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HABITAT DISTRIBUTION, LIFE HISTORY AND BEHAVIOR OF *TETRAGNATHA* SPIDER SPECIES IN THE GREAT SMOKY MOUNTAINS NATIONAL PARK

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ABSTRACT. Habitat distribution patterns of five species of *Tetragnatha* Latreille 1804 were studied by analyzing 1163 one-hour samples collected at 17 focal sites representing 16 major biotic communities (habitats) in the Great Smoky Mountains National Park. *Tetragnatha versicolor* Walckenaer 1841 is a habitat generalist, being common over a wide range of elevations (520–1755 m) and in 10 of the 16 habitats, including seven forest habitats as well as wetland, high grass bald, and grassland habitats. *Tetragnatha laboriosa* Hentz 1850 is virtually restricted to non-wetland grassy habitats, *T. elongata* Walckenaer 1805 to streams, *T. viridis* Walckenaer 1841 to hemlock trees, and *T. straminea* Emerton 1884 to non-forested wetlands (marshes). Microhabitat segregation exists in the high grass bald community between *T. versicolor* (prefers trees and shrubs) and *T. laboriosa* (prefers herbs). Size frequency histograms of seasonal samples of *T. straminea* specimens indicate that this species has a one-year life cycle with six post-emergent instars, and that most individuals overwinter in the antepenultimate instar and mature and mate in May and June. *Tetragnatha straminea* is able to capture prey with or without using a web and adopts stick-like cryptic postures in three different contexts.

Keywords: *Tetragnatha*, spider, habitat preference, life cycle, cryptic behavior

Being highly diverse and abundant predators, spiders are important regulators of terrestrial arthropod populations (Riechert & Bishop 1990; Coddington & Levi 1991; Moran et al. 1996) and may prove to be useful indicators of the overall species richness and health of terrestrial communities (Noss 1990; Kremen et al. 1993; Colwell & Coddington 1994; Hänggi et al. 1995). But progress toward understanding the ecological roles of spiders is limited by a lack of knowledge of the habitat preferences and life histories of many species (Duffy 1978; Hänggi et al. 1995). Ecologists must know the autecology and life histories of important constituent species before they can gain key insights into food web dynamics and other aspects of a community's dynamics (Olive 1980; Strong et al. 1984; Wilson 1992; Polis et al. 1996).

Tetragnatha Latreille 1804 may be the most widespread and abundant orb-weaving spider genus in the world (Levi 1981). *Tetragnatha* species live in tropical, temperate, and arctic climates and on all continents (except Antarctica) and many islands. On the Hawaiian Islands a major adaptive radiation of *Tetragnatha* species has been discovered (Gillespie & Croom 1995). Fifteen *Tetragnatha* species are known from North America north of Mexico (Levi 1981), and some of these are numerically dominant spiders in particular habitats and over whole regions (Lowrie 1953; LeSar & Unzicker 1978). Despite the prominence of this genus, the life histories of only one North American species (*T. laboriosa* Hentz 1850) and a few species in other parts of the world have been rigorously analyzed and described (Juberthie 1954; Toft 1976; LeSar & Unzicker 1978), and knowledge of the habitat preferences of North American *Tetragnatha* species consists of collecting records and comments scattered widely in the literature.

In this study, we describe the habitat distribution patterns of five *Tetragnatha* species found in the Great Smoky Mountains National Park Biosphere Reserve (GSMNP) by using large sets of spider samples collected from 16 major habitats with a standardized protocol used to inventory the spiders of the GSMNP. Located in the southern Appalachian Mountains, the GSMNP, due partly to its wide elevation range (275–2013 m), large size (207,000 ha), and low temperate latitude

(35°35′N), comprises a rich mosaic of biotic communities appropriate for investigating habitat preferences on a landscape scale. We also provide the first analysis and description of the life history, phenology, and behavior of *Tetragnatha straminea* Emerton 1884. Our main goal is to make this important assemblage of spiders more accessible to ecologists.

METHODS

Habitat distribution.—Teams of 3–5 (usually 4) collectors used a modified Coddington sampling protocol (Coddington et al. 1996) to obtain the 1163 one-hour ground (408), aerial (310), beat (360), and sweep (85) samples of spiders used in this project. Ground sampling involved searching below knee level mostly on hands and knees, exploring leaf litter, logs, rocks, and plant surfaces. Aerial sampling involved searching foliage, branches, tree trunks, and spaces in between, from knee height up to maximum overhead arm's reach. Beating consisted of striking vegetation with a 1 m long stick and dislodging spiders onto a 0.5 m^2 canvas sheet held horizontally below the vegetation. Hands and aspirators were used to collect the spiders into vials containing 80% ethanol. One sample unit equaled one hour of uninterrupted effort using one of these three methods during which the collector attempted to collect every spider encountered. During each hour the team as a whole typically used all three methods in the same area. In non-forest communities (grass bald, wetland, and native grassland sites) one-hour sweep sampling was substituted for aerial and/or beating methods; sturdy sweep nets with 38 cm diameter hoops were used, and the number of sweeps per hour (175–400, mean and SD $= 268 \pm 48$) depended primarily on vegetation structure and spider abundance.

