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Between Population Comparison of Resource Acquisition in the Long Jawed Orb Weaving Spider *Tetragnatha elongata*

Rosemary Grace Gillespie
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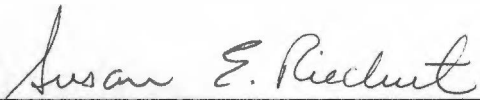
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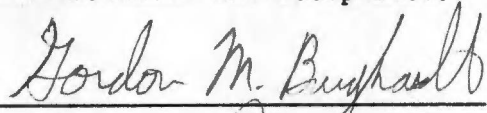
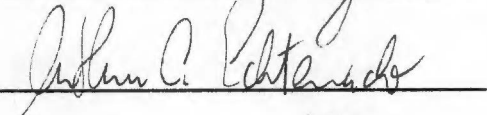
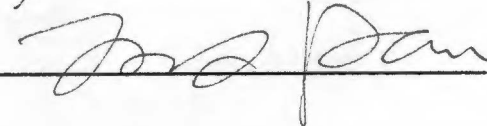
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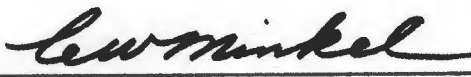
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Accepted for the Council:


Vice Provost
and Dean of The Graduate School

BETWEEN POPULATION COMPARISON OF RESOURCE ACQUISITION IN THE LONG JAWED
ORB WEAVING SPIDER TETRAGNATHA ELONGATA

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Rosemary Grace Gillespie

June 1986

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ABSTRACT

Behavioral adaptations for resource acquisition in the long jawed orb weaving spider Tetragnatha elongata Walckenaer (Araneae : Tetragnathidae) are documented in this study. It examines the form and mechanism of spider foraging behavior, an essential prerequisite to the realization of the commercial use of spiders in integrated pest management. Being the most common and ubiquitous of insect predators, spiders offer tremendous potential as stabilizers in agroecosystems with unstable cycling of phytophagous insects. The initial part of this study examines the mechanisms employed by T. elongata in selecting a habitat, and demonstrates that spiders do not build webs where the abiotic environment is unsuitable; under these circumstances there is increased random locomotion. Where the immediate physiological requirements of the spider are satisfied, web building may occur when a spider can locate suitable support structures. Residence time at a site is determined by an interaction of spider hunger level and prey availability.

The nature of this interaction is further examined in the second part of this study by comparing two populations with marked differences in behavioral activity patterns and prey capture rate. The specific foraging strategy adopted in any given situation is highly plastic. Where prey availability is low, a "sit-and-wait" strategy is adopted; where high, they are "mobile" predators. A model is developed to explain this dichotomy in terms of "risk"; i.e., hunger-specific responses to variability in resource abundance. The model is validated. The behavior of sit-and-wait foragers is "risk prone": predators capitalize on variability in resource abundance by remaining for extended periods at

any site offering a sustainable prey capture rate. A mobile predator is "risk averse", avoiding variability in resource abundance by continual sampling to exploit the habitat average.

The model developed also suggests a positive advantage to aggregative behavior in T. elongata at high prey densities. The extent and form of this behavior is examined in the final part of this study through experimental manipulation to allow the establishment of very high levels of prey availability. Such conditions induce a degree of cooperation: reduced individual web building and silk sharing.

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CHAPTER I

INTRODUCTION

The interactions between spiders and their environment have been investigated systematically only within the past few decades, during which time information on spider ecology has burgeoned. Only in the last few years, however, has this been considered with respect to the behavior of the spider. This study is concerned with the behavioral adaptations exhibited by spiders for the acquisition of resources.

There are two distinct approaches to an adaptationist study of the phenotype-environment interaction of an individual. Firstly, the "a posteriori" approach: given that certain phenotypic characters are correlated with particular ecological circumstances, what is it that renders them more appropriate for gene transmission? Secondly, the "a priori" approach: what kinds of characters might be expected to be more appropriate as aids for gene transmission in prescribed ecological circumstances? The first question uses the comparative approach, analyzing characters of different species, or populations of the same species living in different or similar ecological circumstances. The second question attempts to predict, by means of conceptual or algebraic models, what characters ought to promote fitness and hence what characters ought to be selected in carefully defined environmental conditions. Both these approaches are employed in this study in order to gain insight into the behavior of the long jawed orb weaving spider Tetragnatha elongata Walckenaer (Araneae : Tetragnathidae) and its effect on the ecology of the species. I also consider the universality

of some of the explanations used to describe certain behavioral phenomena in T. elongata.

Rationale

Natural ecosystems exhibit considerable resistance, resilience, or both, to periodic, severe or acute disturbance (Odum 1983). Many organisms actually require stochastic disturbance, such as fire and storms, for long term persistence. Accordingly, ecosystems may recover rather well from many anthropogenic disturbances, such as episodes of pollution or periodic harvesting. If, however, a disturbance is persistent or continued, the effects on an ecosystem may be pronounced. The maintenance of monotypic stands of vegetation for the efficient management of food crops, for example, has led to unstable cycling in associated phytophagous insects (Li 1982). This type of situation is a major concern in agroecosystems (Coppel and Mertins 1977) as it frequently leads to excessive economic damage.

The modern approach to management of insect pests is an integrated one. The strategy involves using short season varieties of a crop (which mature before pest populations can build up) and cultural practices (tilling, irrigation, fertilizing) that discourage pests and encourage their natural enemies, combined with judicious use of several kinds of insecticides. The new control system is based on the premise that the "war" on pests can never be "won", but pests can be controlled in order to minimize the probability of an outbreak and thereby allow an agroecosystem to maintain a margin of profit to the grower. In recent years, therefore, insect pest management has changed its emphasis from

specialist predators, which may eradicate insects, to generalists, which serve to "buffer" the system. For this reason, spiders, being the most common and ubiquitous of insect predators (Bristowe 1958), are receiving increasing attention as possible agents for use in insect pest suppression (Riechert and Lockley 1984). As yet, there is a marked paucity in the literature on the interaction of spiders with their insect prey. (See Riechert [1975], Nentwig [1980] and Louda [1982] for notable exceptions and in which the effect of spiders on pest species was found to be significant.) Before their commercial use can be realized, therefore, a considerable amount of work is required in order to understand the mechanics involved in spider foraging. The present study is a contribution towards this end.

Study Subject

Spiders, which constitute the order Araneae, one of the 11 orders of the Arachnida, occupy almost every possible habitat, largely as a result of a great diversity of prey capture techniques (Bristowe 1958). As a group, they exhibit several striking peculiarities. Although wingless, a spiderling can float its threads on the breezes, and can be carried up through the air, often reaching tremendous heights, and sailing for long distances. This "ballooning" behavior of spiders permits their colonization of areas at a rate not possible even for winged insects (Gertsch 1979). Unless they arrive in an environment favorable for survival, however, they are unlikely to survive for very long.

Another unique feature of spiders is their copious use of silk:

spiders are born in a silk nursery; they escape danger on a silk rope; they wrap their eggs in a silk cocoon; and they hibernate in a silk chamber. Many groups of spiders have further expanded their use of silk to make a trap for capturing prey. By their morphology, these traps are identified as tube webs, purse webs, sheet webs, tangled webs and orb webs. The orb web is the most highly evolved of all the space webs developed by sedentary spiders (Gertsch 1979).

Spiders also have a characteristic mating strategy. The palp of the male is specialized to receive sperm by a process of "sperm induction." After courting a female, mating is accomplished by means of a series of accessory apophyses on the palpi, on the legs, or on other parts of the body, which seize and orient the bodies of both sexes in such a way that the male palpus can come into contact with the apparatus of the epigynum, the genital opening of the female specialized to receive the male palpi.

Of all the Araneae, species in the genus Tetragnatha are among the most abundant worldwide. The spiders constituting this taxon are very distinct, with long slender bodies and legs, and large mandibles (Kaston 1948). Until recently, they were considered a small and primitive family (Bristowe 1958). This assignment was based on the simplicity of their genitalia. The assumption is made that the higher taxa have evolved increasingly complex genitalia, which is generally true (Gertsch 1979). Levi (1978), however, proposes that the tetragnathids are best considered an advanced group, and should be placed in a subfamily of the large orb weaving family Araneidae to avoid the problem of placing them in an intermediate taxon. He bases his proposition on examination of the

structure of the eyes. These are simple in all spiders and tetragnathids have eight positioned across the front of the head. In conjunction with the genitalia, Levi considers these to be the most useful character in the study of spider phylogeny. The tapetum is a canoe shaped structure found in the eyes of primitive spiders. As the lateral eyes move farther away from the medians (generally correlated with the switch to an aerial existence), the tapetum shrinks; and wide separation of the eyes (from the medians) indicates specialization in many groups.

Due to the complete absence of a tapetum, Levi (1981) does not consider the tetragnathids to be primitive. Further evidence comes from details of the morphology of the chelicerae, the front jaws, which consist of a stout basal segment and a terminal fang. As a group, tetragnathids have very powerful chelicerae which, in addition to their function in feeding, serve as modified holdfasts for mating. This characteristic may be responsible for the absence of an epigynum. In T. elongata, the need for such an epigynal coupling is obviated by the strong coupling of the male and female chelicerae. Indeed, the type of cheliceral armature is correlated with the genital characters of tetragnathids (Lehtinen 1978).

It appears, therefore, that the genus Tetragnatha is specialised, spinning an orb web homologous to that of the araneids (Levi 1978). Species of this genus are found on all continents and islands that have been surveyed, and in arctic, temperate and tropical climates. In North America, 15 species have been described (Levi 1981).

Tetragnatha elongata is easily distinguishable from other species of the genus by its exceptionally long chelicerae (Fig. 1). The palp of

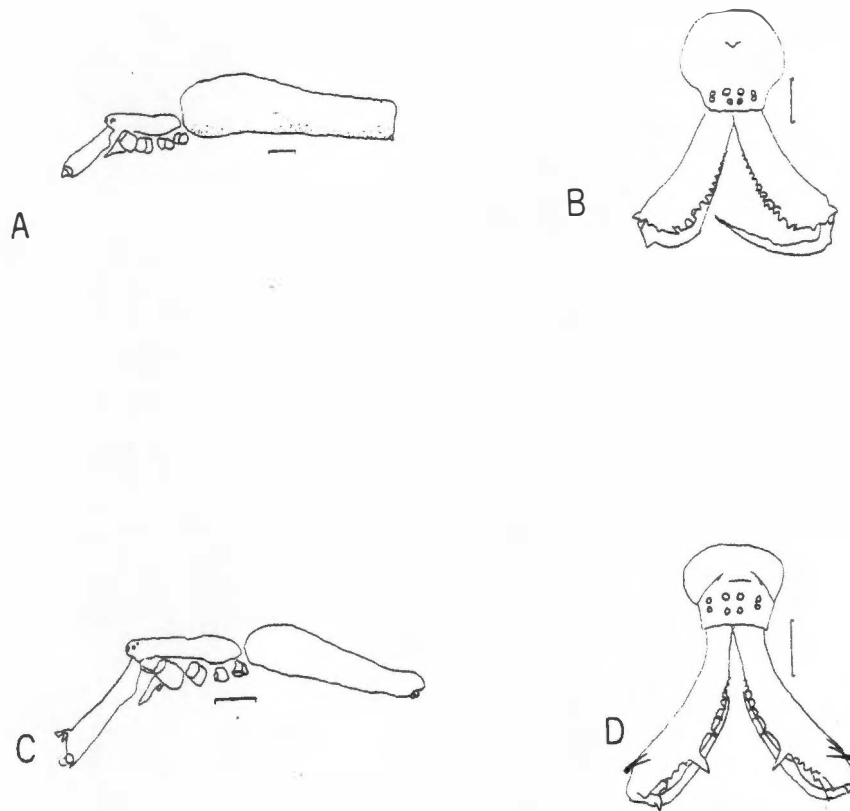


Figure 1. Morphological features of Tetragnatha elongata Walckenaer. (A) Lateral view of female. (B) Chelicerae and eye region of female. (C) Lateral view of male. (D) Chelicerae and eye region of male. (Scale lines. 1.0mm.) (From Levi 1981)

the male is also a distinguishing feature: during the final molt of all spider species the palpal tarsus of a male becomes modified to carry a more or less complex copulatory organ. The palp may be provided with one to several apophyses, which, because of the infinite variety of shapes assumed in different species, are of the utmost taxonomic value. The tarsus generally has a stout bowl shaped cavity on its ventral surface, and hence is called the cymbium. This carries an extension, the palpal organ, made up of hard parts (sclerites) and soft areas (hematodochae). One sclerite, the conductor, so called for its function as a coupling guide, is a key taxonomic character of T. elongata. In this species the conductor tapers evenly to its tip, and terminates in a minute hook bent towards the cymbium. In the female, the median of each of the two pairs of seminal receptacles is characteristically elongate, and they are placed paraxial in the abdomen, parallel to each other. This species is generally found over streams or other running water (Levi 1981).

In common with others of the genus, the orb web of T. elongata ranges from horizontal to vertical, having an open hub, cut out after the web is completed (Wiehle 1963). The orb web is built by immature spiders and mature females, and is generally located over streams or other water, often in woods or other shaded places (Levi 1981). It is delicate and short lived, being taken down and ingested daily if not more frequently. Such activity reduces the caloric cost of a given web by 95% (Peakall 1971). Being, in addition, an extremely light and fragile structure, the web of T. elongata must have a minimal calorific value. The cost of web construction will, therefore, be derived almost exclusively from the activity involved in building (Prestwich 1977).

Mature males do not build webs: they feed by scavenging off the webs of females. The spider is generally found in one of three positions (Fig. 2): A) At the hub of the web, legs extended in a paraxial direction; B) climbing along silk threads suspended from the substrate; or C) flat against the substrate. Adults are found almost all summer, and live for the season. Because males are almost as common as females, they are generally considered to have a similar life span (Levi 1981). Mating occurs without any obvious courtship. A secure coupling is achieved when the male grabs the female's chelicerae with his fangs, The male uses his palpaе alternately, and the female coils her abdomen under to receive them. A week after mating, the female may produce several eggsacs: fluffy structures broadly attached to the vegetation. The young hatch soon after this, and overwinter in immature stages.

The species was chosen on the basis of its universality and ease of manipulation. Further, its general confinement to riparian habitats stimulated the initial study of how such specificity might be achieved. Marked differences in foraging behavior between habitats were noted early on in the study and subsequent work focused on the extent and nature of these differences.

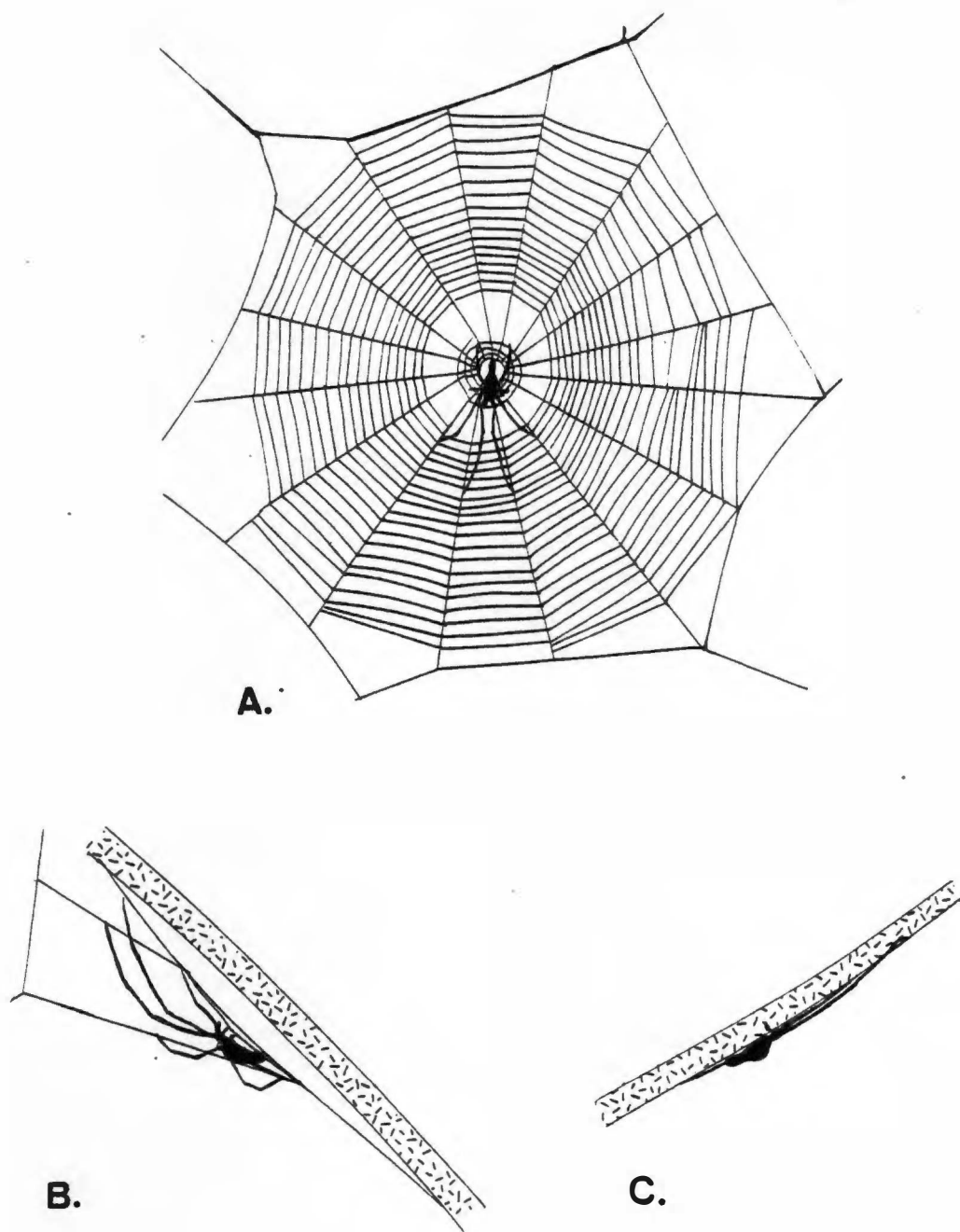


Figure 2. Typical positions adopted by Tetragnatha elongata. (A) Actively foraging (spider at the hub of the orb: ventral view). (B) Wandering (spider walking along silk threads suspended from the substrate). (C) Inactive concealment (spider stretched out flat against the substrate).

CHAPTER II

ANALYSIS OF STUDY AREAS

Introduction

Data were collected from two habitats differing in terms of exposure to the elements as well as abundance of insects. One study site was a heavily wooded section of creek (altitude 1140 m) (fig. 3) beside Highlands Biological Station in North Carolina. The site is cool and sheltered, wind speed never having reached a measurable level during the study period. The shallow creek running through the site flows out of a man-made lake, Lake Ravenel, and is a tributary of Mill Creek.

The other study site was an area near the edge of the east side of Lake Sequoyah (altitude 1121 m) (fig. 4), near the point where it is fed by the Cullasaja River, 3.2km west of Highlands. Here is an area where the dead branches and twigs of a beaver-felled conifer jut out of the water, the rest of the tree being submerged.

Methods

Topography of Aquatic Area

On the creek, measurements were taken of width and depth at 5 m intervals over 30 m. The rate of flow of water was estimated using an anemometer, the cup of which was held so as to just touch the water's surface. The r.p.m. of the head, which was registered automatically on the main body of the anemometer, was converted so as to obtain a value for the linear velocity of the stream. The lake was a very large body of water (area approximately 0.9 km^2); width measurements were not



Figure 3. Photograph taken in the creek habitat.

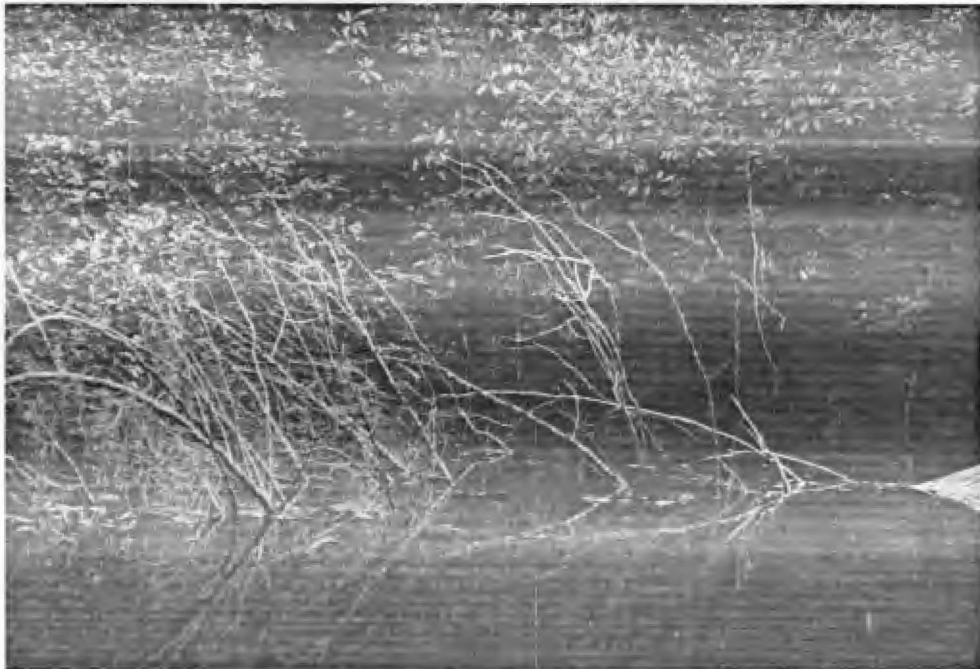


Figure 4. Photograph taken in the lake habitat.

considered necessary. Depth measurements were, however, taken at 5 m intervals from the bank to 30 m out into the water. The current was too slow to allow measurements of water flow rate. In both habitats, qualitative measurements of number and type of plant species were estimated.

Climatic Features

Wind measurements were taken using an anemometer, the wind induced r.p.m. being translated into a linear velocity. Temperatures were taken using a copper constantan thermocouple modelled and painted so as to have a similar size, shape and color of an individual T. elongata. A light meter was used to measure light intensity (lumens/m²). The temperature and light intensity profiles and wind velocity were compared between habitats by taking hourly recordings over a three day period. During this time, rapid shuttling backwards and forwards between the creek and the lake on a given clear, sunny day, allowed comparable measurements from the two habitats. Measurements were taken in both the sun and the shade at each site.

Structures Used For Web Attachment

A total of 63 webs on the creek and 91 on the lake were examined to find the structures used for attachment. Potential structures were categorized as follows: Twigs (i.e., branches of diameter 2 cm or less), branches (greater than 2 cm diameter), logs / tree trunks (diameter 30 cm or more), leaves, moss and wire fencing.

Availability of Emergent Aquatic Insects

In order to estimate the diversity of aquatic insects in the two habitats, two methods of collecting were used. On the creek, a Surber sampler was employed to sample five locations, picked at random, at three intervals through the summer. Insects were identified to family, and the number of each was recorded. Surber sampling was performed in a similar manner on the lake, but another method of sampling was used in addition. The study site on Lake Sequoyah was over a fairly stagnant basin of water, most likely oxygen deficient in its lower depths, and available for colonization here only by species that can survive anaerobically. It was found necessary, therefore, to sample the aquatic fauna in the upper section of the lake. Random samples of surface water were collected (sample volume 2 litres) and the number of insects (including the number of pupal and larval cases) were recorded after identification to family. As with the surber sampling, five locations were sampled at intervals (approximately 3 weeks) throughout the field season.

Results

Topography of Aquatic Area

Except during periods of flooding and drought, the width of the creek varies from 0.7 - 1.2 m; its depth ranges from 0 to a maximum of 65 cm. The rate of flow of the water ranges from 0 - 3.34 m/s, faster moving water being associated with shallower sections. The woodland is mixed deciduous, with rhododendrons in the understory. Ground vegetation in the area is sparse, comprising mainly shrubby plants of the genera

Gaylax and Leucothoe. Twigs, branches and leaves from all vegetation levels overhang the creek extensively, all being potential structures for web attachment.

The lake habitat is very exposed. One side of the site adjoins a dense cover of beech branches which overhang the water from an area of dense mixed deciduous forest. The other side adjoins the main body of the lake.

Climatic Features

The graph (Fig. 5) shows the temperature (in both the sun and the shade) impinging on a model spider at different times of the day on the creek and the lake (averaged over 3 days). As can be seen, the temperature on the lake was consistently higher than that on the creek, but the difference was far more pronounced in the direct sunlight on the lake, where the temperature reached 10°C higher than the shade temperature. On the creek, the temperature differential between sun and shade was far less pronounced. The difference in temperature between the lake and the creek was less pronounced at night, although it was consistently lower on the lake. Similarly, recordings of light intensity (Fig. 6) showed a consistently higher reading on the lake than on the creek.

Wind velocity was not measurable on the creek, as it never attained sufficient force to drive the anemometer at any time during the course of the measurements. On the lake, though the area is very exposed, the average variation in wind speed ranges only from 0 to 0.02 m/s.

