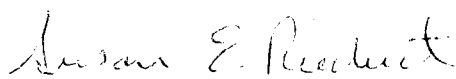


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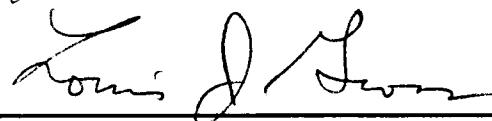
I am submitting herewith a dissertation written by Louis Provencher entitled "AN INDIVIDUAL BASED APPROACH TO UNDERSTANDING PREY REGULATION BY SPIDERS." I have examined the final copy of this dissertation for form and content and recommended that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.



Susan E. Riechert, Major Professor

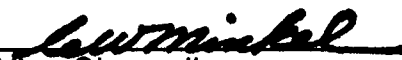
We have read this dissertation
and recommend its acceptance:







Accepted for the Council:



Vice Chancellor
and Dean of the Graduate School

**AN INDIVIDUAL BASED APPROACH TO UNDERSTANDING
PREY REGULATION BY SPIDERS**

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

Louis Provencher
December 1990

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ABSTRACT

In this thesis I investigate the processes by which spiders may regulate associated prey populations. The general hypothesis is that spiders, as generalist predators, should regulate prey if they exhibit a foraging phenotype that maximizes their relative fitness.

Theoretical Treatment. Using an individual based, stochastic computer model I simulated the feeding of individual spiders on prey subpopulations in a patchy habitat. I examined the foraging success of spiders and prey numbers with respect to various environmental and behavioral treatments. Increased patchiness decreased prey numbers and spider foraging success, whereas a higher number of prey species increased spider success. The greater the number of spider species and the broader the range of prey sizes present in the system, the greater was the level of predation by spiders on the insects. The greater the range of body sizes of spiders present, however, the less was their predation effect. The prey selection strategy effect was significant: the superior strategy also captured the greatest biomass of prey in competitive phenotype simulations. Spider aggressiveness towards other spider in the simulation had no significant effect on results.

Experimental Treatment. A series of experiments was devised to test model assumptions. First, it was established that hunger had no effect on the foraging activity of the spiders *Tetragnatha laboriosa* and *Lycosa rabida* nor on the predation of insects by *Tetragnatha*. In an experiment designed to test spider response to prey variability, the spider, *Lycosa rabida*, avoided prey variability treatments presenting the greatest probability of food

deprivation. The test spiders generally switched positively between two prey species. Forecasting tests revealed that *Lycosa* preference for prey significantly exhibited a dependence on experience with past numbers of prey.

The final experiment was a field validation of the model's qualitative predictions concerning the number of species of prey and spiders, and the number of patches. Increasing the number of species of spiders decreased prey biomass and increases in prey numbers with fewer patches occurred only without spiders. A greater number of prey species increased the biomass of prey only in with spiders.

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PART 1

A PHENOTYPIC VIEW OF PREY REGULATION BY GENERALIST PREDATORS

INTRODUCTION

Students of biological control have too often dichotomized predators as specialists or generalists, an oversimplification which, however, has fueled some controversy (Beddington et al. 1978, Hassell 1978, Riechert and Lockley 1984, Murdoch et al. 1985, Erlinge et al. 1984, 1988, Kidd and Lewis 1987). The fundamental difference between the two types of predator is in (genetic) dietary diversity. By specialist predator I refer to an animal which can (1) only consume one or very few and related prey species, (2) may have a short generation time relative to its prey species, and (3) may have high active dispersal capabilities. On the other hand, a generalist predator is polyphagous and may possess some or all of the following characteristics: (1) has a longer generation time than most of its prey species, (2) disperses actively and passively to varying degrees, (3) exhibits aggressive behaviors such as territoriality and cannibalism, and (4) has the physiological potential to resist starvation (Riechert and Lockley 1984, Murdoch et al. 1985). It has long been assumed that only specialists are capable of the density-dependent tracking required to regulate a prey population (Beddington et al. 1978, Hassell 1978). This accepted view has been seriously challenged for several reasons: (1) previous theoretical models have unfavorably represented generalist predators and their dynamics (Murdoch et al. 1985), (2) the idea of a one-to-one relationship between populations of prey and predator applies perhaps well to specialists, but in the case of generalist predators a species assemblage approach may be more appropriate (Riechert and Lockley 1984, Erlinge et al. 1984, Riechert and Bishop 1990), (3) field studies support instead the

idea that generalist predators may have yielded the greatest cases of successful biological control (Kiritani and Kakiya 1975, Riechert and Lockley 1984, Murdoch et al. 1985), and (4) community ecology models of food webs provide theoretical evidence that the self-damping effects of generalist consumers increase stability with greater diversity (DeAngelis et al. 1975, Tanner 1975, Post and Travis 1979) and that generalist consumers may have devastating effects on their prey (Pimm 1982).

The relative ability of generalists or specialists to limit prey populations is to me less interesting than the analysis of the traits of the generalist predator, in particular the specific foraging strategy that individuals exhibit. The set of characters making up a predator type will be referred to as its foraging phenotype, which I will treat in the manner of quantitative genetics (Falconer 1981): a foraging phenotype can be partitioned into genetic and environmental components. Given that at least some generalist predators have successfully limited to acceptable levels the economic damage inflicted by prey (pest) populations, it is then appropriate to identify the combination of foraging traits and the environmental factors which accomplish this.

A first step is to assume that foraging traits are correlated quantitative characters and, thus, have a statistical distribution within a species. Within a population some foraging phenotypes are expected to achieve stronger prey limitation than others. This approach is, however, anthropomorphic; it is difficult to see that higher prey regulation has any bearing on individual predators. The primary concerns of a predator may instead be to survive and reproduce. Hence the important goal is to identify generalist phenotypic

characters maximizing fitness and permitting strong prey limitation relative to other phenotypes. This is because increased reproductive output should demand greater prey consumption. An agent of biological control which fails to reproduce or produces fewer offsprings more than another possessing a different set of traits, will simply not be expected to last in any open system subject to immigration and emigration. The predator must be competitive with other conspecific predators in the system.

My approach is to identify the problem of prey regulation by generalist predators, and then bring it to the level of competing foraging phenotypes. I have taken an individual based approach (Huston et al. 1988), since prey regulation is the result of a distribution of predator strategies acting locally (Chesson 1978). Furthermore, the foraging behaviors of the generalist predator make more sense at the individual level because local conditions are forced upon generalists by their aggressive behaviors. Territorial behavior characteristic of spiders, for example, establishes resource inequalities between the individual predators (Lomnicki 1988), which in turn introduces between-territory (inter-individual) variability in prey selection. The outcome of interactions between individuals is also sensitive to the identities of the animals involved. For example, differences in body sizes among individuals interacting agonistically can make a difference between retaining or losing a territory, injuries which decrease future fitness, and death (Hammerstein and Riechert 1988). An aggregate view of predation would miss many of the behaviors relevant to prey regulation by generalist predators. This approach has proven very valuable in a recent model by

Kareiva and O'Dell (1987) for ladybird beetles predation on swarms of aphids.

Foraging strategies: phenotypes. The set of probable foraging strategies found within a generalist species depends on critical features of the animals. I chose spiders because they exhibit all of the traits that characterize a generalist predator (Turnbull 1973, Riechert and Lockley 1984). An important aspect of spiders is their peculiar physiology related to their extreme tolerance to starvation (see review in Riechert and Harp 1986). The best eco-physiological growth functions for spiders are found in Nakamura (1982) which takes into account the facts that they can store large amounts of energy reserves in their flexible abdomens, and also shut down their metabolisms when food deprived.

Less is known about the foraging behavior of spiders in conditions of varying food deprivation. It has been observed that web size changes with levels of food intake in the desert spider *Agelenopsis aperta* (Riechert and Tracy 1975, Riechert 1981). Although not much data are available on the subject of hunger related foraging behavior in spiders, two models have been made concerning the less active searchers referred to as sit-and-wait foragers. Gillespie and Caraco (1987) proposed a risk-sensitive foraging model for the tetragnathid, *Tetragnatha elongata*, in which food deprived spiders are predicted to become risk-prone by adopting the strategy of not changing web-site (increased variance), while spiders doing well energetically should be risk-averse and aim for the mean prey reward by changing web-sites frequently (decreased variance). Field studies completed on *T. laboriosa* indicate that this spider conforms to model

predictions (Gillespie and Caraco 1987); field experimentation is needed for an adequate test. Mangel and Clark (1988) reconsidered the Gillespie and Caraco (1987) model from the perspective of dynamic optimization theory and predicted opposite behaviors. This is due in part to the inclusion of predation risk in the dynamic optimization model. Mangel and Clark (1988) predicted that a food deprived spider should hunt even at a great risk of predation upon itself, whereas satiated spiders should hide from predators.

Most spiders are generalist feeders, are territorial (Riechert 1981), are often predators of other spiders (Turner 1979, Turnbull 1973), and present an impressive variety of contest behaviors (Witt and Rovner 1982). They are also very varied in their capture tactics. The most notable difference is between web and non-web spiders. There is further division among taxonomic groups, especially at the family level, associated with still other strategies (Turnbull 1973: e.g., ambushers versus active searching among the non-web builders).

Spiders are just one group of generalist predators, yet the diversity of foraging behaviors they exhibit does raise the issue of whether there exists a multitude of successful generalist types. Coming back to the original goal, what specific strategy or strategies make a generalist predator successful as an individual and does this strategy(ies) also lead to the control of associated prey populations? Generalist predators that switch positively between prey types are generally considered more likely to limit prey than predators which do not switch or switch negatively (Oaten and Murdoch 1975, Chesson 1984). Positive switching consists of having a disproportionately greater capture rate for the more abundant prey type

(Chesson 1984). Switching can also be negative, meaning a disproportionately greater capture rate for the rarer prey type. (Negative switching does not lead to prey control.) Switching in predation is similar to diet optimization in foraging theory (Charnov 1976, Stephens and Krebs 1986). The difference, however, between switching and diet optimization is that the most abundant prey type is not necessarily the most preferred by a forager. Hence, in theory, diet optimization could lead to negative switching and actually foster prey outbreaks through the exclusion of the most abundant prey type from the predators diets. Note, however, that the negative effect in the system by one individual predator's behavior may be offset by other predators of the same or other species.

An individual predator should switch to a more profitable prey species if it is expected to be present, or abundant enough (Stephens and Krebs 1986). Note, however, that for switching to be a successful strategy, I hypothesize that the forager should be able to estimate its future prey supply. The inability to predict future prey abundance might be caused by environmental variability or inaccurate forecasting (time series estimation of future numbers). Switching between prey types may maximizes fitness, but it is a potentially unsafe strategy than the proportional use of all prey types in a variable environment, which allows at least the consumption of some food if something were to happen to the preferred type.

