A STRUCTURED INVENTORY OF APPALACHIAN GRASS BALD AND HEATH BALD SPIDER ASSEMBLAGES AND A TEST OF SPECIES RICHNESS ESTIMATOR PERFORMANCE

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ABSTRACT. The current rate of species attrition necessitates the development of quick and accurate sampling protocols and species richness estimators. Four time-based and one area-based methods were used to sample spiders of a grass bald and a heath bald in the Great Smoky Mountains National Park in late spring and early fall of 1995. Eighty-four samples were collected at each site; 1853 adults and 91 species were found in the grass bald, 573 adults and 60 species in the heath bald. The data were analyzed with 11 species richness estimators: Chao & Lee 1, Chao & Lee 2, ACE, ICE, bootstrap, Chao 1, Chao 2, first-order jackknife, second-order jackknife, Michaelis-Menten runs, and Michaelis-Menten means. All but the Chao & Lee estimators generated richness estimates that clustered within a reasonable range, 106–160 species for the grass bald and 68–90 species for the heath bald. The failure of the observed species accumulation curve to level off for our data sets showed that more sampling would be needed to determine the number of species present as adults during the two sampling seasons. Although this prevented us from rigorously testing richness estimator performance, we found that the Michaelis-Menten means estimator performed better than the other estimators when judged by two indirect criteria of good estimator performance—the estimator curve should reach an asymptote with fewer samples than are required for the observed species accumulation curve to reach an asymptote, and the estimates should be close to reasonable visual extrapolations of the asymptote of the observed species accumulation curve. We postulate that the differences we found in species richness and taxon and guild composition between the spider assemblages of these two bald communities are, at least in part, a consequence of striking differences in the physiognomy, richness, and taxonomic composition of the plant associations of the two communities.

Keywords: Spiders, species richness, richness estimators, Appalachian balds

In order to know how and where to protect biodiversity, it is imperative that we learn more about the patterns of diversity of terrestrial arthropods, which may comprise 80% or more of the Earth's species but have too often been neglected by resource managers and conservation planners (Wilson 1988, 1992; Kremen et al. 1993; Colwell & Coddington 1994; Longino 1994). Spiders, which include about 36,000 described species and are estimated to number 60,000–170,000 species (Coddington & Levi 1991; Platnick 1999), comprise a significant portion of this terrestrial arthropod diversity. Spiders are abundant and ubiquitous,

employ a remarkable diversity of predation strategies, occupy a wide array of spatial and temporal niches, are characterized by high within-habitat taxonomic diversity, exhibit taxon- and guild-specific responses to environmental change, and are relatively easy to sample and identify. They are important regulators of insect populations (Riechert & Lockley 1984; Riechert & Bishop 1990; Wise 1993) and may prove to be useful indicators of the overall species richness and health of biotic communities (Kremen et al. 1993; Colwell & Coddington 1994; Norris 1999).

Coddington et al. (1991) pioneered the development of a sampling protocol and estimation procedure for rapid assessment of spider diversity at tropical forest sites. This and similar protocols can be structured to provide replicated data sets that reflect the relative abundance of species in the sites and habitats studied and may therefore provide comparable views of species richness, taxonomic compo-

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sition, and guild structure across diverse communities and regions (Coddington et al. 1996; Silva & Coddington 1996; Dobyns 1997). Colwell & Coddington (1994) reviewed and explored the performance of richness estimators and emphasized the need to test these with real data sets.

Balds, natural tree-less communities located on well-drained high-elevation sites below the climatic tree-line, are among ''the most distinctive and celebrated'' communities of the southern Appalachian Mountains (Whittaker 1956; Mark 1958). Despite considerable research, there is no clear understanding of the factors responsible for the origin and maintenance of these communities (Cain 1930; Whittaker 1956; Billings & Mark 1957; Mark 1958; Stratton & White 1982). Grass balds, because of their high plant species richness, asthetic appeal, and shrinking size (due to forest encroachment), are currently the focus of special monitoring and management efforts by resource specialists in the Great Smoky Mountains National Park (GSMNP) (Keith Langdon pers. com.). Heath balds, which are dense thickets of evergreen ericaceous shrubs on highly acidic soil, support far fewer plant species and a more homogeneous architecture than grass balds, but attract considerable attention because of their colorful floral displays.

In the current study we employ a modified Coddington protocol and eleven richness estimator algorithms and other analytical methods to provide the first estimates of the species richness and structure of spider assemblages in a grass bald and a heath bald. Additionally, we use these data sets to evaluate the performance of the richness estimators.

METHODS

Study sites.—The two sites are 40 km apart in the GSMNP. Gregory Bald, the grass bald site, covers a very gently rounded peak (UTM grid coordinates: E2400, N39343) and ranges from 1490–1510 m elevation. This bald covers about 3 hectares and contains 175 vascular plant species, more than any other bald in the GSMNP (Stratton & White 1982). It consists of large open grassy areas interrupted by patches of shrubs (up to 2 m tall) and, occasionally near its edge, small trees (up to 15 m tall). The dominant grasses are mountain oats (*Danthonia* spp.) and blue grasses (*Poa* spp.);

the dominant shrubs are blueberries (*Vaccinium* spp.), hawthorns (*Cretaegus* spp.) and azaleas (*Rhododendron* spp.). The ground surface is covered by thin mats of dead grasses and sedges in grassy areas and a thin layer of leaf litter below the shrubs.

The heath bald site (UTM grid coordinates: E2788, N39460) covers 0.5 hectares at 1380–1410 m elevation on the southeast-facing slope both above and below a 50 m stretch of Alum Cave Trail immediately below Inspiration Point (which is on a ridge extending south from Peregrine Peak). Cain (1930) found that nearby heath balds supported only 12 plant species. The heath bald at this site is a homogeneous, dense, woody mass of interwoven ericaceous shrubs about 3–4 m tall; rhododendron (*Rhododendron catawbiense*) and mountain laurel (*Kalmia latifolia*) dominate; *Vaccinium*, Carolina rhododendron (*R. minus*), greenbriar (*Smilax*), and sand myrtle (*Leiophyllum buxifolium*) are also present. The ground, virtually devoid of herbaceous plants, is covered by a thick layer of leaf litter (interrupted in places by patches of short compact moss) over thick, moist, spongy humus.

Data collection.—Our sampling procedure included five methods chosen to access all microhabitats in these two communities: aerial hand collection, ground hand collection, beating, Tullgren funnel litter extraction, and sweep-netting. The first four methods were used in the heath bald; sweep-netting was substituted for aerial hand collection in the grass bald due to the predominance of low vegetation in that community. The aerial and ground hand collection methods are synonymous with the ''looking up'' and ''looking down'' methods, respectively, of Coddington et al. (1991). Aerial sampling involves searching leaves, branches, tree trunks, and spaces in between, from knee height up to maximum overhead arm's reach. Ground collection involves searching on hands and knees, exploring the leaf litter, logs, rocks, and plants that are below knee level. Beating consists of striking vegetation at any level with a 1 m long stick and catching the falling spiders on a tray held horizontally below the vegetation. Because the dense maze of shrub branches throughout the heath bald and in some parts of the grass bald made it difficult to maneuver the standard 0.5 m² beating sheet, we used instead a smaller (0.24 m²), rigid, rectangular (57 × 42 cm)

plastic tray with a 1.5 cm high rim. The opening of the heavy sweep net used for sweep-netting was 0.37 m in diameter; at 225–425 sweeps per hour (mean = 327.5) and a mean sweep length of 1.4 m, an average of 49 m^3 of habitat volume was sampled per hour. For all of these methods, fingers, glass vials, and aspirators were used to collect spiders into 80% ethanol. Each litter sample consisted of 1 m^2 of leaf litter and underlying loose humus that was placed in a plastic bag, transported to the lab, and processed in 50–60 cm diameter Tullgren funnels fitted with 6–8 mm mesh screens and 60 watt light bulbs for two–four days until the litter was dry. In grassy areas of the grass bald, where much of the litter was interlocked with grass and low herbs, a long knife was used to cut away and collect thin sections of sod.