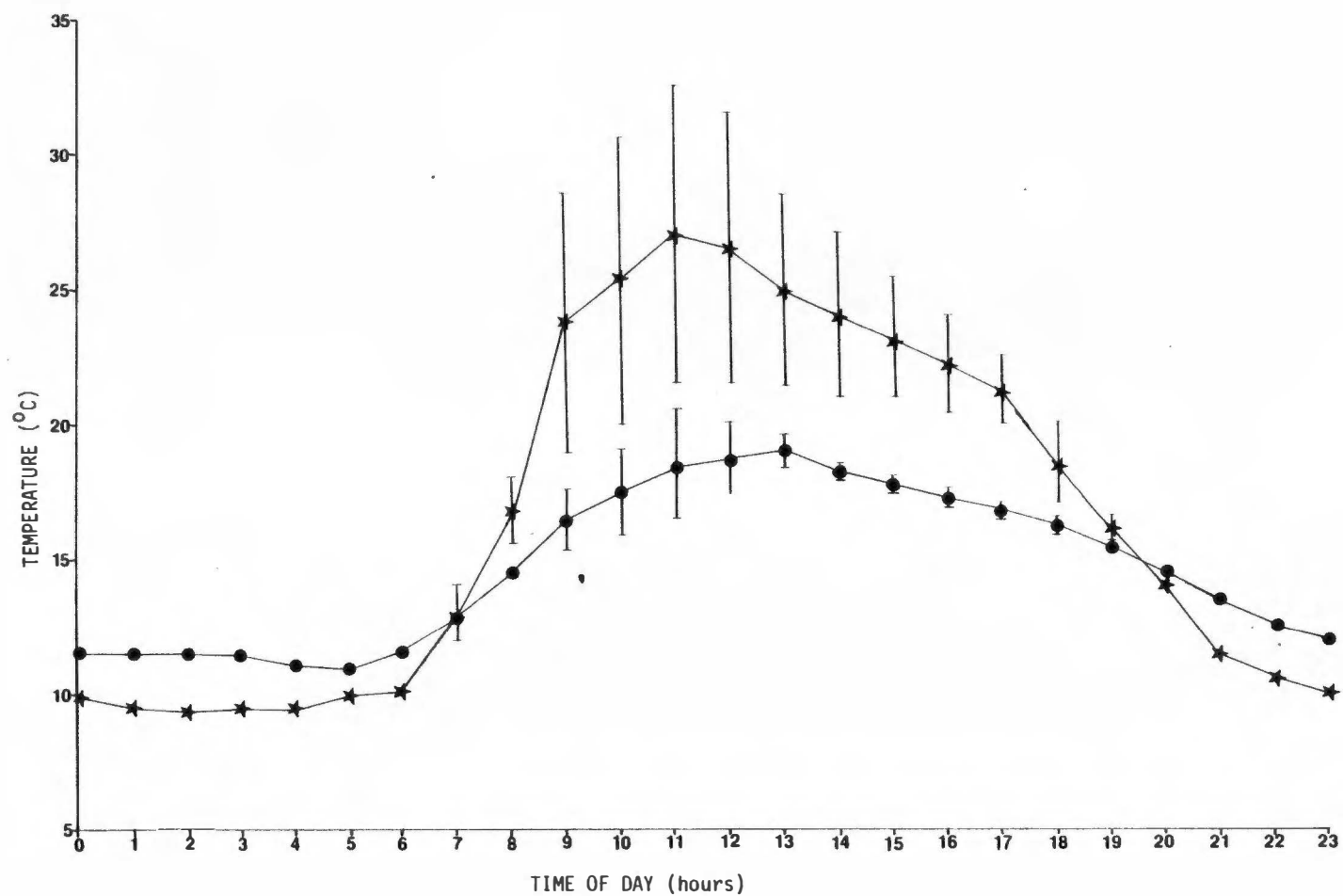


Figure 5. Temperature profile for spider models located over the creek (•) and the lake (*). Temperature spans are shown on the graph as range bars.

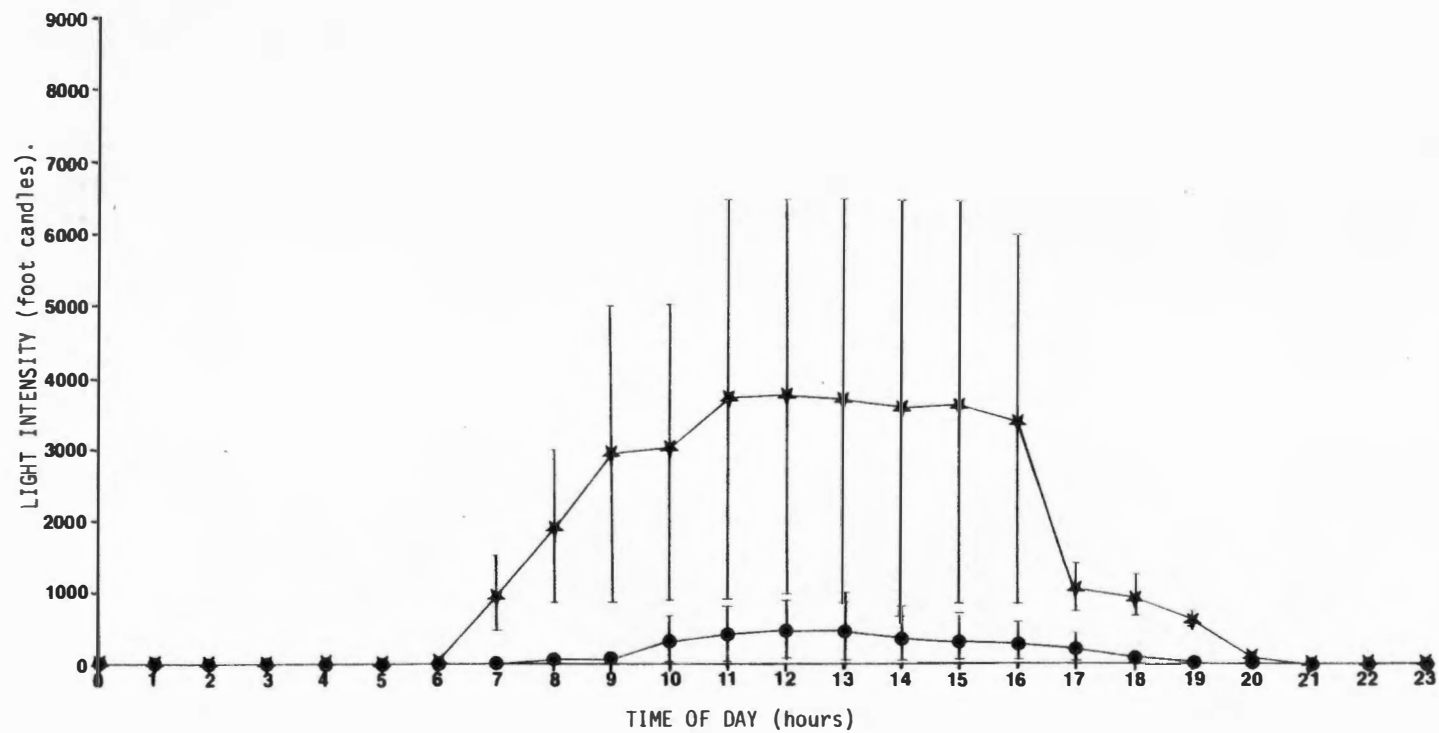


Figure 6. Light intensity profile for creek (.) and the lake (*). The span of measurements (sun versus shade) is indicated on the graph by range bars.

Structures Used For Web Attachment

Considering both habitats together, it was found that twigs (usually dead) are by far the most frequently used structures. Considering all structures used for web attachment, they are used 47.7% of the time. Other structures used are leaves (mostly Leucothoe)(25.7%), branches (15.9%), logs or tree trunks (5.0%), wire fencing (4.1%) and moss (1.6%).

Availability of Emergent Aquatic Insects

Results from sampling of the aquatic habitat (averaged over the three sampling periods) are shown in Table 1. The numbers serve as an estimate of the relative diversity and abundance of the aquatic insect fauna in the two habitats. The numbers on the lake indicate the number of adults present or the numbers that have emerged (pupal cases) over approximately the last 2 days (the rate of disintegration of cases) over an area (approximately $5m^2$) of the lake. The numbers on the creek indicate how many insects are potentially available for emergence over the entire season from an area of approximately $5m^2$. As can be seen, the numbers of emergent insects are very much higher on the lake than on the creek. Indices of diversity were calculated for both creek and lake samples. The Shannon-Wiener Index (H'), which gives greater weight to rare species, gave a value of 3.30 for the creek and 1.40 for the lake. The Simpson Index (C), which gives greater weight to common species, gave a value of 0.86 for the creek and 0.65 for the lake. Both these indices, therefore, indicate a much higher species diversity on the creek than on the lake.

TABLE 1. COMPARING WATER SAMPLES IN LAKE AND CREEK HABITATS.

	CREEK (surber)	LAKE (surface)	LAKE (surber)
DIPTERA			
Culicidae			
Lg pupal cases		7.5+0.96	
Sm pupal cases		4.5+0.49	
Larvae	0.7+0.13		
Adults		3.0+0.49	
Chironomidae			
Pupal cases		8.7+0.36	
Larvae	14.0+0.85		8.0+2.14
Adults		2.0+1.16	
Tipulidae	5.7+0.44		
Simuliidae	2.0+0.21		
PLECOPTERA			
Perlidae	0.5+0.13		
Capniidae	5.5+0.41		
EPHEMEROPTERA			
Heptageniidae	4.3+0.34	0.5+0.13	
Ephemeridae	0.3+0.13		
Beatidae	0.3+0.13		
Leptophlebiidae	0.7+0.13		
ODONATA			
Aeschnidae			
Nymph case	1.0+0.21		0.7+2.27
Adults		0.7+0.16	
COLEOPTERA			
Elmidae			
Larvae	5.3+0.44	0.5+0.10	
Adults	1.7+0.26		
TRICHOPTERA			
Limnephilidae	0.7+0.13		
Hydropsychidae	4.7+0.47		
Hydrophilidae	0.3+0.10		
Leptoceridae	4.3+0.52		
Polycentropodidae	0.3+0.08		
HEMIPTERA			
Gerridae			
Nymph cases		1.7+0.13	
Adults		3.0+0.21	
OSTRACODA			
		0.5+0.08	41.0+5.09

Discussion

This analysis shows that the two study areas were markedly different in terms of both biotic and abiotic parameters. The creek habitat offers a cooler (on average), sheltered environment, with a minimal amount of daily fluctuation. The lake habitat undergoes marked daily climatic fluctuations, often being very warm in the middle of the day and very cool at night. Prey availability is much higher on the lake than on the creek, but the species diversity of the aquatic insect fauna is much lower in the lake, being almost all dipteran (midges or mosquitos).

Before this study was started, populations of T. elongata were found in both these habitats. It was the early recognition of very marked differences in the behavioral repertoire of the two populations that triggered the present research.

CHAPTER III

HABITAT SELECTION IN TETRAGNATHA ELONGATA: A SEQUENCE OF THREE COMPONENTS

Introduction

One of the most important decisions web building spiders make during their life cycle is that of selecting a site in which to build. As in other animals (Fretwell and Lucas 1970, Fretwell 1972, Stearns 1977) these decisions are known to strongly influence spider growth, survival and reproduction (Riechert and Tracy 1975). Studies that delimit the extent of a spider's ability to select a habitat are vital in order to determine their potential as pest control agents (Riechert and Lockley 1984). Habitat utilization has been described in a large number of spiders, strong associations being found with abiotic factors such as structural features (Barnes 1953, Cherrett 1964, Duffey 1966, Hallander 1967, Hollander and Lof 1972, Enders 1973, 1974, Colebourn 1974, Curtis and Morton 1974, Greenquist and Rovner 1976, Cutler et al. 1977, Cady 1978, LeSar and Unzicker 1978, M.H. Robinson and Lubin 1979b, J.V. Robinson 1981, M.H. Robinson 1982, Horton and Wise 1983, Stevenson and Dindal 1982), temperature (Coventry 1967, Almquist 1970, 1973, Edgar and Loenen 1974, Robinson and Robinson 1974, Biere and Uetz 1981, M.H. Robinson 1982), wind (Eberhard 1971), rain (M.H. Robinson 1982) and humidity (Cloudsley Thompson 1957, Almquist 1973, Cady 1978). They have also been found to aggregate in areas of high prey availability (Cherrett 1964, Turnbull 1964, Dabrowska Prot and Luczak 1968a and b, Hardmann and Turnbull 1974, Greenstone 1978, Lubin 1978, Holldobler

1970, Uetz and Burgess 1979, Bishop 1981, Gillespie 1981, Wise 1981, Mackay 1982, Morse and Fritz 1982). Such associations need not, however, imply habitat selection. Random dispersal is known to occur in spider populations. Many of the araneids that colonize old fields and early successional stage vegetation for instance produce large numbers of offspring (in excess of a thousand individuals for each female) which disperse as spiderlings through aerial ballooning (Tolbert 1977). In these species, less emphasis is placed on the survival of individuals and more on the dispersal of one's offspring into new habitats. Dispersal by mass ballooning has also been linked with habitat variability: the more variable the local environment occupied, the higher the frequency of ballooning in a given species (eg. Pardosa, Richter 1970, Greenstone 1981). But dispersal may not be totally random. Tolbert (1976), for example, has shown that araneid spiderlings may reinitiate ballooning, presumably after sampling the local environment encountered following initial dispersal. Changing environmental conditions have also been found to cue dispersal in later life history stages in, for example, linyphiids (Duffey 1956, 1963, Wingerden and Vughts 1974, Vughts and Wingerden 1976). Only in the desert funnel web spider Agelenopsis aperta, however, has there been a conclusive demonstration of active habitat selection (Riechert 1976).

In this chapter, I examine various aspects of habitat selection by the spider Tetragnatha elongata. Previous work on this genus has shown that habitat use may be associated with prey availability (Dabrowska Prot and Luczak 1968a and b, Dabrowska Prot et al. 1968, Luczak 1970, Luczak and Dabrowska Prot 1971) and / or the presence of suitable

structural supports for web building (Lesar and Unzicker 1978). These studies, however, provide little insight into the role of active selection in habitat choice. My initial examination of this problem involved investigation of dispersion "pattern", the organization of a population through the spatial arrangement of its individuals in the environment (Pielou 1969). Patterns of distribution of the desert funnel web spider Agelenopsis aperta have been examined in grassland and recent lava bed habitats of south central New Mexico (Riechert et al. 1973, Riechert 1974) and webs were found to be aggregated in specific habitat patches. The same technique was used to study the pattern of T. elongata. I then determined whether the pattern of distribution observed is a consequence of differential survival, or whether it is caused by active selection.

Methods

Pattern

Field methods. Two plots, one on the creek (fig. 7) and the other on the lake (fig. 8), were selected and mapped in July 1982. The size of the creek plot was 64 m x 16 m; that of the lake 16 m x 16 m. Webs on the creek were examined and their exact locations mapped over a period of 32 days (July 12th - August 11th 1982). An index of web site suitability was obtained by using the frequencies with which each site was used over a period of 32 days. Webs on the lake were far more dense. Data on web locations here were taken from censuses on two consecutive days, during which time approximately the same number of webs were mapped as in the creek habitat. On each plot, the distribution of

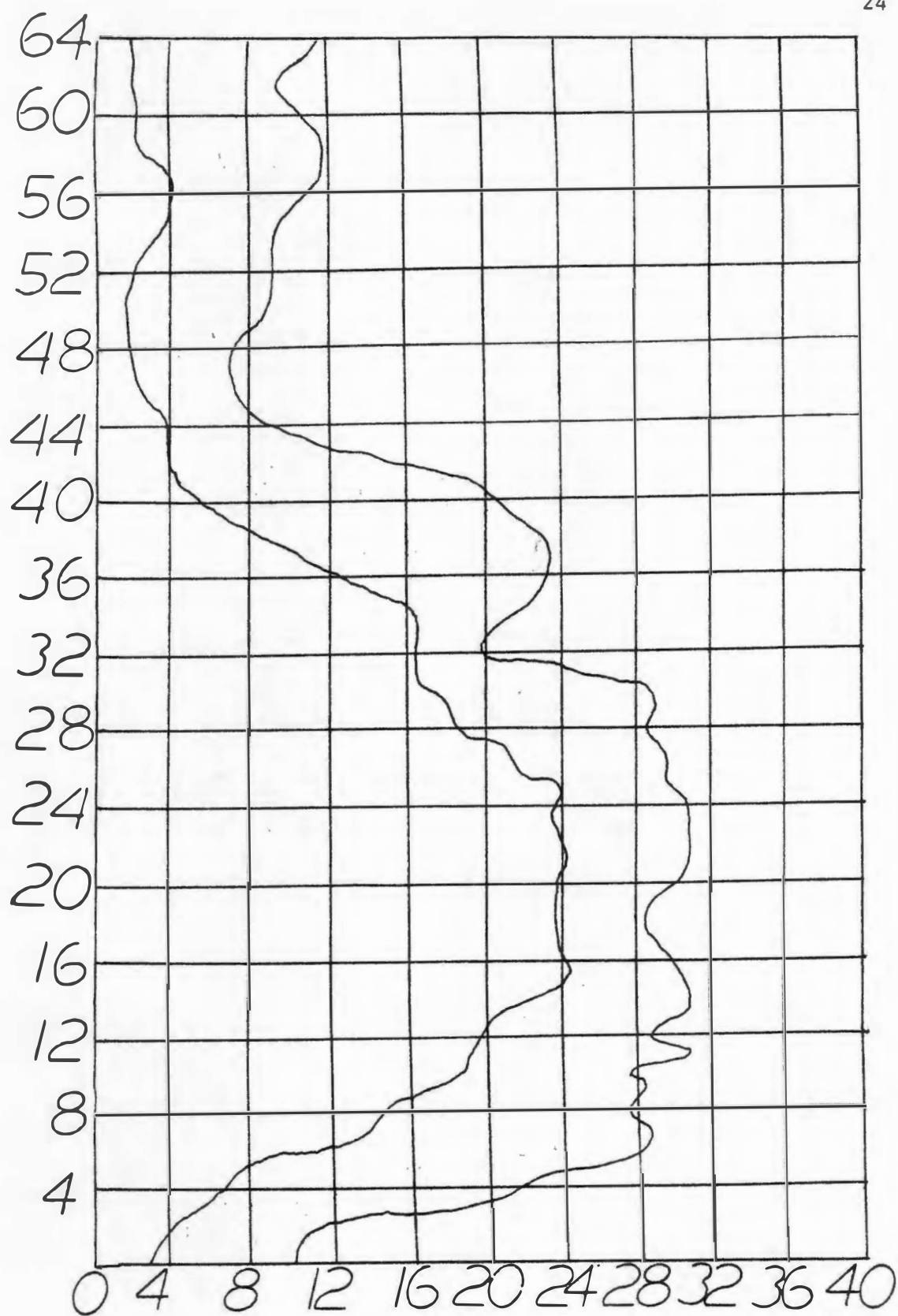


Figure 7. Map of creek plot used in pattern analysis. Shading indicates creek water.

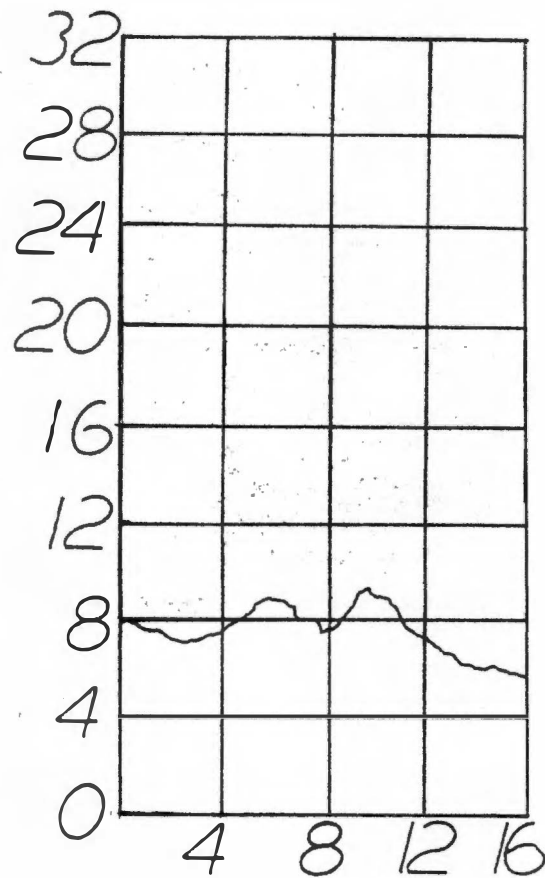


Figure 8. Map of lake plot used in pattern analysis. Shading indicates lake water.

habitat features (e.g. water, sand, moss, leaf litter, twigs, branches and leaves) were also mapped.

Method of analysis. Block size analysis of variance was used to examine the distribution of webs in the study areas. This type of pattern analysis was developed by Grieg Smith (1952, 1961, 1964) and Kershaw (1960, 1964); it measures the departure from randomness. The basis of this approach involves partitioning the total variance of a grid or line of quadrats into parts appropriate to comparisons between adjacent pairs of blocks of different sizes. When mean square (variance) of densities is plotted against block size, those blocks exhibiting peaks are equal to the mean areas of mosaic or pattern units; highest variance will occur at the block sizes in which individual blocks cover areas of especially high or low density. A peak of variance above the mean value signifies that maximum heterogeneity occurs among quadrats of that size. Troughs in variance below the mean value indicate dispersion (or regular spacing) among quadrats of that size.

Pattern analysis is useful in dealing with most natural situations in which not only presence or absence are involved, but also ranges of density (Grieg Smith 1961). Moreover, this method has given consistent results and has proved accurate where independent measurements of pattern were possible (Grieg Smith 1952).

In the present study a rectangle and square system (Grieg Smith 1952) was used for the analysis of pattern. The fundamental quadrat, block size (BS) 1, equalled 1.0 m^2 , the basic field quadrat. The following samples were used in the analysis: A) Creek study area: a

total grid area, BS 1024 (this being equivalent to the area in m^2), was made of contiguous quadrats containing water, bank terrain and woodland.

B) Lake study area: a total grid area of BS 256 (m^2) was made of contiguous quadrats containing open lake water, overhanging trees near the bank, and woodland near the water's edge.

Block size analyses of variance were carried out on all webs of T. elongata in the selected quadrats and on the distributions of water, leaf litter, sand and moss on the ground; branches, twigs and leaves at heights of 0-50 cm, 50 cm-1 m, 1 m-2 m and 2 m-4 m; light intensity, temperature, humidity, wind speed and water speed. Covariance was calculated between web distribution and that of each of the habitat features on all plots by use of the methods described by Kershaw (1960).

Factors Responsible for Survival and Web Building

In order to determine whether T. elongata was exhibiting active selection of web sites, it was necessary to examine 1) those parameters which allowed survival as well as those required for construction of the web trap; and 2) the probability that a spider would move from a site where it had built a web versus situations where no web was built. The variables I chose to examine (on the basis of the results from the pattern analysis) were:- 1) temperature 2) light intensity 3) humidity 4) presence of open water and 5) prey availability. Within its natural distributional area, the parameter most likely to have an immediate effect on individual survivability is desiccation resulting from high temperature, low humidity or the absence of water. The relative effects of each of these parameters was measured in the laboratory through a series of experiments as outlined in Table 2. For each treatment (A-F)

TABLE 2. SET OF EXPERIMENTS TO TEST SURVIVORSHIP UNDER VARIOUS EXTREMES OF THE ABIOTIC ENVIRONMENT.

	TREATMENT					
	A	B	C	D	E	F
TEMPERATURE (°C)	37.5	37.5	37.5	18.0	18.0	18.0
ACCESSIBILITY OF OPEN WATER	NO	YES	NO	NO	YES	NO
RELATIVE HUMIDITY (%)	4	75	75	4	75	75
EXPERIMENTAL SET UP						
Dessicator	yes	yes	yes	no	no	no
Water	none	present	covered	none	present	covered

six spiders were used. After being weighed, individuals were placed in small cylindrical vials (height 5 cm, diameter 2.5 cm) covered with cheesecloth. The weight of each was recorded at 15 minute intervals during each 10 hour treatment. For spiders that died, the time until death, as well as the total weight loss, was also recorded.

The most likely parameters to exert a direct effect on web building behavior in T. elongata were considered to be one or more of the following:- 1) vulnerability to desiccation; 2) light intensity (acting as a cue to humidity); and 3) prey availability. Results from the tests on survivorship (as outlined in Table 2) showed that direct access to open water was needed to prevent desiccation. Field cage experimentation was used to examine this. Two cages were set up, identical except that the floor of one was covered with wire mesh (to allow the passage of small emergent aquatic insects, but prevent direct access to the water by spiders); the other was open to the water's surface. These cages were 1.5 m x 0.6 m; height 0.6 m. The sides were covered with clear polythene and the top with fine wire netting. Wooden bars criss crossed the cages to provide structural support. The effects of incident solar radiation were examined by dividing each of the cages into two equal portions along their length by means of a polythene sheet. One of these sections in each cage was covered with aluminum foil and black polythene to block out a large portion of both visible and infrared wavelengths of the solar spectrum. Any time that measurements were made on the spiders, recordings were taken of temperature ($^{\circ}\text{C}$) and illuminance (lumens/m^2) in both covered and open sections of the cages. In order to control for any differences in these variables that might exist between the two

cages, recordings were taken from both at approximately the same time, and humidity was also measured.

Two experimental procedures, adopted one after the other, were employed to examine the respective effects of desiccation and light intensity on web building. In the first, 12 adult female spiders were collected, weighed and marked, and six were placed in each section on a clear, sunny day. Individuals were removed and weighed at hourly intervals from 0600 to 2100 hours. Spiders were taken in rotation (in order to minimize time out of the cage), weighed and then returned to the cage. The experiment was replicated on the next clear, sunny day with 12 new spiders. In the second experiment, six of 12 newly collected spiders were placed, as before, in each section, having been weighed and marked. Spider activity and web lifespan were monitored at hourly intervals each day for a 16 day period. The procedure was replicated over the next 16 days.

