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The Effect of Architectural Variation in Habitat on a Spider Community: An Experimental Field Study -- with Special Reference to Resource Partitioning

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THE EFFECT OF ARCHITECTURAL VARIATION IN HABITAT ON A SPIDER COMMUNITY:

AN EXPERIMENTAL FIELD STUDY -- WITH SPECIAL REFERENCE TO

RESOURCE PARTITIONING

by

James Vincent Robinson

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Biology
(Ecology)

Approved:

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Major Professor   Committee Member

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UTAH STATE UNIVERSITY
Logan, Utah

1978

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The Effect of Architectural Variation in Habitat on a

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-- with Special Reference to

Resource Partitioning

by

James Vincent Robinson, Doctor of Philosophy

Utah State University, 1978

Major Professor: Dr. James A MacMahon
Department: Biology

Spider community acceptance of, and segregation by, architectural configuration was investigated for the spiders of Green Canyon in northern Utah. Modular habitat units consisting of 30.48 centimeter (1 foot) cubes of chicken wire supporting internal strands of macrame jute tied in different orthogonal configurations were used. Configurations including all three axes were tested at two strand densities.

The primary null hypothesis tested, that spider species use structures independent of architecture, was rejected in favor of the alternate hypothesis that spider species differentially use structures dependent upon architecture. Of the eight most abundant species, two showed preferences for horizontal substrata and one chose vertical substrata. All spiders strongly responded to the amount of jute available in each module. The two most abundant jumping spiders were biased toward modules with widely spaced jute, while the two most abundant web-builders preferred closely spaced jute.

Of the eight most abundant species, two species fell within each of the following four hunting guilds: jumpers, ambushers, pursuers, and web-builders. Within each pair of species, juveniles of the larger species emerged earlier in each of the two field seasons studied. In three of the species pairs, the body lengths were sufficiently different to fulfill theoretical requirements for their coexistence based upon differential prey size use. The remaining species pair, ambushers, had sufficiently different cryptic coloration and abundance patterns to suggest that their coexistence was determined by a combination of microhabitat and seasonal separation.

(87 pages)

INTRODUCTION

Spatial segregation is one way in which spiders may partition habitat resources. This may take the form of horizontal or vertical separation, or it may be more subtly the result of differential preferences for available architectural configurations. Tretzel (1955, in Turnbull 1973) and Chew (1961) found horizontal separation in spiders. More frequently, vertical specialization is reported. MacMahon (in prep.) observed that a species of Diguetia was consistently found at the same height above ground where desert shrubs of the proper minimum height were available. Despite considerable diurnal and seasonal movement by spiders, Turnbull (1960) found that these spiders had highly developed vertical stratification. Enders (1974) reports that immature Argiope aurantia and Argiope trifasciata place their webs at different heights. In late summer this vertical separation disappears. Enders attributes the stratification of the young to competition induced by high juvenile population densities. At maturity fewer individuals survive and more spatial overlap is tolerated.

More subtle spatial segregation was found by Hatley (1978). She found that guilds of spiders, based on different hunting strategies, differentially used experimentally manipulated sagebrush (Artemisia) in a manner which depended on the foliage density of the shrub. Her experimental design consisted of decreasing the foliage density of a set of shrubs through pruning and increasing

the foliage density of another set of shrubs by binding branches
together with twine. Her results suggest that, for those species
present, the jumping spiders were more abundant in open shrubs,
while the ambushers (subfamily Misumeninae) and web-builders were
prevalent in denser shrubs. This is the most significant experimen-
tal field study to date on the fine grained effect of vegetational
architecture on spiders. Another experimental study of spider
response to architecture was performed on lycosid species in labora-
tory terraria (Greenquist and Rovner 1976). They furnished the
terraria with cardboard leaves having controlled surface areas and
slopes. Their results indicate that Lycosa punctulata and L. rabida
spend significantly more time on artificial foliage than do Schizo-
cosa crassipes and S. saltatrix. These results lend credence to
the concept that preferences for structural features within a habitat
play a role in the microhabitat distribution of wandering spiders.
Waldorf (1976) found that in an area containing numerous Mahonia
(Berberis) aquifolium, all size classes of spiders were distributed
nonrandomly on the leaflet types of this plant. In addition, during
the winter small spiders (1-2 mm) were found in high frequency beneath
the leaflets at their junction with the petiole. Other workers
observe that habitats occupied by various web-building spiders are
affected by the availability of specific structural features (Duffey
1962, Judd 1965). Enders (1975a) found that Argiope aurantia
abandoned its web sites following removal of nearby vegetation. He
suggests that this might be the result of greater wind damage to webs
where surrounding vegetation was insufficient to provide a windbreak.

Studies of other taxa indicate an equal variety of spatial segregation. Anolis lizards display vertical and structural separation (Andrews 1971, Rand 1964, Williams 1972). MacArthur (1958) in a classic study of sympatric warbler species found that each species is differentially partitioned from others within conifers on the basis of tree architecture.

Differential use of food is another common form of resource partitioning. In higher animals this often occurs through prey preference, which may result from search image development (Croze 1970; Holling 1965; Tinbergen 1960, in Edmunds 1974). The question of whether spiders demonstrate prey preference is rather controversial. One common view is that spiders are very catholic in their food preference and will eat most living animals of the appropriate size that they can obtain (Savory 1928). Surely most spiders feed on a wide range of organisms (Jackson 1977, Riechert 1974), although data exist indicating rejection of apparently potential prey by some spiders (Bristowe 1939, Turnbull 1960). Even in a case where prey rejection was reported, a species fed on 150 of the 153 prey species available in the habitat (Turnbull 1960).

Despite the apparent euryphagous predation by spiders, food resource partitioning is still feasible if some attributes of a spider species' ecology make some components of the prey spectrum differentially more available to it than to other spiders. Discriminant use of the habitat architectural continuum is a plausible mechanism. Another predatory characteristic influencing prey availability to any species is its hunting strategy (Cody 1974, Diamond

1975). This may influence spider community structure (Balogh and Loska 1974, in Turnbull 1973; Enders 1975b; Hatley 1978; Petrusewicz 1938, in Turnbull 1973; Uetz 1977). Spiders have adaptively radiated leading to considerable variation in hunting strategies (Gertsch 1949, Kaston 1948). These strategies may be grossly lumped into four categories: pursuers, ambushers, jumpers and web-builders. Each of these categories may conceivably be broken into numerous subcategories.

Temporal variation in spider abundance and activity patterns may also affect prey availability. Uetz (1975) found that seasonal species richness patterns of a spider community were strongly correlated with the pattern of seasonal insect abundance. He suggested that increases in prey abundance permit more predatory niche overlap, hence more spiders might temporally "fit" into the community. Tretzel (1955, in Turnbull 1973) felt that temporal variation was important for spider species coexistence.

Finally, one of the most common methods postulated for sympatric species of similar ecologies to partition food is the choice of different sized prey (Andre 1978, Dumas 1956, Hespenheide 1971, Schoener 1968). Food preference studies are difficult, especially with spiders (Turnbull 1973), thus investigators are often forced to make inferences about likely prey from morphological features of the predators (Hutchinson 1959, Lack 1947). Often when reasonable inferences like this are subjected to experimental scrutiny, they are substantiated (Bowman 1961, Holling 1964). Such inferences usually assume that a predator's body size or feeding apparatus size

will reflect the relative size of suitable prey (Hutchinson 1959,
Schoener 1969). This assumption is supported for the spider Phiddipus
johnsoni, which captured prey one quarter to three quarters its size
(Jackson 1977). Enders (1976) inferred from linear body measurements
of several midwestern lycosid species that coexistence is based on
use of different prey sizes.

Much of the concept of food partitioning, based on inferences
made from measurements on the predator, originated from the obser-
vations of Hutchinson (1959) on corixid insects and his tabulation
of data concerning sympatric birds and mammals. He concluded that
sympatric species of similar ecologies are separated by a mean ratio
of 1.28 (range 1.1 to 1.4) for linear body measurements correlated
with feeding. He also suggested that organisms obtaining their own
nourishment throughout life, and that have annual life cycles, are
under different selective pressures than those which procure most of
their own food at or near their adult size. He hypothesized that
for coexistence of sympatric species of the former type, the larger
of the two must begin its development prior to the smaller. This
second hypothesis has not been verified. Enders (1976) used field
and laboratory data obtained from the literature to support this
theory when applied to lycosid spiders. Turnbull (1973) conjectured
that "... except perhaps immediately after spiderling dispersal from
the family cluster, probably few spiders starve." If this is true,
then the time of juvenile emergence (the second instar) may be the
focus of the majority of competitive selection. This reasoning is
strengthened further by his observation that "... female spiders

produce an average of well over 100 eggs, most spiders die before maturity." While this second instar stage may be most important to spiders, competition for food during later stages may still affect fitness, hence selective pressures will probably operate to reduce this competition also.

May (1975) demonstrated that, for mathematical models of species competing along a single resource dimension, the persistence of the community is dependent upon all species using the resource in a sufficiently separate manner. He concluded that the mean value of a species' utilization of the resource must be separated from the mean value of the species with the most similar resource use characteristics by approximately one standard deviation of its utilization function. When this criterion is applied to food resources and projected back onto the morphological features of the predator, May concluded that sympatric predators must have their linear dimensions separated by a ratio of 1.2 to 1.4 for them to successfully coexist in one resource dimension. He further suggested that these ratios can be reduced when multiple resource dimensions are being used. May's analysis provides a theoretical basis for Hutchinson's empirical observations.

Some aspects of resource use of spiders near Green Canyon, northern Utah were studied to address some of the aforementioned hypotheses. Emphasis was placed on assessing spider community acceptance of, and segregation by, architectural configuration.

The primary null hypothesis tested, along with its alternative, may be stated as follows:

H_0: Spider species use structures independent of architecture.

H_1: Spider species differentially use structures dependent upon architecture.

In addition, data pertaining to the juvenile emergence dates, the seasonal abundances and the nominal body lengths of the most abundant species collected were appraised as possible factors permitting coexistence.

PLOT DESCRIPTION

The research site used was the same as that studied by Hatley
during the field seasons of 1974 and 1975. She describes the area
as being

> ... located 3.2 km (2 mi) northeast of Logan on the
> Bonneville Lake terrace of the Bear River Range, 100 m
> south of the mouth of Green Canyon, Cache County, Utah.
> Mean annual precipitation is between 38.1 and 43.2 cm,
> mean annual temperature is between 7 and 9 ^{o}C, and
> frost-free days average between 100 and 120 (USDA Soil
> Conservation Service and Forest Service, 1974). The
> plot is at an elevation of 1477 m and faces southwest
> (20% slope). Land is used mainly for watershed and
> wildlife.
> The area is dominated by big sage (Artemisia
> tridentata). Other shrubs present include Purshia
> tridentata, Gutierrezia sarothrae, Chrysothamnus
> nauseosus. Major herb and forb species include Balsa-
> morhiza sagittata, Wyethia amplexicaulis, Bromus tec-
> torum, and Bromus brizaeformis. (Hatley 1978, p. 4)

My sampling, conducted during the 1976 and 1977 field seasons,
occurred on the Bonneville bench section of this plot, thus level
sites for the modular habitat units were available.

METHODS

Description of habitat
modules used

Spider community acceptance of ten sets of six different architectural configurations was tested for two field seasons (Table 1). Externally, these structures consist of 30.48 cm (1 foot) cubes of 2.54 cm (1 in) mesh chicken wire; internally, various designs were constructed from five ply macrame jute. The "basic cube" (referred to as 222) consists of sets of parallel strands of jute arranged at intervals of 5.08 cm (2 in) in each of three orthogonal directions (Fig. 1). Without altering the density of jute along any axis, four modifications of this basic design exist. These four configurations logically fall into two pairs of structures in which both member configurations can be made identical by a 90° rotation of one of them. The first pair of configurations is comprised of cubes with no vertical component (referred to as H22) and cubes with one set of orthogonal horizontal strands eliminated (referred to as V22) (Fig. 2). The H22 and V22 modules can be aggregated under the heading $\perp$22 which refers to the jute arrangement common to both (i.e., a set of parallel strands of jute every 2 inches arranged perpendicular to an identical set of parallel strands). The second pair consists of cubes with only vertical strands (referred to as V2) and cubes with only parallel horizontal strands (referred to as H2) (Fig. 3). The H2 and V2 modules can be combined under the heading $\parallel$2 which refers to the jute arrangement common to both (i.e., a

Table 1. Pertinent physical dimensions of the six architectural configurations of modules tested

Configuration		Spacing of strands along axes (cm)			Linear Substratum Available (meters)
		Vertical	Horizontal #1[c]	Horizontal #2[c]	
	222[a]	5.08	5.08	5.08	51.2
⊥22	H22[a]	N.A.[b]	5.08	5.08	34.1
	V22	5.08	5.08	N.A.	34.1
∥2	H2	N.A.	5.08	N.A.	17.1
	V2[a]	5.08	N.A.	N.A.	17.1
	444[a]	10.16	10.16	10.16	18.3

