RESEARCH NOTE

A USEFUL PROCEDURE FOR ESTIMATING THE SPECIES RICHNESS OF SPIDERS

Many authors have noted that the abiotic structure of the environment is particularly important to spiders (Luczak 1963; Lowrie 1973; Stratton et al. 1978; Uetz 1979; Hatley & McMahon 1980; Bultman & Uetz 1983; Gunnarson 1983, 1992; Greenstone 1984; Rushton 1991; Sundberg & Gunnarson 1994; Moring & Stewart 1995). By and large, spiders are without the biochemical mandates characteristic of many organisms; for example, they are not bound to particular plant species as are many insects. Spiders are often exceptionally vagile and in addition may occupy different aspects of their environment as they mature. It is suggested here that given the dominant role of the structure of the habitat, a simple saturation model might best be used to estimate the species richness of a habitat. Some of the assumptions relevant to the development of the model include: 1) Rarely collected spiders are largely a consequence of the vagility of spiders and reflect to some degree the size of the regional pool, the propinquity of other habitats, and the status of the populations of particular species at the time observations are made. For these reasons, species assemblages will tend to differ somewhat from year to year in any particular habitat (Rypstra & Carter 1995). 2) Spiders have fairly discreet requirements based on the spatial structure of the habitat and to a lesser degree on other factors such as humidity, temperature, light intensity, etc. (Rushton 1991; Morley & Stewart 1995). 3) Some species of spiders have different spatial requirements as they mature. 4) Within the regional pool there is a species assemblage that is adapted to a considerable degree to the niche-spatial options at any particular time offered by a habitat (more exactly, perhaps, the contained set of "microhabitats"). Spiders that are not suited to a particular habitat and wander in may soon leave or become prey for other organisms, including other spiders that are well

adapted to the habitat. 5) Combining samples taken in different years may lead to an overestimate of the number of species characteristic of any particular habitat as a result of the accumulation of records of species that result simply from the vagaries of vagility (Edwards 1997). As the model developed, it soon became apparent that it was analogous to the equation for adsorption isotherms created by Langmuir (1918).

It is postulated that within any habitat there is a set of n species or species-specific niches representing the maximum potential number of species in the habitat. At any time, n_q of these niches are occupied. When the habitat is saturated, $n_q = n$. The number of n potential and n_q occupied niches may vary with season, with the availability of other suitable habitats, and with changes in the regional pool (immigrants, introduced species, population changes both within and without the spider community that modify interactions, etc.).

Let n = total number of species-specific niches,

The rate of entry into the habitat:

$$dn_d/dt = k_a(n - n_q)q$$

where ka = rate constant of arrival in the habitat and q = number of samples (quadrats). The rate of species entrance is proportional to the number of unoccupied niches, and to the sampling intensity.

The rate of species disappearance is:

$$-dn_d/dt = k_d n_q$$

where k_d = the rate constant of species disappearance. Rate of species disappearance is proportional to space already occupied. Departure may be voluntary, but includes other factors such as predation and disease.

Equating entry and departure (equilibrium):