Two sets of samples (one in the spring and one in late summer) were collected in each of two years (1996 and 1997) from 15 sites and in 1995 from two other sites, the low grass bald and heath bald sites. These 17 focal sites were selected by GSMNP ecologists to represent the 16 major habitat (community) types found in the GSMNP. Habitat type, locality data, collecting dates, and sampling effort for each focal site are given in the Appendix. Two montane wetland focal sites were chosen because each one was too small to support the sampling effort judged necessary for this study. For a given focal site, the number of samples collected in the spring and summer were equal or very nearly so, as were the number of samples collected in 1996 and 1997. At each site (with the exception of the high grass bald and both montane wetland sites) nearly equal numbers of samples were collected with each of the methods employed. Descriptions of most of the sampled community types can be found in Whittaker (1956). Vegetation is being analyzed at each focal site by GSMNP botanists, and the results of these analyses will be posted in one or two years on the World Wide Web.

Adult and juvenile *Tetragnatha* specimens were sorted from each sample and identified to species. By using eye arrangement, pigment pattern, and abdominal shape, we were able to identify all but about 1% of the juveniles. *Tetragnatha versicolor* Walckenaer 1841 and *T. laboriosa* juveniles cannot be separated by eye and body shape characters, but can be distinguished by the following: in *versicolor* the black pigment area surrounding each lateral eye touches that of its neighboring lateral eye (clearly separate in *laboriosa* except in some of the youngest individuals), the abdominal venter is light (dark in *laboriosa*), and the silver pigment dorsally on the abdomen of the smallest specimens is often interrupted by a median dorsal line of no pigment (not interrupted in *laboriosa*). All specimens will be deposited in the Smithsonian Institution.

The relative abundance (mean number of individuals per one-hour sample) of each species in each year was computed for each of the 17 sites. It is important to note that this index of abundance does not reveal the often wide variation in number of individuals among one-hour samples at each site, variation due largely to method bias to particular microhabitats, spatial environmental variation within each site, and seasonal changes in spider abundance correlated with species' phenologies. An ANOVA (StatView 4.5 from Abacus Concepts) was used to examine the effect of year and method on spider abundance; $P < 0.05$ was our significance criterion.

Life history.—We measured the length of the left tibia I (ITL) (along the dorsal surface) of all 220 *T. straminea* specimens collected at the two montane wetland sites, Meadow Branch marsh (15 May and 17 July 1996; 23

May, 1 August, and 7 October 1997) and Indian Creek marsh (27 May and 16 August 1996; 12 May and 29 July 1997). Toft (1976) demonstrated that ITL often distinguishes spider instars more clearly than does either the length or width of the carapace. Measurements were performed with a Wild M-5 stereomicroscope at 24× and 12× magnification and are accurate to ± 0.077 mm. We used the StatView 4.5 computer program to generate ITL frequency distribution histograms. By examining these histograms of seasonal subsets (spring, summer, and fall) of data pooled from both sites, it was possible to reveal phenology (seasonal timing of development) and generation time (life cycle length). The histogram for all data pooled revealed the total number of instars.

Behavior.—We observed and photographed live specimens in the field. Several *T. straminea* juveniles (antepenultimate instar) were placed in separate terraria and maintained for several weeks on *Drosophila* flies while we observed prey capture and cryptic postures, sometimes using a hand-held magnifier.

RESULTS

Habitat distribution.—Five species of *Tetragnatha* were collected in the GSMNP: *T. elongata* Walckenaer 1805, *T. laboriosa*, *T. straminea*, *T. versicolor*, and *T. viridis* Walckenaer 1841. Table 1 and Fig. 1 show the relative abundance of these species at each focal site. *Tetragnatha versicolor* was found at 16 of the 17 focal sites and was common (relative abundance = 0.5–2.0) or abundant (relative abundance > 2.0) in 10 of the 16 habitats, including seven forest habitats as well as montane wetland, high grass bald, and native grassland habitats. It was especially abundant in mixed oak forest. *Tetragnatha laboriosa* was found at nine sites, but was rare at all but two of these sites, native grassland and high grass bald. *Tetragnatha versicolor* and *T. laboriosa* were found over a wide elevational range (520–1830 m). *Tetragnatha straminea* was collected at only three sites, the montane wetland and native grassland sites, and was common or abundant at all three. *Tetragnatha elongata* was found only at the two sites through which streams flow. *Tetragnatha viridis* was found only at the two sites where hemlock trees are abundant.