[a]Colonization trials were run on these configurations.
[b]Not applicable.
[c]Horizontal #1 refers to horizontal parallel strands; Horizontal #2 refers to horizontal parallel strands in an orthogonal direction to Horizontal #1.
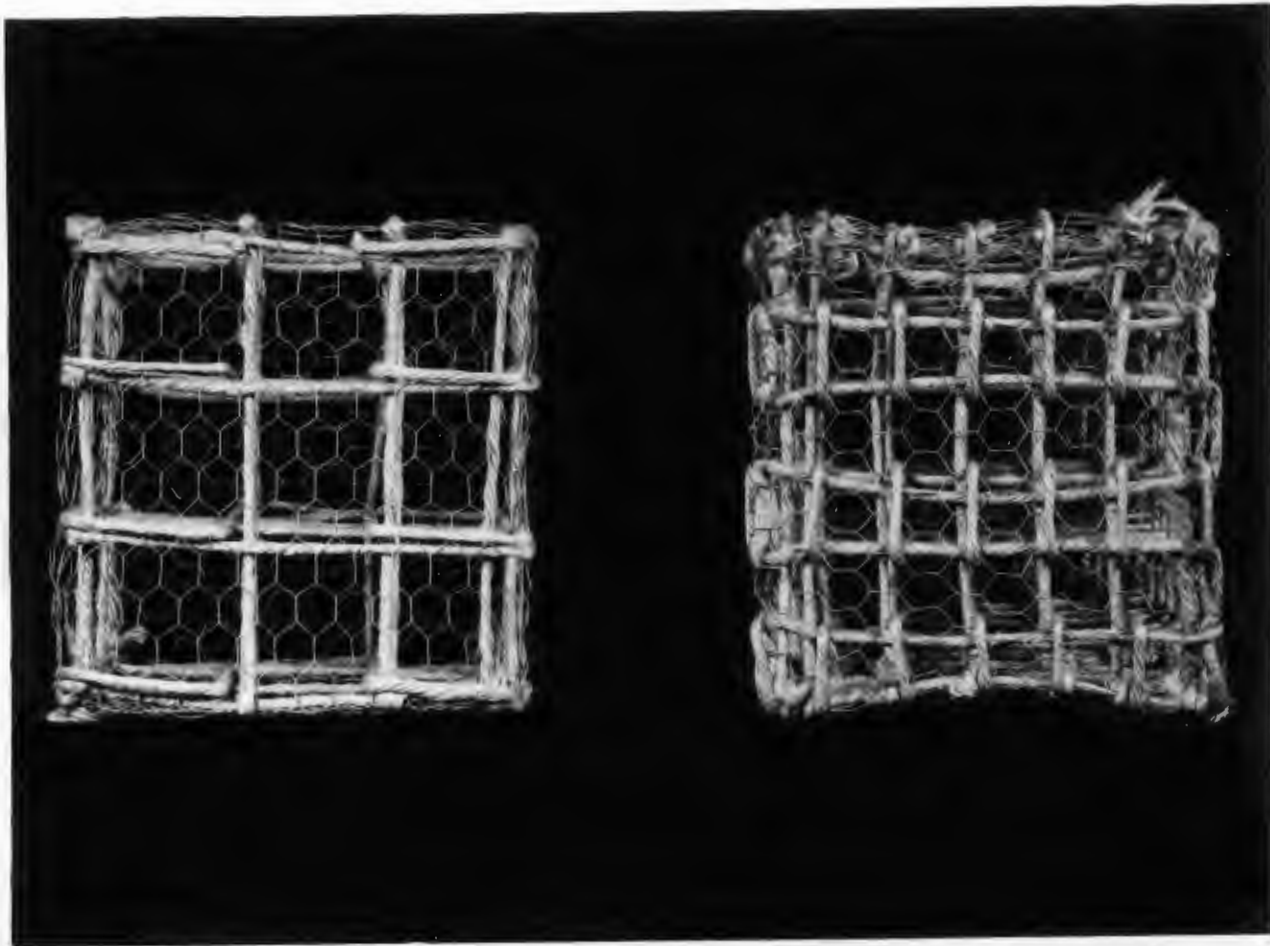
Figure 1. Photographic comparison of modules 444 and 222
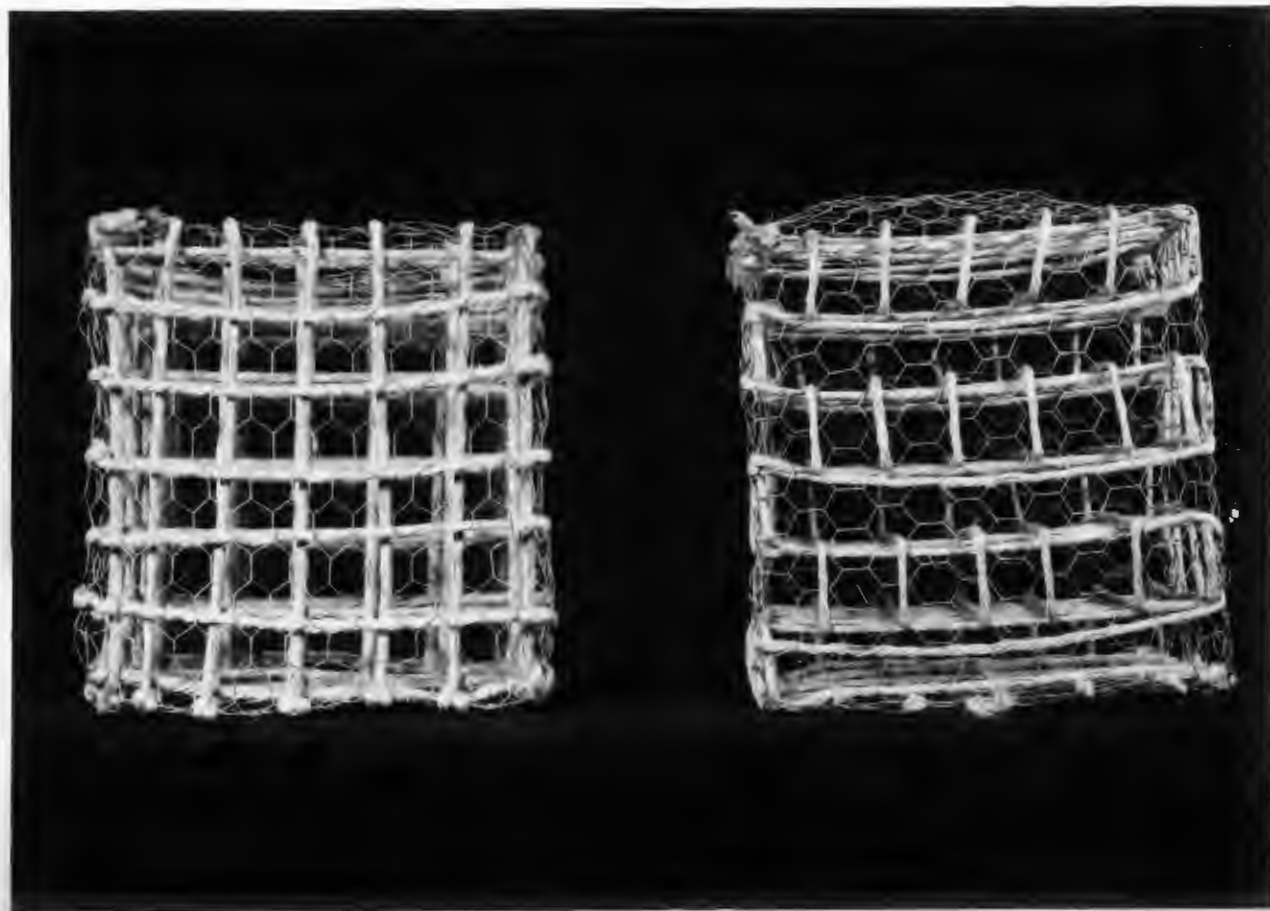
Figure 2. Photographic comparison of ⌐22 (V22 and H22) modules
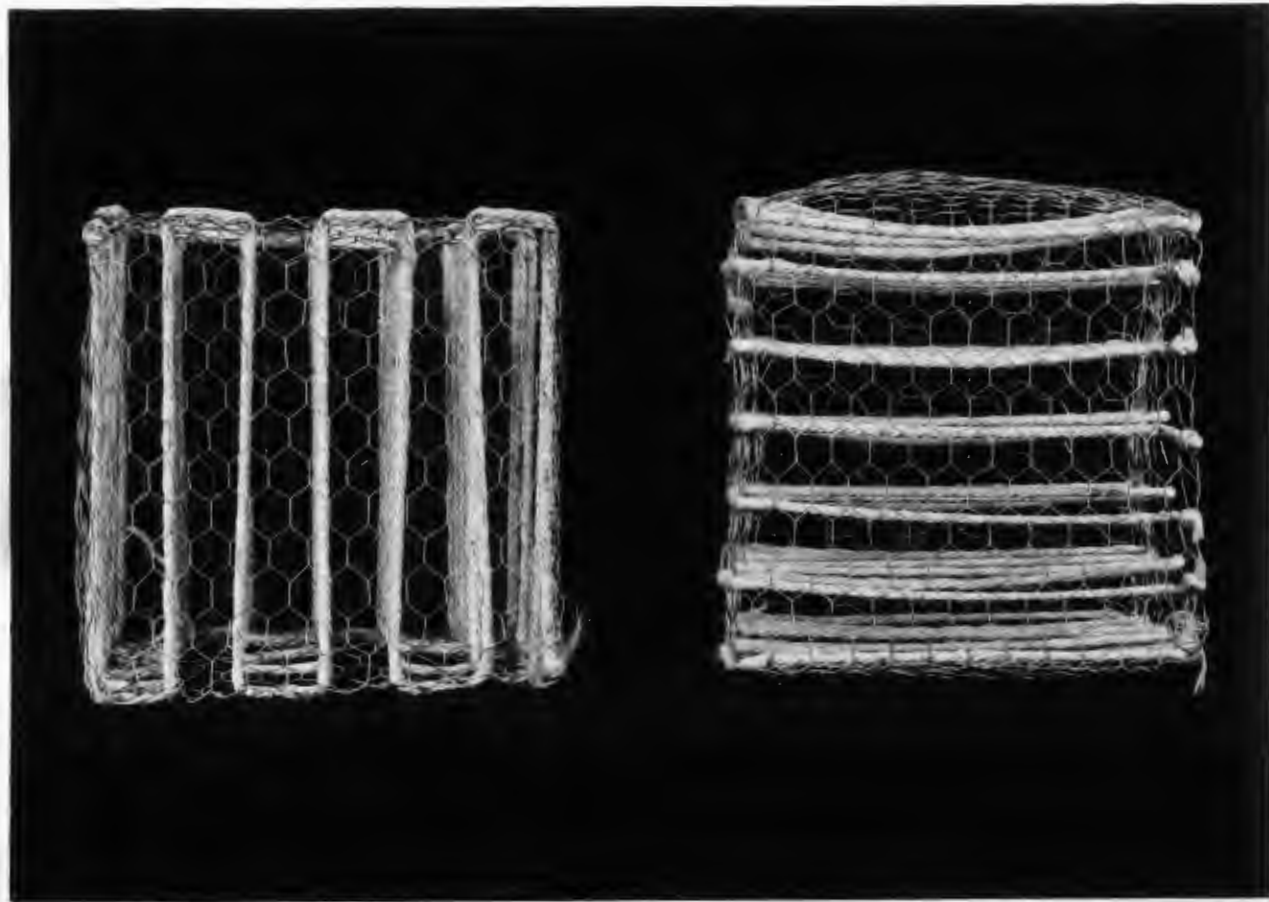
Figure 3. Photographic comparison of ‖2 (V2 and H2) modules

set of parallel strands of jute every 2 inches). These five sets of architecture were designed to indicate which and how many substrate dimensions are of significance to different species.

An additional variation of the basic design was tested. This variation (referred to as 444) consisted of removing every other strand of jute, in each of the three orthogonal directions, increasing the spacing between strands to 10.16 cm (4 in) (Fig. 1). Spider acceptance of this configuration versus the previous five gives an indication of the effect structural density has on their microdistribution. These results were compared with the study by Hatley (1978) in which shrubs were made more or less dense through pruning and binding.

Sampling procedures

Collection and extraction. A sample consisted of collecting a cube which had been left in the field for a predetermined number of days. Cubes were placed in muslin bags and transported to the laboratory. During handling of the 1055 samples taken in this manner only one individual was seen to leave a cube during bagging. In the laboratory each cube was placed into a large funnel for spider extraction. All bags were carefully examined for spiders lost from cubes. The funnel led to a bucket of water. Floating spiders were transferred to vials of 70% ethanol for preservation. To extract the spiders, each cube was banged against the inner surface of the funnel repeatedly and periodically rotated so that each side of the cube was oriented toward the bottom for at least ten blows. This technique yielded over three thousand spiders. Approximately fifty

cubes were reprocessed a second time to estimate the technique's effectiveness. Only four additional individuals were obtained. Each cube was repaired following sampling. This hand manipulation revealed no new individuals, suggesting that the sampling method was adequate. Species identification was aided by collections developed by Hatley and Abraham and determined by W. Gertsch.

Spider identifications and measurements. All spiders collected were identified to species with the exception of several members of the subfamily Erigoninae. Spider body lengths were measured using low power on a WILD model M4 binocular microscope fitted with an ocular micrometer; this permitted resolution to approximately 0.07 mm. Spinnerets were not included in measurements.

Insect identifications and measurements. In addition to spiders, all other invertebrates (predominantly insects) were collected. Some bias was introduced in this procedure because it was not uncommon for active winged forms to escape from the funnel. However, the data pertaining to insects collected probably represent a reasonable indicator of relative prey availability. The insects were separated taxonomically to order and their body lengths were measured. Ovipositors were not included in measurements.

Collection of colonization data. During the first field season the majority of traps were left in the field for eight consecutive days, others were sampled at different intervals (1, 2, 4, 8, and 16 days) to obtain colonization rate data. While preliminary colonization data were being collected, structural types H2 and V22 were rotated 90° to increase the sample size of the V2 and H22 modules. Hence colonization data are pertinent to structures V2, H22, 444,

and 222 only. After evaluating the preliminary colonization data it was decided to sample at fourteen day intervals in 1977.

Analytical procedures

Patterns of spiders as a group. In 1977, following the review of 1976 data, a randomized complete block experimental design was used (Ostle 1963). The blocks consisted of groups of all six configurations aggregated proximate to each other. This design was maintained for 38 sampling dates. Its purpose was to test the null hypotheses that the total number of spider individuals per module and the species richness per module were independent of the structural types of the modules. These hypotheses were examined using one way analysis of variance (ANOVA) tests. Prior to analysis it was necessary to modify the data, due to the moderate number of occurrences of zero spiders within the samples. Zeroes in the data precluded the assumption that the underlying statistical distributions were normal. To obviate this problem, couplets of sampling dates were randomly chosen from among the 38 available. The data within each couplet were summed and the analysis of variance was applied to these summed data. By invoking the central limit theorem of statistics (Miller and Freund 1965) it can be shown that these summed data have a normal distribution. Following the analysis of variance, Duncan's multiple range test was used to determine which structural couplets were used in significantly different ways by the total spider community.

Choice of abundant species. All species for which fifty individuals or more were collected during the two field seasons

were considered sufficiently abundant to warrant individual analysis.
Because of the relatively low numbers per sample for any one species
and the correspondingly high number of samples which did not contain
any individuals of these species, the statistical distributions could
not be assumed normal, but instead were assumed Poisson. This created
difficulties with precise statistical analysis because apparently no
multiple-comparison test for Poisson populations with low mean values
is available (Lehman 1959). However, two-sample comparison tests are
available (Hoel 1945, Lehman 1959).

Effect of horizontal vs vertical substrata. All sufficiently
abundant species were evaluated for their proclivity to horizontal
vs vertical substrate. This was tested for each species by making
pairwise comparisons of structures H2 vs V2 and H22 vs V22. The
probabilities that the number of individuals of each species found
in those structures with only horizontal substrate would be equal to,
or greater than, the number actually found due to chance, were then
ranked and a Kruskal and Wallis multi-sample test for identical
populations, sensitive to unequal locations, was performed (Bradley
1968). This test was applied to determine whether the species in
this species set were using these habitat modules in a significantly
different way due to the amount of horizontal vs vertical substrate.

Effect of open vs dense modules. Due to the rotation of the
H2 and V22 structures for colonization trials and their analogous
rotation during surface area tests (to be described later in this
section), V2 and H22 structures were sampled more often than the
H2 and V22. However, both the H2 and V2 have the same basic

architecture of parallel strands of jute spaced 5.08 cm (2 in) apart, while the H22 and V22 units consist of two sets of parallel strands, each of which is spaced 5.08 cm (2 in) apart, arranged perpendicular to each other. The next set of analyses lumps H2 with V2 under the common heading ∥2 and V22 with H22 under the heading ⊥22. All data collected during both field seasons were then used in a series of six sets of pairwise comparisons of the relative use these type structures had by the abundant spider species. Since these populations express Poisson distribution properties, statistics analogous to those presented above are used. Due to independence constraints, when the Kruskal-Wallis test was applied, only three sets of pairwise comparisons were used. These comparisons were chosen so that a structure of open aspect (444) was compared with each of the three other more closed appearing units (i.e., ∥2, ⊥22, 222).