$$k_a(n - n_q)q = k_d n_q \qquad (1)$$

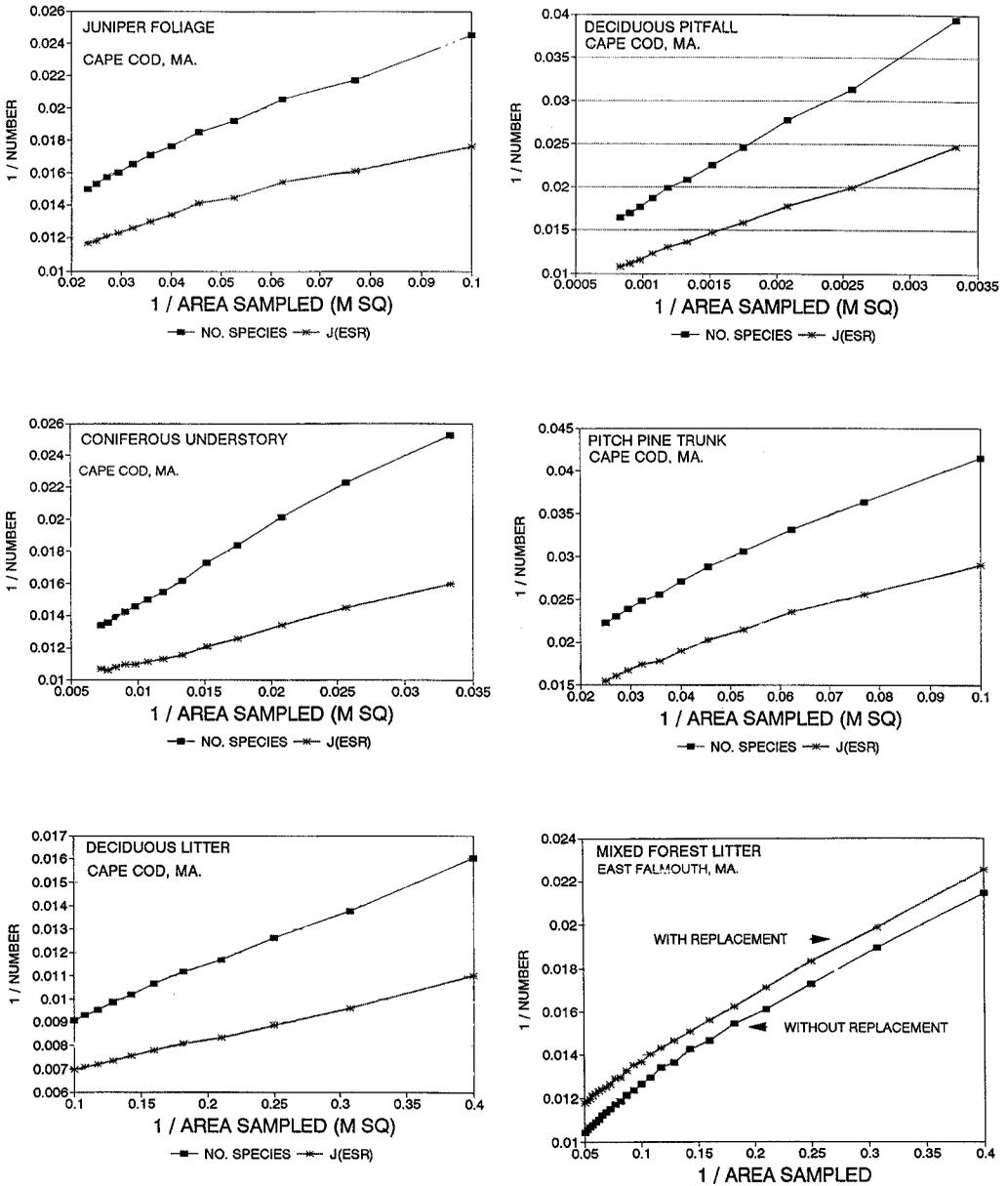Taking reciprocals after setting equation equal to q:

Figure 1.—Six examples of Cape Cod habitat data, with the reciprocals of the number of quadrats plotted against the reciprocals of the number of species collected and the reciprocals of the number of species calculated using the jackknife estimator. Each of these was sampled over a 3½ month period, 15 June–September 1989 and 1990.

$$1/q = k_a(n-n_q)/k_d n_q$$

Rearrangement gives:

$$1/n_q = [(k_d/k_a n)(1/q)] + 1/n \qquad (2)$$

Note that a plot of $1/n$q against $1/q$ is a straight line, with the slope $= k_d/k_a n$ and the intercept $= 1/n$. The reciprocal of the intercept provides the estimated number of species, $n(esr)$, at saturation, and $n = n_q$.