No *Tetragnatha* species were common at the spruce-fir, spruce, northern hardwood, low grass bald, or heath bald sites, and none were collected at the pine-oak (395 m) site (Table 1, Fig. 1). Sites with two or more common species of *Tetragnatha* were the high grass bald (*versicolor* and *laboriosa*), both wetlands (*versicolor* and *straminea*), and the native grassland (*versicolor*, *laboriosa*, and *straminea*) (Fig. 1).

There were significant relative abundance differences between 1996 and 1997 for *T. versicolor* at the mixed oak, Table Mountain pine, hemlock/hardwood cove, hardwood cove, and Meadow Branch wetland sites, and for *T. laboriosa* at the native grassland (Fig. 1). In each case, the relative abundance was higher in 1997.

Microhabitat distribution.—At the high grass bald, *T. laboriosa* was more abundant in sweep samples (collected from herbaceous vegetation) than in beat samples (collected from shrubs and trees) ($F = 5.64$, $df = 1$, $P = 0.025$), whereas *T. versicolor* was more abundant in beat than in sweep samples ($F = 5.64$, $df = 1$, $P = 0.025$) (Fig. 2). At the Indian Creek wetland site, *T. straminea* was more abundant in sweep samples than in beat samples ($F = 5.17$, $df = 1$, $P = 0.041$), but *T. versicolor* was equally common in both sweep and beat samples ($F = 0.24$, $df = 1$, $P = 0.632$) (Fig. 3). Although we were unable to make this kind of microhabitat comparison at the Meadow Branch wetland or native grassland sites (because the beat method was not used at these sites), we observed that *T. straminea* was more common in the low grassy vegetation of the wetter parts of these habitats than was *T. versicolor*. The few specimens of *T. viridis* that were found were collected only by beating the foliage of hemlock trees. *Tetragnatha elongata* was collected only over the small streams flowing through the hemlock and native grassland sites.

Life history of *T. straminea*.—The size frequency histogram of all *T. straminea* individuals collected at the wetland sites during both years indicates a total of six size/age classes and, therefore, six post-emergent instars (instars living outside the egg sac) (Fig. 4). As is typical for spiders (Toft 1976; Coyle 1985) the older the instar, the greater the variation in size. For two reasons, we suspect that the ITL frequency peak between 4.5 and 5.0

Table 1.—Relative abundance of *Tetragnatha* species at 17 focal sites representing 16 biotic communities in the Great Smoky Mountains National Park in both 1996 and 1997 (1996 and 1997 values are separated by a comma). Low grass and heath balds were sampled in 1995 only. Elevation (m) of each site is given in parentheses. Relative abundance value is underlined if at least one adult was collected.

	Relative abundance (mean number of individuals per sample)				
Habitat/focal site	*elongata*	*laboriosa*	*straminea*	*versicolor*	*viridis*
Spruce-fir (1830)		0, 0.04		0, 0.08	
High grass bald (1755)		0.88, 1.67		1.46, 2.25	
Spruce (1715)		0, 0.08		0.13, 0.04	
Beech gap (1645)				0.50, 0.21	
Northern hardwood (1615)				0.16, 0.30	
Red oak (1555)				0.40, 1.08	
Low grass bald (1505)		0.17		0.40	
Heath bald (1390)				0.10	
Mixed oak (1115)				5.82, 18.0	
Table Mtn. pine (1005)		0.02, 0		0.06, 0.58	
Hemlock-hardwood cove (945)				1.15, 2.75	0.04, 0.06
Hemlock (885)	0.17, 0.19			1.73, 3.36	0.02, 0.03
Hardwood cove (740)		0, 0.02		0.43, 1.25	
Wetland (Indian Cr.) (685)		0.06, 0	2.00, 3.31	0.24, 1.38	
Wetland (Meadow Br.) (535)		0, 0.19	2.00, 3.94	0.24, 3.31	
Native grassland (520)	0, 0.13	0.13, 2.17	0.08, 0.80	0.04, 0.54	
Pine-oak (395)					

mm does not represent the modal value of one instar with a very broad size range, but is instead the result of size overlap between postemergent instars IV and V: 1) The size range of adult females should be greater than that of any younger instar. 2) The ITL range of the penultimate male cohort (recognized by swollen palpal tarsi) should approximate that of the penultimate females. Adult females were distinguished by their protuberant genital area (and by fully developed spermathecae whenever dissections were performed). Penultimate females (instar V) were distinguished on the basis of size and the absence of a protuberant genital area. Size frequency histograms of seasonal subsets of *T. straminea* specimens collected at both wetland sites show in late spring (12–27 May) adult and penultimate males, adult and penultimate females, and relatively large juveniles, most of which are presumably antepenultimate (Fig. 5). The summer (17 July–16 August) sample set contained a smaller number of adult females and younger juveniles (instars I-III) than were present in the spring. The fall (7 October) sample set (from Meadow Branch wetland) was composed only of a juvenile class (instars III-IV) with a mean ITL between that of the spring and summer samples. These seasonal patterns strongly support a life history pattern of one generation per year with most individuals overwintering in the antepenultimate instar. Males and females appear to mature and mate in May and June. Many adult females persist well into the summer months, but males are absent then, suggesting that they die soon after mating.

