1996. The Journal of Arachnology 24:111–128

ESTIMATING SPIDER SPECIES RICHNESS IN A SOUTHERN APPALACHIAN COVE HARDWOOD FOREST

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ABSTRACT. Variation in species richness at the landscape scale is an important consideration in conservation planning and natural resource management. To assess the ability of rapid inventory techniques to estimate local species richness, three collectors sampled the spider fauna of a "wilderness" cove forest in the southern Appalachians for 133 person-hours during September and early October 1991 using four methods: aerial hand collecting, ground hand collecting, beating, and leaf litter extraction. Eighty-nine species in 64 genera and 19 families were found. To these data we applied various statistical techniques (lognormal, Poisson lognormal, Chao 1, Chao 2, jackknife, and species accumulation curve) to estimate the number of species present as adults at this site. Estimates clustered between roughly 100–130 species with an outlier (Poisson lognormal) at 182 species. We compare these estimates to those from Bolivian tropical forest sites sampled in much the same way but less intensively. We discuss the biases and errors such estimates may entail and their utility for inventory design. We also assess the effects of method, time of day and collector on the number of adults, number of species and taxonomic composition of the samples and discuss the nature and importance of such effects. Method, collector and method-time of day interaction significantly affected the numbers of adults and species per sample; and each of the four methods collected clearly different sets of species. Finally, we present recommendations to guide future research on the estimation of spider species richness.

Measures that describe or discriminate populations or communities, such as standing crop, basal area, population abundance, or species diversity indices, are useful tools for conservation, natural resource management, environmental monitoring, and land use planning (Magurran 1988). Many of these statistics, such as Shannon's diversity index or Fisher's log series, have been thoroughly tested by theoretical studies of their statistical behavior and accuracy and by use in many practical situations. It is a curious fact that similarly proven techniques to estimate species richness of conservation units or communities are lacking, given that the number of species is surely a fundamental, important and simple community parameter (May 1975, 1988, 1992; Pielou 1975; Palmer 1990; Bunge & Fitzpatrick 1993; Colwell & Coddington 1994; Gaston 1994; Samu & Lövei 1995). Quick, inexpensive and reliable methods for estimating the species richness of taxa at particular sites (alpha diversity) could provide useful input to conservation and land management decisions (Coddington et al. 1991). Although species richness is but one component of biological diversity and only one of many criteria conservationists and planners may use when evaluating sites (compare Vane-Wright et al. 1991; Williams et al. 1991; Faith 1992; Williams & Humphries 1994), it becomes especially important as the global loss of species by extinction accelerates and the need for species preservation increases. Regional or landscape diversity depends both on alpha (local) and beta (habitat) diversity; but because the latter measure also depends on estimates of alpha diversity that are repeated across the larger spatial scale at which beta diversity operates, the ability to estimate alpha diversity accurately assumes special importance. Estimating local richness for a defined place at a defined time is fundamental to estimates of biodiversity at larger spatial and temporal scales.

Our knowledge of the structure and pattern

of biodiversity at landscape scales is especially poor for those "megadiverse" groups such as terrestrial arthropods that are responsible for the vast majority of extant species diversity (May 1988, 1992; Stork 1988); yet it is at a landscape scale that conservation often operates, and at which faunas may actually be preserved or fragmented, as the case may be (Cornell & Lawton 1992). Various attributes and research initiatives point to the potential usefulness of spiders as indicators of arthropod species diversity in terrestrial communities. Spiders are a typical "megadiverse" group of substantial ecological importance. They are 1) among the most speciose orders of animals (Coddington & Levi 1991), 2) generalist predators which have an important collective impact on invertebrate herbivore populations (Riechert 1974; Riechert & Bishop 1990), 3) ubiquitous and easy to collect, and 4) nonspecialists can be quickly trained to make remarkably accurate counts of spider morphospecies (Oliver & Beattie 1993). Coddington et al. (1991) developed and field-tested a relatively simple protocol to sample and estimate the species richness (alpha diversity) of spiders in tropical forests.

This study assesses the usefulness of this protocol in estimating species richness in a temperate forest community by 1) examining the effects of method, time of day and collector on the number of individuals, number of species and species composition of the sample, and 2) comparing the richness estimates provided by different analytical approaches. Secondarily, we are interested in comparing the species richness of a site in one of the floristically richest regions of temperate North America (Whittaker 1972) with that of the tropical Bolivian sites sampled by Coddington et al. (1991). While the collecting methods used here were chosen for their efficiency in sampling spiders, we hope the overall approach, and especially the analytical methods, can be generalized to other diverse taxa. The fundamental rule is to choose sampling methods according to the natural history of the taxon without sacrificing heuristic measures of sampling effort.

METHODS

Study site.—The study site is a southern Appalachian cove hardwood forest at 750–850 m elevation, located in the Ellicott Rock Wilderness Area in Rabun County, Georgia (34°59′N, 83°06′W). The US Forest Service classified this site as a mature white oak/northern red oak/hickory timber stand originating in about 1858. Winter aerial photos reveal that white pine trees are more common here than in most southern Appalachian hardwood coves. Schafale & Weakely (1990) classify this site as a rich cove forest with a transition into montane oak-hickory forest. The site contains one of 57 permanent vegetative diversity plots established in 1990–1991 for monitoring habitat change in the Ellicott Rock Wilderness Area (Patterson 1994).

Data collection.—Four collection methods were chosen to access the most diverse components of the spider fauna: aerial hand collection, ground hand collection, beating and Tullgren funnel litter extraction. We used time as a measure of sampling effort to make the first three methods comparable. One sample unit equalled one hour of uninterrupted time during which all putatively adult spiders were collected into 80% ethanol. A 1 h sample unit yielded a statistically tractable number of individuals per sample and allowed for a sufficient number of replicate samples to conduct statistical analyses. Day (900–1800 h) and night (2000–0300 h) samples were collected in order to access both diurnal and nocturnal species. Each collector was limited to five or fewer sample hours for each day or night collection period. Total sampling intensity was dictated by the number of adult spiders required for richness estimation. Coddington et al. (1991) guessed that roughly ten times as many specimens as species in diverse tropical communities might yield sufficiently accurate estimates of species richness. Since Coyle's (1981) study suggested that 60–120 species were accessible in a mature pine-hardwood forest within 5 km of our site, and since preliminary sampling (2 September 1991) at our site averaged 12 adult spiders per hour, we judged that 100 sampling hours would be adequate.