An analogous data analysis procedure was followed to the one described in the above paragraph. However, instead of assuming the null hypothesis that all cubes have equal utilization probabilities, it was assumed that every centimeter of jute had an equal probability of use.

Additional experimental designs

Effect of exposed surface area of module. To assess the effect that different amounts of available cube surface area have on spider response to architecture, an experiment was designed consisting of a cluster of four identical habitat modules immediately adjacent to each other that were surrounded by four similar cubes each standing separately (Fig. 4). This design was used for twenty five sampling
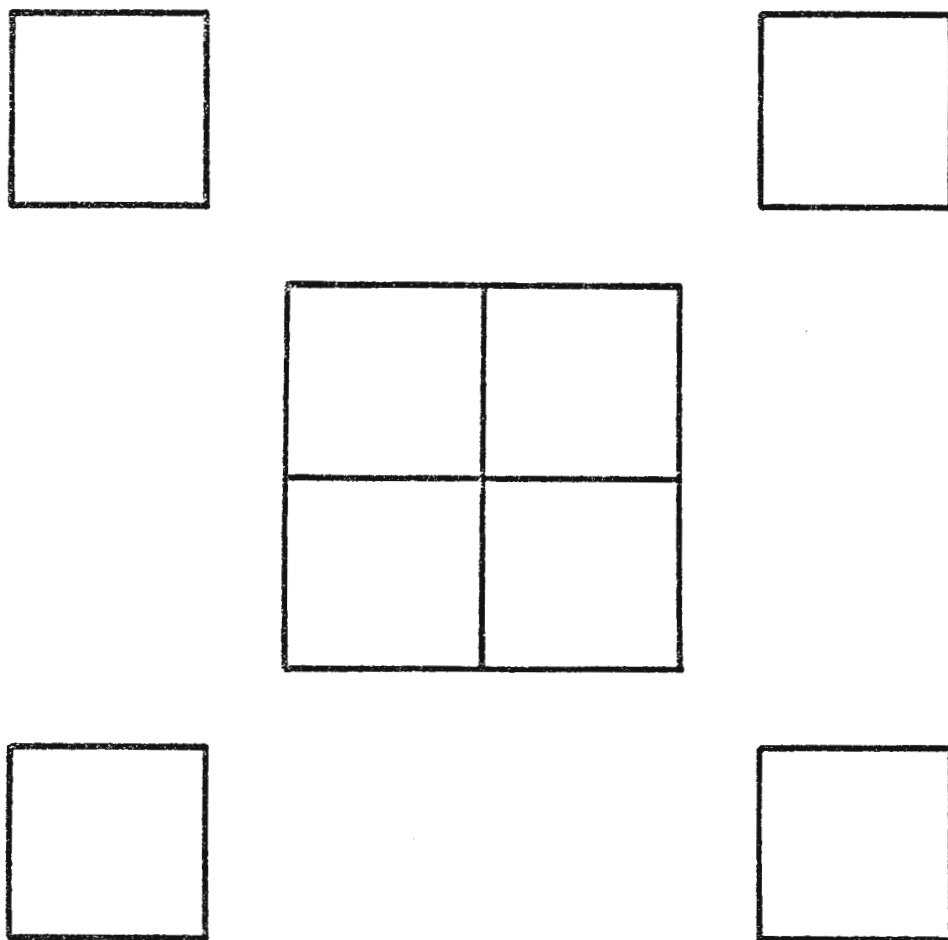
Figure 4. Arrangement of modules during experiments testing the
effect of module exposed surface area on spider use

dates, during which one hundred clustered cubes and one hundred solitary cubes were sampled. The data were analyzed via a pairwise comparison of the number of spider individuals in the solitary versus the clustered cubes, once more using a test for two Poisson populations. During this manipulation the H2 and V22 structures were rotated to provide additional data for the V2 and H22 configurations.

Effect of total jute removal. A final experiment involved sampling a cube of chicken wire which contained no jute. This cube was sampled ten times to evaluate the potential effect of spider use of the juteless wire.

Determination of nominal body
lengths and juvenile
emergence dates

Data pertaining to the number of individuals collected per ten day interval and the measured body lengths of the most abundant species were plotted as functions of time. Individuals were separated into two cohorts, assumed to represent current and previous years' animals. Separation was based on either the presence of adult characteristics or the approximate body size expected for a given date. This latter method has precedence in entomology (Drooz 1965, Enders 1976). Linear regression analyses were then performed on the body length data for each abundant species. The current year's cohorts were separately analyzed for the 1976 and 1977 field seasons, while the previous year's cohorts were analyzed only for the 1977 field season (the beginning process in 1976 was sufficiently delayed so that only marginally complete data were obtained). The

regressions of body length on Julian date were tested to insure significant nonzero slopes using a standard F-ratio test. Only those sections of the lines were graphed that coincided with the range of collection dates for the cohort. The earliest emergence date for which individuals were collected was thus indicated for each abundant species by the left most portion of its regression line. To minimize the visual effect of extreme values, the beginning of the second quartile of individuals and the end of the third quartile were marked with brackets on the regression lines. These quartiles refer to the number of individuals, of that cohort, collected during the respective field season.

RESULTS

Spiders as a group

Specimens collected. This study includes 3025 spiders, representing 12 families, 35 genera and 45 species (Table 2). These species expressed a broad tolerance for a variety of architecture. This was exhibited by the fact that no structural configuration type had fewer than 33 nor more than 40 species. No abundant species was missing from any unit type. More than 50 individuals were collected for only 8 species (Table 3). These 8 species constituted 71% of the total number of individuals collected. The next 8 species amounted to less than 10% of the individuals. Two each of the most abundant 8 species had been assigned to each of the four major hunting guilds prior to experimentation (Table 3).

Colonization data. Colonization data (Table 4) were obtained for four structural types (V2, H22, 444, 222). While it is obvious that those cubes left in the field longest had greater numbers of individuals and species, there was no apparent asymptote in these values. In fact, a 22 module which was lost from sampling, due to vandalism, for 71 days before being located was found to have 11 individuals. These were significantly more individuals than would be found due to chance in modules left in the field for 16 days or less ($P = 0.037$).

Differential use of modules. In aggregate, spiders responded differentially to the structural types provided for them. This differential use was statistically significant when analyzed

Table 2. List of spider species collected in Green Canyon
during this study

Argiopidae

      Aculateira packardi (Thorell)

      Araneus gemma (McCook)

      Argiope trifasciata (Forskal)

      Hyposinga singaeformis (Scheffer)

      Metepeira foxi Gertsch and Ivie

Clubionidae

      Castianeira sp.

      Chiracanthium inclusum (Hentz)

Dictynidae

      Dictyna idahoana Chamberlin and Ivie

      Dictyna completa Chamberlin and Gertsch

Gnaphosidae

      Drassodes saccatus (Emerton)

      Herphyllus sp.

Linyphiidae

      Erigoninae (Unidentifiable)

      Frontinella communis (Hentz)

      Meioneta sp.

      Spirembolus mundus Chamberlin and Ivie

Lycosidae

      Schizocosa sp.

Mimetidae

      Mimetus aktius Chamberlin and Ivie

Oxyopidae

      Oxyopes scalaris (Hentz)

Salticidae

      Metaphidippus aeneolus (Curtis)

      Metaphidippus helenae Chamberlin

      Metaphidippus verecundus (Chamberlin and Gertsch)

Table 2. Continued

Salticidae (Continued)

Pellenes hirsutus (Peckham and Peckham)

Phidippus johnsoni (Peckham and Peckham)

Sassacus papenhoei (Peckham and Peckham)

Synageles sp.

Tetragnathidae

Tetragnatha laboriosa

Theridiidae

Dipoena tibialis Banks

Euryopsis scriptipes Banks

Enoplognatha ovata (Clerk)

Lactrodectus hesperus Chamberlin and Ivie

Steatoda americana (Emerton)

Theridion neomexicanum Banks

Theridion petraeum L. Koch

Theridion rabuni Chamberlin and Ivie

Thomisidae

Misumeninae

Misumenops asperatus (Hentz)

Misumenops lepidus (Thorell)

Xysticus cunctator (Thorell)

Xysticus gulosus Keyserling

Xysticus montanensis Keyserling

Philodrominae

Ebo evansae Sauer and Platnick

Philodromas californicus Keyserling

Philodromas histrio (Latreille)

Thanatus formicinus (Clerk)

Tibellus chamberlini Gertsch

Tibellus oblongus (Walckender)

Table 3. Relative abundances and hunting strategies of the

eight most abundant species collected

Species	% of total individuals captured	Hunting Strategy
Theridion neomexicanum	28.10	web-builder
Misumenops lepidus	9.79	ambusher
Theridion petraeum	7.87	web-builder
Sassacus papenhoei	7.44	jumper
Thanatus formicinus	7.40	pursuer
Pellenes hirsutus	5.09	jumper
Xysticus montanensis	3.07	ambusher
Oxyopes scalaris	2.12	pursuer

Table 4. Colonization data regarding architectural types V2, 444, H22, and 222 based on the number of consecutive days the modules were left in the field

Type of Structure

Days out	V2			444			H22			222		
	Samp. size	Mean ind./ sample	Mean spp./ sample	Samp. size	Mean ind./ sample	Mean spp./ sample	Samp. size	Mean ind./ sample	Mean spp./ sample	Samp. size	Mean ind./ sample	Mean spp./ sample
1	10	1.38	1.00	9	2.00	2.00	10	1.50	1.20	9	1.00	1.29
2	9	1.22	0.82	7	1.67	1.14	9	2.00	1.67	7	2.43	1.57
4	11	0.83	1.20	10	1.56	1.33	11	2.42	1.83	10	2.18	2.00
8	54	1.35	1.11	55	2.36	1.78	54	1.64	1.20	55	3.30	1.93
14	120	2.31	1.57	54	2.16	1.50	120	4.05	2.20	54	5.15	2.78
16	42	2.47	1.63	28	3.07	2.31	42	5.22	2.39	28	5.73	3.40

on the basis of the total number of individuals per random couplet of identical units (Table 5). A Duncan multiple-range test applied to these data indicated that the mean number of individuals in V2 was not significantly different than the mean number in H2, but both means were significantly less than the mean number in any other structural type. There was no significant difference between 444 and H22; 444 was significantly less than V22 and all cubes had significantly lower means than 222. Finally, V22 and H22 were not significantly different.

Analysis of species richness variation in this randomized complete block experiment indicated that there was a statistically significant difference between different structural types (Table 6). The Duncan multiple range test indicated that architecture type 222 had significantly more species using it at any given time than any other type configuration. All other configurations showed no significant difference in species richness from each other.

Abundant species

Effect of horizontal vs vertical substrata. Comparisons made on the eight most abundant species for their preference of horizontal or vertical substrata suggest that Xysticus montanensis prefers horizontal strands of jute over vertical strands, as does Theridion neomexicanum (as demonstrated by the higher frequency of its collection on H2 than V2) (Table 7). Pellenes hirsutus prefers vertical strands to horizontal strands (cf., H22 and V22). The

Table 5. Results of one-way ANOVA testing the null hypothesis
that spider individuals use random couplets of the
same architecture with equal probability independent
of architecture

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-Ratio
Treatment	5	195.27	39.05	4.82[*]
Error	102	826.83	8.11	
Total	107	1022.10		

[*]Reject null hypothesis at $\alpha = 0.001$

Table 6. Results of one-way ANOVA testing the null hypothesis that
spider species richness in random couplets of the same
architecture is independent of architecture

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-Ratio
Treatments	5	103.18	20.63	4.76[*]
Error	102	442.33	4.33	
Total	107			

[*]Reject null hypothesis at $\alpha = 0.001$

Table 7. Probabilities that the number of individuals of the eight abundant spider species found in unit A are ≥ the numbers in unit B. A and B are defined in the table.

Species	Structures Compared	
	A=H2, B=V2	A=H22, B=V22
Sassacus papenhoei	0.3063	0.5993
Pellenes hirsutus	0.7282	0.9579
Misumenops lepidus	0.6563	0.6108
Xysticus montanensis	0.0313	0.0234
Thanatus formicinus	0.6865	0.5433
Oxyopes scalaris	0.3770	0.6531
Theridion neomexicanum	0.3982	0.8948
Theridion petraeum	0.0081	0.1817

statistical significance of these findings is a moot point because of the necessity of making pairwise comparisons instead of multi-sample comparisons.

The results obtained from the above pairwise comparisons were analyzed with a Kruskal-Wallis test to determine if the abundant species were segregated from each other by differential use of horizontal and vertical substrata (Table 8). This test indicated no statistical separation at $\alpha = 0.05$.

Effect of open vs dense nodules. The four architectural types (444, ||2, |22 and 222) were compared, pairwise, for use by the eight most abundant species (Table 9). All probabilities were arranged so that low numbers reflect a species bias for structures with an open aspect. Once again, the statistical significance is debatable due to the number of pairwise comparisons made. It must be emphasized that these results were obtained under the assumption that nodules should all be used with equal probability, regardless of their amount of jute. It was demonstrated earlier that spiders respond to the amount of jute (Table 5). Since 444 and ||2 are the only nodules with approximately equal amounts of jute (Table 1), comparisons between them are the only ones unaffected by the amount of jute.

The results in Table 9 were treated as data for a Kruskal-Wallis test to determine if the eight most abundant spider species used open architectural configurations (444) differently than more closed configurations (||2, |22, 222). This test demonstrated a significant difference in their use (Table 10). Only 3 pairs were

Table 8. Ranks of the probabilities that the number of individuals of the eight most common spider species found in unit A are $\geq$ the number of individuals in unit B due to chance. A and B are defined in the table for each row.

	Species							
Structural Comparison	Sassacus papenhoei	Pellenes hirsutus	Misumenops lepidus	Xysticus montanensis	Thanatus formicinus	Oxyopes scalaris	Theridion neomexicanum	Theridion petraeum
A=H2, B=V2	12	3	5	14	4	11	10	16
A=H22, B=V22	8	1	7	15	9	6	2	13

Kruskal-Wallis H = 11.74[*]

*P(H $\geq$ 11.74) = 0.109

Table 9. Probabilities that the number of individuals of the eight most abundant spider species found in structure A are ≥ the numbers in structure B due to chance. A and B are defined in the table column headings.

Species	Structures compared					
	A=444 B=∥2	A=444 B=⌊22	A=444 B=222	A=∥2 B=⌊22	A=∥2 B=222	A=⌊22 B=222
Sassacus papenhoei	0.00211	0.83299	0.89332	0.99999	0.99998	0.70941
Pellenes hirsutus	0.02043	0.12829	0.83925	0.81994	0.99832	0.99103
Misumenops lepidus	0.10655	0.91034	0.79121	0.99843	0.98026	0.40860
Xysticus montanensis	0.00102	0.83132	0.99999	0.99999	0.99999	0.99999
Thanatus formicinus	0.02821	0.88082	0.99958	0.99987	0.99999	0.99754
Oxyopes scalaris	0.24567	0.18600	0.93167	0.28500	0.98620	0.99741
Theridion neomexicanum	0.08398	0.99999	0.99999	0.99999	0.99999	0.98626
Theridion petraeum	0.31671	0.99999	0.99963	0.99999	0.99999	0.30251

Table 10. Ranks of the probabilities that the number of individuals of the eight most common spider species found in unit A are $\geq$ the numbers in unit B due to chance. A and B are defined in the table for each row.

