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Foraging Tactics of Two Guilds of Web-Spinning Spiders

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Summary. The foraging behavior of orbweaving and sheetweb weaving guilds of spiders was investigated. Orbweavers move among web-sites frequently, but sheetweb weavers do not. A simple model that examines the adaptive advantages of active foraging and sit-and-wait strategies leads to three predictions: 1) Orbweavers should have a simple decision rule for leaving web-sites, 2) Orbweavers' web-sites should have more variable payoffs than do the web-sites of sheetweb weavers, and 3) Orbweavers should have a lower cost of moving than do sheetweb weavers. Field and experimental data bear out each prediction. In addition, analysis of the residence times of spiders at web-sites that are used more than once reveals that members of the two guilds do not compete with each other for web-sites.

The distinction between active foragers and sit-and-wait predators stems from the relative frequency of the decision to leave a foraging site. Thus active foragers are those predators that move often from patch to patch, and sit-and-wait predators are those that leave patches infrequently. In this sense, orbweaving spiders are active foragers and sheetweb weavers are sit-and-wait predators.

Introduction

Sitting-and-Waiting vs Active Foraging

The characterization of predators as sit-and-wait foragers or active foragers is widespread (Pianka 1966; Schoener 1969, 1971; MacArthur 1972; Pianka et al. 1979; Griffiths 1980; Pianka 1978; Huey and Pianka 1981; Fitzpatrick 1978; Smith 1974a, b; Eckhardt 1979). Some differences in terminology exist, which Griffiths (1980) has attempted to reconcile.

The behavioral distinctions of searching for and pursuing prey are obvious. The important ecological appropriation of time is between that spent searching simultaneously for all types of prey and time that is allotted to one particular prey item for pursuit and capture. The most important aspect of the latter is that time spent on pursuit and capture of prey is unavailable for any other activity (MacArthur 1972). To the extent that this is not true (and it certainly is not entirely true for some predators), the distinctions break down.

The time spent moving from one foraging site (patch) to another should be included in the former category. Thus, because the behavioral decision of whether to stay in a patch or leave is the strategically important one, especially in those cases where the predator cannot evaluate a new patch in advance (Charnov 1976b; Krebs et al. 1974; Krebs 1978), the distinction between sit-and-wait predators and active foragers is really between those predators that do not leave their foraging sites often and those that do.

In related work (Janetos 1980, 1982), I derived a simple model for predicting situations in which sit-and-wait foraging or active foraging is favored. The model applies to the situation where predators do not deplete the supply of food available at foraging sites and the sites vary in quality independently of predators' actions, as will be the case for many filter feeders. Sites yield high (G) or low (B) net payoffs and the predator makes its decision to move or stay at the end of each day. Predators have two options: they may remain in a site without moving (sit-and-wait) or they may move to a new site after experiencing one poor day in their current site (active foraging). Good sites occur with frequency p, but active foragers encounter them at frequency $p'=p/(a+p)$, where a is the probability that a good site becomes poor. The active foraging tactic is favored when $(p'-p)$ $(G-B)>q'C$, where $(p'-p)$ is the difference between the

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frequencies of encountering good sites for an active forager and for a sit-and-wait predator, $(G-B)$ is the difference in quality between good and poor sites, $q' = 1\text{-}p'$ and C is the cost of moving to a new foraging site. All costs and payoffs can be measured in units of calories/time, as is usual for foraging studies (Schoener 1969, 1971; Charnov 1976a, b; Mac Arthur and Pianka 1966; Pulliam 1974; Pyke et al. 1977).

Field Predictions

In this paper, I shall apply this model to two guilds of web-spinning spiders: orbweavers and sheetweb weavers. I shall first show that there are gross differences in the characteristic residence times at web-sites between the two guilds. The model then generates several field predictions:

1. Orbweavers should have a simple decision rule for giving up at a web-site.
2. Orbweavers' web-sites should vary more in the payoffs to their occupants than will the web-sites of sheetweb weavers. This prediction follows from the term $(G-B)$ in the model. Since the real world is not black and white, the variance of payoffs at web-sites is a measure of this difference.
3. Orbweavers should have a lower cost of moving than do sheetweb weavers.

