Habitat distribution, life history and behaviour of *Neriene* species in the Great Smoky Mountains National Park (Araneae, Linyphiidae)

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Summary

Habitat distribution, life history and other natural history data generated for four *Neriene* (Araneae, Linyphiidae) species from 668 1-hr samples collected at 17 focal sites representing 16 major habitats in the Great Smoky Mountains National Park (GSMNP) revealed the following: All four species present in the GSMNP (*N. radiata*, *N. variabilis*, *N. clathrata* and *N. redacta*) are either uncommon or absent in high-elevation habitats (>1200 m). One or two of the first three species are common or abundant in each of the middle and low elevation habitats, except in native grassland. *Neriene radiata* utilises the broadest range of habitats and microhabitats. *Neriene redacta*, hitherto known only from brief descriptions, is restricted to grassy non-forest habitats. There is only one habitat (wetland) where more than two *Neriene* species coexist. Two or three of the ground stratum species (*variabilis*, *clathrata* and *redacta*) coexist in only two habitats, whereas *N. radiata*, which builds its distinctive dome web both in and above this stratum, coexists with ground stratum species in six habitats. Life cycles appear to include seven (*N. radiata* and *N. variabilis*) or six (*N. clathrata* and *N. redacta*) post-emergent instars. Well-sampled populations of *N. radiata* and *N. clathrata* have simple annual life cycles, as does one of two populations of *N. variabilis* subjected to analysis, but the other *N. variabilis* population appears to exhibit a mixed annual/biannual pattern. *Neriene redacta* leaves its web to deposit egg sacs on the ground. *Neriene redacta* and *N. clathrata* build similar saucer-shaped sheet webs, while the web of *N. variabilis* is slightly domed. *Neriene clathrata* and *N. variabilis* males appear to be ant mimics. Van Helsdingen's (1969) hypothesis that *Linyphia davisi* Gertsch is a junior synonym of *Neriene redacta* Chamberlin is shown to be correct.

Introduction

In order to gain important insights into the impact of particular animal taxa on community dynamics and explore their potential as useful indicators for tracking community change and assessing biodiversity, it is important to understand their life histories, behaviours, and habitat preferences (Strong *et al.*, 1984; Wilson, 1992; Hanggi *et al.*, 1995; Polis *et al.*, 1996). Twenty years ago Duffey (1978) urged arachnologists to collect these kinds of autecological data for spider species, but still there are many common North American spiders whose natural histories are very poorly known.

Many of the 55 described species of the linyphiine spider genus *Neriene*, which are distributed throughout the northern hemisphere and the Old World Tropics (van Helsdingen, 1969; Brignoli, 1983; Platnick, 1989, 1993, 1997) and are often locally abundant, deserve greater attention. Surprisingly little is known about the natural history of the nine North American species of

Neriene, except for the common and widespread *N. radiata* (Walckenaer) (e.g. van Helsdingen, 1969; Wise, 1973, 1976, 1984; Martyniuk, 1984; Herberstein, 1997). Only scattered and brief observations on two other *Neriene* species living in the GSMNP (*N. variabilis* (Banks) and *N. clathrata* (Sundevall)) have been published (Emerton, 1909; Comstock, 1948; van Helsdingen, 1969; Toft, 1976; Kaston, 1981; Alderweireldt, 1994; Hanggi *et al.*, 1995), and nothing has been published about the biology of the fourth species, *N. redacta* Chamberlin.

In this paper we describe the habitat distribution of these four *Neriene* species in the Great Smoky Mountains National Park (GSMNP), present life history and other natural history data for each species, and confirm van Helsdingen's (1969) hypothesis that the two previously known specimens of *N. redacta* — a female (holotype of *Linyphia davisi* Gertsch) from Mississippi and a male (holotype of *N. redacta*) from Florida — are conspecific. We hope that these discoveries will make this species assemblage more accessible to ecologists and resource managers interested in understanding and conserving biodiversity.

Methods

Habitat distribution

A team of three to five collectors used a modified Coddington sampling protocol (Coddington *et al.*, 1996) to obtain the 668 1-hr ground (235), aerial (172), beat (206) and sweep (55) samples used in this study. Aerial sampling involved searching leaves, branches, tree trunks, and spaces in between, from knee height up to maximum overhead arm's reach. Ground collection involved searching (often on hands and knees) leaf litter, logs, rocks, plant surfaces, and other substrates and spaces below knee level. Beating consisted of striking vegetation with a 1 m long stick and catching the falling spiders on a 0.5 m^2 canvas sheet held horizontally below the vegetation. Aspirators and hands 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 appropriate sampling methods and confined sampling to one portion of the study site. Sampling was restricted to daylight hours. In non-forest communities (grass bald, 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 ± 48) depended primarily on vegetation structure and spider abundance.

Two sets of samples (one in spring and one in late summer) were collected from each of 17 focal sites (see Appendix), each site representing one of 16 major habitat (community) types found in the GSMNP, a 207,000 ha International Biosphere Reserve located in the southern Appalachian Mountains of eastern North America. Two of the sites (low grass bald and heath

bald) were sampled in 1995. The other 15 sites were sampled in 1996. At each site (except for the high grass bald, wetland, and Table Mountain pine sites) nearly equal numbers of samples were collected with each of the methods employed (Appendix). Long-term vegetation analysis plots are being established at each site by GSMNP botanists, and vegetation data will be available on the World Wide Web in a few years.

All adult and juvenile *Neriene* specimens were sorted from each sample and identified to the species level. The pigment patterns of all instars living outside the egg sac are distinctive for each species. The relative abundance (mean number of individuals per 1-hr sample) of each species 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 by spatial environmental variation within each site, by seasonal changes in population age structure, and by the fact that each method samples a different subset of microhabitats.

Life history

For each species, the length of tibia I (ITL) was measured along its dorsal surface on every specimen collected at two or more sites where the species was common. These measurements were performed on 359 *N. radiata*, 434 *N. variabilis*, 146 *N. clathrata* and 48 *N. redacta* individuals (see Figs. 4–7 for the sites and dates represented by these samples). Toft (1976) demonstrated that for many spider species ITL distinguishes instars more clearly than does either the length or width of the carapace. Measurements were performed with a Wild M-5 stereomicroscope at 50 × magnification to the nearest 0.5 micrometer unit (0.0185 mm). StatView 4.5 (Abacus Concepts) was used to generate ITL frequency distribution histograms for all measured individuals and for subsets of these individuals collected at particular sites on particular dates. From these histograms it was possible to determine instar number and then deduce phenology and generation time by examining the relationship between instar distribution and collecting date. Instars were also revealed by the distinctive widths of palpal tarsi of older juvenile males and by the epigyna and palpal organs of adults. Maximum palpal tarsus width (PTW) in dorsal view was measured with a Wild M-5 at 100 × to the nearest 0.5 micrometer unit (0.0093 mm). All measurements are given in mm.

