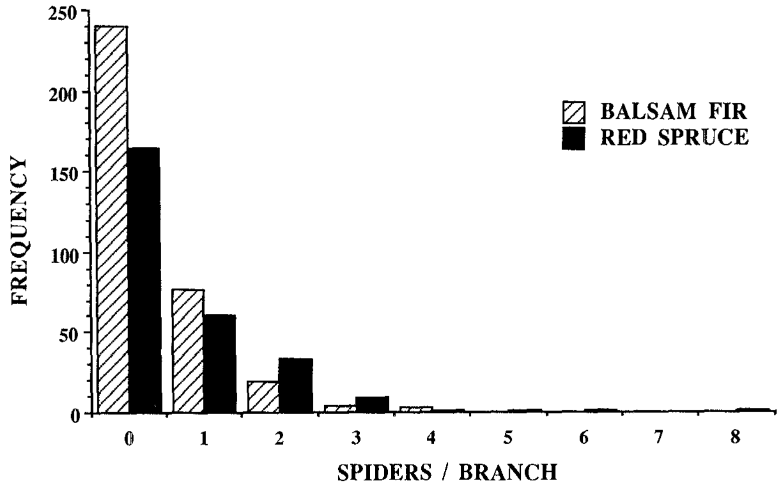

Figure 2.—Frequency distribution of spiders on balsam fir and red spruce branches, east-central Maine, 1987.

males (5.4%), females (48.5%). Sex ratios of males to females were: balsam fir, 1:3.6; red spruce, 1:9.0; both tree species, 1:5.5. All comparisons of spider sex ratios were highly biased ($P \leq 0.001$) in favor of females: balsam fir, $G = 27.2$; red spruce, $G = 66.2$; both tree species, $G = 89.2$.

The number of spiders per branch ranged from 0 to 4 for balsam fir; from 0 to 8 for red spruce (Fig. 2). Red spruce branches tended to have more spiders/branch than balsam fir. For example, 17.0% of the red spruce branches ($N = 270$) had 2 or more spiders/branch, whereas only 7.6% of the balsam fir branches ($N = 343$) had 2 or more spiders/branch.

Spider densities.—For both high- ($>$ 10 branches/site) and low- (10 branches/site) intensity samplings of balsam fir, spider populations/m^2 of foliage area varied among study sites (Table 2, column $\bar{X}$'s). However, spider populations/m^2 of red spruce foliage did not differ significantly among study sites regardless of sampling intensity.

Spider densities generally were greater on red spruce than on balsam fir (Table 2, row $\bar{X}$'s); overall, these differences were significantly greater for the high-intensity sites sampled in 1987. Conversely, overall spider densities were not significantly different between tree species for the low-intensity sites.

Spider densities also varied by sampling date (Fig. 3). Mean densities on red spruce trees exceeded those on balsam fir trees 10 out of 14 sampling dates. For both tree species, mean densities generally declined as the season progressed.

Budworm densities.—Densities of spruce budworm larvae and pupae/m^2 of foliage also varied among study sites for both tree species (Table 3, column $\bar{X}$'s). For high-intensity sites, overall mean densities were not significantly different between tree species (Table 3, row $\bar{X}$'s). However, for low-intensity sites, the overall mean density was significantly greater on balsam fir than on red spruce.

Spider-budworm density relationships.—Spider and spruce budworm densities covaried among study sites for each tree species; however, most of the correlations were weak ((rho) < 0.30) and many were nonsignificant ($P > 0.05$), especially for low-intensity sites. Over all sites and sampling intensities, there was

Table 2.—Densities of spiders/m^2 of balsam fir and red spruce foliage, east-central Maine, 1987. Within each sampling group (high-low), column means (ab, a'b'), and row means (xy) followed by the same letter(s) are not significantly different, SAS Institute (1985), Kruskal-Wallis Test, $P = 0.05$. * = MA classed as both high- and low-intensity site.