Correlated with the tendency to select prey types in certain ways is the important problem of aggression. Territorial behavior can prevent increases in spiders numbers in response to increased numbers of prey (the numerical response) (Greenstone 1978): this is because in defending space

against intrusion by conspecifics, the spiders are limiting the number of spiders that can occupy a given patch of habitat. Territorial behavior is not necessarily a problem for biological control if habitats are managed to foster spider survival (Riechert and Lockley 1984, Provencher and Vickery 1988, Riechert and Bishop 1990) and if more than one species is involved. Riechert and Bishop (1990) have shown that ground protection (mulch) increases dramatically the survival of spiders in garden systems, and, as a result, less damage was inflicted on crop plants. Provencher and Vickery (1988) suggested that intercropping would be a way to prevent pest colonization of crops and to increase the diversity of alternative prey for polyphagous predators such as spiders. These measures could also increase the number of species of spiders, which may make spider packing less of a problem since territoriality is usually intra-specific (Riechert 1981).

Most spiders exhibit territorial behavior; there is variation in the extent to which territories are defended (i.e., in the degree of aggressiveness of the territory holder). Injuries following combat can decrease a spider's future fitness (Hammerstein and Riechert 1988) because the animal's ability to capture prey has decreased. On the other hand, an unaggressive spider is more likely to lose its territory, hence its foraging site. The tradeoff is obvious. One advantage of being territorial and aggressive may be that the spider has a better indication of the prey availability over time and, thus, is more able to "forecast" future trends of prey supply. Its switching may be enhanced. A spider losing a territory for another, unknown area has less information about past prey availabilities at the site and has the added complication of spatial variability to include in its expectation of future prey

numbers. A permanent territorial resident deals mainly with temporal variability, whereas a vagrant spider is constantly confounded by spatial and temporal variability. As an individual moves in space, time goes by. Hence, I would hypothesize that less aggressive or more vagrant spiders do not engage advantageously in complex "forecasting" (Bennett 1979, Pankratz 1984) behavior, whereas the more aggressive or more settled ones do. Switching would thus be more common in more aggressive individuals. One could also imagine conditions where these predictions do not hold; if resources are too variable or too constant. Thus, information has its greatest value at intermediate levels of variability (Stephens and Krebs 1986).

I have argued here for combinations of prey selection and aggressive behaviors assuming that spiders would act in a "clever" manner. Some sobering thoughts are in order. Janetos and Cole (1981) proposed that animals do not always act optimally because of biological constraints imposed on their behaviors. Adding constraints to behavior does not imply suboptimality; the constraints are simply changed. However, Janetos and Cole did show that constrained behaviors can do very well at energy intake compared to the optimal, least constrained strategy. Cases of apparently suboptimal foraging behavior have been reported. Two populations of the funnel-web spider *Agelenopsis aperta*, one in a food-stressed grassland desert and the other in a prey-rich riparian habitat, include a broad range of prey species in their diet. The spiders from the riparian habitat which could (should) specialize their diet by at least rejecting harmful prey, such as ants, continue attacking them (Riechert, submitted). Riechert hypothesizes that this suboptimal behavior is caused by gene flow from migrants originating in

surrounding, food-stressed habitats. A genetic basis to the foraging behavior of this spider has been demonstrated for *A. aperta* (Hedrick and Riechert 1989).

The relationship between all foraging behaviors in a spider species life cycle and their respective contributions to reproductive success were investigated in the crab spider, *Misumena vatia* (Morse and Fritz 1982, Fritz and Morse 1985, Morse 1986, Morse 1988). Several surprising conclusions emerged from this work: (1) A large fraction (30%) of a population of *Misumena* did not seek hunting sites with higher prey visitation rates than theirs (although such sites were in close proximity) (Fritz and Morse 1985). (2) *Misumena* did not generally exhibit an optimal diet choice (Fritz and Morse 1985). (3) Most behaviors, except one, which seemed initially critical, contributed very little to reproductive success (Morse and Fritz 1982, Fritz and Morse 1985, Morse 1986). Females which guarded their eggs against predation while fasting, generally avoided having their clutch destroyed (Morse 1988). The percentage of such predation in unguarded eggs was 55%. (4) Kareiva et al. (1989) mapped by computer simulation the adaptive landscape of two rules of thumb performed by *M. vatia* with respect to average yield. The rules of thumb for spiders were: (1) leave an umbel when some fixed amount of time has elapsed without any prey visiting the umbel, and (2) leave an umbel with a constant probability per unit time, which was calculated from an exponential distribution and changed with environmental conditions. (Conformity to the latter rule was observed in the field.) They obtained a very rugged landscape with multiple peaks, which

means that the a spider's foraging success was not maximized by one behavior.

OBJECTIVES

The main goal of this research was to develop an individual based model testing the role of genetic and environmental factors in prey regulation by generalist predators (Parts 4 & 5 of this dissertation). I tested in the laboratory and in the field 4 major assumptions that were used in the simulations: (1) hunger influences the foraging behavior of spiders, (2) spiders switch between prey types, (3) spiders recognize prey variability, and (4) spiders "forecast" prey numbers. It was necessary for me to evaluate the significance of the 4 assumptions before including any in the behavioral algorithms of the model. In particular, the stochastic algorithm for prey selection could included all of these features and in various forms. These tests are completed in Parts 2 and 3.

The factors tested in the model itself were: patch number, prey species number, the spider species number, range of prey and spider body sizes, the degree of aggression among spiders, and prey selection strategy. In Part 4 of the thesis, I deal with the phenotypes of a single spider species, the patchiness, and the number of species of prey. In Part 5, I examine the hypothesis proposed by Riechert and Lockley (1984): the predator assemblage effect. I completed a validation experiment testing three of the model's predictions in Part 6: the number of patches, and the number of species of prey and spiders, respectively.

RATIONALE

The implications of this research are twofold. The knowledgeable use of generalist predators as agents of biological control may offer a feasible alternative to the harmful and expensive practice of insecticides. Generalist predators are also abundant and widely distributed, which may make them a preferable alternative to the expensive selection and introduction of foreign enemies.

The individual based approach chosen in this research is a promising and relatively new way of looking at old problems. I believe it offers a richer interpretation and greater power of prediction than the aggregate view of modeling. This is because individual based modeling is more mechanistic and testable. It also offers a more unified view of evolution through the intermingling of selection on phenotypes and ecology.

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PART 2

SHORT-TERM EFFECTS OF HUNGER CONDITIONING ON
SPIDER BEHAVIOR, PREDATION, AND GAIN OF WEIGHT

INTRODUCTION

Stochastic foraging models of risk-sensitivity (Real and Caraco 1986) and dynamic optimization (Mangel and Clark 1988) make direct use of an animal's energetic state to predict a behavior that is adopted to maximize fitness. It is, for instance, predicted that starved animals will behave very differently from satiated ones. In experiments testing predictions of risk-sensitive models with small birds (Caraco et al. 1980), small mammals (Barnard and Brown 1985), and social insects (Waddington et al. 1981, Real et al. 1982), the energetic state of interest was always considered on a short time scale of one to several days. In the case of small specialized homeotherms, short-term dynamics seem reasonable since these animals may have stringent energy demands requiring behavioral adjustments on a short-term basis (Clements 1990). As for social insects, it may simply be their short life span which focuses their foraging needs to brief periods of time.

I am concerned here with animals capable of resisting starvation and for which greater food consumption is positively correlated with their reproductive output (Riechert and Tracy 1975). Specifically, the feast-and-famine organisms I study are spiders (Anderson 1974, Riechert and Harp 1986). The problem I foresee is that although food intake is very important to the fitness of spiders, foraging behavior does not seem finely tuned to energy demands precisely because spiders have the physiology to resist starvation. For example, predictions such as 'starved spiders should exhibit risk-prone behavior by choosing the habitat with the highest variance' may not work (but see Gillespie and Caraco 1987). I do think hunger has a short-

term effect on food consumption behavior, but I doubt that this effect influences foraging strategies. For instance, eco-physiological theory when applied to spiders predicts that (1) starved spiders should shut-down their metabolism and activities and wait for prey, (2) exceptionally sated spiders should be active only when necessary and hide from predators otherwise, and (3) spiders of an intermediate energetic condition benefit from exploring new habitats, especially if hungry (Anderson 1974, Riechert and Tracy 1975). Some of the above conclusions have also been reached by Mangel and Clark (1988) through the application of a dynamic optimization model to a spider system.

To examine the potential role of short-term hunger conditioning, I conducted two field experiments with the orb-weaving spider *Tetragnatha laboriosa* (Hentz). The first experiment compared the effect of hunger conditioning on spider movement and relative weight gain, and the second tested for hunger effects on the control of prey numbers in multi-species assemblages. I compare these results with hunger conditioning data available for the spider *Lycosa rabida* (Walckenaer) (Provencher and Riechert, submitted).

METHODS

The work was conducted in an old field habitat in Knox County of east Tennessee, during the summer of 1987. I used adult females of the spider *Tetragnatha laboriosa* (Hentz) which were first hunger conditioned in the laboratory. Adult females of this orb-weaving spider measured between 1 and 1.5 cm from chelicerae to spinnerets. I conditioned the spiders to

different food levels by separating field collected adult females into two groups; individuals in the 'deprived' group were given two fruit flies, *Drosophila melanogaster* Meigen (Diptera), per day, whereas individuals in the 'satiated' group received seven fruit flies daily. (My prior experience with rearing *T. laboriosa* indicates that adult females cannot survive for long at a feeding level of two fruit flies per day. Thus, the food conditioning was continued for only one week.) Spiders were weighed just after hunger conditioning. During this period the subjects were individually housed in 5 x 10 x 2 cm plastic boxes in the laboratory with access to water.

Hunger Patterns and Prey Availability Effects on Spider Activity. I randomly selected spiders from each feeding level group and assigned them to one of four prey covariability treatments, involving 2 prey species: fruit flies, *D. melanogaster*, and termites, *Reticulitermes flavipes* (Isoptera). The four covariability treatments, offered over a 3-day period in the laboratory, were (1) constant, (2) varying (but weakly and negatively covarying), (3) negatively covarying, and (4) positively covarying prey numbers (Table 2.1). The purpose of these variability treatments was to present spiders with four different types of food availability which they may naturally encounter. For each treatment a mean of 3 prey items/prey type was offered. I color-coded the spiders according to prey availability treatments and released them at dusk in field enclosures. These enclosures had a crossed polyethylene pipe supporting structures which was covered with cheesecloth. The structure was fitted to a wooden frame (1.5 by 2 m). The enclosures were 1.3 m high at the center. The floor of each was bare ground stripped of all vegetation and covered by fiberglass insect netting on

Table 2.1. Covariability between fruit flies and termites as post-hunger conditioning treatments offered to the spider *Tetragnatha laboriosa* in the laboratory. Variability is temporal. Each spider received only one of the treatments.

	DAY						VAR ^a		COV
	1		2		3				
	^b F	T	F	T	F	T	F	T	
TREATMENT									
constant	3	3	3	3	3	3	0	0	0
variable	3	4	2	3	4	2	1	1	-0.5
+covariance	1	1	3	3	5	5	2	2	4
-covariance	5	1	3	3	1	5	2	2	-4

^a : VAR = temporal variance of the number of fruit flies and termites. COV = temporal covariance between the number of fruit flies and termites.

^b : F = fruit flies, T= termites.

which I placed a sheet of poultry netting (i.e., "chicken wire") which provided for spider web attachment-sites. Starved and satiated spiders were released in separate, adjoining enclosures (block). Each enclosure contained four spiders, each of the four spider representing a different variability treatment. Hence, I used a total of 32 different spiders. The content of a sweepnet full of insect (25 sweeps) was also added to each enclosure to stimulate spider activity. Observations were started the evening on the day spider's were introduced to enclosures.