	Species							
Structural comparison	Sassacus papenhoei	Pellenes hirsutus	Misumenops lepidus	Xysticus montanensis	Thanatus formicinus	Oxyopes scalaris	Theridion neomexicanum	Theridion petraeum
A=444, B=∥2	9	11	14	4	6	7	3	5
A=444, B=⌊22	12	18	8	13	10	17	1	2
A=444, B=222	23	22	19	24	21	16	20	15

Kruskal-Wallis $H = 82.12^{*}$

*Significant at $\alpha = 0.01$

tested, so that the requirement of the Kruskal-Wallis test for independent samples was fulfilled. Since there were no tied observations for this test, it was felt that recording more than five decimal places (Table 9) was unwise.

The same four structural types (444, ‖2, ⌊22, 222) were compared pairwise for use by the spider dominants (Table 11). This time it was assumed that each centimeter of jute had an equal probability of being occupied by spider individuals. Low numbers (Table 11) indicate a preference for an open structure. The statistical significance of these numbers is equivocal, as described previously. These numbers, with the probable exception of the 444 vs ‖2 comparison, are likely to appear low because each cube, being of similar volume, is probably impinged upon by spiders at the same rate, hence cubes with more jute will take longer to reach saturation. Since none of these cubes remained in the field longer than 16 days, all had their normal colonization truncated. This truncation would be more evident in those cubes further from saturation.

The results from Table 11 were used as data in a Kruskal-Wallis test to examine whether the abundant species of spiders segregated their use of substrata (jute) simply because of its positioning and the positioning of surrounding architecture. This test was performed for pairwise comparisons of 444 with ‖2, ⌊22 and 222. The result indicates that these spiders do partition architecture in this manner (Table 12).

Table 11. Probabilities that the number of individuals of the eight most abundant spider species found per centimeter of macrame jute in structure A are $\geq$ the numbers in structure B due to chance. A and B are defined in the table column headings.

Species	Structures compared					
	A=444 B=‖2	A=444 B=⌊22	A=444 D=222	A=‖2 D=⌊22	A=‖2 B=222	A=⌊22 B=222
Sassacus papenhoei	0.00986	0.01094	0.00024	0.67714	0.12172	0.03526
Pellenes hirsutus	0.06403	0.00013	0.00102	0.01046	0.04428	0.71950
Misumenops lepidus	0.24500	0.01105	0.00002	0.03140	0.00002	0.00351
Xysticus montanensis	0.00672	0.18877	0.82818	0.99404	0.99999	0.99712
Thanatus formicinus	0.08344	0.03717	0.07679	0.41448	0.55162	0.67565
Oxyopes scalaris	0.44902	0.00893	0.12027	0.00054	0.13152	0.95176
Theridion neomexicanum	0.97094	0.48950	0.05233	0.02350	0.00000	0.01147
Theridion petraeum	0.41960	0.91046	0.21351	0.96408	0.17215	0.00141

Table 12. Ranks of the probabilities that the number of individuals of the eight most common spider species found per centimeter of macrame jute in unit A are $\geq$ the numbers in unit B due to chance. A and B are defined in the table for each row.

Structural	Species							
	Sassacus papenhoei	Pellenes hirsutus	Misumenops lepidus	Xysticus montanensis	Thanatus formicinus	Oxyopes scalaris	Theridion neomexicanum	Theridion petracum
A=444, B=‖2	21	23	24	3	12	10	14	8
A=444, B=│22	17	22	16	9	15	19	4	2
A=444, B=222	18	13	7	20	11	5	1	6

Kruskal-Wallis H = 97.45[x]

[x]Significant at α = 0.01

Additional experiments

Effect of the exposed surface area of module. The experiment designed to evaluate the effect of module surface area on spiders (Fig. 4) yielded 348 individuals from clumped units and 347 individuals from solitary units. The closeness of these numbers reinforces the null hypothesis that spiders do not respond to changes in exposed module structural surface area (i.e., number of module sides that are in contact with the surrounding air space).

Effect of total jute removal. When a juteless chicken wire cube was sampled ten times only three spiders were obtained. This suggests that spiders may use the wire part of these cubes, but this is infrequent and in numbers such that they do not affect the results of these experiments.

Comparisons of seasonal
collection abundances

The total numbers of each of the abundant species collected during ten day intervals were plotted against date for each of the two field seasons. For comparative purposes, each pair of species having the same hunting strategy was plotted on the same graph. The two jumping species, Sassacus papenhoei and Pellenes hirsutus, overlap each other seasonally, each occurring in all seasons (i.e., are seasonal generalists) (Fig. 5a and b). The two ambusher species, Misumenops lepidus and Xysticus montanensis, may subdivide the field season with Misumenops active early and late, and Xysticus active more toward mid-season (Fig. 6a and b). The pursuers, Thanatus formicinus and Oxyopes scalaris, are apparent

Figure 5. Numbers of individuals of the two dominant jumping
species collected per ten day interval plotted against
date for 1976 and 1977

Figure 6.   Numbers of individuals of the two dominant ambushing
            species collected per ten day interval plotted against
            date for 1976 and 1977

seasonal generalists with considerable overlap (Fig. 7a and b).
The web-builders, Theridion neomexicanum and T. petraeum, are
apparently separated seasonally; T. neomexicanum is active early
and late in the season, T. petraeum is active in the middle of the
season (Fig. 8a and b).

Body lengths

Actual measurements. Body lengths of individuals collected
were plotted against date for each of the abundant species. Indi-
viduals were assigned to the present year's cohort or the past
year's cohort as described in the methods section. Body length
information for species of the same hunting guild were plotted on
the same page (Figs. 9 - 12).