Behavior of *T. straminea*.—In the field, the orientation of *T. straminea* orbs varied from horizontal to diagonal. Some spiders were in the center of their web adopting a roughly stick-like posture (legs I and II extended forward fairly close to one another and legs III and IV extended backward near the sides of the abdomen). Others were stretched out on a twig or grass blade with legs I and II held together, the much shorter legs III surrounding and gripping the substrate, and legs IV extended backward along the sides of the abdomen. This second posture, in concert with the slender abdomen and pale yellow-brown color, made the spider exceedingly difficult for us to locate. Sometimes we could not find the captive spiders that had adopted this very cryptic posture without jarring the dead grass stems in their containers. When disturbed in this way, the spider would sometimes drop

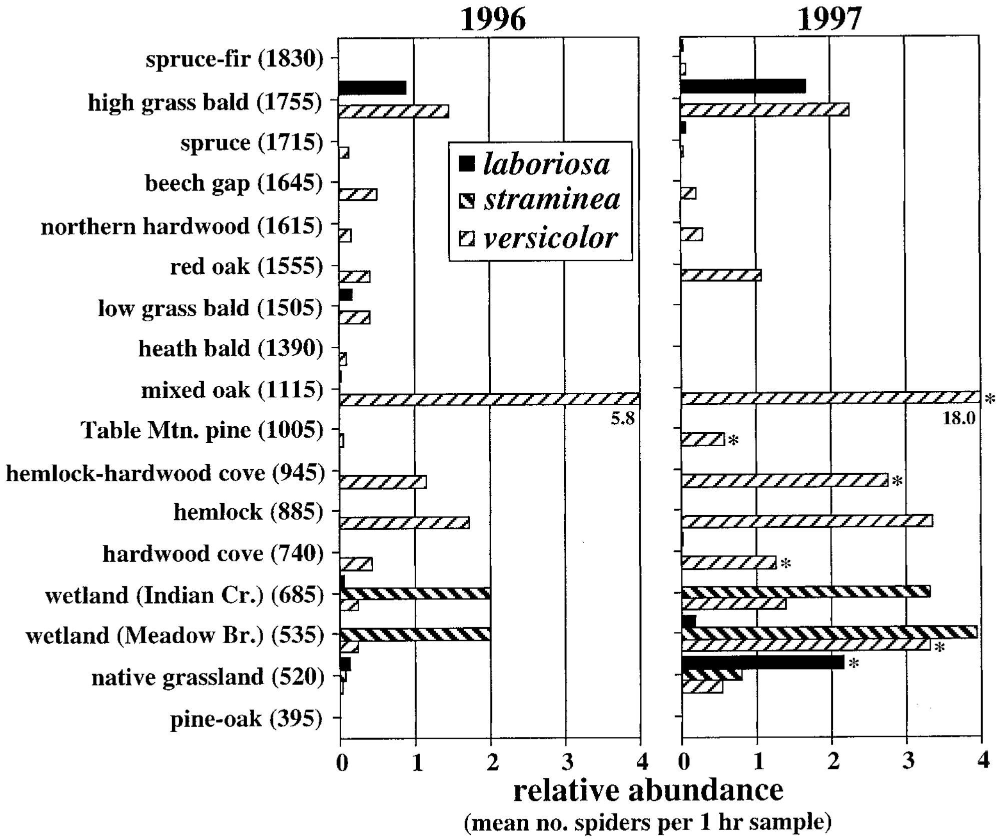

Figure 1.—Relative abundance of the three most common *Tetragnatha* species in 1996 and 1997 at 17 focal sites representing 16 biotic communities in the Great Smoky Mountains National Park. Low grass and heath bald sites were sampled in 1995 only. Focal sites are listed in order from lowest to highest elevation (in meters within parentheses). An asterisk marks any bar representing a relative abundance value significantly higher than one for the same species and site in the other year (ANOVA, $P < 0.05$).