In addition, the data enable me to answer a fourth question not related specifically to the model:

4. Is there competition for web-sites between or within guilds?

Materials and Methods

The Stony Ford Field Station in Princeton, NJ, was my study area. Stony Ford has several different habitats: open fields, parkland, redcedar oldfields, floodplain forest, and some young woods. The habitat in which I concentrated my work is typical of fields in the Northeast that are being reinvaded by shrubs and woody species. It is a scrubby, second-growth habitat characterized by Eastern redcedar (*Juniperus virginiana*), multiflora rose (*Rosa multiflora*), brambles (*Rubus spp.*), and saplings of maples (*Acer spp.*), elms (*Ulmus spp.*), Sassafras (*Sassafras albidum*), dogwood (*Cornus spp.*) and cherries (*Prunus spp.*). There is no closed canopy. The major feature of this habitat is its floristic and structural diversity. Fire trails and deer trails provided access to study sites.

The study ran from June through August in 1978 and 1979. At this time of year, all the orbweaver species in the study site were juveniles and subadults. The sheetweb weaver species were sub-adult or adult. Spiders of both guilds were marked in their webs by applying a dot of model airplane paint with a small brush or blade of grass. Orbweavers occasionally shook the web, dropped from the web or ran to the side of the web when marked. All returned to their webs. Spiders smaller than 2 mm body length were not marked. If I damaged a web or spider severely during marking, it was excluded from the analysis. Bowl and Doily Spiders showed the defensive behavior of running into the tangled silk above the sheet. Filmy Dome Spiders also ran around the web and occasionally dropped into the leaf litter below. Web-spinning and predatory behavior of marked spiders did not differ from that of unmarked spiders observed in the study site and elsewhere.

Marking was the only disturbance due to me. I did not handle the animals any further. Measurements of spider body length and prey body length were made by holding a transparent plastic metric ruler very close to the animal and reading it to the closest half-millimeter.

I censused spiders in the early morning, when the sun's rays catch the dew on the newly spun webs, making them conspicuous. Web-sites were marked by tying numbered strips of flagging tape onto the vegetation that supported webs. All markers were left in place after the original spider disappeared and all sites were checked each day. These methods enabled me to keep track of the residence times of the spiders at web-sites, whether web-sites were re-used, the spiders' sizes, the sizes of their prey, and indications of how often prey hit the web. Because of the markedly non-normal distributions of data, all my statistical tests are non-parametric (Siegel 1956). All means are given ± their standard errors.

All spiders observed were common species that are easily recognizable in the field (Kaston 1978). No difficult taxonomic determinations were necessary.

Results

Guilds of Spiders

A guild is a group of animals that utilize a common set of resources in similar ways (Root 1967). Guilds in web-spinning spiders can be recognized by the form of the web, which is generally characteristic of each family, but there is some overlap, especially among orbweavers.

In looking at the gross patterns of foraging at the level of guilds, one may perhaps obscure a few of the differences between species. However, at this stage a rather gross approach can be rewarding.

Orbweavers. The orbweb may have evolved independently at least twice in different families of spiders (Levi 1978). The basic structure is simple: guy lines support a framework of scaffolding threads. Connected to the framework threads are a series of non-sticky radii, which are joined at the hub. Attached to the radii is the viscid spiral, made of very fine, elastic silk and coated with a sticky, proteinaceous glue (Levi 1978; Witt et al. 1968; Eisner et al. 1964). Prey hit the sticky spiral, which slows them down long enough for the spider to immobilize them completely, either by attack wrapping or by a long bite (Robinson 1969). Only very small and weakly flying prey are completely immobilized by the sticky spiral without the spider having to attack (personal observation). Most of my data come from several species in the family Araneidae. A list of the species on my study site is in Table 1. All the species I studied built their webs shortly before dawn and left them up for most of the day.

Sheetweb Weavers. The sheetweb is typical of the family Linyphiidae. The linyphiid's web is a dense mat of non-sticky silk, on the lower surface of which the spider runs. Strands of silk connect the mat to the

Table 1. Species lists

	Orbweavers		Sheetweb weavers
Araneidae	*Mangora placida* *Mangora gibberosa* *Araneus trifolium* *Araneus diadematus* *Araneus sp.* *Neoscona sp.* *Argiope trifasciata* *Argiope aurantia* *Gea heptagon* *Leucauge venustata*	Linyphiidae	*Frontinella pyramitela* *Neriene radiata*
Tetragnathidae	*Tetragnatha sp.*		
Uloboridae	*Uloborus glomosus*		

vegetation. Tangled threads of silk that function as a knockdown trap extend above the mat and are attached to an overhanging projection in the vegetation. Sometimes a second sheet of silk underlies the first. The two common species in my study site were *Frontinella pyramitela,* the Bowl and Doily Spider, and *Neriene radiata,* the Filmy Dome Spider.