Nominal body lengths. Regression lines representing the
nominal body lengths of these abundant species were developed and
plotted for each cohort in each field season (Figs. 13 - 15). The
first order linear regressions were used as heuristic vehicles
for comparative purposes without substantial theoretical basis for
their use. The values obtained from these regressions do not
represent true estimates for individual nor population body lengths
at different ages, but they are indicative of the size of organisms
collected on different dates; hence these body lengths are best
referred to as nominal. For those species belonging to the same
hunting guilds, the minimum ratios separating the pairs were tabulated
(Table 13). The larger of the two species emerged first as juveniles
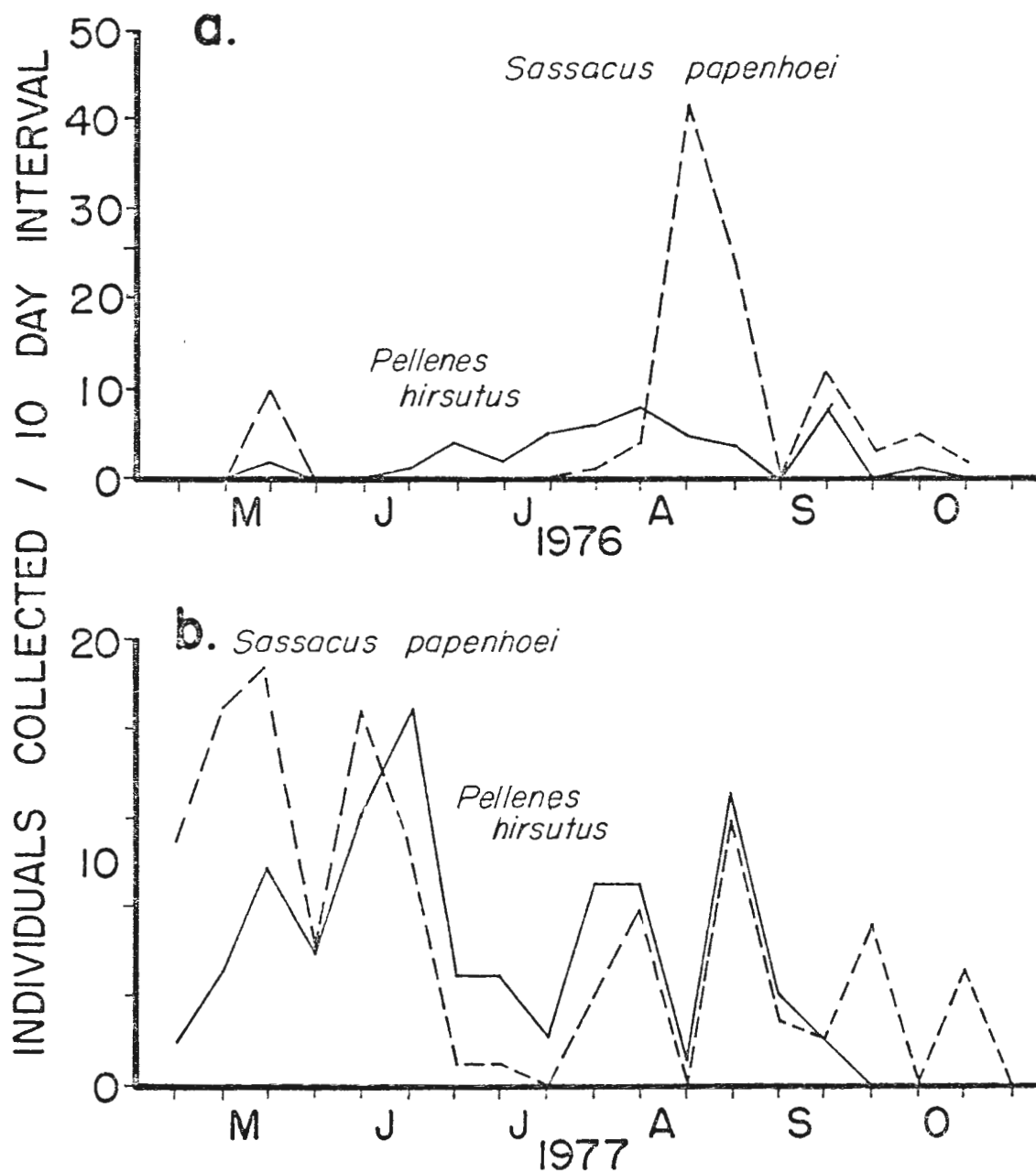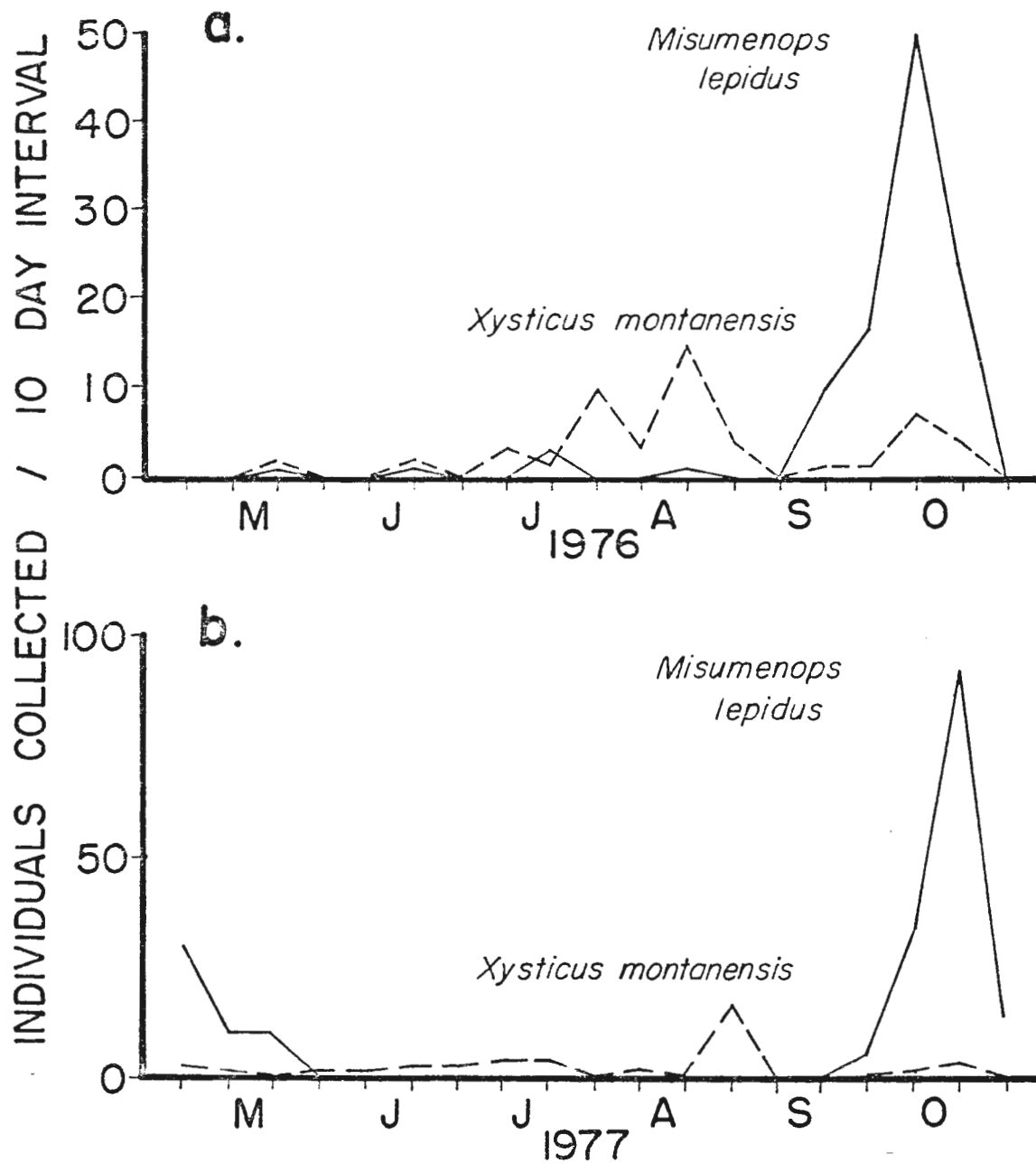in each of the two field seasons for all four species pairs. This
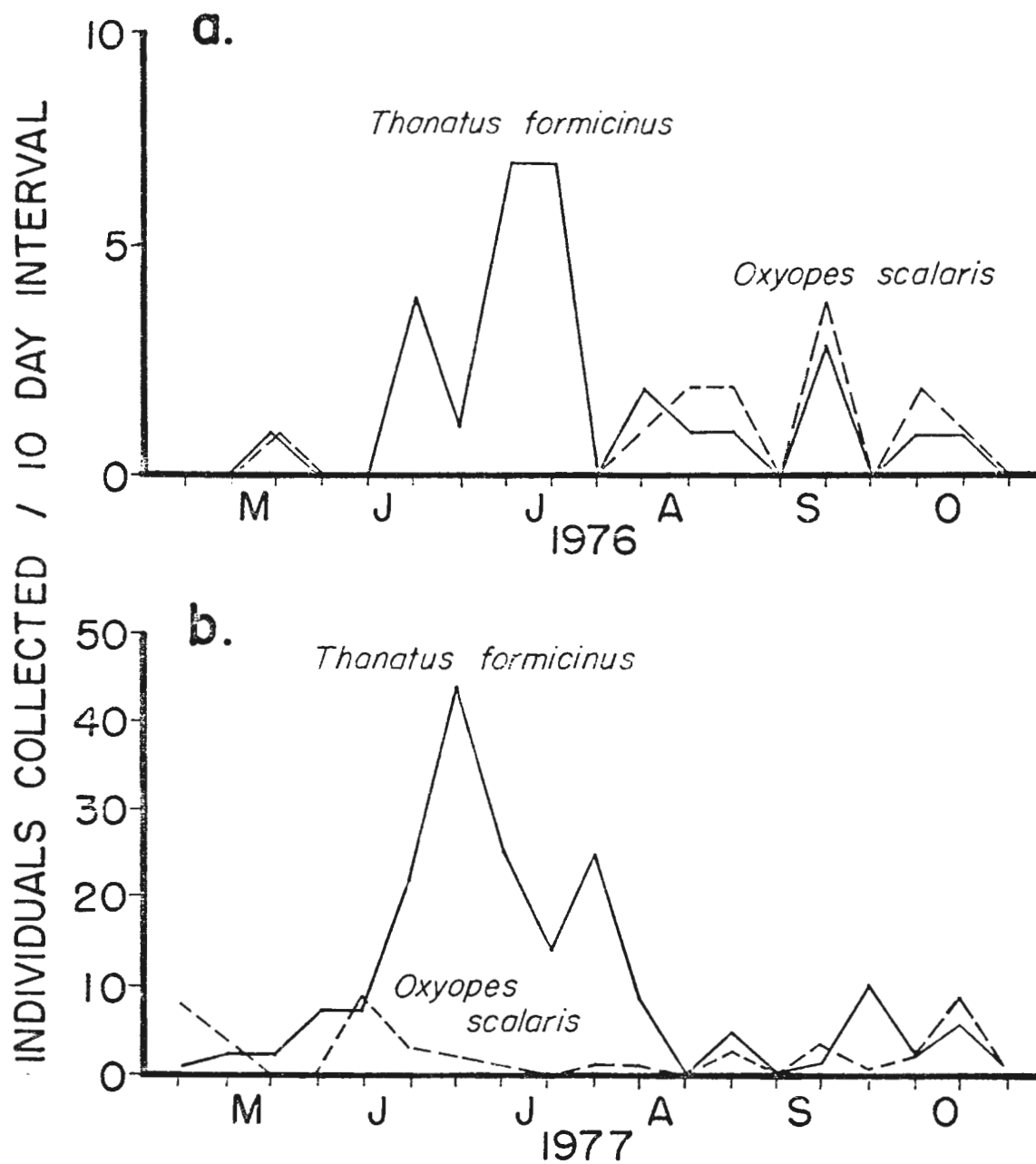
Figure 7. Numbers of individuals of the two dominant pursuing
species collected per ten day interval plotted against
date for 1976 and 1977
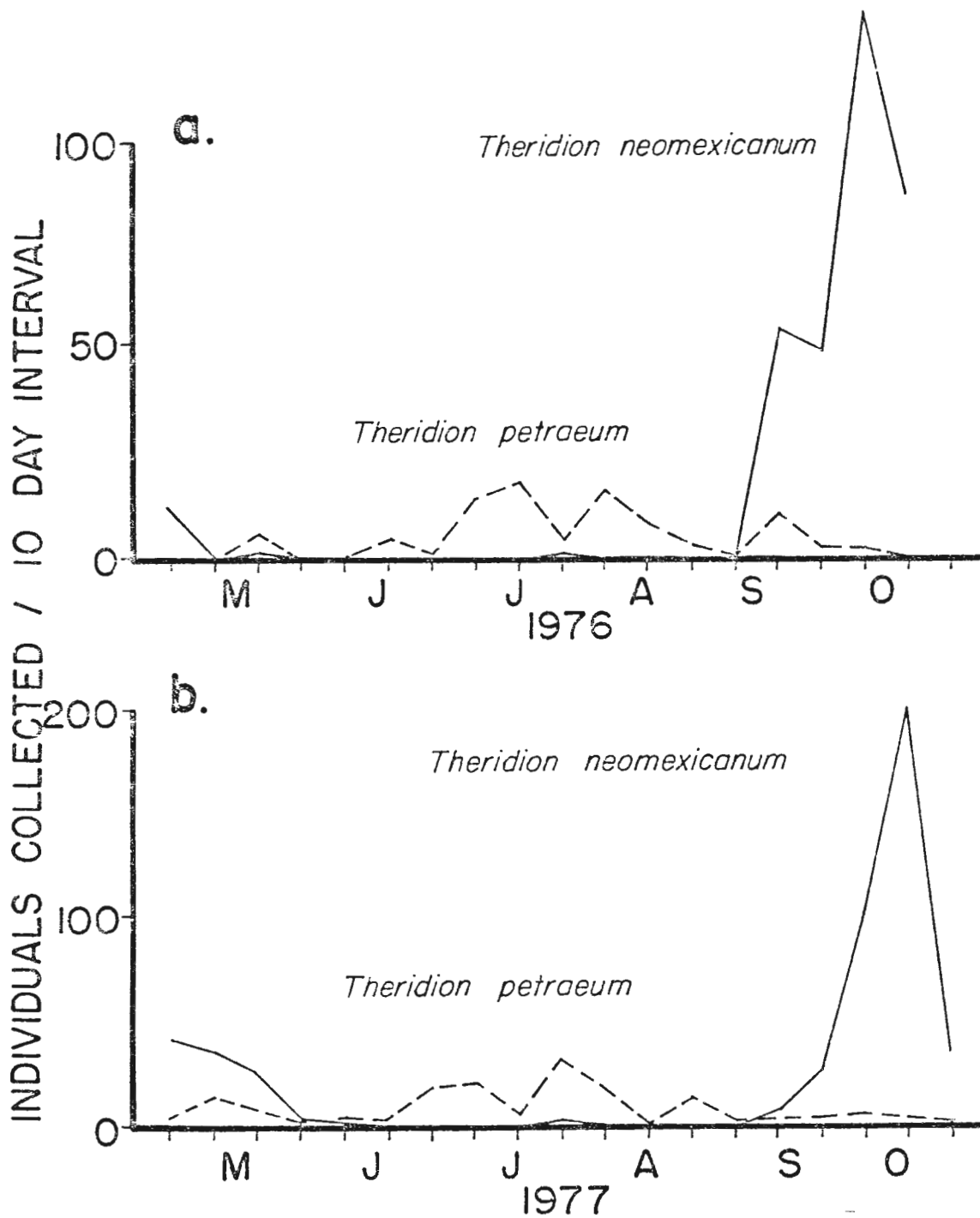
