

Habitat distribution and life history of *Araneus* spider species in the Great Smoky Mountains National Park

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Summary

Habitat distribution patterns of nine *Araneus* species were studied by analysing 1,163 1-hr samples from 17 focal sites representing 16 major habitats in the Great Smoky Mountains National Park. Of the five large-bodied *diadematus* group species, *A. nordmanni* is common or abundant in 12 of the 16 habitats (ten forest types, heath bald, and high grass bald), *A. marmoreus* is common or abundant in five habitats (four forest types and high grass bald), *A. trifolium* is restricted to grass balds, and *A. bicentarius* and *A. iviei* are virtually restricted to (and uncommon in) forest edge and marsh habitats, respectively. In the three forest communities (red oak, northern hardwood, and beech gap) where *A. nordmanni* and *A. marmoreus* coexist at high densities, microhabitat segregation exists, at least in the adult stage; *nordmanni* females use only trees as retreat/web substrates and *marmoreus* females use only the herbaceous vegetation of tree gaps. This preference for tree gaps means that *A. marmoreus* is an indicator of forest decline. Of the four small-bodied *Araneus* species (*A. cingulatus*, *A. miniatus*, *A. pegnia* and *A. pratensis*), only *A. pratensis*, which is restricted to grassland, appears to be common or abundant in any habitat. Size frequency histograms of seasonal samples of *A. nordmanni* and *A. pratensis* specimens indicate that the former species has a two-year life cycle with eight post-emergent (post-eggsac) instars and the latter has a one-year life cycle with seven post-emergent instars. Spiderlings of *A. nordmanni* emerge from the egg sac in the spring, develop to post-emergent instar IV, V or VI before overwintering, and then reach adulthood and reproduce during their second summer. Spiderlings of *A. pratensis* emerge from the egg sac in early summer, develop to the antepenultimate or penultimate instar by winter, and mature and reproduce in the following spring.

Introduction

Because spiders are abundant and highly diverse (Coddington & Levi, 1991; Platnick, 1999) and are important regulators of terrestrial arthropod populations (Reichert & Bishop, 1990; Carter & Rypstra, 1995; Sunderland, 1999), they 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; Norris, 1999). However, progress in understanding the ecological roles of spiders is hampered in part by inadequate knowledge of the habitat preferences and life histories of many species (Duffey, 1978). Ecologists stress the need to understand the autecology and life histories of species before important insights into food web dynamics and other aspects of community dynamics can be unveiled (Olive, 1980; Strong *et al.*, 1984; Polis *et al.*, 1996; Uetz *et al.*, 1999). This view has been broadcast by Wilson's (1992) assertion that "only with a detailed knowledge of the life

cycles and biology of large numbers of constituent species will it be possible to create principles and methods that can precisely chart the future of ecosystems".

The orb-weaver genus *Araneus*, distributed over much of the world, contains some of the commonest and most widespread spider species in the northern hemisphere (Levi, 1971), and may therefore be an important component of many spider assemblages. In North America north of Mexico, Levi (1971, 1973, 1975, 1981) recognises 19 large-bodied species of *Araneus* in the *A. diadematus* species group and another 33 small-bodied *Araneus* species belonging to one or more other species groups. In spite of the probable ecological importance of this genus, only fragmentary knowledge of habitat distribution exists for most of its species, and the life histories of no native North American and only a few European *Araneus* species have been rigorously analysed and described. Although the observations of Bonnet (1930), Wiehle (1931), Nielsen (1932), Colebourn (1974) and Toft (1976) reveal that northern European populations of *A. diadematus* have a two-year life cycle and southern European populations may have a one-year life cycle, Levi (1971) stated (without presenting supporting evidence) that all North American species of the *diadematus* group have a one-year life cycle. Olive (1980), however, on the basis of size-frequency analysis of limited samples, concluded that *Araneus trifolium* (a *diadematus* group species) probably has a two-year life cycle in southern Michigan.

In this paper, we describe the habitat distribution patterns of the nine *Araneus* species found in the Great Smoky Mountains National Park Biosphere Reserve (GSMNP), which, owing 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 rigorous analyses and descriptions of the life histories and phenologies of North American species of *Araneus*. We hope that these findings will help make this interesting assemblage of spiders more accessible to ecologists.

Methods

Habitat distribution

Teams of three to five (usually four) collectors used a modified Coddington sampling protocol (Coddington *et al.*, 1996) to obtain the 1,163 1-hr ground (408), aerial (310), beat (360), and sweep (85) samples used in this project. Ground collection involved searching mostly on hands and knees, exploring leaf litter, logs, rocks, and plant surfaces below knee level. 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 catching the dislodged spiders on a square 0.5 m² canvas sheet held horizontally below the vegetation. Hands and aspirators

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were used to collect the spiders into 80% ethanol. One sample unit equalled 1 hr of uninterrupted effort with one of these three methods, during which the collector attempted to collect every spider encountered. During each hour the team as a whole used all three methods in the same area. In non-forest communities (grass bald, montane wetland, and native grassland sites) 1-hr 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 hr (range 175–400, mean and SD=268 ± 47.7) depended primarily on vegetation structure and spider abundance.

Two sets of samples (one in spring and one in late summer) were collected in each of two years (1996 and 1997) from 15 sites and in 1995 from a low grass bald and a heath bald site. These 17 focal sites represent the 16 major habitat (community) types found in the GSMNP, located in the southern Appalachian Mountains of eastern North America. One of these habitats, montane wetland, was represented by two sites because each was too small to support the sampling effort judged necessary for this study. Habitat type, locality data, collecting dates, and sample sizes for each focal site are given in the Appendix. With the exception of the high grass bald and the Indian Creek wetland sites, nearly equal numbers of samples were collected within each site with each of the methods employed.