Patterns of Residence Times

In both 1978 and 1979, orbweavers averaged less than $^1/_2$ the number of days at a web-site that sheetweb weavers do (1978: 2.2 ± 0.2 ($n=214$) vs 4.8 ± 0.3 ($n=224$); 1979: 2.4 ± 0.1 ($n=458$) vs 5.0 ± 0.4 ($n=220$), $P < 0.0001$ both years, Mann-Whitney U test). A comparison within guilds between years reveals very little difference.

One would like to know whether these differences are randomly generated or not. If a spider's decision to leave a web-site is a Poisson process, the stimuli that induce it to leave occur with a constant small probability in any short time period. Such stimuli could be physical disturbance of the web from excessive wind and rain, predation or the loss of support for the web because of changes in the surrounding vegetation. Regarding each movement as an event, the expected distribution of intervals between events is exponential with parameter λ (Ross 1970). Comparing the actual distribution of residence times of sheetweb weavers and orbweavers to the expected distribution from the hypothesis that the movements occur at random yields Fig. 1.

In both 1978 and 1979, the sheetweb weavers'

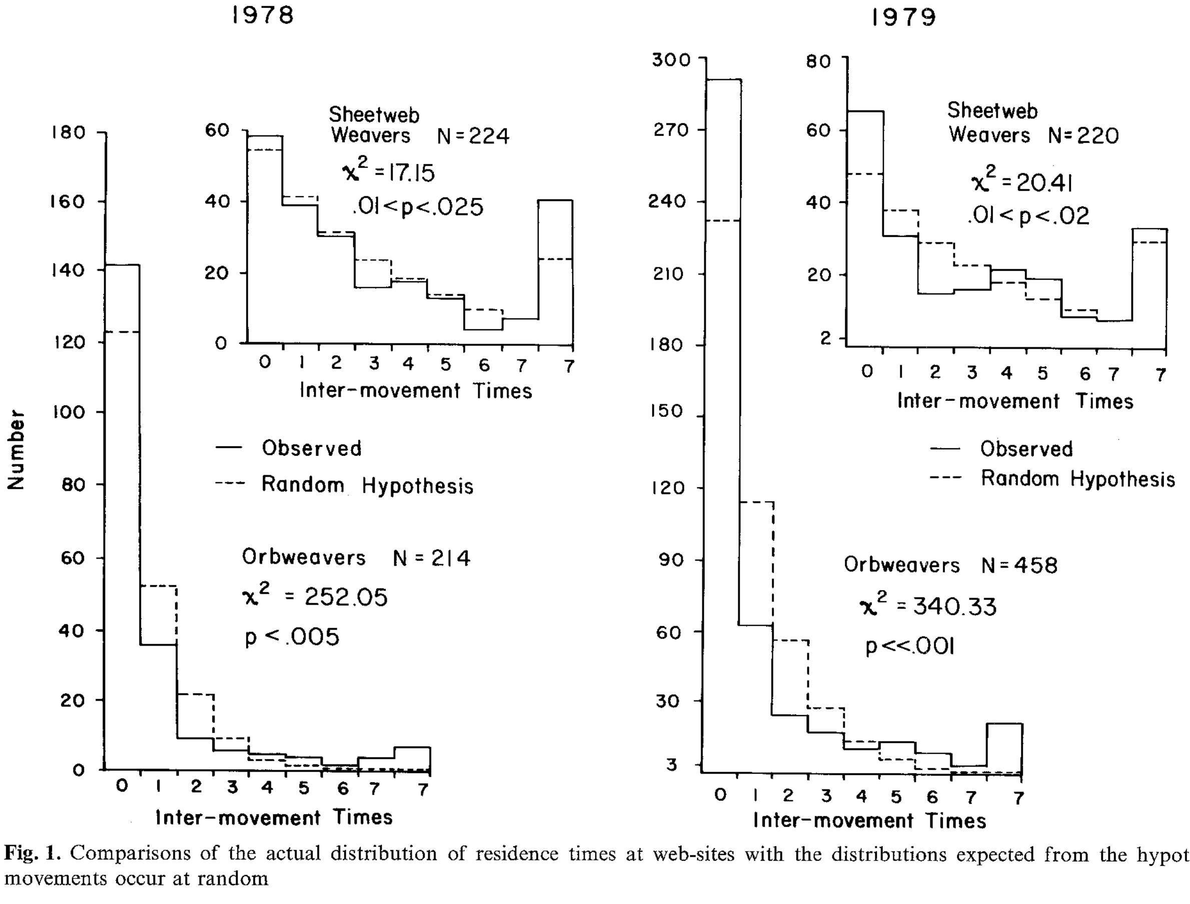

Fig. 1. Comparisons of the actual distribution of residence times at web-sites with the distributions expected from the hypothesis that movements occur at random

distribution of residence times is close to that expected from a random process. The fact that there is a difference is unsurprising; randomness is an extreme hypothesis. However, there is no interpretable difference in the pattern of the sheetweb weavers' residence times and the expected distribution.

The orbweavers' distribution of residence times is significantly different from that expected from a random process ($\chi^2=252$ in 1978 and $\chi^2=340$ in 1979, $P<0.0001$ both years) in an interpretable way. Both short and long residence times are more common than expected, but there is a paucity of residence times in the middle range. The regularity of these patterns is a strong indication that they are produced by behavioral mechanisms that are stable between seasons.

A Simple Decision Rule

What kind of behavioral process could give rise to this pattern? Imagine that orbweavers' tenure at a web-site depends on a very simple behavioral rule. After arriving at a web-site, the spider builds a web and begins to feed. If the spider has not acquired some threshold amount of food at the end of one day, it moves to a new site. Otherwise, it stays in the same site for several days. This rule would produce an excess of residence times of 1 day, from those animals that landed in bad sites, an excess of long residence times from those animals that started in good sites and stayed there, and a paucity of middle-length residence times. This is exactly the pattern that the orbweavers actually exhibit.

