PITFALLS IN SPIDER COMMUNITY STUDIES
(ARACHNIDA, ARANEAE)

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ABSTRACT

Pitfall traps of four types were used at three woodland sites over twelve months in an empirical study of the effect of trap efficiency in describing species composition of spider communities. There was a certain degree of agreement between trap-types in terms of seasonal variations and relative numbers of species and of individuals at the three sites.

Due to the different responses of the various species, distortions were evident in the communities' species frequency curves. This was significantly apparent at one of the sites and less so at the others. The more "efficient" methods used here captured disproportionately more species in relation to the greater number of individuals. The probability of analogous distortions in data from other sampling methods is discussed.

THE PROBLEM

Pitfall traps are commonly utilised by arachnologists, although the validity of their use is questioned by some. Uetz and Unzicker (1976) compare pitfalls with quadrat sampling and give qualified support for the former method in studies of cursorial spiders; they quote further references both for and against the technique. Other considerations may be found in Turnbull (1973) and Duffey (1972). It is generally appreciated that the capture rate in ptifalls depends on both population density and on activity, e.g. Vlijm and Kessler-Geschiere (1967). Trap efficiency is also important and may vary between species and between habitats, as considered by Maelfait and Baert (1973) for arachnids, and for beetles by Baars (1979) whose field experiments and computer simulations indicated that continuous pitfall sampling gave reliable relative measures of carabid populations. A thorough study of pitfall trap efficiency in capturing Coleoptera has been made by Luff (1975).

While there have been criticisms of the accuracy of the method, there has been no explicit consideration of the way in which trapping efficiency may distort information on the relative importance (a function of both density and activity) of species in a community. Based on data from an empirical study, it is with this aspect that this paper is concerned, concentrating on community parameters rather than individual species.

METHODS

To address the question - "Do traps of different efficiency give the same representation of species composition in a community?" - pitfall trap efficiency was varied by using four types of trap:

1. Control—plain plastic jar, 6 cm diameter, 8 cm deep, with drainage holes bored at intervals 1.5 cm below rim.

2. Detergent—as type 1 but with 1-2% solution of the detergent teepol to a depth of 1-2 cm.

3. Detergent + preservative/killing fluid—as type 2 but incorporating 4% formalin solution.

4. Dry—as type 1 but with a horizontal, opaque cover placed over the trap to prevent entry of rain-water and with 2 cm clearance below the cover to allow access for invertebrates active on the soil surface.

To allow for any environmental gradients, the traps were placed in a 4 x 4 Latin square with a pair of similar traps in each 1 m^2 cell. The study commenced in October 1976 and for the initial three months three pairs of traps were placed in each cell and trapping periods of 1, 2 and 4 weeks employed. Analysis of variance applied to each of these sampling periods showed that trap type affected the number of animals caught; trap location in the sampling grid was not correlated with animals captured (Stewart 1977). After this initial experiment, traps were lifted each month. Data obtained over a full year are considered here.

The experiment was carried out in the Loch Lomond National Nature Reserve, Scotland, at three contrasting sites which provide araneid/opilionid communities of different types (Curtis et al. 1978):

Site 1—Oak-dominated deciduous woodland on island of Inchcailloch; ground vegetation includes various grasses, bramble (*Rubus fruticosus* agg.), woodrush (*Luzula sylvatica*) and ferns such as bracken (*Pteridium aquilinum*) and *Dryopteris* spp.

Site 2—Mixed deciduous woodland on mainland, about 4 km from site 1, with fairly similar ground flora including rather more abundant mosses, but with land links to contrasting habitats.

Site 3—Wet birch (*Betula pubescens*) woodland on mainland, only 150 m from site 2, but with markedly different ground flora comprising mainly mosses: *Sphagnum* and *Polytrichum* spp.

RESULTS - DATA AND DISTORTIONS

About 11,000 individuals, representing 130 species, were collected. At all three sites, trap types 2 and 3 were clearly most "efficient," capturing more individuals and more species than types 1 and 4. This can be seen in Table 1, which also gives data for some of the more numerous species. While many species follow the overall trend in trap efficiency, there are important variations. A notable exception is the most abundant species, *Nemastoma bimaculatum* (Fab.), which was captured most in type 1 traps and least in type 2.