Figure 8.   Numbers of individuals of the two dominant web-building species collected per ten day interval plotted against date for 1976 and 1977
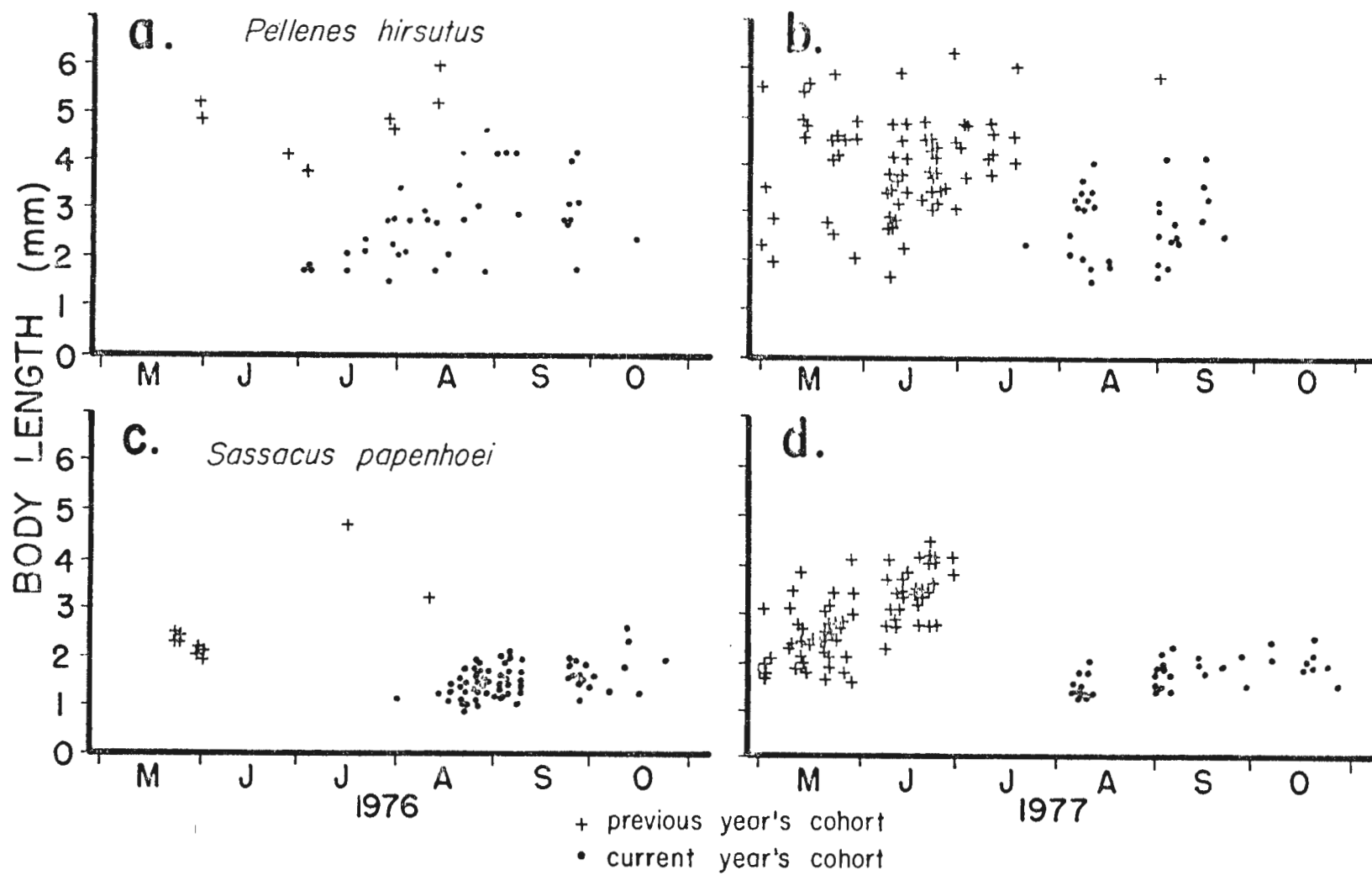
Figure 9. Body length measurements of the two most abundant jumping species collected during 1976 and 1977, for each sampling date
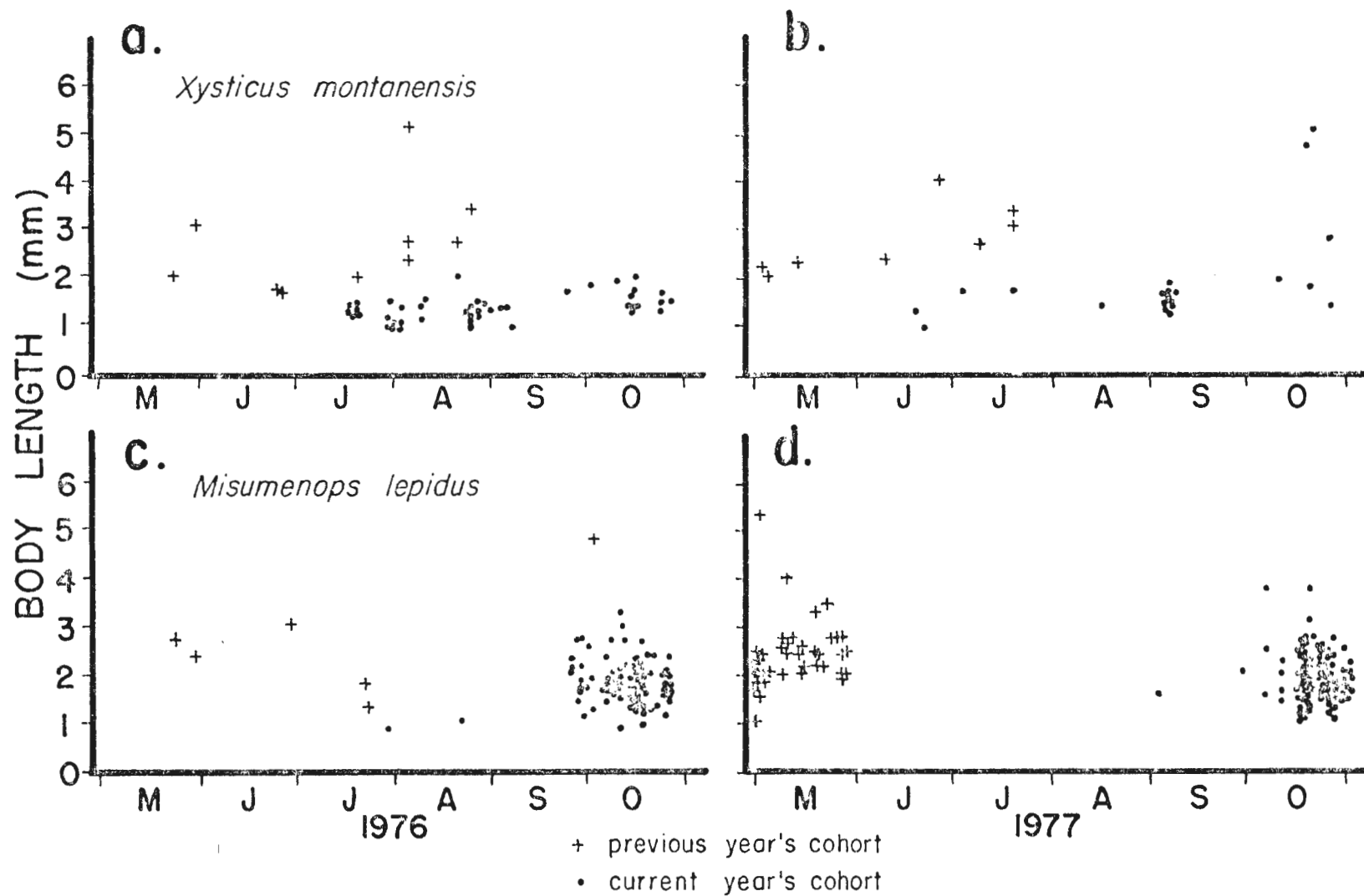
Figure 10. Body length measurements of the two most abundant ambushing species collected during 1976 and 1977, for each sampling date
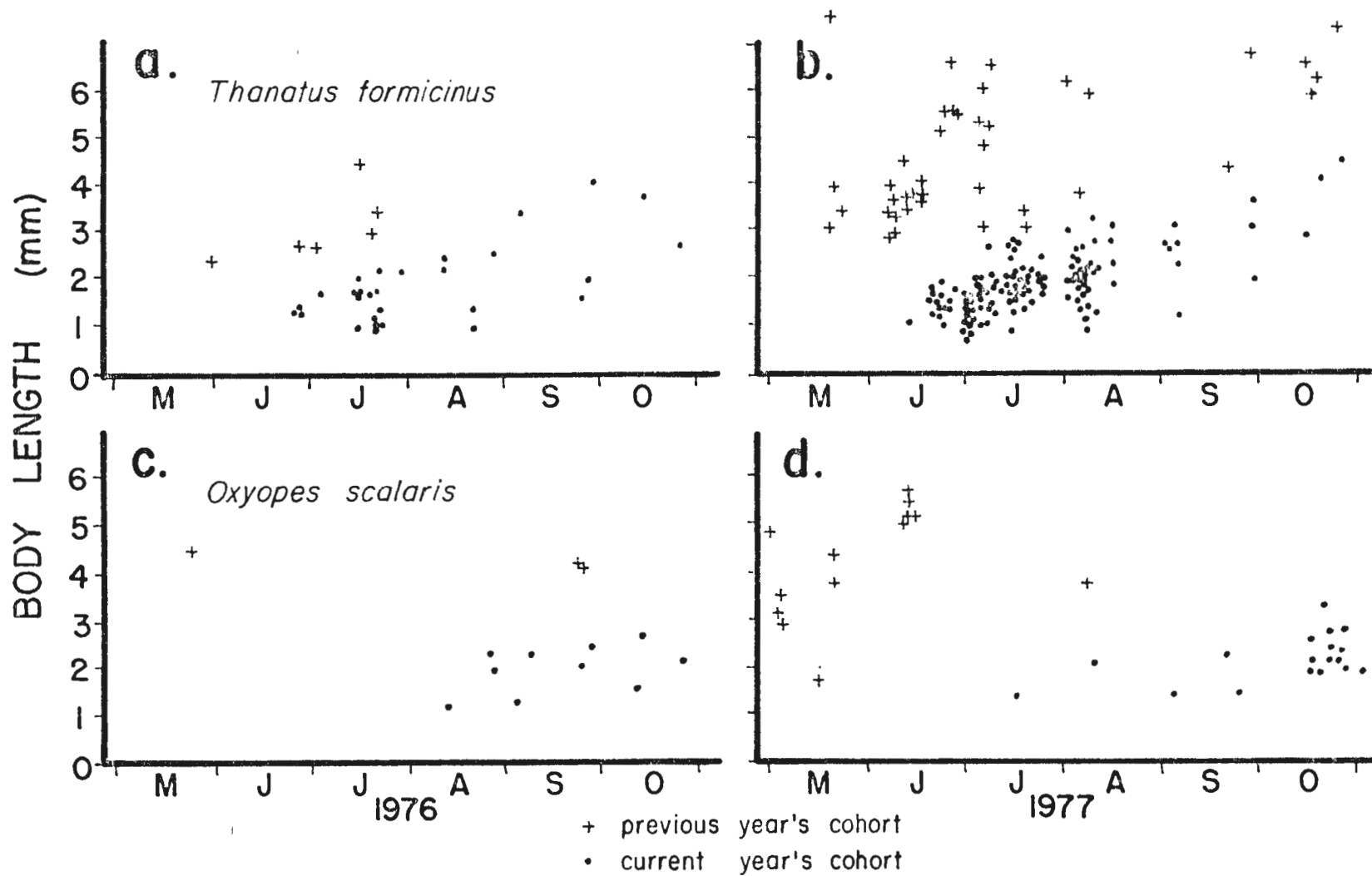
Figure 11. Body length measurements of the two most abundant pursuing species collected during 1976 and 1977, for each sampling date
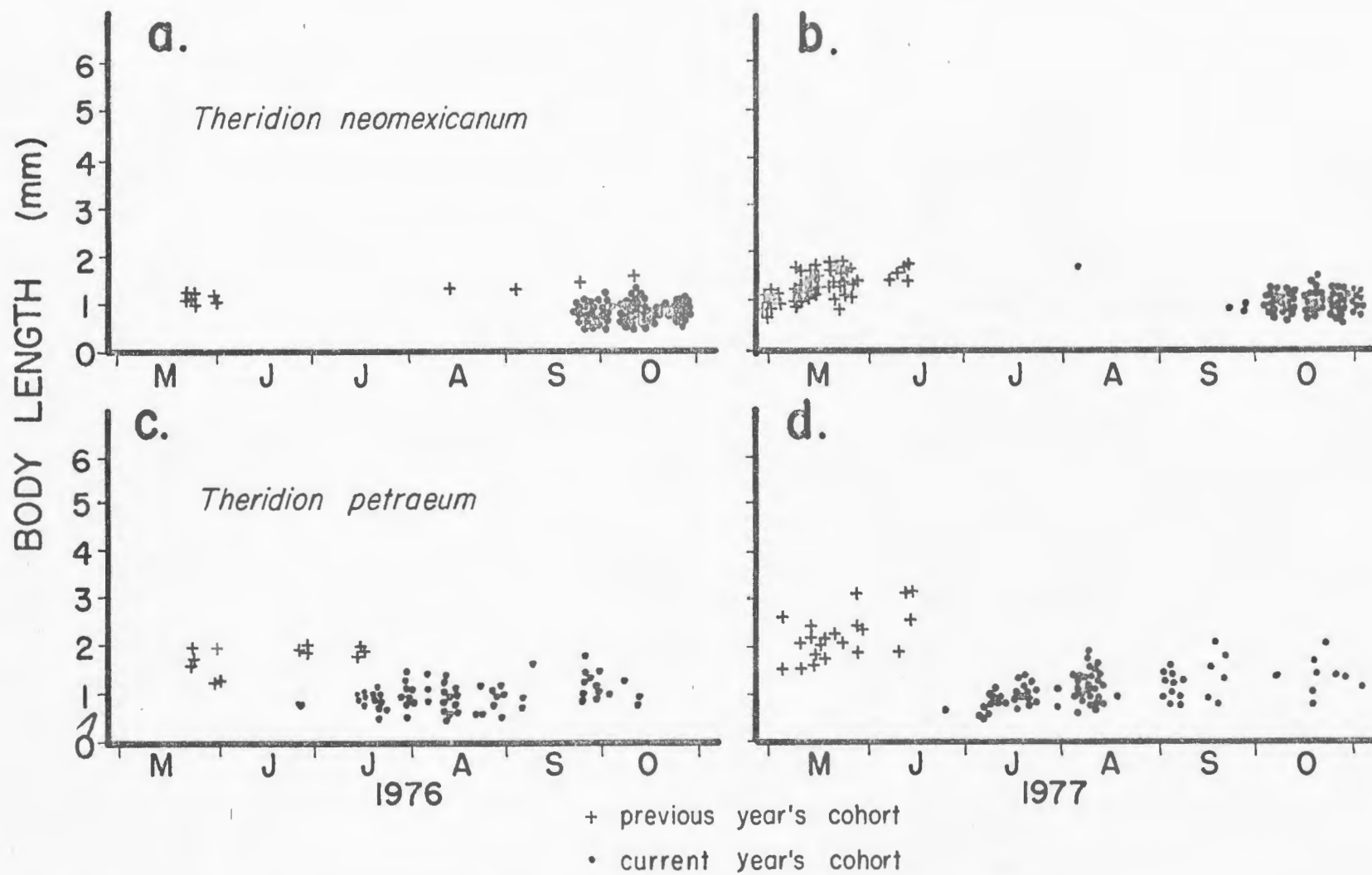
Figure 12. Body length measurements of the two most abundant web-building species collected during 1976 and 1977, for each sampling date
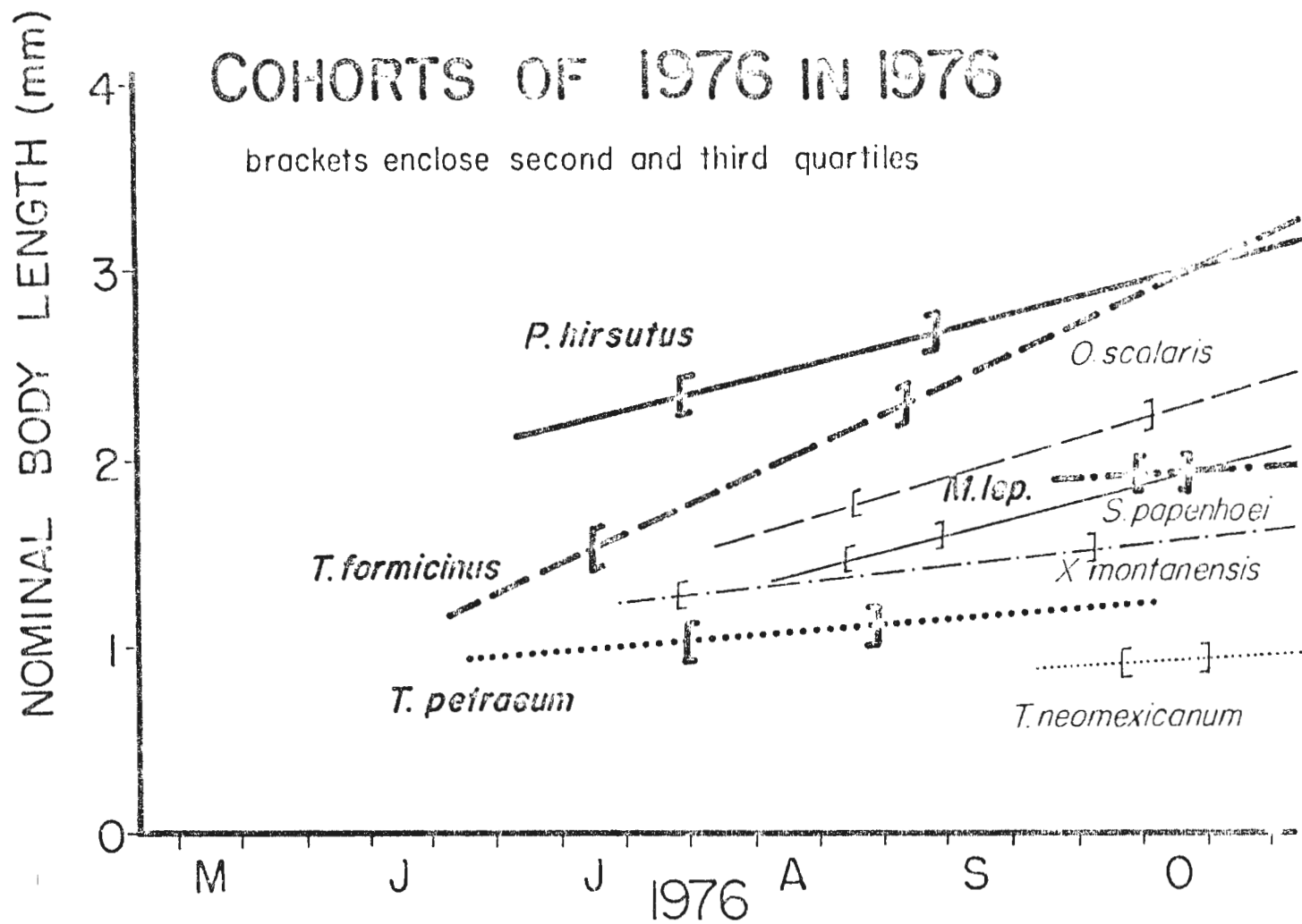
Figure 13. Nominal body lengths of the 1976 cohorts of the eight most abundant spider species during the 1976 field season
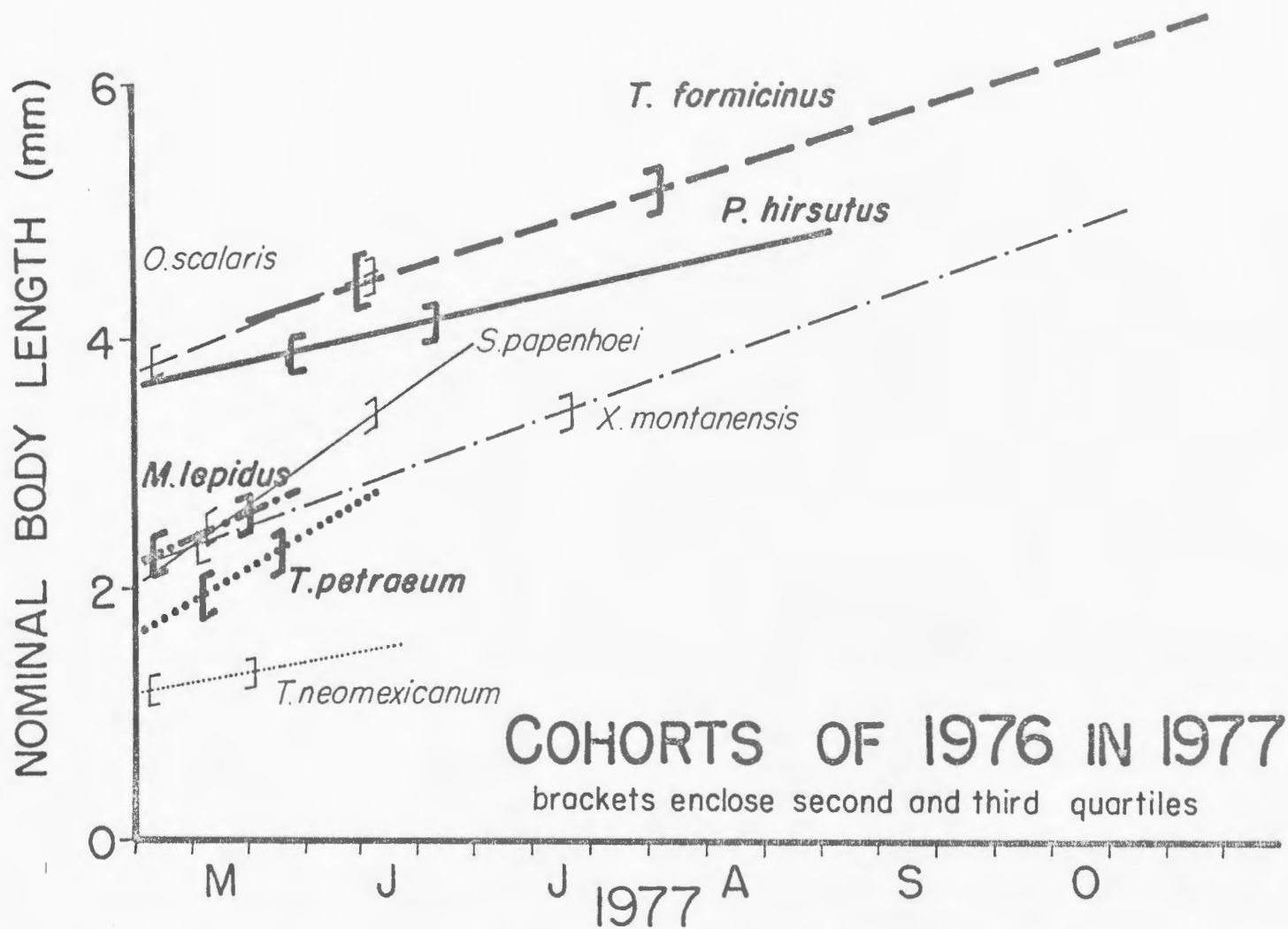
Figure 14. Nominal body lengths of the 1976 cohorts of the eight most abundant spider species during the 1977 field season