Except for the litter samples, time was used to partition sampling effort into replicate samples; one sample unit equals one hour of un-interrupted time during which a collector attempts to collect every spider encountered that is not obviously a juvenile. During any one sampling hour each of the three collectors (the authors) used only one method, but the team as a whole employed all three time-based methods in the same portion of the site. Sampling effort was distributed so that, in each sampling season, no area within the site was sampled more than once with a given method and nearly all of the available habitat area was sampled. Because of the density and height of the heath vegetation, the area sampled per hour was much smaller in the heath bald than in the grass bald. It should be noted that since sweeping was substituted for aerial hand sampling on the grass bald and since it took more time and effort to maneuver in the heath (which biases time-based samples), considerable caution must be exercised when making between-community comparisons of the abundance or relative abundance of taxa. In particular, these differences may bias Kulczynski's index of similarity (see below). Night sampling was tried (3 one-hour samples in the grass bald), but, since the rate of capture of adults was so low (2.3 per hour), sampling was limited to daylight hours. Sampling was conducted in the spring and fall of 1995: 25–26 May and 23–24 September in the heath bald; 3–5 June and 29 September–1 October in the grass bald. Forty-two samples (36 one-hour samples distributed equally among the three time-based methods and six litter samples) were collected at each site in each season. Although many juveniles end up in each sample, only adults were counted, identified, and used in analyses because identifying juveniles to species is often impossible. The specimens, which are being curated temporarily at Western Carolina University, will eventually be deposited in the National Museum of Natural History of the Smithsonian Institution.

Data analysis.—The computer program EstimateS (Version 5.0.1) (Colwell 1997) was used to evaluate the performance of the following 11 species richness estimators with our data sets: Chao & Lee 1, Chao & Lee 2, ACE, ICE, Chao 1, Chao 2, first-order jackknife, second-order jackknife, bootstrap, Michaelis-Menten runs, and Michaelis-Menten means. The two Michaelis-Menten estimators use the same equation, a two-parameter hyperbolic function first used to describe enzyme kinetics, to directly extrapolate the species accumulation curve, but they differ in computational format (Colwell & Coddington 1994; Colwell 1997). The other nine estimators are non-parametric algorithms which estimate the number of species yet-to-be-collected based on a quantification of rarity. Chao & Lee 1, Chao & Lee 2, ACE, and ICE are coverage-based richness estimators based on the statistical concept of sample coverage. ACE (abundance-based coverage estimator) (Chao et al. 1993) and ICE (incidence-based coverage estimator) (Lee & Chao 1994) are modified versions of the two Chao & Lee (1992) estimators, which have been found to consistently overestimate richness, especially with small samples (Colwell & Coddington 1994; Colwell 1997). Chao & Lee 1, Chao & Lee 2, ACE, and Chao 1 are all abundance-based estimators; that is, they use abundance to quantify rarity (for example, the number of singletons and doubletons, which are the number of species represented by only one or two individuals in the entire data set). ICE, Chao 2, both jackknife estimators, and the bootstrap estimator are incidence-based; they rely on incidence (presence/absence) data to quantify rarity (for example, the number of uniques and duplicates, which are the number of species found in only one or two samples in the entire data set). We used the Coleman curve,

which plots the expected richness for random subsamples of the entire data set, to determine whether the samples are uniform enough to justify use of the Michaelis-Menten estimators (Colwell & Coddington 1994; Colwell 1997).

See Colwell & Coddington (1994), Colwell (1997), and Chazdon et al. (1998) for descriptions and discussions of these estimator algorithms and for a demonstration of how EstimateS tracks changes in each richness estimate as samples accumulate. From a species-by-sample abundance matrix, the program selects a sample, calculates the richness estimates based on that sample, selects a second sample, recomputes the estimates using the data from both samples, and so on until all samples are included. By randomizing sample order (we chose 100 randomizations) and computing the mean richness estimate for each sample accumulation level, the program removes the effect of sample order and generates a smoother species accumulation curve, thereby permitting closer comparison of estimator performance. The fact that the Coleman estimator curve was nearly identical to the species accumulation curve in all of our data sets indicates that our samples are not especially heterogeneous, and that randomization of sample accumulation order is therefore justified (Colwell & Coddington 1994). Using the same randomization protocol, we also plotted the mean number of singletons, uniques, doubletons, and duplicates against sample number.

Percentage complementarity (Colwell & Coddington 1994), Kulczynski's index of similarity (also called the Bray-Curtis index) (Bray & Curtis 1957), and Sorensen's index of similarity (Kent & Coker 1992) were used to compare the taxonomic composition of the two bald communities. Percentage complementarity = $100(x/y)$, where x = number of unique species (collected in only one community or the other), and y = total number of species collected in both communities (combined species richness). Kulczynski's index of similarity (K) = $2w/(a + b)$, where a = number of individuals collected in community A, b = number of individuals collected in community B, and w = sum of the lesser abundances for those species present in both communities. Sorensen's index of similarity (S) = $2e/(c + d)$, where c = number of species collected in community A, d = number of spe-

cies collected in community B, and e = number of species common to both communities. Percentage complementarity is a measure of difference. Kulczynski's index is a measure of similarity and, because it uses abundance data, emphasizes the importance of common species. Sorensen's index, also a measure of similarity, does not emphasize the importance of common species.

RESULTS

A total of 2426 adult spiders representing 22 families, 89 genera, and 128 species was present in the 168 samples collected in this study (see Table 1 for breakdowns by community and season). The number of adults collected and the observed richness were much higher in the grass bald than in the heath and were higher in the spring than in the fall in both communities (Table 2). Sampling intensity, the ratio of adults to species, was higher for the grass bald than for the heath bald (Table 2). The inventory completeness index (the percentage of species that is not singletons), another indication of how well a community has been sampled, was slightly lower for the grass bald than for the heath bald (Table 2).