Seasonal variations.—In spite of their different capture rates, the four trap types showed similar seasonal variations of abundance typical in temperate woodland spider communities. This applies to numerical abundance and species richness and is illustrated in Fig. 1. All three sites show an increase in numbers from February. This appears as a peak at sites 2 and 3. At sites 1 and 2 linyphiid species such as *Diplocephalus picinus* (Blackwall) and *Lepthyphantes tenebricola* (Wider) contribute to this spring/early summer peak especially evident in type 2 traps. The lycosid, *Pirata hygrophilus* Thorell is another contributor to the site 2 peak and is involved at site 3 where other lycosids are also prominent together with the linyphiids *Cnephalocotes obscurus* (Blackwall) and

Table 1.—Capture totals over the year for more abundant species, together with number of species and of individuals taken in the four types of trap at the three sites.

SITES:	One				Two				Three			
TRAP TYPES:	1	2	3	4	1	2	3	4	1	2	3	4
Opiliones:												
Nemastoma bimaculatum (Fab.)	306	73	151	123	67	17	25	65	74	18	24	24
Oligolophus tridens (C.L. Koch)	114	279	299	18	55	56	190	5	3	2	4	1
Lacinius ephippiatus (C.L.K.)	42	59	146	3	55	36	65	3	1	–	–	–
Araneida:												
Linyphiidae:												
Macrargus rufus (Wider)	41	71	130	60	9	69	53	3	6	27	10	2
Lepthyphantes zimmermanni Bertkau	14	53	112	28	7	44	91	38	14	23	63	15
Lepthyphantes tenebricola (Wider)	32	147	96	11	11	90	85	19	1	7	11	4
Dicymbium tibiale (Blackwall)	12	106	126	9	2	52	40	1	–	1	–	–
Monocephalus fuscipes (Blackwall)	13	75	84	7	3	12	12	1	–	–	–	–
Diplocephalus latifrons (O.P. Camb.)	8	25	38	2	3	36	46	1	–	–	–	–
Diplocephalus picinus (Blackwall)	–	97	95	2	–	49	45	–	–	1	1	–
Centromerus sylvaticus (Blackw.)	3	55	112	2	–	4	5	1	6	13	33	1
Tapinocyba pallens (O.P. Cambridge)	1	1	1	–	1	34	34	2	4	48	61	1
Crephalocotes obscurus (Blackw.)	–	1	–	–	–	4	–	–	19	25	45	2
Lycosidae:												
Pirata hygrophilus Thorell	–	–	–	–	1	59	51	1	23	129	121	3
Alopecosa pulverulenta (Clerck)	–	–	–	–	–	1	2	1	35	35	76	2
Trochosa spinipalpis (F.O.P. Camb.)	–	1	–	–	–	1	2	2	55	65	74	32
Pardosa amentata (Clerck)	–	1	1	–	–	–	–	–	2	44	34	3
Total number of species:	29	66	66	27	30	72	71	33	34	55	59	23
Total number of individuals:	720	1601	2937	308	326	1046	1621	226	348	730	1031	137

Overall number of species = 130
Grand total of individuals = 11032

Table 2.—Correlations between the patterns of monthly changes in (a) species richness and (b) abundance, shown by the four trap types; expressed as Spearman's rank correlation coefficient with significant (p<0.01) values underlined.

(a) SPECIES RICHNESS

Sites:	1				2				3		
Trap types	1	2	3		1	2	3		1	2	3
4	.51	_.79_	.68	4	.46	.43	.52	4	_.75_	_.82_	_.77_
3	.69	_.90_		3	_.71_	_.86_		3	_.74_	_.88_	
2	_.76_			2	_.70_			2	_.79_		

(b) ABUNDANCE

Sites:	1				2				3		
Trap types	1	2	3		1	2	3		1	2	3
4	_.70_	.61	.62	4	_.72_	.19	.35	4	_.87_	_.81_	_.95_
3	_.84_	_.87_		3	_.72_	.60		3	_.83_	_.92_	
2	_.78_			2	.54			2	_.72_		

Tapinocyba pallens (O.P.-Cambridge). At site 1 the abundance of harvestmen is responsible for the gradual increase in numbers through the year to a peak in September/October. A peak in species richness is evident at each site around May/June and a smaller peak in October/November.