In order to determine the effect of prey availability on web building, a series of small cages (39.3 cm x 39.3 cm x 11.4 cm) were set up along a stream bed, where the incidence of solar radiation was very low (the midday peak being approximately 37.20 lumens/m²). Individual spiders were weighed and then placed in these cages, where they had direct access to open water. The spiders were fed on field collected fruit flies (Drosophila melanogaster: average weight 2.59 mg), caught from a culture of rotten fruit, just prior to feeding. Spiders were fed at 2000 hours daily, insects being placed in the cages by means of specifically designed apertures in their tops. The stoppers in these apertures were removed, and tubes containing the insects inverted over

the top. The presence of soft tissue paper in the tubes prevented the insects from just dropping into the water and drowning. They were left in the inverted position until the next day. In order to find the relationship between prey availability and web building, spiders were subjected to one of three treatments for a period of ten days:- insects administered at a rate of 20, 5 and 0 per day. To measure the extent to which web building occurs in the absence of any stimuli from either light or prey, six spiders were collected, weighed and placed in a cage (1.2 m x 0.6 m x 0.5 m). The cage was placed in a basin of water in a photographic laboratory which was completely devoid of light, insects, wind or water currents. The cages were examined daily. Infrared lights were used (for a minimal period of time) to see whether or not webs were present.

Finally, the probability that a spider would move from a site where it had built a web versus a situation where no web was built was examined using a cage (1.2 m x 1.2 m x 0.6 m high). These cages were placed in an artificially made shallow pool of water, and consisted of wooden struts, the sides of which were lined with clear plastic. The top was covered with cheesecloth and the bottom was open to the surface of the water, which provided a source of mosquito prey. Eight marked spiders were placed in the cage and monitored throughout the season in order to compare the numbers that changed site subsequent to building versus those that moved from a site where no web was built.

Method of analysis. The data were analyzed using the Statistical Analysis System (SAS), a computer software system for data analysis (SAS

Institute 1982). Because the data did not fit into a balanced design, the framework of linear models in the GLM was used. The GLM procedure uses the method of least squares to fit general linear models.

Results

Pattern

Analysis of web pattern showed peaks at block sizes of the largest area (512 m² on the creek; 256 m² on the lake). The factor responsible for this was the patchy distribution of webs due to differences in habitat and the physical environment. The effects of territorial spacing were not detected in this analysis, unlike similar studies on Agelenopsis aperta (Riechert et al. 1973). There are two reasons for this. First, a smallest block size of 1.0 m² is probably too large for detection of inter-individual spacing and, in addition, the analysis does not take into account the three dimensionality of web building in T. elongata (i.e., its vertical distribution).

Creek habitat. Correlation coefficients computed on covariance between web distribution and that of creek water indicate significant correlations at block sizes of 4 ($p < 0.05$), 16 and 32 m² ($p < 0.01$) (Fig. 9). Of the total population of T. elongata sampled, all web sites were located over water. The mean square / block size graph of water (Fig. 10) shows a peak at BS 512 m², which probably represents the area of clustering of water and therefore of webs (webs are clustered at the same block size). The lack of significance of correlation coefficients of water with web sites at block sizes of 1 and 2 indicates that, at these block sizes, there were far more quadrats containing water than

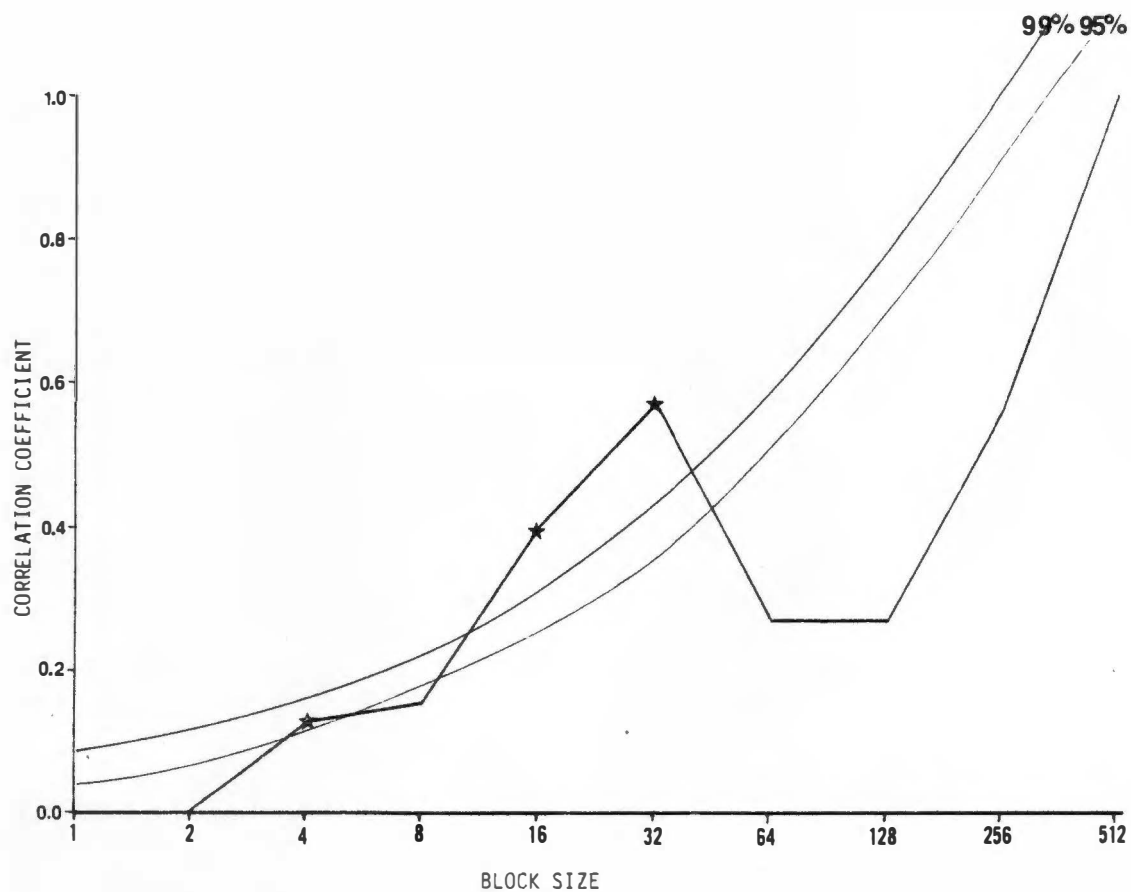


Figure 9. Covariance between web distribution and water (creek). Correlation coefficients computed on covariance between web distribution and that of water (thick line) are plotted along with the curve indicating the level of significance ($p < 0.05$) of the correlation (thin line). There is a significant correlation at three block sizes: 4 (☆: $p < 0.05$), 16 and 32 (★: $p < 0.01$).

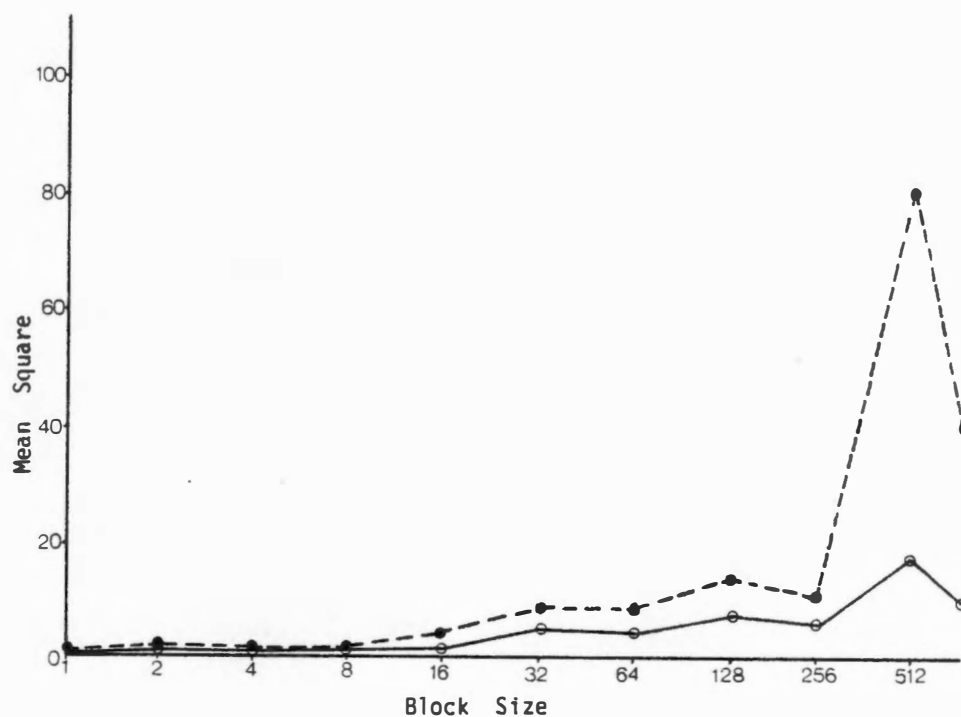


Figure 10. Distribution of creek water (solid line) and webs (broken line) at different block sizes. Mean square analysis was performed at different block sizes and shows a peak at block size 512 for both webs and creek water.

were without webs than there were with webs. An area of 16 m^2 is that which encloses a whole portion of stream: despite the patchy nature of the distribution of webs within this area, webs are always found over water. Significance at BS 16 m^2 and BS 32 m^2 , therefore, indicates that a positive association of webs with water exists, but at a lower block size this effect is masked by the fact that other features are necessary before webs can be built over water. Covariance analysis was completed with water partitioned into fast and slow moving sections. A positive association ($p < 0.01$), similar but stronger than that with water alone, is found with slow water (Fig. 11). There is no significant association with fast water.

Covariance analyses also indicated that webs were associated with other features of the habitat, most importantly, moss at BS 1 and 2 m^2 (Fig. 12). This reflects the fact that webs are always found at the edge of streams and so, at the smallest block sizes, are associated with moss, which is found in similar, coincident patches. The association becomes negative at BS 4 m^2 , indicating that, at this block size, moss is found in clumps where there are no webs. This is because webs stretch from the bank over water, whereas moss stretches farther up the bank.

Webs are also associated with twigs at heights of both 0-50 cm and 50 cm-1 m, at block sizes of 1, 8 and 32 m^2 (Fig. 13). This reflects the use of twigs for web attachment. But webs stretch between twigs; so at block sizes of 2 and 4 m^2 , there are large portions of the webs which are not associated with twigs. The peaks at block sizes of 8 and 32 m^2 indicate the patch size of clusters of the ends of branches from 50 cm

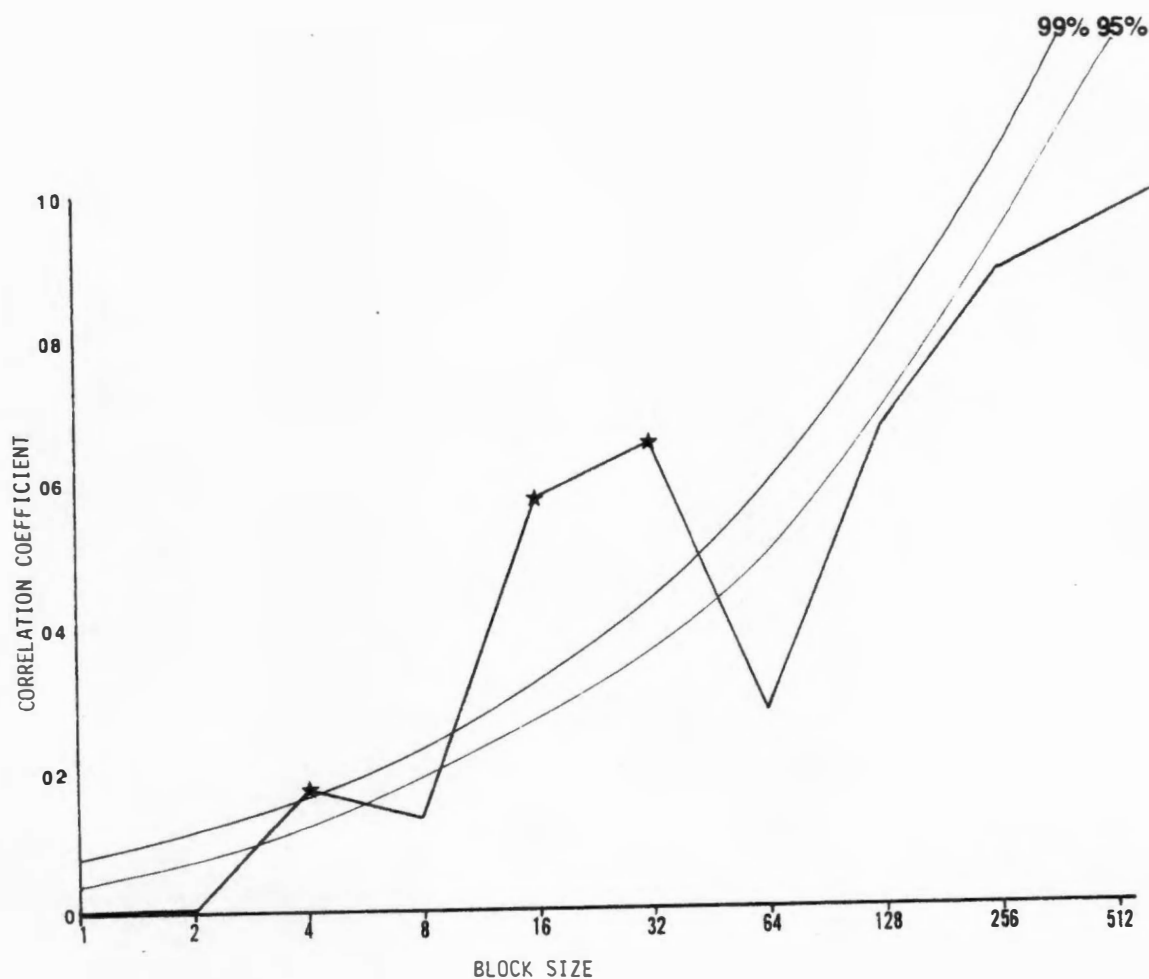


Figure 11. Covariance between web distribution and slow water (creek). Correlation coefficients are plotted (thick line) along with the curve indicating the significance of the correlation ($p < 0.05$) (thin line). The correlation is significant at block sizes of 4 (☆: $p < 0.05$), 16 and 32 (★: $p < 0.01$).

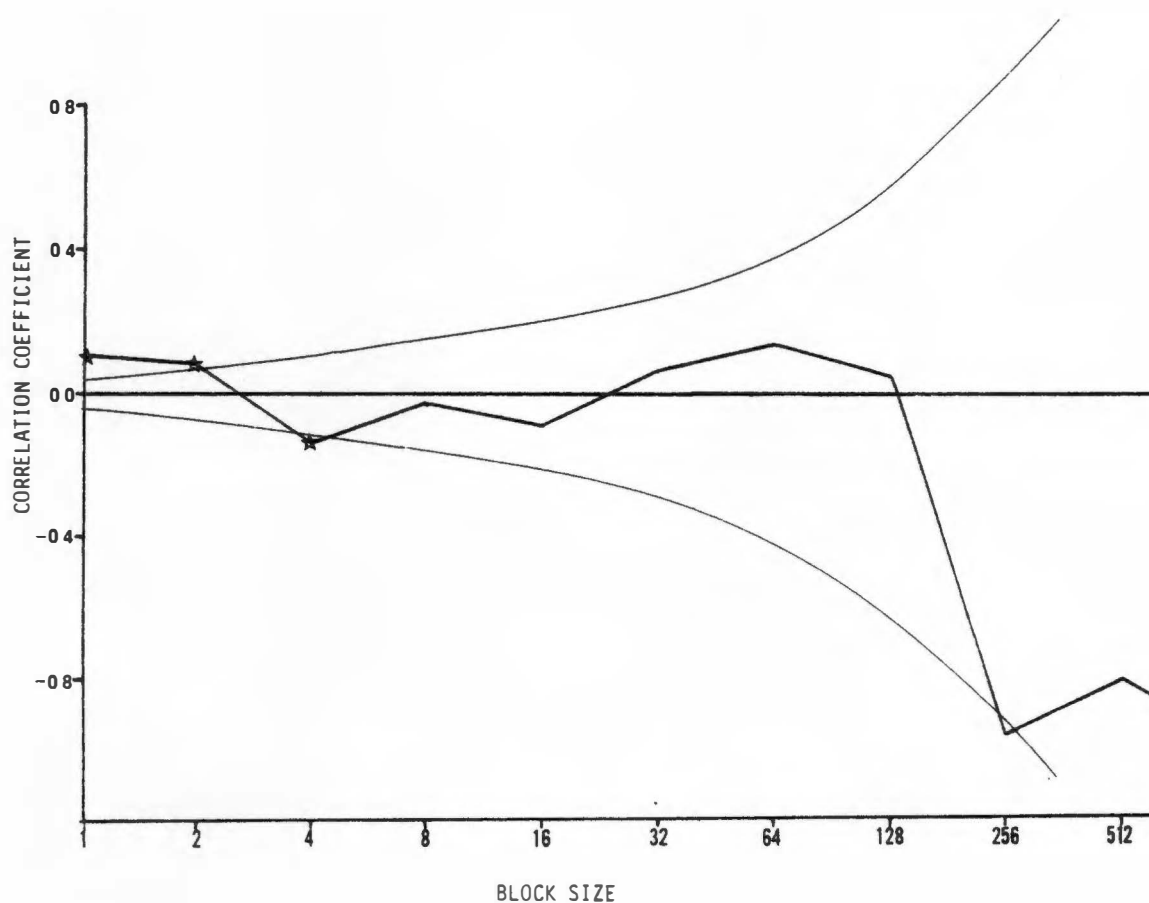


Figure 12. Covariance between web distribution and that of moss (creek). Correlation coefficients are plotted (thick line) along with the curve indicating correlation significance ($p < 0.05$) (thin line). The correlation is positively significant at block sizes of 1 (\star : $p < 0.01$) and 2 (\star : $p < 0.05$). It is negatively significant at block size 4 (\star : $p < 0.05$).

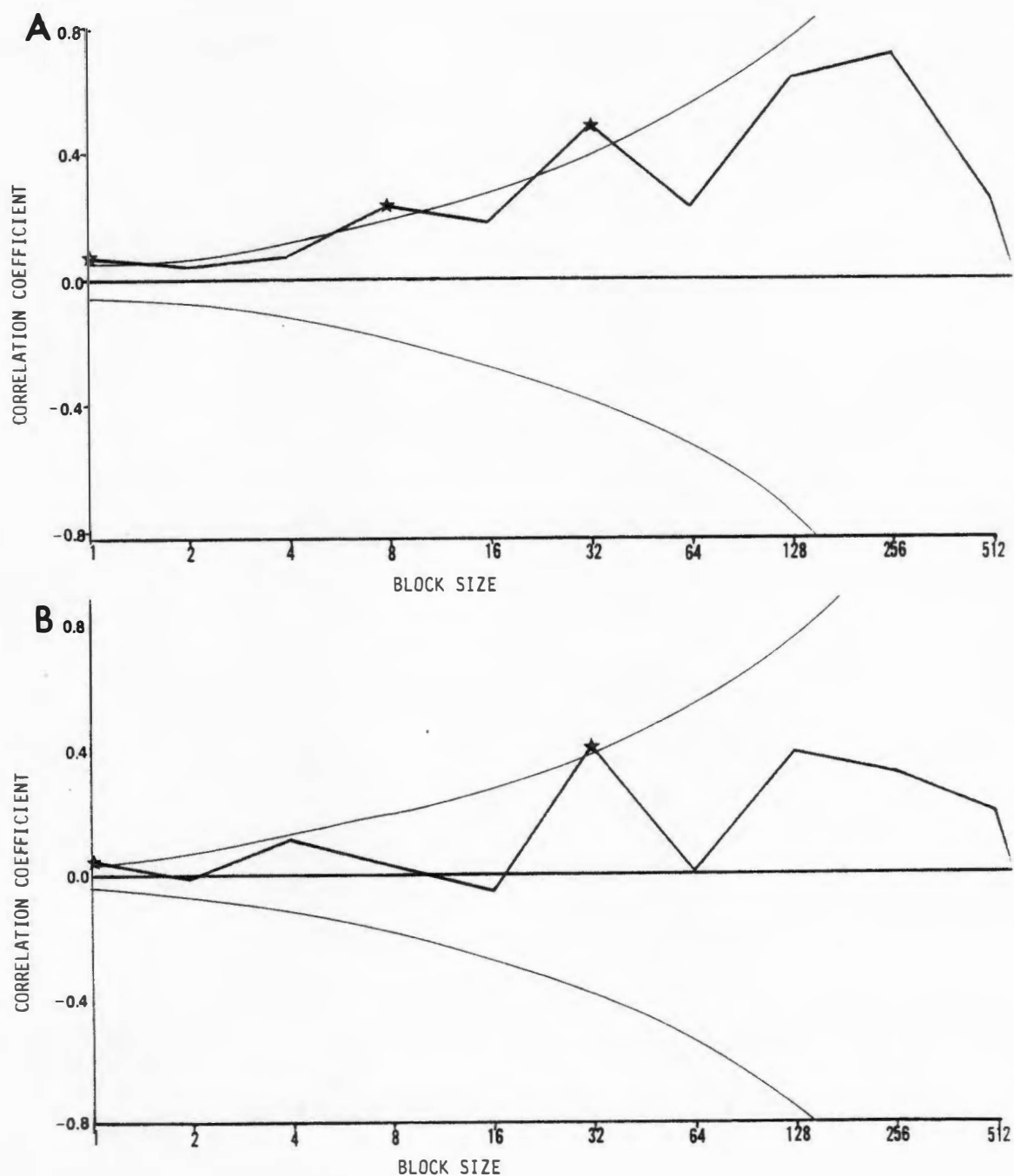


Figure 13. Covariance between web distribution and twigs (creek). Correlation coefficients for the respective heights (thick lines) along with the curves indicating the significance of the correlations ($p < 0.05$) (thin lines). In (A), significant correlations of webs with twigs at 0-50 cm were found at block sizes of 1 (☆: $p < 0.05$), 8 and 32 (★: $p < 0.01$). In (B), significant correlations (☆: $p < 0.05$) of webs with twigs at 50-100cm were found at block sizes of 1 and 32.

to 1 m at BS 2 m². This indicates the size of a block containing a branch which gives off twigs to which the webs are attached.

There is a negative association with leaf litter ($p < 0.05$) at block sizes of 8 and 16 m², indicating that blocks containing webs are never coincidental with areas of leaf litter at these block sizes; i.e., webs are never found away from water in the woods.

Lake habitat. The pattern for webs on the lake shows aggregation only at the largest block sizes (Fig. 14). This is because the area under study incorporated a large body of water; therefore, the difference between bank and water sections was only detected at large block sizes. The mean square / block size graph of water similarly shows a peak at BS 256 m² (Fig. 14).

The distribution of T. elongata on the lake is strongly related to the presence of water, as indicated by the results of the covariance analyses between web and water distributions (Fig. 15). Correlation coefficients show water and webs to be positively associated at block sizes of 2, 4 and 8 m². The absence of any association at the lowest block size reflects the fact that a large proportion of water quadrats were lacking webs. This is because a lot of open water had no structures to which T. elongata could attach its web. At BS 16 m² enough of the water block included land to render any association with this block size insignificant. Webs were associated with water at block sizes of 2, 4 and 8 m², probably the patch sizes of combined water and twig availability.

Correlation coefficients also showed twigs (at height of 0-50 cm, 50 cm-1 m and 1-2 m) and webs to be positively associated at block sizes

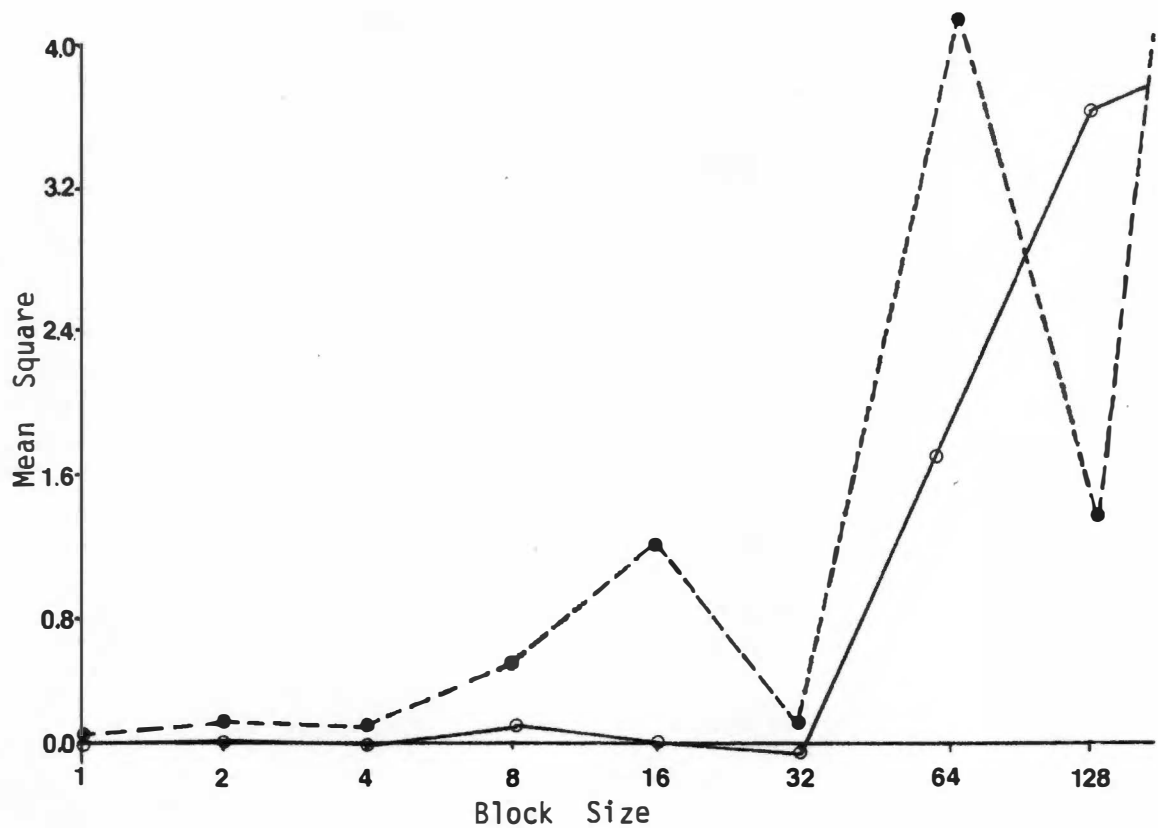


Figure 14. Distribution of lake water (solid line) and webs (broken line) at different block sizes. Mean square analysis shows peaks at the highest block sizes for both webs and lake water. This probably represents the area of clustering of both webs and water.