In order to investigate further the behavioral mechanism responsible for the patterns of residence times in orbweavers, I collected orbweavers from the field and separated them at random into two groups. Both groups were allowed to spin webs in wooden frames, from which the spiders could easily escape. I fed the experimental group by introducing insects that had been captured in a sweep-net from a nearby field. The control group was treated exactly as the experimental group except that the spiders were not fed. Comparison of the distributions of residence times shows a significant difference ($\chi^2=6.23$, $P<0.05$): spiders that were fed stayed in the frames longer than the unfed spiders (2.4 ± 0.2 days vs 1.8 ± 0.2 days).

The experiment is artificial to the extent that sites did not vary in quality, nor were spiders observed after they moved. In the field, orbweavers may take only a day to evaluate a web-site. If they stay, they tend to remain for 4 or 5 days, hinting that the time scale for sites to change is close to a week. Sheetweb weavers seem to be sit-and-wait predators, leaving foraging sites only by some random process.

Variability of Web-Sites

The second prediction is that the profitability of orbweavers' web-sites will vary more than that of sheetweb weavers. High variability is equivalent to large differences between good and poor sites. I have calculated two measures of variability because it is not clear how a spider judges the profitability of its web-site. The first involves the size of prey that the spider captures. The second measures the frequency with which prey of all sizes are ensnared.

a) Variability of prey size at a site. Spiders may use the occasional occurrence of large prey to distinguish good sites from poor (Olive 1980). The prediction is that the web-to-web variance in average prey size is larger for orbweavers than for sheetweb weavers. Both field seasons bear this out (1978: 4.59 vs 2.02, $F=2.27$, $P<0.01$; 1979: 12.51 vs 1.40, $F=8.93$, $P\ll0.01$). If one controls for the effects of spider size by throwing out all orbweavers that are larger than any of the sheetweb weavers, the results are only slightly changed (1978: 2.78 vs 2.02, $F=1.38$, $P\approx0.1$; 1979: 4.25 vs 1.40, $F=3.03$, $P<0.001$).

b) Incidence of prey at a site. The data are from spot samples taken each morning when the spider was censused, not the total number of captures made during the day. Therefore, I assume that the spot samples reflect the situation at each web-site with some accuracy and that the range of variation in the population at any one time is nearly the same as can be encountered by any individual spider over a long time. The spiders live long enough for each to be exposed to all of the conditions that confront the population as a whole. With these assumptions in mind, one can calculate a capture rate for each spider sampled: No. of prey/residence times. Orbweavers' web-sites should show a pattern of either having many prey or very few, while many sheetweb weavers' sites will have moderate amounts of prey.