All adult and juvenile *Araneus* specimens were sorted from each sample and identified to the species level. Pigment pattern and abdominal shape are distinctive for each species in all post-eggsac instars. Before the distinctive anterior lateral prominence appears on each side of the abdominal dorsum of *A. nordmanni* (one or two instars after emerging from the eggsac), this species can be distinguished from *A. marmoreus* by the absence of a dark median longitudinal line on the caput (present in *marmoreus*) and by oblique (slanted) dark bars on the

border of the dorsal abdominal folium (essentially transverse in *marmoreus*).

The relative abundance (mean number of individuals per 1-hr 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 show the often wide variation in number of individuals among 1-hr samples at each site, variation caused largely by method bias in particular microhabitats, by spatial environmental variation within each site, and by seasonal changes in spider abundance correlated with species' phenologies. ANOVA was used to examine the effect of year and method on spider abundance, Fisher's PLSD was used to test for significance in pairwise comparisons, and $p < 0.05$ was our significance criterion. Observations of the form and location of adult female retreats and webs were recorded with field notes and photographs.

Life history

We measured the length of the left tibia I (ITL) (along the dorsal surface) of all *A. nordmanni* specimens collected at the northern hardwood site in 1996 ($n=238$) and at the hardwood cove site in 1997 ($n=187$). We also measured 32 antepenultimate and penultimate males and females collected at several sites in 1996. Similarly, we measured the ITL of 650 *A. pratensis* specimens collected at the native grassland site on 8 August 1996, 15 May and 17 July 1997, and 19 September 1998. Toft (1976) and Lowder & Coyle (in prep.) have demonstrated that ITL typically 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 50× (*A. nordmanni*) and 100× (*A. pratensis*) magnification and are accurate to ± 0.0185 mm and ± 0.00925 mm respectively. We used the StatView 5.0 computer program (SAS Institute, Inc.)

Habitat/focal site	Relative abundance (mean number of individuals per sample)									
	<i>diadematus</i> -group species					small-bodied species				
	<i>bicentenarius</i>	<i>iviei</i>	<i>marmoreus</i>	<i>nordmanni</i>	<i>trifolium</i>	<i>cingulatus</i>	<i>miniatus</i>	<i>pegnia</i>	<i>pratensis</i>	
Spruce-fir (1830)				2.9, 0.3						
High grass bald (1755)			1.4, 0.8	3.2, 0.4	7.4, 13.8				0.3, 0	
Spruce (1715)				7.9, 2.2						
Beech gap (1645)			6.3, 11.0	3.5, 1.6						
Northern hardwood (1615)			1.1, 3.7	22.9, 14.6						
Red oak (1555)			1.5, 7.1	9.7, 12.3	0.02, 0					
Low grass bald (1505)				0.08	1.1					
Heath bald (1390)				0.5						
Mixed oak (1115)			0.02, 0	4.1, 6.8						
Table Mtn. pine (1005)			0.03, 0.1	0.4, 1.8			0, 0.1			
Hemlock-hardwood cove (945)				1.3, 4.2			0, 0.1			
Hemlock (885)			0, 0.03	0.7, 1.1			0.3, 0.6			
Hardwood cove (740)			0.09, 0.07	0.9, 3.1			0.06, 0.02	0.05, 0		
Wetland (Indian Cr.) (685)	0, 0.06	0.06, 0.2	0.1, 0				0.2, 0			
Wetland (Meadow Br.) (535)	0, 0.3	0.4, 0.2	0.1, 0.3	0.06, 0			0, 0.1			
Native grassland (520)										8.0, 21.0
Pine-oak (395)	0.04, 0.02		0.3, 1.0	0, 0.04		0.3, 0		0.04, 0.08		

Table 1: Relative abundance of *Araneus* species at 17 focal sites representing 16 habitats in the Great Smoky Mountains National Park in 1996 and 1997 (1996 and 1997 values separated by comma). Low grass and heath balds were sampled in 1995 only. Elevation (m) of each site given in parentheses.

to generate ITL frequency distribution histograms for these samples. From the histograms of pooled samples for each species, it was possible to determine instar numbers. Instars were also revealed by the distinctive widths of palpal tarsi of older juvenile males, the pre-epigynal rudiments of penultimate females, and the epigyna and palpal organs of adults. Phenology and generation time were determined by comparing histograms of each seasonal data set and examining the relationship between instar distribution and collecting date.

Results

Habitat distribution

Of the nine species of *Araneus* found at the 17 focal sites, five (*A. bicentenarius* (McCook), *A. iviei* (Archer), *A. marmoreus* Clerck, *A. nordmanni* (Thorell) and *A. trifolium* (Hentz)) are large-bodied species belonging to

the *diadematus* species group and four (*A. cingulatus* (Walckenaer), *A. miniatus* (Walckenaer), *A. pegnia* (Walckenaer) and *A. pratensis* (Emerton)) are small-bodied species not belonging to the *diadematus* group. *Araneus nordmanni* was found at more sites and in greater overall abundance than were any of the other *Araneus* species (Table 1, Fig. 1). This species was common (relative abundance=0.5–2.0) or abundant (relative abundance >2.0) in 12 of the 16 habitats (ten forest types, heath bald, and high grass bald). *Araneus marmoreus*, the second most widespread and abundant species, was common or abundant in five habitats (four forest types and high grass bald). *Araneus trifolium* was virtually restricted to grass balds. *Araneus bicentenarius* was uncommon and found only at the wetland (in trees) and pine-oak (in a tree gap) sites. *Araneus iviei* was collected only at the wetland sites, where it was uncommon. Of the four small-bodied species, only *A. pratensis*, which was found only in the native grassland and high grass bald sites, and *A. miniatus*, which was common in