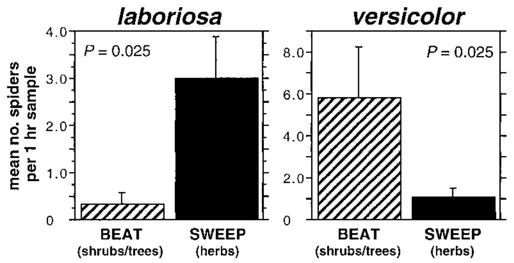

Figure 2.—Microhabitat distribution of *Tetragnatha* species at the high grass bald site. $n = 12$ beat and 18 sweep samples. Standard error is shown on top of each bar. The *P*-value is generated by ANOVA; see text for test statistics.

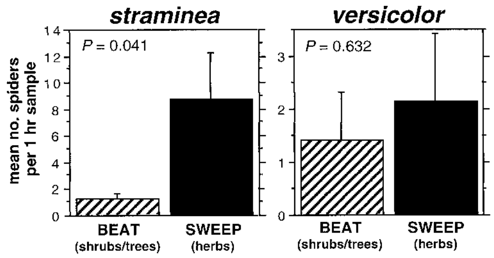

Figure 3.—Microhabitat distribution of *Tetragnatha* species at the Indian Creek wetland. $n = 8$ beat and 7 sweep samples. Standard error is shown on top of each bar. The *P*-value is generated by ANOVA; see text for test statistics.

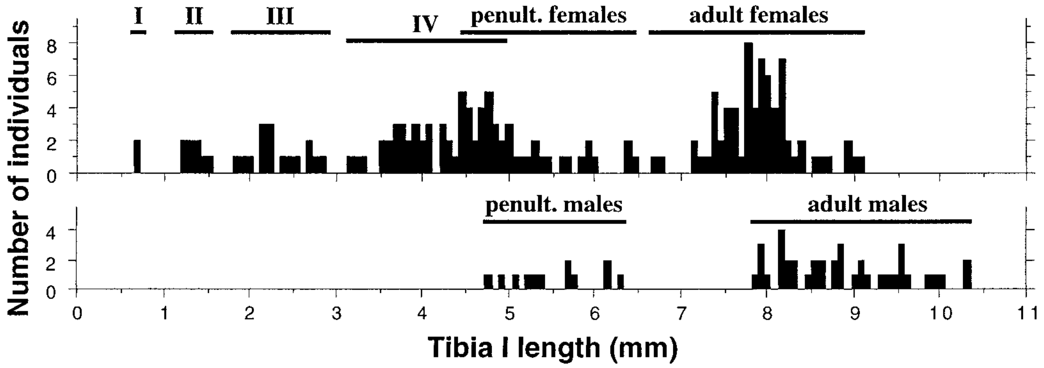

Figure 4.—Size (ITL) frequency distribution histograms of all 220 *Tetragnatha straminea* individuals collected at the two montane wetland sites during 1996 and 1997. Females and individuals too young to be sexed are graphed separately from penultimate and adult males. Labeled horizontal bars indicate ITL ranges of putative and known (adults and penultimate males) post-emergent instars.