The three time-based collection methods involved capturing spiders by hand and with an aspirator. 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 required searching vegetation from knee height up to maximum arm's reach overhead. Ground collection required searching on

hands and knees, exploring the leaf litter, logs, rocks and plant surfaces that were below knee level. Beating entailed striking vegetation with a stick, catching the falling organisms on a 0.5 m^2 canvas sheet held horizontally below the vegetation, and aspirating and picking the spiders off the sheet. The number of such beating/collecting events averaged 22 per one hour sample. Two of the three collectors in this study were experienced collectors with moderate practice at identifying southern Appalachian spiders; the third had no prior experience collecting or identifying spiders.

Plotless areas (*ca.* 500 m^2) that allowed for adequate sampling opportunities and precluded collection interference were roughly delimited in the field. The collectors, each using a different method, operated simultaneously in each such area for one hour. Flagged boundaries prevented resampling on subsequent visits. In order to restrict collecting to a fairly homogeneous vegetative type, distinctly different habitats, such as ridge tops, steep rock outcrops, and *Rhododendron* thickets were avoided. Approximately 2.5 ha were sampled.

Leaf litter was removed by hand from a 2 m^2 area and placed in a plastic bag. In the laboratory this litter was placed in 50–60 cm diameter Tullgren funnels with 60 W light bulbs and 6–8 mm mesh screens, and spiders were extracted into alcohol until the litter was dry or nearly so. Data from the 11 litter samples were included in richness estimates but omitted from time-based comparisons.

Sampling dates and number of one hour samples (n = 122) were as follows: 2 September 1991 (n = 2); 6–9 September (n = 50); 13–15 September (n = 35); 22 September (n = 18); and 5–6 October (n = 17). The October collection was added primarily to see if species represented by penultimate instars in the September collections would mature before winter. Collectors were assigned methods so that analysis of variance cells were equably represented; no more than two replicates of any one collector/method combination occurred in any single 5 h collecting period. Each of the 11 litter samples was treated as equivalent to 1 h of collector effort for the purposes of richness estimation. Total sample number for estimation was thus 133.

This protocol differed from that used by Coddington et al. (1991) by using time as a measure for beating, adding Tullgren-funnel extraction of area-based litter samples, extending sampling to as many as 10 h (rather than only 5) in a 24 h period, avoiding resampling of areas, and in accessing a larger area (2.5 ha) rather than confining collectors to one hectare.

Only adult spiders were identified, counted and used in the analyses because identifying juveniles to species level is difficult, time consuming and fundamentally ambiguous in many cases. Voucher specimens for each species identified in this study and a portion of the duplicates have been deposited in the Smithsonian Institution (USNM).

Statistical analysis.—Richness estimates were obtained using six different approaches that differ in theoretical assumptions and the kind of data required. The classic continuous lognormal distribution (Preston 1948; Magurran 1988; Ludwig & Reynolds 1988; Colwell & Coddington 1994) is a parametric technique requiring relative abundance data. We also fitted the Poisson lognormal (Bulmer 1974) because its assumptions are better suited to discrete data than are those of the continuous lognormal. We tested the fit of both lognormal models to the data with Chi square statistics. The estimator proposed by Chao (1984), hereafter "Chao 1," is non-parametric, but also requires relative abundance data. The remaining three techniques are non-parametric but require only presence-absence data: the "Chao 2" estimator (Chao 1987), the jackknife (Heltshe & Forrester 1983), and species accumulation curves fitted to a rectangular hyperbola (the "Michaelis-Menten equation") (Lamas et al. 1991). We programmed SYSTAT (Version 5.02) routines to calculate all richness estimates except the Poisson lognormal, for which we used Ross (1987). We also used EstiMateS 3.1 (R. K. Colwell unpubl.) to investigate the behavior of estimators under randomized sample orders (see below). Where possible we provide variance estimates for the richness estimates. Point estimates of species richness are most valuable when combined with measures of variability because the reliability or precision of the estimates is conveyed as well.

We followed Magurran (1988) in fitting the lognormal model (Preston 1948) to the data. Octaves falling to the left of the zero octave represent species that could have been collected if more sampling had been done, while

octaves to the right represent actual sampling results. The null hypothesis that relative abundances are lognormally distributed is assessed by a Chi square statistic (df = number of octaves − 3). The area under the normal curve estimates the number of species in the universe being sampled. There is no analytic formula for the variance of the area under the curve (Pielou 1975), so measures of variability are not available for the lognormal estimate.

Chao (1984) proposed the following nonparametric estimator (Chao 1, Colwell & Coddington 1994) for species richness (S^*):

$$S_1^* = S_{obs} + (a^2/2b) \quad (1)$$

where S_{obs} is the number of species observed, a is the number of singletons, and b is the number of doubletons. Chao originally used a bootstrapping procedure to calculate a variance, but later work suggests the same algebraic formula for the variance of the Chao 2 estimator (see below) may serve for Chao 1 (Chao 1984, 1987, pers. comm.). Note that the Chao 1 estimator reaches its maximum of about one-half the square of the observed richness when all species save one are singletons and considers the inventory complete when all species are represented by at least two individuals.

The Chao 2 estimator (Chao 1987; Colwell & Coddington 1994) originally dealt with the estimation of population size when the capture probabilities of individuals vary. This is formally equivalent to estimating the richness of a community when the abundance of species vary, and therefore her technique may also be used to estimate species richness. Chao 2 requires replicated samples (unlike Chao 1) and takes the same algebraic form as the Chao 1 estimator, above. Thus,

$$S_2^* = S_{obs} + (L^2/2M), \quad (2)$$

where L is the number of species found in only one sample ("uniques", regardless of abundance in those samples), and M is the number of species found in just two samples ("dupes", regardless of their abundance). The variance is

$$\text{var} = M\left[\left(\frac{L/M}{4}\right)^4 + (L/M)^3 + \left(\frac{L/M}{2}\right)^2\right]. \quad (3)$$

The formula for var (S_1^*) is the same, but with a replacing L and b replacing M. Note that Chao 2 reaches its maximum of about one-half the square of the observed richness when all species save one are uniques, and, conversely, considers the inventory "complete" when all species occur in at least two samples.

The non-parametric jackknife estimator proposed by Heltshe & Forrester (1983) is

$$S_3^* = S_{obs} + L\left(\frac{n-1}{n}\right), \quad (4)$$

where n is the number of samples. The variance is

$$\text{var}(S_3^*) = \frac{n-1}{n}\left(\sum_0^{S_{obs}} j^2 f_j - \frac{L^2}{n}\right), \quad (5)$$

where f_j is the number of samples with j of the L unique species. The jackknife reaches its maximum of $\approx 2S_{obs}$ when all species are uniques and considers an inventory complete when all species are known from at least two samples.