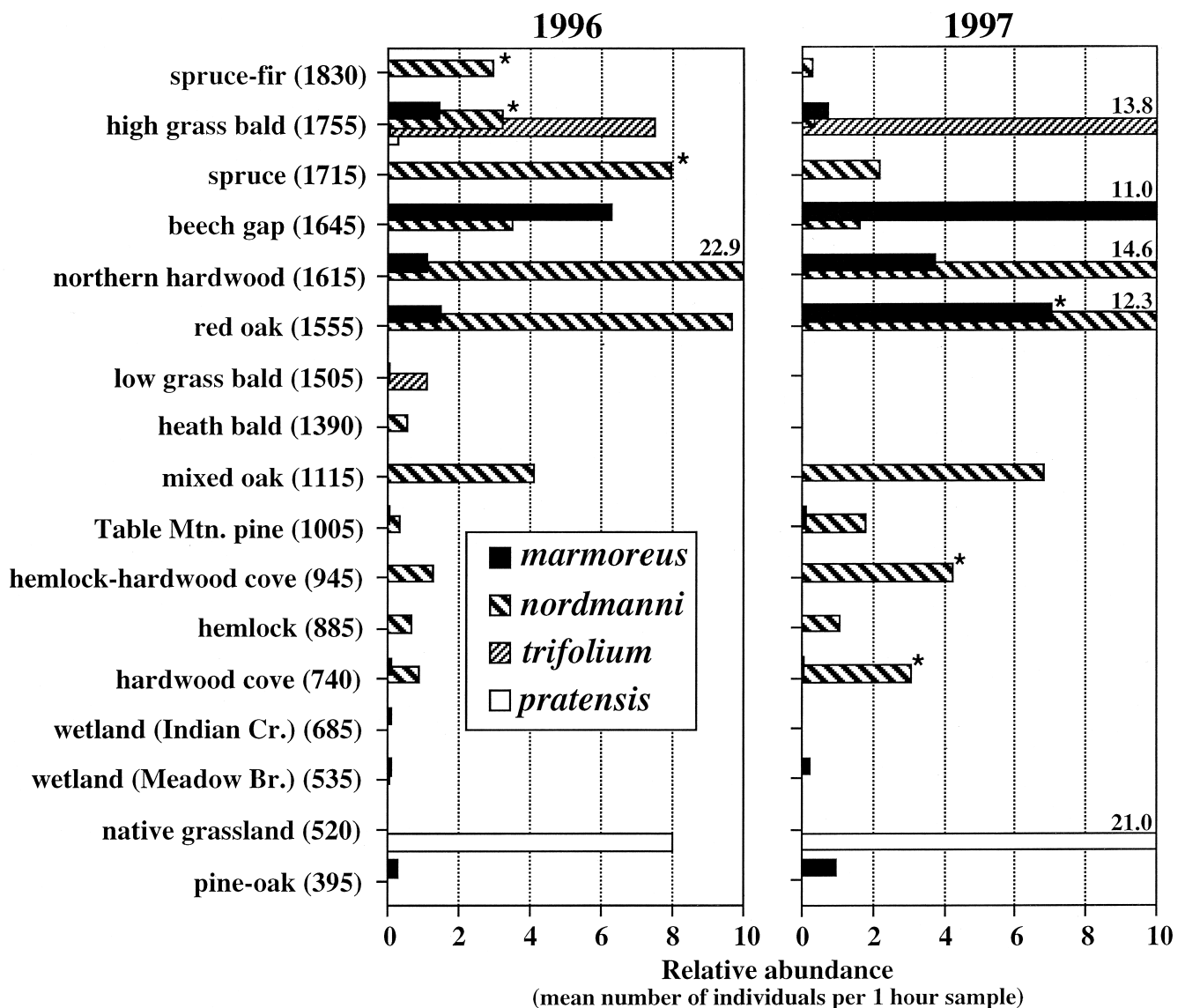


Fig. 1: Relative abundance of the four commonest *Araneus* species collected in 1996 and 1997 in the Great Smoky Mountains National Park at 17 focal sites representing 16 major habitats. Low grass and heath bald sites were sampled in 1995 only. Focal sites are listed in order from highest to lowest elevation (in m). 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, Fisher's PLSD, $p < 0.05$).

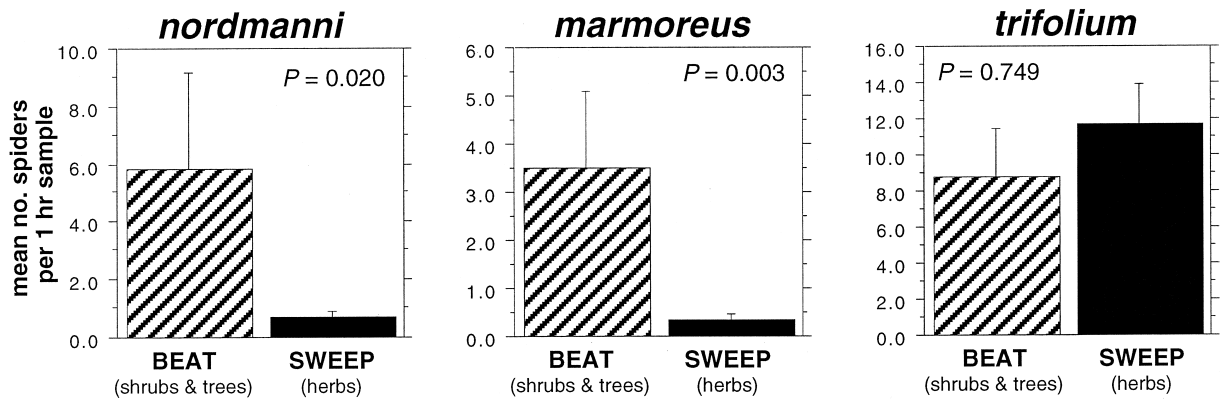


Fig. 2: Microhabitat distribution of *Araneus* species at the high grass bald site. Standard error shown on top of bars; $n=12$ beat and 18 sweep samples; p -values generated by ANOVA, Fisher's PLSD.