Other observations

The vertical microhabitat distribution of each species was analysed by computing its relative abundance in aerial (above knee level) vs. ground (below knee level) samples at all sites where the species was found. Beat and sweep samples were not used because each of these methods sampled spiders both above and below knee level. The Mann-Whitney U-test was used to see if the relative abundance values for ground and aerial samples were significantly different (at $p < 0.05$). Web descriptions were derived from field observations, photographs, and the webs of several captive individuals kept in glass arenas. Captive adult females of *N. variabilis, N. clathrata* and *N. redacta* were observed while capturing
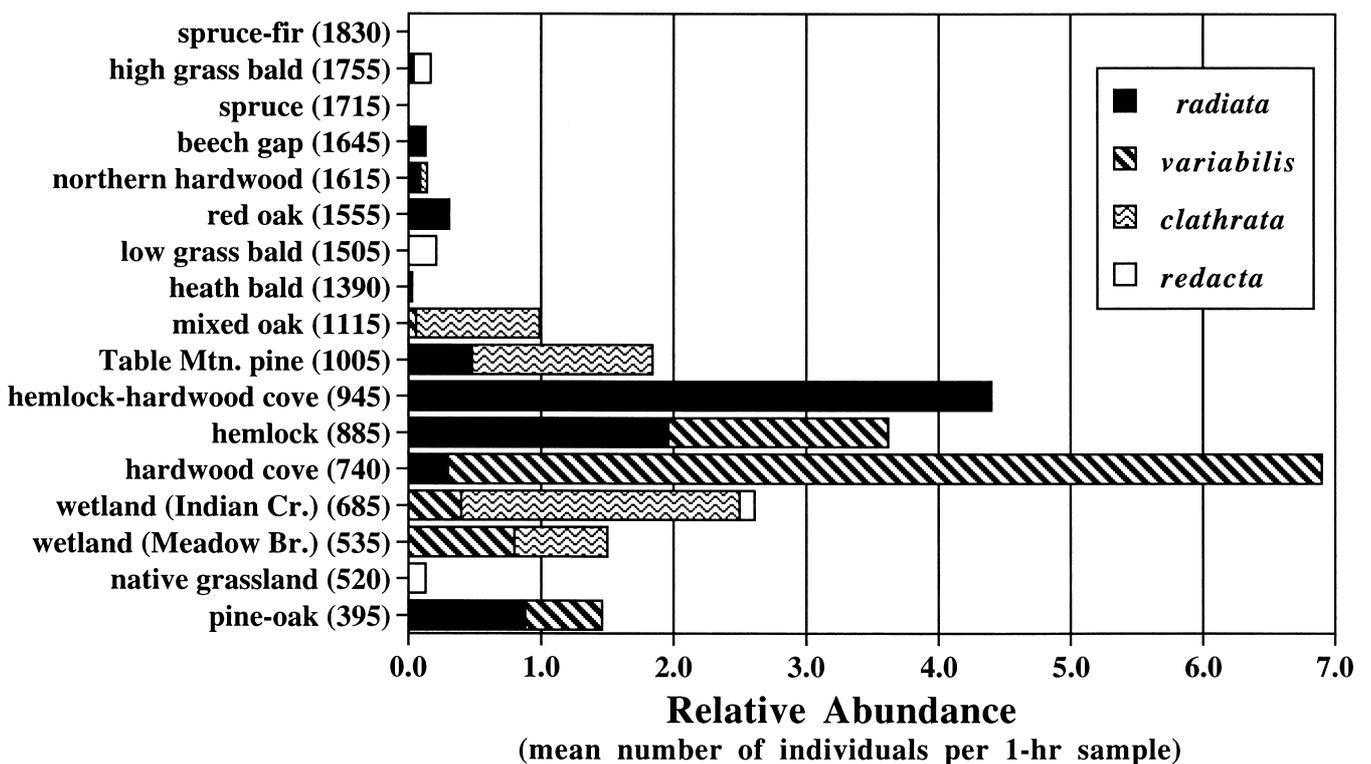
Fig. 1: Stack-bar diagram showing relative abundances of *Neriene* species at 17 focal sites representing 16 major habitats in the Great Smoky Mountains National Park. Elevation (in m) of each focal site given in parentheses after each habitat name.

vestigial-wing *Drosophila* flies that were dropped on to their webs. For each species one capture was video-recorded and two or three additional captures were observed directly. To test van Helsdingen's (1969) hypothesis that *Linyphia davisi* and *N. redacta* are conspecific, we compared our specimens of *N. redacta* with published descriptions and illustrations of the holotypes (Chamberlin, 1925; Gertsch, 1951; van Helsdingen, 1969).

Results and discussion

Habitat distribution

All four *Neriene* species were uncommon (relative abundance <0.5 ind./1-hr sample) or absent in the eight high-elevation (over 1200 m) habitats, whereas all but one of the lower elevation habitats (below 1200 m) supported at least one common (relative abundance = 0.5–2.0) or abundant (relative abundance >2.0) *Neriene* species (Fig. 1). This elevation pattern resembles that of central European *Neriene* species, which are rarely found above 800 m and never found above 1500 m (Hanggi *et al.*, 1995). *Neriene radiata* was found in far more habitats (10) and over a wider elevation range (1360 m) than any of the other species. It was common or abundant in three forest habitats (hemlock-hardwood cove, hemlock, and pine-oak) and was absent or rare at the six non-forested sites. *Neriene variabilis* was found in five habitats, all below 1200 m elevation; it was abundant in hardwood cove forest and common in hemlock, wetland (forest edge), and pine-oak habitats. *Neriene clathrata* was found in four habitats; it was abundant at one wetland site and common at the other wetland site and two forest habitats (Table Mountain pine and mixed oak). *Neriene redacta* was found in only four habitats, all non-forested grassy communities. Even though *N. redacta* was uncommon in all these habitats, it was the only *Neriene* species found in two of them (low grass bald and native grassland) and it spanned nearly as great an elevation range as did *N. radiata*. Seven of the 16 habitats contained two *Neriene* species, one (wetland) contained three species, and no habitat contained all four species (Fig. 1). Only four communities (Table Mountain pine, hemlock, wetland and pine-oak) contained roughly equal densities of two species. These species pairings involved *N. radiata, N. variabilis* and *N. clathrata* in all three possible pairings.

The differences among some of the 16 sampled habitats in the kinds and relative abundances of *Neriene* species (Fig. 1) suggest that this species assemblage, especially when combined with other assemblages such as *Theridion* (Stiles & Coyle, in press), might be a useful indicator of biotic community structure and, therefore, useful in tracking changes in community structure. For example, the two cove forest communities (hemlock-hardwood and hardwood), which are basically at two ends of a short continuum of cove forest assemblages (Whittaker, 1956), exhibit a marked difference in their *Neriene* populations (Fig. 1). However, data on variation in relative abundance from year to year at each site
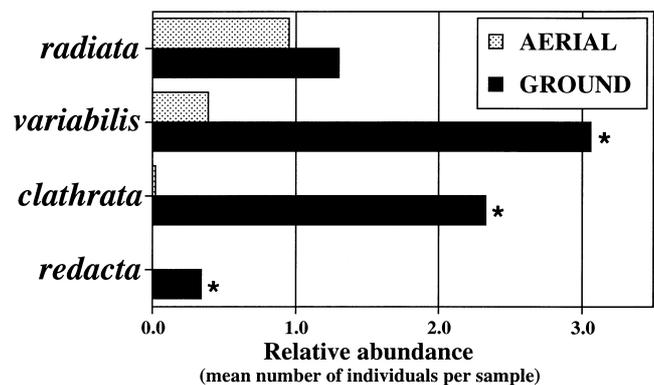
Fig. 2: Vertical microhabitat distribution of *Neriene* species as indicated by relative abundances in aerial and ground samples at those sites where the species in question was collected. Ground samples collected from 0.0–0.5 m above ground; aerial samples from 0.5–2.2 m above ground. Sample size ranged from 53 to 154 1-hr samples per species. Asterisk indicates a statistically significant difference in relative abundance between aerial and ground samples (Mann-Whitney U-test, $p < 0.05$).

are needed before the suitability of this genus as an indicator assemblage can be rigorously assessed.