	Spiders $\bar{X}$ (± SE) / m^2 of foliage					
1987 Sites	No. branches sampled	Balsam fir		No. branches sampled	Red spruce	
		HIGH-INTENSITY SITES				
HM	60	11.5 acx	(3.6)	59	10.3 ax	(2.2)
MR	59	9.8 ax	(1.6)	60	13.9 ax	(2.7)
MY	49	6.0 bcx	(1.6)	50	9.8 ax	(2.5)
DL	60	5.4 bcx	(1.6)	60	13.5 ay	(3.0)
MA*	85	4.4 b	(1.2)			
All	313	7.2 x	(0.9)	229	12.0 y	(1.3)
		LOW-INTENSITY SITES				
GP	10	14.8 a'x	(4.4)	10	18.4 a'x	(5.5)
NL	10	13.3 a'b'x	(5.3)	10	9.2 a'x	(4.3)
SH	10	3.0 b'x	(2.2)	11	10.3 a'x	(4.2)
MA*				10	17.6 a'	(5.5)
All	30	10.4 x	(2.5)	41	13.8 x	(2.4)

little difference between tree species; balsam fir ((rho) = 0.17, $P = < 0.01$, $N = 343$), red spruce ((rho) = 0.15, $P = 0.01$, $N = 270$).

DISCUSSION

Spider taxa.—The species of spiders we collected from foliage of balsam fir and red spruce are typical arboreal spiders of northeastern spruce-fir forests. All of the identified species collected during this study previously have been taken from coniferous-tree foliage in east-central Maine (Jennings and Dimond 1988). Many of the same species also have been found on red spruce foliage in northern Maine (Jennings and Collins 1987). Based on their relative abundance, species common to arboreal habitats of Maine's spruce-fir forests include *Dictyna brevitarsus* Emerton, *Theridion murarium* Emerton, *Pityohyphantes costatus* (Hentz), *Grammonota angusta* Dondale, *Araniella displicata* (Hentz), *Clubiona trivialis* C. L. Koch, *Philodromus exilis* Banks, *P. placidus*, and *Metaphidippus flaviceps* Kaston. Five of these species—*D. brevitarsus, G. angusta, P. exilis, P. placidus*, and *M. flaviceps*—comprised 46.0% of all collected spiders in this study.

Apparently, none of the commonly collected species exhibited a definite habitat preference for either tree species; their relative abundances were about the same on balsam fir and on red spruce. The salticid, *M. flaviceps*, was slightly more abundant on balsam fir (Table 1), which is consistent with our earlier study (Jennings and Dimond 1988). We conclude that the erigonid, *G. angusta*, is much more prevalent on foliage of balsam fir and red spruce than its congeneric, *G. pictilis* (O. P.-Cambridge). Loughton et al. (1963) reported that *G. pictilis* was one of the most abundant spiders on balsam fir foliage at Fredericton, New Brunswick; however, according to Dondale (1959), most early collections and identifications of *Grammonota* in the Northeast refer to *G. angusta*, not *G. pictilis.*