In Figs. 1 and 2 both the number of species at saturation, $n(esr)$ and the calculated number of species using the jackknife estimator, $j(esr)$, developed by Heltsche & Forrester (1983) are shown. The data were resampled randomly
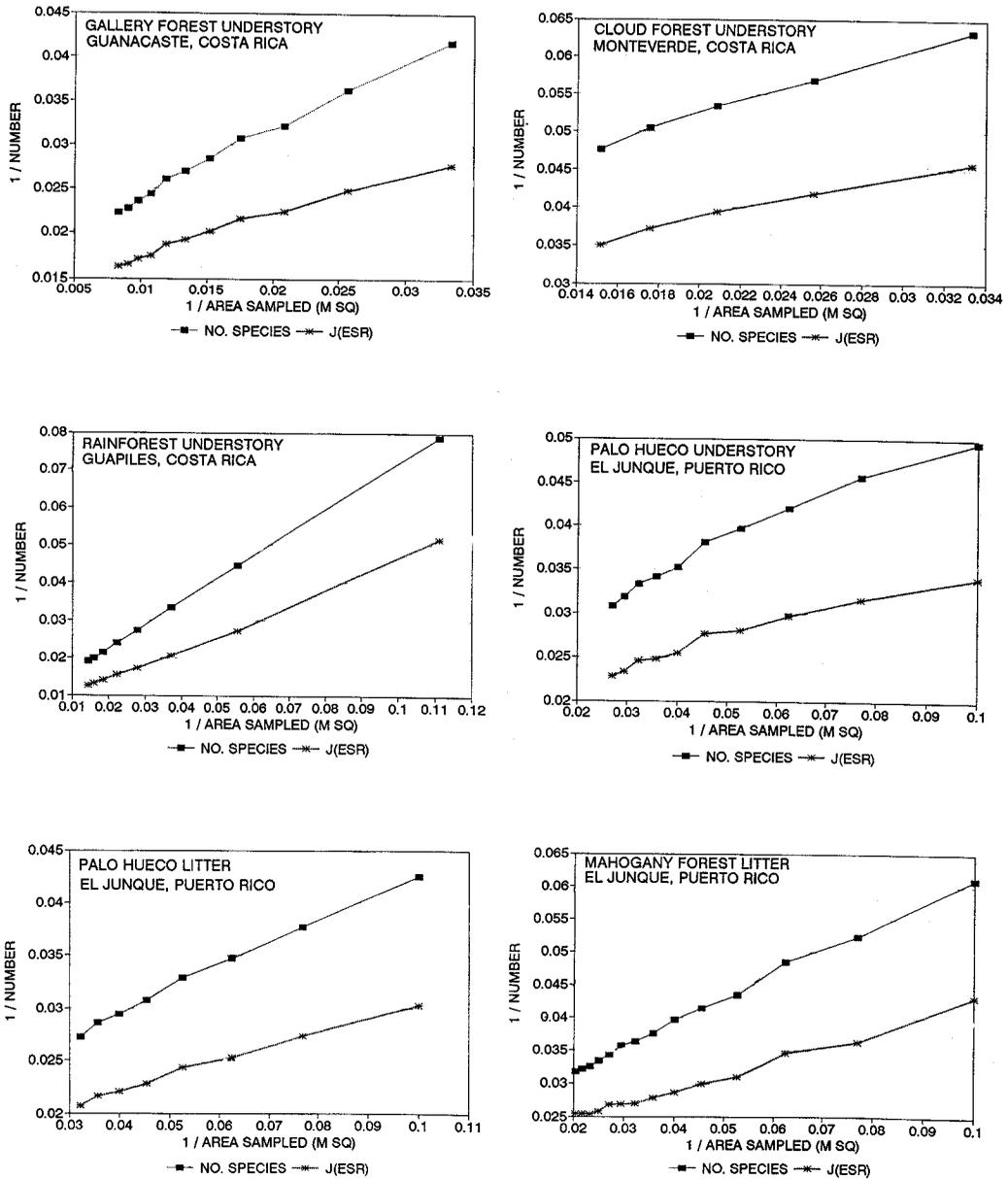
Figure 2.—Plots of the reciprocals of the number of quadrats against the reciprocals of the number of species and number of species calculated using the jackknife estimator for two examples from Costa Rica and four from El Junque, Puerto Rico. The Costa Rican samples were each collected in one day, while those from Puerto Rico were collected at intervals during 1994 and 1995.