Species richness estimates.—For none of the six sample sets (the total sample for each community and the two seasonal subsets for each community) does the mean, randomized, observed species accumulation curve reach an asymptote (Figs. 1–6), although these curves for the three heath community data sets (Figs. 2, 5, 6) appear to more closely approach an asymptote than do those of the corresponding grass bald data sets (Figs. 1, 3, 4). The Michaelis-Menten, ICE, and Chao 2 estimator curves approach an asymptote more rapidly as sample number increases than do the other estimator curves (Figs. 1–6). In all six data sets, the Michaelis-Menten estimate appears to approach an asymptote more closely than do the other estimates. The second-order jackknife estimates climb more steeply for every data set than do the first-order jackknife estimates. The shape of the bootstrap estimator curve departs relatively little from the observed species accumulation curve. As predicted by Colwell (1997), the Michaelis-Menten runs estimator generated especially high and erratic richness estimates early in the curve. Since this estimator leveled off to nearly the same values as the Michaelis-Menten means, only

Table 1.—Species collected in bald communities; numbers of adults given for spring and fall sample sets (42 samples per set). Classification follows Platnick (1997), except that linyphiids are divided into subfamilies. Guild designations (based on our collecting data and literature): AW = aerial web-builder, AH = aerial hunter, GW = ground web-builder (web in, or attached to, ground litter), GH = ground hunter; AG and GA mean, respectively, primarily aerial or primarily ground. Erigonine linyphiids and leptonetids were assigned to web-building guilds even though for many of these species it is not known whether webs are used in prey capture. Singleton status designations (based on identified GSMNP collections): C = common in GSMNP (in one or more other habitats), U = apparently uncommon in GSMNP.

Taxon	Grass bald		Heath bald		Guild	Single-ton status
	Spring	Fall	Spring	Fall		
Agelenidae						
Agelenopsis utahana (Chamb. & Ivie)	0	3	0	4	AW	
Amaurobiidae						
Callobius bennetti (Blackw.)	0	0	0	1	AW	C
Cybaeopsis armipotens (Bishop & Crosby)	4	0	0	0	GW	
Cybaeopsis pantoplus (Bishop & Crosby)	0	0	1	14	GW	
Coras montanus (Emerton)	0	0	1	2	GW	
Wadotes calcaratus (Keys.)	0	3	0	0	GW	
Wadotes hybridus (Emerton)	0	1	0	0	GW	C
Wadotes tennesseensis Gertsch	0	0	3	6	GW	
Antrodiaetidae						
Antrodiaetus unicolor (Hentz)	0	8	12	9	GW	
Anyphaenidae						
Wulfila saltabunda (Hentz)	0	1	0	0	AH	U
Araneidae						
Araneus trifolium (Hentz)	0	12	0	0	AW	
Araniella displicata (Hentz)	2	0	0	0	AW	
Argiope aurantia Lucas	0	2	0	0	AW	
Argiope trifasciata (Forskal)	0	1	0	0	AW	C
Eustala cepina (Walck.)	0	0	1	0	AW	U
Gea heptagon (Hentz)	0	3	0	0	AW	
Hyposinga rubens (Hentz)	13	0	0	0	AW	
Neoscona arabesca (Walck.)	0	3	0	0	AW	
Neoscona hentzi (Keys.)	0	3	0	0	AW	
Clubionidae						
Clubiona canadensis Emerton	4	0	3	0	AH	
Clubiona kastoni Gertsch	1	0	0	0	AH	C
Clubiona rhododendri Barrows	66	34	2	3	AGH	
Clubiona spiralis Emerton	0	0	7	10	GAH	
Clubiona sp. A	1	0	0	0	AH	U
Cybaeidae						
Cybaeus patritus Bishop & Crosby	0	0	0	4	GW	
Dictynidae						
Cicurina breviaria Bishop & Crosby	1	2	1	2	GW	
Cicurina brevis Emerton	0	0	1	0	GW	C
Cicurina minima Chamb. & Ivie	0	0	6	10	GW	
Dictyna maxima (Banks)	0	0	1	0	AW	U
Lathys immaculata Chamb. & Ivie	1	0	1	12	GW	C
Gnaphosidae						
Zelotes hentzi Barrows	4	0	0	0	GH	

Table 1.—Continued.

Taxon	Grass bald		Heath bald		Guild	Single-ton status
	Spring	Fall	Spring	Fall		
Hahniidae						
Calymmaria persica (Hentz)	0	0	2	6	GW	
Cryphoeca montana Emerton	0	0	6	1	GW	
Neoantistea agilis (Keys.)	1	7	0	0	GW	
Neoantistea magna (Keys.)	2	11	5	15	GW	
Leptonetidae						
Appaleptoneta coma (Barrows)	0	0	0	1	GW	C
Appaleptoneta silvicultrix (Crosby & Bishop)	0	0	0	2	GW	
Linyphiidae						
Erigoninae						
Blestia sarcocuon (Crosby & Bishop)	4	36	2	3	GW	
Ceraticelus alticeps Fox	564	434	3	6	AW	
Ceraticelus carinatus Emerton	12	77	6	14	GW	
Ceratinella brunea Emerton	2	3	0	0	GW	
Ceratinops carolinus Banks	1	0	1	0	GW	C
Ceratinopsidis formosa Banks	0	0	0	1	AW	C
Collinsia oxypaederotipus (Crosby)	128	2	85	0	GW	
Eperigone trilobata (Emerton)	1	0	0	0	GW	U
Eridantes erigonoides Emerton	8	0	0	0	GW	
Erigone autumnalis Emerton	11	2	0	0	GW	
Erigone brevidentata Emerton	4	0	0	0	GW	
Floricomus praedesignatus Bishop & Crosby	10	1	11	11	GW	
Gonatium crassipalpum Bryant	0	3	0	0	AW	
Grammonota pictilis (O.P.-Cambr.)	0	0	2	0	AW	
Maso sundevallii (Westring)	6	0	0	0	GW	
Pelecopsis moesta (Banks)	12	12	0	0	GW	
Pocadicnemus americana Milledge	3	0	17	0	GAW	
Scylaceus pallidus (Emerton)	0	7	0	0	GW	
Walckenaeria digitata (Emerton)	4	0	0	0	GAW	
Walckenaeria directa (O.P.-Cambr.)	1	1	3	5	GW	
Walckenaeria minuta (Emerton)	0	0	3	1	GW	
Walckenaeria pallida (Emerton)	0	0	1	0	GW	C
Walckenaeria spiralis (Emerton)	4	0	0	0	GW	
Erigoninae sp. A	0	0	0	1	GW	U
Erigoninae sp. B	0	2	0	0	AW	
Erigoninae sp. C	0	1	0	0	AW	U
Linyphiinae						
Bathyphantes bishopi Ivie	4	50	16	2	GW	
Bathyphantes pallidus (Banks)	0	1	0	0	GW	U
Centromerus denticulatus (Emerton)	0	0	0	1	GW	C
Florinda coccinea (Hentz)	39	7	0	0	AW	
Frontinella pyramitela (Walck.)	0	0	0	1	AW	C
Lepthyphantes zebra (Emerton)	17	0	56	29	GW	
Meioneta micaria (Emerton)	8	1	2	0	GAW	
Meioneta semipallida Chamb. & Ivie	0	5	0	0	GAW	
Neriene radiata (Walck.)	0	0	9	0	AW	
Neriene redacta Chamb.	0	5	0	0	GAW	
Neriene variabilis (Banks)	0	0	0	1	GAW	C
Tapinopa bilineata Banks	0	0	0	1	GW	U
Taranucnus ornithes (Barrows)	0	0	1	1	GW	