the hemlock forest in 1997, were common or abundant in any habitat. *Araneus miniatus* was found at six sites, *A. pegnia* at two, and *A. cingulatus* at one. There was a significant difference in relative abundance between 1996 and 1997 for *A. nordmanni* at five sites (Fig. 1); at three high elevation sites (spruce-fir, high grass bald, and spruce) it was more abundant in 1996, and at two other sites (hemlock-hardwood cove and hardwood cove) it was more abundant in 1997. *Araneus marmoreus* exhibited a significant relative abundance change only at the red oak site (Fig. 1). Although more *Araneus* species (five) were found in the wetland and pine-oak sites than at any others, five other sites (high grass bald, beech gap, northern hardwood, red oak, and hemlock) were the only ones found to support two or three coexisting species with relative abundances of 0.5 or more

(*marmoreus*, *nordmanni* and *trifolium* at the grass bald, *nordmanni* and *miniatus* at the hemlock site, and *marmoreus* and *nordmanni* at the other three sites).

Microhabitat distribution and web structure

Adult female webs and retreats of *A. nordmanni* and *A. bicentenarius* were found only on tree trunks and branches. Two measured adult female *A. bicentenarius* webs were approximately 2.1 and 3.1 m from hub to ground, 0.6 and 0.7 m in diameter (sticky spiral), and 2.7 and 3.7 m from retreat to ground. Webs of adult female *A. marmoreus* were almost always found between knee and chest level in thick herbaceous vegetation. The *marmoreus* female is hidden in a cone-shaped leaf retreat constructed by pulling together and attaching with silk

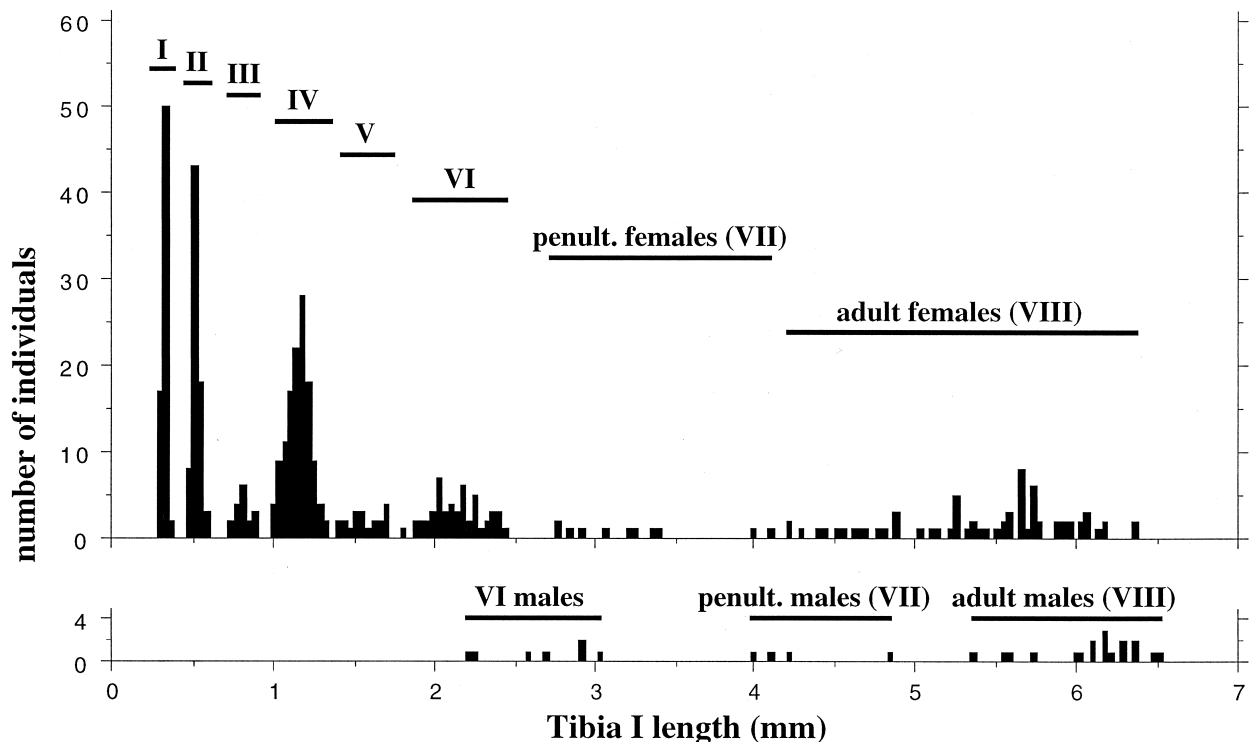


Fig. 3: Size (ITL) frequency distribution histograms of pooled samples of *Araneus nordmanni* collected at the hardwood cove (1997) and northern hardwood (1996) focal sites and all 32 pre-adults (antepenultimate and penultimate males and females) collected at other sites in 1996. Females and individuals too young to be sexed were graphed separately from males. Instars are designated by Roman numerals. Instar I is the first post-emergent instar, i.e. the instar that emerges from the eggsac.