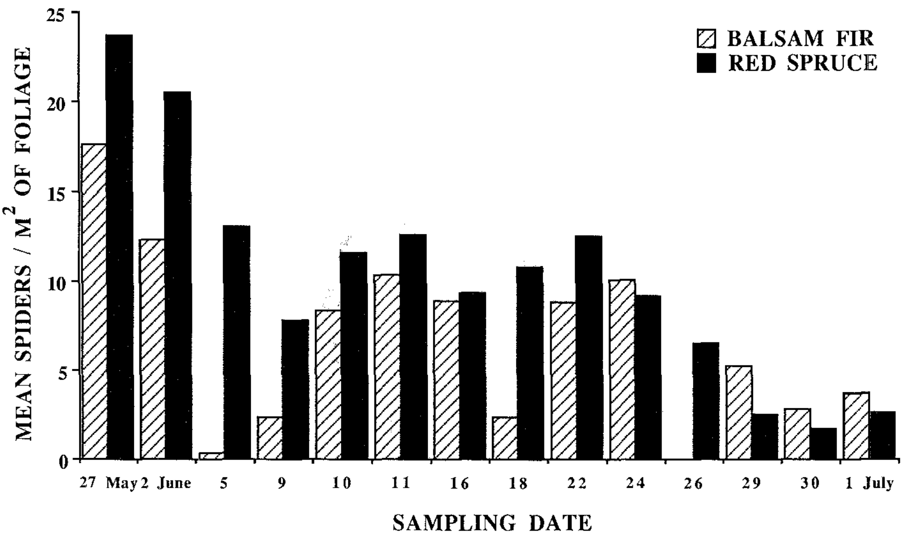

Figure 3.—Mean density of spiders/m^2 of foliage by sampling date, balsam fir and red spruce, east-central Maine, 1987.

Our observed differences in spider species composition by foraging strategy (web spinner, hunter) are consistent with earlier findings (Jennings and Dimond 1988; Loughton et al. 1963). The arboreal spider fauna of northeastern spruce-fir forests is dominated by the web-spinner guild, chiefly species of Erigonidae and Araneidae. The arboreal hunter guild in these forests consists mainly of species of Philodromidae, Thomisidae, and Salticidae.

Spider numbers, life stages, sex ratios.—Our results for these parameters complement and support earlier findings (Jennings and Dimond 1988), namely that: (1) more spiders are found on foliage of red spruce than on foliage of balsam fir; (2) for both tree species, spider individuals are distributed unevenly among life stages (juveniles, males, females); and (3) for both tree species, spider sex ratios (males:females) are biased in favor of females. No doubt, some of the observed differences in spider numbers, life stages, and sex ratios can be attributed to the reproductive cycles, developmental periods, and survivorships of individual species. For example, our sampling period spanned the time when both juveniles and adults of biennial species were present (e.g., *Philodromus placidus* and *Xysticus punctatus* Keyserling, see Dondale 1961, 1977). Because female spiders generally live longer than male spiders (Gertsch 1979), a biased sex ratio in favor of females can be expected. However, this does not fully explain the greater disparity in spider sex ratios on red spruce (1:9.0) as compared to balsam fir (1:3.6) that we observed in 1987. Because of the dense, closely compact foliage of red spruce, we suspect that resident female spiders gain some measure of protection from foliage-searching predators. If so, such females would have greater survival than their conspecifics on balsam fir, which has relatively open, flat foliage.

Spider-budworm densities.—The spider densities observed in 1987 generally are lower than those previously recorded (Jennings and Dimond 1988). For example, the mean overall density for balsam fir was 10.9 spiders/m^2 of foliage in 1985, and 8.5 spiders/m^2 in 1986 (Jennings and Dimond 1988); and 7.2 spiders/m^2 in

Table 3.—Densities of spruce budworms/m^2 of balsam fir and red spruce foliage, east-central Maine, 1987. Within each sampling group (high-low), column means (ab, a'b'), and row means (xy) followed by the same letter(s) are not significantly different, SAS Institute (1985), Kruskal-Wallis Test, $P = 0.05$. * = MA classed as both high- and low-intensity site.

	Spruce budworms $\bar{X}$ (± SE) / m^2 of foliage					
1987 Sites	No. branches sampled	Balsam fir		No. branches sampled	Red spruce	
		HIGH-INTENSITY SITES				
HM	60	169.0 ax	(22.6)	59	79.0 by	(9.6)
DL	60	139.2 ax	(13.1)	60	123.2 ax	(13.2)
MR	59	46.4 bx	(9.3)	60	19.1 cy	(4.5)
MY	49	21.6 bx	(3.9)	50	13.3 cy	(4.2)
MA*	85	9.9 c	(2.4)			
All	313	73.9 x	(6.5)	229	60.5 x	(5.4)
		LOW-INTENSITY SITES				
GP	10	340.1 a'x	(51.3)	10	237.9 a'x	(43.1)
NL	10	83.9 b'x'	(30.8)	10	26.9 b'x	(9.9)
SH	10	80.8 b'x'	(14.6)	11	69.0 bx	(24.7)
MA*				10	27.9 b'	(11.7)
All	30	168.2 x	(30.0)	41	89.9 y	(18.4)