Species accumulation curves are a classic, but informal way to assess the completeness of an inventory (Pielou 1975; Soberón & Llorente 1993). As individuals of a population are sampled, new species are encountered rapidly at first, but subsequently appear less frequently as the asymptote of species accumulation is approached (Miller & Wiegert 1989). An equation for a two parameter hyperbola, popularly known as the Michaelis-Menten equation, has been used to estimate the asymptotes of such curves, simply because it fits many data sets reasonably well (e.g., Lamas et al. 1991). It is

$$S_4^* = S_{obs}(n)\left(\frac{B+n}{n}\right), \quad (6)$$

where S_4^* is the estimate of the asymptote (the species richness) and B is a fitted constant (actually the number of samples needed to collect half the total species). As noted by Raaijmakers (1987) and Colwell & Coddington (1994), most efforts to calculate a variance for this estimator (e.g., by least squares or regression) are flawed by assuming independence among data points. However, one can at least calculate S_4^* for a large number of randomized accumulation orders and calculate the variance of this sample of estimates (Colwell & Coddington 1994). This statistic measures the variability in the data due to sample composition and richness. Richer samples added earlier

Table 1.—Summary values and richness estimates for the Ellicott Rock samples. Sampling intensity is ratio of number of adults to observed species richness. See "Methods" section for explanation of bounds on estimates.

	Sample sets			
	A (Samples collected Sept. 2–13)	B (Samples collected Sept. 14–Oct. 6)	C (All except Oct. samples)	D (All samples)
Summary values				
No. of samples	64	69	114	133
No. of adults	751	878	1452	1629
Observed richness	67	74	85	89
No. of singletons	25	24	25	26
Sampling intensity	11.2	11.9	17.1	18.3
Estimators				
Poisson lognormal	207 ± 315	157 ± 127	179 ± 156	182 ± 126
Chao2	101 ± 35	135 ± 69	131 ± 49	128 ± 40
Chao1	102 ± 37	110 ± 40	124 ± 43	123 ± 35
Jackknife	93 ± 10	101 ± 12	111 ± 11	117 ± 11
Lognormal	98	92	106	114
Michaelis-Menten	89 ± 14	87 ± 18	100 ± 12	104 ± 13

tend to cause a more pronounced shoulder and earlier asymptote. We performed 100 such randomizations and calculated informal bounds on the estimate (2 SD) of the resulting 100 asymptote values.

Finally, to gauge the adequacy of the inventory for estimating richness, we again computed 100 replicate accumulation curves by randomized sample order, and, after the addition of each sample, calculated three estimators (Chao 1, Chao 2, and jackknife), which Colwell & Coddington (1994) found to be especially effective. Means of observed species accumulation and each estimator were plotted against sample number. This analysis reveals the behavior of the richness estimators as information accumulates (the empirical species accumulation curve). A good estimator should reach a stable asymptote long before the empirical curve (i.e., given few data). If the richness estimators do reach a stable plateau, even if the observed curve is still rising by the last sample, the inventory may be adequate to estimate richness of the fauna (Colwell & Coddington 1994). Conversely, if the estimators are still climbing by the end of the inventory, richness estimates may still be subject to undersampling bias.

Effect of sampling methods on results.—Analyses of variance were used to identify significant differences ($P < 0.05$) among the treatment variables (collector, method and time of day) in both number of adults and number of species collected, and Tukey HSD tests were used in determining pairwise significant differences (at $P < 0.05$). Descriptive statistics, ANOVAs, and Tukey tests were calculated using SYSTAT. The Bray-Curtis (1957) index of similarity,

$$C = \frac{2w}{(x + y)} \tag{7}$$

where x is the total number of adults collected by one method, y is the total number of adults collected by the other method, and w is the sum of the lesser values for those species present in both samples, was used to assess the effect of collection method on the taxonomic composition of samples.

RESULTS

A total of 6666 spiders was collected in the 133 samples, including 1629 adults representing 19 families, 64 genera, and 89 species (see Appendix). We define "sample intensity" to be the ratio of individuals (adults) to species, here 18.3:1. We define "inventory completeness" to be the percentage of species represented by singletons, here 29% (Table 1). While inventory completeness rarely goes to zero, in well-sampled faunas it is likely to be low, whereas in sparse samples from rich

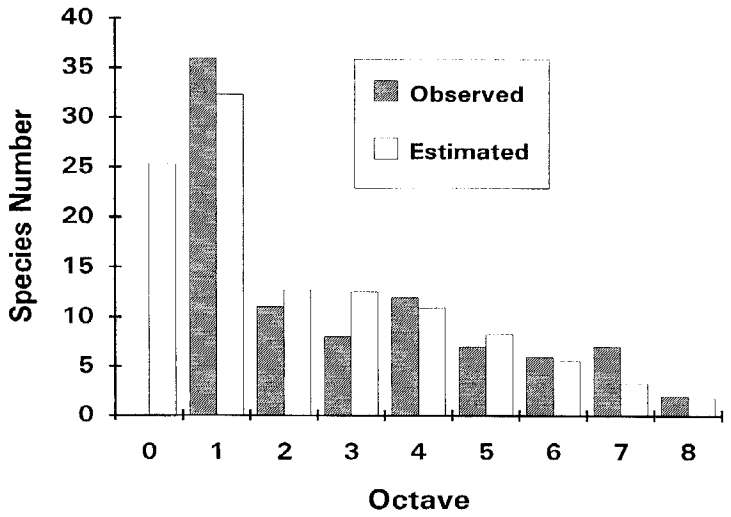

Figure 1.—Fit of the data of Appendix ("observed") to the continuous lognormal distribution (estimated). $X^2 = 6.8$; $df = 6$; $0.5 > P > 0.1$. The distribution is truncated on the left.

communities it is likely to be high. The collected data conformed to an expected skewed frequency distribution (Williams 1964), with many species represented by few individuals and few species by many individuals. Only three species had abundances greater than 100, the most abundant being 186.

Richness estimates.—For the complete data set, the richness estimates derived from all estimators except the Poisson lognormal agreed fairly closely and their confidence intervals overlapped (Table 1). In general, estimates derived from approximate halves of the data (subsets A and B) were lower than those based on nearly all (subset C) or all (set D) of the samples. For all these sample sets but set A, the rank order (from low to high) of estimators was Michaelis-Menten, lognormal, jackknife, Chao 1, Chao 2, and Poisson lognormal.

The truncated species abundance distribution for the complete data set spans eight octaves (Fig. 1). The frequency distribution was slightly bimodal, but the continuous lognormal model fit reasonably well ($0.1 < P < 0.5$). Acceptable fits were also obtained for all four partitions of the data, as judged by a Chi square goodness of fit test.

The species accumulation curve (Fig. 2) reveals that new species were still being added when sampling stopped and that the asymptote had not been reached, despite the relatively high sample intensity. Likewise, curves representing the mean values of the Chao 1, Chao 2, and jackknife estimators at each sample increment for 100 randomizations of sample sequence have not reached asymptotes (Fig. 3).

