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HABITAT DISTRIBUTION AND LIFE HISTORY OF SPECIES IN THE SPIDER GENERA *THERIDION*, *RUGATHODES*, AND *WAMBA* IN THE GREAT SMOKY MOUNTAINS NATIONAL PARK (ARANEAE, THERIDIIDAE)

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ABSTRACT. Based largely on 668 one-hour samples collected during a survey of spiders in 16 major habitats of the Great Smoky Mountains National Park, habitat distributions, life history patterns, and other natural history traits are described for 14 species in the related theridiid genera *Theridion, Rugathodes,* and *Wamba.* Two to eight of these species were found in each of the 16 habitats. Among-habitat differences in the kinds and relative abundance of these species suggest that they may be good predictors of habitat. Richness, diversity, and evenness of this species assemblage are highest in middle to low elevation habitats. *Rugathodes aurantius* and *R. sexpunctatus,* two boreal sister species, are abundant in the highest elevation habitats, but differ sharply in microhabitat and habitat preference. *Theridion frondeum* is much more common in high elevation habitats than is its sister species, *T. albidum,* which is virtually limited to middle and low elevation habitats. *Theridion lyricum* is most common in dry, pine-dominated forests. The three most common species (*R. aurantius, R. sexpunctatus,* and *T. frondeum*) have a simple annual life cycle of five or six instars and similar phenologies: they mate during late spring (*R. aurantius* and *R. sexpunctatus*) and early summer (*T. frondeum*) and over-winter in antepenultimate and/or penultimate instars. Female-biased sex ratios were observed in juvenile cohorts of these species. *Rugathodes aurantius,* its natural history previously unknown, places its webs on the undersides of broad-leafed herbs close to the ground and captures small flying insects. Adult females engineer partly folded leaf retreats, carry the egg sac when disturbed, help their instar II spiderlings exit the egg sac, and then share the retreat with these spiderlings for at least a few days. Rapid early development (about two weeks from oviposition to emergence from the egg sac), the presence of females with egg sacs throughout the summer, and smaller clutch sizes in late summer suggest that a typical *R. aurantius* female produces more than one clutch.

Keywords: Spiders, habitat distribution, life history, *Theridion, Rugathodes*

The spider genus *Theridion* Walckenaer 1805, as defined by Levi (1957, 1959, 1963) is cosmopolitan and large (over 90 species have been recorded from North America alone), and many of its species are abundant in favorable habitats. But published knowledge of these species consists of little more than taxonomic descriptions and brief, scattered natural history observations (e.g., Emerton 1902; Archer 1947; Comstock 1948; Levi 1957; Bristowe 1958; Toft 1976; Kaston 1981; Hanggi et al. 1995; Roberts 1995). Moreover, it is now generally accepted that *Theridion* is polyphyletic, and phylogenetic research is underway to determine the relationships of these species (I. Agnarsson & M. Arnedo pers. comm.). Wunderlich (1987) removed *Rugathodes* Archer 1950 from *Theridion*, and Platnick (1997), following Wunderlich's and Archer's (1950) views, formally transferred from *Theridion* to *Rugathodes* two species included in our current study, *Rugathodes sexpunctatus* (Emerton 1882) and *Rugathodes aurantius* (Emerton 1915). *Wamba crispulus* (Simon 1895), another species in our study and one considered by Levi (1963) to belong to *Theridion*, was transferred to *Wamba* by Wunderlich in 1995. The other eleven of the 14 species included in our study still remain in *Theridion*, but some of these may be removed following phylogenetic analysis (I. Agnarsson & M. Arnedo pers. comm.). Both morphological (Levi 1957) and molecular (M. Arnedo pers. comm.) evidence indicate that *Theridion frondeum* Hentz 1850 and *Theridion albidum* Banks 1895 are sister species and that *R. sexpunctatus* and *R. aurantius* are also sister species. Morphological evidence indicates that *Theridion cheimatos* Gertsch and Archer 1942 will eventually be transferred to *Rugathodes* (I. Agnarsson pers. comm.).

The need to learn more about habitat preferences, life histories, and other facets of species' natural histories before being able to answer important questions about the structure and dynamics of communities has been emphasized by many (e.g., Duffy 1978; Strong et al. 1984; Wilson 1992; Polis et al. 1996). Our goal is to begin providing these kinds of information for North American species of *Theridion, Rugathodes,* and *Wamba,* thereby making them more accessible to ecologists and other evolutionary biologists. The Great Smoky Mountains National Park Biosphere Reserve (GSMNP), due partly to its wide elevation range (275–2013 m), large size (207,000 ha), and low temperate latitude (35°35′N, in the southern Appalachian Mountains), comprises a rich mosaic of biotic communities appropriate for pursuing this goal. By distributing a systematic sampling effort among the major habitats of this park, we have expanded our knowledge of the habitat distribution patterns of these 14 related theridiid species, completed the first life history analyses for three of them, and added knowledge about their reproductive biology.

We also hope that such knowledge will begin to help us evaluate this group's potential as an indicator assemblage (a group of species that can be used to monitor and predict changes or species richness in biotic communities). The search for such indicator groups is an important focus of some ecologists, conservation biologists, and environmental monitoring agencies (Thomas 1972; Kremen et al. 1993; Colwell & Coddington 1994; Russell et al. 1995; Norris 1999). An ideal indicator group should be easily sampled, abundant, diverse, geographically widespread, sensitive to environmental change, and important to community dynamics (Noss 1990; Kremen et al. 1993). Since spider taxa appear to meet these criteria (e. g., Uetz 1979; Coyle 1981; Bracher & Bider 1982; Christenson et al. 1990; Riechert & Bishop 1990; Coddington & Levi 1991; Carter & Rypstra 1995), they deserve to be included in the search for indicator taxa.

METHODS

Habitat distribution.—A team of four collectors used a modified Coddington sampling protocol (Coddington et al. 1996) to obtain the 668 one-hour ground (235), aerial (172), beat (206), and sweep (55) 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 (ca. 0–49 cm above ground). Aerial sampling involved searching leaves, branches, tree trunks, and spaces in between, from knee height up to maximum overhead arm's reach (ca. 50–220 cm above ground). 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. Hands and aspirators were used to collect the spiders into 80% ethanol. One sample unit equaled 1 hour 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 the non-forest communities (grass bald, mountain wetland, and native grassland sites) 1-hour sweep sampling was substituted for aerial and/or beating methods (see Appendix); sturdy sweep nets with 38 cm diameter hoops were used and the number of sweeps per hour (175–400, mean and SD = 268 ± 47.7) depended primarily on vegetation structure and spider abundance.

Two sets of samples (one in the spring and one in late summer) were collected from 17 focal sites, each site representing one of the 16 major habitat (community) types found in the GSMNP. Habitat type, locality data, collecting dates, and sample sizes for each method at each site are given in the Appendix. At each site (except for the high grass bald, Table Mountain pine, and Indian Creek wetland sites) equal or nearly equal numbers of samples were collected with each of the methods employed. Two of the sites (low grass bald and heath bald) were sampled in 1995. The others were sampled in 1996. All adult and juvenile *Theridion, Rugathodes,* and *Wamba* specimens were sorted from each sample and identified to species. The pigment patterns are distinctive for each species in all but the first instar. The most similar species, *T. frondeum* and *T. albidum,* differ in the form of the longitudinal median marks on the carapace; *T. frondeum* has two lines or a broad band and *T. albidum* has one line. Voucher specimens for each species have been deposited in the

National Museum of Natural History, Smithsonian Institution.