without replacement, at three quadrat intervals beginning at 10 quadrats, with 100 iterations for each level of quadrat aggregation. The graphs are double reciprocal plots, with the number of quadrats shown on the abscissa and the number of species on the ordinate.

In Fig. 1, plots of the results of analysis for six habitats from the Cape Cod region are presented. These are some of the habitats and collections reported on earlier (Edwards 1993). These habitats were sampled from the middle of June to the end of September, 1989–1990. In Fig. 2 data for various habitats in Puerto Rico and Costa Rica are plotted. The Costa

Table 1.—Statistical data for habitats using linear regression $1/n_q = (x)(1/q) + c$ (Equation 5). q = number of quadrats, c = constant, SE = standard error, x = slope, $n(esr)$ = estimated total number of species (reciprocal of c), $r_n = r^2$ for calculations based on species, q_{50} = number of quadrats required to collect 50% of $n(esr)$, $j(esr)$ and $r^2_j = r^2$ for calculations based on number of species derived from jackknife estimator. Data in descending order of estimated total number of species $n(esr)$. For habitat codes see Table 2.

Code	q	c	SE c	x	SE x	$n(esr)$	q_{50}	r^2_n	$j(esr)$	r^2_j
CL	50	0.0062	0.0001	0.0899	0.0011	162.09	16.2	0.998	197.23	0.999
DL	41	0.0069	0.0001	0.0911	0.0013	144.91	14.1	0.998	177.38	0.998
CP	123	0.0077	0.0004	0.2122	0.0040	129.73	27.5	0.994	179.92	0.992
DP	41	0.0088	0.0003	0.3011	0.0039	113.25	34.1	0.999	160.23	0.999
XL	80	0.0093	0.0003	0.1277	0.0027	108.07	13.7	0.990	131.35	0.993
GP	52	0.0097	0.0005	0.2724	0.0055	103.07	29.0	0.995	140.31	0.992
DU	45	0.0098	0.0002	0.1037	0.0020	101.62	10.4	0.996	125.33	0.990
FP	43	0.0100	0.0002	0.2204	0.0022	100.16	21.9	0.999	123.82	0.996
CU	47	0.0100	0.0002	0.1560	0.0024	99.65	15.6	0.998	111.75	0.995
RU	23	0.0101	0.0002	0.2063	0.0007	99.31	20.5	1.000	158.73	0.997
FS	53	0.0112	0.0004	0.1198	0.0041	89.63	10.7	0.985	117.47	0.960
GS	45	0.0113	0.0006	0.1899	0.0075	88.18	17.0	0.985	130.04	0.984
PF	40	0.0115	0.0002	0.1422	0.0032	86.98	12.4	0.995	111.35	0.996
JF	44	0.0125	0.0003	0.1229	0.0035	79.76	9.8	0.992	99.59	0.979
DT	41	0.0149	0.0006	0.2856	0.0085	67.10	19.0	0.992	101.05	0.990
GU	40	0.0163	0.0005	0.2582	0.0069	61.37	15.9	0.994	78.65	0.988
CT	40	0.0165	0.0005	0.2575	0.0069	60.68	15.6	0.994	87.21	0.990
SF	25	0.0200	0.0002	0.1985	0.0031	50.08	10.4	0.998	61.82	0.996
HL	32	0.0206	0.0004	0.2224	0.0058	48.54	10.8	0.996	60.36	0.994
MU	71	0.0231	0.0010	0.2793	0.0100	43.35	12.1	0.976	56.38	0.967
ML	46	0.0244	0.0005	0.3688	0.0054	40.93	15.1	0.998	49.34	0.989
HU	39	0.0250	0.0010	0.2595	0.0143	39.97	10.4	0.976	51.38	0.967
BL	30	0.0256	0.0007	0.3337	0.0120	39.09	13.1	0.994	53.71	0.991
TL	61	0.0266	0.0005	0.3953	0.0048	37.53	14.8	0.998	41.99	0.967
BU	32	0.0271	0.0006	0.3408	0.0096	36.96	16.3	0.995	51.26	0.989
FU	14	0.0338	0.0019	0.1451	0.0090	29.63	4.3	0.992	45.52	0.996
VU	22	0.0355	0.0005	0.2790	0.0115	28.16	7.9	0.995	37.11	0.987
Means							15.5	0.993		0.988