Why *N. radiata* is absent or rare in the non-forested communities — even near the edges of the small wetland communities that are surrounded by forest — is puzzling in the light of the fact that this species is relatively common in grass and weeds in some roadside and forest edge habitats near the GSMNP and occurs in many types of forest and non-forest habitats in Europe (Hanggi *et al.*, 1995). However, our observations in the GSMNP are consistent with those of other authors (Fitch, 1963; Kaston, 1981; Wise, 1984; Gaddy & Morse, 1985), who collectively indicate that elsewhere in North America this species is most common in forests, less common in forest edge habitats, and rare in open treeless habitats.

Emerton (1909) and Kaston (1981) both indicated that in New England *N. variabilis* prefers forest over open meadows, which is consistent with our findings. Kaston's (1981) records of *N. clathrata* from both forest and salt marsh habitats, and the extremely wide variety of habitats occupied by this species in Europe (Hanggi *et al.*, 1995), are also consistent with our results. Of the four *Neriene* species living in the GSMNP, *N. redacta*, which is restricted to grassy non-forest habitats, is the only habitat specialist. Since *N. redacta* has hitherto been collected only from relatively low latitudes and elevations (Florida, Mississippi, and southwestern North Carolina at 890 m elevation in Horse Cove near Highlands), it surprised us to find this species living and reproducing in the cold temperate climate of the high grass bald, at an elevation (1755 m) well above those occupied by *N. clathrata* and *N. variabilis*, species whose geographic ranges include much higher latitudes.

Web placement and structure

Although all four *Neriene* species construct sheet webs and hang inverted on the underside of the main sheet, there are differences in web placement and form. *Neriene*
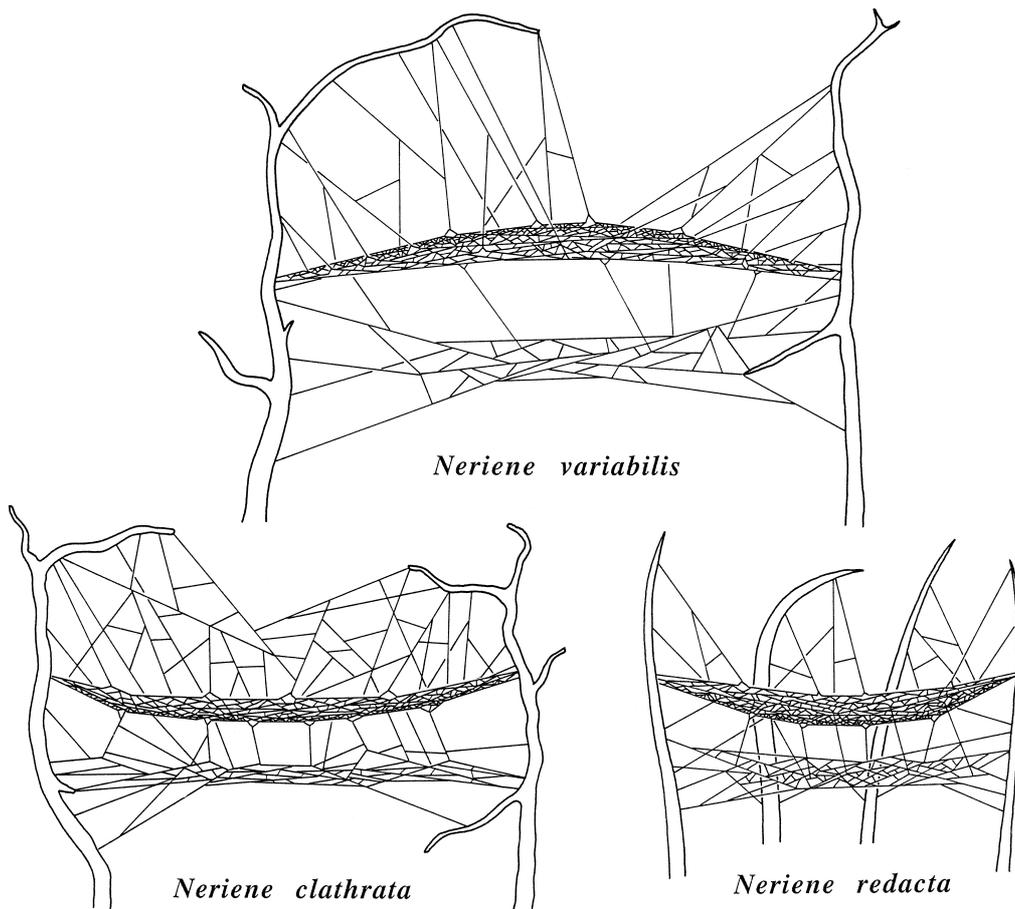
Fig. 3: Webs of adult females of three *Neriene* species. Each drawing based on sketches, notes and measurements taken of webs in the field and webs constructed in captivity. Webs of *N. variabilis* and *N. clathrata* shown at about 30% life size; *N. redacta* web shown at about 50% life size.

radiata webs were about equally common above (50–220 cm above ground) and below (0–50 cm above ground) knee level, but webs of the other three species were much more common below knee level (Fig. 2). *Neriene radiata* webs were located from just above the ground surface to 1 m or more above ground and were commonly attached to small understory trees, shrubs and other plants and substrates. This species' web, characterised by a dome-shaped capture sheet surrounded by a maze of threads extending in all directions, has been described by many authors (e.g. Comstock, 1948; Nielsen, 1932; Gertsch, 1979; Kaston, 1981; Roberts, 1995).

In accord with the observations of Emerton (1909) and Kaston (1981), we found virtually all *N. variabilis* webs close to the ground. They were commonly attached to small dead branches lying on the ground, to ground layer vegetation, and to the bases of small trees. The web, which was very briefly described by Emerton (1909), is primarily a horizontal sheet suspended and bowed slightly upwards by many support lines, forming a very shallow dome, the centre of which is 1–2 cm higher than the periphery (Fig. 3). The spider normally rests suspended from the underside of the sheet near its centre. Below this horizontal sheet there is a tangle of interconnected threads attached to the sheet and surrounding substrates. In a few webs, these interconnected threads form a horizontal sheet-like scaffolding. Five webs that were observed closely (three at Indian Creek

wetland and two at the hardwood cove site) had the following dimensions (minimum and maximum diameter of main sheet in cm): 20 × 30, 11 × 13, 28 × 35, 13 × 16, and 12 × 16. The main sheets of these webs ranged from 8–30 cm above the ground surface (mean and SD = 16.4 ± 7.3). At the Indian Creek wetland site one occupied *N. variabilis* web was observed 19 cm directly above an occupied *N. clathrata* web.