The relative abundance (mean number of individuals per 1-hour sample) of each species was computed for each of the 17 sites. This index of abundance does not show the often wide variation in number of individuals among 1-hr samples at each site. This variation is due largely to the fact that each method samples only a subset of microhabitats, to spatial environmental variation within each site, and to seasonal changes in spider abundance correlated with species' phenologies. Shannon diversity and Pielou's evenness indices were used to measure the diversity of these theridiid species at each site (Magurran 1988).

Life history.—For the three most common species (*R. aurantius*, *R. sexpunctatus*, and *T. frondeum*) tibia I length (ITL) was measured along its dorsal surface in every specimen collected at a site where the species was common. Toft (1976) demonstrated that ITL 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× magnification and are accurate to ±0.0185 mm. StatView 4.5 (Abacus Concepts) was used to generate ITL frequency distribution histograms for these samples. From these histograms it was possible to determine instar number. Instars were also distinguished by the distinctive widths of the palpal tarsi of penultimate and, for *R. aurantius* and *R. sexpunctatus*, antepenultimate males. The maximum width of the palpal tarsus in dorsal view (PTW) was measured at 100× magnification (accurate to ±0.00925 mm) for instar III specimens of *R. aurantius* to confirm this. Phenology and generation time were determined by examining the relationship between instar distribution and collecting date. These life history analyses were based on ITL measurements of 375 *R. aurantius*, 139 *R. sexpunctatus*, and 843 *T. frondeum* individuals (see Figs. 3, 5 and 6 for the sites and dates represented by these samples). The pattern of early postembryonic development was determined by examining (at 24–100× magnification) the spiderlings and shed exuviae in eleven *R. aurantius* and four *T. frondeum* egg sacs containing spiderlings. One field collected antepenultimate male and an antepenultimate female of *R. aurantius* were reared to adulthood.

Other observations.—The vertical microhabitat distribution for each species was analyzed by computing its relative abundance in aerial (above knee level) vs. ground (below knee level) samples. 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 $P < 0.05$). Field notes, sketches, measurements, and close-up photos of webs and spiders were used to characterize web structure and spider behavior. Prey items were collected from webs in the field. Egg diameters were measured with a Wild M-5 stereomicroscope at 50× magnification with an accuracy of ±0.0185 mm. Clutch sizes were determined by counting the number of eggs and spiderlings in each field-collected egg sac. An unpaired *t*-test was used to determine if clutch size and body size differed significantly between early and late summer samples of *R. aurantius* and if egg and body sizes of *R. aurantius* differed significantly from those of *T. frondeum.* Several live specimens (predominantly adult females, most with egg sacs) of *R. aurantius* and *T. frondeum* were kept in small transparent plastic terraria for a few weeks to observe rates of brood development and behavior.

RESULTS

Habitat distribution.—Fourteen *Theridion*, *Rugathodes*, and *Wamba* species were found in the GSMNP. At each of the seven highest elevation sites (over 1500 m) one of these species was much more abundant than any other (Table 1, Fig. 1). *Rugathodes sexpunctatus* was common (relative abundance = 0.5–2.0) or abundant (relative abundance > 2.0) in the spruce-fir (1830 m) and spruce (1715 m) sites, *R. aurantius* was abundant in the high grass bald (1755 m) and beech gap (1645 m) sites, and *T. frondeum* was abundant in the northern hardwood (1615 m), red oak (1555 m), and low grass bald (1505 m) sites. Middle to low elevation sites (below 1400 m) tended to contain more species (2–8, mean and SD = 4.4 ± 1.6) than the high elevation sites (2–4, 2.4 ± 1.0) and to lack abundant species. Shannon diversity and Pielou eveness index values for the sets of these species at each site show this same pattern (Table 2).

Table 1.—Relative abundance of *Theridion*, *Rugathodes* and *Wamba* species at 17 focal sites representing 16 major habitats in the Great Smoky Mountains National Park. Species arranged alphabetically by species name. The single specimen of *T. alabamense* was found in a leaf litter sample.

Habitat and elevation (in m) of focal site	Relative abundance (mean number of specimens per 1-hour sample)													
	alabamense	*albidum*	*aurantius*	*cheimatos*	*crispulus*	*differens*	*flavonotatum*	*frondeum*	*glaucescens*	*lyricum*	*murarium*	*neshamini*	*pennsylvanicum*	*sexpunctatus*
Spruce-fir (1830)			0.13											1.71
High grass bald (1755)		0.04	5.92					0.21						0.13
Spruce (1715)			0.04											3.13
Beech gap (1645)			11.38					1.13						
Northern hardwood (1615)			0.02					8.07						0.02
Red oak (1555)								3.50		0.04				
Low grass bald (1505)					0.03			3.71				0.07		
Heath bald (1390)					0.01	0.03		0.15		0.35				0.43
Mixed oak (1115)		0.02						0.27		0.07				
Table Mountain pine (1005)		0.12			0.06	1.15				1.33				
Hemlock-hardwood cove (945)		0.08				0.15		0.48	0.15	0.21				
Hemlock (885)		0.69			0.10		0.13			0.33				0.48
Hardwood cove (740)	0.02	0.54				0.04	0.14	1.11	0.09	0.48	0.02			
Wetland (Indian Cr.) (685)		0.53		0.06			0.47			0.18			0.06	
Wetland (Meadow Br.) (535)		1.18		0.06			0.71			0.06			0.18	
Native grassland (520)		0.04		0.67				0.04						
Pine-oak (395)						0.02				0.92				