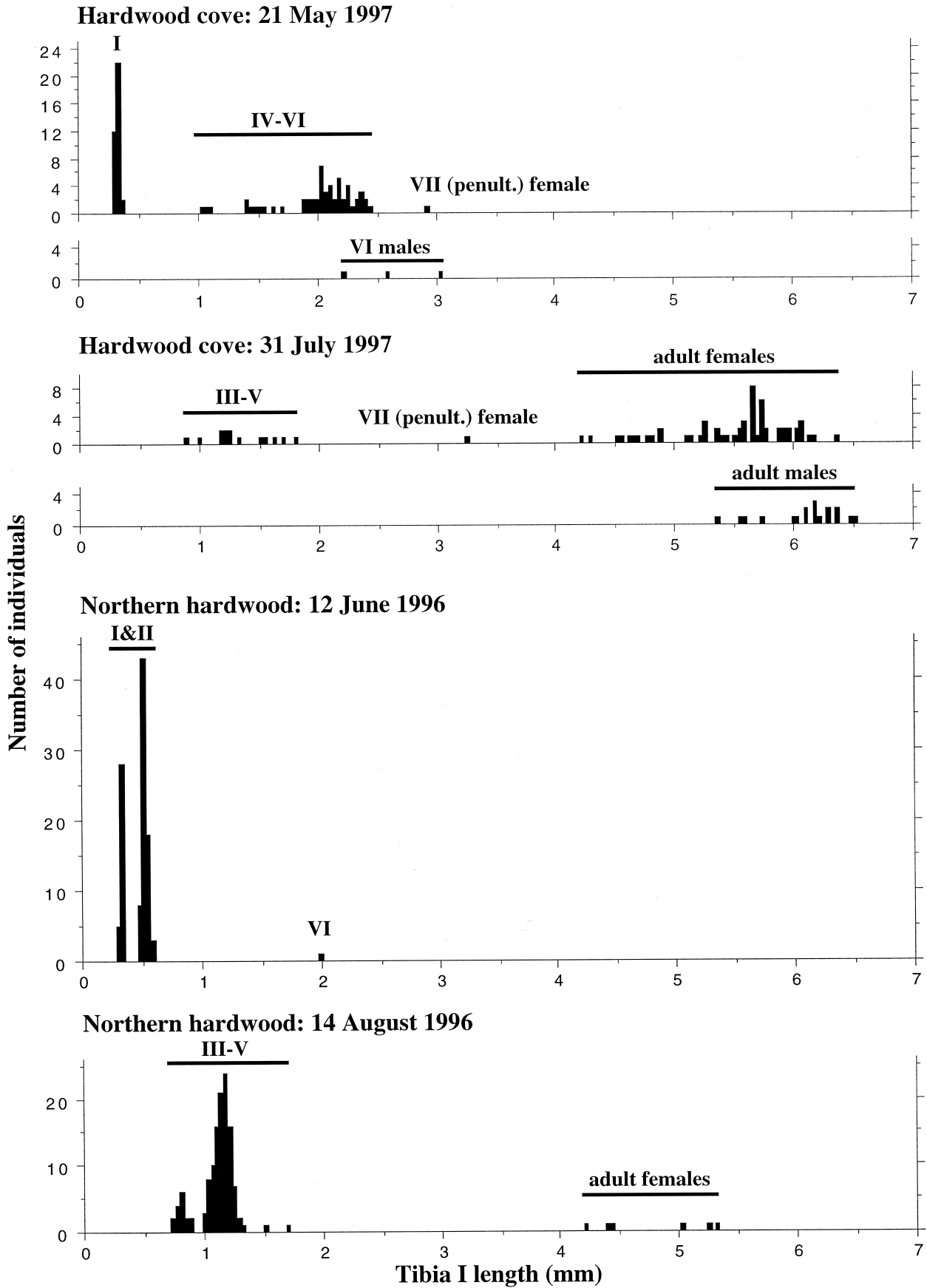


Fig. 4: Size (ITL) frequency distribution histograms of four samples of *Araneus nordmanni* collected in the spring and summer at the hardwood cove and northern hardwood focal sites. Females and individuals too young to be sexed were graphed separately from males. Instars are designated by Roman numerals. Instar I is the first post-emergent instar, i.e. the instar that emerges from the eggsac.

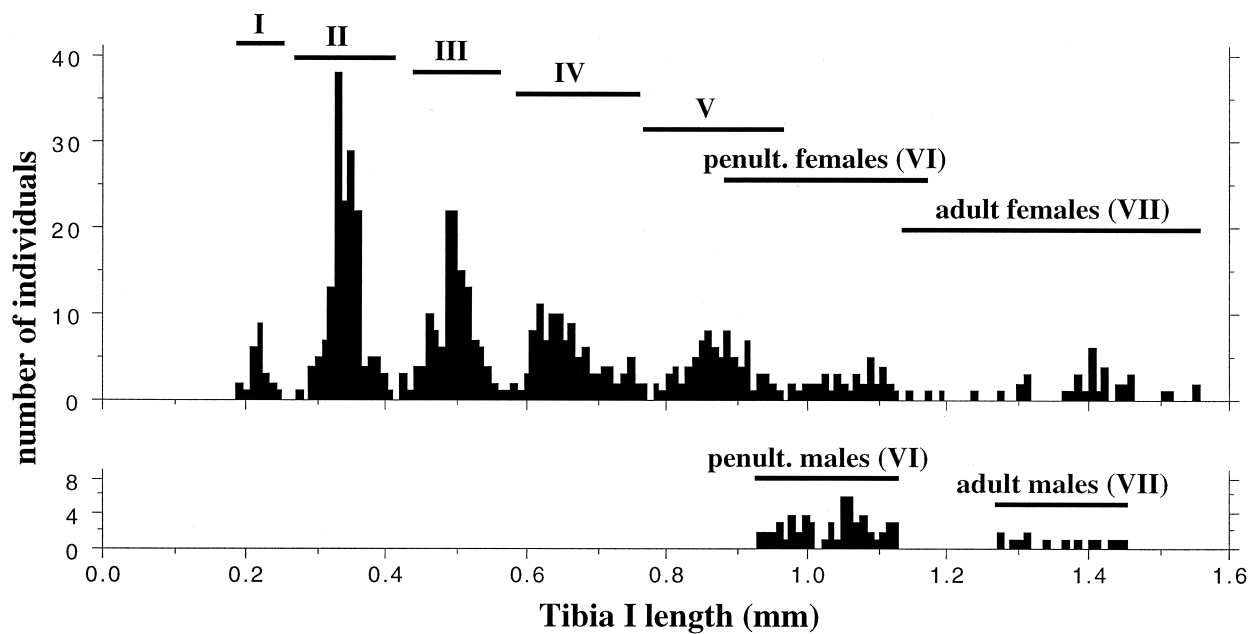


Fig. 5: Size (ITL) frequency distribution histograms of pooled samples of *Araneus pratensis* collected at the native grassland focal site. Females and individuals too young to be sexed were graphed separately from males. Instars are designated by Roman numerals. Instar I is the first post-emergent instar, i.e. the instar that emerges from the eggsac.