Rican habitats were each sampled in one day. The Puerto Rican habitats show data collected at periodic intervals during 1994 and 1995.

The mean r^2 values (Table 1) for the estimated number of species, $n(esr)$, against number of quadrats was $r^2 = 0.9933$ (0.9761–0.9999), while the mean value of r^2 for calculations based on the jackknife estimator, $j(esr)$, was $r^2 = 0.9884$ (0.9597–0.9985). The slightly increased variability of the jackknife data is apparent to the eye in the figures. Estimates of $j(esr)$ averaged about 31% more than $n(esr)$.

In some habitats there is an increase in the slope of the fitted line toward the origin, as may be seen in Fig. 1 for the red cedar foliage (JF) and in East Falmouth mixed forest leaf litter (XL). In Fig. 3, the skew (g_1) and kurtosis (g_2) of the frequency distribution of the numbers of species/quadrat in each habitat for the Cape Cod area is portrayed. The species assemblages of spiders are typically positively skewed and leptokurtic. The downward bend exhibited in some plots is evidence of the existence of a platykurtic and/or a multimodal distribution.

The sampling period for the Cape Cod habitats included at least part of the early fall onset of a different assemblage of species. The frequency distribution of the number of species for red cedar foliage (JF) is platykurtic and distinctly bimodal (Fig. 4a). Separating the data for the months of June-July from that for August-September resulted in the fitted lines shown in Fig. 4b. The second mode is interpreted as representing the incoming as-
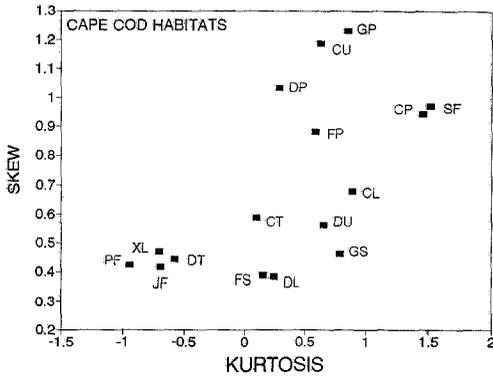
Figure 3.—The central moments, skew ($g1$) and kurtosis ($g2$) for the frequency distribution of the number of species/quadrat in Cape Cod habitats. Habitat codes are given in Table 2. A platykurtic distribution often indicates temporal change and/or environmental disturbance during the period of sampling. This is indicated by the increasing slopes in the red cedar foliage and mixed forest leaf litter data shown in Fig. 1.

semblage, with the vanishing summer assemblage contributing largely to the first mode. The $n(esr)$ for this entire data set was 79.8 species ($r^2 = 0.992$). The $n(esr)$ for June and July was 62.3 ($r^2 = 0.9999$) and for August and September was 74.7 ($r^2 = 0.9971$). Similarly the pine foliage (PF) and deciduous trunk (DT) samples also suggested that seasonal change was involved. The East Falmouth mixed forest leaf litter (XL) data was more difficult to interpret. This habitat was sampled from January–March in 1993 (see Fig. 4c). By and large, the collection contained species to be expected in litter during the colder months. Also present was a fairly large number of arboreal species that could be considered the constituents of a second different assemblage, some or all individuals of which had taken refuge in the litter during the winter months.