I performed four blocks (= plots of hunger conditioning) during the nights of September 11-12 and 14-15, and observed spiders all night from inside the enclosures. Note that the covariability treatments were subplots (this is a split-plot design with no replication; Steel and Torrie [1980]). Spiders were systematically sampled by alternating 20 minute periods of observations between cages. Light was provided by a flashlight covered with yellow cellophane. Previous field work by myself and S. E. Riechert revealed that insects do not react as much to yellow light as red one. The variables measured were the number of times a spider moved and the distance moved. Spiders did not seem aware of my presence and only infrequently interacted with one another. At dawn spiders were collected and weighed again.

Spider Effect on Prey Numbers. For the predation experiment, I used 64 *Tetragnatha* which, after hunger conditioning, were put into field enclosures in groups of four. There were three treatments; no spiders added (control), deprived spiders added, and satiated spiders added. The design was a block design without replication (Sokal and Rohlf 1981), with three

treatments per block and eight blocks. Enclosures had the same basic design as above except that the clover-fescue vegetation was not removed. Furthermore, prey collected by sweepnetting were initially added to the insect fauna already present in the enclosures. Prey numbers were sampled daily for 7 days between 7:00 and 8:00 am EST. The first sample was completed before introducing spiders to enclosures. The easiest non-destructive method for sampling prey that would encounter the webs of *Tetragnatha* was to count prey on the inside surface of the netting. This method yielded relative results which were adequate for among treatment comparisons. Prey types, their average length and energy content (J/mg) are listed in Table 2.2.

Statistical Analyses

Hunger patterns of prey availability effect on spider activity. As noted above, the experiment testing hunger effects on spider activity and weight gain was a split-plot design with hunger conditioning being the plot and covariability treatments the subplots. I tested both the effects of hunger conditioning and covariability treatment by a MANOVA on the number of moves by spiders, the distances they moved, and their relative gains of weight. Relative gain in weight was measured by the logarithm of the ratio of final to initial body weights. I used this transformation to normalize the distributions of the weight data and to homogenize the variances between treatments, which initially were not all normal and were heteroscedastic. I used a MANOVA because the response variables were potentially correlated such that a significant effect for one causes the other to

Table 2.2. Prey types of the prey control experiment with the spider *Tetragnatha laboriosa*. Conversions to Joules/mg from regression relationship to dry weight (mg wet weight = $0.0305(\text{insect length})^{2.62}$; Rogers et al. 1972) and Joules equivalents for different orders (Joules/mg from Riechert, submitted).

TYPE	MEAN LENGTH (mm)	ENERGY CONTENT (J/mg)
brown leaf hopper	2.75	24.03
green leaf hopper	5.17	24.03
aphid (winged)	1.5	24.03
dipteran	7.0	21.14
fruit fly	2.0	21.14
noctuid moth	6.5	22.86
crane fly	15.0*	21.14
house fly	5.0*	21.14
hemipteran	6.0	24.03
parasitic wasp	3.0*	23.20
mosquito	4.0*	21.14
beetle	5.0	23.28

* Length taken from the literature (Borror and DeLong 1971, Milne and Milne 1980). Note that the predominant prey type is the brown leaf hopper.

also be significant (SAS 1985, PROCEDURE GLM). The error term for the hunger conditioning effect was the interaction between the mean squares of blocks and hunger conditioning, whereas the correct error term for the covariability treatment and interactive effects was the interaction of the mean squares of blocks and the covariability treatment, nested in hunger conditioning (in SAS terminology; block*treatment(hunger)) (Steel and Torrie 1980).

Spider Effect on Prey Numbers. Although the basic statistical design of the predation experiment is a simple two-way ANOVA without replication, I resorted to the more complicated multivariate repeated-measures, two-way ANOVA (O'Brien and Kaiser 1985, SAS 1985 PROCEDURE GLM) design to test the effect of hunger conditioning. The repeated-measures MANOVA was the better way of testing an effect measured from the same experimental units over time because it also tests the effect of time. The response variable was the natural logarithm of prey energy (J) summed across prey type per enclosure and per time interval. The logarithmic transformation was necessary to normalize distributions and, mainly, to homogenize variances between treatments and days.

RESULTS

Hunger patterns of prey availability effect on spider activity. The overall effect of hunger conditioning was not significant ($P > 0.0650$); the effect of the prey covariability treatment was significant ($P < 0.0393$) (Table 2.3). The overall effect of their interaction was not significant ($P > 0.5$). The effect of hunger was inconsistent because the response

Table 2.3. MANOVA of the effect of hunger conditioning and covariability treatments on the number of moves, the distance moved, and the log(final weight/initial weight) by *Tetragnatha laboriosa* in field enclosures.

source	Wilks' λ	F	df / df	P > F
hunger ^a	0.0026	127.52	3 / 1	0.0650
covariability ^b	0.3627	2.24	9 / 39.1	0.0393
hunger*				
covariability ^b	0.6520	0.83	9 / 39.1	0.5891

^a Error term is block*hunger.

^b Error term for the covariability and the hunger*covariability tests is block*covariability(hunger) where (hunger) means that covariability is nested within the hunger treatment.

variables for spider activity in the constant treatment behaved in the opposite direction of other treatments (Figures 2.1 & 2.2). Also, because the hunger effect is a plot effect, it is more difficult to detect than subplot effect in split-plot designs. The effect of covariability treatments was certainly caused by the difference between the means of response variables of the constant treatment versus the means of other treatments. With the exception of the constant treatment, satiated spiders moved more and greater distances than deprived ones. On the other hand, starved spiders gained considerably more weight than satiated ones (Figure 2.3). The high variances associated with the mean values of the response variables probably prevented significance.

Spider Effect on Prey Numbers. The effect of time and all interactive effects of time with blocks or hunger treatments were not significant ($P > 0.08$) (Table 2.4). The effect of added spiders (between subject effects) was significant ($P < 0.0023$). However, contrasts completed between the control and the two hunger conditions, and between the two hunger conditions, revealed that this significant effect was due to the control containing much more prey than the enclosures with spiders ($P < 0.0007$ versus $P > 0.4$) (Table 2.4). In other words, spiders significantly reduced prey biomasses regardless of their initial hunger states (Figure 2.4).

DISCUSSION

The general picture concerning hunger effects in this study is that they were not significant (Tables 2.3 & 2.4). The absence of significant hunger conditioning effects on foraging behavior and on the gain of weight has also

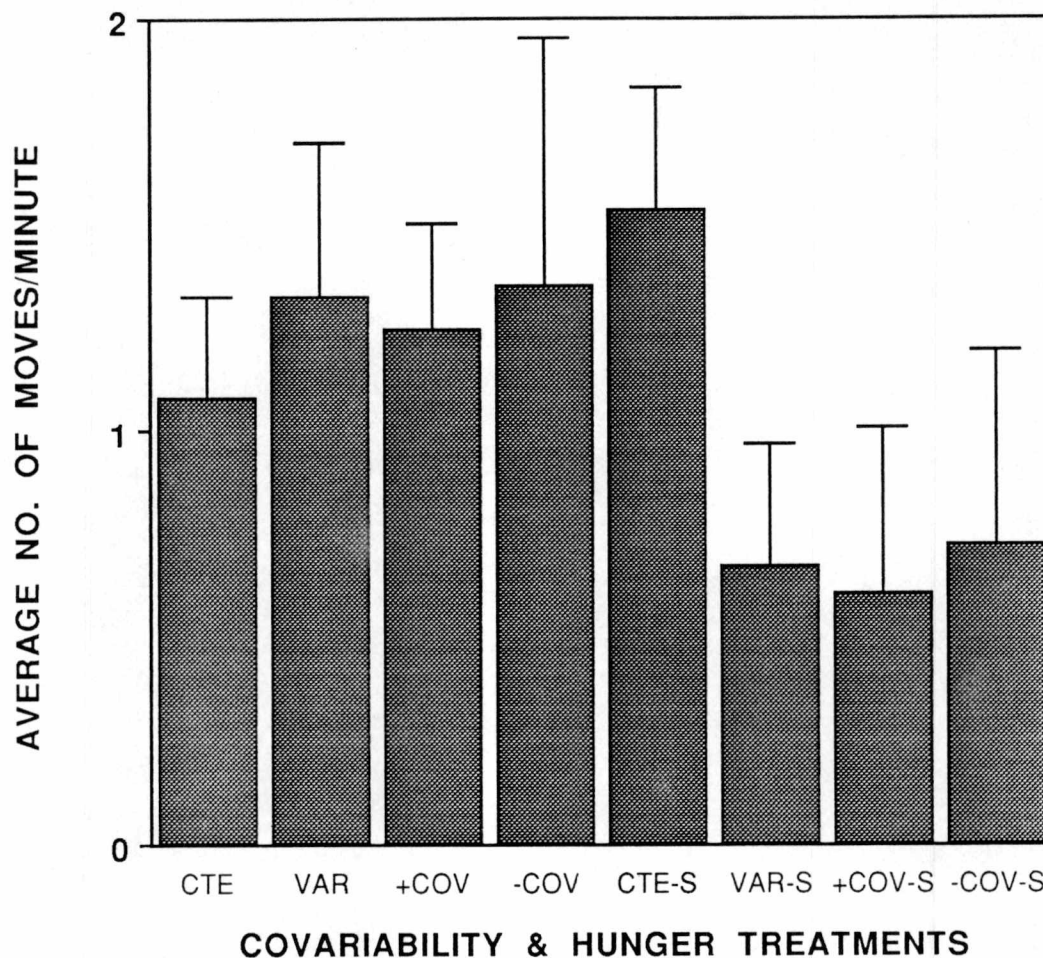


Figure 2.1. Average number of moves per minute made by satiated and food deprived *Tetragnatha laboriosa* exposed to four covariability treatments of prey numbers. cte(-s) = constant (starved), var(-s) = variable but weak covariance(starved), +cov(-s) = positive covariance (starved), -cov(-s) = negative covariances (starved). Error bar is one standard error.