the edges of a green leaf located above or beside the web. Adult females of *A. trifolium* and *A. iviei* also construct similar conical leaf retreats in herbaceous vegetation. At the grassland site, *A. pratensis* was often observed in its small orb web completely supported by a long, strongly arched grass stem or blade.

In the three forest sites where *A. nordmanni* and *A. marmoreus* coexist at high densities (beech gap, northern hardwood, and red oak), *A. marmoreus* females were virtually restricted to the lush tall herbaceous vegetation found in the tree gaps common at these sites, whereas *A. nordmanni* females were restricted to trees. At the high grass bald, where three *diadematus* group species occur together, both *nordmanni* and *marmoreus* were significantly more numerous in beat samples (collected from shrubs and trees) than in sweep samples (collected from low herbaceous vegetation), whereas *trifolium* was not (Fig. 2). None of the 86 *nordmanni* specimens, only four of the 52 *marmoreus* specimens, and 35 of the 509 *trifolium* specimens collected at this site were adults or pre-adults (in the last few instars).

Life history

The distinct gaps between all size classes (except for the penultimate and adult females) in pooled samples of *A. nordmanni* indicate that there are eight post-emergent instars (instars living outside the eggsac) in the life cycle of this species (Fig. 3). Instar VI (antepenultimate) males have a distinctly swollen palpal tarsus. Instar VII (penultimate) males have a much more strongly swollen palpal tarsus. In penultimate females (instar VII) a rudimentary scape is clearly visible. That *A. nordmanni* has a two-year life cycle is demonstrated by the presence, in each sampling season at each site, of two distinct size/age classes separated by gaps of one to three missing instars and by the presence of adults in summer but not

in spring samples (Fig. 4). The temporal pattern of these data shows that individuals emerge from the eggsac in the spring of their first year, overwinter in post-emergent instar IV, V or VI, reach maturity in July and early August of their second year, and reproduce and die off before winter.

Size frequency histograms of ITL for the pooled samples of *A. pratensis* indicate that there are seven post-emergent instars in the life cycle of this species (Fig. 5). Penultimate males have a much more swollen palpal tarsus (PTW=0.39–0.45 mm, $n=59$) than do all other juveniles (maximum PTW=0.20 mm). Penultimate females are distinguished by a distinctive pre-epigynal swelling. The presence of only a single age cohort in May, August and September, and the fact that the older cohort in July consists of a few surviving adult females that will soon die, show us that *A. pratensis* has a one-year life cycle (Fig. 6). The temporal pattern of these data shows that spiderlings emerge from the eggsac in June and early July, reach the penultimate instar before over-wintering, and moult to adulthood and reproduce in the spring.

Discussion

Habitat distribution

Our finding that *A. nordmanni* is a common forest-dwelling species that uses branches as retreat and web substrates is consistent with published observations (Levi, 1971; Kaston, 1981). Although this species may be fairly common on some grass balds, its greater abundance in beat than in sweep samples and the absence of sub-adults and adults suggest that it is largely restricted to the islands of shrubs and trees on the bald and is a non-reproducing population annually replenished by aerial immigration of spiderlings from nearby

forest communities. Also consistent with published accounts are our observations that *A. marmoreus* prefers forest edges and tree gaps (Levi, 1971), that *A. trifolium* prefers meadows with sturdy herbs and shrubs (Levi, 1971; Olive, 1980; Kaston, 1981), and that *A. iviei* prefers wetlands (Levi, 1971). Our study considerably extends the known range of *A. iviei*, which had previously not been found south of Pennsylvania (Levi, 1971). Our observation that *A. bicentenarius* is uncommon and lives in trees in open canopy forest and forest edge is also consistent with literature records (Levi, 1971; Rossman, 1977; Kaston, 1981) and the general collecting experience of one of us (FAC) in the southern Appalachians over the past 30 years. The ability of the

small-bodied *A. pratensis* to utilise grasses and probably other low flexible herbs to support its webs helps explain the abundance of this species in grassland habitats that support few if any other *Araneus* species. Consistent with our observations, Levi (1973) reported that this species is commonly swept from fields, moist open meadows, and alfalfa.

Our observations suggest that the coexistence of relatively dense populations of two *diadematus* group species, *A. nordmanni* and *A. marmoreus*, in three high elevation forest communities (beech gap, northern hardwood, and red oak) is at least partly explained by the different substrate requirements of the adult females (and perhaps pre-adults) of these species and