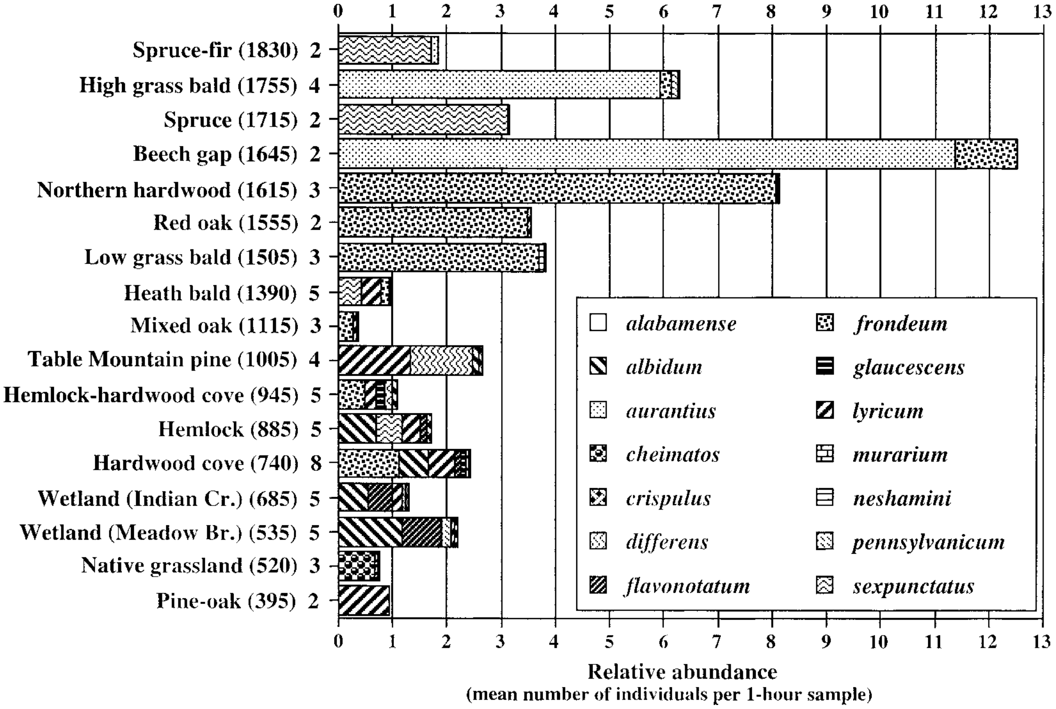

Figure 1.—Stack-bar diagram showing relative abundance of *Theridion, Rugathodes* and *Wamba* species at 17 focal sites representing 16 major habitats in the Great Smoky Mountains National Park. Focal sites are listed by habitat in order from highest to lowest elevation (in m) and number of species found at that site are given after elevation.

Table 2.—Species richness and diversity values for assemblages of *Theridion, Rugathodes* and *Wamba* species at 17 focal sites representing 16 major habitats in the Great Smoky Mountains National Park.

Habitat and elevation of focal site (in m)	No. of samples	Observed richness	Diversity index (Shannon)	Evenness index (Pielou)
Spruce-fir (1830)	24	2	0.25	0.36
High grass bald (1755)	24	4	0.28	0.20
Spruce (1715)	24	2	0.07	0.10
Beech gap (1645)	24	2	0.30	0.44
Northern hardwood (1615)	44	3	0.04	0.03
Red oak (1555)	48	2	0.06	0.09
Low grass bald (1505)	72	3	0.36	0.32
Heath bald (1390)	72	5	1.18	0.73
Mixed oak (1115)	45	3	0.70	0.64
Table Mountain pine (1005)	33	4	0.93	0.67
Hemlock-hardwood cove (945)	48	4	1.42	0.88
Hemlock (885)	48	5	1.40	0.87
Hardwood cove (740)	56	8	1.47	0.71
Wetland (Indian Cr.) (685)	17	5	1.28	0.80
Wetland (Meadow Br.) (535)	17	5	1.10	0.68
Native grassland (520)	24	3	0.64	0.58
Pine-oak (395)	48	2	0.11	0.16

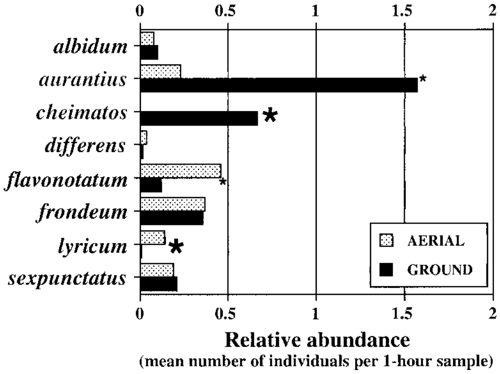

Figure 2.—Vertical microhabitat distribution of *Theridion* and *Rugathodes* species as indicated by relative abundance in aerial and ground samples from those sites where the species has been collected. Only those species found in ground and/or aerial samples at two or more sites are included. Aerial samples from 50 to 220 cm above ground; ground samples below 50 cm. Large asterisks indicate significant differences ($P < 0.05$), small asterisks differences at $0.05 > P < 0.13$.

The only middle to low elevation site with diversity and evenness values as low as those of the high elevation sites was the pine-oak site. The hardwood cove site appears to possess the greatest number of species (8). Both wetland sites had the same five species, and at each of these two sites *T. albidum* and *T. flavonotatum* were more common than the other three species and about equally abundant.

Theridion frondeum was found in more habitats (10 of 16) than any other species, and was especially abundant in the high elevation hardwood communities and the low grass bald, which is surrounded by high elevation hardwood (Table 1, Fig. 1). *Theridion albidum,* the sister species of *T. frondeum,* was found in almost as many habitats (8) but was virtually absent from high elevation habitats. Both of these species occur over a wider elevation range (1220 m) than any other species. *Rugathodes aurantius* is restricted to, and its sister species, *R. sexpunctatus,* is most abundant in, high elevation communities, but wherever one of these species is abundant or common, the other is uncommon (relative abundance < 0.5) or absent. *Theridion lyricum* Walckenaer 1841 was found in nine habitats, including a wide range of middle to low elevation communities, but appears to be most common in dry, pine-dominated, forests. Three of the less common species appear to be associated primarily with a single community type: *T. flavonotatum* Becker 1879 with wetland, *T. differens* Emerton 1882 with Table Mountain pine, and *T. cheimatos* Gertsch and Archer 1942 with native grassland. Six species (*T. alabamense* Gertsch and Archer 1942, *T. glaucescens* Becker 1879, *Wamba crispulus* (Simon 1895), *T. murarium* Emerton 1882, *T. neshamini* Levi 1957, and *T. pennsylvanicum* Emerton 1913) were uncommon wherever they occurred and, with one exception (*Wamba crispulus*), were found in only one or two habitats.

Microhabitat distribution.—Four species, *T. albidum, T. differens, T. frondeum,* and *R. sexpunctatus,* were equally common below and above knee level (Fig. 2). *Theridion cheimatos* was found only below knee level. *Rugathodes aurantius* was more common below than above knee level, but the difference is not significant ($P = 0.12$). *Theridion lyricum* was significantly more common above than below knee level; *T. flavonotatum* exhibits the same pattern, but the difference is not significant ($P = 0.08$). *Theridion flavonotatum* webs were common in the tops of relatively tall leafless stalks of dead herbaceous plants at both wetland sites. Nearly all *R. aurantius* webs were found on the undersides of the leaves of low herbs in clearings (grass balds, trailsides, and areas of sparse canopy in beech gap forest). *Rugathodes sexpunctatus* was collected primarily by beating low branches of young fir or ferns in spruce-fir and spruce forest. All *T. cheimatos* specimens collected at the native grassland site were found on the ground near a drainage ditch. *Theridion glaucescens* appeared only in beat samples. The single specimen of *T. alabamense* was collected in a leaf litter sample.