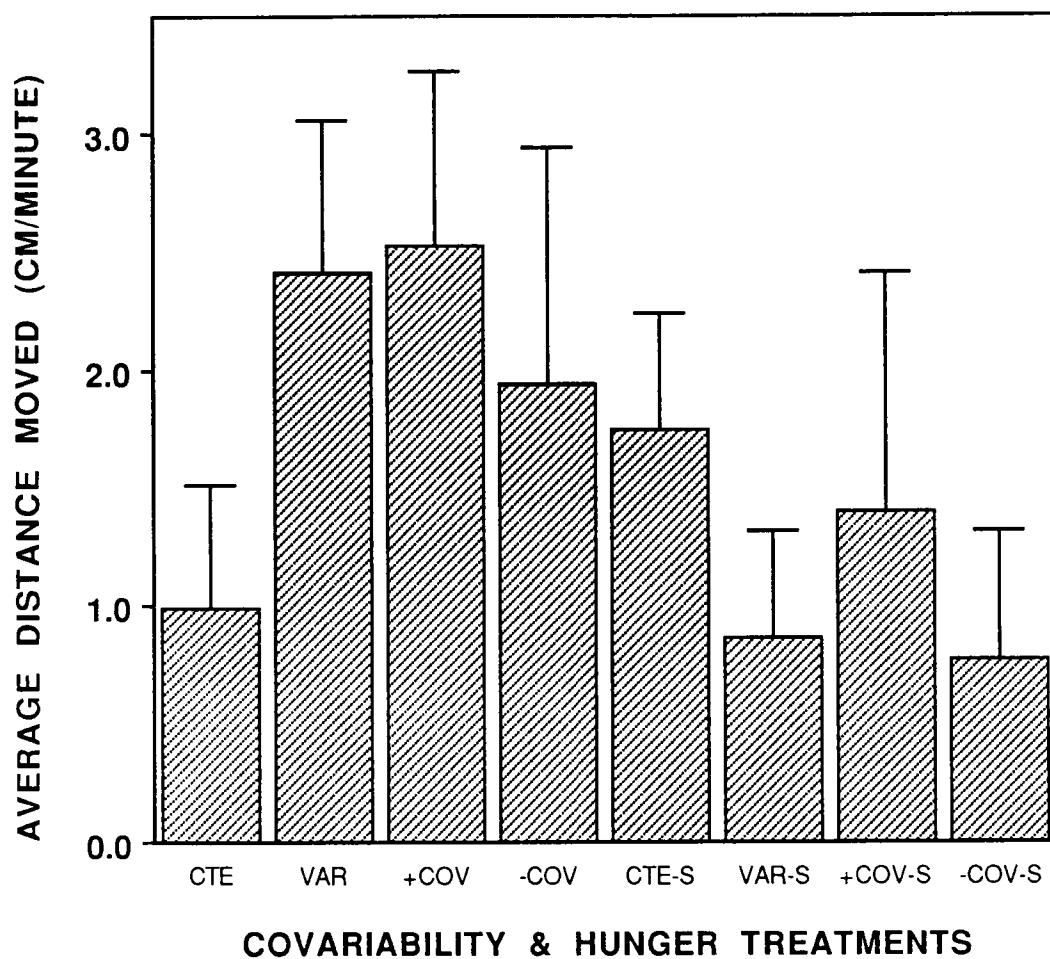


Figure 2.2. Average distance moved per minute made by satiated and food deprived *Tetragnatha laboriosa* exposed to four covariability treatments of prey numbers. Abbreviations as in Figure 2.1.

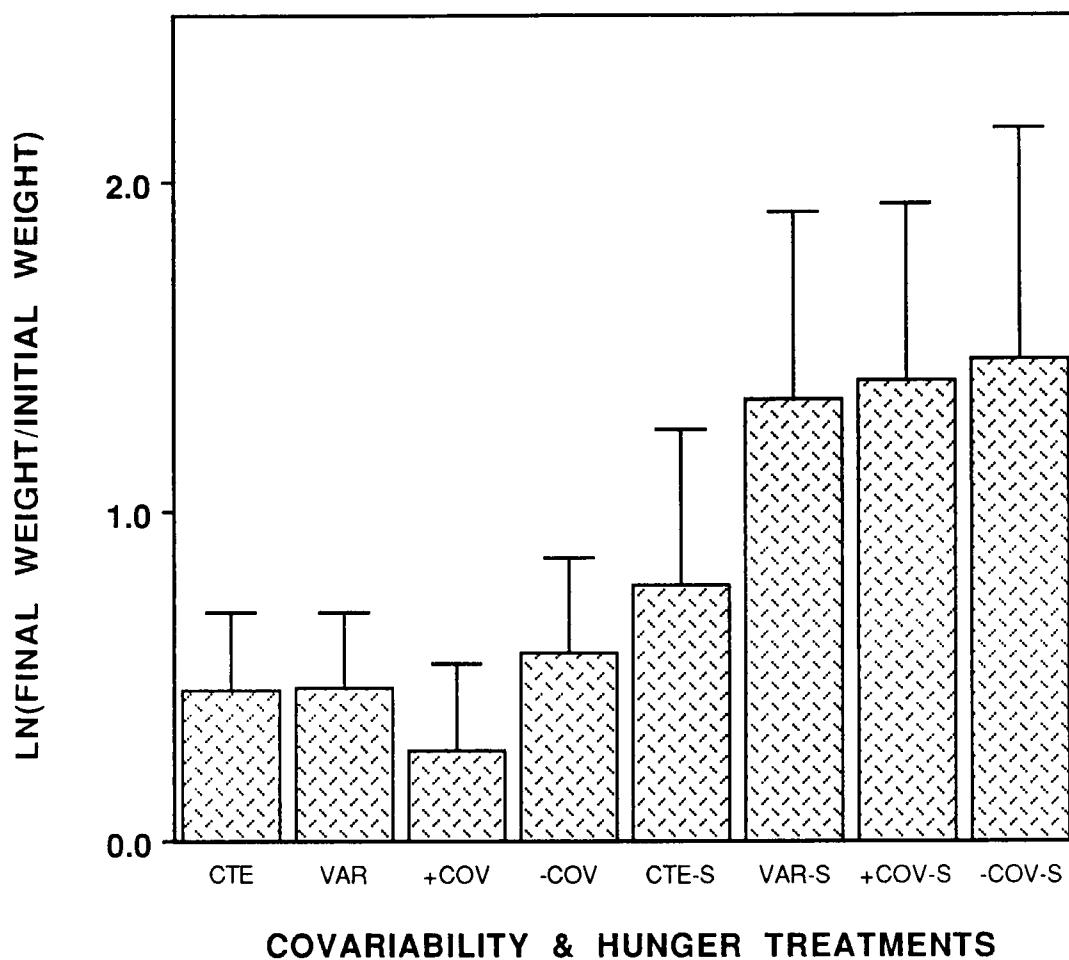


Figure 2.3. Relative gain of weight of satiated and food deprived *Tetragnatha laboriosa* exposed to four covariability treatments of prey numbers. The relative gain of weight is measured by the natural logarithm of the ratio of the final weight / initial weight. Abbreviations as in Figure 2.1.

Table 2.4. Repeated measures MANOVA of the effect of hunger conditioning on prey energy reduction by *Tetragnatha laboriosa* in field enclosures. Analyses were performed on the natural logarithmic transformation of Joules of prey.

A - Temporal effects

source	Wilks' λ	F	df / df	P > F
time	0.3580	2.689	6 / 9	0.0884
time*hunger	0.5894	0.454	12 / 18	0.9170

B - Hunger conditioning effects (between subject effects)

source	df	SS	F	P > F
block	7	14.5943		
hunger	2	29.9073	9.68	0.0023
contrast: 'no spider vs. spider'	1	28.7454	18.61	0.0007
contrast: 'deprived vs. satiated'	1	1.1619	0.75	0.4004
error	14	29.9074		

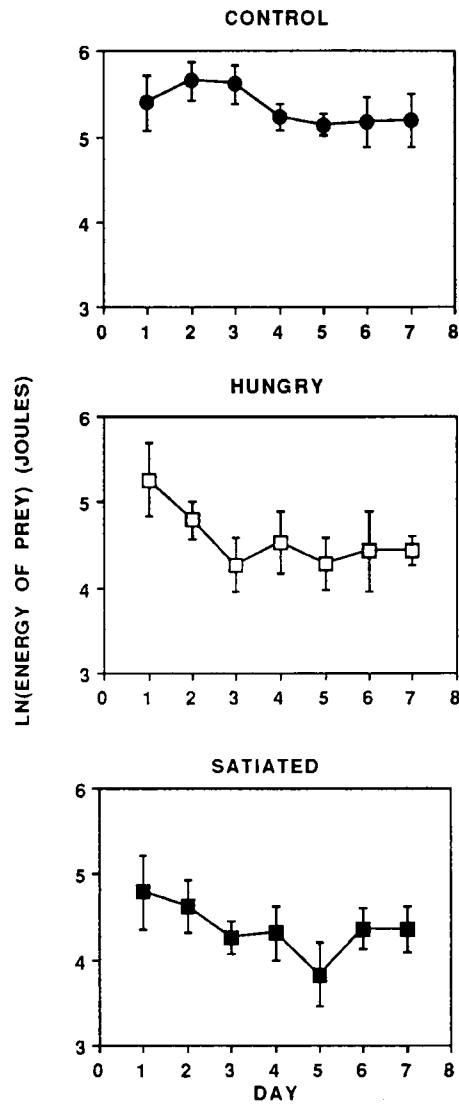


Figure 2.4. Energy of prey biomass in enclosures containing no spiders, satiated spiders, and food deprived spiders, *Tetragnatha laboriosa*, measured over seven days. Notice the natural logarithmic transformation of energy. Error bar represents one standard error.

been observed for the wolf spider *Lycosa rabida* (Provencher and Riechert, submitted). In that study, food deprived and satiated spiders were given a choice between three spatial options of temporal prey covariability established over 11 days. Hunger had no statistical effect on the frequencies of choice and the relative gain of weight. Deprived spiders weighed as much as satiated ones at the end of the experiment, just as in this study. I believe this is the key to understanding spider behavior as related to hunger. Simply, a deprived spider will attack any prey, perform multiple captures (pers. observ., Haynes and Sisojevic 1966) and consume all the prey, thus gaining back its weight deficit on its first prey encounter (spiders can subdue prey larger than themselves). A satiated spider will more likely choose easy to capture prey and eat them partially (pers. observ., Haynes and Sisojevic 1966). Hence after one prey encounter, the food deprivation effect may have vanished. It is thus not surprising that an experiment which exceeds one day may yield non-significant hunger effects. Such is the lesson emerging from the behavioral and predation experiments conducted here.

Deprived spiders which experienced the constant treatment increased their weights less than other deprived spiders and behaved like satiated spiders (Fig. 2.3). On the other hand, satiated spiders which also experienced the constant treatment gained weight like other satiated counterparts, but behaved like deprived spiders. Although a consistent eco-physiological interpretation for these average results can be offered, a detailed examination of individual spiders shows that initial body size may provide a sufficient explanation. Large adults gained little, or even lost

weight, whereas individuals made smaller by found deprivation showed an incredible increase in body mass. The significant covariability effect was actually caused by the (random) presence of the two largest spiders in the constant treatment for both hunger conditions and by the small number of degrees of freedom. Thus the results represent a body size effect: larger individuals move more than smaller ones and also cover greater distances. Larger individuals also better withstand food shortages.