COHORTS OF 1977 IN 1977

brackets enclose second and third quartiles

P. hirsutus

O. scalaris

S. pap.

T. formicinus

M. lon

X. montanensis

T. neomexicanum

T. petraeum

NOMINAL BODY LENGTH (mm)

M   J   J   1977   A   S   O
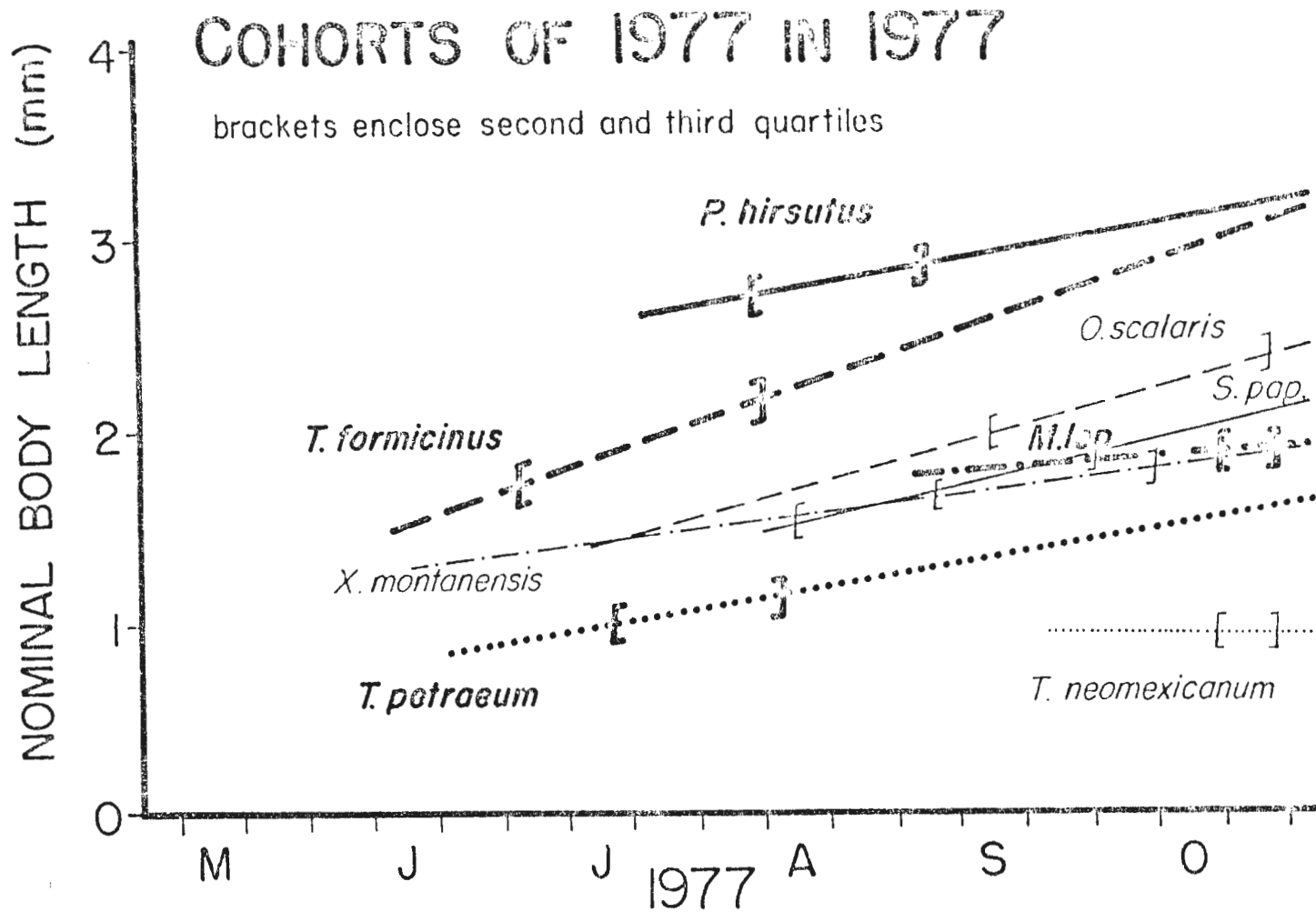
Figure 15.   Nominal body lengths of the 1977 cohorts of the eight most abundant spider species during the 1977 field season

Table 13. Minimum ratios obtained between the nominal body lengths of species cohorts of each hunting guild

Guilds		Ratio for cohorts of		
Larger species as adult	Smaller species as adult	1976 in 1976	1976 in 1977	1977 in 1977
web-builders				
Theridion petraeum[a]	T. neomexicanum	1.35	1.41	1.44[b]
ambushers				
Xysticus montanensis[a]	Misumenops lepidus	1.22[b,c]	1.00	1.00[b]
jumpers				
Pellenes hirsutus[a]	Sassacus papenhoei	1.81	1.18	1.51
pursuers				
Thanatus foricinus[a]	Oxyopes scalaris	1.25[b]	1.00[b]	1.32

[a] Juveniles emerging first in both 1976 and 1977 as measured both by extreme earliest capture and completion of the capturing of the first quartile collected each field season.

[b] At least one of the regressions employed in these comparisons did not have a slope significantly different from zero at the 95% confidence level.

[c] This cohort of X. montanensis had a lower nominal body length than M. lepidus during this field season.

was consistent whether the date of emergence measurement was
based on the earliest capture or on that species which had
the first quartile of its individuals, within that year's cohort,
collected first.

Seasonal comparison of the total
numbers of insects and spiders

The number of insects collected was plotted for each sampling
date (Fig. 16a and b). Since all of the units sampled on any date
were in close proximity, these values should serve as a reasonable
index of prey availability in both a spatial and temporal sense.
Superimposed on these graphs is the number of spiders collected on
each date. Linear correlations were made between the numbers of
insects and the numbers of spiders. The coefficient of determination
(R^2) in 1976 was 0.011 and was not statistically significant at the
95% confidence level, while in 1977, $R^2 = 0.077$ and was statis-
tically significant at the 95% level.
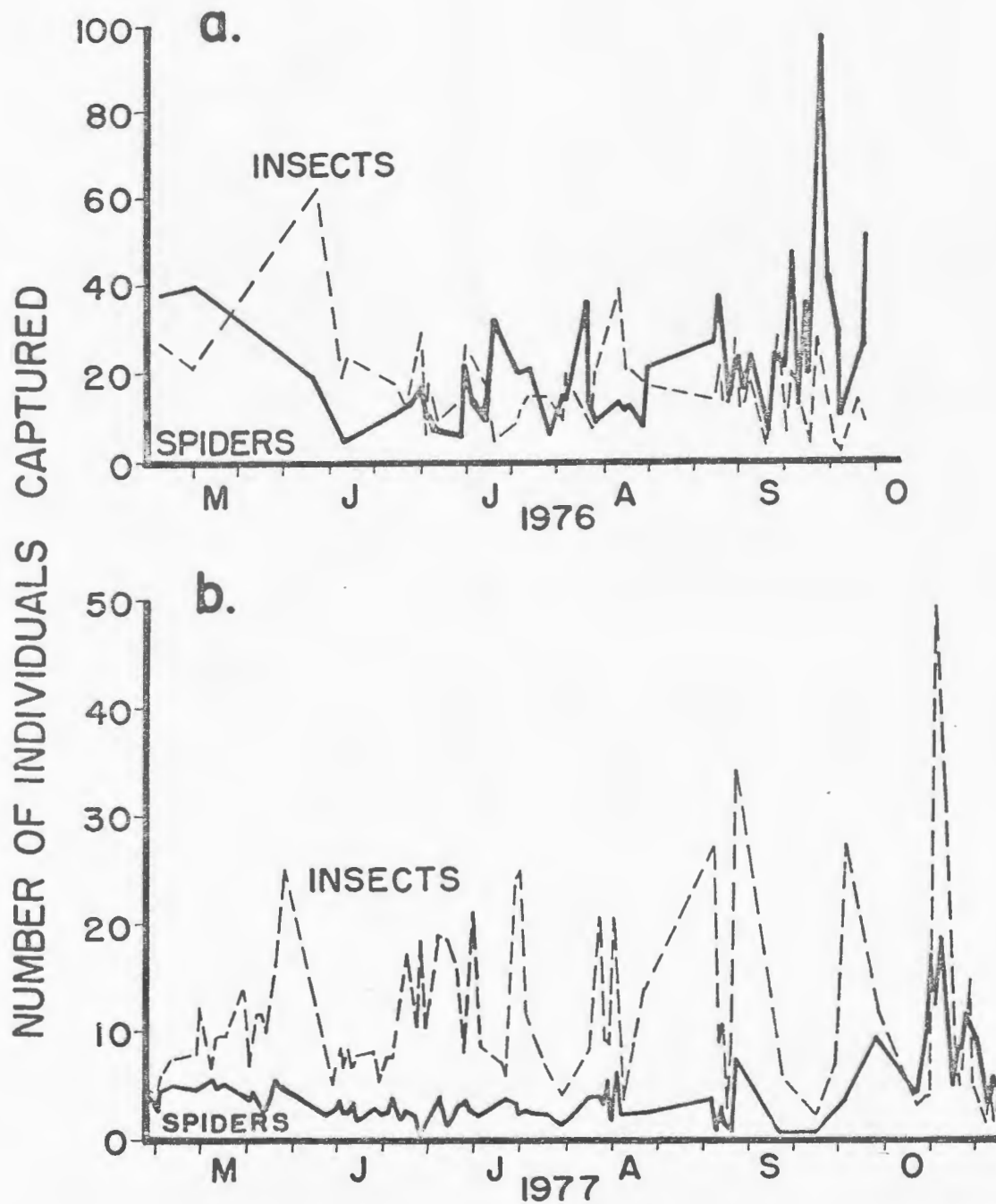
Figure 16. Total number of insects and total number of spiders collected for each sampling date during the 1976 and 1977 field seasons

DISCUSSION

Generalized patterns for
spiders as a group

Observed module patterns. Both the number of spider individ-
uals and the number of species showed strong tendencies to vary
with the amount of available jute (Tables 4, 5, 6 and 9). A plethora
of reports indicate analogous species-area relationships for other
taxa (Brown 1971, Preston 1962, Terborgh 1974). The significantly
greater number of individuals found on 444 modules versus V2 or
H2 modules, which all had approximately the same amount of jute,
suggests that fine grained habitat variations are important to
spiders. Similar conclusions were reached concerning habitat factors
influencing species richness values in other taxa (Lack 1973, Mac-
Arthur and MacArthur 1961, Pianka 1967, Power 1972). The preference
displayed by spiders in general to the 444 modules may be attributed
to either the greater openness of these modules or their three
dimensional complexity. If complexity per se is the primary factor,
V22 modules should contain more individuals than H22 modules because
V22 contains both vertical and horizontal habitat, not just horizon-
tal. Since they did not, I consider the differences observed assign-
able to the openness of the 444 modules.

The results also suggest that spider use of cubes is unaffected
by the addition of adjacent modules (Fig. 4). Therefore, I conclude
that within the size range tested, module volume is insignificant
as a controlling factor of spider distribution.

A model. Assuming that spiders react similarly to vegetational architecture, the deduction is made that the amount of branch and leaf surface area of a shrub is probably the best correlate with spider abundance on that shrub. Since it is inpractical to obtain these surface areas for such correlations, an estimate of shrub mass might suffice (this would require an assumption regarding the relationship between surface area and mass). Because openness was significant, shrub foliage density estimates, based on optical measurements (Hatley 1973, MacArthur and MacArthur 1961), also belong in a predictive model of spider abundance on shrubs. A generalized model of the form

$$S = A \cdot f(m) - \sum B \cdot f(d_i) \qquad (1)$$

$$\text{all } i$$
$$\text{where}$$
$$d_i \neq 0$$

is proposed, where A and B are positive constants, $f(m)$ is some function of mass, $f(d_i)$ is a function of the density in volume i, and S is the expected number of spider individuals. The mathematical forms of these functions must be determined through further experimentation.

Statistical interpretations

Difficulties associated with pairwise comparisons. The need to make pairwise comparisons of differential architectural use by each abundant species makes the interpretation of results difficult. One may consider each pairwise comparison as a distinct experiment.

This approach is useful in exploratory research, such as this, because the power of the statistical test is unaffected by the number of experiments. Hence, differences in architectural use, potentially significant at the 95° confidence level, will show probabilities of greater than 0.975 or less than 0.025 in Tables 7, 9 and 11. An alternative method is to approximate a multi-sample test by applying the Bonferroni method to the series of pairwise comparisons. This method insures that the null hypothesis is not rejected more frequently than $100\alpha\%$ (α = rejection level) of the time due to chance, regardless of how many pairwise comparisons are made. When the number of pairwise comparisons is large it does this by making a significant sacrifice in statistical power (i.e., the probability of accepting the null hypothesis is considerably greater than $(1 - \alpha)$) (Feller 1968, Miller 1966). If this method were chosen, only those probabilities under 0.00022 or over 0.99973 in Tables 7, 9 and 11 can be rejected with 95° confidence. A third method, consistency, may also prove to be a useful heuristic tool for evaluating these results. The fact that Xysticus montanensis was consistently found on horizontal structures much more often than on vertical structures provides a reasonable basis for assuming that it prefers horizontal habitat (Table 7).

Species segregation. The above discussion of methods focused on distinguishing whether an individual species chose one habitat type over another in a significant manner. This may be important in a population study of that species. What is perhaps

more important in a community study is determination of species separations based on their architecture choices. Results of the Kruskal-Wallis test provided this information (Tables 8, 10, and 12).

Coexistence of the abundant species

I assume that the primary method of species separation among the spider community of Green Canyon is the result of alternative hunting strategies. The following is my interpretation of the pertinent results of the architectural experiments under a general discussion of the four hunting guilds.

Jumping spiders. These spiders are all confined to the single family Salticidae (Child 1965). Kaston stated that the Salticidae have the keenest vision of all spiders and that:

> They make use of the visual sense to hunt their prey in broad daylight, and are common in sunny areas. In stalking prey they approach the latter slowly until within a centimeter or two, then make a sudden quick jump. (Kaston 1948, p. 442)

The two abundant jumping spiders appear to be seasonal generalists. The less common of the two, Pellenes hirsutus, was larger, almost always by a ratio exceeding 1.28 (Figs. 13 - 15) and emerged earlier in the season as juveniles during both field seasons than Sassacus papenhoei. Pellenes showed a tendency toward vertical substrata (Table 7). Although this was consistent, it was not statistically significant. Both Pellenes and Sassacus showed marked preferences for open vs closed architectural configurations (see 444 vs ‖2 comparison in Table 9 and the series of 444 comparisons in Table 11).

I conclude that, in Green Canyon, jumping spiders as a guild prefer open habitat. This provides support for the similar results obtained by Hatley (1978). This is reasonable because these species rely on vision for hunting, thus an open habitat is optimal.

Ambushing spiders. The two species of ambushing spiders were Xysticus montanensis and the smaller Misumenops lepidus. X. montanensis emerged earliest seasonally as a juvenile. There was no clear evidence from the individuals collected that Xysticus displayed any size sexual dimorphism. The adult females of Misumenops were obviously larger than the males. This observation, made in the field, has not been quantified, but is consistent with published data on congeneric species (Kaston 1948). The overwhelming number of adults captured in the modules were males. The Misumenops collected in the spring may have been males in search of females, not food. These species showed similar size patterns through the year, however, there was a reasonably marked seasonal separation in the emergence of juveniles. The substantial seasonal differences of the timing of the second instar developmental stages between these species, precludes overlap while individuals of both species are subjected to their most intense food needs.