Life history.—There are five instars in the life cycle of *R. aurantius* (Fig. 3). Instar I, which is confined to the egg sac, lacks eyes, pigment, spigots, and visible hairs (at 100× magnification). Instar II has eyes, pigment around the eyes, functional spinnerets, and many fully developed hairs. It is also the active spiderling instar that emerges from the egg sac; this was confirmed by examining and measuring newly emerged spiderlings reared in the laboratory and by observing that instar II spiderlings inside the sac have the same ITL

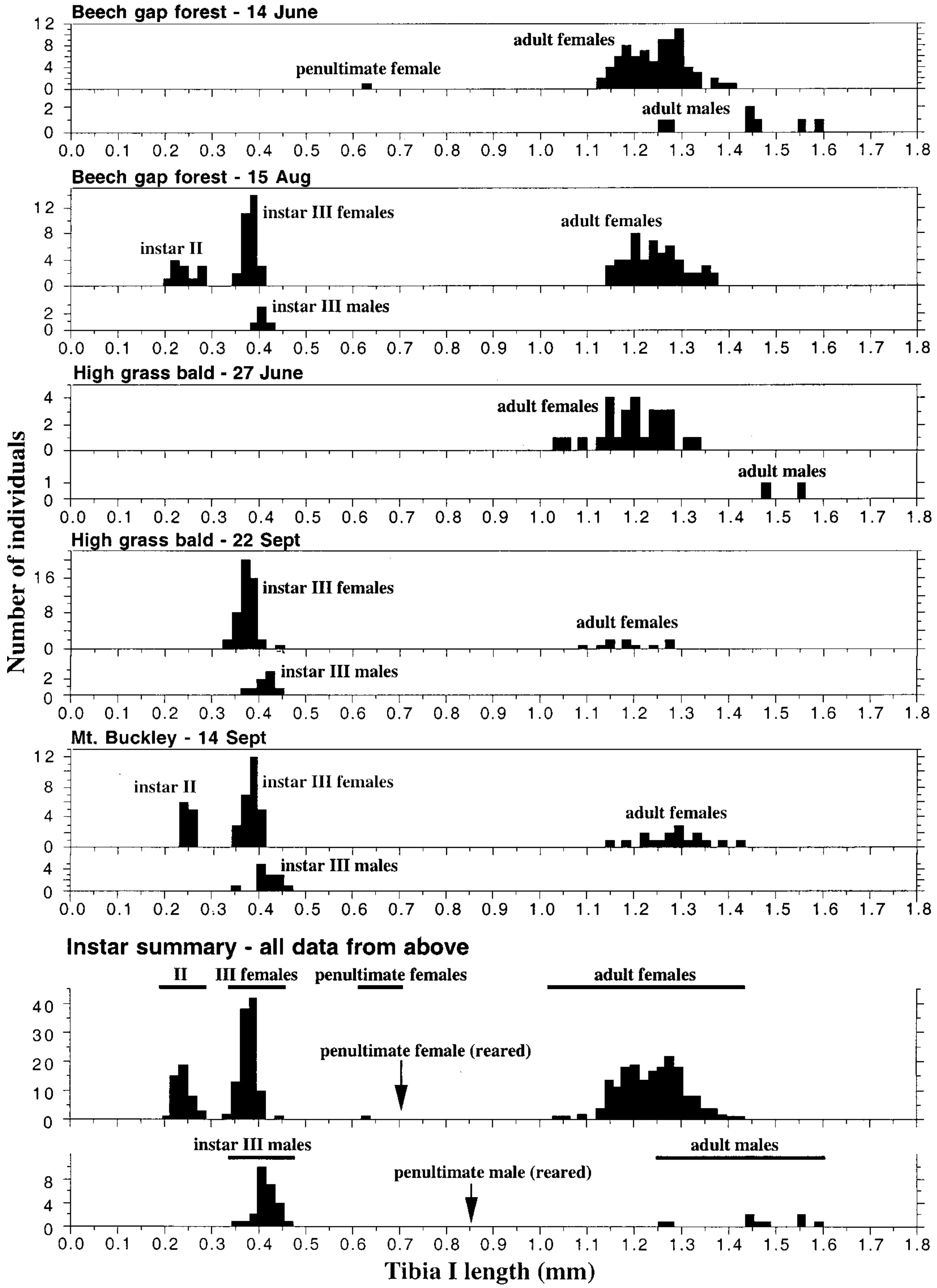

Figure 3.—Size (ITL) frequency distribution histograms for five samples of *Rugathodes aurantius* from three sites. For each sample, females and individuals too young to be sexed are graphed separately from males. All five samples were pooled to generate the instar summary histograms at the bottom. Arrows in instar summary histogram mark ITL values of the penultimate instar exuvia of two specimens reared to adulthood in captivity.

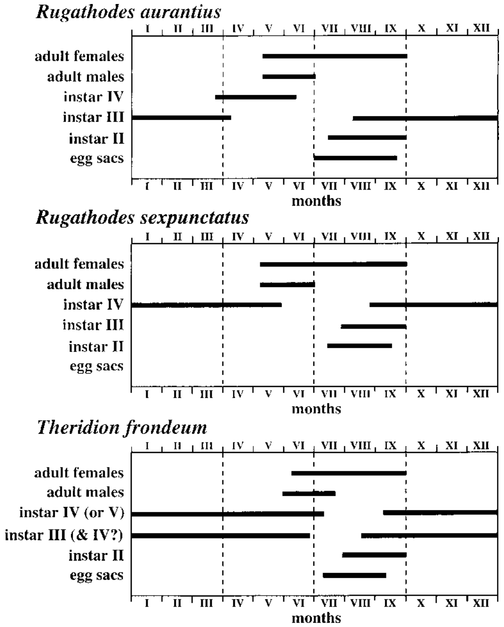

Figure 4.—Postulated phenologies for two *Rugathodes* and one *Theridion* species in the Great Smoky Mountains National Park. Based on size frequency distribution analyses and additional observations.

as the smallest solitary (post-dispersal) instar collected in the field. Instar III is the antepenultimate instar. This was confirmed by rearing an antepenultimate male and an antepenultimate female collected at Mt. Buckley to the adult instar and measuring the exuvia. The palpal tarsi of antepenultimate males were significantly ($P < 0.0001$) wider (PTW = 0.111–0.130, mean and SD = 0.117 ± 0.008, n = 15) than those of same-aged females (0.065–0.074, 0.067 ± 0.004, n = 15). Instar IV is the penultimate instar; this was confirmed by rearing the two aforementioned Mt. Buckley spiders and by finding one female of that size class at the beech gap site with an epigynum visible through her soon-to-be-molted cuticle. Instar V is the adult instar. The life cycle pattern most consistent with these data (Fig. 3) is that of one generation per year, with most individuals over-wintering in the antepenultimate instar and males and females maturing and mating in May and June (Fig. 4). This hypothesis was further supported by finding 15 individuals—all antepenultimate males and females—in leaf litter samples collected under the snow at the beech gap site on 12 February 1997. The absence of adult males from all summer and fall collections made after 27 June suggests that they die soon after mating. Many of the females collected at the beech gap site on 9 July and 15 August and at Mt. Buckley on 14 September were guarding single egg sacs. Sexual dimorphism in ITL first appears in instar III and is much greater in subsequent instars (Fig. 3). We found female-biased sex ratios (females/males) in every sample of instar III (6.0 at the beech gap on August 15 (n = 35), 1.5 at the same site on 12 February (n = 15), 6.0 at the high grass bald on 22 September (n = 57), and 2.1 at Mt. Buckley on 14 September (n = 40)).

There are five instars in the life cycle of *R. sexpunctatus* (Fig. 5). Based on observations of its sister species, *R. aurantius,* we presume that instar II of *R. sexpunctatus* is the active instar that emerges from the egg sac. The males of instars III and IV can be distinguished from each other and from females by distinctive widths of the palpal tarsi. Instar V is the adult instar. The life cycle pattern (Fig. 4) most consistent with the data is that of a single annual generation that over-winters chiefly in the penultimate instar, as indicated by the relatively large number of penultimate spiders collected in September. A collection of six individuals (four penultimate females, one penultimate male, and one instar III female) at Mt. Buckley on 25 September also supports this phenology. Males and females apparently mature and mate in May and June. Adult males are absent from late summer collections, suggesting that they die soon after mating. Some adult females persist until at least mid-September. Sexual dimorphism in ITL first appears in instar III, is much greater in the following instars, and appears to be even more pronounced in *R. sexpunctatus* than in *R. aurantius* (Fig. 5). The sex ratios (females/males) in instars III and IV of the total *R. sexpunctatus* sample are 1.6 (n = 29) and 1.1 (n = 30) respectively.