Table 2 shows the fractions of web-sites which had no prey and which had 1 or more prey per day for both orbweavers and sheetweb weavers. A larger fraction of orbweavers than sheetweb weavers are at poor web-sites and at very good web-sites. A larger fraction of sheetweb weavers occurs at web-sites that provide some prey, but the capture rates are mostly in the intermediate range. Figure 2 shows the full distributions of capture rates. The distributions are obviously qualitatively similar. However, a Kolmogorov-Smirnov two-sample test reveals that for each

Table 2. Numbers (proportions) of webs with 0 prey, between 0 and 1/day, and ≥ 1/day

	Orbweavers		Sheetweb weavers	
	1978	1979	1978	1979
None	162 (0.76)	309 (0.68)	142 (0.63)	118 (0.54)
0–1/day	21 (0.10)	51 (0.11)	60 (0.28)	77 (0.35)
≥ 1/day	31 (0.14)	98 (0.21)	22 (0.09)	25 (0.11)

$P < 0.001$ both years, χ^2 test

year, the orbweavers' distribution of capture rates and that of sheetweb weavers are significantly different (1978: $P = 0.05$; 1979: $P < 0.01$). The difference is quantitative, with orbweavers tending to be in very poor sites or very good sites, while more sheetweb weavers end up in moderate sites.

Web-sites are a boom or bust proposition for an orbweaver; they vary widely in quality, and are either very good or very bad. However, sheetweb weavers have a better chance of winding up in a web-site that is intermediate in reward rate. The element of boom or bust is not gone, as Fig. 2 shows, but it is not as strong as for orbweavers.

Web-sites vary temporally as well as spatially, but it is difficult to show quantitatively because most sites are occupied for too short a time. The occurrence of prey does not seem to be clumped during periods of occupation at those web-sites for which I was able to sample insects for several consecutive days; only 3 of 31 runs tests on the occurrence of prey are significant at the 0.05 level. This was also true at those web-sites that were used more than once.

The surrounding vegetation determines whether a web-site will be profitable. Patches of flowers bloom quickly, last for one or two weeks, and then die. Most of the spiders' prey are Diptera, Hymenoptera and Lepidoptera, many of which are flower visitors. The flight patterns of these insects are strongly influenced by the presence of flowering plants, and since the spatial distribution of flowering plants is constantly changing, the profitability of any web-site will also change during the growing season. The time scale for a change in quality should be about a week, which is approximately the length of time any of the flowers in the habitat remain in bloom.

Cost of Moving

The total cost of moving has two parts: C, the energetic cost of moving between web-sites and spinning a new web, and q', the frequency with which the cost must be paid. One measure of q' is the fraction of webs that had no prey (Table 2). This fraction is greater for orbweavers than for sheetweb weavers, but not dramatically so.

When a spider arrives at a new site, it must produce the first web completely from stored reserves. Because spider silk is a protein (Lucas et al. 1960; Peakall 1962, 1964), the production of a web is an expensive proposition both in terms of energy and