Neriene clathrata webs were very close to the ground and commonly attached to plant debris, ground vegetation, and the bases of small trees. The main sheet is horizontal and usually saucer-shaped (slightly depressed in the middle) (Fig. 3), a feature not noted in previous descriptions (Comstock, 1948; van Helsdingen, 1969; Kaston, 1981). Below the main sheet there is a less developed sheet. The web resembles that of *N. redacta* (see below), although the system of support lines above the main sheet is denser and thus more obvious than that of *N. redacta*. The spider rests suspended from the sheet, often near its edge, from where it may dash to the nearest attachment substrate and hide when disturbed. The main sheet of one adult female web was 11 cm above the ground and was roughly rectangular (9 × 36 cm).

Neriene redacta constructs a horizontal sheet web 5–33 cm (mean and SD = 21 ± 10) above the ground (n = 5 females, 1 male, 1 juvenile) and typically attached to grasses or sedges. The main sheet is suspended from lines attached to adjacent vegetation and is slightly

concave (saucer-shaped), with the centre 1–2 cm lower than the outer edge (Fig. 3). Since the support lines directly above the sheet are few and relatively delicate, the sheet appears very smooth. The sheet's shape varies, but is roughly circular, its diameter ranging from 3–14 cm (mean and SD = 10.4 ± 4.5) in the sample of seven webs referred to above. At 1–1.5 cm beneath the main sheet there is usually another semi-horizontal sheet nearly as large, but not as fine-meshed, as the main sheet and connected to it by thin threads that cause indentations in the main sheet.

We suggest that the lower sheet in the webs of *N. clathrata* and *N. redacta* may be homologous to the less sheet-like maze of threads located below the domes of *N. radiata* (Comstock, 1948) and *N. variabilis* webs, and that all these may help to protect the spider from predators approaching from below. The tall dome and surrounding tangle of *N. radiata* webs may enable this
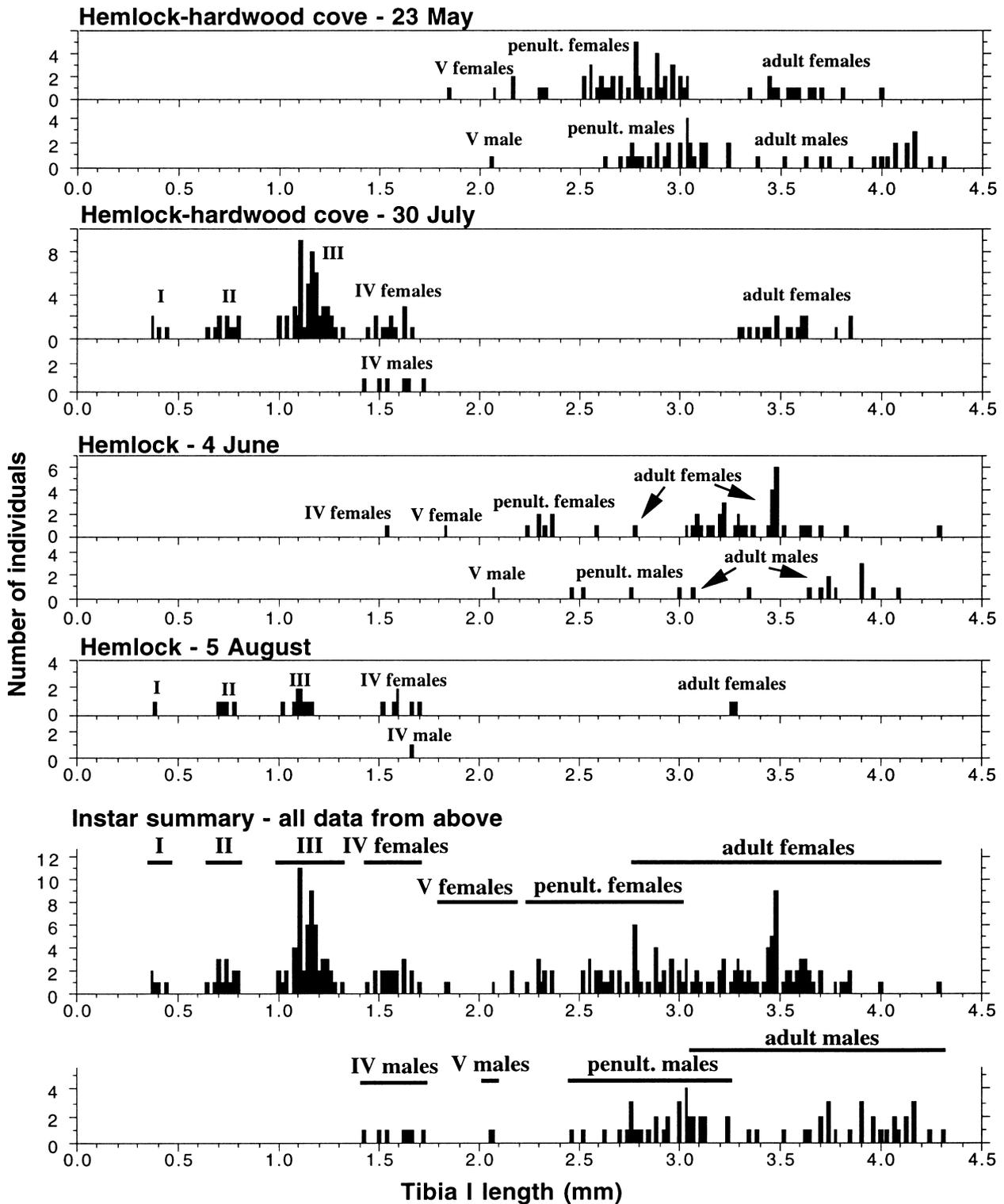
Fig. 4: Size frequency histograms for four samples of *Neriene radiata* collected in the spring and summer at two focal sites. For each sample, females and individuals too young to be sexed were graphed separately from males. Instar summary histograms were generated by pooling these four samples. Instar I is the first post-emergent instar, i.e. the instar that emerges from the egg sac.

species to capture flying insects more effectively than can the webs of the other species. Fitch (1963) and Herberstein (1997) found that flies (in several families), halictid bees, and other relatively active fliers are trapped by *N. radiata* webs.

The observation that two or three of the *Neriene* species that construct relatively similar flat capture sheets close to the ground (*variabilis, clathrata* and *redacta*) coexist in only two habitats (wetland and mixed oak forest), whereas *N. radiata*, the species which often builds its dome-shaped web above this stratum, coexists with others in six habitats, is consistent with, but does not constitute strong support for, the role of competition in organising these assemblages. The observed ability of *N. radiata* to utilise a greater range of heights above ground than its congeners, as well as its unique dome web design, which probably is more effective than the horizontal designs of the other three species in intercepting active flyers, may facilitate its coexistence with congenerics in forest communities. It would be interesting to examine the niche parameters of *N. clathrata, N. variabilis* and *N. redacta*, which all have webs of similar form and placement, at the wetland sites where they coexist.