There are five or six instars in the life cycle of *T. frondeum* (Figs. 6, 7). Development in the egg sac includes the same two instars as in *R. aurantius.* Instar II spiderlings in the sac have the same ITL as the smallest solitary (post-dispersal) field-collected instar; this shows that instar II emerges from the egg sac. Only in the penultimate instar do males have distinctively wider palpal tarsi than females.

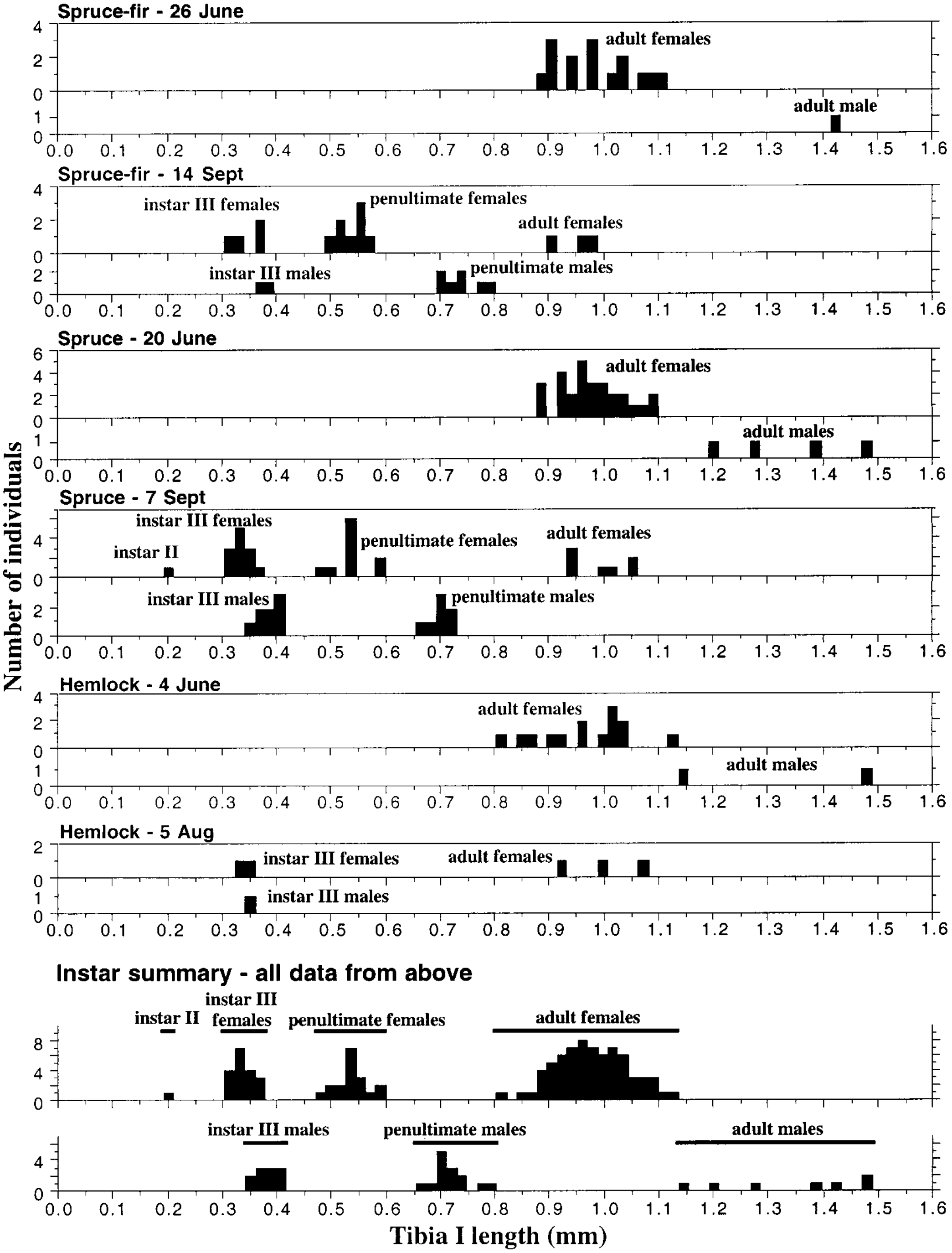

Figure 5.—Size (ITL) frequency distribution histograms for six samples of *Rugathodes sexpunctatus* from three sites. For each sample, females and individuals too young to be sexed are graphed separately from males. All six samples were pooled to generate the instar summary histograms at the bottom.