Table 1.—Continued.

| | Grass bald | | Heath bald | | | Single-ton status |
Taxon	Spring	Fall	Spring	Fall	Guild	
Liocranidae						
Phrurotimpus borealis (Emerton)	3	0	18	0	GH	
Scotinella sp. A	0	0	2	0	GH	
Lycosidae						
Allocosa funerea (Hentz)	0	1	0	0	GH	U
Arctosa virgo (Chamb.)	3	0	0	0	GH	
Pardosa atlantica Emerton	1	0	0	0	GH	U
Pardosa milvina (Hentz)	1	0	0	0	GH	C
Pardosa saxatilis (Hentz)	1	0	0	0	GH	C
Pirata hiteorum Wallace & Exline	0	6	0	0	GH	
Pirata montanus Emerton	1	2	0	0	GH	
Schizocosa bilineata (Emerton)	1	0	0	0	GH	U
Varacosa avara (Keys.)	1	0	0	0	GH	C
Nesticidae						
Nesticus reclusus Gertsch	0	0	2	2	GW	
Oxyopidae						
Oxyopes salticus Hentz	5	0	0	0	AH	
Philodromidae						
Philodromus montanus Bryant	2	0	0	0	AH	
Salticidae						
Eris marginata (Walck.)	0	0	0	2	AH	
Evarcha falcata (Clerck)	5	3	0	0	AH	
Ghelna canadensis (Banks)	5	4	0	0	GH	
Habrocestum pulex (Hentz)	1	0	2	0	AH	C
Habronattus coecatus (Hentz)	1	0	0	0	AH	C
Hentzia mitrata (Hentz)	2	0	0	0	AH	
Maevia inclemens (Walck.)	12	0	0	0	AH	
Maevia sp. A	2	1	14	4	AH	
Neon nellii Peckham & Peckham	17	3	21	0	GH	
Pelegrina montana (Emerton)	1	0	0	0	GH	C
Pelegrina proterva (Walck.)	18	8	0	1	AGH	C
Pelegrina sp. A	1	0	0	0	AH	U
Phidippus clarus Keys.	0	3	0	0	AH	
Phidippus mystaceus (Hentz)	0	1	0	0	AH	U
Talavera minuta (Banks)	1	0	0	0	GH	U
Thiodina puerpera (Hentz)	1	0	0	0	AH	C
Zygoballus bettini Peckham	2	0	0	0	AH	
Zygoballus sexpunctatus (Hentz)	1	0	0	0	AH	C
Tetragnathidae						
Tetragnatha laboriosa Hentz	5	0	0	0	AW	
Zygiella dispar (Kulczynski)	0	0	0	2	AW	
Theridiidae						
Dipoena nigra (Emerton)	1	0	0	0	AW	C
Pholcomma barnesi Levi	0	0	1	0	GW	U
Pholcomma hirsuita Emerton	0	0	1	1	GW	
Robertus frontatus (Banks)	1	0	0	0	GW	C
Theridion differens Emerton	0	0	2	0	AW	
Theridion frondeum Hentz	0	1	0	0	AW	C
Theridion intervallatum Emerton	0	1	0	0	AW	U

Table 1.—Continued.

| Taxon | Grass bald | | Heath bald | | Guild | Single-ton status |
	Spring	Fall	Spring	Fall		
Theridion lyricum Walck.	0	0	7	0	AW	
Theridion neshamini Levi	1	0	0	0	AW	U
Theridion sexpunctatum Emerton	0	0	30	0	AW	
Theridula opulenta (Walck.)	23	2	0	0	AW	
Theridiosomatidae						
Theridiosoma gemmosum (L. Koch)	0	0	7	0	GW	
Thomisidae						
Misumena vatia (Clerck)	0	0	1	0	AH	U
Misumenoides formosipes (Walck.)	0	1	0	0	AH	C
Misumenops asperatus (Hentz)	3	0	0	0	AH	
Misumenops oblongus (Keys.)	5	0	0	0	AH	
Ozyptila distans Dondale & Redner	0	0	0	3	GH	
Xysticus triguttatus Keys.	1	0	0	0	GH	U
Total	1072	781	378	195		

Table 2.—Richness estimates and other summary values for each bald community and for each seasonal sample set from each community. Each richness estimate represents the mean (and, for some estimators, the SD) for 100 randomizations of sample order. Sampling intensity is the ratio of individuals to species. Inventory completeness is the percentage of species that are not singletons. Adjusted estimate range is the range of all but the Chao & Lee richness estimate values divided by the observed number of species.

| | Grass bald | | | Heath bald | | |
	All samples	Spring samples	Fall samples	All samples	Spring samples	Fall samples
Richness estimates						
Chao & Lee 1	948.1	558.3	262.7	106.5	90.4	59.5
Chao & Lee 2	9147.8	4307.1	1260.1	150.9	144.1	73.0
ACE	120.9	93.6	59.4	75.6	57.5	53.6
ICE	125.3	99.8	65.0	76.8	57.9	52.5
Chao 1	159.6 ± 36.7	110.6 ± 25.5	62.0 ± 9.9	72.8 ± 8.4	54.4 ± 6.8	51.1 ± 8.8
Chao 2	139.2 ± 22.7	101.6 ± 18.2	71.1 ± 14.8	82.6 ± 13.9	61.6 ± 11.0	53.1 ± 9.6
first-order jackknife	124.6 ± 6.0	93.3 ± 5.9	65.6 ± 4.2	78.8 ± 4.5	59.6 ± 3.7	53.6 ± 3.9
second-order jack-knife	146.2	109.8	76.2	89.6	67.4	60.5
bootstrap	105.8	77.9	56.0	68.3	51.7	45.7
MM runs	112.4	85.6	72.9	70.7	59.5	59.5
MM mean	110.8	83.1	69.4	72.3	58.9	55.9
Observed richness	91	66	48	60	45	39
No. of samples	84	42	42	84	42	42
No. of adults	1853	1072	781	573	378	195
No. of adults/sample	22.1	25.5	18.6	6.8	9.0	4.6
No. of singletons	31	25	14	16	13	13
No. of doubletons	7	7	7	10	9	7
No. of uniques	34	28	18	19	15	15
No. of duplicates	12	11	7	8	7	8
Sampling intensity	20.4	16.2	16.3	9.6	8.4	5.0
Inventory completeness	66	62	71	73	71	67
Adjusted estimate range	0.59	0.50	0.42	0.37	0.33	0.38

the curves of the latter estimator are presented here. Chao 1, Chao 2, and ICE estimator curves were also especially erratic, even at high sample numbers. Because the two Chao and Lee estimators gave unrealistically high estimates (Table 2), their curves are not presented in Figs. 1–6. Plots of singletons and uniques rise quickly, level off, and do not decline. There are always more uniques than singletons. Plots of doubletons and duplicates rise more slowly, level off, and, in some data sets (grass total and grass fall), begin to fall.