Effects of method, time of day and collector.—Table 2 summarizes the data in the Appendix on numbers of adults and species collected by method and time of day. The number of adults collected per sample was highly variable for all methods but especially so for the litter samples. Three-way ANOVA's of the 122 time-based samples (litter samples omitted) showed that method and collector, but not time of day, significantly affected both the number of adults and species per sample and that the method-time of day interaction significantly affected both the number of adults and species per sample. Tukey tests showed that aerial and ground collecting yielded significantly more adults per sample than beating, and significantly more species than litter sampling.

The Bray-Curtis similarity indices are low for all pairwise comparisons of the samples of each of the four collection methods (Table 3). Even samples collected with the most similar methods (aerial and beating; ground and litter), were quite distinct taxonomically. Of the 57 species collected by aerial and/or beating methods, 17 (30%) were unique to aerial collections and 13 (23%) were unique to beating. Of the 59 species collected by ground search-

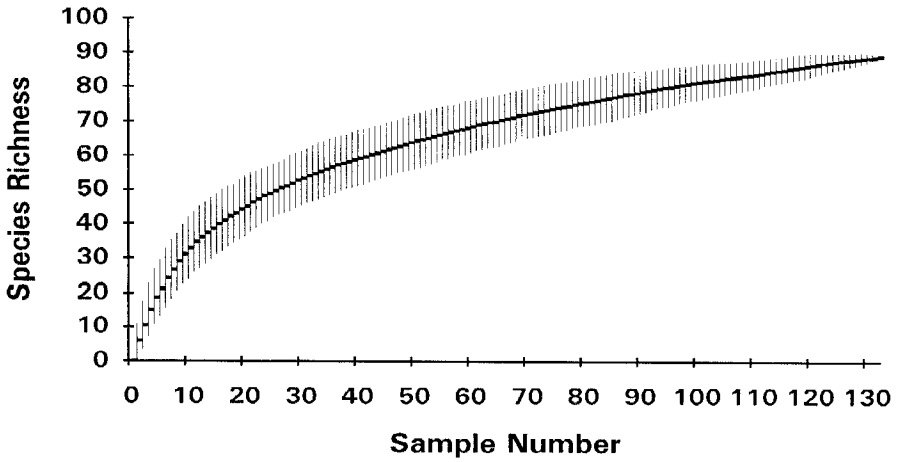

Figure 2.—The empirical species accumulation curve for the data of Appendix. Samples were accumulated randomly 100 times, and the mean ± two standard deviations plotted.

ing and/or litter extraction, 37 (63%) were unique to ground samples and 6 (10%) were unique to litter. Of the total 89 species observed, 12 species were caught only by aerial collecting, 15 only by ground collecting, 8 only by beating, and 5 only by litter extraction. Of these 40 species, 26 (65%) were singletons. Day and night samples for a given method have much higher indices of similarity than do samples collected by different methods (Table 3), indicating that contrasts between methods are much stronger than contrasts between day and night. Nevertheless, 14 species (16% of the total) were collected only at night and 18 species (20% of the total) were collected only during the day.

Tukey tests attributed the significant effect of collector on both the mean number of adults and species to the difference between collectors 1 and 2 (the most *versus* the least

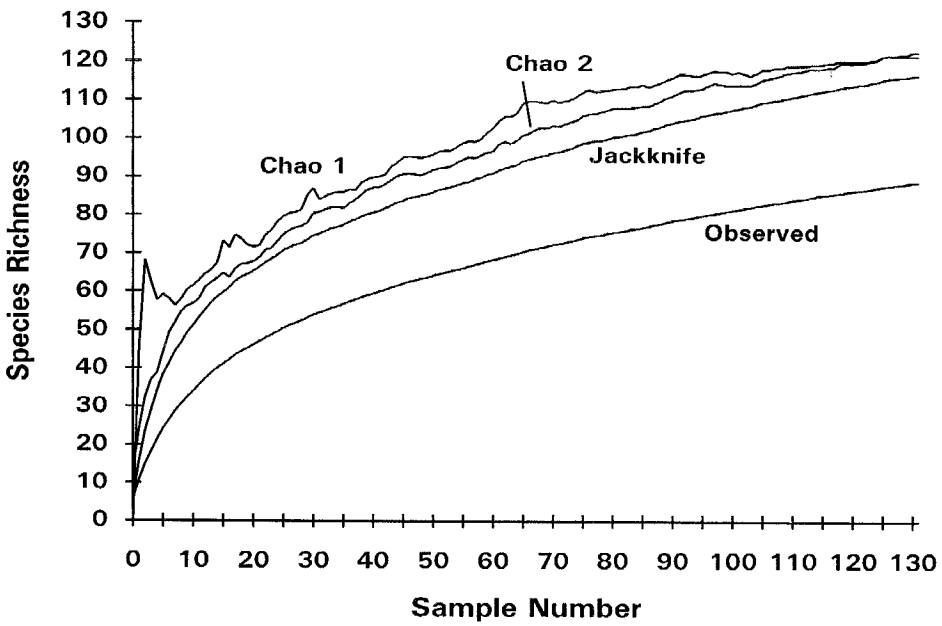

Figure 3.—Mean values of observed species richness and Chao 1, Chao 2, and jackknife estimators at each sample increment for 100 random orders of sample addition.

Table 2.—Summary of numbers of adults and species by collection method and time of day. Standard deviations of the mean number of adults and species per sample are given for method subtotals and for totals. *n* = number of samples.

	n	No. of adults	Mean no. of adults per sample	% of total adults	No. of species	Mean no. of species per sample	% of total species
Aerial							
Day	21	322	15.3	20	28	6.0	31
Night	21	315	15.0	19	33	6.5	37
Subtotal	42	637	15.2 ± 7.8	39	44	6.2 ± 2.1	49
Ground							
Day	20	222	11.0	13	41	6.1	46
Night	20	351	17.6	22	34	6.7	38
Subtotal	40	573	14.3 ± 6.7	35	53	6.4 ± 2.4	60
Beating							
Day	20	195	9.8	12	30	5.0	34
Night	20	113	5.7	7	26	3.8	29
Subtotal	40	308	7.7 ± 4.5	19	39	4.3 ± 2.0	44
Litter	11	111	10.1 ± 14.9	7	22	3.8 ± 3.4	25
Total	133	1629	12.2 ± 8.1	100	89	5.5 ± 2.5	100

experienced and productive collectors, respectively). Each collector's performance (measured by average number of adults/sample) varied considerably during the study (Table 4). A two-way ANOVA of the effects of date and collector indicated a significant effect of collector on the number of adults collected, due to the difference between collectors 1 and 2 during the first sampling period. After this first period, there were no significant productivity differences among the collectors. Although not significant, the average number of adults collected per sample did decrease slightly during the final sampling period (Table 4).