Life history

Neriene radiata: The size frequency histograms of the pooled *N. radiata* samples indicate that there are seven post-emergent instars (Fig. 4), i.e. seven instars beginning with the spiderling instar that emerges from the egg sac. Each of the last four male instars can be recognised by a distinctive palpal tarsus configuration: the adult tarsus has a functional palpal organ; the penultimate tarsus is very swollen (PTW=0.53–0.63 mm, mean and SD=0.58 ± 0.03, n=16); the antepenultimate tarsus is swollen (PTW=0.22, 0.24 mm, n=2); and the pre-antepenultimate tarsus is slightly but distinctively swollen (PTW=0.11–0.15 mm, mean and SD=0.12 ± 0.01, n=9) when compared with those of pre-antepenultimate and antepenultimate females from the same population. In addition, there are three distinct and smaller ITL classes which exhibit no obvious sexual dimorphism; these represent three earlier instars, the first almost certainly being the one that disperses from the egg sac. The phenology most consistent with the temporal pattern of these data is as follows: individuals overwinter in the antepenultimate or penultimate instar; these mature, mate and begin producing eggs in the spring; spiderlings emerge from egg sacs, disperse in June and July and develop to the antepenultimate or penultimate instar by winter. This is a simple annual life cycle.

Wise's (1976, 1984) careful studies of the life history patterns in one Michigan and two Maryland populations of *N. radiata* revealed in all three populations both annual and biannual life cycles. This "polymorphic phenology" is characterised by the production of both slowly and rapidly developing offspring by adults that mature and reproduce in the spring. The slow developers overwinter and mature the following spring (annual life

cycle) while the fast developers mature and reproduce in their first summer (biannual life cycle). Wise pointed out that the proportion of a population exhibiting each of these two strategies probably varies with climate and, consequently, latitude and elevation. Kaston's (1981) observation of mating pairs in Connecticut as early as 30 May and as late as 13 August, and Fitch's (1963) observation of mating from April through September in Kansas, are consistent with the hypothesis of polymorphic phenology. Martyniuk (1984) reported an annual life cycle for this species near Albany, NY, and Herberstein (1997) recently discovered a strictly annual population of *N. radiata* in eastern Austria.

If the two populations we have studied embody the mixed life cycle pattern described by Wise (1984), we should see in our late July and early August samples a newly maturing cohort of smaller adults or at least a large cohort of penultimate or antepenultimate individuals. The absence of antepenultimates, penultimates, and adult males, and the presence of relatively few females which are as large as the springtime females, during this time period (Fig. 4) indicates that these populations are strictly or predominantly annual. The absence of early juvenile instars and the extremely small number of instar IV and V (antepenultimate) individuals in our spring (late May and early June) samples also argues against a biannual component in these populations. However, without one more observation window in late August or early September, we are not in a position to completely rule out the possibility of a polymorphic phenology; it is remotely possible that in these populations a biannual cohort may become evident later in the summer than is the case in the populations studied by Wise. If, as our data suggest, these two populations in the Great Smoky Mountains are predominantly or completely annual, they fit Wise's (1984) prediction that populations at higher elevations or latitudes (with shorter, cooler growing seasons) should have reduced numbers of rapid developers; these Great Smoky Mountains populations live in well-shaded understories at 885 and 945 m elevation.

Neriene variabilis: The data indicate that most individuals of *N. variabilis* pass through seven post-emergent instars (Fig. 5). Each of the last four male instars can be recognised by a distinctive palpal tarsus configuration: the adult tarsus has a functional palpal organ; the penultimate tarsus is very swollen (PTW=0.56 and 0.57 mm for the only two penultimate males collected); the antepenultimate tarsus is swollen (PTW=0.19–0.30 mm, mean and SD=0.26 ± 0.02, n=34 from the hardwood cove site); and the pre-antepenultimate tarsus is slightly but distinctively swollen (PTW=0.12–0.21 mm, mean and SD=0.16 ± 0.02, n=18 from the hardwood cove site) when compared with those of pre-antepenultimate and antepenultimate females from the same population. Three distinct and smaller ITL classes exhibit no obvious sexual dimorphism; these represent three earlier instars, the first almost certainly being the one that disperses from the egg sac. The paucity of penultimate males and the apparent lack of penultimate females in these samples may be the result

of a lack of sampling during the seasons (presumably autumn, winter and early spring) when that instar is common. Alternatively, the considerable overlap in ITL between penultimate and antepenultimate male cohorts suggests that penultimate females may be present but "hidden" in the upper end of the large size class labelled
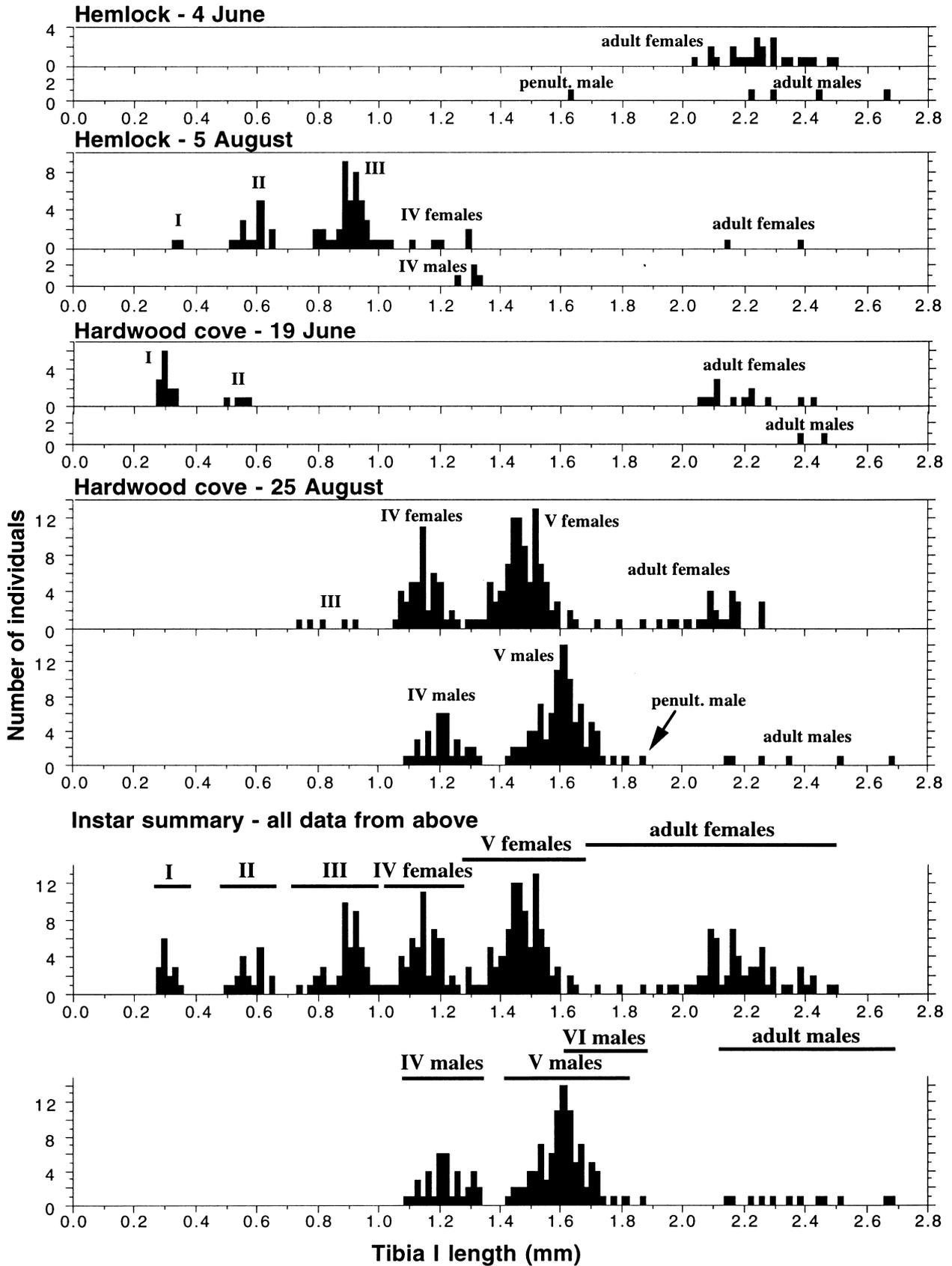
Fig. 5: Size frequency histograms for four samples of *Neriene variabilis* collected in the spring and summer at two focal sites. For each sample, females and individuals too young to be sexed were graphed separately from males. Instar summary histograms were generated by pooling these four samples. Instar I is the first post-emergent instar.