1987 (Table 2). Similarly, for spruces (red and white), mean overall density was 16.3 spiders/m^2 in 1985 (Jennings and Dimond 1988); and, for red spruce, only 12.0 spiders/m^2 (high-intensity sites) and 13.8 spiders/m^2 (low-intensity sites) in 1987 (Table 2). Spruces were not sampled in 1986. We suspect that these declines in spider populations can be attributed to similar declines in potential prey populations (i.e., spruce budworms) in east-central Maine. Mean overall densities of spruce budworms generally were greater than 100/m^2 of foliage in 1985 and 1986 (Jennings and Dimond 1988); however, in 1987, similar densities usually were less than 100/m^2 of foliage (Table 3).

Despite individual site differences, our observations in 1987 further indicate that red spruce has more spiders than balsam fir. This conclusion is supported by the between-tree differences for overall site means (Table 2, red spruce, $\bar{X} = 12.0$ spiders/m^2; balsam fir, $\bar{X} = 7.2$ spiders/m^2; Kruskal-Wallis $\chi^2 = 7.7$, $P = 0.005$), and by the number of sampling dates (10 out of 14, Fig. 3) that mean spider densities on red spruce exceeded those on balsam fir. Nevertheless, sampling intensity affected these population-density estimates because between-tree differences were not detected for the low-intensity sites (Table 2, red spruce, $\bar{X} = 13.8$ spiders/m^2; balsam fir, $\bar{X} = 10.4$ spiders/m^2; Kruskal-Wallis $\chi^2 = 0.89$, $P = 0.35$). For future between-tree comparisons of spider densities, we recommend that trees be sampled over several dates and with sample sizes > 10 branches/tree species. Large sample sizes should help to stabilize variances within tree species and among study sites.

Spider-budworm relationships.—Our observations in 1987 further indicate that spiders may have been responding to available prey (budworm) populations in east-central Maine. This conclusion is supported by the fact that both spider and budworm populations generally declined together over the 3-year period, 1985-87, (this study; Jennings and Dimond 1988). Although the possible effects of density-independent factors (e.g., weather) on these populations cannot be ruled out, we suspect that declines in budworm population densities concomitantly affected spider populations in a density-dependent fashion. However, more detailed studies are needed before we can fully understand spider-budworm interactions and their possible population density-relationships. Apparently, the weak correlations between spider-budworm densities/m^2 of foliage area observed during this study are to be expected; similar weak correlations were observed for spider-budworm densities on red spruce foliage in northern Maine (Jennings and Collins 1987).

Interestingly, individuals and species of all three spider families (Erigonidae, Theridiidae, Salticidae) previously identified as potentially important in spruce budworm dynamics (Loughton et al. 1963) were common among foliage samples taken from balsam fir and red spruce in east-central Maine. Future studies of spider-budworm interactions should concentrate on abundant species like *Grammonota angusta, Theridion murarium*, and *Metaphidippus flaviceps*. Because of their frequencies in coniferous-tree samples, relative abundances, and active foliage-searching behaviors, species of Thomisidae and Philodromidae also are likely predators of spruce budworm larvae. In laboratory feeding trials (Jennings, unpubl.), *Xysticus punctatus* readily accepted and fed on late instars (L_5 - L_6) of the spruce budworm. The predatory habits of this thomisid spider that frequents coniferous-tree foliage (Dondale and Redner 1978) warrant further investigation.