DISCUSSION

These methods estimate only the portion of the total Ellicott Rock spider fauna present as adults in the area we sampled, during the time we sampled, and accessible to the methods we used. These are, therefore, estimates of the "instantaneous" species richness of the ground and understory strata of that forest site. They certainly underestimate the true species richness, meaning all those species

Table 3.—Bray-Curtis similarity indices.

A. Collecting methods

	Ground	Beating	Litter
Aerial	0.091	0.261	0.003
Ground		0.066	0.175
Beating			0.029

B. Method and time of day combination

	Aerial night	Ground day	Ground night	Beating day	Beating night	Litter (day)
Aerial day	0.575	0.088	0.048	0.116	0.128	0.005
Aerial night		0.086	0.084	0.180	0.257	0.005
Ground day			0.496	0.077	0.167	0.144
Ground night				0.059	0.082	0.147
Beating day					0.494	0.163
Beating night						0.045

Table 4.—Mean number of adults collected per sample by collector and sampling period. Number of sample hours in parentheses.

	Sampling period			
	1 (Sept. 6–9)	2 (Sept. 13–15)	3 (Sept. 22)	4 (Oct. 5–6)
Collector				
1	14.8 (20)	15.5 (14)	21.0 (4)	10.6 (5)
2	9.0 (20)	12.5 (14)	9.0 (9)	6.0 (6)
3	13.0 (10)	11.6 (7)	16.4 (5)	12.0 (6)

that successfully bred at that site during the annual cycle in which we sampled. Even given this definition of the "local" fauna, species may go locally extinct or immigrate from one year to the next, to say nothing of showing great variation in abundance (Wolda 1978). "Local species richness" necessarily varies with the time scale on which it is defined. These estimates are snapshots—they should underestimate species richness over longer time scales. On the other hand, if a proportion of the species actually observed are "tourists" or waifs, the richness estimate will be high because such rare species increase the estimates but are not permanent members of the community being estimated. These two effects will tend to counteract each other. While field guides or checklists may provide accurate lists of species for larger areas accumulated by years of observation, it is difficult to know the "true" species richness of an area small enough to be feasibly sampled in a short time period. Since the true species richness is generally not known in such circumstances, and certainly not for Appalachian spider faunas, the accuracy of the richness estimates can only be assessed indirectly. The agreement among the estimates and the coverage of their associated confidence intervals can be assessed, the estimates can be compared against common sense guesses, checklists, and other studies, and the performance of the estimators on subsets of the data can be assessed. Among the estimators we used, only the continuous lognormal and poisson lognormal are based on models that allow explicit tests of the fit of the model to the data.

Temperate richness estimates.—Five of the six estimators used in this study suggest that the species richness of late summer adult spiders living on the ground and in the understory of this hardwood cove forest was roughly 100–130 species (Table 1). The Poisson lognormal gave consistently high estimates with almost unusably broad confidence limits. The similarity among the former estimates suggests either that they were measuring the true species richness, or that, if biased, they all were affected similarly. The somewhat lower estimates generated for the partitioned data sets of this study reveal that most estimators show substantial negative bias with small sample size (Colwell & Coddington 1994; Chao & Lee 1992), although the confidence intervals usually overlap and the effect is not consistent (Table 1). Since Chao 1, Chao 2, and the jackknife estimators are explicit functions of the number of species observed, such sensitivity is to be expected. This is not necessarily true for the continuous lognormal nor the Michaelis-Menten models, although the former is well-known to require extremely large samples (Magurran 1988). We partitioned the data by date rather than a random selection of samples, and thus our test of the effect of sample size may have confounded the influence of sample size with that of date, collector experience, or climate effects. When sample order was randomized, the same trend was observed (Fig. 3).

Fitting the continuous truncated lognormal model to these sample data was problematic, and different estimates of species richness can be obtained depending on the method used. May (1975) did not recommend fitting the lognormal to data sets containing many fewer than 100 species, and certainly the grouped and log-transformed data in Fig. 1 do not form anything approaching a smooth curve. Although the three Bolivian data sets reported by Coddington et al. (1991) were based on many fewer collecting hours and included fewer adults (Table 5), each fit a lognormal distribution. Since the sampling intensity at the Ellicott Rock site was roughly four times higher than at the Bolivian sites, the relative abundances of species at the Ellicott Rock site are better known. May (1975) pointed out that a lognormal pattern of species abundance is often observed in stable (equilibrium) communities, while disturbed communities will show increased dominance and exhibit instead a log series distribution, but this pattern is far from reliable. Most really diverse communi-

Table 5.—Summary values and richness estimates for the Ellicott Rock and Bolivian sites. Bolivian data from Coddington et al. (1991 and unpubl. data). Sampling intensity is ratio of number of adults to observed species richness. See "Methods" section for explanation of bounds on estimates.

	Ellicott Rock	El Trapiche	Rio Tigre	Cerro Uchumachi
Summary values				
No. of samples	132	51	69	37
No. of adults	1629	875	1109	654
Observed richness	89	191	329	158
No. of singletons	26	89	147	70
% singletons	29	47	45	44
Sampling intensity	18.3	4.6	3.4	4.1
Estimators				
Poisson lognormal	182 ± 126	616 ± 428	691 ± 200	375 ± 188
Chao2	128 ± 40	329 ± 77	583 ± 105	278 ± 73
Chao1	123 ± 35	319 ± 73	506 ± 77	256 ± 63
Jackknife	117 ± 11	283 ± 27	497 ± 40	235 ± 26
Lognormal	114	247	374	191
Michaelis-Menten	104 ± 13	322 ± 104	578 ± 152	277 ± 113

ties are likely to have been so sparsely sampled that either model will fit the data adequately. For example, Turnbull (1966) found a log series fit for spider species abundance data collected from May to September in a north temperate early field succession where dominance by colonizers would be predicted, but the lognormal fits his data also (our calculations).

The greater seasonality of temperate communities should foster narrower, species-specific breeding seasons and thus may cause a sample of adults collected in a short period (a few weeks or less) to mimic the dominance of a low diversity, early successional stage. Just three species (*Micrathena mitrata*, *Micrathena gracilis*, and *Wadotes hybridus*) comprised 29% of all adults in the Ellicott Rock samples. Sampling methodology may also affect the observed species abundance distribution. We may have been biased toward the collection of more apparent (less cryptic and/or more active) species (Stork 1988), especially since the plotless areas sampled in this study were not resampled as they were in the Bolivian study. On the other hand, unbiased samples are unobtainable in practical terms, and our use of experienced collectors is probably no more biased than many other collecting techniques. The ideal is to use an array of collecting techniques that complement each other, rather than trying to design one technique with minimal bias.