The richness estimates generated by the 11 estimators varied widely (Table 2). The two Chao & Lee estimates were always distinctively high (especially for the grass bald). The bootstrap estimates were consistently the lowest of the remaining nine estimators, and the second-order jackknife and, occasionally, Chao 1 produced the highest estimates. The estimates of the other six estimators tended to cluster more tightly and varied in rank depending on community and season. The ranges spanned by these six estimates (ACE, ICE, Chao 2, first-order jackknife, and Michaelis-Menten runs and means) are smaller for the heath bald data sets than for the corresponding grass bald sets.

These six richness estimates (106–160 for the grass bald and 68–90 for the heath) and the observed richness (91 and 60) indicate that more spider species live in the grass bald community than in the heath bald community. This conclusion is also supported by the observation that the heath bald data set produced a smaller adjusted estimate range (the ratio of the range of all but the two Chao & Lee estimators divided by the observed richness; Table 2), which suggests that the heath bald inventory is more nearly complete than is the grass bald inventory. The conclusion is further reinforced by the observation that the observed species accumulation curves for the grass bald data sets appear to be further from reaching an asymptote than are those for the corresponding heath bald data sets (Figs. 1–6). We found this same pattern when we plotted species accumulation curves using number of specimens for the independent variable instead of number of samples; at an x-axis value of 573 specimens (the total number found in the heath bald sample set), the grass bald curve is steeper than the heath bald curve. This suggests that the observed difference in

species richness between the two spider assembalges is not a result of sampling bias due to reduced sampling maneuverability in the heath bald.

Community structure.—Values of the complementarity and similarity indices (Table 3) show that these two communities differ greatly in spider species composition; only 23 species were common to both communities. Even if the effect of ''rare'' species is reduced by deleting, before computing these indices, all singleton species that were found in only one community, the index values still indicate a large (although reduced) difference in species composition. In addition, there is a considerable, although smaller, difference between spring and fall samples within each community in the species present as adults (Table 3).

Both assemblages exhibit the commonly encountered skewed frequency distribution of few common species and many rare ones (Williams 1964) (Table 1). In the grass bald only 7 of the 91 observed species each comprise 2% or more of the adults collected. Of these 7 ''dominant'' species, one (*Ceraticelus alticeps*, an erigonine linyphiid) is superabundant, comprising 54% of all adults collected at the site. In the heath bald 19 of the 60 observed species each comprise 2% or more of the adults collected. The two most abundant of these ''dominants'', *Collinsia oxypaederotipus* (an erigonine linyphiid) and *Lepthyphantes zebra* (a linyphiine linyphiid), make up 15% and 14% respectively of all adults collected.

In both communities, linyphiids were far more common than any other family in terms of numbers of species and adults (Table 4). The next three most species-rich families in the grass bald (Salticidae, Lycosidae, and Araneidae) were much less well represented in the heath bald; the absence of lycosids and the presence of only one araneid species in the heath samples are particularly noteworthy. Very small juveniles of *Araneus* orbweavers (probably *A. nordmanni*) were common in the heath; we saw only two or three large orb webs, but did not find their owners. Two families were notably more species-rich in the heath samples than in the grass bald: Dictynidae and Leptonetidae.