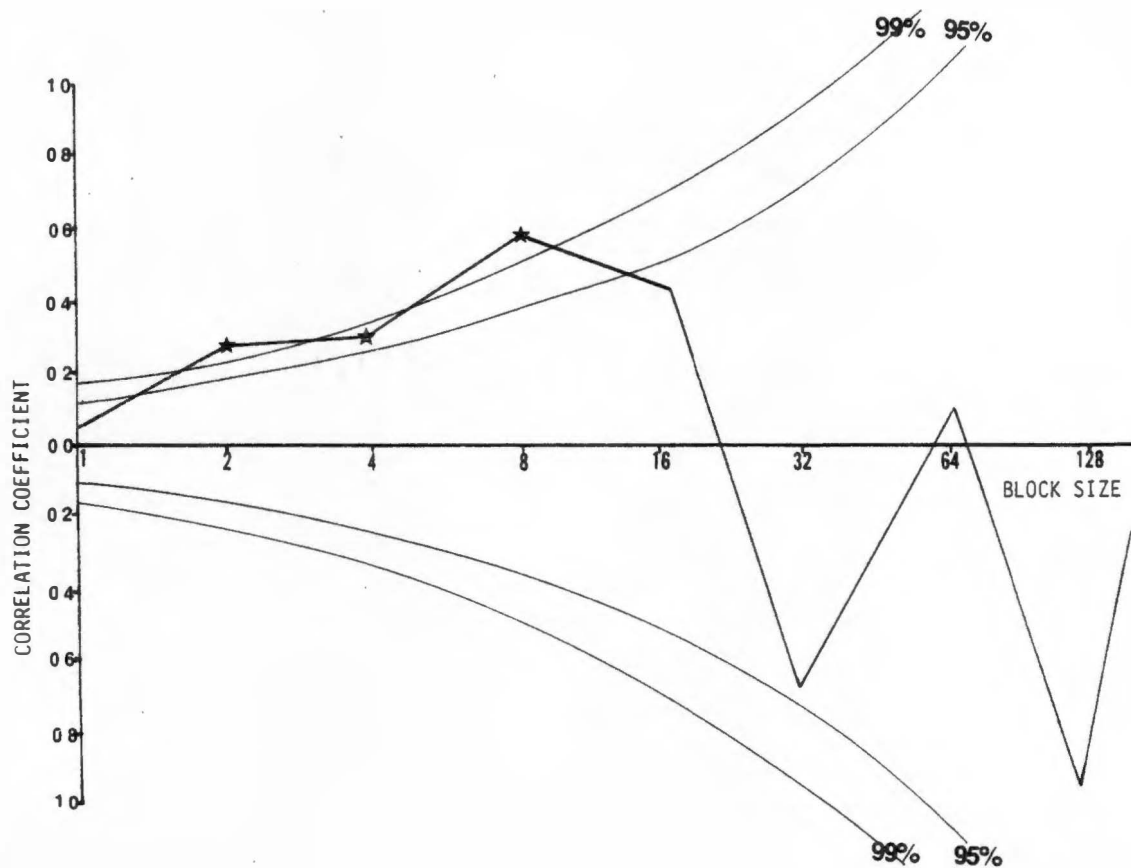


Figure 15. Covariance between web distribution and that of water (lake). Correlation coefficients are plotted (thick line) along with the curves indicating the significance of the correlation ($p < 0.05$) (thin line). Significant correlations were found at block sizes of 2 (★: $p < 0.01$), 4 (☆: $p < 0.05$) and 8 (★: $p < 0.01$).

of 1 and 2 m² (Fig. 16). This reflects the fact these structures were used as points of attachment for webs. Webs were built through these structures at heights of up to 2 m above the surface of the water. A similar association was found between webs and branches (0-50 cm and 50 cm-1 m), primarily at block size 1 m² (Fig. 17). This indicates that branches may also be used for web attachment in the lake habitat. Positive associations were also found at higher block sizes, which probably reflects the fact that twig distribution (with which the webs are generally more intimately associated) is correlated with branch distribution.

Three features associated with areas of open water are associated with webs at block sizes of 2 and 8 m² (or 2 and 4 m² in the case of light). These are 1) some air movement (the average velocity never exceeded 0.02 m/s), 2) high light intensity and 3) high temperature (see chapter II for methods used in measuring these parameters). The lack of significance at the lowest block sizes indicates that these factors alone are insufficient to account for the immediate presence of a web. The patchy nature of the significance of these associations is probably an artifact of the method of analysis: the more exposed stretches of water were all on the same side of the area examined.

Comparison of creek and lake habitats. Structures used for web attachment in both creek (Fig. 13) and lake populations (Fig. 16) were primarily twigs, although only the lower layers were used on the creek. Association with these structures was significant at the lowest block sizes on the lake; the significant associations in the creek habitat

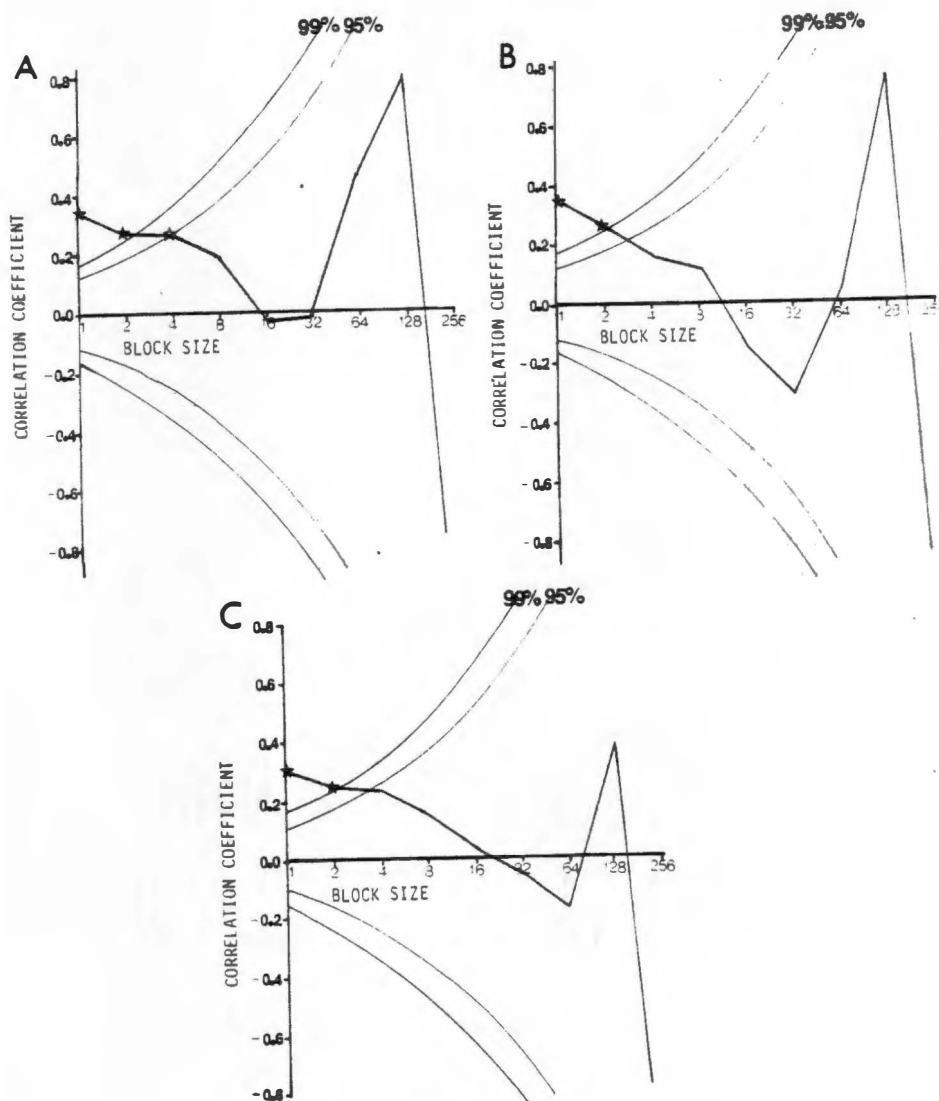


Figure 16. Covariance between web distribution and twigs (lake). Correlation coefficients are plotted for the respective heights (thick lines) along with the curves indicating the significance of the correlation ($p < 0.05$) (thin lines). In (A), significant correlations were found at block sizes of 1 and 2 (★: $p < 0.01$) and 4 (☆: $p < 0.05$). In (B), significant correlations were found at block sizes of 1 and 2 (★: $p < 0.01$). In (C), significant correlations were found at block sizes of 1 and 2 (★: $p < 0.01$).

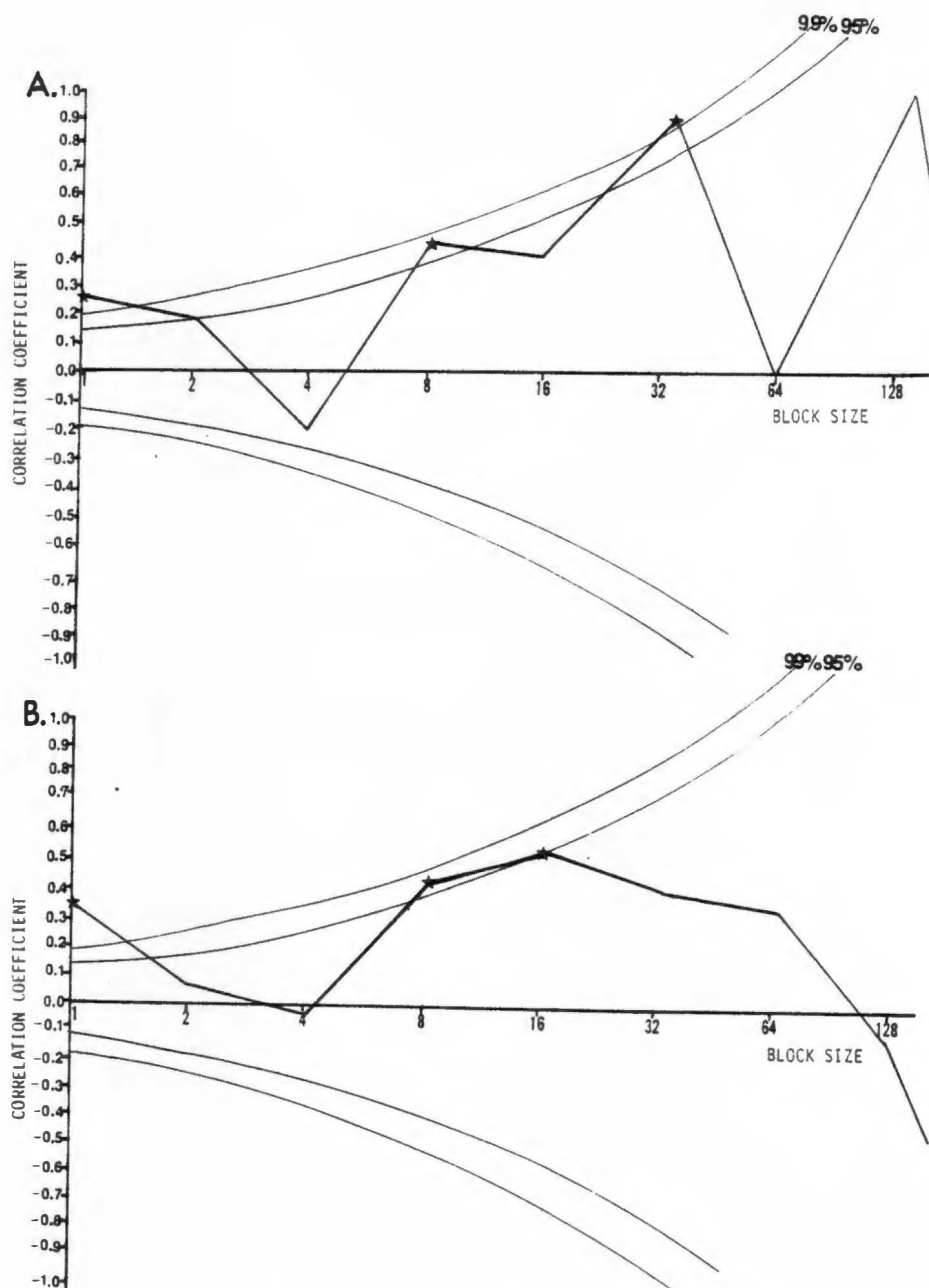


Figure 17. Covariance between web distribution and branches (lake). Correlation coefficients are plotted for the respective heights (thick lines) along with the curves indicating the significance of the correlation ($p < 0.05$) (thin lines). In (A), significant correlations were found at block sizes of 1 (★: $p < 0.01$), 2 and 8 (☆: $p < 0.05$) and 32 (★: $p < 0.01$). In (B), significant correlations were found at block sizes of 1 (★: $p < 0.01$), 8 and 16 (☆: $p < 0.05$).

were only at block sizes of 8 and 32 m² (and less so at 1 m²). In other words, webs are more intimately associated with twigs on the lake, which is a reflection of the higher web density in this population. Similarly, the association with water was significant at lower block sizes on the lake, indicating a more dense aggregation of webs in this habitat.

Factors Responsible for Survival and Web Building

The results from experiments to determine the effect of abiotic parameters on survival are shown in Table 3. From the table it is clear that, in any given situation, the factor generally responsible for death is desiccation. The rate of desiccation appears to be more a function of temperature than humidity, although the rate of weight loss was considerably reduced at high humidities. In any situation where spiders are denied direct access to water, however, desiccation appears to occur. But, even at high temperatures, virtually no weight loss was detected if individuals had direct access to open water.

The water loss suffered at different times of the day, and, at corresponding times, the effect of light intensity and temperature on web building are shown in Table 4 for both the cage where spiders had access to open water and the cage where this was denied. Also shown is the proportion of spiders with webs that were observed occupying the hub during a given time period. The primary determinant of web building is accessibility to open water. Without water, spiders were found never to build orbs. Under these circumstances, individuals suffered dehydration, the rate of which was determined by the temperature. Light intensity, although it does not appear to exert a significant effect on the presence of a web, does determine the activity pattern of the spider: at

TABLE 3. THE EFFECT OF TEMPERATURE, HUMIDITY AND OPEN WATER ON SPIDER SURVIVAL.

TREATMENT	MEAN RATE OF DESICCATION (wt. loss, mg/hr)	INITIAL WT. (MEAN) (mg)	% WT. LOSS TOLERATED (MEAN)
High temperature, low humidity, no water.	5.15 <u>+0.27</u>	56.13 <u>+5.92</u>	14.82 <u>+1.15</u>
High temperature, high humidity, no water.	4.42 <u>+0.34</u>	59.30 <u>+5.70</u>	15.12 <u>+0.41</u>
High temperature, high humidity, open water.	0.05 <u>+0.02</u>	60.93 <u>+5.70</u>	-
Low temperature, low humidity, no water.	0.13 <u>+0.02</u>	55.80 <u>+5.16</u>	-
Low temperature, high humidity, no water.	0.21 <u>+0.04</u>	60.35 <u>+4.73</u>	-
Low temperature, high humidity, open water.	0.00	64.08 <u>+5.68</u>	-

TABLE 4. DAILY VARIATION IN WATER LOSS, LIGHT INTENSITY, WEB BUILDING AND OCCUPATION OF THE HUB OF AN ORB, WHERE WATER IS AND IS NOT ACCESSIBLE.

TIME (hrs)	Mean light reading (lumens/m ²)	Mean temp. °C	WATER ACCESSIBLE		WATER NOT ACCESSIBLE	
			Mean water loss(mg)	% at hub (mean web #=2.8+.5)	Mean water loss(mg)	% at hub: No webs built
0600	-	0.00	-	100	11.0	-
0900	0.08	5.58	0	73	14.5	-
1200	0.34	6.05	0	70	19.5	-
1500	0.46	5.58	0	74	19.0	-
1800	0.21	3.72	0	80	19.0	-
2100	0.02	0.00	0	100	17.0	-
0600	-	0.00	-	100	11.0	-
0900	0.06	46.50	0	0	20.0	-
1200	5.34	186.00	0	0	29.5	-
1500	4.42	186.00	0	0	28.5	-
1800	2.83	65.10	0	0	19.0	-
2100	0.00	1.86	0	0	17.0	-

high light intensities spiders move off the hub of the orb. They do, however, continue to monitor prey impinging on the orb through tarsal contact with one of the bridge lines.

Total movement was also documented by recording the position of individuals in the uncovered (illuminated) sections of both cages each day. The average distance moved by an individual on any given day (averaged over 6 days) was found to be 74.0 cm (SD:49.57) in the cage with the bottom covered, and 29.6 cm (SD:20.2) in the cage providing accessibility to open water.

The effect of prey availability on web building was determined by counting the number of days on which webs were built for each spider. The average number for each feeding regime is shown in Table 5. As can be seen, there is a marked effect of prey availability on web building: spiders generally built webs daily when administered 20 flies per day (capture success was estimated at approximately 30%). In most natural situations, animals should encounter at least this number of insects. At very low prey availability (5 or 0) web building frequency was found to drop sharply, though even when prey were absent spiders were still found to build orbs, albeit at a low frequency. Indeed, where spiders were deprived of all external stimuli, webs were still built, though very infrequently. Over a period of ten days, a total of four webs were built (by different spiders) by the six individuals. None of these were maintained for more than 1.5 days (average 1.25 days).

The final experiment was a comparison of translocation frequency in spiders that had built webs versus those that moved from a site where they had not built. This showed that, if a spider had built an orb,

TABLE 5. THE EFFECT OF PREY AVAILABILITY ON WEB BUILDING.

TREATMENT (No. of insects)	AV. NO. WEBS BUILT (Mean & C.L.: taken over 10 day period)	NO. SPIDERS USED
20	10.92 (<u>+1.33</u>)	18
5	3.75 (<u>+1.88</u>)	9
0	1.28 (<u>+0.53</u>)	16

there was a 27% chance that it would move. If it had not, however, the chance of moving was 83%.

Discussion

The results from this study show that 1) The pattern of distribution of T. elongata is non random, spiders being found to be positively associated with areas over water that are suitable for web building. 2) In terms of abiotic parameters, the ability of a spider to survive in a given environment is determined by the rate of desiccation, this being a function of humidity and temperature. The effects of desiccation can be counteracted by access to open water (Table 4). 3) Where abiotic conditions are suitable, spiders will build orbs, but the frequency of web building is determined by prey availability (Table 5). 4) The probability of changing site is much higher where no web has been built. These results suggest a three component mechanism of habitat selection in T. elongata: 1) Random movement curtailed upon encountering a favorable abiotic environment. Alternatively, if they do not move, temporal variability may cause the environment surrounding the spider to change. The end result of either spatial or temporal change might trigger off 2) active search for a specific microhabitat within this environment which satisfies the requirements for web construction. 3) Site sampling occurs once the web has been built and leads to a repetition of the process if the spider's foraging requirements necessary for maintenance and egg production are not satisfied. (T. elongata loses weight, and will eventually die, when administered prey at a level much below ten insects per day; see Chapter IV)

The first component, the random search phase, has been recognized and described in a number of spider groups (Riechert and Gillespie, in press). The mechanism behind this procedure has been considered in terms of negative feedback (Sale 1969): where the environment is inadequate, low intensity feedback causes a high level of exploratory activity. As shown in this study, T. elongata does not build webs where or when the environment is unfavorable (i.e., there is no open water accessible). During this period, their activity may be largely non-directed exploratory movement, which would frequently enable them to locate a suitable environment. It may be that a similar mechanism is used by other species that are associated with specific forms and strata of vegetation that permit efficient perception and capture of prey (Hallander 1967, 1970, Kronk and Riechert 1979).

The second component involves active search for a specific microhabitat. The importance of spatial / architectural features of the habitat in determining the specific location of webs has been documented in araneids (Colebourne 1974) and linyphiids (Schaefer 1978). Such features may be even more important in social species where the colony is generally relatively permanent; structures of similar permanence in the habitat are therefore a prerequisite to its formation (Lubin 1974, Buskirk 1975b, Uetz and Burgess 1979). In this study, twigs appeared to be the structures of primary necessity for web building in T. elongata.

The final component considered to be involved in the habitat selection process of T. elongata is web relocation if the long term physiological needs of the animal are not satisfied. It differs from the first component of random search in that it cannot be explained by the

idea of negative feedback (Sale 1969). Rather, it is a continual trial and error procedure. Also, due to the effect of temporal variation superimposed on spatial variation, no one site can be optimal for any length of time. This component of the habitat selection process has been documented in many species that require web traps to be built before they can estimate the availability of prey in particular patches. Hildrew and Townsend (1980) report this type of behavior in the caddis fly larva Plectrocnemia conspersa. Amongst spiders, Turnbull (1964) found that individuals of the house spider Achaearanea tepidariorum, when released into an empty room, will continue to change web locations until all have built webs in the vicinity of a localized prey source (in this case a window, where flies were attracted to the light). In two studies on theridiid ant specialists, a change in web location has been shown to be associated with predation avoidance tactics of the ants: Holldobler (1970) noted that Steatoda fulva changes web location from one ant mound to another following cessation of ant usage of particular entrances. Mackay (1982) found that Latrodectus hesperus migrates from a nest of ants that have ceased to forage. The crab spider Misumena vatia leaves flowers that yield insufficient prey (Morse and Fritz 1982). And among tetragnathids, T. montana has been shown to base its web building activity on mosquito abundance: the frequency of web building decreases and overall movement increases with prey availability (Dabrowska Prot et al. 1968, Luczak 1970). Olive (1982) has shown that this process of web relocation occurs when the current rations a spider is receiving fall below its previous rations, and the effect of this tendency is aggregation of animals in quadrats with high ration levels. This

"decision" rule of when to leave a given site has been examined in terms of optimality theory in a number of spider groups (Janetos 1982a and b) and its application to T. elongata is discussed in the next chapter.

The three component sequence of habitat selection that I have proposed may well explain the mechanism by which a suitable habitat is located by most web building spiders. Numerous studies have shown the association of various spider groups with specific abiotic parameters in the microhabitat within a defined area (see Riechert and Gillespie, in press, for review). The mechanism of sampling at a given site is less well documented and is likely to vary, depending on the investment made in a web at any given site (Rypstra 1983). Spiders with a high investment are unlikely to build complete webs to sample prey availability, as the cost incurred by such behavior would be inordinately high. Gillespie (1981) showed that the cribellate spider Amaurobius similis (which has a very high web investment) continually lays single silk threads during the sampling period. This may enable the animal to monitor prey availability with only a minimal cost.

CHAPTER IV

RISK SENSITIVE FORAGING STRATEGIES AND THE TWO POPULATIONS

Introduction

One of the most active areas of behavioral ecology research concerns predation, and more particularly that on pest species. Holling (1959, 1966) introduced the concept of the functional response to describe how a predator responds to changes in prey density. This model does not, however, account for the fact that each of the many prey items available to a predator may vary according to nutritional value, spacing pattern and abundance, although cost of capture and processing can be incorporated into the model. In addition, each food exposes the animal to a different level of competition with other consumers and to a different risk of predation. Because an animal generally has only limited amounts of time and energy, its mechanism of resource acquisition and allocation may critically affect its survival and reproductive success. Even if food is not effectively limited, selection should favor efficient exploitation, because the most efficient foragers will have the most time for other activities (Morse 1980).

The benefit to the predator of capturing prey is clearly the energy gained from the environment. This is then available for metabolism and synthesis. Optimal foraging theory is a way of conceptualizing resource utilization to allow the generation of a testable hypothesis (Krebs 1978). Optimization models are designed in an attempt to recreate short term evolution in the imagination, and are currently the most widely used tools to predict the impact of predators on their prey (Hassell

1980). The general approach to their use in foraging theory involves three components. 1) A set of possible behavioral responses of the animal must be delineated, i.e., its "phenotype set" (Maynard Smith 1978). This phenotype set specifies the range of responses which is assumed to be available to the population through the action of evolution. 2) The state equations of the system must be delineated. These are the constraints describing how an organism's response is coupled to the environment. 3) The fitness criterion must be defined by giving a function over the phenotype set, which gives a specific fitness to each phenotype.