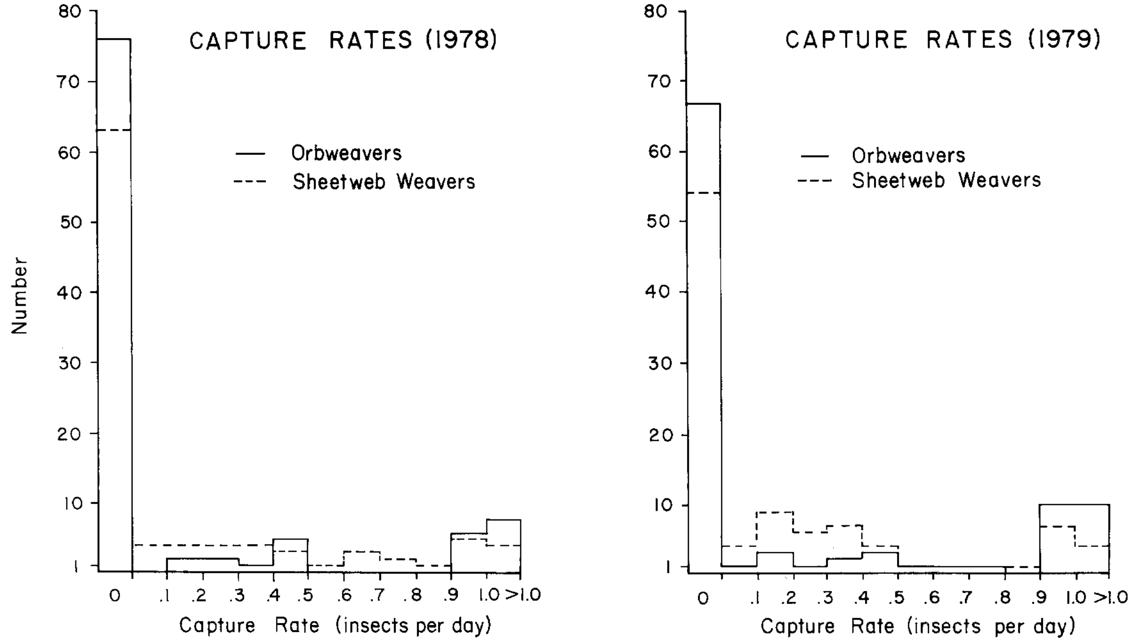

Fig. 2. Frequency distributions of capture rates at web-sites. Rates are no. of insects sampled/residence time

materials, particularly if the animal has just left a poor web-site.

Orbweavers recycle the silk in their old webs. At the end of the day, the spider eats its old web and uses the amino acids to synthesize new silk. *Araneus diadematus* can be at least 90% efficient in recycling the amino acids from old silk (Peakall 1971). Sheetweb weavers do not possess this behavior. Prestwich (1977) and Peakall and Witt (1976) have found that the metabolic activity costs can be approximated by a factor of 0.9 cal/0.1 mg silk, and the cost of the silk is $S = 4.57\,W$, where W is the weight of silk in mg, for a spider that does not recycle its silk. Recycling reduces the synthesis cost 95%.

Assuming that Prestwich's (1977) and Peakall and Witt's (1976) results can be applied to other species, one can estimate the caloric costs of building a web per mg of spider by simply knowing the weights of the web and spider. In order to compare orbweavers' and sheetweb weavers' cost of making new webs, I brought specimens of each guild into the laboratory, where they were weighed and allowed to spin webs in boxes without feeding. After collecting and weighing the silk produced, the caloric costs per mg of spider are 1.27 cal/mg for orbweavers ($n = 9$) and 10.9 cal/mg for sheetweb weavers ($n = 3$) ($P < 0.01$, Mann-Whitney U test). The results show clearly that sheetweb weavers pay a much higher energetic cost for constructing a new web from body reserves than do orbweavers.

Competition for Web-Sites?

Figure 3 shows the height distribution of sheetweb weavers and orbweavers in the second-growth habitat in 1978. The question of whether these spiders are competing for web-sites immediately comes to mind. One way to answer this question is to look at web-sites that are used more than once during the season. If orbweavers and sheetweb weavers compete for web-sites, then any web-site should be equally attractive to both groups, and abandoned sites should be taken over by each group according to its abundance. However, a 2 × 2 contingency table (Table 3) showing the four possible series for re-used web-sites (orbweaver to orbweaver, orbweaver to sheetweb weaver, sheetweb weaver to orbweaver, sheetweb weaver to sheetweb weaver) shows that these events are not independent ($P < 0.005$ in 1978 and $P < 0.001$ in 1979, χ^2 test). Orbweavers take over sites previously occupied by orbweavers and sheetweb weavers take over sites previously occupied by sheetweb weavers far more often than would be expected at random, and switches occur less often than expected. Thus, sites that are attractive to orbweavers are not to sheetweb weavers and vice versa.