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PART 3

SPIDER RESPONSE TO VARYING PATTERNS OF PREY ABUNDANCES:
TESTS FOR SWITCHING AND FORECASTING BEHAVIORS

INTRODUCTION

In association with possessing a broad diet (polyphagy), generalist predators exhibit territorial behavior or cannibalism and may have some physiological mechanism to resist starvation (Erlinge et. al. 1984,1988; Riechert & Lockley 1984; Murdoch et. al. 1985). The ability to maximally exploit associated prey patterns of availability is another trait that has been postulated for the generalist predator (Provencher & Vickery 1988). In this paper I test the idea that generalist predators are "multivariate time series statisticians," capable of forecasting expected resource availability on the basis of prior experience. (Note that I do not imply any conscious predictive capability on the part of the predator, but rather a response to cues that imitates forecasting.) If a predator is capable of processing information concerning the future availability of various prey types, then forecasted availability of a prey type should be included in the predator's estimate of its profitability (See Heller 1980; Juliano 1989). Classically, the profitability of a prey has included only the caloric value of that prey divided by the handling time necessary to procure it (Stephens & Krebs 1986). Why might forecasting be included in a predator's foraging decision as to whether to attack a given prey type or not? It is because forecasting predictions have fitness consequences. The magnitude of the fitness effect will depend on the behavioral rules followed by the generalist predator in its utilization of prey. The forager that attacks prey in proportion to their relative abundance is less in need of forecasting than is the predator that specializes on the most profitable prey type for a specific time interval (as in density-dependent

switching between prey types). Although density-dependent switching can afford greater food reward than proportional prey selection (Charnov 1976), the cost of an error, no food, is greater for this strategy. The critical factor is whether the supply of the preferred prey can be forecast accurately enough to permit temporary specialization on the prey type.

In the study reported here, I manipulate the temporal pattern of variability of two prey types to the spider, *Lycosa rabida* Walckenaer (Lycosidae), a generalist predator, to determine the extent to which this spider recognizes patterns of prey availability and responds to them. I used a spider as the model generalist predator because most Araneae are highly polyphagous, territorial, abundant, and easy to manipulate without disruption to their foraging behavior. In the first of two experiments I completed in the study, I test the hypothesis that individual spiders avoid certain types of temporal variability and covariability of encounter with prey. In the second experiment, I test for switching between prey and the prey forecasting that would be necessary for successful use of this temporal prey specialization strategy.

METHODS

Study Animals

I collected adult female wolf spiders, *Lycosa rabida*, from an old field habitat in east Tennessee. These animals averaged 700 mg in weight and were between 2-3 cm in length. *Lycosa rabida* is a nocturnal forager that I have observed feeding on crickets (Gryllidae), grasshoppers (Acrididae),

katydids (Tettigoniidae), scarab beetles (Scarabidae), lepidopteran larvae, and leafhoppers (Cicadellidae) during the course of my field collections.

In the first experiment (1988), I used field collected crickets (*Gryllus pennsylvanicus*) and katydids (*Orchelimum vulgare*) of approximately 1 cm in length as the two prey types. In the second experiment (1989), I used field collected *G. pennsylvanicus* and laboratory supplied European crickets (*Acheta domesticus*) of 1 cm as the prey. (The need for larger quantities of prey in the second experiment underlies the substitution of *A. domesticus* for *O. vulgare*.)

Design of Experiments

Spider and prey collections were made and field enclosures set up in a mowed old field in Knox Co. of east Tennessee during the summers of 1988 and 1989. I completed the experiments in a field setting rather than in the laboratory because I wished to incorporate the results into a computer simulation of spider-prey interactions that includes the stochastic effects of the environment. My interest, then, is in results that would not be overshadowed by the kinds of weather effects that might occur in the natural habitat. Completing the experiments in the field ensured this degree of robustness.

The same basic cage design was used in both experiments. It measured 1 X 1 m at the base and was 1 m high. The frame was constructed of polyethylene pipes and it was covered with netting (cheesecloth in the first year and insect netting in the second year.) The enclosure was completely sealed off by being designed as a bubble with

netting totally surrounding the inner structured. The prey were introduced into each cage through a slit in the netting which was folded and closed with clamps at other times. Peat moss and straw were laid on the netting floor of each cage to provide shelter to the prey and predator. Each cage was placed on a sheet of black plastic to limit ground beetle entrance and to slow the deterioration of the cage floors. In addition an extra layer of netting was laid over the top of the cage for shade.

Choice of Pattern of Prey Availability. I completed a pilot experiment between July 15 and 26 of 1988 to determine what was the minimum average level of prey that could be provided without compromising the prey availability treatments. The design was completely randomized with 10 replicates and an average of 6 individuals of the two prey species provided, *G. pennsylvanicus* and *O. vulgares*. In the subsequent main experiment, I used an average level of 5 individuals of prey species and a complete randomized block design with 10 replicates per block within 2 temporal blocks (August 1-11 and August 13-24).

Two fixed factors, food level and prey number variability, were tested in the experiment. The food level treatments were imposed before the initiation of the choice trials. Half of the test subjects were deprived of food for the week prior to the trials and the other half were fed ad libitum on *A. domesticus* for this period. Three prey number variability treatments were provided in the enclosure design shown in Figure 3.1. These were (1) constant numbers, (2) positively covarying numbers and (3) negatively covarying numbers (Fig. 3.2a & b). The constant prey number treatment afforded the spiders the highest resource predictability and the covariance

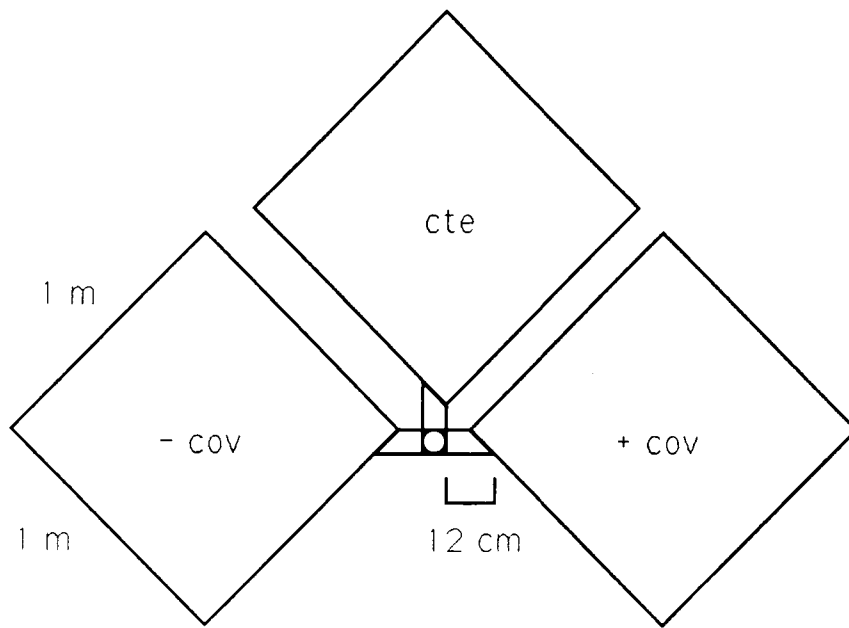


Figure 3.1. Aerial view of an enclosure system of choice experiments. Drawing is not to scale. Shaded areas are enclosures. Connections between enclosures are the PVC pipes with the central hole. An arbitrary layout of treatments is presented: cte = constant prey numbers, -cov = negatively covarying prey numbers, and +cov = positively covarying prey numbers.

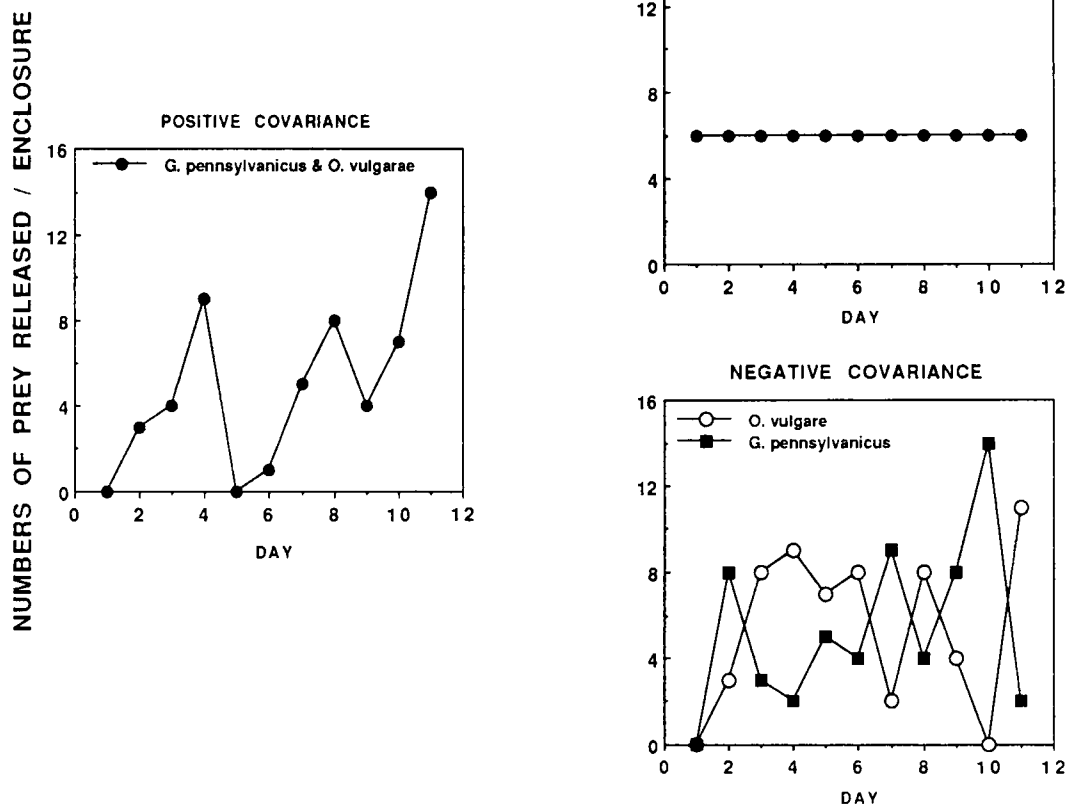


Figure 3.2.a. Number of katydids and crickets released in field enclosures as treatments for the pilot choice experiment. The three treatments are (1) constant, (2) positively covarying, and (3) negatively covarying prey numbers over 11 days and each treatment was assigned to a single enclosure of a triplet. Each line represents the number of individuals of each prey species released; a single line per plot means that the two species have equal abundances. All species per test have the same mean value, thus treatments differ only in variability and covariability. The average number of prey in the pilot test is 6.