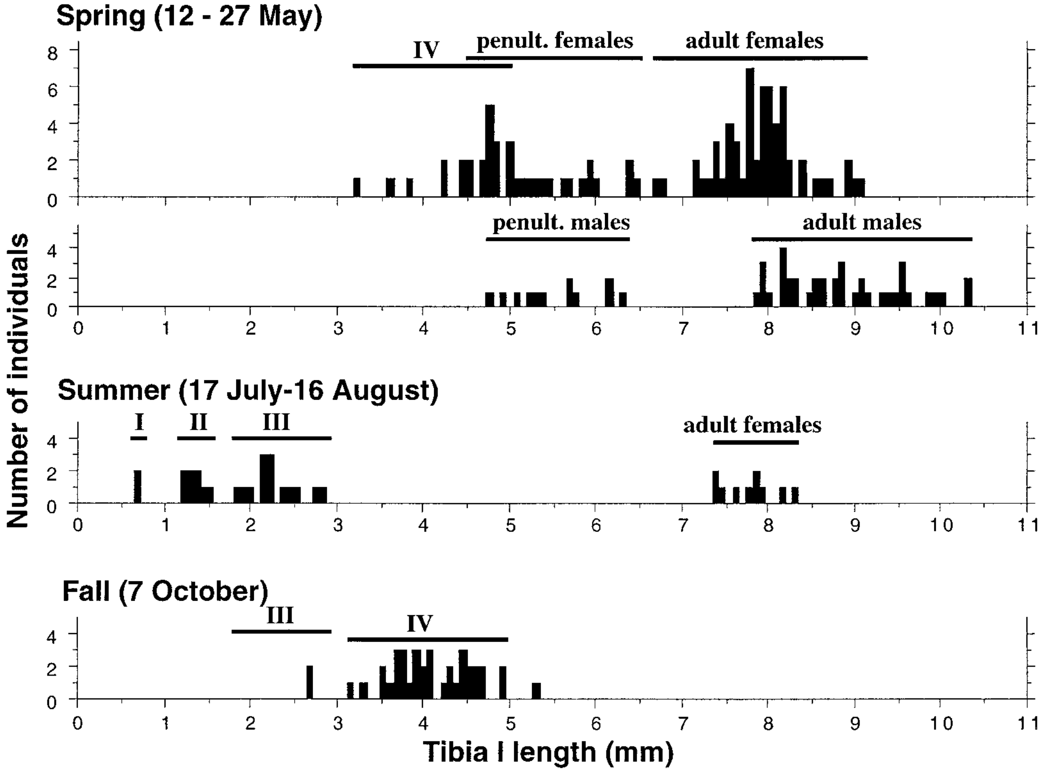

Figure 5.—Size (ITL) frequency distribution histograms of seasonal subsets of all 220 *Tetragnatha straminea* individuals collected at the two montane wetland sites during 1996 and 1997. Females and individuals too young to be sexed are graphed separately from penultimate and adult males. Labeled horizontal bars indicate ITL ranges of putative and known (adults and penultimate males) postemergent instars.

and assume this cryptic stick-like posture while hanging suspended in mid-air from its dragline.

Twice we were able to directly observe these spiders capture *Drosophila* flies without using a web. In the first observation, the fly was walking on the twig under which the spider was positioned cryptically. The fly appeared to hit one of the spider's third legs (which were wrapped around the twig) and it was seized instantly. In the second observation, the spider was ascending the side of its glass cage when a fly walked into it. The spider's first two pairs of legs instantly surrounded the fly for a brief moment until the spider could grasp it with its chelicerae. Silk was not used to immobilize either of these flies. Following these and other less closely observed capture attempts not involving webs, the spider crushed and manipulated the prey with its chelicerae and pedipalps. We often observed individuals holding in their chelicerae 1–5 flies which had been captured without a web. Occasionally, such spiders with two or more flies in their mouthparts would capture additional live flies (that we held in contact with the web) by grabbing them with the first legs and immediately wrapping them in silk with the hind legs. These immobilized flies were left attached to the web, and since we could not find them on the following day, we presume they were eaten.

DISCUSSION

Habitat and microhabitat distribution.—Clearly, *T. versicolor* is a habitat generalist. Our finding that it is common or abundant over a wide elevation range in a wide variety of forest communities as well as wetland, grass bald, and grassland habitats, is consistent with collection records cited by Levi (1981). Although it appears to prefer woody vegetation and can thrive in dryer situations than many of its congeners, it can also be found on herbaceous vegetation in marshy areas. Our observations, which are consistent with those of Comstock (1912), Lowrie (1953), Levi (1981), and Kaston (1981), show that *T. laboriosa*, like *T. versicolor*, often lives far from aquatic habitats, but, unlike *T. versicolor*, rarely occurs in forests and is virtually restricted to non-wetland grassy habitats. In spite of this restriction, it thrives over a wide range of natural and agricultural communities and elevations (Levi 1981) and is the most abundant spider in New York alfalfa fields (Wheeler 1973) and central Illinois soybean fields (LeSar & Unzicker 1978). We suspect that the very few individuals of *T. laboriosa* collected at forest sites within the GSMNP were immigrants that had ballooned from non-forest habitats and would not have matured and reproduced where we found them; this view is supported by LeSar & Unzicker's (1978) observations that early instars of *T. laboriosa* are good ballooners and colonizers and by the fact that every forest-dwelling individual we collected was an early instar juvenile.

Our data indicate that *T. straminea*, *T. viridis*, and *T. elongata* are all habitat specialists. The restriction of *T. straminea* to non-forested wetlands in the GSMNP is consistent with collection records cited by Levi (1981). Levi's (1981) observation that *T. viridis* is restricted to conifers matches our findings. We suspect that our data underestimates the abundance of *T. viridis* at the two sites where we found it because 1) it may frequent the large volume of hemlock canopy foliage above our sampling zone, 2) its green color and abandonment of web-building make it difficult to locate visually, and 3) it may be especially difficult to dislodge (Levi 1981). Our observation that *T. elongata* is strictly riparian and nearly always builds its webs over open water match those of Lowrie (1953), Levi (1981), Kaston (1981), and Gillespie (1987). According to the distribution records in Levi (1981), there are only two other species of *Tetragnatha* that we think might eventually be found in the GSMNP, *T. guatemalensis* O.P.-Cambridge 1889 and *T. pallescens* F.P. Cambridge 1903. If these two are living in the GSMNP, they are not common.