According to Chao (1984), her method generates lower bounds on estimates and ought to work best when "most of the information is concentrated on low order occupancy numbers," i.e., when most species in the sample are observed as singletons or doubletons. About 40% of the species were singletons or doubletons in the Ellicott Rock data *versus* an average of 62% in the Bolivian data. Since tropical samples often have a greater proportion of "rare" species than temperate samples, Chao 1 ought to yield better estimates of tropical richness than of temperate richness. However, despite great disparities in the frequency ranges of the temperate versus the tropical data, this estimator clustered about in the middle of other estimates. If poor behavior of an estimator due to violation of assumptions shows up in aberrant values, we did not observe it for Chao 1.

By generating richness estimates from quadrat sampling of a known community of forest floor herbs and shrubs, Palmer (1990, 1991) determined that Heltshe & Forrester's jackknife procedure yielded the best richness estimates out of several estimators tested (although he did not test Chao's estimators). The jackknife method is biased by dominance, but this effect can be reduced by increasing sample size (Heltshe & Forrester 1983). The heavy dominance in the Ellicott Rock samples may have been offset by a large sample size because, although lower than some of the oth-

er estimates, the jackknife estimate is not markedly deviant.

All six of these estimators rely on the proportion of "rare" species, whether the latter, somewhat intuitive, notion is defined more precisely as either uniques or singletons. Common sense suggests that if all species in the sample are known from "many" individuals after much sampling, the sample is probably exhaustive. Therefore, a better understanding of the status of singleton species may help to evaluate and refine estimator performance. (Since propinquity in time and space are highly related in this protocol, species unique to a sample is more a question of patchiness than rarity.) The 26 singleton species collected in our study are distributed rather evenly among collecting methods, families, and guilds (see Appendix). A survey of the taxonomic literature, the third author's multiyear collecting records from this region, and data from a springtime inventory at our study site (Dobyns in press) indicate that 22 of these species are spatially uncommon, i.e., more common either outside the southern Blue Ridge Province (14 species) or in other habitats (6 species) or in the forest canopy (2 species) (see Appendix). The other four singletons are temporally uncommon, i.e., they are species that are common at the site but whose breeding seasons are past.

One can view these rare species as caused by a variety of "edge" effects, of which the most important are habitat, time and method. Habitat edge effects explain the singleton status of canopy species in subcanopy samples, or of species not usually found in mature hardwood forest, but known to be more common elsewhere. Time edge effects explain the four species in fact common at the site, but that were "out of season" at the time we sampled. Finally, method edge effects may explain some of the 14 species not known to be anywhere common in the region. It is a ecological truism that all species must be common somewhere, or, alternatively, that breeding populations have a species-specific spatial structure. Although we cannot be certain, we doubt that few of these 14 species naturally occur at such low densities that nearest neighbor distances are greater than 100 meters. More likely, these "rare" species occur in the area we sampled, but have natural histories that make them difficult to collect by the methods we used. Nevertheless, although "edge" effects may explain rare species to some extent, they still are valid indicators that an inventory is incomplete.

The richness estimates derived from this study must be interpreted critically due to the spatial and temporal (seasonal) bias of the sampling methods utilized. This study estimated only that proportion of the total fauna that was 1) available to the collecting methods used and 2) adult during the course of the study. Perhaps the most significant omissions are the canopy fauna and those species present only as juveniles. Examination of about 4200 of the 5037 juveniles (76% of all specimens collected in the samples) revealed that between 25–40 species were not represented by adults in any of the samples. As noted above, richness estimates are biased upwards by inclusion of "tourist" or waif species that may be ecologically "out of place" or merely passing through the site, and they are biased downwards by low sampling effort and phenology. However, if one presumes that the total fauna available to the methods during the collecting period was observed either as adults or juveniles, then the true species richness of the site was 114–129 species. The estimates of Table 1 all agree fairly well with this common sense figure.

On the other hand, the behavior of all estimators in Fig. 3 is reason to believe that the true species richness is still underestimated. Colwell & Coddington (1994) reported one data set in which even the empirical curve reached an obvious asymptote. As expected, "good" estimators achieved this asymptote (or very close to it) much sooner than the empirical curve. The sampling intensity of that data set was over 30:1; but the Ellicott Rock inventory was 18:1, and the three Bolivian inventories were less than 4:1. If sampling intensity is a rough guide to required effort, then it appears that the 10:1 figure guessed at by Coddington et al. (1991) is seriously low.

The only previous study of spider species richness in a southern Appalachian forest is that of Coyle (1981). Using aerial hand (2.25 h), ground hand (2.25 h), Tullgren litter (ten 0.25 m^2 samples), sweep net (about 2 h), and pitfall trap (eight traps for 15 weeks) methods between June and October, he collected 217 individuals and 51 species as adults (and 9 more as juveniles) from a mature mixed pine-

hardwood site in the Ellicott Rock Wilderness Area, and about 5 km from the site we sampled. Only 29 species, or 33% of the species present in our total sample, are common to his sample and ours. Both samples are similar in the percent of sampled species of adults in three (ground web-builders, aerial web-builders, and aerial hunters) of the four guilds, but the Coyle sample had 18% ground hunters *versus* 9% in ours (9 of 51 *versus* 8 of 89 species, respectively). The greater duration of the Coyle study and his low ratio of hand collecting effort to pitfall trap effort (which biased his study in favor of ground hunters) help account for these differences.

Comparison of temperate and tropical richness estimates.—It is no surprise that the species richness estimates for tropical sites (Coddington et al. 1991; Silva & Coddington in press) are much greater than for the temperate (Ellicott Rock) site (Table 5). Of the tropical sites, Rio Tigre was most nearly comparable in elevation to the Ellicott Rock site (500 m *versus* 800 m). Comparison of observed species richness indicates that Rio Tigre had 3.7 times more species than Ellicott Rock, but comparison of the six estimated species richness values indicates ratios from 3.8–5.6. Comparing Georgia to Bolivia is not the point, but rather that comparisons of raw sample data can mislead. In this case, the lower intensity tropical sample apparently accessed a much smaller proportion of the total fauna present. Use of statistical procedures may emend such biased comparisons and enable better comparison of the results of inventories that differ in method, circumstances and completeness. This higher tropical species richness resembles the north temperate to tropical latitudinal gradient observed for many other taxa (Fischer 1960; Ehrlich & Wilson 1991; Platnick 1991). Interestingly, all the estimators for the tropical data sets show the same rank order. With the exception of the species accumulation curve, the same ranking is repeated in the temperate data set. This rather startling consistency in rank order among estimators suggests a systematic bias with respect to each other (and therefore with respect to the true richness), at least for the data sets tested thus far. It therefore remains to be demonstrated, perhaps through simulation studies, which estimator most accurately tracks the true richness.