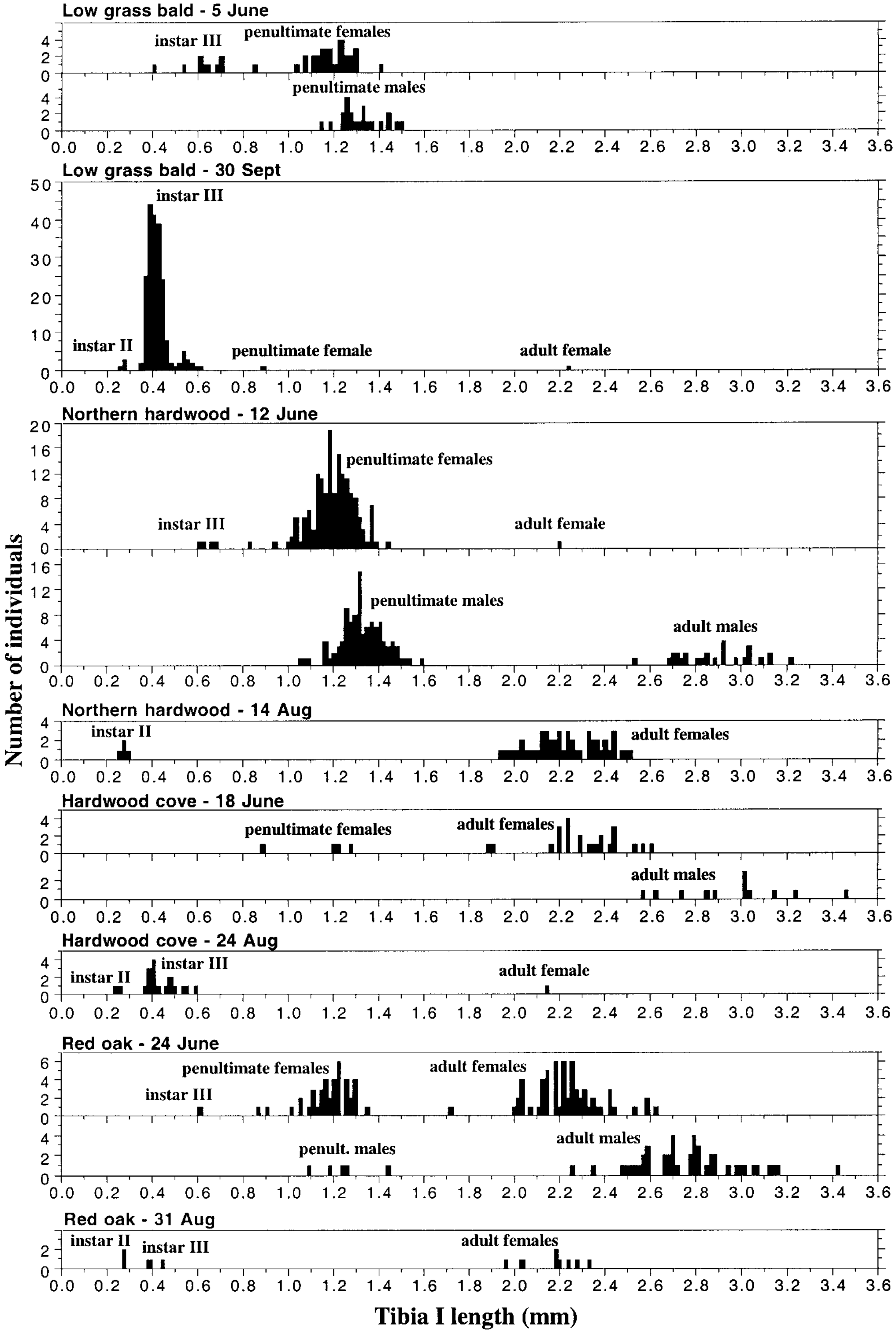

Figure 6.—Size (ITL) frequency distribution histograms for eight samples of *Theridion frondeum* from four sites. For each sample, females and individuals too young to be sexed are graphed separately from males.

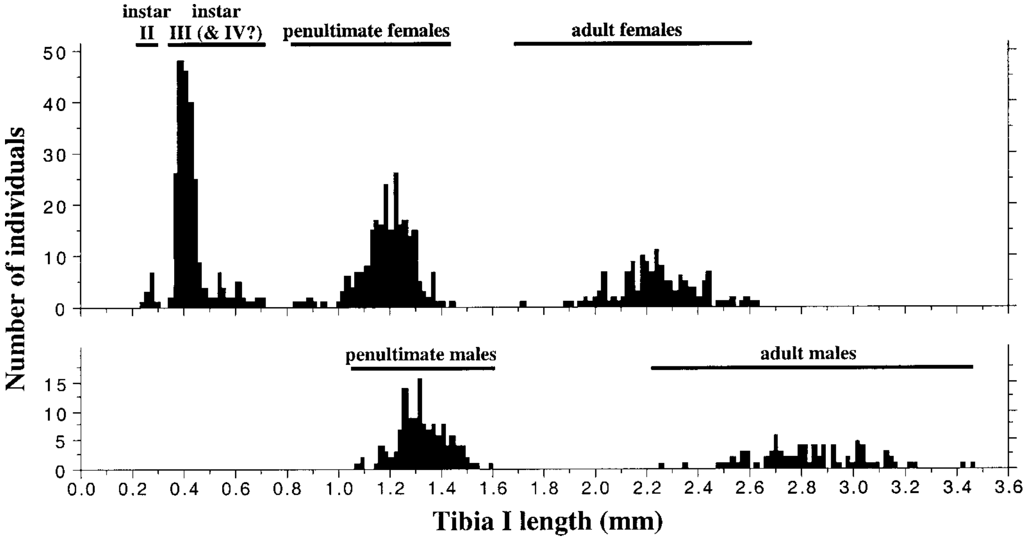

Figure 7.—Instar summary histogram for *Theridion frondeum.* Generated by pooling all data in Fig. 6.

An epigynum was visible through the soon-to-be-molted cuticle of several penultimate females. There are two lines of evidence suggesting that the size class labeled instar III in Fig. 7 may actually include instar IV individuals as well. This size class is broad and skewed strongly to the left. And the seasonal histograms (Fig. 6) show that many of the individuals that comprise the low right shoulder of this size class were collected in early June (Fig. 6), suggesting that a mid-May collection may have contained a large proportion of individuals with ITL values between 0.5 and 0.7 mm. Such a class, if present, would have to be instar IV, and would mean that at least many adults of *T. frondeum* are in their sixth instar. The life cycle pattern most consistent with the data is that of one generation per year, with over-wintering primarily in the antepenultimate instar (Fig. 4). Males and females apparently mature and mate in June and July. Since males at each site in June exhibit a higher ratio of adults to juveniles than do females, it is clear that males tend to mature before females. The absence of adult males from late summer collections suggests that they die off soon after mating. Sexual dimorphism in ITL is apparent in penultimate and adult instars. The sex ratio (females/males) in the total *T. frondeum* penultimate instar sample is 1.9 (n = 362) (Fig. 7).

Other natural history observations.—*Rugathodes aurantius*.—*Web placement and structure: Rugathodes aurantius* webs are virtually restricted to the herb layer. Most adult female webs were found on the broad-leafed herbs *Solidago glomerata* Michaux, *Angellica* sp., *Agertina altissima* King & Robinson var. *roenesis*, and *Aster divaricatus* L. All of these species were common at the beech gap forest site wherever tree gaps permitted the development of a rich herb layer. Most *R. aurantius* collected in the high grass bald were found in dense patches of *S. glomerata.* At Mt. Buckley (1998 m) webs were found almost exclusively in a small clearing dominated by *S. glomerata* (11 adult females and 40 juveniles were collected in a 1-hour ground sample) and were virtually absent from the adjacent spruce-fir forest (only one adult female was collected—from ferns—in 3 hours of ground collecting and beating). Adult female webs are primarily confined to the underside of a single leaf or leaflet. Roughly parallel strands of silk attached to the leaf edges bend or fold the leaf, and the bulk of the web is an asymmetrical cobweb sheltered within the resultant concavity. The spider typically rests near the center of the web on or within a few mm of the retreat leaf's ventral surface. Three types of leaf modification were observed in detail at the beech gap site on 9 July (n = 9 webs). The first type was characterized by strands of silk running from the tip to the base of the leaf and bending the leaf tip and adjacent edges downward and toward the leaf base, the second by lines pulling the lateral edges of the leaf to within 5 cm of each other to form a length-wise fold, and the third by lines connecting a lateral edge fold near the base of the leaf to the tip fold, forming a cone-shaped retreat. Juvenile spiders do not appear to modify leaf shape; those collected at Mt. Buckley on 14 September were found, like adult females, on the undersides of *S. glomerata* leaves, but their webs were smaller and positioned in the natural concavity of the leaf undersurface.

Diet: Prey items found in the webs of two adult female and two instar II spiders at Mt. Buckley included three Homoptera (two green leaf hoppers [Cicadellidae] 3.5 and 3.4 mm long and one other homopteran 1.3 mm long), three small muscoid Diptera (2.1–3.5 mm long), and two other small unidentified winged insects. Beside the trail to the high grass bald site, the web of one female contained her recently emerged instar II spiderlings and the exoskeletal remains of four midges (2.2–2.5 mm long) and one small (8.5 mm long) cranefly.