In the grass bald, the percentages of aerial (47) and ground-dwelling (53) species are
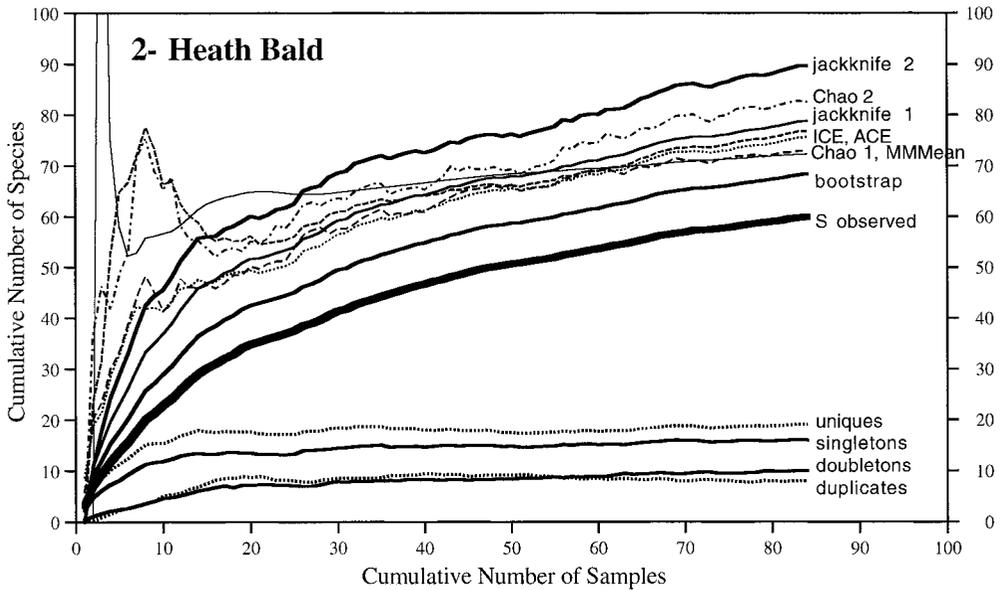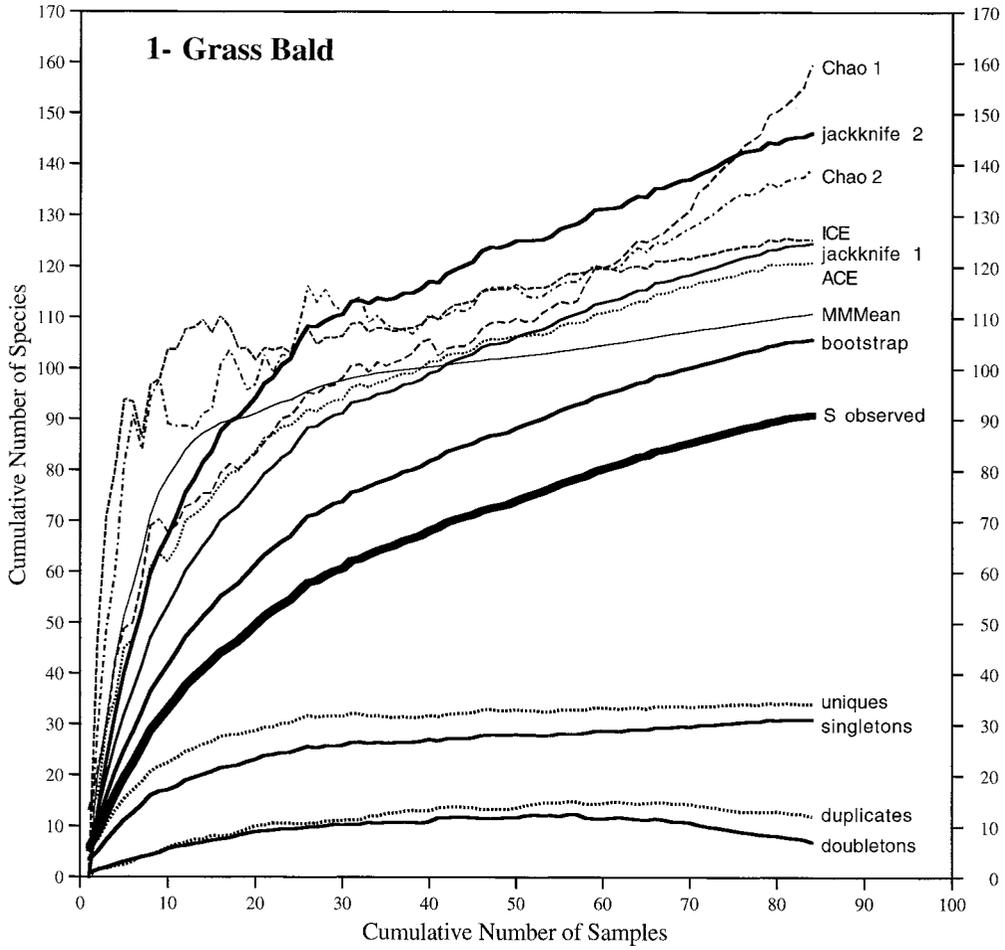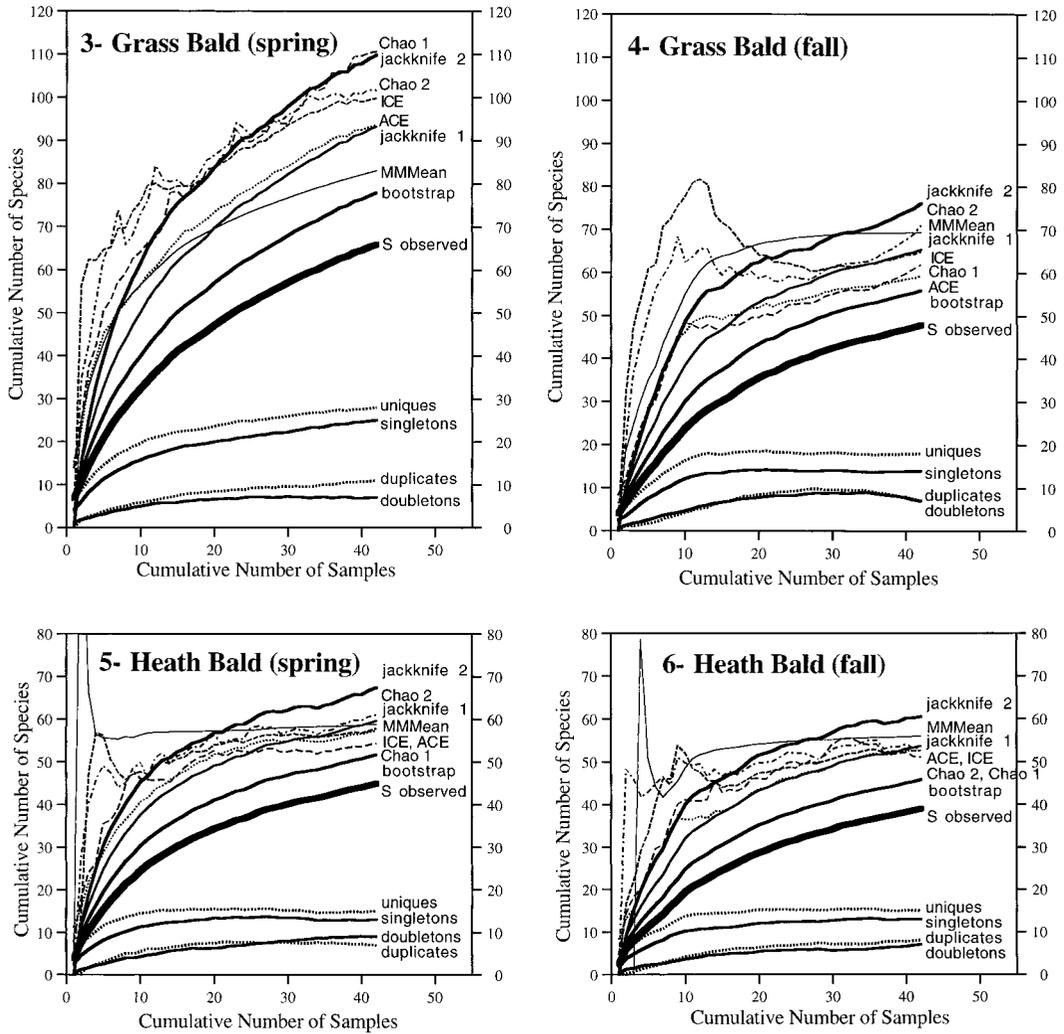
Figures 3–6.—Plots comparing the performance of eight estimators of species richness with the observed species accumulation curve, using data from the four sets of spider samples. 3. Spring samples from the grass bald; 4. Fall samples from the grass bald; 5. Spring samples from the heath bald; 6. Fall samples from the heath bald. Scales, line symbols, variables, and computation protocols are the same as for Figure 1.

←

Figures 1, 2.—Plots comparing the performance of eight estimators of species richness with the observed species accumulation curve, using data from all 84 samples (spring and fall) of spiders from the grass bald (Figure 1) and the heath bald (Figure 2). The species accumulation curve (S observed) plots the observed number of species as a function of the number of pooled samples. The eight curves above the species accumulation curve show the estimated species richness based on successively larger numbers of samples. The estimators used are ACE, ICE, Chao 1, Chao 2, first-order jackknife (jackknife 1), second-order jackknife (jackknife 2), bootstrap, and Michaelis-Menten means (MMMeans). All values were generated by EstimateS, version 5.0.1 (Colwell 1997). The four curves at the bottom of the graph plot mean numbers of singletons, doubletons, uniques, and duplicates as a function of cumulative number of samples. For all 13 curves, each point is the mean of 100 values based on 100 randomizations of sample accumulation order.

Table 3.—Values of complementarity and similarity indices for the two communities and for the spring and fall data sets of each community. See text for definitions of the indices. Index values in parentheses were generated after deleting all singletons found in only one community.

	Grass bald to heath bald	Grass bald spring to fall	Heath bald spring to fall
% Complementarity	82 (73)	75	60
Kulczynski's index of similarity	0.196 (0.229)	0.584	0.363
Sorensen's index of similarity	0.305 (0.422)	0.397	0.571

about equal, and the ground web-building guild is the most species-rich (35% of all species present) (Table 5). In the heath bald, 67% of the species are ground-dwellers, with the great majority of these (58.3% of all species present) probably being ground web-builders. Pronounced seasonal changes occurred in the (adult) guild composition of the grass bald community but not in the heath community (Table 5). The number of aerial web-builder species present as adults increased and the number of aerial and ground hunter species present as adults decreased between spring and fall in the grass bald.

Collecting methods: taxonomic characterization of yields.—The complementarity matrices reveal—for both communities—generally large differences among the methods in the taxonomic composition of the spider samples these methods yield (Table 6). The smallest differences are those between ground and litter samples, beating and sweeping samples, and beating and aerial samples. In terms of number of species per sample, it appears that aerial and beating methods are the least productive (Table 7). Each method yielded some unique species not collected by any other method; aerial hand collecting in the heath yielded the smallest number of unique species (Table 7). From 33–60% of these unique-to-method species were singletons.