Inspection of Fig. 1 shows differences between the different trap-types, which depend on their relative efficiencies for particular species. Note especially the high capture totals for type 1 traps at site 1 towards the end of the sampling period. This is due to the greater importance of *N. bimaculatum* at this site relative to sites 2 and 3. Nonetheless, there is a good deal of agreement between the trap types in terms of the relative numbers of individuals and of species recorded each month. Rank correlation coefficient values comparing the patterns of monthly variations are given in Table 2. Considering as significant values for which $p < 0.01$, all four types of trap agree with each other at site 3. More disagreement is evident at sites 1 and 2 with their greater proportion of opilionids, especially at site 2 with strong agreement only of type 1 with type 3 and with type 4.

Community structure.—To examine this aspect, the data were considered in terms of four quarterly periods: Q1 - October, November, December; Q2 - January, February, March; Q3 - April, May, June; Q4 - July, August, September. This approach avoids the problems of small sample size for single months but still gives an indication of variations over the year. Species frequency distributions are used here, plotting S(n) - the number of species represented by n individuals - versus n on a logarithmic (to the base 2) scale. This is just one of several alternative ways of presenting species abundance relationships (May 1975) and serves well to illustrate the distortions present in these pitfall trap results.

Species frequency distributions for the three sites in each quarter are illustrated in Fig. 2. Comparison of the three sites in any one period shows differences between the curves
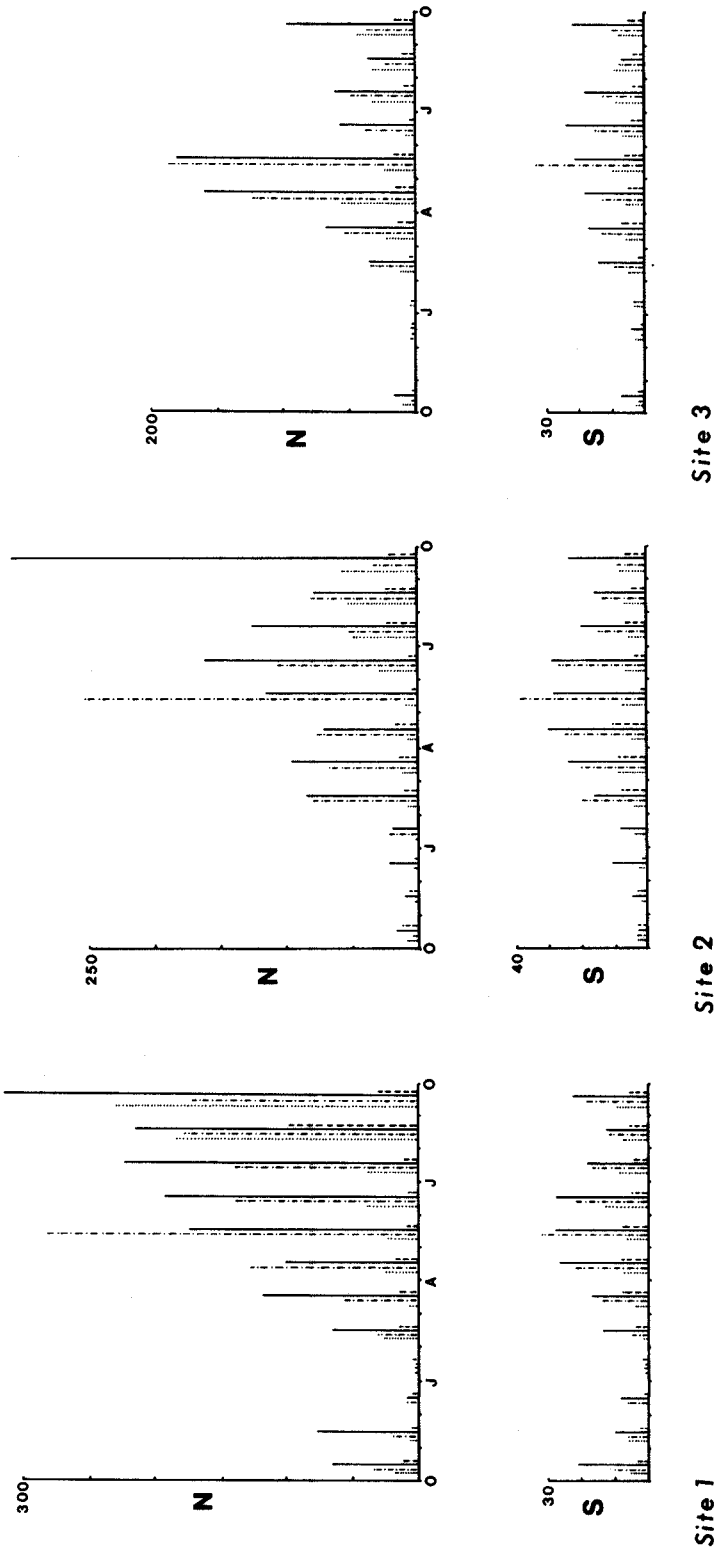
Fig. 1.–Variations in number of individuals (N) and of species (S) taken in each month. Four bars are drawn in each month referring to the four types of trap: dotted line - type 1, dots/dashes - 2, solid line - 3, broken line - 4. The months marked (O - October, J - January, A - April, J - July) indicate the start of the quarterly periods considered.
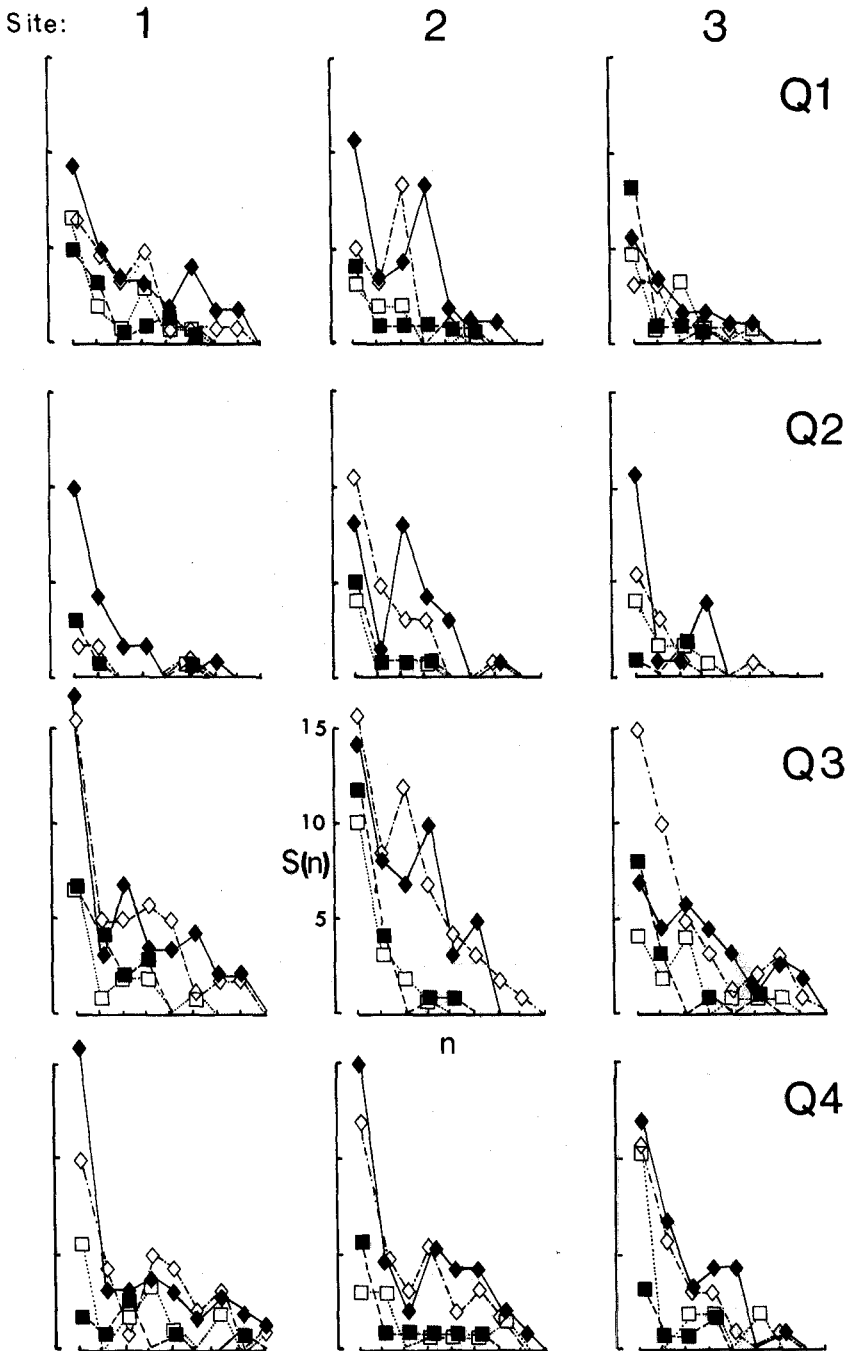
Fig. 2.—Species frequency diagrams showing S(n) = number of species represented by n individuals plotted against n with the n axis in terms of octaves, i.e. 1, 2, 4, 8, 16, 32, 64, 128 and 256: S(4) = no. of species with capture total of 3-4 individuals, S(8) with 5-8, etc. Note differences in the shape of these curves between sites and between quarterly periods. In particular, observe differences between trap-types at site 2, where clear separation between the curves is evident for moderately abundant species, especially in Quarter 3. Open squares represent trap-type 1, open diamonds - 2, solid diamonds - 3, solid squares - 4.