Reproduction and brood care: Rugathodes aurantius females were found in nature guarding egg sacs close to the undersurface of their retreat leaf from early July to mid September. No female was observed with more than one egg sac. The spherical white egg sac is composed of a single fairly dense layer of kinky/looped threads. The diameters of 5–10 *R. aurantius* eggs in each of nine clutches (egg sacs) ranged from 0.48–0.59 mm (mean and SD = 0.54 ± 0.03 mm). Clutch sizes at two sites (beech gap forest and Mt. Buckley clearing) ranged from 3–47 (24.6 ± 13.7, n = 30). Clutch size was significantly larger (P < .0001) at the beech gap forest site on 9 July (11–47, 35.5 ± 9.7, n = 15) than on 15 August (3–23, 12.2 ± 6.2, n = 11). Clutch size of the 14 September Mt. Buckley sample was also significantly lower (14–24, 17.8 ± 4.3, n = 4, P = .003) than that of the 9 July beech gap sample. Females collected with egg sacs at the beech gap site on 9 July were significantly larger (P = .0001) (ITL = 1.18–1.39, 1.30 ± 0.05, n = 14) than those collected on 15 August (1.15–1.30, 1.22 ± 0.04, n = 11).

When disturbed, females with egg sacs typically maintained contact with the sac and often moved it. At least one of the fourth legs was used to position and move the sac, which, in a few cases, was clearly seen to be attached to the spinnerets. The time between oviposition and emergence of instar II spiderlings from the sac was 13 days for the only brood oviposited in captivity. Spiderlings emerged from the eight field-collected egg sacs between 2 and 9 days (mean and SD = 5.9 ± 2.3) after they were collected, also suggesting that the normal period of development in the egg sac is about 2 weeks or less. Several hours before spiderling emergence, the female repeatedly and vigorously bit at the egg sac, pulling and stretching the silk to create a hole through which instar II spiderlings soon began to emerge. In the field, females were commonly found with emerged instar II spiderlings, and in one case the remains of several Diptera were present in such a web, but we saw no evidence of communal feeding. One captive female captured *Drosophila* flies and placed them near her recently emerged instar II spiderlings, which appeared to increase in size (abdominal volume) over the course of three weeks; however we never actually observed the spiderlings feeding.

Theridion frondeum.*—Retreat placement and structure:* Adult females were found inside partly folded living leaf retreats from 30 to 220 cm above ground in a great variety of plants, both herbaceous (stinging nettle, ferns, blackberries, etc.) and woody (striped maple, sugar maple, etc.). Part of the leaf is folded downward longitudinally, transversely, or diagonally. Some, for example, were folded downward sharply near the middle at one side with the opposing edges on that side fastened together with silk to make a roughly cone-shaped retreat.

Diet: A wrapped and partly consumed 5.4 mm long adult female *Pityohyphantes costatus* (Hentz 1850) spider was found in a web occupied by a 3.3 mm long *T. frondeum* female and her emerged instar II spiderlings.

Reproduction and brood care: Theridion frondeum females were found in leaf retreats with egg sacs from early July to late August. No female was observed with more than one egg sac. The spherical white egg sac is composed of a single fairly dense layer of kinky/looped threads. The diameters of ten eggs in each of two clutches ranged from 0.67 to 0.78 mm (mean and SD = 0.72 ± 0.03 mm). Clutch size ranged from 13–40 (26.8 ± 11.5, n = 5). The time from oviposition to the emergence of instar II spiderlings from the egg sac took 13 days for the only viable brood oviposited in captivity. Two females were observed vigorously biting their egg sacs prior to spiderling emergence. In the summer spiderlings are often found with the mother in her web, suggesting that they remain there for at least a few days before dispersing.

***Theridion albidum*.**—One female was found at the hardwood cove site on 24 August in a partly folded leaf retreat at knee level guarding an egg sac containing ten spiderlings that emerged from the sac as instar II spiderlings about 4 days later in captivity.

***Theridion differens*.**—One female was found at the Table Mountain pine site on 6 August 1997 guarding her pale grey-brown egg sac attached to her small conical silk retreat in the junction of a leaf petiole and twig on a mountain laurel branch at about head height. She continued to cling tightly to her egg sac after being transported to the lab in a glass vial. Her entire clutch of 25 instar II spiderlings emerged from the sac by the following morning.

***Theridion lyricum*.**—One female was collected at the hardwood cove site on 25 August with her egg sac containing 82 instar I spiderlings. The pale grey-brown sac was composed of kinky/looped strands of silk, some of which were brown, not white.

DISCUSSION

Habitat and microhabitat distribution patterns.—The differences among the 16 sampled habitats (and the great similarity of the two widely separated wetland sites) in the kinds and relative abundances of *Theridion* and *Rugathodes* species (Fig. 1) suggest that these species may be good predictors of habitat. The presence of more of these species in the habitat (hardwood cove forest) celebrated for its high plant diversity (Whittaker 1956), than in some of the habitats (spruce fir, spruce, beech gap, and pine-oak forests) characterized by relatively low plant diversity (Whittaker 1956), suggests a positive correlation between the species richness of this set of spider species and plant species richness. However, the finding of only three of these spider species in the plant-rich (175 species (Stratton & White 1982)) low grass bald and five in the plant-poor (12 species (Cain 1930)) heath bald completely negates this correlation. Evidently, the number of *Theridion* and *Rugathodes* species present at a site is not a reliable predictor of plant species richness.

It is of interest that the species found in the greatest number of habitats and over the greatest range of elevations (*T. frondeum, T. albidum, R. sexpunctatus, T. lyricum,* and *T. differens*) all have relatively wide geographic and latidudinal ranges (Levi 1957), while some of the species found in only one or two habitats (*T. alabamense, T. cheimatos, T. neshamini,* and *T. pennsylvanicum*) have much smaller ranges (Levi 1957). This tendency for habitat specialists to occupy relatively small geographic ranges has been observed in many taxa (Stevens 1989), including species of *Tetragnatha, Neriene,* and *Araneus* spiders living in the GSMNP (Aiken & Coyle 2000; Wright & Coyle 2000; Davis & Coyle 2001).

Our observation that the sister species *T. frondeum* and *T. albidum* are often found at the same sites and that *T. frondeum* is generally more common than *T. albidum* is consistent with Levi's (1957) and Kaston's (1981) observations. The much greater abundance of *T. frondeum* at high elevation sites is consistent with the geographic ranges of the two species; T. *frondeum* is more common and widespread at higher latitudes (Levi 1957), and is therefore probably better adapted to cold climates, than is T. *albidum. Rugathodes aurantius* and *R. sexpunctatus*, another pair of sister species (Levi 1957; I. Agnarsson pers. comm.), are most common in high elevation communities—which is consistent with their basically boreal geographic ranges (Levi 1957)—but they exhibit striking habitat segregation. The distinctively different web placement substrates of the two species suggests that this segregation is based upon different microhabitat requirements. *Rugathodes aurantius* builds its webs on the undersides of broad-leaved herbs, which are rare on the heavily shaded ground of spruce-fir and spruce forests, whereas *R. sexpunctatus* typically lives on the foliage of young fir trees, which are rare or absent in the high grass bald and beech gap forest communities. The restriction of *R. aurantius* to high elevation habitats may be the result of climatic requirements, since an ample broad-leaved herb substratum is present at some of the other forest sites (especially northern hardwood) where *R. aurantius* is extremely rare or absent. Since *R. sexpunctatus* is found at some of our middle elevation sites, it seems to be less narrowly restricted to boreal climates. Our data suggest that it may be restricted to fine-needle conifers, which is consistent with Levi's (1957) observation that it is ''usually found on coniferous trees.'' Our observations of *T. cheimatos* and *T. neshamini* are consistent with Chamberlin and Ivie's (1944) note that the former species was collected in moderately damp places on the ground and with Levi's (1957) observation that the latter species is associated with tall grass.