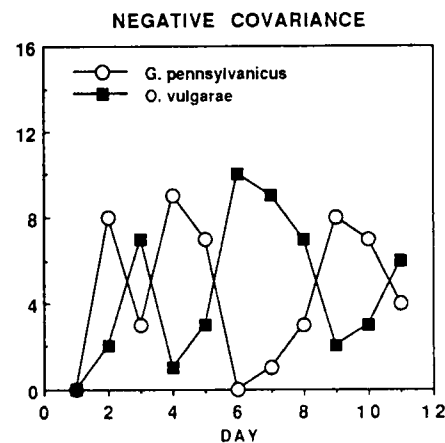
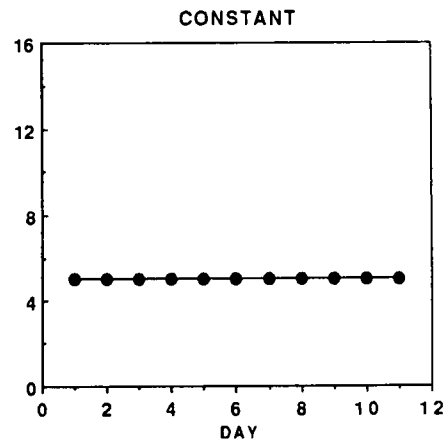
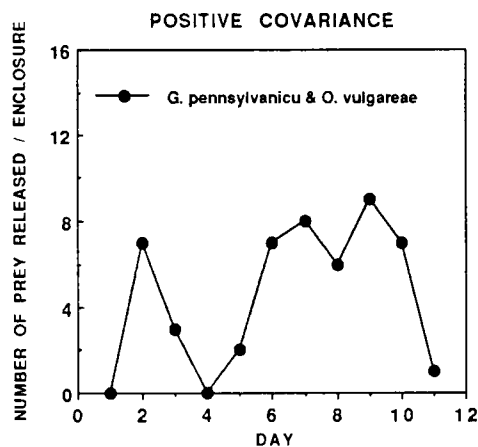


Figure 3.2.b. Number of katydids and crickets released in field enclosures as treatments for the main choice experiment. The three treatments are (1) constant, (2) positively covarying, and (3) negatively covarying prey numbers over 11 days and each treatment was assigned to a single enclosure of a triplet. Each line represents the number of individuals of each prey species released; a single line per plot means that the two species have equal abundances. All species per test have the same mean value, thus treatments differ only in variability and covariability. The average number of prey in the main test is 5.

treatments afforded less predictability. They differed in the way relative prey numbers changed through time. In the case of negative covariance, low numbers of one prey type (*G. pennsylvanicus*) corresponded to high numbers of the other prey type (*O. vulgares*) and vice versa. This treatment provided a constant supply of prey, making it a "safe" treatment relative to positively covarying prey numbers in which both prey types were either present in high numbers or low numbers.

I hypothesized that *Lycosa rabida* would avoid the positive covarying treatment because it would receive no food on some days in this treatment and more food than it could utilize on other days. If the spiders preferred one prey type over another, then I also expected to see greater residence time in the constant prey supply cages where both prey were present at average levels than in the negative covariance treatment where a given prey type was abundant on some days and scarce on others.

Each replicate of the choice experiment consisted of one *L. rabida* released into the 3-cages enclosure shown in Fig. 3.1. Each cage contained one of the three prey availability treatments and the 3 cages were connected centrally at ground level by a T-joint PVC pipe measuring 2.54 cm in diameter. I had drilled a hole in the top of this T-joint through which I introduced the test subject. The hole was stoppered at other times.

Following the completion of the pre-trial feeding regimes in the laboratory, I released individual *L. rabida* that had been weighed and paint-marked with white enamel paint into each of the enclosures (one per enclosure). (Marking the spiders aided in relocating them.) The releases were completed between 1300 and 1500 hrs EST and coincided with the

introduction of the two prey types into the respective cages. New prey were introduced into the cages each evening of the 11 day trial period, following the removal of all prey remaining from the previous 24 hr sampling period. The prey were collected fresh each day from the surrounding field. I checked each enclosure after dark each day and noted the prey availability treatment (cage) within which each spider was foraging. (Preliminary runs indicated that *L. rabida* does not change cages during a night foraging period once it has initiated foraging.) The spiders were removed from the enclosures and were reweighed after completion of the 11 day trial.

Switching and Forecasting. Prior to completing the full-scale experiment to test for the presence of switching and forecasting behaviors, I tested for spider preference between the two cricket species to be used in the experiment. I released one newly collected *L. rabida* into each of twenty-five field cages. At the same time, I added 8 crickets of each species to each cage. An additional 3 cages were set up as controls with the crickets present but no spiders. As in the experiment already described, the releases were made between 1300 and 1500 hrs EST. The cages were checked 24 hrs later and the number of crickets of each type remaining was recorded for each cage.

The main experiment consisted of 14 treatments, 7 test treatments and 7 controls (test treatments without spiders). There were two types of test treatments, 'continuous' pattern and 'stopped' pattern. The 4 test treatments of the continuous pattern type consisted of placing newly collected *L. rabida* for 14 day periods into field cages (1/cage), each of which offered one of the following prey availability patterns: (1) constant, (2) negative covariance

(covarying), (3) negative autocovariance (alternating) and (4) cyclic (Fig. 3.3). Negative autocovariance refers to alternating days of high and low numbers of a given prey type and cyclic to the progressively increasing and decreasing numbers of a single prey type over a longer period. These patterns tested for spider response to the temporal patterning of a single prey species rather than to the mixed species effects that are measured in the constant and negatively covarying treatments.

In testing for predator switching between the two prey species, I kept the numbers of the preferred prey type, *A. domesticus*, generally higher (average of 8) than the less preferred type, *G. pennsylvanicus*, (average of 4) except where the treatment specified that the numbers of *A. domesticus* decrease below those of *G. pennsylvanicus* (Fig. 3.3). My choice of *A. domesticus* as the numerically predominant prey makes the test for switching conservative rather than powerful.

The 3 treatments designated as stopped pattern entailed spider exposure in field cages for 10 days to one of three prey availability patterns, cyclic, negative autocovariance (alternating) and negative covariance (covarying) (as in Fig. 3.3 to Day 10), followed by 4 days of exposure to a constant prey availability (as in Fig. 3.3 in the constant treatment for days 11-15).

The experimental design was a complete randomized block with 14 treatments and 3 temporal blocks (July 18-31, Aug. 19-Sept. 1 and Sept. 7-20). Each treatment was replicated 3 times per block except the controls which had only 1 replicate per block. Each morning following the nighttime foraging by *L. rabida*, I collected all of the prey remaining in each cage and

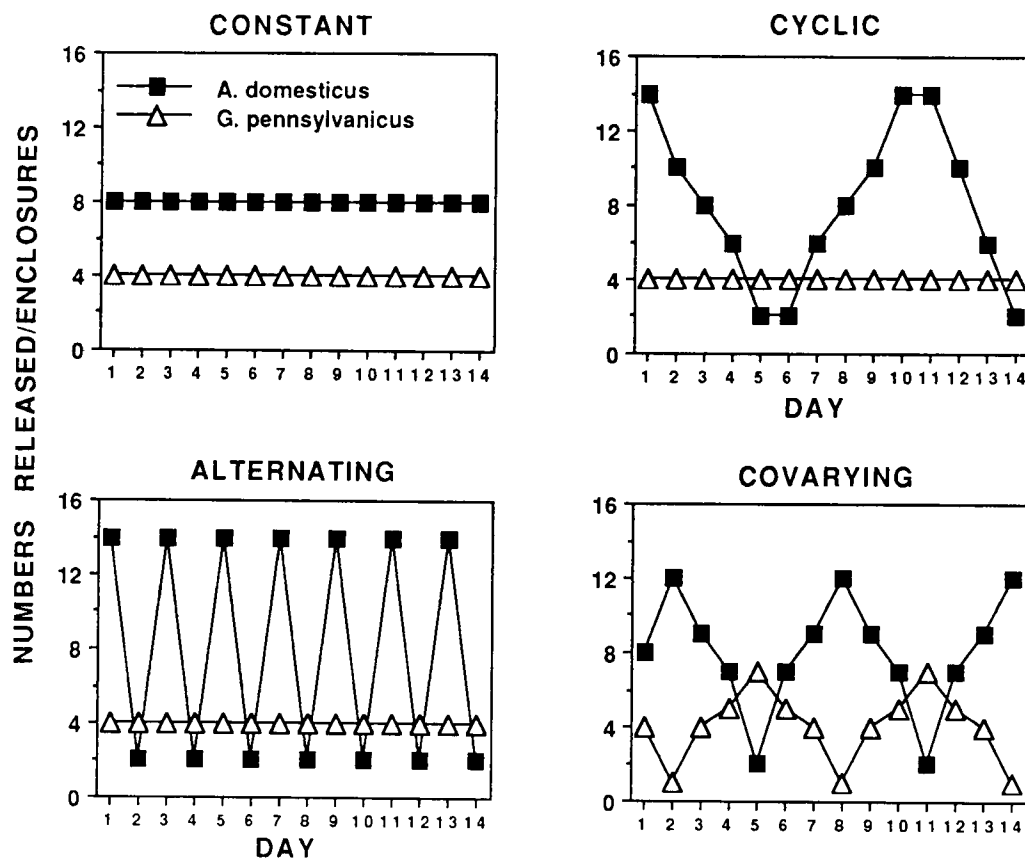


Figure 3.3. The number of European and wild crickets released daily in field enclosures as treatments of the prey regulation experiment. Presented are only the 4 basic treatments ("continuous" treatments). The 3 "stopped" treatments apply to the covarying, alternating and cyclic prey numbers and are obtained by setting the numbers of *A. domesticus* equal to 8 for days 11 to 14. Some of above patterns were computer generated by a simple autoregressive model (Bennett 1979). Enclosures were individually and randomly attributed a specific treatment or control.

noted the number of each type. The next foraging period's prey allotments were then introduced.

RESULTS

Choice of Pattern of Prey Availability.

In examining the data from the 1988 experiment, I sought to test both for spider choice among patterns of prey availability treatments and differences in weight gains associated with these choices. This is not statistically possible in one analysis, since there is no test that includes both mixed categorical and continuous data. I tested by ANOVA the effect of hunger condition on changes in body weight, computed as the difference between final and initial spider weights at the time of the trials. Hunger conditioning had no significant effect on weight gain over the 11 day trial period for either the pilot ($P < 0.11$) or main ($P < 0.18$) choice experiments (Table 3.1).

I applied a runs test (Sokal & Rohlf 1981) to the daily cage choices made by each spider to test for non-randomness in its temporal sequence of choices. (Note that most of the *L. rabida* sheltered in the T-joint pipes that separated the three cages of each enclosure when not foraging.) Because the runs test deals with only 2 alternative sequences, I combined the safe treatments (constant and negative covariance cages) in completing the analysis. Twelve of the 15 test subjects that I was able to relocate each night (combined results of pilot and main experiments) exhibited non-random ($P < 0.05$) sequences of runs. (Using the more conservative level of $P < 0.003$, only 9 individuals had non-random runs [Bonferroni protection where

Table 3.1. The effect of hunger conditioning on *Lycosa rabida* weight gain during the course of 11 day pattern of prey availability choice trials.

MEANS			
Pilot Experiment			
treatment	n	weight change (g.)	1 s.d.
starved	4	.30	.07
satiated	4	.17	.11
Main Choice Experiment			
treatment	n	weight change (g.)	1 s.d.
starved	9	0.12	0.21
satiated	5	0.03	0.13

ANOVA				
Pilot Experiment				
source	df	SS	F	P > F
hunger	1	0.031	3.71	0.1023
error	6	0.051		
Main Choice Experiment				
source	df	SS	F	P > F
block	1	0.215		
hunger	1	0.028	2.02	0.1828
error	11	0.154		

0.05/15= 0.003: Sokal & Rohlf 1981])). Most of the runs were in the safe (constant and negative covariance) treatments indicating that the positive covariance treatment was avoided by *L. rabida*. I tested this hypothesis by applying the binomial expansion sign test (Siegel and Castellan 1988) to the choice frequency data, using the expected probabilities of 2/3 for "safe" treatments (constant and negative covariance) and 1/3 for the "risky" treatment (positive covariance). The observed frequencies of association with different prey availability treatments departed significantly from random ($P < 0.05$) for 10 of the 15 test spiders.