Although it is virtually impossible to delineate a complete phenotype set, an approximation can generally be made as to the range of possibilities. Delineation of the number and relative importances of the various constraints impinging on a system may be even more complex. The role of predators and competitors, for example, may have considerable influence on observed foraging behavior (MacArthur and Pianka 1966). Similarly, which optimization criterion is most applicable to any given situation is subject to debate (DeBenedictus et al. 1978, Pyke et al. 1977, Sih 1979). The most frequently applied criteria include the rate of net energy gain (Pulliam 1974, Charnov 1976, Oaten 1977, DeBenedictus et al. 1978, Waddington & Holden 1979), optimal use of time (Katz 1974, DeBenedictus et al. 1978, Craig et al. 1979, Pyke 1979, Hixon 1980) and total food uptake or reward (Oster 1976, Craig et al. 1979, Pyke 1979, Hixon 1980). Other criteria suggested include energy gain efficiency (Pyke 1979, DeBenedictus et al. 1978), survivorship (Caraco 1979a) and utility (Caraco 1980).

The classical optimal foraging models were developed for a deterministic environment. In the first paper on the subject, MacArthur and Pianka (1966) assumed that animals are capable of recognizing patches of food and accepting or rejecting them prior to entry. Patches, in these models, are considered to be concentrated food sources separated by areas of lower density, and most of the literature on foraging is organized around this concept. A predator is visualized as foraging on a number of different patches which vary in the quantity and quality of prey available. The question of interest concerns how a predator apportions its time between various patches so as to maximize fitness. The currency is assumed to be caloric gain, and the fitness criterion is taken as the net rate of energy gain.

A central concept in models of patch use is that of resource depression (Charnov et al. 1976) in which it is assumed that a predator's foraging activity causes a steady decrease in prey availability. This could come about by direct depletion of prey, or because prey take evasive action. An example of the latter context occurs in dungflies (Scatophaga stercoraria) which leave cowpats for surrounding grass when the presence of a hunting yellow wagtail (Motacilla flava) is detected (Davies 1977). The result is that the predator incurs diminishing returns with time in a patch.

In order to maximize its intake from a set of patches that suffer from resource depression, a predator should follow the rules of the Marginal Value Theorem (Charnov 1976). Suppose the time taken to travel between patches is T_1 , which is interpreted as a mean in this model, as are all other variables. We let t_1 be the time spent searching for food

in patch type i , these being the control variables. Suppose that p_i is the proportion of patches of type i , $i=1,2,\dots,n$; $E_i(t)$ is the net energy gain obtained by searching a time t in patch i , and E_r is the locomotory cost per unit travel time between patches. Then the average time between leaving one patch and leaving the next is

$$T = T_r + \sum_{i=1}^n p_i t_i \quad (1)$$

and the average net energy gain during this time is

$$E = \sum_{i=1}^n p_i E_i(t_i) - E_r T_r \quad (2)$$

The fitness criterion is

$$F = E/T = \frac{\sum_{i=1}^n p_i E_i(t_i) - E_r T_r}{T_r + \sum_{i=1}^n p_i t_i} \quad (3)$$

and the objective is to choose t_i^* , $i=1,2,\dots,n$ so as to maximize (3).

It can easily be seen by differentiating (3) that if dE_i/dt is a decreasing function, then the optimal t_i^* s are such that $dE_i(t_i)/dt = E/T$ for all $i = 1,2,\dots,n$, where E and T are calculated at the optimum $t^* = (t_1^*, \dots, t_n^*)$. This leads to two testable predictions. 1) That the optimal time to leave a patch is when the instantaneous rate of energy gain in that patch has reached the value of the overall rate of energy gain from all patches; i.e., the marginal value. All patches will be depleted to this same value. 2) If a comparison is made between habitats with different average profitabilities (E/T values), then the result implies that predators should remain a longer time in a patch with a given number of prey in the less profitable habitat than a similar patch in the more profitable habitat. Similarly, if travel time increases (for example, when patches are farther apart) the optimal time to stay in a patch also increases; the longer it takes to travel, the

lower the value of moving, and so the animal will tolerate a lower value for the instantaneous rate of energy gain.

This classical model of patch choice has a daunting list of simplifying assumptions. The forager, for instance, must be omniscient, recognizing a patch type instantaneously and knowing the travel time between patches. Once in a patch, the forager must feed according to the optimal diet (see Morse 1980) for prey types within that patch. Patches of type i are assumed to be at a constant density, and their proportion in the habitat does not vary with time. Travel time between patches is independent of the patches visited and incurs a constant locomotion cost. For each patch type there is an energy gain $E_i(t)$ after time t spent foraging in patch type i . The curve obtained by plotting $E_i(t)$ against time is smooth, continuous and decelerating. Finally, it is assumed that the forager, as well as being able to control the time spent in patch type t_i , will always act in such a way as to maximize its net rate of energy gain. Despite all these assumptions, however, the models seem to do quite well in predicting behavior for a wide range of animals such as, for example, great tits (Cowie 1977), wheatears (Carlson & Moreno 1982), starlings (Kacelnik 1984) and paper wasps (Kasuya 1982).

Deterministic models, such as the classical model of patch choice outlined above, are the most common approach to optimal foraging theory (Schoener 1971, Katz 1974, DeBenedictus et al. 1978, Caraco 1979a, Craig et al. 1979, Pyke 1979, Hixon 1980, Sih 1980). But, as has been argued by Oaten (1977), the stochasticity inherent in foraging problems should not be ignored. From the outset optimal foraging theory recognized that

most, if not all, parameters, such as the amount of energy obtained from an individual of a particular prey type, are random variables; i.e., they take different values with certain probabilities. In the classical models, like that outlined above, this type of random variability was adequately dealt with by the use of mean values. But there must be numerous cases in nature where the fitness of a foraging animal is a function not only of the mean values of certain parameters, but also their variances. Under such circumstances an animal cannot be omniscient (as is assumed in the deterministic models): it will only have an imperfect knowledge of what it may encounter at a future time and place (Pyke 1984). There are two major consequences arising from this effect of stochasticity (Stephens and Charnov 1982): 1) A forager may be uncertain about resource quality, so the acquisition of information becomes important. Rewards obtained at the start of a patch visit could be used to estimate patch quality and thus how long to stay (Oaten 1977, Kacelnik 1979, Green 1980, McNamara 1982, Iwasa et al. 1981). For this reason, an animal's foraging efficiency may depend on its sampling efficiency (Krebs et al. 1978, Houston et al. 1982, Lima 1984). Currently there is great interest in ecological questions concerning information in foraging processes (see Commons et al. in press).

2) The second consequence of stochasticity arises in environments where resource quality is not a function of time and therefore initial sampling of any given patch is less important. In this case, and when the outcome of a foraging decision is a random variable, there is a problem of "risk" (Keeney and Raiffa 1976). That is, the forager may possess full information concerning probability distributions of

benefits associated with available options, but the variation in those benefits and costs may still impose survival (and sometimes fecundity) risk (Caraco 1980, Real 1981, McNamara and Houston 1982, Pulliam and Millikan 1982, Stephens and Charnov 1982). In this case, experience does not reduce uncertainty. The rest of my discussion will be confined to this type of situation.

To study an animal's preference for a given survival / fecundity risk, we initially characterize a probability distribution of a foraging currency by its statistical moments: mean, variance (or standard deviation) and skew. The random variable of interest is either the cost of obtaining a required amount of food (Caraco 1981a) or the rate of energy intake (Stephens and Charnov 1982).

Consider the statistical moments of a set of benefit or cost distributions; i.e., the moments that describe that distribution, measure its properties, and, in certain circumstances, specify it (Hines and Montgomery 1980). For each member of this set of distributions these moments can be related to the probability that the forager will obtain less than its physiologically required intake in the time available for feeding. The probability of an energetic deficit is taken as the estimate of fitness in the following models (Caraco et al. 1980c, Pulliam and Millikan 1982), and the assumption is made that natural selection favors discrimination abilities (e.g. Commons 1981, Commons and Ducheny 1982). Therefore, a forager should always prefer the benefit distribution associated with the smallest attainable probability of an energy deficit (Caraco et al. 1980c, Houston and McNamara 1982, Pulliam and Millikan 1982, Stephens and Charnov 1982). Furthermore, these

probabilities should allow one to predict a preference ranking over available foraging options (Caraco 1983). The prediction from risk sensitive foraging theory is that, unlike deterministic approaches to foraging theory, the forager's preference for one reward over another need not be fixed, but can depend on a comparison of required and expected food intake (Caraco et al. 1980a, Stephens 1981, Houston and McNamara 1982).

As with other foraging models, risk sensitive foraging theory purposes to elucidate the optimal consequences of possible selective forces governing Darwinian evolution. Suppose an animal exploiting a stochastic environment has n foraging opportunities during a finite time interval. Denote the reward at trial i ($i=1,2,\dots,n$) with the independent random variable x_i . The mean and variance of each x_i are finite: $E[x_i], V[x_i] < \infty$. $Y = \sum_{i=1}^n x_i$ is the total reward acquired during the day. Then $E[Y] = \sum_{i=1}^n E[x_i] = n\mu$ and $V[Y] = \sum_{i=1}^n V[x_i] = n\sigma^2$. $F(Y)$ is the distribution function; $F(y) = \Pr[Y \leq y]$. As long as one x_i does not dominate the sum and the x_i s are not uniformly skewed, y should approach normality for sufficiently large n by the central limit theorem (Caraco and Lima 1985).

Assume that the forager must accumulate a total reward exceeding R to satisfy its daily physiological requirements. Let $F(R) = \Pr[Y \leq R]$ be the probability of an energy deficit, and the assumption is made that selection on survival favors minimizing this probability. Caraco and Lima (1985), following Stephens and Charnov (1982), have used a simple transformation to characterize the forager's problem. Since Y approaches normality, the random variable z ($z = (Y - \mu_Y) / \sigma_Y$) will be approximated by

the standard normal distribution. Minimizing $F(R)$ is then equivalent to minimizing

$$\Pr[z < (R - \mu_Y)/\sigma_Y] = \Phi(z_R)$$

Suppose the forager (fully informed by assumption) must choose to allocate its time to one of a series of reward probability distributions. In making a choice, larger means are always attractive since $\delta\phi(z_R)/\delta\mu < 0$. The influence of the standard deviation depends on the sign of $(R - \mu_Y)$. That is

$$\delta\phi(z_R)/\delta\sigma_Y > 0 \text{ if } \mu_Y > R \quad (4)$$

$$\delta\phi(z_R)/\delta\sigma_Y < 0 \text{ if } \mu_Y < R \quad (5)$$

When a forager can expect its intake to exceed its requirement ($\mu_Y > R$, a positive energy budget), increasing variance decreases an option's value. But when the forager can expect an energy deficit ($\mu_Y < R$, a negative energy budget), increasing reward variance enhances the value of an option (Caraco et al. 1980a, Houston and McNamara 1982, Pulliam and Millikan 1982, Stephens and Charnov 1982).

The following hypotheses can be derived immediately from (4) and (5). Consider an animal presented with experimental choices between a constant ($\sigma=0$) and a variable ($\sigma>0$) rate of energy intake, with both having the same expected value. According to (4), the animal should prefer the constant rate if its expected energy budget is positive. However, according to (5), the animal should prefer the variable rate if the expected energy budget is negative. These predicted behaviors are termed respectively "risk aversion" and "risk proneness" (Keeney and Raiffa 1976) since risk ordinarily is assumed to depend on a measure of variability (eg., Pollatsky and Tversky 1970).

The hypothesis is based on the premise of minimization and considers only immediate survival, taking fitness (W) as a step function of the total rate of energy intake over a given period. That is

$$W = 0, \text{ if } Y \leq R$$

$$W = 1, \text{ if } Y > R$$

$E[W]$ then becomes $\Pr[Y > R]$.

McNamara and Houston (1982) point out that this step function neglects the effect of the energy intake during one period on the future survival and reproduction of the animal. That is, all foragers with a daily food intake exceeding the physiological requirement need not be equally "fit". When energy can be stored on one day and used the next, it is very possible that $dW/dY > 0$ for at least some $Y > R$. Caraco (1980) and McNamara and Houston (1982) adopt a convex-concave fitness function where $dW/dY > 0$ and

$$d^2W/dY^2 > 0 \quad \text{for } Y < R \quad (6)$$

$$d^2W/dY^2 < 0 \quad \text{for } Y > R \quad (7)$$

These two expressions are analogous to (4) and (5) in that convexity (i.e. bowed downwards) implies that the expected fitness increases with reward variability and concavity (i.e. bowed upwards) implies that the expected fitness decreases with reward variability (Caraco 1980, Caraco and Lima 1985). A risk sensitive animal is expected to exhibit a sigmoidal fitness function, switching from convex to concave at the point at which it changes from a positive to a negative energy budget.

Most of the tests of this model have been performed using small granivorous birds: yellow eyed juncos (Junco phaeonotus) (Caraco 1980, Caraco et al. 1980a), dark eyed juncos (Junco hyemalis) (Caraco 1981a

and 1981b) and white crowned sparrows (Zonotrichia leucophrys) (Caraco 1983); or hymenopteran pollinators (Real 1980a, Waddington et al. 1981, Real et al. 1982). Labile risk sensitive foraging preferences have also been found in rodents (Sorex araneus L.) (Barnard and Brown 1985) and may be common in small homeotherms that must regulate their food intake over relatively short periods of time. Demonstration of preference for different levels of reward variability may indeed be a fairly universal phenomenon amongst animals that are governed by severe time constraints, where a negative energy budget will reduce fitness to zero, and incur diminishing returns from further exploitation of food while on a positive energy budget.

In this chapter I examine the possibility that dichotomous foraging modes, observed in a large number of species and species groups, may be explained in terms of differential risk responses. Pianka (1966), working with lizards, recognized two extreme types of foragers on the basis of the relative importance of searching and pursuit in their foraging repertoires: 1) Those that "sit and wait" for prey, capturing it by ambush; and 2) those "mobile" predators that hunt actively for their food. Subsequent studies have developed this concept (Pianka, Huey & Lawlor 1979, Huey & Pianka 1981). More recently, spiders have been used to examine dichotomous foraging strategies (Janetos 1982a and b, Nakamuru 1982, Riechert and Luczak 1982) and their possible ecological correlates (Richter 1970, Olive 1981a and b). Comparative studies like this, as with those on the lacertid lizards, do, however, suffer from being made across different species. As a result, there are numerous confounding variables making definitive conclusions unreliable at best

(see Clutton Brock and Harvey (1984) for a discussion on the problems of interspecific comparison). Nevertheless, spiders are ideal tools for examining foraging behavior, numerous studies having documented its intimate behavioral dependence on prey availability (Cherrett 1964, Turnbull 1964, Dabrowska Prot and Luczak 1968a and b, Hardmann and Turnbull 1974, Greenstone 1978, Lubin 1978, Holldobler 1970, Uetz and Burgess 1979, Bishop 1981, Gillespie 1981, Rypstra 1981, Wise 1981, Mackay 1982, Morse and Fritz 1982). The present chapter examines the foraging strategies of the two local populations of Tetragnatha elongata in the context of the sit-and-wait versus mobile search dichotomy. It is based on the premise that this species exploits "patches" in the environment: i.e., units between which fitness prospects differ (Wiens 1976). Tetragnatha elongata exploits a wide variety of riparian habitats in the eastern U.S. (Levi 1981), which exhibit high temporal and spatial variability. Across a gradient in patch quality, a single species might be expected to exhibit phenotypic plasticity, exploiting resources in different ways under changing conditions (Morse 1971, Slater 1981). The extent and form of plasticity in foraging behavior is little known in spiders, apart from sexually related differences (Givens 1978). This study is confined to different populations of adult female T. elongata. A model is presented which is designed to relate a given foraging strategy to the costs / benefits encountered by an individual, in the light of stochastically changing resource availability. This model is based on risk sensitivity and suggests a parallel to the sit-and-wait / mobile search dichotomy. A test of the model's predictions is made using the two populations of T. elongata which occupy markedly different

habitats already described.

A complete study of optimal foraging must include three components (Oster and Wilson 1978): 1) Construction of a model on the basis of natural history experiments and intuition, taking into account the animal's state space, its collection of strategic alternatives, the most applicable fitness criterion and the relevant constraints (part I); 2) derive a set of predictions from the model analysis (model); and 3) test these predictions using empirical observations (part II). Following reconnaissance observations (Lehner 1979) the present study was accordingly divided into two parts: 1) Determination of the parameters pertinent to a given foraging behavior to allow the formulation of a reasonable model to describe its behavior; and 2) testing the validity of the model developed. The study was conducted over three field seasons (June -September of 1982-1984). Following reconnaissance observations during the first field season, I set out to determine the relevant parameters to describe the foraging behavior of the species. A model was then developed to describe the behavior, its validity being tested in the final field season.

Methods I

Correlates of Foraging Mode

This part of the study was divided into descriptive comparison of behavior and experimental manipulation:

Demography. A total of six aspects of the behavior of the two populations were examined and compared: activity patterns, spider

densities, web relocations, distance moved during web relocation, number and types of prey items caught and web take overs.

Activity patterns. During the first field season (1982), the activity patterns of the two spider populations were determined by documenting the activity of individuals through a 24 hour cycle. At 1/2 hour intervals, all spiders that could be censused (lake spiders, $n = 98$; creek spiders, $n = 52$) were monitored as to their activity: wandering / travelling, stationed at the hub of the orb, actively monitoring prey impingent on the web, or inert (stretched out so as to be camouflaged against the substrate). A total of seven 24 hour sampling periods were collected for each habitat.

Comparison of spider densities. In order to estimate local spider density, individuals were marked on their abdomen with Airfix^(R) paint, a fast drying enamel, applied with a paintbrush bristle. Only adult females were used, thereby avoiding problems arising from spiders molting. A color code was adopted using different legs and colors to positively characterize individuals. The number and position of specific individuals in a given area was then monitored at weekly intervals throughout the field season (June 14th - August 31st). The position of marked individuals was recorded, any unmarked individuals being caught and marked as they were found. In this way individuals in the area could be tracked throughout the field season. On the lake, a total of 149 spiders were marked in 16 observation periods, made at approximately 4 day intervals from June 20th to August 31st. Data were collected from a 5 m x 5 m study area only. On the creek, a total of 71 spiders were marked in the course of daily observations over the 79 day field

session. The area used was a 26 m section over the creek (width 0.7-1.2 m). These measurements allowed an estimate of spider density (number of individuals per m^2) and its variation through the season. This was found by counting all marked and unmarked individuals and dividing this value by the area under study ($25 m^2$ on both the lake and the creek).

The number of web relocations made by individuals. Marked spiders were used again to determine the frequency at which they changed the location of their webs. An index was obtained on the lake by tallying all spiders that had changed web sites between consecutive observation periods. In order to make the creek results comparable to the lake, only the data gathered during the same 16 days from this population was used in the estimate.

Estimation of the distance moved during web relocation. Marked spiders were used again to estimate the distance moved when spiders changed web location, with only those spiders that were observed to relocate between observation periods included. A metric tape was used to measure the shortest distance between web locations used by an individual on consecutive observation periods.

The numbers and types of prey items caught. Focal animal sampling (Lehner 1979) was used in studying prey capture behavior (1/4 hour observation period). Animals were selected at random and the number and size of prey items (in mm) caught within the sample period was recorded. Samples were taken throughout the day. A minimum of eight replicates were made for each 1/4 hour interval in the 24 hour cycle. A headlamp, covered with red / orange plastic and directed away from the

web to minimize the effect of light on insect activity, was used for night time observations.

Experimental manipulation. The nature of the behavioral differences between the two populations was farther examined through two experimental manipulations: prey availability and habitat crossplants.

The effect of prey numbers on web building. Twenty four individual cages were set up along the stream bed. The cages consisted of wooden rims (39.3 cm x 39.3 cm x 11.4 cm), the entire inner surfaces of which were lined with fine wire screening. Nine circular apertures (diameter 9 cm) on the top and sides allowed for aeration. Glass plates were latched on to the front and back of these structures to facilitate observations. Weighed spiders were placed individually inside the cages. The spiders were fed field collected fruit flies (Drosophila melanogaster: average weight 2.59mg). The methods used have already been outlined in the "Factors responsible for survival and web building" in the previous chapter. Spiders were subjected to one of six treatments for a period of 14 days: insects administered at a rate of 40, 20, 10, 5, 2 and 0 D. melanogaster per 24 hour period. The cages were examined for the presence of an orb at 0600 and 2100 hours daily.

The plasticity of foraging behavior. The effect of habitat on foraging behavior was examined by means of reciprocal transfer experiments. Two identical cages (2 m x 2 m x 1 m) were constructed using wooden struts. Plastic (clear polythene) was used to cover the sides. Netting covered the top of the cages. One cage was placed on the gravel floor of the creek. The other was suspended over the lake by means of a rope from an overhanging tree. The floor of both cages was

uncovered so as to allow insects to emerge from the water into the cage. Five spiders from the lake were placed in the cage on the creek, and five from the creek in the cage on the lake. The activity of individuals was recorded at intervals throughout the day for comparison with the activity patterns of the animals naturally occupying the respective habitats. A total of three replicates were made over consecutive 16 day periods, using different spiders in each replicate.

Results I

Correlates of Foraging Mode

Demography. Table 6 summarizes the various population parameters and foraging differences between the lake (n=132) and creek (n=61) spiders.

Activity patterns. The proportional number of individuals engaged in various behaviors at a given time were used to investigate activity pattern. For each of the three primary activities (Fig. 2), the t-statistic generated indicated a significant difference between habitats ($p < 0.01$ in each case). The activity most affected by site, however, was the time spent at the hub of the orb. Comparison of this activity on the creek versus the lake is shown for a 24 hour period in figure 18.

Comparison of spider densities. In order to determine the spider density in the two habitats, comparable areas were used on both the creek and the lake (a 5 m x 5 m section over the water on the lake; a 26 m stretch along the main stream [0.8-1.2 m wide] of the creek).

TABLE 6. SUMMARY OF VARIOUS POPULATION PARAMETERS AND FORAGING DIFFERENCES ON THE CREEK VERSUS THE LAKE HABITATS.

	CREEK	LAKE
SPIDER DENSITY		
mean, C.L.	0.55+0.38 spid./m ²	3.13+1.96spid./m ²
range	0.3-0.9 spiders/m ²	2.0-5.3 spiders/m ²
NO. SITE CHANGES / DAY (mean, C.L.)	0.056+0.082	0.753+0.909
DISTANCE MOVED BETWEEN SITES (m) (mean, C.L.)	4.417+6.662	1.586+2.979
NO. PREY CAUGHT / HOUR (mean, C.L.)	0.745+2.666	2.126+4.873
FREQUENCY WEB SITE TAKE OVERS	0.15 (n=25)	0.00 (n=58)
MEAN PROPN FEMALES RAIDING THE WEB OF ANOTHER PER DAY	0.00 (n=25)	0.37 (n=58)

Values for spider density, frequency of site change, distance moved between sites and number of prey caught per hour were taken over the 1983-1984 field seasons (n=132 for the lake; n=61 for the creek). A t-test was used to find the significance of the difference in frequency of web relocation ($t=4.55$ $p<.001$). A GLM analysis of variance was used to test the significance of the differences between the lake and the creek with regard to distance between sites ($F=30.42$ $p<.001$) and prey capture rate ($F=39.45$ $p<.001$).

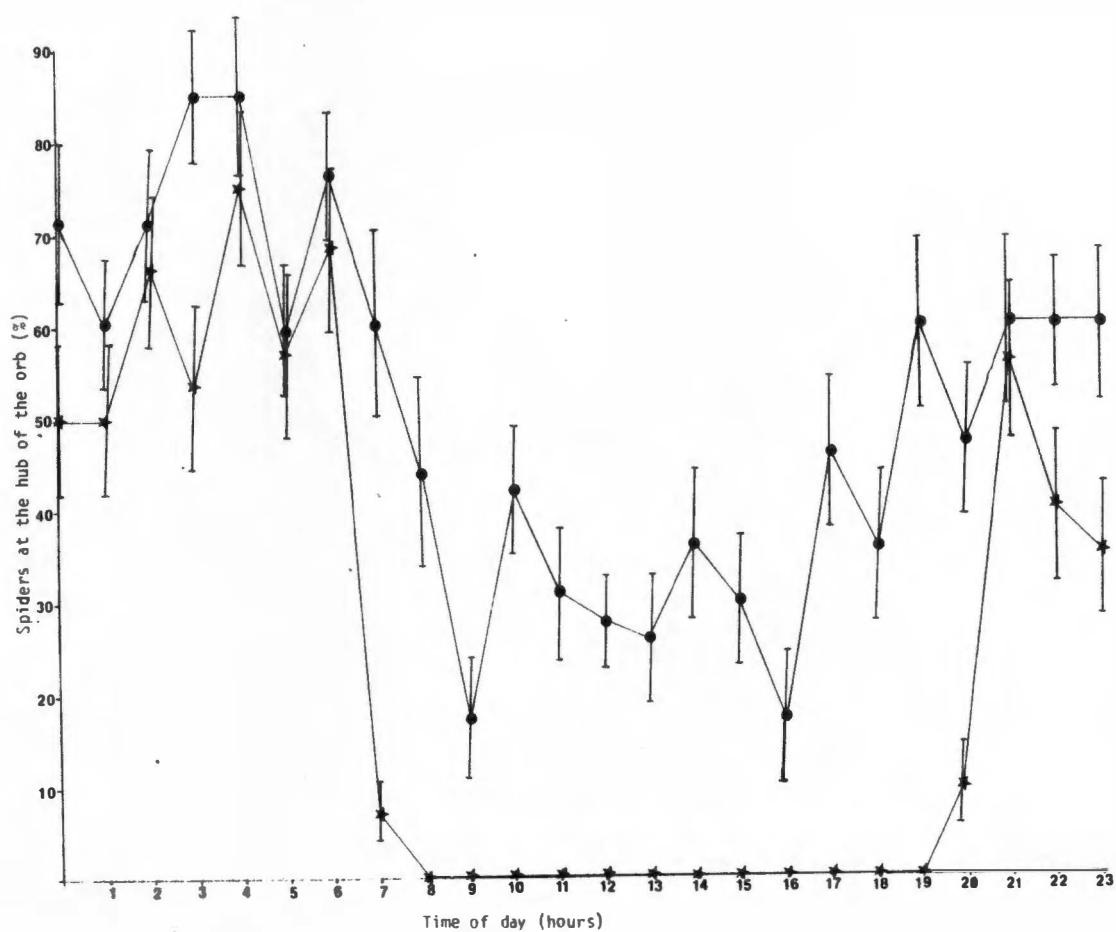


Figure 18. Percentage of spiders found at the hub of the orb (lake $n=98$, creek $n=52$) at hourly intervals throughout the day on both the creek (•) and the lake (*) spiders.