Apparently Xysticus montanensis tended toward structures containing the most horizontal jute, while Misumenops showed no particular tendency. Neither species preferred closed vs open architecture. This appears to contradict Hatley's (1978) findings that ambushing species were more abundant where foliage was dense. These contrary results may reflect the lack of precision of her control

on foliage density or may reflect the short period of time my modules were left in the field prior to sampling. More probably they reflect the different relative abundances of species constituting the ambusher guild, between our studies. Her dominant ambusher was Xysticus cunctator which was not one of my dominants. Misumenops lepidus (the same species as her Misumenops celer which was reidentified recently by W. Gertsch), peaked at the beginning and end of my six month field seasons. Undoubtedly she collected this species relatively less frequently during her four month field seasons. The sensitivity of her conclusion regarding architectural type modalities of the ambushing guild, to species composition, is significant.

How then do these two ambushing species coexist? Gertsch (1939, p. 289) says of the subfamily Misumeninae that "obviously the microhabitat of the species will determine the type of prey that may become available for food." He further commented on the typical capture of prey by these ambushing species.

> The spider takes up a position in any part of the flower and sits patiently with its long front legs extended upward. If the spider is not hungry, it pays no attention to insects and will allow them to crawl all over its body. However, if it is hungry, it immediately siezes the insect in its strong front legs and buries the chelicerae in its body. (Gertsch, 1939, p. 290)

These details suggest that the ambushing species are likely to have distinctly different microhabitats. In the spring, Misumenops occupy the flowers of Wyethia and Balsamorhiza. The microhabitat preference of Xysticus montanensis is less easily

determined. Kaston (1948, p. 421) describes the genus as one whose individuals "... live on and under loose bark, under leaves and stones of the forest floor and on low plants." Misumenops is yellow in color, blending well with its preferred habitat, the yellow petals of Wyethia and Balsamorhiza. Xysticus is a mottled gray and brown which would be less conspicuous on woody plant parts or dead leaves. Clearly the cryptic coloration (which should be extremely important to ambushers) of these species is adaptive for different microhabitats.

Why then are these species found in abundance on these modules? The answer is probably multifold. Xysticus' coloration is not markedly different from that of the jute, hence the modules might be acceptable hunting sites for it. Adult male Misumenops collected were probably searching for females, not hunting. The juvenile emergence of Misumenops is not obviously tied phenologically to any local flowering. Juvenile Misumenops may use hunting locations for which they are less well adapted.

Pursuing spiders. This hunting guild contains the large species Thanatus formicinus which emerged earlier in the year than its smaller counterpart, Oxyopes scalaris. Both of these species are seasonal generalists.

This guild is composed of those species which are able to secure their prey through their ability to run fast. Kaston (1948, p. 429) said of the subfamily Philodrominae, which includes Thanatus, that "the members of this group are very fast runners and pursue their prey with great rapidity. Most of them live on plants... ." Thus

the assignment of Thanatus to this guild is clear cut; the proper

assignment of Oxyopes is more confusing. Hatley (1978) decided

to group the family Oxyopidae with the jumping species, perhaps

because of statements like this:

> These spiders build no snares, or retreats, or
> molting nests, and live among low bushes and herba-
> ceous vegetation where they hunt their prey. They
> run rapidly and can also jump. (Kaston 1948, p. 339)

However, Brady (1975), an authority on the family (see also

Brady 1964), states of the genus Oxyopes:

> They ran swiftly over plants where they occurred
> and when disturbed exhibited characteristic erratic
> leaps which allowed them to be immediately recognized
> in the field. Although Oxyopes do not actively pursue
> their prey by sight, they are much more active than
> thomisids, and exhibit a general searching behavior
> when observed. Long spines on the legs, another field
> characteristic of lynx spiders, are apparently used to
> subdue prey. Much remains to be learned about prey
> capture and other forms of behavior. (Brady 1975,
> p. 189-190)

It would seem that by virtue of their not pursuing their prey

by sight they differ distinctly from salticids. The comment by

Brady that they are more active than the thomisids (the only family

to which he compares them in terms of prey capture behavior) suggests

that the thomisids are a closely related family in terms of hunting

technique. The use of their spines for prey capture may qualify

them for status as a unique hunting guild. I believe that the value

of the guild concept, defined by Root (1967, p. 335) as "... a

group of species that exploit the same class of resources in a

similar way," is in clustering ecologically similar species;

splitting spider hunting guilds too finely would negate the value

of the concept. Therefore, I conclude that *Oxyopes scalaris* is best considered a member of the pursuer hunting guild.

No significant regression line of nominal body length on Julian date was found for adult *Oxyopes*; this may be due to both its size sexual dimorphism and its low abundance (with 67 individuals it was the least abundant species analyzed). If one takes the approach of Schoener (1970) and measures the largest one third of the individuals collected, for the previous year's cohorts, the ratio of *Thanatus* to *Oxyopes* is 1.23. In addition, this difference is also maintained in the regressions for the juvenile cohorts. Since neither species showed any tendency to respond differentially to architecture and since they are both seasonal generalists, I conclude that their size separation is sufficient for coexistence.

Web-building spiders. This guild containing species that construct various kinds and sizes of traps is a likely candidate for splitting into multiple groups. However, the two most abundantly collected species of this group are congeneric, hence probably build similar webs. *Theridion petraeum*, the larger of the two species, emerged as juveniles earlier in the year than *T. neomexicanum* and was collected decidedly more toward midsummer. *T. neomexicanum* appeared most frequently at the beginning and end of the field season. *T. petraeum* always had a nominal body length of at least 1.35 times that of *T. neomexicanum* (Table 13). According to theory they are sufficiently separated on this one resource axis for coexistence.

Both of these species preferred closed habitats when compared
to the other abundant species (Tables 10 and 12). T. petraeum
chose horizontal vs vertical jute strands (Table 6). This conclu-
sion is strengthened by the lack of difference between the number
of individuals of T. petraeum found in 122 vs 222 type structures
(Table 9); the majority of both of these structural types had the
same amount of horizontal jute.

These results seem reasonable in light of the natural history
of species similar to these two. Waldorf (1976) and Duffey (1962)
observed Theridion spp. beneath leaflets at the junction of the
leaflet blades with the petiole; this habitat would seem to be
distinctly horizontal.

The conclusion that this set of web-builders preferred closed
habitat is in accord with Hatley's (1978) data. Her web-building
guild was also dominated by the genus Theridion, but she had not
developed taxonomic criteria for separating the various species.

It should not be concluded that all web-builders have a tend-
ency toward closed habitat. The genus Theridion is a special sub-
set of the large array of web-builders; this analysis pertains, in
its most general form, to this genus.

Generalized patterns. The pattern that emerges for the abun-
dant spider species from Table 9 is that each species becomes
decidedly more abundant in any given volume as the amount of sub-
strate increases. The trend depicted in Table 11 is that these
abundant species do not use a centimeter of substrate as fully when
there is a high concentration of substrate per unit volume as they

do when there is less substrate. This may be attributed, to a large degree, to the truncation of the colonization process due to sampling, as noted in the result section; but it may also reflect a limitation on the packing of individuals within any given volume. The validity of these two hypotheses cannot be judged from my experiments.

The modalities in architectural use expressed by the jumping species for open architecture and the web-building species, of the genus Theridion, for closed architecture suggest a plausible mechanism for interguild separation. This, in concert with the assumption that different hunting strategies are likely to be most efficient for different prey species, may permit coexistence of these guilds in Green Canyon with minimum competition.

The predominant intraguild method of species partitioning is concluded to be based on differential prey size use, although some architectural specialization was noted. This prey size partitioning may have arisen through natural selection at Green Canyon, or it may simply reflect the assortment of species. Species assortment may be expected to produce a spatially defined community of high persistence (Robinson in manuscript). If the first of these possibilities were true the spider community seen in Green Canyon might be the result of character displacement (Brown and Wilson 1956), a phenomenon observed with some frequency for other taxa (Grant 1968, Hutchinson 1959, Schoener 1965). However, I believe that the diffuse competition (MacArthur and Wilson 1967) resulting from both intra-guild and inter-guild interference (guild species richness values and relative abundances between guilds are:

jumpers 7 sp, 17.1%; ambushers 5 sp, 15.9%; pursuers 14 sp, 14.9%;
and web-builders 19 sp, 52.2%), probably precludes such fine adapta-
tions to single competitors. I suggest that these abundant species
most probably represent fortuitous combinations which have attributes
that are sufficiently varied to reduce their levels of food competi-
tion to a level permitting coexistence.

SUMMARY AND CONCLUSIONS

The eight most abundant spider species of this study react differentially to architecture. The two most abundant jumping spiders Pellenes hirsutus and Sassacus papenhoei showed a proclivity for open habitat, while the two most abundant web-builders, Theridion neomexicanum and T. petraeum preferred more closed habitat.

Both T. petraeum and Xysticus montanensis (an ambushing species) were found most often on horizontal substrate, while Pellenes hirsutus was most frequent on vertical substrate.

The general trend for spiders was to respond primarily to the amount of substrate available. However, they did show evidence of using open habitat most frequently.

Of the eight most abundant species collected, one pair belonged to each of the four hunting guilds proposed. In each pair of species, the larger one consistently emerged earlier as a juvenile than the corresponding smaller species. These data support the hypothesis (Hutchinson 1959) that for annual, sympatric species to minimize competition through size dissimilarities, the larger species should begin development earlier. The ratio of nominal body lengths between species within any of these pairs (with the exception of the ambushing species) are sufficiently different to suggest that food size partitioning may permit coexistence. These ratios are shown to persist during most of the activity period for each of these three species pairs. Different cryptic coloration and natural histories suggest that the ambushing species Xysticus

montanensis and Misumenops lepidus differ in primary microhabitats
as adults, minimizing spring competition. Seasonal differences in
juvenile emergence dates precluded overlap during the critical
second instar stages in the fall. It was concluded that these
combined adult and juvenile differences are sufficient to explain
the coexistence of these ambushing species.

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APPENDIX

Table 14. Mean monthly temperatures and precipitation totals for
the U.S. Weather Station nearest to Green Canyon (Utah
State University Experimental Station)

Month	1976		1977	
	Mean monthly temp $^\circ F$	Monthly precip. inches	Mean monthly temp $^\circ F$	Monthly precip. inches
Jan	22.5	.78	19.8	.97
Feb	22.8	2.84	27.3	.45
Mar	27.1	2.74	35.1	1.92
Apr	46.4	2.94	51.3	.39
May	59.0	1.39	53.0	3.52
Jun	62.7	1.97	69.1	.13
Jul	72.6	1.02	71.2	1.13
Aug	67.1	1.87	70.3	4.34
Sep	62.7	.55	61.6	1.59
Oct	48.2	.66	51.8	1.36
Nov	37.8	.04	38.5	1.45
Dec	27.6	.05	33.9	2.16

CURRICULUM VITAE

James V. Robinson
Department of Biology
Utah State University
Logan, Utah 84322

(801) 752-6745 Evenings
(801) 752-4100 X7629 Days

PERSONAL

Age: 32
Marital Status: Married
Children: 2
Height: 5'9"
Weight: 155 lbs
Health: Excellent

EDUCATION

Utah State University
   PhD Biology (Ecology) - due early 1978
     Grade Point Average 3.96/4.00
Polytechnic Institute of Brooklyn
   MS Operations Research
   BS Electrical Engineering

DISSERTATION TOPIC

The effect of architectural variation in habitat on a
   spider community: an experimental field study.

EXPERIENCE

Dept. of Biology
Utah State University
Logan, Utah

**Sept. 1975
to
Present**

Position Title: Teaching Assistant

As Teaching Assistant, my responsibilities include:

--Directing operations for a variety of laboratories
--Lecturing prior to laboratory sessions
--Preparing and grading examinations

During this period, I have been involved with the following courses:

1) Invertebrate Zoology - three times
2) Genetics
3) General Biology (for biology majors) a three quarter sequence
4) General Biology (for non-majors)
5) General Botany - twice
6) Plant Physiology

**Jan. 1974
to
Sept. 1975**

US/IBP Desert Biome
Utah State University
Logan, Utah

Position Title: Research Assistant

As Research Assistant, my responsibilities included:

--Design and development of ecosystem computer simulation models
--Programming the animal section of the primary desert
  ecosystem model

Sept. 1971
to
Jan. 1974

RCA Records
New York, New York

Position Title: <u>Manager, Systems Planning and Development</u>

As Manager, my responsibilities included:

--Initiation and cost justification of project proposals to
  divisional management
--Direction of a staff of analysts and programmers toward the
  implementation of these projects
--Presentation of the results of these projects to management
--Budgetary responsibility for more than $500,000 per year

During this period of time, I was involved in the following areas:

1) Simulation of the production/inventory system
2) Design of a short interval scheduling system for the
   production of lacquers
3) Development of both a heuristic and an integer programming
   approach to sequencing tape product
4) Design and development of a management information system
   to control recorded assets

April 1969
to
Sept. 1971

Sperry and Hutchinson Company
New York, New York

Position Title: <u>Operations Research Analyst</u>

As an Operations Research Analyst, my responsibilities included:

--Preparation of new project proposals
--Troubleshooting problem areas for corporate management

During this period of time, I was involved in the following areas:

1) Forecasting wholesale cost effect on catalog profit potential
2) Statistical analysis of the square foot requirement for a
   proposed warehouse
3) Optimization of a Mail Order Physical Distribution System

June 1967
to
April 1969

Grumman Aerospace Corp.
Bethpage, New York

Position Title: <u>Systems Analyst</u>

As a Systems Analyst, my responsibilities included:

--Feasibility studies and mathematical modeling of new proposals
  regarding the Lunar Excursion Module
--Evaluation of test results regarding the control electronics
  system on the Lunar Excursion Module

SCHOLARSHIPS   New York State Regents Scholarship
New York State Incentive Award
Child of Deceased Veteran Scholarship

PAPERS PRESENTED   Community assortment -- Rocky Mountain Guild of Population
Biologists Annual Meeting. 1977.

Island biogeography: current theory and implications --
Association of American Geographers Annual Meeting
(Invited Paper). 1977.

An animal simulation model -- US/IBP Desert Biome Annual
Meeting. 1975.

PUBLICATIONS   The concepts of elasticity, invulnerability and invadability.
(With W. D. Valentine. Amer. Natur., submitted)

An assortative model of island biogeography. (Amer. Natur.,
submitted)

The effect of architectural variation in habitat on a spider
community: an experimental field study. (In preparation,
projected journal Ecology)

Seasonal trends in spider populations. (In preparation with
C. Hatley-Beedlow, projected journal J. Arach.)

Levels of biological organization: an organism centered
approach. (In preparation with J. MacMahon, D. Phillips
and D. Schimpf, projected journal Bioscience)

PROFESSIONAL SOCIETIES

American Arachnological Society
American Association for the Advancement of Science
American Institute of Biological Sciences
American Society of Naturalists
Ecological Society of America
Society for the Study of Evolution
Society of Systematic Zoology

REFERENCES   Provided upon request