DISCUSSION

Species richness estimates.—The best way to test the performance of species richness estimators is to use data sets from a site where the actual species richness is known; the germinating seed bank data set used by Colwell & Coddington (1994) and Butler & Chazdon (1998) essentially meets this requirement. Unfortunately, we cannot use this direct approach to evaluate estimator performance because none of our observed species accumulation

curves reached an asymptote; evidently we have not collected all the species present as adults at either site during the seasons when we sampled. However, we can employ other less rigorous (indirect) ways to assess estimator usefulness—observing how rapidly estimation curves approach an asymptote as sample number increases (Colwell & Coddington 1994; Coddington et al. 1996; Chazdon et al. 1998), looking for a consensus among a majority of estimators (Coddington et al. 1996), and comparing the estimator curves to subjective visual extrapolations of the possible asymptotes of an observed species accumulation curve. A good estimator 1) should reach (or at least closely approach) a stable asymptote with fewer samples than are required for the observed species accumulation curve to reach an asymptote, 2) is unlikely to yield estimates that differ widely from those of all other estimators, and 3) should give estimates that are close to reasonable visual extrapolations of the asymptote of the observed species accumulation curve.

The two Chao & Lee estimators generated unrealistically large estimates, especially so with the grass bald data sets. Colwell & Coddington (1994) observed the same tendency of these two estimators to overestimate species richness with a seed bank data set. The newer, modified coverage-based estimators, ACE and ICE, the latter of which performed especially well in a recent study by Chazdon et al. (1998), generate much more realistic richness estimates for our sample sets than do the Chao & Lee estimators. Although the rankings of richness values generated by all 11 estimators vary somewhat among our data sets and from study to study (Coddington et al 1996; Silva & Coddington 1996; Dobyns 1997; Chazdon et al. 1998), the relatively tight clustering of the ACE, ICE, Chao 2, first-order jackknife,

Table 4.—Percent (of community total) of species and adults collected in each family. Number of species is in parentheses.

	Grass bald		Heath bald	
	% of species	% of adults	% of species	% of adults
Agelenidae	1.1 (1)	0.2	1.7 (1)	0.7
Amaurobiidae	3.3 (3)	0.4	6.7 (4)	4.7
Antrodiaetidae	1.1 (1)	0.4	1.7 (1)	3.7
Anyphaenidae	1.1 (1)	0.1		
Araneidae	8.8 (8)	2.1	1.7 (1)	0.2
Clubionidae	4.4 (4)	5.7	5.0 (3)	4.4
Cybaeidae			1.7 (1)	0.7
Dictynidae	2.2 (2)	0.2	8.3 (5)	5.9
Gnaphosidae	1.1 (1)	0.2		
Hahnidae	2.2 (2)	1.1	5.0 (3)	6.1
Leptonetidae			3.3 (2)	0.5
Linyphiidae	30.8 (28)	80.6	36.7 (22)	51.7
Liocranidae	1.1 (1)	0.2	3.3 (2)	3.5
Lycosidae	9.9 (9)	1.0		
Nesticidae			1.7 (1)	0.7
Oxyopidae	1.1 (1)	0.3		
Philodromidae	1.1 (1)	0.1		
Salticidae	18.7 (17)	5.0	8.3 (5)	7.3
Tetragnathidae	1.1 (1)	0.3	1.7 (1)	1.2
Theridiidae	6.6 (6)	1.6	8.3 (5)	7.3
Theridiosomatidae			1.7 (1)	1.2
Thomisidae	4.4 (4)	0.5	3.3 (2)	0.7

and Michaelis-Menten estimator values suggests that they are either estimating the same real value or are being biased in the same manner. When we apply the above-mentioned three criteria of a potentially good estimator to the performance of the estimators with all six of our data sets, the Michaelis-Menten estimator appears to perform best. ICE and ACE also perform rather well but do not approach an asymptote as quickly as the Michaelis-Menten estimator. Chao 2 and the first-order jackknife show some promise, but the former is sometimes quite unstable and neither closely approach an asymptote. The poor performance of the bootstrap estimator on our data

sets echos the findings of others (Colwell & Coddington 1994; Chazdon et al. 1998). Although they used tropical forest seed, seedling, and sapling data sets that differed greatly from ours, Colwell & Coddington (1994), Butler & Chazdon (1998), and Chazdon et al. (1998) did not come to conclusions that were radically different from ours about the performance of these richness estimators. However, they did give ICE (Chazdon et al. 1998) and Chao 2 (Colwell & Coddington 1994; Chazdon et al. 1998) the highest overall ratings.

The failure of the observed species accumulation curve and most of the estimator curves to reach an asymptote with our data

Table 5.—Percentage of species in each guild for each community and for spring and fall samples from each community. Any species in two guilds (see Table 1) was assigned to its primary guild.

			Grass		Heath	
	Grass	Heath	Spring	Fall	Spring	Fall
Aerial web builders	22.0	21.7	12.1	31.3	17.8	15.4
Ground web builders	35.2	58.3	37.9	41.7	62.2	69.2
Aerial hunters	25.3	11.7	28.8	16.7	11.1	10.3
Ground hunters	17.6	8.3	21.2	10.4	8.9	5.1

Table 6.—Percent complementarity of the samples collected by different methods. See text for definition of percent complementarity. Number of sample units in parentheses.

Grass bald

	Beating (24)	Sweeping (24)	Ground (24)	Litter (12)
Beating	—	70	80	87
Sweeping	—	—	80	87
Ground	—	—	—	67

Heath bald

	Beating (24)	Aerial (24)	Ground (24)	Litter (12)
Beating	—	72	78	87
Aerial	—	—	84	90
Ground	—	—	—	57

sets is directly related to the fact that the numbers of singleton and unique species failed to decline as sample size increased (Figs. 1–6). Indeed, the relatively steep ''final'' slopes of the Chao 1, Chao 2, and first- and second-order jackknife curves for the grass bald data sets (Figs. 1, 3, 4) were caused by this failure of singletons and uniques to decrease with increased collecting effort while doubletons and, to a lesser degree, duplicates decreased.

Since rare species (especially singletons and uniques) play such an important role in generating most of these estimates, it may be instructive to examine the ecological and taxonomic status of singletons in our data sets. Most of the singletons in each community (55% of bald and 63% of heath singletons) are common in other habitats in the GSMNP, and most of the rest appear to be common only in regions beyond the GSMNP boundary (Table 1). Consequently, many of these species may not be permanent (breeding year after year)

members of these bald communities. However, it is also possible that some or many of these singletons may be temporal singletons, artifacts of temporally patchy sampling; we will not know without collecting early spring, summer, and late fall samples of adults from these balds. For those families represented by five or more species in either or both bald communities, the percentage of that family's species that are singletons ranges from 22–67%: Araneidae (22%), Linyphiidae (28%), Amaurobiidae (29%), Clubionidae (40%), Salticidae (50%), Thomisidae (50%), Theridiidae (55%), Dictynidae (60%), Lycosidae (67%). Why lycosid species should more often be rarer than araneid or linyphiid species in these habitats, especially in the meadow-like grass bald, is not obvious. Sampling bias is not a likely explanation, because our ground and litter sampling methods collect large numbers of lycosid individuals and/or species in some other non-forest and forest communities in the GSMNP.