Densities on the lake increased from 2 spiders per m^2 (June 16th 1984) to 5.3 spiders per m^2 (25th August 1984) during the season. On the creek, densities gradually declined from .95 spiders per m^2 (14th June 1984) to .30 spiders per m^2 (22nd August 1984) during the season. Densities were therefore always very much higher on the lake than on the creek.

The number of web relocations made by individuals. The frequency of web relocation was determined by dividing the total number of individuals that had changed web sites between two consecutive observation days by the total number of spiders that were observed in both these consecutive periods. These values were summed and divided by the total number of observation periods (16) to give the average number of moves made by an individual in any given 4 day period between observation days, and are shown in Table 6. As can be seen, movement on the lake was over an order of magnitude greater than that on the creek.

Estimation of the distance moved during web relocation. The average distance moved during these relocations was found to be 4.42 m on the creek (SD=3.33, n=24). On the lake the distance moved was only 1.59 m (SD=1.52, n=58). Creek spiders covered over twice the distance of lake spiders during web relocation. Analysis of variance (GLM) indicated that this difference was highly significant ($F=30.42$, $p<0.001$).

The numbers and types of prey items caught. The mean prey capture rate was found to be 0.75 insects per hour (SD=1.33, n=237) on the creek. On the lake, however, the capture rate was 2.13 insects per hour (SD=2.49, n=187). A t-test was used to compare these prey capture rates and indicated a highly significant difference ($t=7.31$, $p<0.001$).

Figure 19 shows the variation in prey capture rate through the day for both habitats and indicates that the pattern and amount of prey capture is markedly different in the two habitats. On the lake the capture rate is much higher, and is also confined to the hours of approximately 2000 - 0700. Prey are captured at a very low rate throughout the 24 hour period on the creek.

Experimental manipulation.

The effect of prey numbers on web building. Spiders were found to be highly responsive to prey availability at both upper and lower extremes. Web building frequency dropped sharply when five or fewer insects were administered daily. A basal level (webs built, on average, on 9% of the 14 day period) was found when no prey were administered. At very high prey availability (40 insects per day), the decline was more gradual. At all intermediate levels, however, web building frequency was fairly constant. As most habitats occupied by the spiders would offer prey within this range, web building frequency in the natural habitat might be expected to be relatively independent of prey availability.

The plasticity of foraging behavior. The effect of habitat on foraging behavior was examined by calculating the frequency of each activity (walking, at the hub and flat against the substrate) for each time period (0000, 0100, ..., 2400 hours) for spiders transferred from the creek to the lake and vice versa. A series of t-values were generated to compare the activity patterns of the translocated spiders with those characteristic of its parent population as well as of its new habitat (Table 7). The proportion of spiders changing web site on

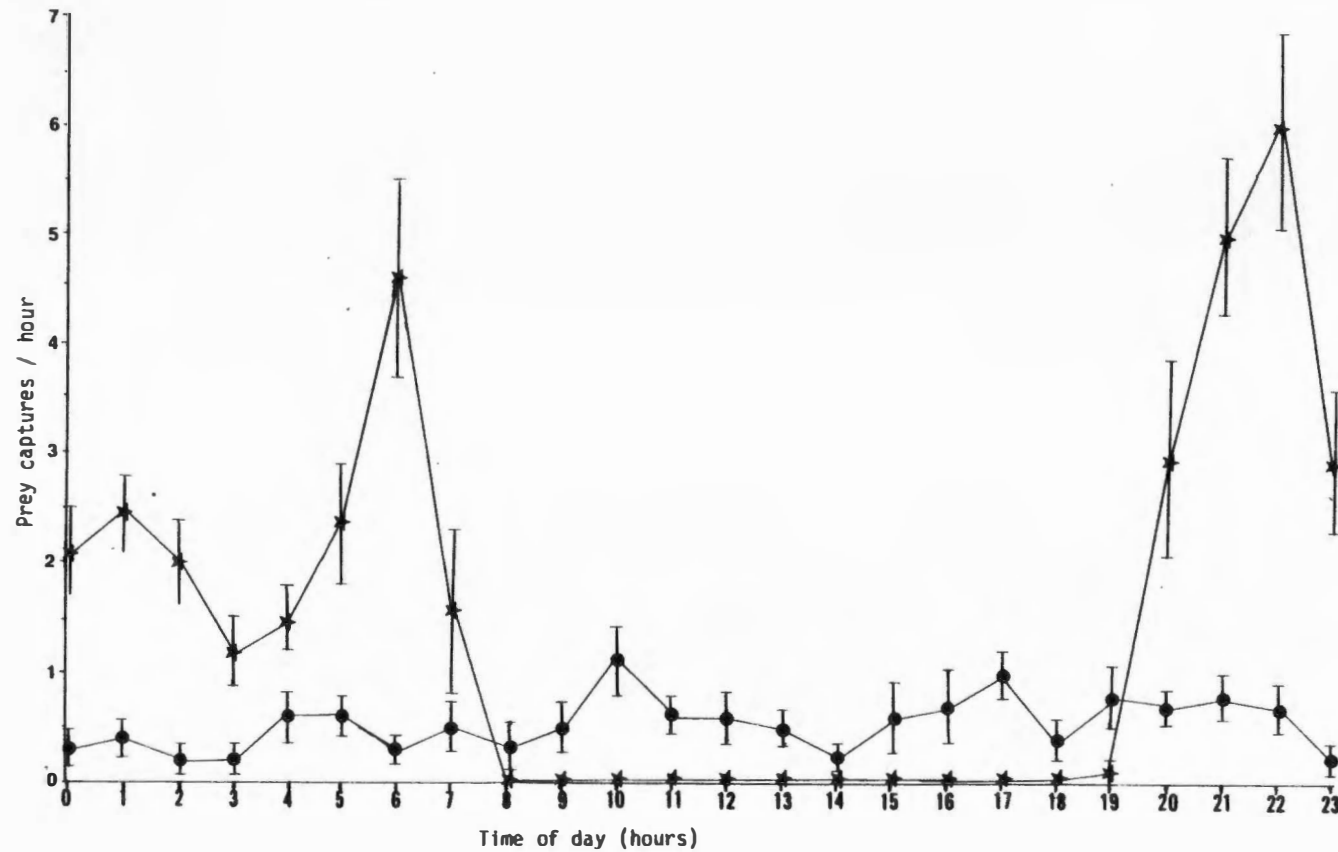


Figure 19. Comparison of daily prey capture rates by spiders on the lake (*) and the creek (.). Mean and standard deviations of the hourly prey capture rate.

TABLE 7. RECIPROCAL TRANSFER EXPERIMENTS: COMPARISON OF PRIMARY ACTIVITIES IN CREEK AND LAKE TRANSPLANTS.

	LAKE	TRANSFERRED LAKE- CREEK	TRANSFERRED CREEK- LAKE
CREEK	walk	t=2.97 p<.01	t=0.85 N.S.
	hub	t=8.17 p<.0001	t=4.83 p<.001
	flat	t=2.92 p<.005	t=7.98 p<.001
LAKE	walk	t=1.27 N.S.	t=6.67 p<.001
	hub	t=2.40 p<.05	t=0.63 N.S.
	flat	t=6.14 p<.001	t=0.14 N.S.
TRANS- FERRED LAKE- CREEK	walk		t=0.11 N.S.
	hub		t=3.44 p<.01
	flat		t=8.97 p<.001

The table shows a series of t values calculated to compare the observed foraging pattern of a translocated spider with its parent population and with the population to which it is transferred (N.S.=not significant, i.e., $p > .05$).

consecutive days was also calculated. Creek spiders were found to change sites at a frequency (average 0.812; SD=0.413) comparable to lake spiders when translocated; there was no significant difference between the respective values for relocation frequency (t-test: $t=1.821$, $p>0.05$). Lake spiders changed site at a frequency (average 0.160; SD=0.409) only slightly higher than creek spiders when translocated; but again, the difference between the values for relocation frequency was not significant (t-test: $t=1.821$, $p>0.05$). The distance moved between sites did not, however, differ significantly between the two sets of translocated spiders. This latter finding is almost certainly due to the constraining influence of the cage to which the spiders were confined. These results demonstrate, therefore, that spiders adopt the activity patterns characteristic of the habitat to which they have been translocated. This indicates that foraging mode in T. elongata is not constrained genetically; rather it varies with environmental characteristics.

The Model

Based on the results obtained in the first part of this study (see above), the following model was developed, in collaboration with Dr. Thomas Caraco of the State University of New York at Albany, to describe the behavioral differences between the spiders from the two habitats. Consider two theoretical strategies: a spider chooses to be a sit-and-wait predator or a mobile predator. Neither strategy uses information that might be gained from recent experience. This may be realistic for certain invertebrate predators that have a limited ability to process

information. Since: 1) a female will generally build a web each evening (having ingested the remains of the previous orb) independently of foraging mode; and 2) movement takes less time (and probably less energy) than web construction, the overall costs of the two strategies are initially taken as equivalent. In the discussion I examine the applicable criterion when the mobile strategy is more expensive.

Suppose that a spider must capture more than R prey over a season lasting n ($n > 1$) days in order to survive and successfully produce an egg sac. Then it fails to reproduce if it captures a total of R or fewer prey. To examine the potential effects of environmental stochasticity and risk-sensitivity on choice of foraging mode, the model's assumed objective is minimization of the probability of reproductive failure.

The Environment

At any particular web site the probabilistic rate of prey capture is λ . Site quality varies spatially, so λ itself can be assumed to be a random variable. Specifically, the distribution of λ across possible web sites can be assumed to follow a gamma density:

$$f(\lambda) = \lambda^{\theta-1} \alpha^{-\theta} e^{-\lambda/\alpha} / \Gamma(\theta) \quad (1)$$

$$\lambda > 0; \alpha, \theta > 0; \Gamma(\theta) = \theta \Gamma(\theta-1)$$

The expected rate of prey capture in the environment is $E[\lambda] = \alpha\theta$, and its variance is $V[\lambda] = \alpha^2\theta$. The gamma density accomodates a wide variety of shapes; hence it is a good model for many continuous, non-negative random variables (Bury 1975).

Sit-and-Wait Predator

A sit-and-wait predator selects a foraging site and builds a new

web at the same location on each of n days. The selection of a site can be equated with sampling randomly from the distribution of λ . That is, the predator "knows" $f(\lambda)$, but the capture rate at any particular site is unknown at the time of deciding to sit and wait. Once λ has been determined, the count of prey captured becomes a conditional Poisson process. However, the marginal probabilities for the number of captured prey and the consequent probability of reproductive failure must be calculated at the decision point, before the particular value of λ is realized.

Let the non negative discrete variable Y_s represent the total number of prey captured by a sit-and-wait predator over the n days of the season. Given a particular prey capture rate λ (i.e., given selection of a particular web site), Y_s is a conditional Poisson process:

$$\Pr[Y_s=y | \lambda] = e^{-\lambda n} (\lambda n)^y / y! \quad (2)$$

Since λ is a random variable, the marginal distribution of Y_s at the decision point depends on $f(\lambda)$. Marginally,

$$\Pr[Y_s=y] = \int_0^\infty \Pr[Y_s=y | \lambda] f(\lambda) d\lambda \quad (3)$$

$$= \int_0^\infty [e^{-\lambda n} (\lambda n)^y / y!] [\lambda^{\theta-1} \alpha^{-\theta} e^{-\lambda/\alpha} / \Gamma(\theta)] d\lambda \quad (4)$$

The Y_s follows a negative binomial probability function:

$$\Pr[Y_s=y] = \binom{\theta+y-1}{y} \left(\frac{1}{n\alpha+1} \right)^\theta \left(\frac{n\alpha}{n\alpha+1} \right)^y \quad (5)$$

This is a standard result (e.g., Pielou 1975). Given that Y_s is a negative binomial variate

$$E[Y_s] = n\alpha\theta; \quad \text{and} \quad (6a)$$

$$V[Y_s] = n\alpha\theta(n\alpha+1) \quad (6b)$$

The probability of a reproductive failure for the sit-and-wait predator is $\sum_{y=0}^{\infty} \Pr[Y_S=y]$.

Mobile Predator

A mobile predator changes its foraging site on each of the n days. This strategy can be equated with n random and independent samples from $f(\lambda)$. Let the non-negative discrete random variable X_i represent the number of prey captured by a mobile predator on day i ($i = 1, 2, \dots, n$). Given a particular capture rate λ , X_i is conditionally a Poisson variate:

$$\Pr[X_i=x | \lambda] = e^{-\lambda} \lambda^x / x! \quad (7)$$

Since λ is also a random variable, the marginal distribution of the number of prey captured on day i depends on $f(\lambda)$:

$$\Pr[X_i=x] = \int_0^{\infty} \Pr[X_i=x | \lambda] f(\lambda) d\lambda \quad (8)$$

The nX_i must follow a negative binomial probability function, and

$$\Pr[X_i=x] = \binom{\theta-x-1}{x} \left(\frac{1}{\alpha+1} \right)^{\theta} \left(\frac{\alpha}{\alpha+1} \right)^x \quad (9)$$

Now let Y_m represent the total number of prey captured by a mobile predator over the n days of the season; $Y_m = \sum_{i=1}^n X_i$. Since each X_i is an independent and identically distributed negative binomial variate with parameters α and θ , their sum (Y_m) is a negative binomial variate with parameters α and $n\theta$ (DeGroot 1970). Therefore,

$$\Pr[Y_m=y] = \binom{n\theta+y-1}{y} \left(\frac{1}{\alpha+1} \right)^{n\theta} \left(\frac{\alpha}{\alpha+1} \right)^y \quad (10)$$

Since Y_m is a negative binomial variate,

$$E[Y_m] = n\alpha\theta; \quad \text{and} \quad (11a)$$

$$V[Y_m] = n\alpha\theta(\alpha + 1) \quad (11b)$$

The probability of a reproductive failure for a mobile predator is

$$\sum_{y=0}^R \Pr[Y_m=y].$$

In the same environment, i.e., given a particular $f(\lambda)$, the two strategies yield identical expected values for the total number of captured prey; $E[Y_s] = E[Y_m] = n\alpha\theta$. However, the variance of the total number of prey captured is greater for the sit-and-wait strategy; $n\alpha\theta(n\alpha + 1) = V[Y_s] > V[Y_m] = n\alpha\theta(\alpha + 1)$. This result suggests that under certain conditions risk-aversion might favor the mobile strategy, and risk-proneness might favor the sit-and-wait strategy (Caraco et al. 1980a, Caraco 1981a, McNamara and Houston 1982, Stephens and Charnov 1982, Barnard and Brown 1985). This possibility will now be examined.

Comparing the Strategies

For the sit-and-wait predator, the probability of reproductive failure is

$$\Pr[Y_s < R] = \sum_{y=0}^R \left(\frac{\theta+y-1}{y} \right) \left(\frac{1}{n\alpha+1} \right)^\theta \left(\frac{n\alpha}{n\alpha+1} \right)^y \quad (12)$$

For the mobile predator the corresponding probability is

$$\Pr[Y_m < R] = \sum_{y=0}^R \left(\frac{n\theta+y-1}{y} \right) \left(\frac{1}{\alpha+1} \right)^{n\theta} \left(\frac{\alpha}{\alpha+1} \right)^y \quad (13)$$

Each of the probabilities is a distribution function of a negative binomial, designated by F_{NB} , evaluated at the foraging requirement R . F_{NB} can be expressed in terms of the distribution function of a beta variate, designated by F_β (Peitzner and Pratt 1968):

$$F_{NB}(Y_j; p_j, c_j\theta) = F_\beta(p_j; c_j\theta, Y_j+1) \quad (14)$$

The probabilities given in equations (12) and (13) lead to the following representation in terms of F_β :

$$\Pr[Y_j < R] = \int_0^{p_j} x^{c_j\theta-1} (1-x)^R dx / \int_0^1 x^{c_j\theta-1} (1-x)^R dx \quad (15)$$

For the sit-and-wait predator the entries in equation (15) are $Y_j = Y_s$, $c_j = 1$, and

$$p_j = p_s = (n\alpha + 1)^{-1} \quad (16)$$

For the mobile predator the corresponding quantities are $Y_j = Y_m$, $c_j = n$, and

$$p_j = p_m = (\alpha + 1)^{-1} \quad (17)$$

Given the constraints of the model, an efficient predator should choose the strategy yielding the smaller $\Pr[Y_j \leq R]$.

Equation (15) is an incomplete beta function that, in general, requires numerical evaluation (see below). Bury (1975), however, provides for an approximation for F_β that is useful when $(\theta+R)$ is not too small:

$$F_\beta(p_j; c_j\theta, R+1) = F_N(z(p_j); 0, 1) \quad (18)$$

$F_N(z; 0, 1)$ is the standard normal distribution function, and

$$z(p_j) = \frac{(p_j) - R - (c_j\theta + R)(1 - p_j)}{[(c_j\theta + R)p_j(1 - p_j)]^{1/2}} \quad (19)$$

Expressions (15) and (18) directly imply that the sit-and-wait strategy provides the lower probability of reproductive failure when $z(p_s) < z(p_m)$, and the mobile strategy yields the lower probability of reproductive failure when $z(p_m) < z(p_s)$.

Recall that $E[Y_s] = E[Y_m] = n\alpha\theta$; for convenience we designate this common expectation by μ . After substituting for c_j and p_j in equation (19), simple algebra shows that for the sit-and-wait strategy

$$z(p_s) = (R - \mu)/[n\alpha(\theta + R)]^{1/2} \quad (20)$$

For the mobile strategy

$$z(p_m) = (R - \mu)/[\alpha(n\theta + R)]^{1/2} \quad (21)$$

Since $n > 1$, $n\alpha(\theta + R) > \alpha(n\theta + R)$. That is, the denominator of $z(p_s)$ is greater than the denominator of $z(p_m)$. Then the approximation to the beta distribution leads to the following conclusions:

(1) When $\mu > R$, so that the predator's expected intake exceeds its requirement, $z(p_m) < z(p_s)$ and the mobile strategy is superior. Since $V[Y_m] < V[Y_s]$, risk-aversion is favored when the forager can expect to surpass its requirement (Caraco et al. 1980a; Houston and McNamara 1982, Pulliam and Millikan 1982, Stephens and Charnov 1982).

(2) When $\mu < R$, so that the predator's requirement exceeds its expected total intake, $z(p_s) < z(p_m)$ and the sit-and-wait strategy is superior. Since the sit-and-wait strategy induces the greater variance in food intake, risk prone behavior is favored when the forager cannot expect to surpass its requirement.

Numerical Results

Using equations (12) and (13), the probability of reproductive failure was calculated for both the sit-and-wait and mobile over a range of values for θ , α , and n . Equation (18) (the analytic approximation) suggests that $\Pr[Y_m \leq R] < \Pr[Y_s \leq R]$ when $R < \mu$, and $\Pr[Y_s \leq R] < \Pr[Y_m \leq R]$ when $R > \mu$. In most cases the approximation does quite well. Under certain circumstances, however, an individual should choose the mobile strategy, i.e., the strategy yielding the lower variance, for values of R somewhat larger than μ .

The analytic approximation performs best when $\theta > 1$ and $\alpha < 1$. Since $E[\lambda] = \alpha\theta$ and $V[\lambda] = \alpha^2\theta$, the normal approximation appears quite reliable when the variance of λ is less than its expected value. When $\alpha > 1$, so that $V[\lambda] > E[\lambda]$, the approximation's performance declines; the approximation may not perform especially well when $\alpha > 1$, $\theta < 1$ and n is large. All such cases are, however, similar in that the mobile strategy should be favored not only when $R < \mu$, but also over an interval where R exceeds μ . Consequently, the mobile strategy can be advantageous over a greater range of physiological requirements as the spatial heterogeneity in prey capture rates increases.

Figure 20 shows an example where the normal approximation fares poorly. Parameter values are $\theta = 0.1$, $\alpha = 5$, and $n = 40$. Y_s has a strong mode at 0; modal values of Y_m are 14 and 15. The common expected value is $\mu = 20$, but $\Pr[Y_m \leq R] < \Pr[Y_s \leq R]$ for $R \leq 31$. That is, the mobile strategy remains favored as R increases until $R > 1.55\mu$.

Parameter values for Fig. 21 are $\theta = 1$, $\alpha = 0.1$ and $n = 100$. When $\theta = 1$, Y_s follows a geometric probability function (as a special case of the negative binomial), and so has a mode at 0. Y_m has a mode at 9. The normal approximation performs very well. As R increases, the shift from risk-averse to risk-prone behavior, i.e. from the mobile to the sit-and-wait strategy, should occur close to the common expectation $\mu = 10$. Similarly, the approximation proves reliable for the parameter values used for Fig. 22, $\theta = 2$, $\alpha = 0.1$ and $n = 100$. In this case both Y_s and Y_m have positive modes, so that the accuracy of the normal approximation should not be surprising.

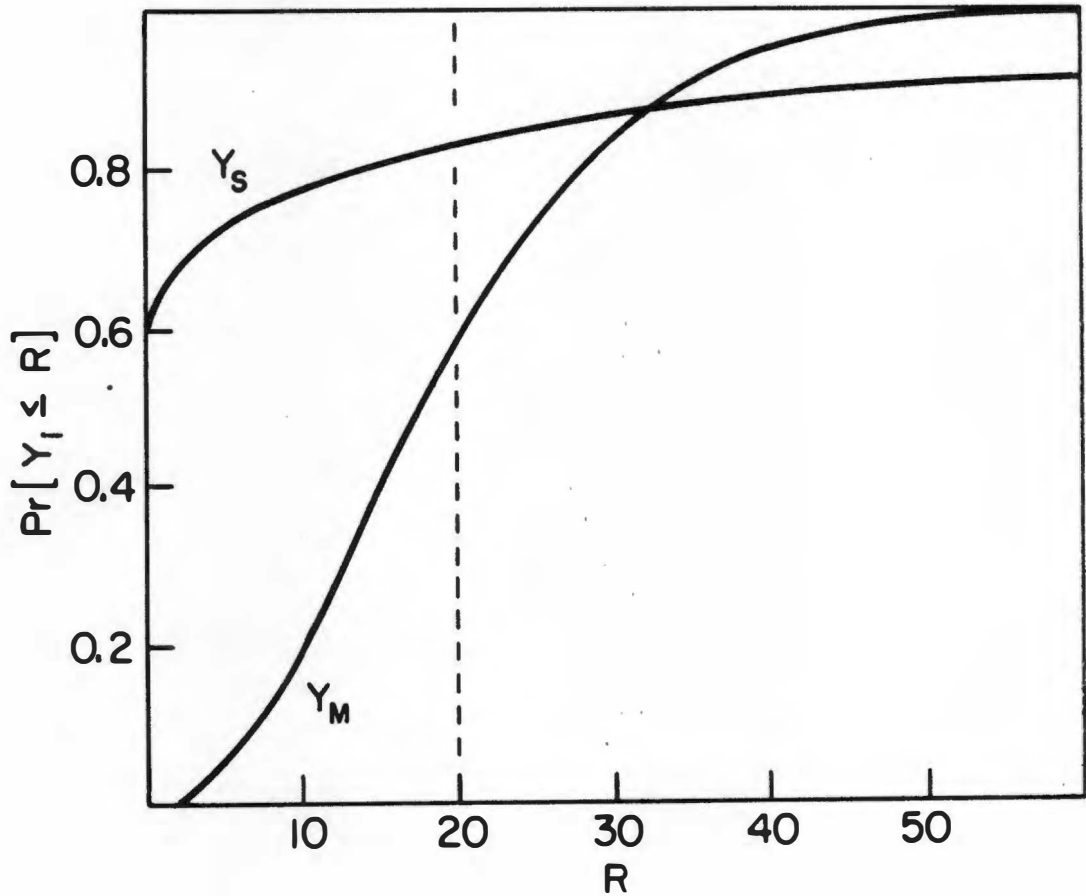


Figure 20. Distribution functions showing the relationship between the probability of acquiring fewer prey than are necessary to reproduce against the number they require; $\theta=0.1$, $\alpha=5$, $n=40$. For convenience the calculated discrete distributions are drawn as continuous functions. Y_s refers to the sit-and-wait strategy; Y_m refers to the mobile strategy. The vertical line at $R=20$ identifies the common expectation of Y_s and Y_m . With $\theta < 1$ and $\alpha > 1$, the mobile strategy is superior not only for $R < \mu$, but also over a range of values where $R > \mu$.