from the sites, presumably reflecting different community structures at the sites. Also, at each site the shape of the species frequency plot changes from one period to another. At sites 1 and 3 the curves from the different types of trap are similar, but there are noticeable variations at site 2. Here, trap types 2 and 3 strongly increase the frequency of moderately abundant species, a phenomenon which is most clearly evident in Q3, but also present at other times of the year.

Fig. 3 shows species frequency plots for data amalgamated over the full year and emphasises the different distortions evident at the different sites. At sites 1 and 3 there is no significant difference between distributions from different trap types, but at site 2 trap types significantly altered the frequency distribution ($\chi^2 = 40.1$, d.f. = 12, p $<$0.001). This clearly has implications for data interpretation.

Number of species recorded (S) is plotted against number of individuals (N) for each trap-type at each site in Fig. 4. The usual curvilinear relationship is apparent but there is also clear separation of trap-types 2 and 3 from 1 and 4. This was also seen in data from each quarter, with a most noticeable separation of types 2 and 3 from 1 and 4 occurring in Q3.

DISCUSSION AND CONCLUSIONS

A reassuring feature of Fig. 4 is that the data points for the more "efficient" trap-types 2 and 3 lie about the asymptote of the curve. This suggests that best representation of species richness would be achieved by using these types of trap (preferably type 3, in which the preservative keeps specimens in better condition).

Use of a rarefaction technique (Heck, van Belle and Simberloff 1975) to calculate E(S), estimated species richness for a standard sample size, is an effective way of describing species diversity. A general trend apparent in each quarterly period was for trap types 2 and 3 to yield higher E(S) values than 1 and 4. This is demonstrated in Fig. 5 which shows E(S) values for a standard sample size of 100 adults, using the full year's data. The higher E(S) values at site 2 accord with the noted distortion in species frequency distribution, but this marked pattern in E(S) is also shown at sites 1 and 3. Clearly the use of traps of different efficiency will give different impressions of species richness in a com-
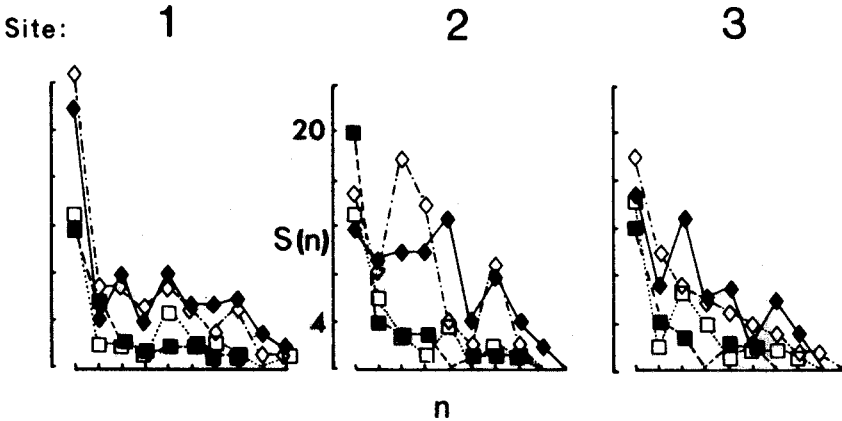

Fig. 3.—Species frequency diagram for three sites' data over whole year. Symbols as Fig. 2. Again the most obvious variations with trap-type may be seen at site 2 with the deviation of types 1 and 4 (squares) from types 2 and 3 (diamonds).

munity. Fig. 5 indicates that in the more "efficient" traps the increase in S is *not* a direct consequence of increase in N.