Effects of method, time of day and collector on results.—Although some methods (aerial and ground) were more productive than others (beating and litter), the Bray-Curtis indices and the numbers of collected species unique to each method suggest that each method is sampling a distinctly different array of species. Of course, species that are singletons cannot appear in more than one sample, and these may artificially inflate the distinctiveness suggested by such comparisons. Although aerial collecting and beating both accessed similar vegetative habitats, aerial sampling accessed larger spiders (araneids) while beating accessed a higher proportion of smaller cryptic species (especially linyphiids; see Appendix) which are likely to be overlooked during aerial hand collection. Ground hand collection accesses far more microhabitats than does litter collection, but is less likely to sample the smallest-bodied litter-dwelling species. The extensive use of aspirators in ground hand collection probably reduces this difference between the two methods in the size of the spiders collected. It is logical to expect that methods which depend heavily on visual searching (aerial and ground) are biased against small-bodied species. The higher ratios of large to small spiders in the aerial and ground samples compared to beating and litter samples, respectively, conform to that prediction. Additional evidence of this bias is the high female to male ratio (13.5:1) for aerial collections of three common species with much larger females than males (*Micrathena gracilis*, *Micrathena mitrata*, and *Spintharus flavidus*) and the much more normal ratio (1.5:1) for ground collections of large-bodied species with little sexual size dimorphism (*Wadotes hybridus*, *Wadotes bimucronatus*, and *Gladicosa gulosa*). As Poole (1974) has noted, the whole question of "true" relative abundance of species in nature as compared to relative abundance in samples is nearly insoluble, however fundamental it may be to assessing bias.

The especially high variability of the litter sample data may be the result of heterogeneity in spider distribution, variation in litter depth (Uetz 1975), or variation in Tullgren funnel technique (funnels were sometimes overloaded and the litter not allowed to dry completely). Sampling equal volumes (rather than areas) of litter, placing a constant and moderate

volume in each funnel and continuing the extraction process until the litter is completely dry should reduce this variability and make comparisons between sites more meaningful. Sorting spiders from litter by hand in the field on a white tray for one hour might allow litter to be analyzed as a time-based method, but this probably would not be as efficient as Tullgren funnel extraction and would be less likely to capture very small spiders.

Although time of day had no significant effect on the number of adults and number of species collected, and Bray-Curtis indices indicated that time of day affected the taxonomic composition of samples less than method did, the relatively large number of species unique to either day or night samples indicates that both night and day collecting may be desirable if the sampling is to approach closely the real species richness of the site. These data (see Appendix) support the generalization that many spider species are either predominantly night or day active. *Wadotes hybridus*, *Gladicosa gulosa*, *Mimetus interfector*, *Thiodina sylvana*, *Spintharus flavidus*, and *Hyptiotes cavatus* were species whose collection was strongly skewed toward the night (nocturnally active species), while *Micrathena gracilis*, *Ceraticelus fissiceps*, *Ceratinopsidis formosa*, and *Gonatium crassipalpum* were far more abundant in day collections (diurnally active species). *Micrathena mitrata* was the only commonly sampled species that appeared to be equally active both night and day. Unlike these results, night sampling in the Bolivian forests was significantly more productive (numbers of adults and species per sample) than day sampling (Coddington et al. 1991), supporting the oft quoted generalization that most kinds of spiders are most active at night, and perhaps that diurnal predation pressure may be more intense in tropical than in temperate forests.

We should note, however, that collector fatigue may have markedly reduced the productivity of night collecting in our study. While the collectors in the Bolivian study in general collected only 5 one-hour samples in any 24 h period, the temperate sampling was done primarily on weekends with as many as 10 h of sampling per collector in a 24 h period. For example, the total numbers of adults collected by the three collectors on the night of 14 September were 48 for hour 1, 51 for hour 2, 36 for hour 3, and 22 for hour 4; and the plan to collect for another hour was aborted due to fatigue.

The data analysis suggests that naive and experienced collectors do differ in their abilities and that the sampling time required for a richness survey can be reduced by selecting particularly able collectors. We suspect that the collectors in the Bolivian study, who averaged 16.4 adults per sample (Coddington et al. 1991), would have averaged significantly more than the 12.2 adults per sample average productivity of the Ellicott Rock team because the most experienced Ellicott Rock collector almost equalled the Bolivian average but had far less spider-collecting experience than four of the five collectors in Bolivia. However, this study and the Bolivian study both showed that the sampling productivity of inexperienced collectors can improve so that they soon became statistically indistinguishable from the more experienced collectors. This improvement in collector performance is encouraging since it suggests that it is possible to train naive collectors rather quickly and thus to implement efficient, long-term, continuous monitoring in the tropics.

Collector (and method) productivity may have been affected by climate-induced changes in adult spider activity and/or abundance. The reduced average sample size during period 4 (Table 4) was probably a result of a diminished number of active spiders due to markedly colder and windier weather and not a reduction in collector performance.

Recommendations for future research.—Since sampling protocols should access all components of a fauna without bias, and since the protocol used by Coddington et al. (1991) under-samples the litter fauna, methods that access this fauna (litter extraction, pitfall traps) should be added wherever feasible. Hand sorting of litter for one hour on a tray would be logistically easier in remote areas due to the scarcity of electricity, but Tullgren funnel extraction may be more productive and a study is needed to test that hypothesis; either way it would be more informative to also record the volume of litter processed. We have shown that beating can be performed as a time-based sampling method to make data analysis more straightforward. This study provides some, albeit weak, evidence for the importance of night sampling; and it suggests that sampling should be limited to 5–6

sample hours per 24 hour period to minimize the effects of collector fatigue. Additional sampling of this and other hardwood coves in the southern Appalachians should be undertaken in September, in May, and in July: 1) to see if the species richness estimates of 104–128 are repeatable, 2) to explore the effect of season on richness estimates (see Dobyns in press), 3) to compile a more accurate species list to which the performance of richness estimators can be compared, and 4) to facilitate the identification of juveniles so that the effect of their inclusion on species abundance distributions and richness estimates can be studied. Simultaneous plotless and quadrat sampling studies should be performed to compare plotless richness estimates with those based on 1) pooled quadrats (Pielou 1975) and 2) species-area relationships (Palmer 1990, 1991). The hypothesis that repeated (intensive) sampling in a plot will collect more covert species than does non-repetitive collecting requires testing (see Dobyns in press). Statistical research to develop confidence intervals for species accumulation curves and lognormal estimates is required, as is further study of the dependence of estimates on sample size and their performance on data sets that display different degrees of ecological dominance (i.e., range of frequencies). Spider richness studies should be located at sites where other animal or plant diversity plots already exist so that the correlation between spider richness and the richness of other taxa can be explored.