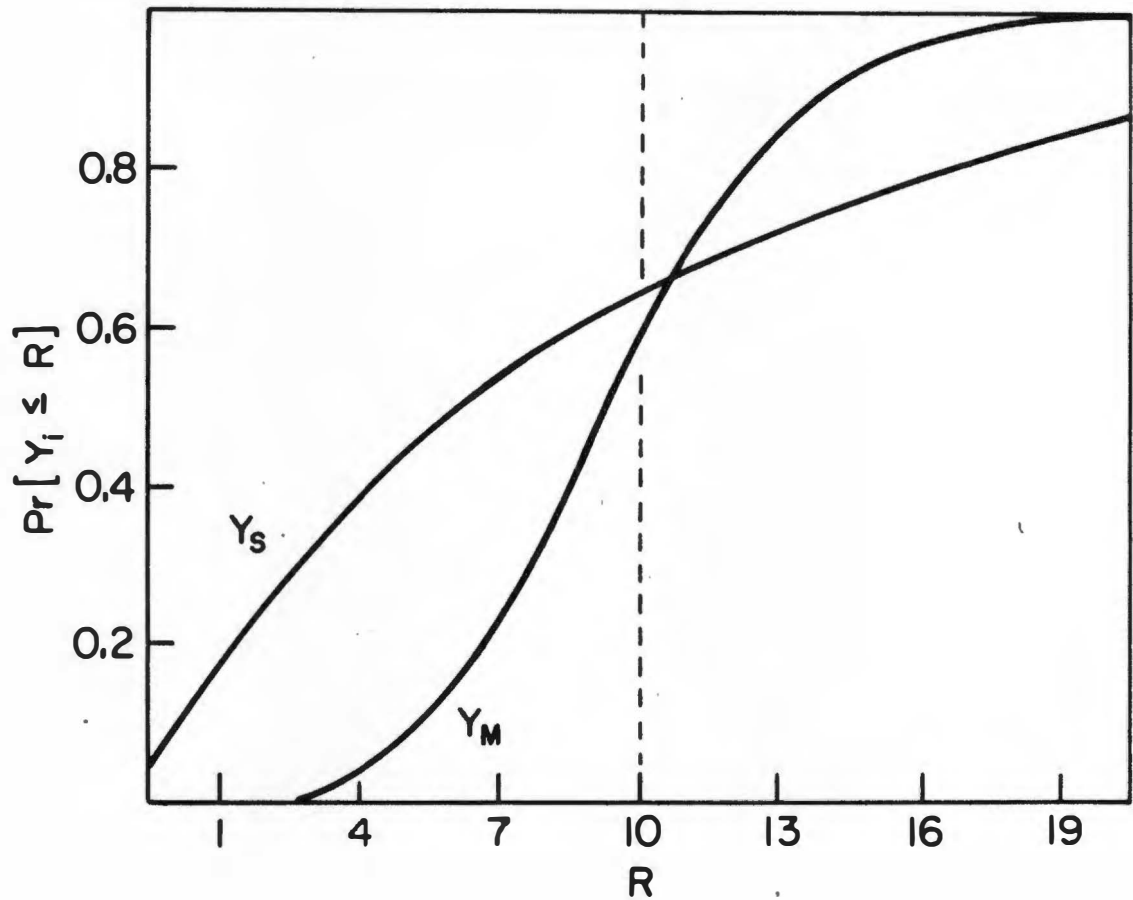


Figure 21. Distribution functions showing the relationship between the probability of acquiring fewer prey than are necessary to reproduce against the number they require; $\theta=1$, $\alpha=0.1$, $n=100$. The vertical line at $R=10$ identifies the common expectation of Y_s and Y_m . The mobile strategy is superior for $R < \mu$; the sit-and-wait strategy is superior for $R > \mu$.

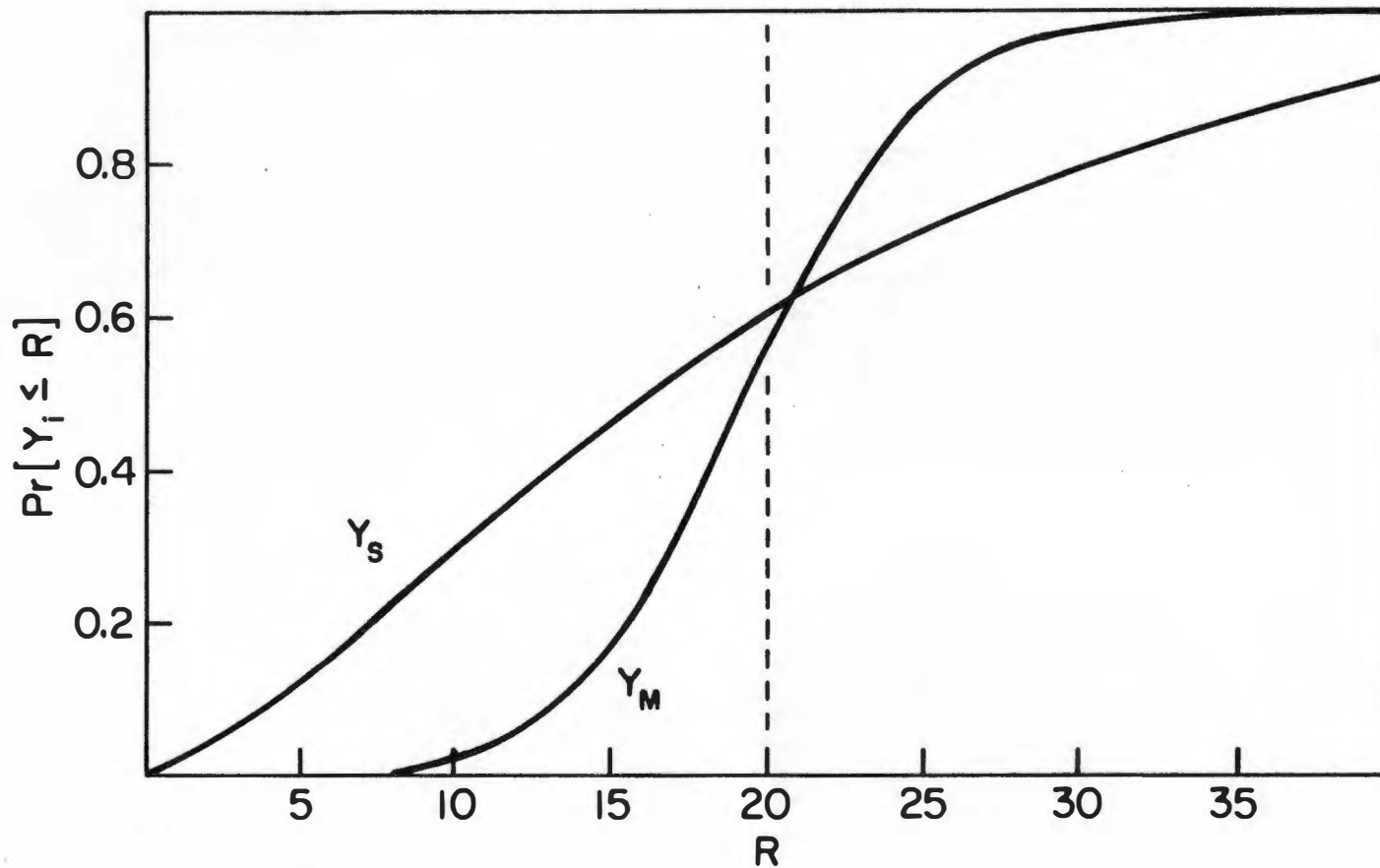


Figure 22. Distribution functions showing the relationship between the probability of acquiring fewer prey than are necessary to reproduce against the number they require; $\theta=2$, $\phi=0.1$, $n=100$. The vertical line at $R=20$ identifies the common expectation of Y_s and Y_m . The mobile strategy is superior for $R < 20$, the sit-and-wait strategy for $R > 20$.

Conclusions from the Model

In its analytical form, the model proposes that a predator should be risk-averse and adopt the mobile strategy when the individual can expect to capture more prey than is required to survive and reproduce. But when it can expect to capture fewer prey than required, a predator should be risk-prone and adopt the sit-and-wait strategy.

One of the assumptions of this model is that a forager responds to the global pattern of prey abundance, but not to information that might be acquired concerning local variation in the probabilistic rate of prey capture. This simplification may be inappropriate for many vertebrate foragers, but may not be unrealistic for spiders. Olive (1982) found that juvenile spiders could discriminate between no food and more food than minimally required for growth, but patterns of mobility and web site selection were independent of prey abundance whenever food was available (a treatment with some food, but less than required for growth, was not included in the study). The assumption also appears to be consistent with the observed behavior of T. elongata outlined in the previous section of this dissertation.

The assumption that the energetic costs of the two strategies are effectively equivalent may be quite reasonable for orb weaving spiders that are capable of ingesting their webs (though it is clearly inappropriate for most birds and mammals (Norberg 1977; see Janetos 1982a)). But what would happen if the mobile strategy were more expensive? The sit-and-wait strategy could be advantageous at values of n exceeding R . Suppose the cost of moving amounted to the equivalent of k prey per move. Then the probability of a reproductive failure for a

sit-and-wait predator would remain $\Pr[Y_s < R]$, but the probability of a reproductive failure for a mobile predator would become $\Pr[Y_m \leq R + nk]$. Equation (12) for $\Pr[Y_s \leq R]$ would still apply. Minor modification of equation (13), replacing R by $R + nk$, would give the exact currency of fitness for the mobile strategy, and the two alternatives could then be compared numerically for any given value of k . With respect to the normal approximation given by equation (18), $z(p_s)$ for the sit-and-wait strategy would remain exactly as shown in equation (20). For the mobile predator $z(p_m)$ would become

$$(p_m | k > 0) = [(R + nk) - \mu] / [\alpha(n\theta + R + nk)]^{1/2} \quad (22)$$

The sit-and-wait strategy has the advantage when $z(p_s) < z(p_m | k > 0)$, and the mobile strategy is superior when $z(p_m | k > 0) < z(p_s)$. Therefore, the assumption of equivalent energetic costs for the two strategies does not impose a limitation on the model. The analytic approximation would not, however, reduce to a simple comparison of μ with R if the two strategies incur different costs.

Methods II

Testing the Validity of a Model Designed to Describe Behavior

The validity of the model proposed above hinges on the demonstration of 3 facets of the foraging behavior of T. elongata: 1) spiders must be capable of varying their intake according to prey availability; 2) spiders on the lake must store more food (measured by fat content) than those on the creek; and 3) the foraging mode exhibited must parallel threshold levels of prey availability: the number of insects required to sustain an individual must be below some minimal

value on the creek, above on the lake. In order to examine these predictions, experiments were performed to determine: 1) the constraint on the number of prey consumed per day: is T. elongata capable of exploiting variability in prey abundance? 2) the fat content of spiders on the creek relative to those on the lake, 3) the energetic needs of the spider for both survival and reproduction and 4) the prey availability levels afforded by the creek and lake habitats, respectively.

Can T. elongata vary its intake with prey availability? In order to measure the extent to which spiders are capable of exploiting variability in prey abundance, the effect of hunger level on the duration of a single foraging period was determined. Individual spiders were placed in cages (39.3 cm x 39.3 cm x 11.4 cm) over water in the laboratory, where they could generally be stimulated to build webs by introducing fruit flies (Drosophila melanogaster) into the cage for a three hour period before allowing them to escape. They could not, however, be forced to build exactly on cue and introduction of a spider on to another's web would generally damage the web. Starvation times were therefore divided into periods: 0-5 days, 10-15 days and 20-30 days, during which times the spiders were not fed. Ten spiders were tested at each of these periods and the periods were used to categorize the hunger level (low, medium or high) of a spider. The manufacture of an orb was a necessary prerequisite to a feeding session since the spider would not take food without a cue. Spiders were fed individually weighed noctuid moths. These were held with forceps on the orb, being released only when they had been secured by the spider. As soon as the

spider had finished sucking on the first moth, another was held on the web, and the remains of the first extracted from the web and weighed. This process was repeated until the spider would no longer respond to vibrations of a moth on the web. The end of a feeding session was indicated when the spider was without a web and had adopted a "prone" position (legs and chelicerae stretched out) on the side of the cage.

Between habitat comparison of spider fat content. To estimate how much food was exploited by spiders on the lake relative to those on the creek, 20 spiders were collected from each habitat and lipid assays were completed on each. The protocol used for lipid extraction was as follows (Bligh & Dyer 1959). The abdomens of individual spiders were homogenized in a methanol (with acetic acid added to make up 2% of the volume) / chloroform mixture (1:1). Water was added to this mixture in the ratio 5.0 : 2.25 (methanol and chloroform mixture : water). Following mixing, the solvents were centrifuged to give a compact interface. A syringe was then used to take out the bottom chloroform layer, which was put in a clean test tube and saved. Chloroform (an amount approximately equal to that removed) was then added to the methanol layer, and the extraction (homogenization, centrifugation and removal of the chloroform layer into the test tube) repeated in order to extract any remaining lipid. This process was repeated twice more, during which time approximately 30 mls of chloroform mixture (with lipid dissolved in it) was collected and reserved. The test tube was then placed under a gentle stream of nitrogen to dry off the chloroform. Subsequently, the tube with lipid in it was placed in a vacuum dessicator for 15 mins, and weighed. The lipid

in the tube was then dissolved in chloroform and rinsed out of the tube, leaving it clean. After returning the clean tube to the vacuum dessicator for a farther 15 mins., it was reweighed, and the difference between the two tube weights gave the lipid content weight of an individual spider.

Energetic requirements for survival and reproduction. To find the minimum number of insects required to sustain the spider. I placed individual weighed spiders in cages (39.3 cm x 39.3 cm x 11.4 cm) and allowed them to build webs. Moths (small noctuids) were captured, anaethsetized and weighed. Once it had recovered, an individual moth was held on the web until the spider had secured it. Once the spider had finished eating the moth, the remains were taken out and weighed so as to give an estimate of the amount consumed. Spiders were fed continuously, until they ingested the web, this marking the end of a given feeding session. They were allowed to rebuild before being given any more prey. This web building behavior was used as a gauge to indicate that the spider had reached a certain threshold hunger level. The experiment was performed using 16 spiders, each of which were subjected to this feeding regime for 50 days. After this time, the numbers of egg sacs laid were counted, and the spiders reweighed and frozen in chloroform and methanol prior to lipid extraction. Estimates of lipid content were used to gauge the level of starvation / satiation of an individual. The protocol used in this lipid extraction was the same as that outlined above. In order to estimate the energy expenditure incurred during the laying of an egg sac, other spiders that were in similar cages in the laboratory were used. A total of 16 spiders were

weighed both before and after laying an egg sac, and the resultant weight loss after completing the process was recorded for each.

Comparison of prey availability in the two habitats. Sticky traps were used in prey availability determinations. Traps were made to simulate orb webs as follows: Nylon thread was woven across the inner portion of an embroidery hoop (30 cm diameter), the threads separated by a distance of 5 mm, and secured in place by the outer ring of the hoop. Threads were then woven across at 4 cm intervals. After completion, this entire structure was dipped in "Stickem Special," a non-drying sticky substance, which had been heated to render it less viscid. A total of 16 traps were made in this way. Sites were then selected at random over the creek and the lake (8 in each habitat type). Traps were placed at the modal angle / height of the webs in the two habitats: an angle of 30° to the water's surface, with the center of each 30cm above. Traps were left in these positions for a period of 21 days, insects being picked off the traps daily.

The average prey availability of the habitat was determined as follows. An estimate of the weight of each prey type was found by collecting, killing and weighing 40 of each, and using the average weight in subsequent calculations. Criticism of the use of artificial webs to determine the prey available to orb weaving spiders come from the general ignorance of the rate of spider capture failure and prey rejection (Castillo et al. 1983), These factors were therefore taken into account as follows: Previous work on prey capture in T. elongata have shown that, of all insects hitting the web, an estimated 61.3% are

actually captured; the rest escape before the spider has time to secure them. Once captured, only a certain percentage of the insect is consumed. The estimated percentage of any prey item actually consumed was found to be 81.6%. Having accounted for these two effects, the average prey availability (in terms of the weight that a spider could ingest) could be found from the total number of insects caught in the traps. This analysis does, however, ignore the possibility of nutritional intake in the form of microscopic organic matter that sticks to the web (Smith and Mommsen 1984).

Results II

Testing the Validity of a Model Designed to Describe Behavior

Can *T. elongata* vary its intake with prey availability? The ability of spiders to exploit sporadic prey abundances was examined first by studying the effect of length of starvation period on the duration of a given feeding bout. Analysis of variance indicated that the time over which a spider was starved prior to a test could be used as a predictor of the period over which a spider would continue to feed: The longer a spider was starved, the longer it would feed when prey became available to it ($F=216.76$, $p<0.0001$). This indicates that *T. elongata* is potentially capable of exploiting periodic abundance in prey availability.

Between habitat comparison of spider fat content. Lipid weight was used to compare the energetic condition of spiders on the lake relative to those on the creek. The mean lipid weight of creek spiders was found

to be 17.38 mg (SD=10.18, n=16). On the lake the mean weight was 25.92 mg (SD=13.46, n=13). This difference was found to be highly significant ($F=12.14$, $p<0.002$). Multiple regression was used to show that the best model for accounting for the behavior of lipid weight was site (creek, lake) once the effect of spider weight had been taken into account. The F value for this model was highly significant ($F=36.27$, $p<0.001$).

Energetic requirements for survival and reproduction. The minimum number of insects required to sustain the spider was found by regression of the total weight change of a spider (over a 50 day period and taking egg sac production into account) against weight of insects consumed during this period. The formula of the regression line was found to be:

$$Y = 0.60X - 26.48$$

where Y is the total weight change of the spider (with egg sac production accounted for) in the period (range 0-325 mg, including the weight of the egg sac); and X is the total weight of insects consumed (range 0-580 mg). This line of best fit was highly significant ($F=58.02$, $p<0.0001$). The weight of insects that must be consumed by a spider over a 50 day period in order to suffer zero weight loss during that time is found to be 44.11mg or 8.90mg per day. The same equation shows that, assuming an egg sac to weigh 45.00 mg, a spider must consume 117.75 mg over the period in order to produce a single egg sac. This can be translated as a daily intake of 2.40 mg in order to produce one egg sac over the season.

Comparison of prey availability in the two habitats. Table 8 shows the results from the analysis of prey availability levels in the creek

TABLE 8. COMPARISON OF INSECT AVAILABILITY IN A GIVEN HABITAT RELATIVE TO THE REQUIREMENT OF A SPIDER.

	CREEK	LAKE
MEAN WEIGHT OF INSECTS CAUGHT ON TRAPS (mg)		
Mean	3.48 mg/day	24.93 mg/day
Temporal variance	4.79	53.74
Spatial variance	3.58	48.60
INSECTS POTENTIALLY AVAILABLE FOR INGESTION BY SPIDER (mg). (Mean & C.L.)		
Number of traps	1.74 mg/day (+0.25) n=8	12.47 mg/day (+1.44) n=8
NUMBER OF EGG SACS THAT COULD BE LAID IF SPIDER WAS EXPLOITING PREY AT THIS LEVEL		
	0	7

Values of insect weight potentially available for ingestion were obtained by counting the number of insects caught on sticky traps each day over the field season (July and August 1983). These values are shown, along with both temporal and spatial components of variability. In reality, a spider will only capture an average of 61.3% of the insects hitting the web; the numbers of prey caught on the sticky traps were deducted accordingly. An estimate of the weight of each prey type was found by collecting, anaesthetizing and weighing 40 of each, and using the average weight in subsequent calculations. Once captured, an estimated 81.6% of the insect is consumed. Deductions were made accordingly from the total estimated weight of insects that the spider can capture, to give the weight of prey actually available for ingestion. Assuming an egg sac weighs 45.00 mg, and requires (from regression analysis) 117.75 mg to produce, the number of egg sacs that can be laid are shown.

and lake habitats. The total number of insects caught on the traps over a 21 day period were divided into three classes, and an estimate of the weight and average amount of the insect that the spider could consume, was found for each size class. As shown in the table, both temporal and spatial components of variability in prey abundance were extremely high. The average insect weight potentially available for consumption by the spider, caught in the traps on any given day was markedly different on the creek versus the lake. On the creek the value was found to be only 1.74 mg (SD=0.30, n=8); on the lake the value was found to be almost an order of magnitude higher: 12.47 mg (SD=1.72, n=8). (Note: because insect numbers were totalled over the 21 day period, this analysis ignores temporal variability). Comparing these values to the spider's requirements, it can be seen that, if the spider were to exploit the habitat at the average availability, it could not produce a single egg sac on the creek (from the regression analysis above, a minimum intake of 2.40 mg is required for a single egg sac). On the lake, however, exploitation of the habitat average would allow the spider to lay seven egg sacs (from the regression analysis) over the season. That is, the analysis suggests that the lake spiders (mobile strategy) can expect to consume more than enough prey to survive and reproduce. The creek spiders (sit-and-wait strategy), however, cannot expect to consume the number minimally required for reproduction.

Discussion

The foraging strategies of the two populations in this study clearly contrast in frequency of movement. Spiders on the creek, where

prey are sparse, change foraging sites only once every 18 nights, on average. Spiders on the lake, where prey availability and capture rates are much greater, change foraging sites nightly. This study suggests that the dichotomy in foraging patterns can be explained in terms of risk sensitivity. Compared to a sit-and-wait predator operating in the same environment, a mobile forager achieves a lower probability of spending n nights at sites of very low prey availability. This benefit requires that the mobile forager accepts a lower probability of spending n nights at sites of very high prey availability. Where the average prey availability is sufficient to allow survival and egg production over the season, the mobile strategy (risk averse) implies the lesser probability of reproductive failure. Fitness averaged over low and high possible prey capture rates is less than the fitness at intermediate rates. This is a consequence of limits imposed by handling time, physiological constraints, etc., which mean that the spider receives diminishing returns as the levels of prey exploitation increase up to extremely high levels. In an environment that exhibits both temporal and spatial variability, risk averse behavior can only be achieved by continually sampling from the habitat in order to exploit the average thereof. Mobile foragers (the lake spiders in this study) adopt such a strategy by building short-lived webs and changing sites frequently, perhaps using a level close to the average prey availability as a criterion of when to leave a given site. The trigger involved is most likely a physiological hunger threshold.

Where the average prey availability is insufficient to allow the production of one egg sac over the season, the sit-and-wait strategy

(risk prone) implies the lesser probability of reproductive failure. In this case mean fitness (in terms of egg production) averaged over low and high possible prey capture rates is greater than the fitness at intermediate prey capture rates. Initial habitat selection would allow spiders to exploit the peak of spatial variability in resource abundance. Subsequently, in order to minimize the risk of never attaining sufficient resources to lay an egg sac, the individual must remain at this site, for extended periods, despite temporal fluctuations in resource abundance. The decision rules used for leaving a site in such a situation are likely to be more complex (see Pyke [1984] for examples of possible sources of information under these circumstances): the average of the habitat cannot be used as it is unknown, and below the level required for reproduction. It may be that the spider only leaves a site when it is actually starving (receiving less than that required to sustain it without weight loss, which requires an average intake of 8.90 mg per day). It should be emphasized, however, that the decision making process for any given situation is quite separate from the ultimate foraging pattern (Krebs et al. 1983). These "rules of thumb" are proximate cues used to attain the optimal foraging behavior (McFarland 1977, McCleery 1978). As pointed out by Janetos and Cole (1981, but see Houston & MacNamara 1982), these are likely to be simple rules, approximating to optimality. Most likely they are mediated by differences in responsiveness to the same eliciting stimuli, as has been found in garter snakes, Thamnophis elegans (Drummond and Burghardt 1983) and aquatic invertebrates (Meadows and Campbell 1972).

Can the dichotomy in foraging patterns be explained in terms of

different levels of intraspecific disturbance arising from the differential in spider density between the two habitats? This is unlikely: as I will show in chapter V (table 10), the density of conspecifics has no significant effect on the probability that an individual will move from a given site. Sensitivity to risk appears to be the most plausible explanation for the different behavior types observed, although it is unlikely that the distinction between the two types is always as clear as that found in this study. Within its distributional area, the habitats I chose to examine imposed opposite extremes in terms of abiotic parameters. Examination of foraging strategies in intermediate habitats is likely to reveal a continuum, the presence of which has already been noted in discussions of predators in terms of sit-and-wait / mobile search foraging (Riechert and Luczak 1982) and risk sensitivity (Barnard and Brown 1985).

A recent criticism of risk sensitive models is: Why do we not find animals starving to death (Krebs and McCleary 1984)? This arises from the fact that nearly all the studies on risk sensitive behavior have been performed under conditions where the crucial determinant of fitness is survival from one day to the next. Houston and MacNamara (1982) proposed that the animals adopt a sequential approach to risk taking: animals face a series of choices through a single day. If they start off risk prone, at each choice a proportion of animals will get enough food to ensure that they are risk averse at the next decision; so by the end of the day, far fewer than the original proportion of risk prone animals will still be in the negative expected energy budget. Spiders, however, in direct contrast to the animals used in these studies, demonstrate the

astonishing ability to survive for several months without food. Like the species used in previous studies, however, they are under a severe time constraint to produce an egg sac during the season.