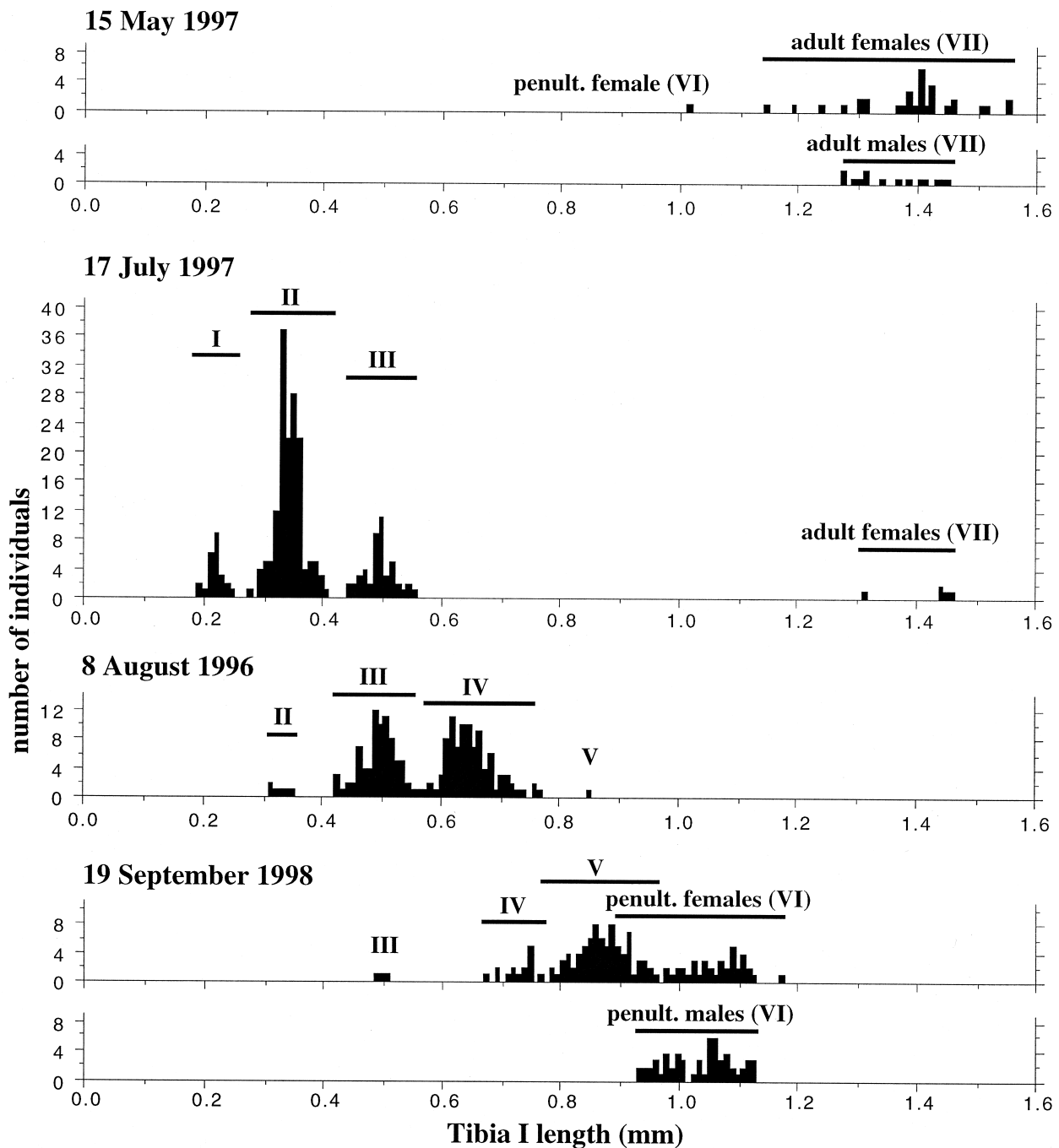


Fig. 6: Size (ITL) frequency distribution histograms of four samples of *Araneus pratensis* collected at different seasons at the native grassland focal site. Females and individuals too young to be sexed were graphed separately from males. Instars are designated by Roman numerals. Instar I is the first post-emergent instar, i.e. the instar that emerges from the eggsac.

the frequent tree gaps in these communities. These gaps permit the lush growth of tall sturdy herbs needed by *marmoreus* for leaf retreats. Such retreat substrates are lacking in adjacent closed canopy areas where an abundance of tree branches provides retreat and web attachment surfaces for *nordmanni* adults. We predict that the observed increase of tree gaps in these three forest types, apparently caused by the spread of introduced tree pathogens and increased air pollution (Anonymous, 1996; R. Dellinger, pers. comm.), will result in increases in *marmoreus* populations. In effect, *A. marmoreus* is an indicator of decline in these forests.

The three *diadematus* group species (*nordmanni*, *marmoreus* and *trifolium*) that are especially abundant at high elevation sites are also the ones which range into the most northerly latitudes (Levi, 1971). This correlation presumably results from the common effect of increasing latitude and increasing elevation on temperature and, therefore, climate. Similarly, the virtual absence of the four small-bodied species in samples from high elevation sites is not unexpected, given the warmer climates of the latitudes (8–45°N) inhabited by these species. This observation must be tempered, however, by the possibility that some of these small-bodied species are principally forest canopy dwellers (Levi, 1973; Coddington, 1987) which are not adequately sampled by our methods. The finding that *A. nordmanni* and *A. marmoreus* are distributed among more habitats in the GSMNP than are other *Araneus* species, coupled with the observation that these two species have larger latitudinal (36 and 37°) and geographic (c. 30 million mi²) ranges than the other seven species (14–36°; 3–7 million mi²) (Levi, 1971; 1973), fits 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).

Life history

Our demonstration that *A. nordmanni* requires two years to complete its life cycle in middle and high elevation southern Appalachian forests, Olive's (1980) evidence for a biennial cycle in a Michigan population of *A. trifolium*, our casual observations that seasonal size class distributions of *A. trifolium* and *A. marmoreus* are similar to those of *A. nordmanni*, and life history data for northern European populations of *A. diadematus* (Wiehle, 1931; Nielsen, 1932; Colebourn, 1974; Toft, 1976) all force us to reject Levi's (1971) hypothesis that North American *diadematus* group species have one-year life cycles.