Temporal change in the species assemblages during the period of sampling is a possibility that must be recognized. It should not, however, mitigate against comparable sampling from one year to the next providing relevant factors are kept constant.

Two examples of habitats sampled in Costa Rica are shown in Fig. 2. These habitats were each sampled in one day. The Puerto Rico samples were taken in the rainforest on El Junque during periodic visits from May 1994–
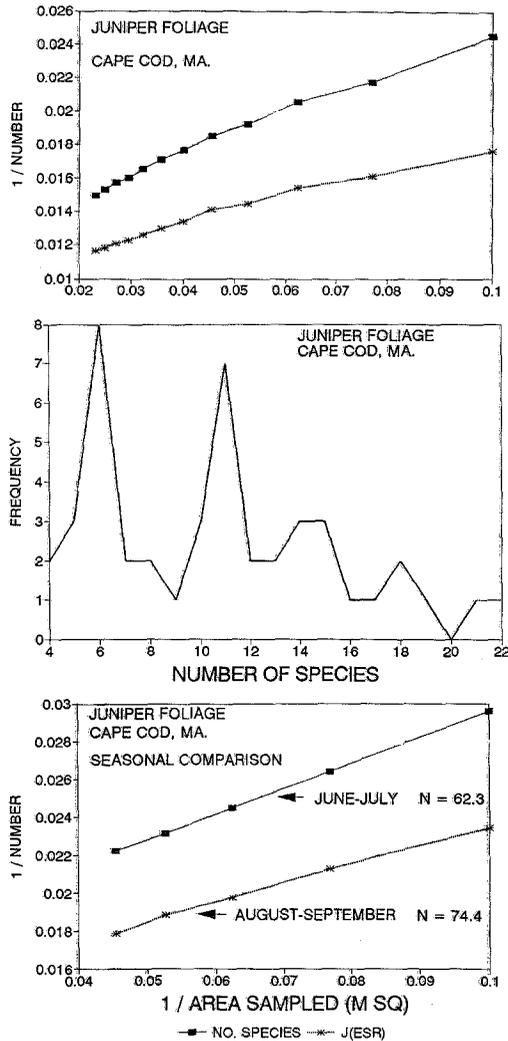

Figure 4.—4a, Frequency distribution of the number of species taken in red cedar (juniper) foliage (RF); 4b, Plot of the number of species for the period June-July, and the period August-September; 4c, The frequency distribution of species in the East Falmouth mixed forest leaf litter habitat (XL), collected January–March 1993.

March 1995 in the understory of a mahogany plantation (ML, MU) and September 1994–March 1995 in the leaf litter at Palo Hueco, a young mixed second forest area (HL, HU). During this period the area suffered a severe drought. This event may have contributed to some of the irregularity shown in the understory samples, although not in the leaf litter collections. An examination of the mahogany

Table 2.—List of codes used in Table 1, locality sampled, habitat, and estimated quadrat area and sampling method. CC = Cape Cod, CR = Costa Rica, PR = Puerto Rico (El Junque). For further details on sampling methods, see Edwards (1993).