The finding that *T. versicolor* is distributed among more habitats in the GSMNP and elsewhere than are *T. straminea*, *T. viridis*, and *T. elongata*, and the observation that this species has a higher (67°N) and larger (54′) latitudinal and geographic (ca. 20.7 billion km^2) range than the other three species (46–57°N; 16–34′; 1.6–7.8 billion km^2) (Levi 1981), appear to fit a taxonomically widespread biodiversity pattern where habitat generalists in many taxa tend to occupy broader latitudinal and geographical ranges than do habitat specialists (Stevens 1989; Wilson 1992). However, *T. la-*

boriosa, which appears from our data to be less of a habitat generalist than *T. versicolor*, has much the same geographic range as *versicolor*. Apparently, the ability of *T. laboriosa* to colonize and reproduce in open habitats suits it well to utilizing a wide array of edaphic and early successional non-forest habitats which have proliferated because of increased human impact on landscapes and which are simply not well represented in the GSMNP. In other words, its status as a habitat generalist cannot be fully expressed in the GSMNP landscape.

Our results indicate that the coexistence of *T. versicolor* and *T. laboriosa* at the high grass bald site involves microhabitat segregation in a patchy community; *versicolor* lives primarily in the shrubs and small trees that are scattered within and surround the open areas of grass and other herbs where *laboriosa* lives. It is puzzling why no adults of *T. versicolor* were collected here despite the abundance of juveniles (Table 1). Perhaps this population is largely or wholly maintained by aerial immigration from high density forest-dwelling populations at lower elevations; this hypothesis remains to be tested. The beat vs. sweep data from the Indian Creek wetland site suggest that the *T. versicolor* population there is not as distinctly segregated from the *straminea* population. However, observations during an autumn sampling effort in the Meadow Branch wetland, as well as *T. versicolor*'s ability to prosper away from aquatic habitats, suggest to us that an appropriate sampling design would reveal that the *straminea* population is concentrated in grasses and other herbs in the wetter part of these wetlands while the *versicolor* population is chiefly found on taller and more sturdy vegetation in the dryer areas.

The significantly higher relative abundance values in 1997 as compared to 1996 for *T. versicolor* at several sites and for *T. laboriosa* at one site may be the result of population increases. However, we suspect that the 1997 sampling team devoted more effort to collecting small juveniles (particularly from beating sheets and sweep nets) than did the 1996 team, thus creating a bias which might have caused these relative abundance differences.

Life history.—Ours is the first life history analysis of *T. straminea*. This and other life history analyses of north temperate *Tetragnatha* species show that one-year life cycles may be the rule in this genus; Finnish populations of *T. extensa* (Linnaeus 1758), *T. obtusa* C.L. Koch 1837, and *T. montana* Simon 1874, and Illinois populations of *T. laboriosa* all have annual cycles (Toft 1976; LeSar & Unzicker 1978). Much like *T. straminea*, these species overwinter in mid-to-late juvenile instars and mature and mate in late spring or early summer. However, Juberthie (1954) showed that in southern France *Tetragnatha* species may have two generations per year. LeSar & Unzicker (1978) found that lab-reared *T. laboriosa* has eight postemergent instars, rather than the six our field data indicate for *T. straminea*, but the natural phenologies of these two species are very similar.

Behavior.—The cryptic, stretched-out stick-like postures of *T. straminea* (on its web, on vegetation, or hanging in mid-air), like similar postures adopted by other species of *Tetragnatha* and unrelated spiders like *Deinopis* MacLeay 1839 (Comstock 1912; Bristowe 1958; McKeown 1963; Forster & Forster 1973; Levi 1981; Kaston 1981; Gillespie & Croom 1995; Getty & Coyle 1996), surely must serve to reduce an individual's chances of being detected or recognized as prey by visual predators. The remarkably flexible prey capture behavior we have observed in *T. straminea*—the ability to catch prey both with and without the use of a web—has also been observed by Luczak & Dabrowska-Prot (1966) in a Eurasian species, *T. montana*. This versatile capture program, which may be more widespread in the genus than is currently appreciated, may help explain the origin of non-web-building cursorial spiny-legged lineages represented by *T. viridis* (Levi 1981) and several Hawaiian species (Gillespie & Croom 1995).

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APPENDIX

Habitat type, locality data, collecting dates, and sampling effort for each of the 17 focal sites (listed in order from highest to lowest elevation). Number of ground, aerial, beat, and sweep samples given in parentheses after total number of one-hour samples.

Spruce-fir forest: NORTH CAROLINA: *Swain County*, 0.5 km SW Mt. Collins, N & S sides of Appalachian Trail, E2755, N39403, 1815–1845 m elev., 26 June 1996, 14 September 1996, 11 June 1997, 23 August 1997. 48 samples (16–16–16–0).