ACKNOWLEDGMENTS

We thank Bob Dellinger and Trey McGarity for helping to collect the spider samples, Dick Bruce, Allen Moore and Jackie Palmer for their advice, encouragement and comments on early drafts of this paper and Joe Beatty for identifying *Graphomoa theridioides*. Bob Robbins offered helpful advice throughout on statistical issues, Rob Colwell made helpful comments on the penultimate draft, and C. J. Humphries and M. W. Palmer provided helpful reviews of the manuscript. We particularly thank Rob for making EstiMateS 3.1 available. The Highlands Biological Station, the Western Carolina University Department of Biology, and the Smithsonian Institution (through its Scholarly Studies, Neotropical Lowlands, and Biological Diversity of Latin America Programs) provided logistic support and funds. This paper is based on a Master's Thesis presented by the second author (LY) to the Department of Biology, Western Carolina University. This is contribution no. 83 from the Smithsonian Biological Diversity Program.

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Manuscript received 8 September 1995, revised 14 March 1996.

Appendix.—Species and number of adult spiders collected in Ellicott Rock species richness study. Collection method and time of day indicated (D = day, N = night). Guild designation: A = aerial, G = ground, W = web building, H = hunting. Status of singleton species: R = rare in southern Blue Ridge Province; U = uncommon to moderately common in southern Blue Ridge Province; J = juveniles common in samples (adults common at another time of year); P = at periphery of its geographic range; H = common locally in other, usually more open, habitats; C = probably common in forest canopy (Coddington 1987).

Taxon	Guild	Collection method							Singleton status
		Aerial		Ground		Beating			
		D	N	D	N	D	N	Litter	
Agelenidae									
Agelenopsis pennyslvanica	AGW	10	2	4	3	1	1		
Calymmaria cavicola	GW			22	40				
Cicurina arcuata	GW			3	7			12	
Cicurina breviaria	GW			6	3			2	
Cicurina sp. A	GW			2					
Cicurina sp. B	GW			1					R
Coras aerialis	AW		1						U
Coras taugynus	GW			2	9				
Cybaeus silicis	GW		2	6	4				
Wadotes bimucronatus	GW			28	41			5	
Wadotes hybridus	GW			18	101			3	
Amaruobiidae									
Callioplus armipotens	GW			1	2			4	
Anyphaenidae									
Anyphaena pectorosa	AH						1		U
Wulfila alba	AH						1		U
Araneidae									
Araneus cingulatus	AW		1						C
Araneus marmoreus	AW	25	10				1		
Araneus niveus	AW		1						C
Araneus nordmanni	AW	17	6	1		3	1		
Araneus pegnia	AW		1						H
Araneus saevus	AW		1						P
Araneus thaddeus	AW	1	5			2			
Mangora maculata	AW	1				1			
Metepeira labyrinthea	AW	7	1				1		
Micrathena gracilis	AW	111	39	1	1	4	1		
Micrathena mitrata	AW	77	99	1	2	1	6		
Micrathena sagittata	AW	1							U
Neoscona arabesca	AW	1							H
Neoscona domiciliorum	AW	18	17	1	1	2	1		
Neoscona hentzi	AW	1							U
Wixia ectypa	AW		3			2	2		
Clubionidae									
Clubiona spiralis	AH		1						P
Clubionoides excepta	AH	1	1		1	5	3		
Phrurotimpus alarius	GH			1				1	
Scotinella redempta	GH			4				2	
Trachelas similis	AH		2			3	4		
Trachelas sp. A	AH		1						R
Ctenidae									
Anahita punctulata	GH				1				J
Hahniidae									
Neoantistea agilis	GW			1	3				

Appendix.—Continued.

Taxon	Guild	Collection method							Singleton status
		Aerial		Ground		Beating			
		D	N	D	N	D	N	Litter	
Hypochilidae									
Hypochilus pococki	GW	2		11	3				
Leptonetidae									
Leptoneta gertschi	GW			13	7			19	
Linyphiidae									
Bathyphantes albiventris	GW			1	1				
Centromerus denticulatus	GW							2	
Ceraticelus carinatus	GW			1			1	36	
Ceraticelus fissiceps	AGW			3		51	18	2	
Ceraticelus minutus	GW							3	
Ceratinopsidis formosa	AW	3	1	1		53	13	1	
Drapetisca alteranda	AW	11	8			2			
Erigone autumnalis	GW					1			J
Frontinella pyramitela	AW	6	4	1					
Gonatium crassipalpum	AW					15	2	1	
Graphomoa theridioides	GW	1		50	32		1		
Lepthyphantes sabulosa	GW			4	6			6	
Lepthyphantes sp. A	GW			1	2				
Lepthyphantes turbatrix	AGW		1		2				
Meioneta micaria	GW			1					H
Meioneta sp. A	AW		1						R
Neriene radiata	AW	2							
Neriene variabilis	GW			2	1				
Pelecopsidis frontalis	GW			1					R
Scylaceus pallidus	GW							1	P
Walckenaeria brevicornis	GW							2	
Lycosidae									
Gladicosa gulosa	GH		7	3	61		3		
Pirata montanus	GH			6	1			1	
Mimetidae									
Mimetus interfector	AH	1	5		1		1		
Mysmenidae									
Mysmena guttata	GW							1	J
Salticidae									
Eris marginata	AH	1		1		8	6		
Habrocestum parvulum	GH			4				3	
Habrocestum pulex	GH	1		2					
Maevia intermedia	AH	1	1		1	8	2		
Metaphidippus protervus	AH					3			
Thiodina sylvana	AH					1	8		
Tetragnathidae									
Glenognatha foxi	AW					1			H
Leucauge venusta	AW	9	5	2		1			
Meta menardi	AGW			1	1				
Tetragnatha elongata	AW			1					H
Theridiidae									
Argyrodes trigonum	AW	2	1		1	1			
Euryopis funebris	AW		1			1			
Paratheridula perniciosa	AW					1			P
Pholcomma hirsuta	GW			1				3	

Appendix.—Continued.

Taxon	Guild	Collection method							Singleton status
		Aerial		Ground		Beating			
		D	N	D	N	D	N	Litter	
Spintharus flavidus	AW	1	44		4	11	18		
Theridion albidum	AW	2			1				
Theridion flavonotatum	AW	1				1			
Theridion lyricum	AW		7		4	5	5		
Theridula opulenta	AW						3		
Theridiosomatidae									
Theridiosoma gemmosum	AGW				1				J
Thomisidae									
Misumena vatia	AH					1			H
Xysticus fraternus	GH				1	1		1	
Uloboridae									
Hyptiotes cavatus	AW	7	35	8		5	9		
Uloborus glomosus	AW				1				U
Totals		322	315	222	351	195	113	111	