Switching and Forecasting

Equal Density Preference. T-test results indicate that the mean numbers of crickets that died in the control enclosures from causes other than predation by *L. rabida* were not significantly different from 0 for either prey species (Table 3.2). I applied an ANOVA to the spider predation results to test for differential capture of one prey type over the other. *Lycosa rabida* captured significantly more ($P < 0.001$) *A. domesticus* than *G. pennsylvanicus* when they were offered in equal numbers. I label this result as *L. rabida* shows a 'preference' for *A. domesticus* for convenience in this paper, recognizing that the differential capture of *A. domesticus* by *L. rabida* could have any of several underlying causes (e.g., ease of capture).

Switching. Switching between prey types in terms of capture frequency was calculated by:

$$S_d = U(\exp(-K_p/N_p) - \exp(-K_d/N_d)),$$

where S is the value of the switching index for *A. domesticus* if subscript = d and for *G. pennsylvanicus* if subscript = p, K is the number of that prey type

Table 3.2. Number of crickets dying in cages during exposure to the spider *Lycosa rabida* for one day at equal abundance per species in field enclosures. Twenty-five replicates with 8 crickets of each species in each replicate. Spiders were absent from controls.

A. T test results for differences from 0.

MEANS

treatment	<i>G. pennsylvanicus</i> P > T				<i>A. domesticus</i> P > T		
	<u>n¹</u>	<u>mean sd</u>			<u>mean sd</u>		
control	3	0.33	0.88	0.42	0.67	1.15	0.42
predation	25	3.24	1.80	0.0001	5.2	1.61	0.0001

B. ANOVA

source	df	SS	F	P > F
enclosure	24	51.08		
species	1	48.02	14.14	.0010
error	24	81.48		

¹ n is the sample size; sd is one standard deviation.

captured, N is the number of that prey type introduced into the cage and U is the step function where $U = -1$ if $N_p > N_d$ and $U = 1$ if $N_p \leq N_d$. This formula simply compares relative capture rates of the two prey types, such that the higher the proportion of prey killed of one prey type, the smaller is the negative exponential term for that type. Thus, switching is density-dependent; negative S values represent inversely density-dependent switching for the prey type indicated by the subscript, positive values represent density-dependent switching for the prey type indicated by the subscript and a value of 0 for S indicates that no switching has occurred. For example, if $N_d = 10$, $N_p = 5$, $K_d = 0$, and $K_p = 5$, then $U = 1$ and the expression in parenthesis, which measures preference in the sense used in this paper, is $e^{-1} - e^{-0} = e^{-1} - 1 < 0$. This result indicates that the predator preferred *G. pennsylvanicus* over *A. domesticus*, but since *A. domesticus* was the more abundant prey ($U = 1$), inversely density-dependent switching (higher preference shown for the rarer prey type) is observed. Note that I adopted this formula because it was the only one which produced the normal and homoscedastic results needed for the statistical analyses: Manly's index (Chesson 1983) and variants of it did not meet these criteria.

The switching values were normally distributed for most treatments and days (84%) as measured by the Shapiro-Wilk statistic (10 days * 4 continuous pattern treatments: SAS 1985). Likewise, the variances among treatments were homogeneous (F-max test: $P > 0.05$; Sokal & Rohlf 1981) for all trial days. T-tests applied to the switching data by treatment by day indicate that 2.5% of the averages for treatment days were significantly negative reflecting inversely density-dependent switching while 35% were

significantly positive (Fig. 3.4). That the negative switching values generally occurred on days when *A. domesticus* was less abundant than *G. pennsylvanicus*, indicates the magnitude of *L. rabida* preference for *A. domesticus* over *G. pennsylvanicus*.

The effect of pattern of prey availability treatment, time, and their interaction on switching by *L. rabida* was tested with a repeated measures MANOVA (O'Brien and Kaiser 1985). There were significant overall effects for spider behavior over time ($P < 0.005$), for the interaction of time and prey variability treatment ($P < 0.00001$), and for spider behavior in different prey variability treatments (Table 3.3). Contrasts performed between the constant prey treatment and the variable prey availability treatments were significant for both the time * variability treatment interaction ($P < 0.009$) and for the between treatment effect ($P < 0.0073$).

Forecasting. Spider forecasting was tested with a repeated time measures MANOVA on preference values for the last 4 days for the seven treatments (4 continuous and 3 stopped treatments). I utilized the equation for switching without the step function (U) in obtaining the preference estimates:

$$P_d = \exp(-K_p/N_p) - \exp(K_d/N_d).$$

This measure is maximally bounded between -0.63 and 0.63 in this system, is equal to 0 at indifference, and positive and negative values indicate, respectively, preference for and avoidance of *A. domesticus*.

The distribution of preference values for the last 4 days of the stopped and continuous pattern trials were normal in 78.6% of the treatment combinations (4 days * 7 treatments: Shapiro-Wilk statistic). Likewise the

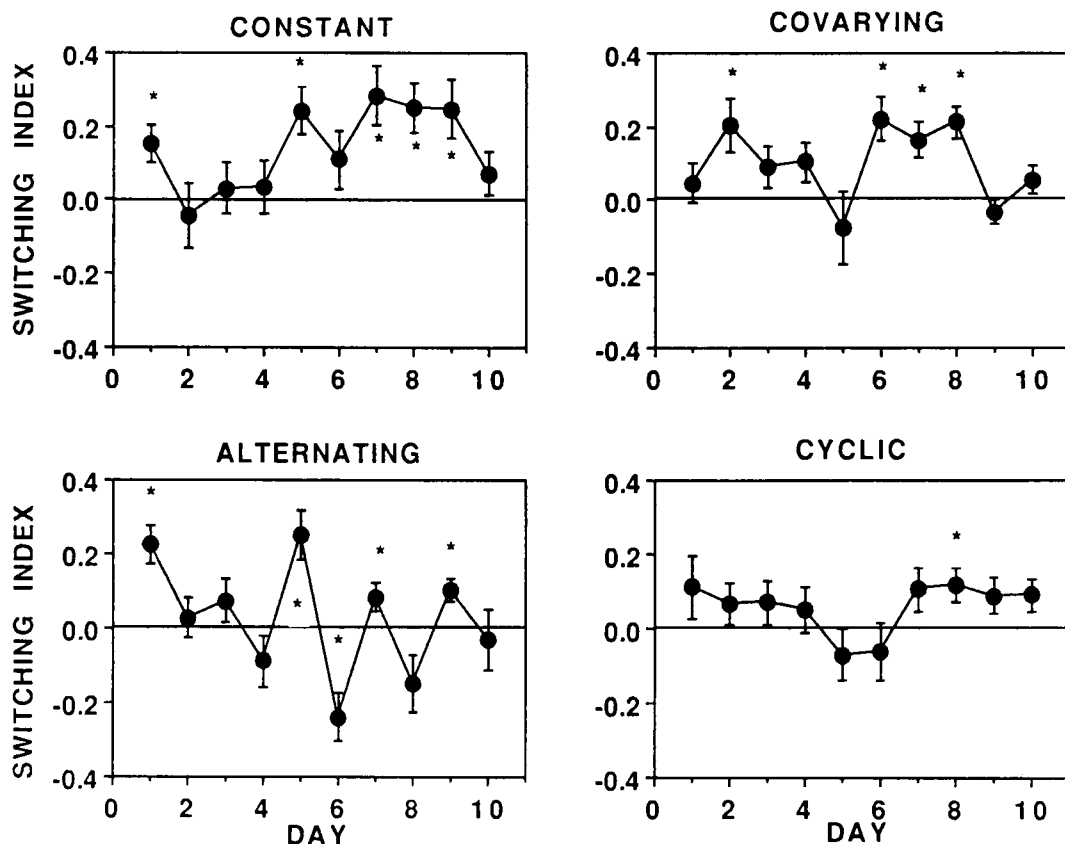


Figure 3.4. Switching values for *Gryllus pennsylvanicus* obtained in field enclosures with the spider *Lycosa rabida* over the first 10 days for the four "continuous" variability treatments. Errors bars are ± 1 standard error. The * indicates that the average is significantly different from 0, as calculated from the t test.

Table 3.3. Repeated time measures MANOVA of switching values for the spider *Lycosa rabida* in field enclosures. Switching values of the first 10 days only were used in order to increase replication by the consideration of "continued" and "stopped" treatments. Switching values are for *Gryllus pennsylvanicus*.

MANOVA				
source	Wilks' lambda	F	df	P > F
time	0.64	2.92	9, 47	0.0078
time*treatment	0.25	2.864	27, 137.9	0.0001
time*variability				
contrast ¹	0.64	2.86	9, 47	0.0089
Variability Treatment Effects (between subject effects)				
source	df	SS	F	P > F
block	2	.347		
treatment	3	1.25	7.34	.0003
variability				
contrast ¹	1	.55	9.70	.0029
error	55	3.12		

¹: Contrast is between the constant prey number treatment and all other continued variability treatments.

variance among treatments was homogenous for all 4 days (F-max test: $P > 0.05$). Preference scores were significantly positive in 53.6% of the cases and non-significantly different from 0 otherwise (T-tests: $P < 0.05$; Fig. 3.5). The MANOVA results did not show a significant continuous pattern versus stopped pattern effect ($P > 0.06$) though the interaction of this time effect and the type of prey variability pattern the spider was exposed to was significant ($P < 0.03$; Table 3.4). Contrasts completed between the interaction of time and prey variability treatment differing only in their 'stopped' versus 'continuous' patterning show significant differences for alternating (negative autocovariance) ($P < 0.05$) and cyclic ($P < 0.03$) prey availability patterns (Table 3.4). No significant between treatment effects were observed in the analysis (Table 3.4).