Table 7.—Comparison of total number of species and number of unique species (here defined as species collected by only one method) sampled by each method in each community. Number of samples in parentheses after each method heading. The number of unique species which are singletons is given in parentheses after the number of unique species.

Grass bald

	Beating (24)	Sweeping (24)	Ground (24)	Litter (12)
No. of species	27	44	45	32
No. of species per sample	1.1	1.8	1.9	2.7
No. of unique species	7 (4)	20 (11)	15 (9)	11 (5)

Heath bald

	Beating (24)	Aerial (24)	Ground (24)	Litter (12)
No. of species	23	14	38	27
No. of species per sample	1.0	0.6	1.6	2.3
No. of unique species	9 (4)	4 (2)	18 (6)	7 (3)

As in similar inventories of spider assemblages (Coddington et al. 1996; Dobyns 1997), it is difficult to judge from these data sets and estimates the true species richness at either study site, primarily because we identified and counted only adults and therefore do not know how many resident species populations consisted only of juveniles during the two brief sampling periods at each site. The diversity of phenologies in a typical spider community is so great (Toft 1976) that it may be difficult or impossible to estimate true richness until sampling bouts for adults are distributed more evenly throughout the annual cycle of seasons or juveniles are identified to species. This is demonstrated by the differences in species richness (observed and estimated) and species composition between spring and fall samples at each of our bald sites. Accurate estimation of true richness from snapshot sampling may only be feasible where spider faunas are extremely well known, because it will require either accurate sampling and identification of all age classes or the use of estimator formulas derived in part from extensive knowledge of the life cycle patterns of relevant spider assemblages. It is possible that late spring and early fall are the two best times to inventory spiders in temperate communities, and that two such samples will prove adequate for estimating species richness, but these possibilities need to be tested by year-round sampling.

One goal of species richness inventories should be to help predict how many samples are required for a complete (observed species accumulation curve reaches asymptote) or adequate (accurate estimate of true richness) survey. Indices like sampling intensity or inventory completeness may be useful. Our results indicate that one drawback of the sampling intensity index is that a superabundant species (like *Ceraticelus alticeps* in the grass bald) can inflate the index; even though our sampling intensity at the grass bald was 20.4, the species accumulation curve generated for that site was not as close to its asymptote as was the curve for the heath bald, which had a much lower sampling intensity (9.6). Excluding species with abundances of more than 100 or 200 would be a way to avoid such inflated sampling intensity values. As noted by Coddington et al. (1996), the rough estimate by Coddington et al. (1991) that a sampling intensity of 10 should be adequate for an accurate survey is low, at least for some spider assemblages. The inventory completeness indices for our two fall data sets (71, 67) are comparable to that for the Ellicott Rock forest fall data set (71) (Coddington et al. 1996). While the latter data set consisted of three times as many samples as either of our fall data sets, it also contained over twice as many species. The similar slopes of the observed species accumulation curves for the forest and both fall bald data sets suggest that all three inventories may have reached roughly the same degree of completeness.

It is clear that more sampling is needed at both bald sites to determine whether any of these estimators can provide meaningful estimates of the species richness of these spider assemblages. However, a few results suggest that our heath bald inventory is more nearly complete than the grass bald inventory, in spite of roughly equal sampling effort; the heath data set yields 1) observed and estimated richness curves that are more closely approaching an asymptote, 2) smaller gaps between observed and estimated richness curves, and 3) a smaller interval between the lowest and highest richness estimates. This last result is expressed by the adjusted estimate range (Table 2), which may be a useful indicator of inventory completeness. The intensity and seasonal frequency of sampling needed to generate samples of adult spiders that may yield useful estimates of species richness will only be determined by analysis of data from concerted year-round sampling effort at a particular site and will certainly differ from region to region and habitat to habitat.

Community structure.—The large differences between these two bald spider assemblages in both taxon and guild composition are not surprising considering the big differences in community physiognomy and plant species composition. The grass bald contains large patches of low grass and herb-dominated meadow habitat not found in the heath bald; the impact of this difference in the plant component of the communities on the spider component is demonstrated by the observation that 19 (26%) of the 76 grass bald spider species found elsewhere in the GSMNP are found only in non-forested meadow habitats whereas in the heath bald this is true for only one (2%) of 54 species. The fact that many of these

meadow species are salticids, lycosids, and araneids helps explain the much better representation of these three families in the grass bald. We suggest that the very low richness and abundance of adult orb weavers in the heath bald, in spite of moderate numbers of very young juveniles, may be due to a paucity of flying insects, which we noticed while sampling in the heath. Perhaps juvenile orb weavers colonize the heath from adjacent habitats but find survival difficult. The striking dominance of ground-dwelling guilds, and especially the ground web-builders, in the heath bald may be due in part to a litter and humus layer that is thick and well-shaded (and therefore probably relatively stable microclimatically) and to the low diversity and abundance of herbivorous insects supported by the relatively unpalatable ericaceous foliage. Other studies demonstrate the positive correlation between litter depth, litter microclimate stability, and ground spider species richness (Uetz 1979; Coyle 1981). Furthermore, while sampling spiders, we observed a high density of detritivore arthropods in this heath litter. Perhaps the diterpene antifeedents and insecticides that make ericaceous leaves unpalatable to many herbivores (Rosenthal & Janzen 1979; Klocke et al. 1991; Harborne 1993) are leached out of the litter or reabsorbed by the plant before leaf abscission.

For the reasons given earlier in the Results section, we feel confident that the differences between the two sample sets in observed (91 *vs.* 60) and estimated (106–160 *vs.* 68–90) species richness mean that the grass bald spider assemblage is significantly richer than that of the heath bald. The much higher plant species richness and much more varied physiognomy (patches of meadow and shrubs, and scattered trees) of the grass bald, the dominance of relatively unpalatable foliage in the heath bald, and the greater diversity and abundance of herbivorous insects in the grass bald, are likely to be important (and interrelated) causes of this marked difference in spider species richness.

The apparent temporal shift in taxonomic and guild structure from spring to fall within each of these two spider assemblages is, of course, an artifact of our ignorance of juvenile spiders. The distinct differences in the life cycles and adult phenologies within an assemblage of spider species (Toft 1976) guarantees that adult-only samples taken in one season will be different taxonomically from those taken from the same site at another season. The increase in aerial web-builders and the equally marked decrease in hunting guilds between spring and fall (adult) samples at the grass bald are consistent with the tendency of most north temperate araneids to be late summer and fall breeders and most north temperate hunting guild taxa to breed in the spring and early summer (Toft 1976; Gertsch 1979).

Collecting methods.—Longino & Colwell (1997) stressed the importance of using sampling methods that collect complementary sets of species. The large differences among our five collecting methods in the taxonomic composition of the samples these methods yielded, as well as the fact that even the least productive method (aerial hand sampling) collected four species not collected by any other method in the heath bald, justify their continued use in future sampling in these habitats. The very high productivity and distinctiveness of the sweep samples suggests that we were justified in substituting this method for aerial hand sampling in the grass bald. Such a substitution in the heath bald would not be appropriate; the physiognomy of the heath bald makes sweeping very difficult and is such that sweeping would probably sample the same taxa that beating does.

ACKNOWLEDGMENTS

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