As considered by Uetz and Unzicker (1976), N may be increased by increasing the number of traps, or trap density. Unpublished data from an experiment carried out in October 1977 show this. A 5 x 5 Latin square of 1 m^2 quadrats was used. Trap densities of 1, 2, 4, 8 and 16 per square metre over this area showed that mean number of captures per trap was not affected by trap density. Curtis (1978) used 20 plain pitfalls within 1 m^2 quadrats to increase sample size. However, this dodges the question - Does the species abundance pattern in pitfall samples reflect the pattern in the community being sampled? Obviously at site 2 the disagreement between trap-types indicates that at least some types do not give an accurate picture of the field situation. Even at the other sites, where there is agreement between the types of trap, one cannot be certain that the species frequency distribution recorded in the pitfall samples also applies to the community under study.

It is well appreciated that pitfall trap capture rate depends on (e_{ih}, a_{ih}, d_{ih}), where e_{ih} = trapping efficiency, a_{ih} = species' activity and d_{ih} = species' density, for species i in habitat h. Variations in these parameters cause distortions and have implications for the use of many ecological approaches based on species' relative abundances. Examples include the Shannon (1948) diversity measure as used by Uetz (1975, 1976), Levins' (1968) formulation for niche breadth (Uetz 1977), its corollary as a measure of species diversity and Hurlbert's (1971) probability of interspecific encounter used by Curtis (1978), as well as the index of overlap used by both of these authors.

A traumatic development is to re-define e_{ih} as the efficiency of any other method of sampling. Just as e_{ih} applied to a pitfall reflects the probability that a spider having fallen into the trap cannot escape, it could also be taken to represent the probability of retention in a sampler's hand, or of separation in a thermal extraction apparatus. Just as the likelihood of a spider falling into a pitfall trap depends on its activity, a_{ih}, the probability of its capture by hand is greatly increased by its activity rendering the specimen more noticeable to the searcher; a physiologically inactive individual will not respond to the temperature/humidity gradient in an extraction apparatus such as a Berlese or Tullgren funnel. So the types of distortion described explicitly in this paper are also applicable to the other sampling methods employed by ecological arachnologists.
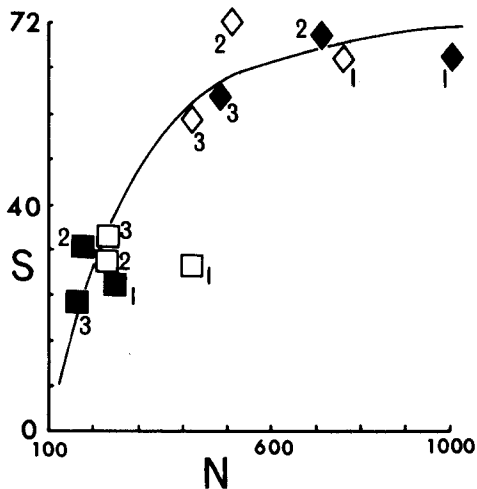

Fig. 4.—Plot of number of species (S) versus number of individuals (N) captured over the year in the four trap-types (symbols as in Fig. 2) at the three sites (site numbers beside symbols). Clear separation of types 2 and 3 (diamonds) from 1 and 4 (squares) is obvious. Curve is fitted by eye.
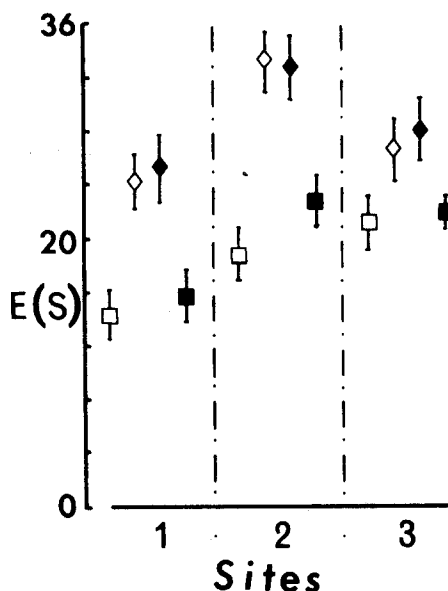
Fig. 5.–Values of E(S) - estimated number of species for a standard sample size of 100 adults. Based on full year's data. Symbols relate to trap-types as in Fig. 2 and the bar extends one standard deviation above and below symbol. Markedly higher values are evident for trap-types 2 and 3 (open and closed diamond symbols).

Perhaps the high numbers of species recorded in pitfall traps, coupled with the continuous nature of their sampling, argue in favour of their use. In any case, although great caution is required in attempting to describe spider communities, the hypotheses generated in these studies are useful from a heuristic point of view.

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