"V females" in the 25 August hardwood cove sample (Fig. 5). Two individuals, a penultimate male (ITL=1.83) and a penultimate female (ITL=1.59), were found in the leaf litter samples collected at the hardwood cove site on 23 February 1997.

The temporal pattern of data at the hemlock site indicates that this population overwinters in the penultimate instar and then matures, mates and begins egg-laying in the spring; spiderlings emerge and disperse in June; these develop to the penultimate instar by autumn. This is a simple annual life cycle. However, the hardwood cove data suggest that this population may have a mixed annual/biannual life history pattern like that of the *N. radiata* populations studied by Wise (1976,
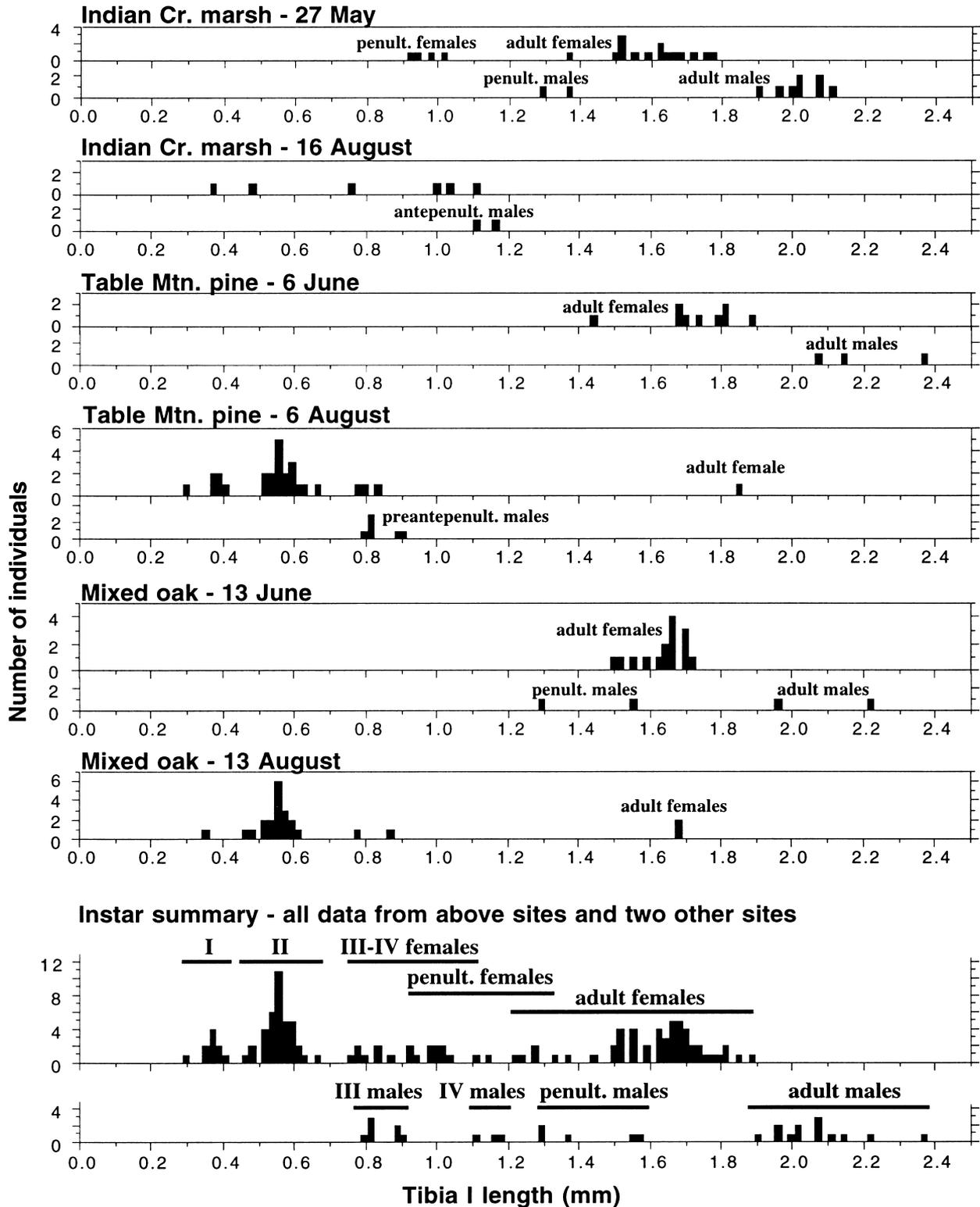
Fig. 6: Size frequency histograms for six samples of *Neriene clathrata* collected in the spring and summer at three focal sites. For each sample, females and individuals too young to be sexed were graphed separately from males. Instar summary histograms were generated by pooling these six samples and two others (from the Meadow Branch wetland focal site and a wetland beside Big Cove Road near the Oconaluftee entrance to the GSMNP). Instar I is the first post-emergent instar.

1984). Adult females and males are present in June and August, and the mean ITL of the August adult females is significantly smaller than that of the adult females collected in June. Kaston's (1981) observation that *N. variabilis* males occur in Connecticut only in May and June suggests that this species has an annual pattern there, but van Helsdingen's (1969) claim that *N. variabilis* adults have been collected as late as October is consistent with a biannual cycle.