It seems likely that, as Burch (1979) observed for *A. diadematus*, *A. nordmanni* spiderlings emerge from the egg sac in their second instar and therefore become adults as they enter the tenth instar. Toft (1976) tentatively concluded that *A. diadematus* in Denmark probably passes through only six post-emergent instars, but indicated that he wished he had more data. Other than this possible difference in instar number, the phenologies

of *diadematus* in Denmark and *nordmanni* in the GSMNP are similar.

Because *A. pratensis* is so much smaller than *A. nordmanni* or any other *diadematus* group species, it is not surprising that it reaches maturity within a year. We are not aware of any published life history studies of any other small-bodied *Araneus* species, but predict that they will prove to be annual like *A. pratensis*. The literature indicates that at least some other small *Araneus* species, like *A. pratensis*, mature in the spring rather than summer and autumn (as do *diadematus* group species) (Levi, 1973; Kaston, 1981; Roberts, 1995).

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- small gray beech trees (*Fagus grandifolia*) and typically located on a south-facing slope in a high mountain gap. Appalachian cove forests are found in sheltered middle elevation sites and are characterized by a high species diversity of large tree and understory plants.
- Spruce-fir forest*: NC: Swain Co., 0.5 km SW Mt. Collins, N & S sides of Appalachian Trail, E2755, N39403, 1815–1845 m elev., 26 June and 14 September 1996, 11 June and 23 August 1997, 48 samples (16-16-16-0).
- High grass bald*: NC: Swain Co., Andrews Bald, E2738, N39354, 1755 m elev., 27 June and 22 September 1996, 12 June and 6 September 1997, 48 (18-0-12-18).
- Spruce forest*: NC: Swain Co., just SW junction of Noland Divide Trail and road to pumping station, E2755, N39382, 1715 m elev., 20 June and 7 September 1996, 10 June and 23 August 1997, 48 (16-16-16-0).
- Beech gap forest*: NC: Swain Co., in hog enclosure below Appalachian Trail at 350 m E Road Prong Trailhead, E2786, N39433, 1645 m elev., 14 June and 15 August 1996, 10 June and 13 August 1997, 48 (16-16-16-0).
- Northern hardwood forest*: NC: Haywood Co., Cataloochee Divide just above Hemphill Bald Trail at 200 m E Garrett's Gap, E3055, N39359, 1615 m elev., 12 and 15 June and 14 August 1996, 6 June and 12 August 1997, 84 (29-27-28-0).
- Red oak forest*: NC: Swain Co., Roundtop Knob, E of Noland Divide Trail about 3 km SE Clingman's Dome Road, E2770, N39364, 1555 m elev., 24 June and 31 August 1996, 4 June and 11 August 1997, 88 (30-28-30-0).
- Low grass bald*: NC: Swain Co., Gregory Bald, E2401, N39343, 1505 m elev., 3–5 June and 22–24 September 1995, 72 (24-0-24-24).
- Heath bald*: TN: Sevier Co., Inspiration Point on Alum Cave Trail, E2789, N39461, 1390 m elev., 25–26 May and 23–24 September 1995, 72 (24-24-24-0).
- Mixed oak forest*: TN: Sevier Co., E, S, & W slopes of Chinquapin Knob, E2639, N39512, 1083–1144 m elev., 13 June and 13 August 1996, 2 June and 7 August 1997, 85 (29-26-30-0).
- Table Mtn. pine forest*: TN: Sevier Co., about 200 m N of route 441 loop NW of Chimneys picnic area, E2738, N39471, 976–1037 m elev., 6 June and 6 August 1996, 27 May and 6 August 1997, 64 (23-18-23-0).
- Hemlock-hardwood cove forest*: TN: Sevier Co., N & E Grotto Falls Trailhead at Roaring Fork Motor Trail, P. White veg. plot, E2772, N39512, 945 m elev., 22 May, 30 July and 1 August 1996, 19 May and 4 August 1997, 96 (32-32-32-0).
- Hemlock forest*: NC: Haywood Co., Cataloochee, 150 m S mouth of Palmer Branch at Caldwell Fork, E3107, N39436, 854–915 m elev., 4 June and 5 August 1996, 18 May, 1 June, 10 and 24 August 1997, 84 (29-26-29-0).
- Hardwood cove forest*: TN: Sevier Co., along Porter's Creek Trail at 200 paces above bridge over Porter's Creek, E2830, N39508, 740 m elev., 18–19 June and 24–25 August 1996, 21–22 May and 31 July 1997, 116 (39-37-40-0).
- Wetland (Indian Creek)*: NC: Swain Co., marsh between Indian Creek Trail and Indian Creek at 3 km NE of junction with Deep Creek Trail, E2817, N39296, 685 m elev., 27 May and 16 August 1996, 12 May and 29 July 1997, 33 (14-4-8-7).
- Wetland (Meadow Branch)*: TN: Blount Co., marsh along Meadow Branch at 0.5 km ENE of Dosey Gap, E2527, N39470, 535 m elev., 23 May and 1 August 1996, 15 May and 17 July 1997, 33 (13-8-0-12).
- Native grassland*: TN: Blount Co., Cades Cove, S side Abrams Creek about 0.5 km upstream from Cades Cove Loop Road bridge, E2426, N39423, 520 m elev., 5 June and 8 August 1996, 15 May and 17 July 1997, 48 (24-0-0-24).
- Pine-oak forest*: TN: Blount Co., 300 m N of junction of Tabcat Creek and Maynard Creek, E2301, N39347, 395 m elev., 28–29 May and 2 August 1996, 14 May and 15 July 1997, 96 (32-32-32-0).

Appendix

Habitat type, locality data, collecting dates, and sample sizes 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 1-hr samples. When vegetation surveys at these sites are completed in a year or two, results will be posted on the WWW. Whittaker (1956) provides descriptions of the vegetation of most of these habitats. A bald is a natural tree-less community on a well-drained high elevation site below the climatic tree-line. A beech gap forest is an orchard-like forest dominated by