Life history.—Except for reports that *T. frondeum* matures in late June or July and that adult females produce eggs in July and survive through September (Emerton 1902; Comstock 1948; Kaston 1981), there are no published descriptions of the life cycles of the three species we have analyzed (*R. aurantius, R. sexpunctatus,* and *T. frondeum*). Based on our observations and those of Toft (1976) on several *Theridion* species living in a Danish beech forest, we postulate that in most *Theridion* and *Rugathodes* species the life cycle contains five or six instars, with instar II emerging from the egg sac. Like the three species we studied, four of the six *Theridion* species whose life cycles Toft resolved have annual (one-year) life cycles and overwinter in the antepenultimate or penultimate instars. The three species we studied differ from one another in two aspects of their phenologies (Fig. 4): *R. aurantius* overwinters in the antepenultimate instar; *R. sexpunctatus* overwinters in the penultimate instar; and *R. aurantius* and *R. sexpunctatus* mature a few weeks and possibly one instar earlier than does *T. frondeum.*

The female-biased sex ratios we observed in antepenultimate and penultimate instars of these three species may be artifacts of sampling error or may be real. The strongly female-biased ratios in the adult samples of all three species could be the result of the earlier maturation and/or shorter longevity of males, but the basis for bias in earlier instars is not so evident. Group living, which should favor selection of female sex-biasing mechanisms in social spiders (Aviles 1986, 1993), does not exist in these species.

Web placement and structure.—The diversity of leaf retreat architectures engineered by adult females of *R. aurantius* and *T. frondeum* is probably the result of a flexible response to variation in leaf form. We hypothesize that leaf retreat construction is an adaptation to protect the spider and her brood from rain, intense sunlight, and/or visual predators.

Diet.—The few prey items collected from *R. aurantius* webs suggest that small flying insects are a significant part of their diet. The data also show that both *R. aurantius* and *T. frondeum,* like other *Theridion* species (Bristowe 1958), can capture prey considerably larger than themselves.

Reproduction and brood care.—Given that *T. frondeum* females with egg sacs were significantly ($P < .001$) larger (mean carapace width = 1.12 mm ± 0.04; $n = 5$) than those of *R. aurantius* (0.85 ± 0.19; $n = 5$), it is not particularly surprising that the eggs in the two observed egg-stage clutches of *T. frondeum* were significantly larger than those of *R. aurantius* ($P < .001$). In the light of Marshall & Gittleman's (1994) findings that clutch size increases with body size across spider taxa, it is interesting that the observed clutch sizes of these two species did not differ. It is also noteworthy that the only clutch of *T. lyricum* we observed (carapace width of the mother = 0.96 mm) was nearly twice as large as the largest clutches of the other species.

Toft (1976) found that females of some *Theridion* species produce two or more (up to five) egg sacs over the course of the summer. He postulated that this ability to produce multiple clutches is a widespread fecundity-enhancing trait of small spiders that compensates for a relatively small number of eggs per egg sac. Two of our observations strongly suggest that *R. aurantius* females also produce multiple clutches: 1) the single annual cohort of adult females is found in nature guarding egg sacs throughout a 2.5 month period, even though the interval from oviposition to spiderling emergence from the egg sac is about 2 weeks; 2) there was a significant decrease in the beech gap forest site population's mean clutch size between 9 July and 15 August, a pattern commonly observed in multi-clutch spiders (Toft 1976; Marshall & Gittleman 1994). Nevertheless, we cannot rule out the possibility that *R. aurantius* females produce only one clutch and that the observed decrease in clutch size is the result of delayed oviposition by smaller females. This second hypothesis is consistent with the observation that adult females in the 15 August beech gap sample had a significantly smaller mean ITL value than those of the 9 July sample.

Our observations of *R. aurantius* and *T. frondeum* indicate that females devote considerable effort to brood care. Bent-leaf retreat construction and egg sac guarding have been observed in other *Theridion* species (for example Archer (1947) and Bristowe (1958)), and Emerton (in McCook 1890) described an unidentified *Theridion* female assisting her spiderlings in exiting the egg sac with the same behaviors we observed in *R. aurantius* and *T. frondeum.* Our observations that instar II spiderlings of these two species remain with the mother in her retreat for at least a few days after emerging from the egg sac suggests the interesting possibility of nutritional parental care like that observed in some European and Central American *Theridion* species (Nielsen 1932; Bristowe 1958; Kullman 1972; and authors' personal observations in Costa Rica). We have observed no compelling evidence of such care, but the possibility deserves closer scrutiny.

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APPENDIX

Habitat type, locality data (with UTM coordinates), collecting dates, and sample sizes are given for each of the 17 focal sites (listed in order from highest to lowest elevation) and one accessory site. For focal sites, the number of ground, aerial, beat, and sweep samples are given in parentheses after total number of 1-hr samples. Whittaker (1956) provides descriptions of the vegetation of most of these habitats. A bald is a natural treeless 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 is typically located on a south-facing slope in a high mountain gap. Hardwood cove forests are found in sheltered middle elevation sites and are characterized by a high species diversity of large trees and understory plants.

Focal sites.—*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 and 14 Sept. 1996, 24 (8-8-8-0).

High grass bald: North Carolina: Swain County, Andrews Bald, E2738, N39354, 1755 m elev., 27 June and 22 Sept. 1996, 24 (10-0-4-10).

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 and 7 Sept. 1996, 24 (8-8-8-0).

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 and 15 Aug. 1996, 24 (8-8-8-0).

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&15 June and 14 Aug. 1996, 44 (15-15-14-0).

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 and 31 Aug. 1996, 48 (16-16-16-0).

Low grass bald: North Carolina: Swain County, Gregory Bald, E2401, N39343, 1505 m elev., 3–5 June and 29–30 Sept. 1995, 72 (24-0-24-24-24).

Heath bald: Tennessee: Sevier County, Inspiration Point on Alum Cave Trail, E2789, N39461, 1390 m elev., 25–26 May and 23–24 Sept. 1995, 72 (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 and 13 Aug. 1996, 45 (15-14-16-0).

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 and 6 Aug. 1996, 33 (13-8-12-0).

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 and 30 July and 1 Aug. 1996, 48 (16-16-16-0).

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 and 5 Aug. 1996, 48 (17-14-17-0).

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 and 24–25 Aug. 1996, 56 (19-18-19-0).

Wetland (Indian Cr.): 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 and 16 Aug. 1996, 17 (7-3-4-3).

Wetland (Meadow Br.): Tennessee: Blount County, marsh along Meadow Branch at 0.5 km ENE of Dosey Gap, E2527, N39470, 535 m elev., 23 May and 1 Aug. 1996, 17 (7-4-0-6).

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 and 8 Aug. 1996, 24 (12-0-0-12).

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 and 2 Aug. 1996, 48 (16-16-16-0).

Accessory site.—Tennessee: Sevier County, small clearing near top of Mt. Buckley and adjacent area of young fir on N slope near top of Mt. Buckley, E2720, N39380, 1980–2000 m elev., 14 Sept. 1996.