Neriene clathrata: The size frequency histograms (Fig. 6) indicate that there are six or seven post-emergent instars in the life cycle of *N. clathrata*. Each of the last four male instars can be recognised by a distinctive palpal tarsus configuration: the adult tarsus has a functional palpal organ; the penultimate tarsus is very swollen (PTW=0.56–0.63 mm, mean and SD=0.59±0.03, $n=3$); the antepenultimate tarsus is moderately swollen (PTW=0.28–0.30 mm, mean and SD=0.28±0.01, $n=3$); and the pre-antepenultimate tarsus is slightly but distinctively swollen (PTW=0.11–0.19 mm, mean and SD=0.17±0.02, $n=7$) when compared with those of pre-antepenultimate and antepenultimate females from the same population. In addition, there appear to be two distinct and smaller ITL classes which exhibit no obvious sexual dimorphism; these represent two earlier instars, the first probably being the one that disperses from the egg sac. If, however, the smallest individual represents an undersampled instar distinct from the rest, the number of post-emergent instars would be seven. The size frequency distribution pattern for juvenile females older than post-emergent instar II does not permit resolution of age (instar) classes. *Neriene clathrata* exhibits marked sexual dimorphism in ITL, especially in the last two instars.

The temporal pattern of these data indicates that the population overwinters in the antepenultimate and/or penultimate instar and then matures, mates and begins egg-laying in the spring; spiderlings emerge and disperse in June and July; and these develop to the antepenultimate or penultimate instar by autumn (Fig. 6). This is a simple annual life cycle. The absence in August of penultimate and adult males and penultimate females, and the paucity of adult females in these August samples, rule out any biannual component in these populations. Further support for the annual life cycle hypothesis is provided by a 15 September 1996 collection of nine individuals (from a marsh near the Oconaluftee entrance to the GSMNP) which included one antepenultimate and one penultimate male and seven antepenultimate and penultimate females. Toft (1976) reported a simple annual life cycle (with mating and egg-laying in June and July) for a population of *N. clathrata* in Denmark. Kaston's (1981) observations also strongly suggest an annual pattern in Connecticut. Van Helsdingen (1969), however, reports that males of *N. clathrata* are common during most of the year, suggesting the possibility of a mixed annual/biannual life history strategy in some populations of this widespread species.

Neriene redacta: The pooled size frequency data (Fig. 7) suggest that there are six post-emergent instars in this species. Since egg sac dissections reveal that the active emerging spiderling instar is the second post-hatching instar (see below), there are seven instars altogether in this life cycle. Each of the last four male instars can be recognised by a distinctive palpal tarsus configuration: the adult tarsus has a functional palpal organ; the penultimate tarsus is very swollen (PTW=0.34–0.37 mm, mean and SD=0.35±0.01, $n=3$); the antepenultimate tarsus is moderately swollen (PTW=0.16–0.19 mm, mean and SD=0.18±0.01, $n=5$); and the pre-antepenultimate tarsus is slightly but distinctively swollen (PTW=0.09–0.11 mm, mean and SD=0.11±0.01, $n=4$) when compared with those of instar IV through penultimate females (PTW= 0.07 mm, $n=6$). In addition, there are two smaller ITL classes which exhibit no obvious sexual dimorphism; these represent two earlier instars. There is marked sexual dimorphism in ITL, especially in the last two instars. The reduced number of instars for this species (when compared with *N. radiata* and *N. variabilis*) may be causally related to its much smaller body size.

Sample sizes are too small to resolve the phenology and generation time of this species. Pooling all samples into high (>1505 m) and low (520–685 m) elevation groupings and subdividing each of these into comparable seasonal categories fails to shed much light on the matter (Fig. 7), although it does indicate that adults of both sexes may be present throughout much of the summer and autumn and that many of the juvenile instars are present at a high elevation site (low grass bald) in the autumn (29 September).

Reproduction and early development

One *N. redacta* female collected at a wetland site (615 m elev.) beside Big Cove Road near the Oconaluftee entrance to the GSMNP on 15 September constructed four egg sacs in captivity over 1.5 months. All four egg sacs were hidden from view, deposited in and under moist crumpled paper towels lying beneath her web on the floor of the arena. These egg sacs were flattened, lenticular, and 6–13 mm diameter. A white fluffy layer of silk surrounded the eggs. The diameters of 10 eggs in the only sac with unhatched eggs ranged from 0.48–0.56 mm (mean and SD=0.52±0.02). Examination of the egg sac contents revealed that development in the egg sac includes two post-hatching instars. Moulted first instar exoskeletons lack visible hairs (at 100 × magnification). The second instar spiderlings have eyes, eye pigment, numerous well-developed hairs, and spinnerets with spigots. When we first discovered one of the egg sacs, several of these second instar spiderlings had just emerged from the sac. Clutch size ($n=5$, four from this female and one from another female collected at the same place and time) ranged from 15–49 (mean and SD=26.8±13.8). The four clutches of the first female were fully fertile. Although we do not know the exact oviposition date for any of these clutches, our observations show that (1) the first clutch developed to the second instar and emerged from the egg sac less than 15 days after oviposition, (2) the third clutch

required fewer than 12 days to develop to early stage embryos, and (3) the fourth clutch required 7 or more days to develop to the second instar and emerge from the egg sac.

Our observations suggest that in nature *N. redacta* females leave their webs and attach their egg sacs to substrates within nearby ground litter, which is also what *N. radiata* and *Neriene montana* (Clerck) females do (Staveley, 1866; McCook, 1890; Wise, 1973). Consequently, this trait may be widespread in the genus *Neriene*. The egg sac of *N. redacta* is the same shape and texture as described for those of *N. clathrata* (Kaston, 1981) and *N. radiata* (McCook, 1890; Wise, 1973). The mean clutch size of *N. redacta* is smaller than that of any Michigan (78) or Maryland (49–66) sample of *N. radiata* observed by Wise (1973, 1984) and the three clutch sizes (49, 50, 140) reported for *N. clathrata* by Toft (1976) and Kaston (1981). Also, *N. redacta* eggs are smaller than the Maryland *N. radiata* eggs measured by Wise (1984) (mean diameters for several samples=0.59–0.65 mm). That *N. redacta* clutch and egg sizes are smaller than those of *N. radiata* and *N. clathrata* is not surprising in the light of the much smaller size of *N. redacta* adults.