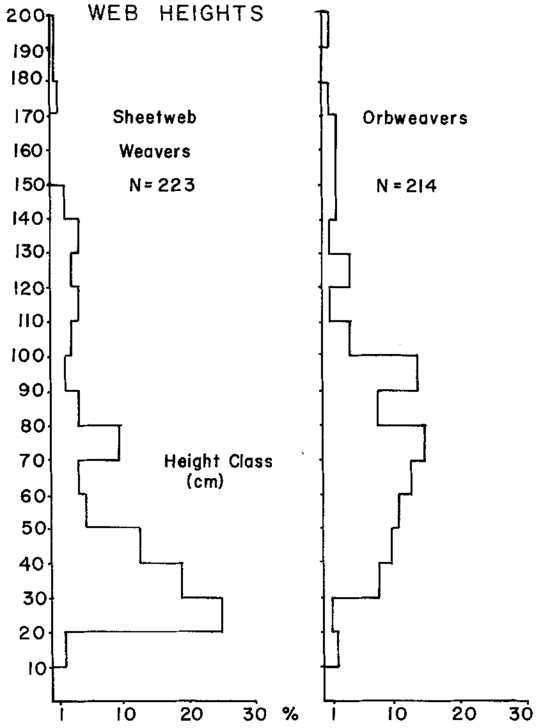

Fig. 3. Height distribution of orbwebs and sheetwebs in 1978

Table 3. Patterns of re-use of web-sites

	Taken over by	Orbweavers	Sheetweb weavers
	1978		
Deserted by	Orbweavers	31	3
	Sheetweb weavers	8	26
	$\chi^2 = 31.8$, $P < 0.005$		
	1979		
	Orbweavers	64	13
	Sheetweb weavers	4	21
	$\chi^2 = 35.3$, $P < 0.001$		

If there is interference competition within guilds, then in cases where a spider disappeared from a web-site and the subsequent occupant appeared the next day, one expects the second spider to be larger. A sign test reveals no trend for the second occupant to be larger than the first in either orbweavers or sheetweb weavers. Thus it does not appear that web-sites are taken over by force, with the larger spider winning, in contrast to Riechert's (1976, 1978, 1981) findings with a desert grassland species.

Influence of Body Size

The main danger associated with an analysis at the level of guilds is that significant variation among spe-

Table 4. Average body sizes and residence times of orbweavers

Orbweaver	Body length (mm)	Residence time	*n*
Tetragnathidae	11.7	1.5	21
Mangora gibberosa	3.8	2.9	113
Acacesia hamata	4.4	1.9	39
Araneus trifolium	10.5	3.7	21
Argiope trifasciata	8.4	6.4	9
Argiope aurantia	12.6	4.1	38

Kruskal-Wallis one-way ANOVA: Body size: $H=887.30$, $P<0.0001$; Residence time: $H=10.39$, $0.1>P>0.05$

cies will be overlooked. In this system, the main variable that I have not considered is the body size of orbweavers. The body sizes of the two sheetweb weavers are similar, but a Kruskal-Wallis nonparametric ANOVA on the body sizes of orbweavers reveals significant variation (Table 4). It is possible that large body size is associated with an increased cost of moving from one web-site to another. If so, then large body sizes should be correlated with long residence times. However, Table 4 also shows that there is no significant variation among species in average residence time. More importantly, a Spearman rank correlation of average body size and average residence times shows no significant relationship between the two ($r_s=0.14$, NS). Thus, the data do not support the contention that the cost of moving increases with body size.

Discussion

Other Factors

The statistical analysis of residence times at web-sites does not require a knowledge of all the possible factors that could serve as a stimulus for a spider to leave a web-site. I have tried to show that the cost of moving to a new web-site, the variation among sites and a simple decision rule based on feeding are mainly responsible for the observed patterns of residence times at web-sites. There are several reasons to assume that most of the disappearances from web-sites are not due to predation, parasitism or excessive web damage.

Since I sampled the same route in the study site every day, I know that spiders that built webs along those paths moved there from other web-sites. I was also able to re-find some spiders that moved, despite the difficulty of doing so in such a complex habitat. Therefore, it is likely that disappearances from web-sites are most often the results of movement and not death.