Spider-tree relationships.—Why does red spruce have more spiders/m^2 of foliage area than balsam fir? Stratton et al. (1979) attributed the greater spider diversity on white spruce foliage, as compared to that on foliage of red pine and northern white-cedar, to differences in plant physiognomy. We suspect that differences in foliage shape, structure, and density (number of needles per internode) also influence arboreal spider populations on red spruce and balsam fir. The availability of suitable habitat structures can limit spider population numbers (Riechert and Gillespie 1986); hence, the open, relatively flat needles of balsam fir probably provide less microhabitat space for web-spinning and foraging than the compact, curved needles of red spruce.

In Sweden, Gunnarsson (1988) found that percentage needle loss affected population densities of spiders on Norway spruce, *Picea abies* (L.). The density of large spiders (length $\geq$ 2.5 mm) was about twice as great in a stand with low needle loss as that in a stand with high needle loss. Because spiders are easier to detect on branches with few needles, Gunnarsson (1988) postulated that large spiders might be more vulnerable to bird predation.

Similarly, in the spruce-fir forests of Maine, defoliation by the spruce budworm could adversely affect resident spider populations on balsam fir, red spruce, and other host-tree species. Balsam fir is extremely sensitive to defoliation by the spruce budworm (Witter et al. 1984), and balsam fir usually receives more feeding damage and is more vulnerable to mortality than red spruce (Blum and MacLean 1984). Although we did not measure tree or branch defoliation during this study, balsam fir branches generally had fewer needles and more budworm feeding damage than red spruce. Such differences in foliage quantity may have contributed to the lower spider densities that we observed on balsam fir.

Pest management implications.—Results of this and our earlier study (Jennings and Dimond 1988) confirm that balsam fir generally has fewer spiders/m^2 of foliage area than red spruce. Balsam fir is the principal host of the spruce budworm in eastern North America (Miller 1963); it is the tree species most severely damaged by the spruce budworm (Kucera and Orr 1981). The spruces—white, red, and black (*Picea mariana*)—on the other hand, are less vulnerable to damage by the spruce budworm (Blum and MacLean 1984). Forest entomologists have long attributed this relative "immunity" of spruces to host-insect asynchrony. The emergence of young budworm larvae from overwintering hibernacula in the spring may precede budbreak of spruces by several days; consequently, the larvae are forced to feed on old, less nutritious foliage (Morris et al. 1956; Greenbank 1963). Because balsam fir buds burst some 13 days before red or black spruce (Greenbank 1963), young instars of the spruce budworm are able to feed on new, nutritious foliage of balsam fir before similar foliage is available on spruces. These differences in host-foliage phenologies affect budworm survival and subsequent tree damage (Morris 1963; Greenbank 1963). However, based on our findings, we suggest that abundant spider populations also contribute to the apparent "immunity" of spruces to damage by the spruce budworm. If true, then management of forest stands to favor spruces over balsam fir may provide an indirect, cultural method to enhance these natural enemies of the spruce budworm.

But, can spider populations be enhanced or increased indirectly through silvicultural treatments designed to favor spruces over balsam fir? We believe that they can, because habitat-structural features are important determinants of spider populations (Riechert and Lockley 1984; Riechert and Gillespie 1986; Riechert and Bishop 1990). Silvicultural methods and guidelines are already available for increasing species composition and basal areas of spruces in northeastern spruce-fir forests (Frank 1979, 1985; Frank and Blum 1978). Such silvicultural treatments are advocated as a means to minimize forest-stand vulnerability to budworm damage (Blum and MacLean 1984). We predict that forest-stand treatments designed to favor spruces will also have a positive influence on resident spider populations through increases in favorable habitat structure. Our prediction needs to be tested by carefully designed and controlled experiments where both spider and potential prey densities are monitored before and after silvicultural treatments. Such information is needed before the onslaught of the next spruce budworm epidemic, which is expected in 25 or 35 years (Blais 1983; Royama 1984; Eidt 1989). Because of potential adverse impacts on prey diversity for spiders (Provencher and Vickery 1988), monocultures of red spruce, or any other conifer, should be avoided. Diversification of coniferous-tree habitats in northeastern spruce-fir forests is much more desirable and ecologically sound.

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