Feeding behaviour

All these *Neriene* species hang inverted from the underside of the main sheet and run on that surface to struggling prey that have fallen on to the sheet. *Neriene variabilis, N. clathrata* and *N. redacta* deliver
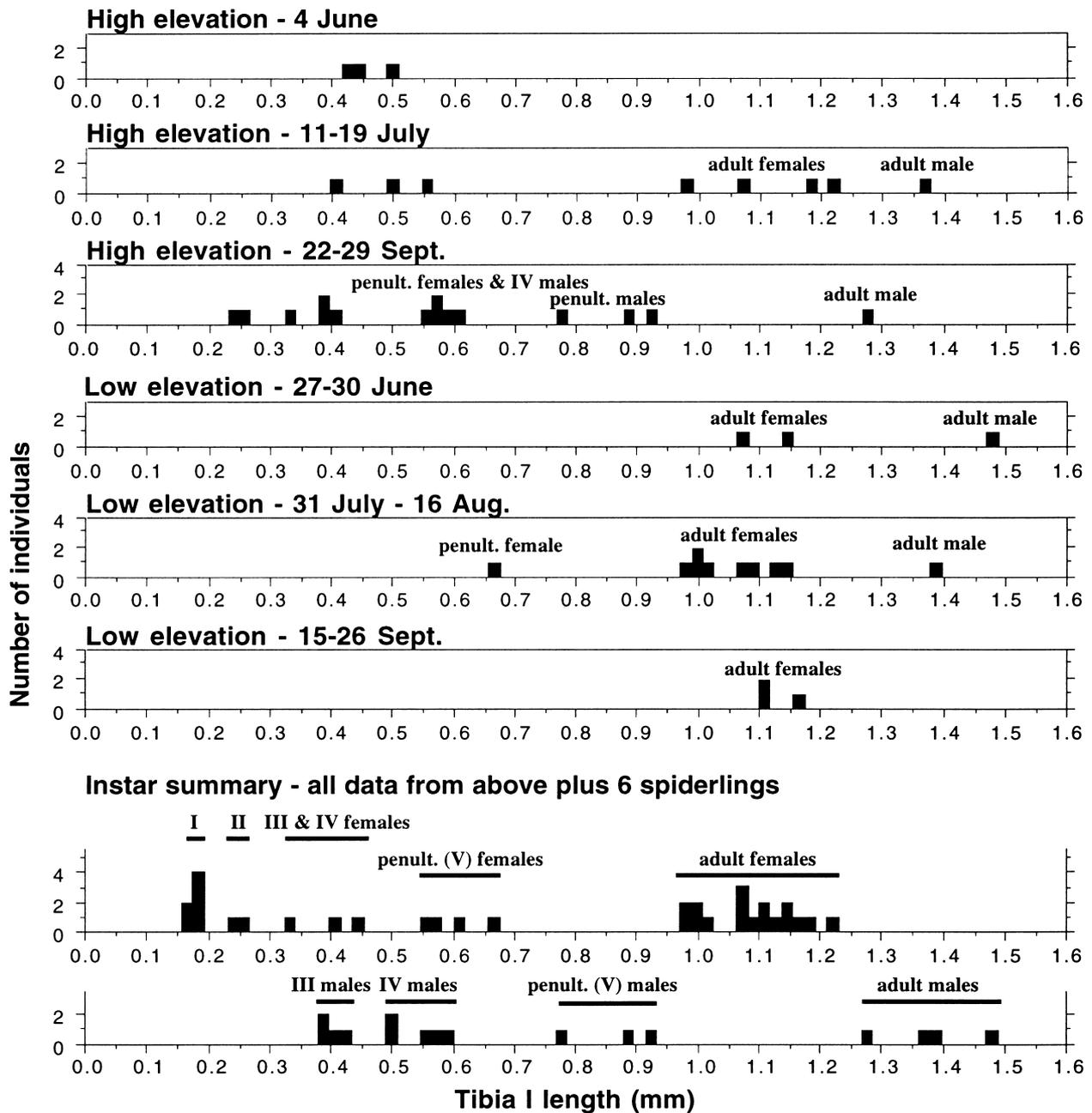
Fig. 7: Size frequency histograms for all individuals of *Neriene redacta*, grouped into high elevation and low elevation samples, each further subdivided into three comparable seasonal samples. Instar summary histograms were generated by pooling these samples and adding six spiderlings that had just emerged from an egg sac in captivity. For the instar summary, females and individuals too young to be sexed were graphed separately from males. Instar I is the first post-emergent instar.
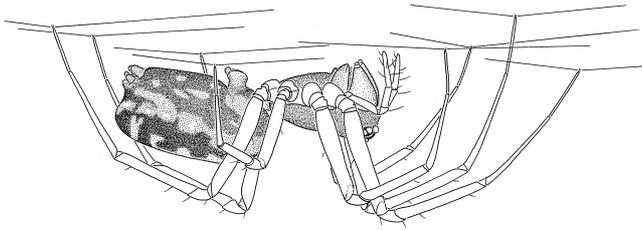
Fig. 8: Adult female of *Neriene redacta* in typical posture on underside of her sheet web, × 10.

"peck-like" bites to the prey (*Drosophila*) from underneath the sheet, grab it with the fangs, pull it through the web, carry it to the centre of the web, wrap it in silk, and then feed. This is the typical prey capture behaviour described for *Linyphia triangularis* (Clerck) by Bristowe (1958) and for *N. radiata* by Gertsch (1979). The only departure we observed from this sequence was the failure of the *N. variabilis* female to wrap the prey before she began feeding, something Bristowe observed whenever *L. triangularis* captured especially small prey.

Ant-like appearance of males

We noticed that males of *N. variabilis* and *N. clathrata* look very ant-like in the field, especially when they are running. One *N. variabilis* male was observed closely in the lab. Its very rapid and jerky gait, the occasional antenna-like movements of its first legs (which were sometimes lifted and moved about when it was not running), and the narrow body and long legs, all caused it to resemble an ant. *Neriene clathrata* males displayed similar behaviour in the field, and their dark (almost black) shiny colour helped them resemble workers of syntopic *Formica* ants. Although we are not aware of any previous reports of ant-like behaviour in species of *Neriene*, other observers have noted the ant-like appearance of *N. clathrata* and *N. furtiva* (O. P.-Cambridge) males (Donisthorpe in Bristowe, 1941; Jones, 1983; P. Merrett, pers. comm.). We suggest that the ant-like traits of these ambulatory males, which may spend a considerable time searching for mates, are the result of selection by visual predators that are repelled by the defences of ants. This function of ant-like traits, which have evolved many times in the Araneae (often perhaps in response to other selection pressures), has been discussed by numerous authors (Bristowe, 1941; Reiskind, 1977; Foelix, 1996).

Systematics

All our female (Fig. 8) and male specimens of *N. redacta* very closely match the published descriptions and illustrations of the female holotype of *Linyphia davisi* Gertsch and the male holotype of *N. redacta* Chamberlin. This provides convincing support for van Helsdingen's (1969) hypothesis that these holotypes are conspecific. Furthermore, it should be noted that the web structure similarities (particularly the slightly concave horizontal main sheet and the sheet-like tangle of threads below it) and marked sexual dimorphism in ITL of *N. clathrata* and *N. redacta* might be synapomorphies supporting van Helsdingen's (1969) hypothesis that these species are close relatives.

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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 small gray beech trees (*Fagus grandifolia*) and typically located on a south-facing slope in a mountain gap. Appalachian cove forests are found in sheltered middle elevation sites and are characterised by a high species diversity of large trees 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, 24 samples (8–8–8–0).

High grass bald: NC: Swain Co., Andrews Bald, E2738, N39354, 1755 m elev., 27 June and 22 September 1996, 24 (10–0–4–10).

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, 24 (8–8–8–0).

Beech gap forest: NC: Swain Co., in hog exclosure below Appalachian Trail at 350 m E Road Prong Trailhead, E2786, N39433, 1645 m elev., 14 June and 15 August 1996, 24 (8–8–8–0).

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, 44 (15–15–14–0).

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, 48 (16–16–16–0).

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, 45 (15–14–16–0).

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, 33 (13–8–12–0).

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 and 30 July and 1 August 1996, 48 (16–16–16–0).

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, 48 (17-14-17-0).

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, 56 (19–18–19–0).

Wetland (Indian Cr.): 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, 17 (7–3–4–3).

Wetland (Meadow Br.): 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, 17 (7–4–0–6).

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, 24 (12–0–0–12).

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, 48 (16–16–16–0).