Code	Locality	Estimated quadrat area
CL	Coniferous leaf litter, CC.	0.25 m^2—sample
DL	Deciduous leaf litter, CC.	0.25 m^2—sample
CP	Coniferous forest pitfall, CC.	±3.0 m^2—sample
DP	Deciduous forest pitfall, CC.	±3.0 m^2—sample
XL	Mixed forest leaf litter, CC.	0.25 m^2—sample
GP	Grass field pitfall, CC.	±3.0 m^2—sample
DU	Deciduous forest understory, CC.	2.4 m^2—sweeping
FP	Old field pitfall, CC.	±3.0 m^2—sample
CU	Coniferous understory, CC.	3.0 m^2—beating
RU	Guapiles rainforest understory, CR.	3.0 m^2—sweeping
FS	Old field foliage, CC.	10.0 m^2—sweeping
GS	Grass field foliage, CC.	10.0 m^2—sweeping
PF	Pine foliage, CC.	1.0 m^2—beating
JF	Red Cedar foliage, CC.	1.0 m^2—beating
DT	Oak trunk, CC.	1.0 m^2—brushing
GU	Taboga Gallery Forest understory, CR.	10.0 m^2—sweeping
CT	Pitch pine trunk, CC.	1.0 m^2—bark removal
SF	Spruce foliage, CC.	1.0 m^2—beating
HL	Palo Hueco mixed forest litter, PR.	0.25 m^2—sample
MU	Mahogany forest understory, PR.	3.0 m^2—sweeping
ML	Mahogany forest leaf litter, PR.	0.25 m^2—sample
HU	Palo Hueco understory, PR.	3.0 m^2—sweeping
BL	Mt. Britten Dwarf Forest leaf litter, PR.	0.25 m^2—sample
TL	Tabonuco forest leaf litter, PR.	0.25 m^2—sample
BU	Mt. Britten Dwarf Forest understory, PR.	3.0 m^2—sweeping
FU	Guapiles rainforest fern understory, CR.	10.0 m^2—sweeping
VU	Monteverde cloud forest understory, CR.	3.0 m^2—sweeping

understory data showed some ambiguous evidence of seasonal change.

There is one further attribute of the saturation model that should be noted. At equilibrium (Equation 1), the number of quadrats needed under ideal circumstances to achieve 50% of the estimated number of species may be calculated. This is simply the reciprocal of the intercept/slope of Equation 2 (see Table 1, q_{50}). In general, with the exception of the pitfall trap collections, when the number of quadrats reaches ±16, 50% of the estimated total number of species has been achieved (Table 1). In the case of pitfall traps, the number of quadrats needed to reach 50% is considerably more. Again, with the exception of pitfall trap collections, approximately 40 quadrats were necessary to achieve ±75% of the estimated total number of species. The ground level is the principal route traveled by wandering spiders, thus pitfall traps provide a sample of the immediate habitat as well as a

sample of wandering spiders, especially adult males, from other habitats. The number of quadrats required to reach the q_{50} level (or any other desired level) is not directly determined by the number of species to be found in the habitat, or the number of quadrats, but rather by the rate at which additional species enter the collection. Within reasonable limits the size of the quadrat chosen should not alter the $n(esr)$ although smaller quadrats are intuitively to be preferred, particularly where there is evidence of aggregation. The sampling method used and an estimate of the area sampled for the data presented here is provided in Table 2.

In summary, the data appear to be well fitted using a double reciprocal plot of the number of quadrats against the number of species. Simply using the number of species observed results in a relatively easy to understand estimate of species richness since there are no abstract mathematical considerations in-

volved. The procedure appears to be amenable to interpretation; that is, identifying and quantifying temporal change and other environmental changes. It is suggested that the jackknife estimator of Heltshe & Forrester (1983), an approach that involves giving weight to the number of unique species, will tend to overestimate the number of species. Combining samples taken in different years will result in an ever increasing overestimate of the species richness of a particular habitat, given the vagility of spiders.

The regional pool of spiders in the Cape Cod, Massachusetts area is estimated to be approximately 500 species (Edwards 1993). The results presented (see species estimates in Table 1) support the suggestion that specific Cape Cod habitats have a high beta diversity, are inhabited by interactive assemblages of spiders and tend to be saturated (Cornell & Lawton 1992; Edwards 1997).

ACKNOWLEDGMENTS

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