High grass bald: NORTH CAROLINA: *Swain County*, Andrews Bald, E2738, N39354, 1755 m elev., 27 June 1996, 22 September 1996, 12 June 1997, 6 September 1997. 48 samples (18–0–12–18).

Spruce forest: NORTH CAROLINA: *Swain County*, just SW junction of Noland Divide Trail and road to pumping station, E2755, N39382, 1715 m elev., 20 June 1996, 7 September 1996, 10 June 1997, 23 August 1997. 48 samples (16–16–16–0).

Beech gap forest: NORTH CAROLINA: *Swain County*, in hog exclosure below Appalachian Trail at 350 m E Road Prong Trailhead, E2786, N39433, 1645 m elev., 14 June 1996, 15 August 1996, 10 June 1997, 13 August 1997. 48 samples (16–16–16–0).

Northern hardwood forest: NORTH CAROLINA: *Haywood County*, Cataloochee Divide just above Hemphill Bald Trail at 200 m E Garrett's Gap, E3055, N39359, 1615 m elev., 12 and 15 June 1996, 14 August 1996, 6 June 1997, 12 August 1997. 84 samples (29–27–28–0).

Red oak forest: NORTH CAROLINA: *Swain County*, Roundtop Knob, E of Noland Divide Trail about 2 mi SE Clingman's Dome Road, E2770, N39364, 1555 m elev., 24 June 1996, 31 August 1996, 4 June 1997, 11 August 1997. 88 samples (30–28–30–0).

Low grass bald: NORTH CAROLINA: *Swain County*, Gregory Bald, E2401, N39343, 1505 m elev., 3–5 June 1995, 29–30 September 1995. 72 samples (24–0–24–24).

Heath bald: TENNESSEE: *Sevier County*, Inspiration Point on Alum Cave Trail, E2789, N39461, 1390 m elev., 25–25 May 1995, 23–24 September 1995. 72 samples (24–24–24–0).

Mixed oak forest: TENNESSEE: *Sevier County*, E, S, & W slopes of Chinquapin Knob, E2639, N39512, 1083–1144 m elev., 13 June 1996, 13 August 1996, 2 June 1997, 7 August 1997. 85 samples (29–26–30–0).

Table Mountain pine forest: TENNESSEE: *Sevier County*, about 200 m N of route 441 loop NW of Chimneys picnic area, E2738, N39471, 976–1037 m elev., 6 June 1996, 6 August 1996, 27 May 1997, 6 August 1997. 64 samples (23–18–23–0).

Hemlock-hardwood cove forest: TENNESSEE: *Sevier County*, N & E Grotto Falls Trailhead at Roaring Fork Motor Trail, P. White veg. plot, E2772, N39512, 945 m elev., 22 May 1996, 30 July and 1 August 1996, 19 May 1997, 4 August 1997. 96 samples (32–32–32–0).

Hemlock forest: NORTH CAROLINA: *Haywood County*, Cataloochee, 150 m S mouth of Palmer Branch at Caldwell Fork, E3107, N39436, 854–915 m elev., 4 June 1996, 5 August 1996, 18 May 1997, 1 June 1997, 10 and 24 August 1997. 84 samples (29–26–29–0).

Hardwood cove forest: TENNESSEE: *Sevier County*, along Porter's Creek Trail at 200 paces above bridge over Porter's Creek, E2830, N39508, 740 m elev., 18–19 June 1996, 24–25 August 1996, 21–22 May 1997, 31 July 1997. 116 samples (39–37–40–0).

Wetland (Indian Creek): NORTH CAROLINA: *Swain County*, marsh between Indian Creek Trail and Indian Creek at 2 mi. NE of junction with Deep Creek Trail, E2817, N39296, 685 m elev., 27 May 1996, 16 August 1996, 12 May 1997, 29 July 1997. 33 samples (14–4–8–7).

Wetland (Meadow Branch): TENNESSEE: *Blount County*, marsh along Meadow Branch at 0.5 km ENE of Dosey Gap, E2527, N39470, 535 m elev., 23 May 1996, 1 August 1996, 15 May 1997, 17 July 1997. 33 samples (13–8–0–12).

Native grassland: TENNESSEE: *Blount County*, Cades Cove, S side Abrams Creek about 0.3 mi. upstream from Cades Cove Loop Road bridge, E2426, N39423, 520 m elev., 5 June 1996, 8 August 1996, 15 May 1997, 17 July 1997. 48 samples (24–0–0–24).

Pine-oak forest: TENNESSEE: *Blount County*, 300 m N of junction of Tabcat Creek and Maynard Creek, E2301, N39347, 395 m elev., 28–29 May 1996, 2 August 1996, 14 May 1997, 15 July 1997. 96 samples (32–32–32–0).