The ability of spiders to withstand starvation is due to a set of physiological adaptations to variable prey availability and is a logical corollary to the demonstration of risk sensitivity. The primary physiological adaptations include a very low metabolic rate (Anderson 1970, Carrel and Heathcote 1976, Peakall and Witt 1976, Greenstone and Bennett 1980, Tanaka and Ito 1982) and an extensively developed intestinal system (Foelix 1982). In addition to secretory and resorptive cells, the intestinal epithelium contains adipose tissue, also known as the "fat body" (Comstock 1940). This is made up of 2 cell types: 1) urate cells, which contain glycogen, guanine and urate crystals; and 2) trophocytes, which are packed with rough endoplasmic reticulum and are the major site of protein synthesis (Riechert & Harp in press). After a fixed period of food deprivation, the rough endoplasmic reticulum is shut off. This probably occurs coincidentally with a marked drop in the spider's metabolic rate (Ito 1964, Miyashita 1968, Anderson 1974, Humphreys 1977). Also, during starvation, urate crystals accumulate in the urate cells. A similar phenomenon has been found to occur in some insects, but its function is unknown. The net effect of the combined action of the trophocytes and the urate cells is to allow a starving spider to carry on all normal functions. This ability to withstand starvation makes spiders physiologically ideally adapted to variable environments, where they may expect to experience periods of energy shortage. As I have shown in this chapter, their foraging behavior may

also be sensitive to variability in prey abundance, allowing them to exploit a resource in such a way as to minimize the probability of reproductive failure. Because they are capable of both maintaining a negative energy budget for extended periods, as well as exploiting conditions of high prey availability, they are ideal tools for studying risk sensitive behavior.

Several studies have demonstrated the ability of spiders to exploit the average prey availability of the habitat (Morse and Fritz 1982, Olive 1982, Janetos 1982b). But it has also been shown that a spider's foraging strategy itself is responsive to prey availability: Luczak (1970) found that Tetragnatha montana responds to very high prey densities by a reduction in the time spent sitting on the web and increased overall activity, relative to lower prey densities. This latter study lends support to the conclusions from the present study, i.e., that certain spiders may respond to risk, and that the strategy adopted in a given situation depends on their energetic condition. Further support comes from a study by Uetz et al. (1982) in which the flexible spacing (solitary versus colonial) of Metepeira spinipes was found to fit predictions of risk sensitive foraging in a patchy environment. As predicted (Caraco 1981b, 1983), a risk averse animal reduces the variance in food available to it by aggregating in a colony; a risk prone animal, facing the prospect of physiological deficiency, remains solitary. Rypstra (1983) has found similar social grouping tendencies under conditions of high prey availability in three tangle and two orb weaving spiders. Under conditions of low prey density, the colonial orb weaver Metabus gravidus becomes more solitary and

aggressive (Buskirk 1975a and b). A similar relationship between prey availability and social grouping tendencies was found in Tetragnatha elongata and will be described in the next chapter.

If, as this study suggests, switches in foraging strategy can be explained in terms of risk sensitive models, it would greatly enhance our understanding of the effect of stochastic variability on foraging behavior. Diversification in any behavior might be expected to confer maximal fitness in every environment that presents the animal with uncertainty with regards the returns (Real 1980b).

CHAPTER V

THE ROLE OF ENERGY BUDGETS IN THE DEVELOPMENT OF AGGREGATIVE BEHAVIOR
IN TETRAGNATHA ELONGATAIntroduction

Many, if not most, animals spend part or all of their lives in groups, which vary enormously in both size and complexity. The range encompasses everything from many fish and amphibian species that occur in groups only in temporary spawning aggregations, to some birds, mammals, insects and spiders that live their entire lives in large, highly structured societies.

There are two primary reasons why animals might aggregate into social groups. Firstly, they may gain directly from group living; and secondly they may be "forced" to remain in groups as a result of high costs or risks associated with departure (Caraco and Wolf 1975, Emlen 1984). Considering only the former, more common, case, the two most frequently cited benefits derived from gregarious living are increased alertness and defense against predators and increased capabilities for detecting and harvesting food resources that are difficult to locate (Alexander 1974, Hoogland and Sherman 1976, Bertram 1978). In such instances the average fitness of an individual group member (W) will increase as some function of increasing group size (k) up to some optimum size, and decrease thereafter (Emlen 1984). I will confine this discussion to the benefits derived from the relationship between foraging and group size (Pulliam and Caraco 1984).

Demonstrations that the time required to discover a patch of food

decreases with group size have been carried out with minnows and goldfish (Pitcher et al. 1982) and with birds (Krebs et al. 1972). Aggregative behavior will impart maximum benefit if: 1) patches are large relative to individual requirements (so that only one or a few patches need be discovered); 2) if the individual seeks to minimize the time until it acquires any food at all (Caraco 1981b); or 3) if the resources are highly ephemeral (Pulliam and Millikan 1982). It is, however, difficult to unravel the primary and secondary factors responsible for the evolution of group living: the establishment of one advantage will stimulate rapid development of others (Morse 1980). Speculation as to the primary and secondary determinants of group living have become increasingly futile over recent years.

In the last chapter I emphasized the importance of incorporating environmental stochasticity in the examination of behavioral patterns, particularly those related to foraging. I described how spiders might change foraging mode (sit-and-wait to mobile search, or vice versa) according, not only to the expected benefits and costs of their resource distribution, but also to its associated variance. Similar models, developed for small, granivorous birds, have shown that, where variance reduction increases the probability of averting starvation (risk aversion) it will be advantageous for individuals to aggregate (Thompson et al. 1974, Caraco 1980, Caraco 1981b, Real 1981, Pulliam and Millikan 1982, Caraco and Pulliam 1984). If survivorship is instead proportional to variance, solitary foraging may be preferred. The present chapter will discuss the use of risk sensitive foraging theory to describe aggregative and / or cooperative behavior in spiders.

Spiders are generally considered solitary animals, exhibiting aggressive behavior towards others including conspecifics (Riechert 1974, 1982, Rovner 1968, Hallander 1970). Studies confined specifically to orb weavers, however, have frequently remarked on the absence of intraspecific competition and / or aggression (Burlacu 1972, Burch 1979, Horton and Wise 1983, Lubin 1974, Olive 1982, Robinson and Lubin 1979a, Rypstra 1983, Schoener and Toft 1983, Uetz et al. 1982, Wise 1981). Species from many spider groups exhibit a tendency towards aggregation, the pattern of which may range from simple, temporary aggregations to communal web building, cooperative prey capture and indiscriminate brood care (Shear 1970, Burgess 1978, Buskirk 1981, Burgess and Uetz 1982). There are a few species from several families that exhibit highly cooperative living patterns (Krafft 1966, Shear 1970, Kullman 1972, Darchen 1973, Lubin 1974, Buskirk 1975a and b, Burgess 1976, Barch 1977, Fowler and Diehl 1978, Jackson 1978a and b, Christenson 1984).

In order to understand fully what benefits can be derived from communal living, it is necessary to examine a species that is found in both colonial and solitary states, and compare the conditions under which these two states are found. Within a single species, several studies have shown that generally territorial spiders may exhibit plasticity in spacing patterns in response to prey availability (Riechert 1978). Normally communal spiders may also exhibit variation in grouping tendencies in response to prey availability (Uetz et al. 1982). The present study is an attempt to understand what conditions might favor group living and speculate as to how this might lead to the evolution of cooperative behavior and subsequent sociality

(Slobodchikoff 1984). The most commonly cited advantages of group living in spiders are: increased prey capture efficiency, protection from predators and competing heterospecifics, architectural stability and sharing the cost of parental care (Buskirk 1981, Uetz et al. 1982, Christenson 1984). To date, however, there have been no formal analyses of the two crucial issues in the evolution of social behavior: 1) its phylogenetic origins; and 2) its adaptive significance (Brockmann 1984). In this chapter I use risk sensitive foraging theory to examine the extent and nature of aggregative behavior in T. elongata, a species which exhibits flexible spacing patterns. I test the validity of this application by manipulating insect densities and examining the response of different densities of spiders to this differential in prey availability.

Methods

The study was conducted during the summer field season (June - September) of 1984. Results from previous work on the two populations used in the study (see Chapter IV) stimulated further application of risk sensitive foraging theory to the system. This allowed the generation of two predictions as to how individuals might aggregate as a risk averse response to variance in resource abundance: 1) High prey densities lead to a reduction in interindividual spacing. 2) Aggregation serves some benefit at high prey densities. The most likely benefit would be that derived from an individual's use of pre-laid silk. Silk removal should, therefore, negate these possible benefits. Two separate manipulations were carried out in order to test these predictions.

Variation in Web Building Frequency with Prey Availability

The extent to which web building frequency is determined by prey availability was examined using a large cage (2.5 m x 1.5 m x 0.6 m) divided into 4 sections. The partition dividing the cage in half longitudinally was lined with black plastic to prevent light from penetrating between sections. In each section, the black plastic was lined with white cheesecloth. The sides opposite this partition were covered with clear plastic. The ends of the cage were also covered with plastic. The partition dividing the cage transversely was made of white cheesecloth. A black light was placed against one of the cheesecloth partitions, so that one entire longitudinal section was illuminated, the other not. The top of the cage was covered with fine plastic netting, and the entire structure was placed in an artificial, shallow pool of water lined with industrial grade clear plastic. At night, the half of the cage without the black light was covered with black plastic so as not to be illuminated by the black light in any way. The cover was lifted in the illuminated sections for 15 mins. both before sunrise and after sunset each day. This allowed larger insects to enter these sections, being attracted to the black light. Mosquitos emerging from the water were also attracted by the light on the black cheesecloth, on which they landed in very large numbers. Fifteen weighed and marked spiders were placed in one of the illuminated sections, 4 in the other. Corresponding numbers were placed in the half of the cage that was not illuminated. The position of individuals and the size of any orbs was recorded at 0500 and 2200 hours daily over a 20 day period. An estimate of exactly how many insects were being captured in the illuminated

section versus the non-illuminated section was estimated through counting the presence and type of prey present in the jaws of all individuals in each of 4 time periods (00-03, 03-06, 06-21 and 21-24 hours; ten recordings were made in each time period). Results were averaged over 4 days' recordings and converted to daily consumption rates by determining the average weight of the prey items consumed and multiplying by the total intervals spent foraging.

The weight of prey items consumed was estimated by means of a second experiment in which 20 spiders of approximately the same size were placed individually in cages. Once they had built webs, weighed moths of approximately the same size were held on the webs, and the spiders were allowed to capture them. The time taken for an individual spider to consume a moth was recorded, as was the weight of the discarded moth remains. The experiment was repeated using mosquitos instead of moths. Two replicates of the original experiment were carried out.

The Effect of Silk Removal on Web Building

The degree to which web building frequency is affected by removal of silk was tested using 2 cages (1.2 m x 1.2 m x 0.6 m high) which were placed in an artificial, shallow pool of water lined with clear plastic. The cages consisted of a framework of wooden struts, the sides of which were lined with clear plastic. The top was covered with cheesecloth, and the bottom was open to the surface of the water. Eight weighed and marked spiders were placed in each of these cages. In one of the cages silk was removed every 4 days by rubbing all surfaces with a cloth

saturated in alcohol. The other was left as a control. In both cages web building and individual movement were monitored at 0500 and 2200 hours daily over a 12 day period. After this time the spiders used were reweighed, and the experiment was repeated using new spiders. Five replicates (12 days each) were carried out.

Results

Variation in Web Building Frequency with Prey Availability

Table 9 gives estimates of the number and weight of insects that were being captured in the illuminated versus the non illuminated sections. In the illuminated sections an average of 13.3% of spiders were eating moths and 20.0% eating mosquitos during the period 2100-2400 hours. In the non-illuminated sections there were no moths, but 31.1% of spiders were eating mosquitos during this time. The availability of mosquitos declined during the night, and feeding was confined almost exclusively to moths in the illuminated section during the daylight period. Table 9 also shows the weight of prey consumed by the spiders in the different sections of the cage through various intervals of the day. In the non-illuminated section the average daily intake is 10.34 mg, which would allow the spider to lay approximately 6 egg sacs during the course of the season (see previous chapter). In the illuminated section the average daily intake is 38.53 mg, which, if this rate were maintained through the season, would allow the spider to lay 24 egg sacs. It is not known whether this number can ever actually be realized, although other orb weavers have been found to exhibit radical increases

TABLE 9. INSECT CONSUMPTION IN ILLUMINATED AND NON-ILLUMINATED CAGE SECTIONS.

PERIOD	NON ILLUMINATED		ILLUMINATED			
	MOSQUITOS		MOSQUITOS		MOTHS	
	PROP. EATING	AV. INTAKE (mg)	PROP. EATING	AV. INTAKE (mg)	PROP. EATING	AV. INTAKE (mg)
00-03h	.19	3.42	.15	2.72	.15	4.70
03-06h	.07	1.21	.10	1.83	.18	5.58
06-21h	.00	0.09	.00	0.05	.10	15.85
21-24h	.31	5.63	.20	3.62	.13	4.18
AV. DAILY INTAKE			AV. DAILY INTAKE			
		10.34 mg				
			38.53 mg			

Rate of consumption for moths and mosquitos:

Moths: n=20. Time for consumption: Mean=4.38 hrs. (+0.71 hrs)

Weight administered: Mean=2745.72 mg (+506.15 mg)

Weight eaten by spider: Mean=2040.37 mg (+456.16 mg)

It follows that: Rate of consumption = $\overline{10.45}$ mg / min.

Mosquitos: n=134

Rate of consumption = 6.03 mg / min.

A t-test was carried out to test the difference in average daily intake between the sections: $t = 33.45$, $p < 0.001$ (highly significant).

in the number of egg sacs laid as prey availability increases (Palanichamy 1984, Palanichamy and Baranikumar 1984).

The effect of prey and spider density on web building was examined by calculating the means and standard deviations of: percentage of spiders building, web diameter, percentage not moving and distance between site locations, for each treatment. Results from this analysis are shown in Table 10. In order to test the significance of the treatments on the various aspects of web building, analysis of variance was used to generate F values (SAS). For the spiders in the high density, high prey treatment (the section illuminated with the black light) the frequency of web building was found to be significantly lower than the other treatments ($F=74.07$; $p<.001$). The same treatment caused a significant reduction in web diameter ($F=123.06$; $p<.001$). Neither the percentage of spiders remaining at a web site on successive days, nor the distance moved between web sites were found to be affected by the treatments. Under conditions of low spider density, however, web building, distance moved and the tendency to remain at a site, show no significant difference between the two sections.

In order to give a clearer picture of the extent of aggregation, nearest neighbour distances were recorded for individuals with webs, as well as those without, in the respective sections. Considering the high spider density sections, the average nearest neighbour distances for those that built webs was found to be 28.76 cm (SD: 22.84), and did not differ significantly between the two sections (t-test: $t=0.47$; $p>0.05$). In the same sections of the cage, spiders without webs in the high prey density section, maintained close proximity (average 16.28 cm apart [SD:

TABLE 10. COMPARISON OF WEB BUILDING ACTIVITY UNDER 4 TREATMENTS: HIGH SPIDER DENSITY, HIGH PREY; HIGH SPIDER DENSITY, LOW PREY; LOW SPIDER DENSITY, HIGH PREY; AND LOW SPIDER DENSITY, LOW PREY.

TREATMENT	% BUILDING	WEB DIAMETER (cm)	% NOT MOVING	% MOVING >2m
High spider High prey	33.40* (+2.90)	13.73** (+0.71)	51.30 (+3.21)	0.71 (+0.07)
High spider Low prey	76.47 (+1.47)	24.13 (+0.55)	55.00 (+4.33)	0.59 (+0.06)
Low spider High prey	65.87 (+2.23)	29.39 (+1.93)	68.30 (+1.08)	0.43 (+0.07)
Low spider Low prey	67.57 (+1.46)	30.97 (+1.88)	65.27 (+0.54)	0.48 (+0.04)

* F=74.07; p<0.001

** F=123.06; p<0.001

12.44]) relative to the same spiders in the low prey density section (average 37.73 cm apart [SD: 29.61]) and web builders in either section. These differences are highly significant (t-test: $t=6.05$ and 5.06 respectively; $p<0.001$). Considering the low spider density sections, the average nearest neighbour distances for those with and without webs was found to be 53.28 cm (SD: 45.87) and 55.61 cm (SD: 47.15) respectively, and did not differ significantly between the two sections. The separation distance between spiders not building webs, in both sections, was, again, significantly higher than that of the same spiders in the high density, high prey availability section.

It appears, therefore, from these results, that prey availability has a marked effect on web building activity under conditions of high spider density. Where spider density is low, however, prey availability has little effect on any of the parameters measured.

Effect of Silk Removal on Web Building

Data on web building behavior under the two treatments (silk removed and control) were analyzed as in the previous experiment. Means were generated as shown in Table 11. It can be seen from this that the average web area in cages where the silk is removed is over double that where silk is not removed ($F=37.01$ $p<.0001$). Also, the percentage of webs which were attained by a spider by taking over from another is much higher in cages where the silk was removed ($F=73.03$ $p<.0001$), as is the percentage of spiders moving a distance of more than 2m between sites ($F=61.26$ $p<.0001$). The two sections were not significantly different in percentage of spiders building webs, nor the percentage that remain at a given web site on successive days.

TABLE 11. COMPARISON OF WEB BUILDING ACTIVITY IN CAGES FROM WHICH SILK IS REMOVED VERSUS CONTROL (SILK NOT REMOVED).

	CONTROL	SILK REMOVED	SIGNIFICANCE OF DIFFERENCE
AREA(cm)	444.95 (<u>+33.51</u>)	992.85 (<u>+32.09</u>)	F=37.01 (p<.0001)
% TAKE OVERS	13.40 (<u>+1.83</u>)	44.80 (<u>+1.88</u>)	F=73.03 (p<.0001)
% MOVING > 2m	7.96 (<u>+0.45</u>)	20.84 (<u>+0.81</u>)	F=61.26 (p<.0001)
% BUILDING	71.62 (<u>+3.38</u>)	75.42 (<u>+3.47</u>)	F=5.44 (p>.01)
% NOT MOVING	43.76 (<u>+5.94</u>)	43.96 (<u>+5.24</u>)	F=0.05 (p>.01)

Discussion

Web building spiders, as a group, are preadapted to sociality purely through their possession of a web (Shear 1970). The ability of individuals to make use of prelaid silk threads of conspecifics has long been recognized (McCook 1889, Tilquin 1942, Enders 1974); they may also use the silk of heterospecifics (Crocker and Felton 1972). Such behavior could provide the communication necessary for tolerance and cooperation (Krafft 1982). Luczak (1971) has suggested that the tendency of spiders to congregate into groups is based on the existence of webs, and the resultant social characters are independent of the stage of evolutionary development of the web form. Orb web spiders, although orbs themselves require stereotyped individual behavior, could still derive benefits from sharing colony drag and support lines. Buskirk (1981) cites economy of silk expenditure as the primary advantage these spiders derive from being in a group, although predator defense and prey capture have also been suggested as adaptive functions for elementary coloniality (Schoener and Toft 1983). These advantages can only prevail after mutual tolerance of conspecifics has been established: the potentially lethal aggressive response of a spider to conspecifics is a primary deterrent to the development of sociality (Brach 1977, Riechert 1981). Buskirk (1981) considers that, if a food source is available in excess, intraspecific tolerance and cooperation may evolve. But, as she points out herself, interpretation of previous studies have been hampered by the lumping together of all individuals of the same species and ignoring ecological differences between populations of one species.

The present study was based on the proposition that variability of grouping tendencies within a species is a response to variable levels of prey availability (Uetz et al. 1982). By manipulating predator and prey densities, I have found that high prey densities allow a significant reduction in web building activity and a much higher inter-individual tolerance by spiders without specific orb webs. This reduction was, however, only observed when spiders themselves were at high densities. This can only be explained if: 1) satiated spiders suffer a decrease in aggressive behavior; and 2) individuals benefit from aggregating together at high prey densities. This benefit may be derived from the use of comunally laid silk for capturing insects. Where spider density is low, silk sharing is unlikely to arise, as spiders will not come into contact with the silk of another individual: nearest neighbour distances are very much greater for both those with webs and those without. Similarly, if prey is available at a lower level, spiders build webs more frequently, and the orb webs are larger. Because the orbs themselves are defended areas, the aggressiveness of individuals towards conspecifics is never reduced sufficiently to allow mutual tolerance.

That the presence of silk itself does indeed affect the foraging process in T. elongata is given farther support in the second experiment, where spiders spin larger webs and are significantly more aggressive where silk is removed. One could imply from this that individuals are responding to the reduced energy budget under these conditions as a consequence of the increased expenditure in terms of silk production. But then the question would remain: when spiders do not share silk, and there is a differential in the energy budget in terms of

prey availability (the 2 sections with spiders at low density), why do spiders not spin larger orbs at the lower prey availability? An alternative explanation to the increased size of orbs when silk is removed is that silk serves as a mechanism for compensating for the reduction in prey detectability. This implies that silk, though it need not be energetically expensive, is essential for determining the availability and location of prey, as well as capturing it. The second explanation is also more likely when one considers the very low cost involved in the manufacture of an orb web that is ingested prior to rebuilding (Peakall 1971, Prestwich 1977).

As Pulliam and Millikan (1982) point out: whenever the amount eaten is independent of the size of an aggregation (i.e., food is not limiting and intraspecific tolerance prevails), even a marginal increase in the efficiency of locating and / or capturing prey will benefit members of the foraging group. Aggregative behavior may then develop where the organism suffers an increased probability of averting starvation through variance reduction (Caraco et al. 1980c). Risk sensitivity and subsequent aggregation at high resource availability has been demonstrated in a number of studies on passerine birds (Baker et al. 1981, Caraco 1979b, 1981a and b, 1982, Caraco and Pulliam 1980, Caraco et al. 1980b and c, Krebs et al. 1972, Powell 1974, Pulliam and Millikan 1982, Thompson et al. 1974, Wolf et al. 1975). These birds are almost all small and energetically stressed; studies conducted on them were generally during periods of relative food shortage. Time and energy expenditures are therefore likely to be the primary currency of economy (Pulliam and Millikan 1982): if the birds suffer starvation, their

Darwinian fitness will be reduced to zero. This makes them ideal tools for relating short term behavior to lifetime fitness (McNamara and Houston 1982); the immediate response of an individual to resource variability is directly related to its fitness.

Similar constraints (the ability to produce an egg sac over the season) have been shown to cause T. elongata to respond to variance in prey availability in a way that can be predicted in terms of risk responses (see Chapter IV). Aggregating and subsequent sharing of silk could reduce the variance in prey capture rate to an individual by allowing the spider to monitor a much larger area for prey availability. Where spiders are solitary, the localized area over which an individual can detect and capture prey necessitates a higher variance in prey capture rates, though the mean capture rate may be the same. This type of risk sensitive response to resource variance may be an alternative route to sociality avoiding the need for elaborate hypotheses as to why aggregative behavior may have originally evolved.

CHAPTER VI

CONCLUSION

This study documents behavioral interactions between spider predators and their prey. There is a marked paucity of data documenting such interactions, although those data that are available suggest that the tactics involved may be very complex (Morse 1980). A large proportion of studies on foraging behavior are concerned with the many ways that mean fitness maximization (i.e., a single value: the average of the habitat) can be incorporated into biological models and in what ways application of this principle leads to new insights into the evolutionary process. The present study points to the inadequacy of this approach. Simple mean maximization will not account for the diverse behavioral repertoires frequently found in a single species, particularly when behaviors are bimodal (Real 1980b) as was found here between populations of Tetragnatha elongata.

Consideration of the role played by diversification in foraging behavior lends new insight to the role of spiders as possible agents of pest control. Those criteria which make it beneficial for an organism to diversify in time and space will also be those criteria that stabilize populations (Real 1980b). Changes in prey density caused the spiders in this study to change their foraging strategy. Consequently, the behavior of these predators may impart stability to the population as a whole.

It has frequently been argued that the tendency of spiders to maintain a certain inter-individual distance will limit their use in agroecosystems that are actually undergoing unstable cycling of a pest:

they may only serve to maintain existing stability. Studies on orb weavers, however, invariably refute the concept of a fixed inter-individual tolerance limit under variable levels of prey availability. As shown in this study, spiders may tend towards coloniality at very high prey numbers. The potential of T. elongata, and perhaps orb weavers in general, appears, therefore, to have been underestimated in their consideration as pest control agents.

Initial control of pests in a given ecosystem is only effective if the predator is small, is specialized in its choice of prey and has a high biotic potential. In this regard, insect parasites do have one great advantage over orb web spiders: their resource serves as their habitat and they are therefore generally both habitat and prey specialists. Spiders, on the other hand, tend to be generalist feeders (but see Riechert and Lockley (1984) for a review of some notable exceptions). Habitat specificity may also, however, allow spiders to specialize on a given prey type. Integrated pest management wherein natural vegetation is mixed with cultivated areas may serve to maintain stability in an agroecosystem but only once the numbers of a given pest species have been controlled. What if a pest is present in epidemic numbers? Spiders may only serve as effective control agents if they have a specialized habitat which, if coincident with that of the pest, may necessitate a degree of specialization on that pest. Such a situation does occur with T. elongata, which will build a web in exactly those situations where mosquitoes pupate and emerge; i.e., almost anywhere over water that provides adequate structural support; and, if prey is available in excess, they may reach extremely high densities in these

areas. Tetragnathids, therefore, offer potential as agents in both the initial control and subsequent maintenance of stability in situations where mosquitoes are pestilent (see Dabrowska Prot and Luczak 1968a for suggestions of the potential of T. montana as an agent for use in pest control).

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