One could argue that orbweavers' shorter average residence times are due to higher predation rates on them than on sheetweb weavers. However, only on *Frontinella pyramitela* did I observe external parasitoids. Species in both guilds also suffer damage to their webs. Large prey damage spiral and radii in orbwebs, and the spiders routinely repair such damage when they extract prey from the web (personal observation). Sheetwebs apparently do not suffer much damage from capturing prey, but the spiders do repair damage done by other sources. It is possible that excess damage to webs in some web-sites could lead to spiders moving from those sites. However, there is no consistent tendency for spiders to spend longer times in their second web-site, as this hypothesis would predict (sign test, sheetweb weavers $P=0.05$ ($n=5$), orbweavers $P=0.36$ ($n=8$)).

One cannot claim that predation, parasitism and disturbance have no influence on a spider's decision to leave or stay at a web-site. However, none of these can explain why orbweavers' residence times show the particular deviation from random expectation and sheetweb weavers' do not. Thus, while their influence cannot be discounted, in this system it does seem to be minor.

Application to Other Systems

One would like to know whether the results of this study are generalizable to other systems. It has been known for some time that some non-orbweavers leave old web-sites and re-build webs in new sites that are more profitable (Turnbull 1964). Wise (1975) has reported a food supplementation experiment on *Neriene radiata (Linyphia marginata)* in which juveniles do not respond, but adults do by increasing their residence times at web-sites. The observed residence times of *N. radiata* in my study cannot be distinguished from random expectation (Janetos 1980). The discrepancy probably arises from a low variance of payoffs at suitable natural web-sites.

Riechert and her associates have documented the behavior of a desert ageleniid, *Agelenopsis aperta,* which builds sheetwebs. In this case, a combination of thermal and structural characteristics and food determines the quality of a site (Riechert and Tracy 1975; Riechert et al. 1973; Riechert 1974, 1976). The spiders give up either when evicted by intruders or when the energetic return at the site declines too far (Riechert 1976). Web-sites are limiting and the spiders defend their sites vigorously against intruders (Riechert 1978, 1981).

However, studies of orbweavers have concentrated mostly on diet choice and its relationship to web placement, structure and the spider's morphology (Uetz and Biere 1980; Uetz et al. 1978; Uetz and Burgess 1979; Olive 1980, 1981a, b; Enders 1973, 1974, 1975, 1977). These are important topics and these studies have elucidated much of the variation of foraging behavior within the orbweaving guild. Yet there has been surprisingly little attention paid to the web-spinning spiders that live in the same habitats as orbweavers and eat the same insects.

It appears that the distinguishing characteristic of each guild, the form of the web, is the controlling factor in the typical foraging tactic of the guild. The reason may be found in the relationship between the web structure and the vegetation structure needed to support it. The orbweb is a relatively simple structure to support. The spiders need two supports across which to string a bridge thread, which then forms the beginning of the framework that supports the orb (Levi 1978; Witt et al. 1968). Early in the growing season, orbweavers commonly use dead grass stems as supports for their webs (personal observation). Later, when the vegetation has grown, other tall grass stems and emergent vegetation are used, as are twigs and small branches.

However, a linyphiid web requires much more support from the vegetation. A triangular fork supports the main sheet of silk and an overhanging projection supports the tangled threads which form the knockdown trap. The outside branches and twigs of redcedars and small shrubs, where most of the webs are found, supply the needed support for these linyphiid webs. The height distribution reflects the distribution of available supports more than any competition among orbweavers and linyphiids for web-sites.

Because orbwebs can be put nearly anywhere, there will be an intrinsically higher variance in their payoffs than for sheetwebs, whose vegetational supports are more uniform. Thus, it is to the orbweavers' advantage to invest relatively less in their web and to move among potential web-sites to find hot spots. If there is competition for web-sites, then the costs of invading an occupied web make moving less attractive. However, only in social orbweavers is there documentation of common invasions of neighbors' webs (Uetz and Burgess 1979; Buskirk 1975). Enders' (1974) calculations to the contrary, I saw no evidence that intra- or interspecific competition for web-sites was important among orbweavers in second-growth habitats.

Thus there is a complicated interplay among the web form of a spider, the structure of the vegetation in its habitat, and the variability of the resources available to it. Systems in which web-sites are more limited in number or are intrinsically less variable because of the habitat structure will provide another interesting test of these ideas.

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