DISCUSSION

Can generalist predators, such as spiders, regulate associated prey populations? Although the conventional answer has been "no" (Beddington et al. 1978, Hassell 1978), others have argued to the contrary (DeAngelis et al. 1975, Tanner 1975, Kiritani & Kakiya 1975, Post and Travis 1979, Erlinge et al. 1984, 1988 [but see Kidd and Lewis 1987], Riechert and Lockley 1984, Murdoch et al. 1985, Provencher and Vickery 1988, Riechert and Bishop 1990). However, both sides of the debate have borrowed from population-level assumptions, when in fact predation is an individual based and stochastic phenomenon (Chesson 1978, 1984, Kareiva and O'Dell 1987, Huston et al. 1988, Provencher and Vickery 1988). While this study does not provide a definitive answer to this question, it does indicate that the foraging

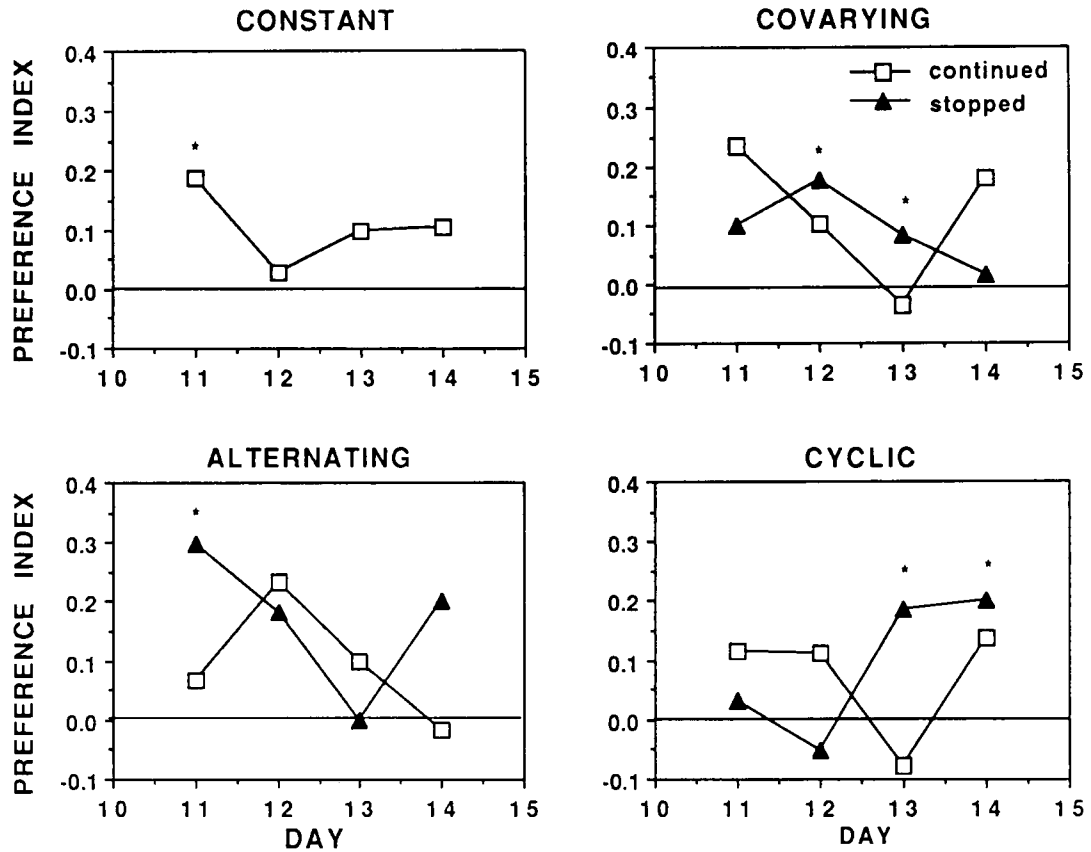


Figure 3.5. Preference values for *Gryllus pennsylvanicus* obtained in field enclosures with the spider *Lycosa rabida* over the first 10 days for the “stopped” variability treatments. The constant treatment box is there for the sake of comparison and is not a forecasting treatment. Other symbols as in Figure 3.4.

Table 3.4. Repeated time measures MANOVA of preference values of forecasting for the spider *Lycosa rabida* in field enclosures. I used the preference values calculated between days 11 and 14, inclusively. Preference values are for *Gryllus pennsylvanicus*. The important tests of forecasting are the contrasts in the **Variability Treatment Effects** part.

MANOVA

source	Wilks' lambda	F	df	P > F
time	0.86	2.55	3, 50	0.0659
time*treatment	0.56	1.78	18, 141.9	0.0326
time*variability				

contrasts between the continued and stopped variability treatments:

-covariance	0.90	1.73	3, 50	0.1712
alternating	0.85	2.86	3, 50	0.0462
cyclic	0.83	3.25	3, 50	0.0294

Variability Treatment Effects

source	df	SS	F	P > F
block	2	0.32		
treatment	6	0.17	0.64	0.6985
variability				

contrasts between the continued and stopped variability treatments:

-covariance	1	0.006	0.15	0.6961
alternating	1	0.079	1.78	0.1877
cyclic	1	0.006	0.15	0.7045
error	52	2.32		

strategies adopted by individual generalist predators when faced with spatial and temporal variability of prey numbers permit their survival to reproduction and is consistent with local prey limitation.

The results of the choice experiments, for instance, show one way in which spiders deal with variation in prey availability: they choose foraging sites that provide a constant level of prey over those that fluctuate between high and low numbers --- feast and famine. Another method of dealing with temporal variability in local prey abundances is by feeding on alternative prey. As pointed out by Murdoch et al. (1985), generalist predators can cause local extinctions of prey species and tolerate these extinctions by switching to other prey types. Even under the conservative test for switching used in this study, I observed *L. rabida* to exhibit significant levels of density-dependent (positive) switching in all 4 of the different patterns of variable prey numbers it was exposed to (35% of all switching exhibited was significantly positive: Fig. 3.4).

Although switching behavior is only one component of predation, along with the functional and numerical responses (Holling 1965, Riechert and Lockley 1984), density dependent (positive) switching by generalist predators for associated prey populations fosters regulation (Oaten and Murdoch 1975). On the other hand, inverse density-dependent (negative) switching will prevent the regulation of assemblages of prey species even though capture rates may be density-dependent since most of the density-dependent effects will be directed on the least abundant or least profitable prey species. I observed only 2.5% of the switching by *L. rabida* to be significantly negative. The only significant negative switching average

obtained was for day 6 in the alternating prey availability treatment when the preferred prey, *A. domesticus*, was at a low (Fig. 3.4). The most negative values (but not significantly different from 0) for switching in other treatments also occurred when *A. domesticus* was the least abundant prey type. Two points need to be made. First, some negative values may arise by chance when spiders capture very few prey of the least abundant species on days where total prey abundance is low. Secondly, negative values are expected since *L. rabida* exhibited greater preference for *A. domesticus* than *G. pennsylvanicus* (Table 3.3), probably due to the differential vulnerability and/or activity of the two prey types. This points to another important aspect of switching: a certain percentage of the variation in it is due to the behavior of the prey, which can be highly dependent on weather conditions (personal observations), and, consequently, the predator's behavior may not be subject to natural selection unless predator and prey share common responses to weather. This latter source of variation could explain some of the temporal variation I observed in switching and preference values in the constant, and other, treatments.

The significant time effects noted for switching between prey types by *L. rabida*, suggest the possibility of learning or conditioning since they occurred within the 10-day chronology of individual spiders. Increased attack by *L. rabida* on one prey species over another following sampling over days can cause such time effects. Time effects might also result from varying levels of hunger, though this was not a probable explanation for time effects in this study where prey levels were very high. (The non-significant weight gain results between starved and satiated treatments in the 1988

experiment (Table 3.6) indicate that energetic considerations are not a factor under the high prey levels offered in these experiments.)

The presence of significant time effects in switching and in preferences exhibited by *L. rabida* towards the two prey species in the absence of underlying hunger control, indicates that this spider does forecast prey abundance. Forecasting is also supported by the results of the choice experiment. Individual *L. rabida* avoided cages that provided alternate days of highs and lows in prey availability (positive covariance) in favor of cages offering a more constant food supply (negative covariance and constant prey availabilities) even though they could have accessed these cages on the high days. Finally, forecasting is supported by the lack of between treatment effects (continued variability versus stopped variability in the 1989 experiment). Having experienced a given pattern of variation in prey abundances over a 10 day period, *L. rabida* continued the pattern of attack corresponding to this past experience even though the pattern of prey availability was changed in half of the cages to a constant one for the last 4 day period.

Though present, prey forecasting by *L. rabida* does not seem to be fine-tuned to different prey availability patterns, since it fails to exhibit between prey availability treatment variability in switching and preference behavior towards prey. For instance, I observed some negative switching values in the alternating prey availability treatment, corresponding to highs and lows in the preferred prey, *A. domesticus*. Spiders probably do not experience naturally this type of variability, and thus may not have recognized it in the tests. Few, if any, insect prey populations exhibit such

rapid oscillations in time and in one place. Moreover, given that spiders have a remarkable resistance to starvation (Anderson 1974, Nakamura 1982), there may not be a need to track resources on such a fine temporal scale.

Lycosa rabida's response to variable patterns of prey abundance might be summarized as conservative. The term conservative refers to the importance of low prey numbers in damping future preference towards zero (e.g., alternating and cyclic treatments: Fig. 3.4), at the cost of missed opportunities (Stephens and Krebs 1986). There seems to be greater weight given to the lows in the abundance of the preferred prey than in the highs as best evidenced in the switching values for cyclic prey abundances (Fig. 3.4). Conservative behavior has been observed in the territory size of the spider *Agelenopsis aperta* (Riechert 1981), which was explained as a strategy for avoiding the worst possible events. The peculiar physiology of spiders (Anderson 1974, Nakamura 1982) probably allows the cost of missed opportunities. A temporally weighted-average of prey numbers with high weights assigned to low values may suffice to forecast future abundance.

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PART 4

THE ROLE OF GENERALIST PREDATOR PHENOTYPES IN THE LIMITATION OF ASSOCIATED PREY POPULATIONS

INTRODUCTION

In this study I explore the relationship between foraging strategies that maximize reproductive potential in generalist predators and those that lead to prey regulation. Many of the traits that characterize generalist predators do not appear to be conducive to density-dependent predation (e.g., their broad diets and aggressive within species competitive behaviors). Yet, successful cases of biological control with generalist predators have been reported (see review in Riechert & Lockley 1984 and Murdoch et al. 1985, Riechert & Bishop 1990). Here I attempt to identify what combination of traits, if any, contribute to both greater fitness and prey limitation than other sets of traits.

In particular, I am interested in partitioning the contributions of the genotype and the environment. The environmental component to individual fitness and predator control of prey includes such factors as the degree of patchiness of the prey and shelter for the predators as well as the species composition of both predator and prey assemblages. The genotypic component consists of physiological and foraging traits such as aggressiveness towards prey (Hedrick & Riechert 1989), prey and foraging site selection and territory or home range sizes. The genotypic component to the analysis is particularly difficult to manipulate experimentally. Thus, I used computer simulations in my initial investigation of the hypothesized relationship between fitness and prey limitation. Specifically, I used an individual based model (Huston et al. 1988) of natural selection on conspecific competing phenotypes foraging in a stochastic environment.

Selection was achieved through the differential mortality and fecundity between the phenotypes of the parents and their offsprings phenotypes within one generation, which correspond to the duration of an annual crop. The model predator is the spider (order Araneae), a generalist predator with which I have had considerable experience and for which I have a good data base.

SIMULATION

In this computer model I simulate the growth of individual spiders of a population which feed on n prey species in a 20 m^2 area of annual crop that is fragmented into k patches. Prey body size did not change with time, only their numbers did. The immigration and dispersal of prey items into and from this patch system is stochastic with the prey composition updated every 2 hours over a 30 day period. A general flow diagram for the model is presented in Figure 4.1.

The equation for local prey population growth is a time varying logistic one and has 5 contributing components: 1) growth rate of the species, 2) mortality due to predation, 3) immigration, 4) dispersal and 5) stochastic weather effects (Table 4.1):

$$X_{jit} = X_{ji(t-1)} (r_j - 0.01 \text{ er}_{(t-1)} - 0.001nk X_{ji(t-1)} / t) - \sum_{a=1}^m \sum_{b=1}^{L(a)} y_{jab} / c_j + u_j / k + 0.001 \left(\sum_{h=1}^k X_{jh(t-1)} / k - X_{ji(t-1)} \right) \quad (1)$$

where X_{jit} is the number of prey of species j in patch i at time t , r_j is the average maximum rate of increase of prey species j , er is a uniformly distributed pseudo-random number (DURAND subroutine, E.S.S.L. 1988)

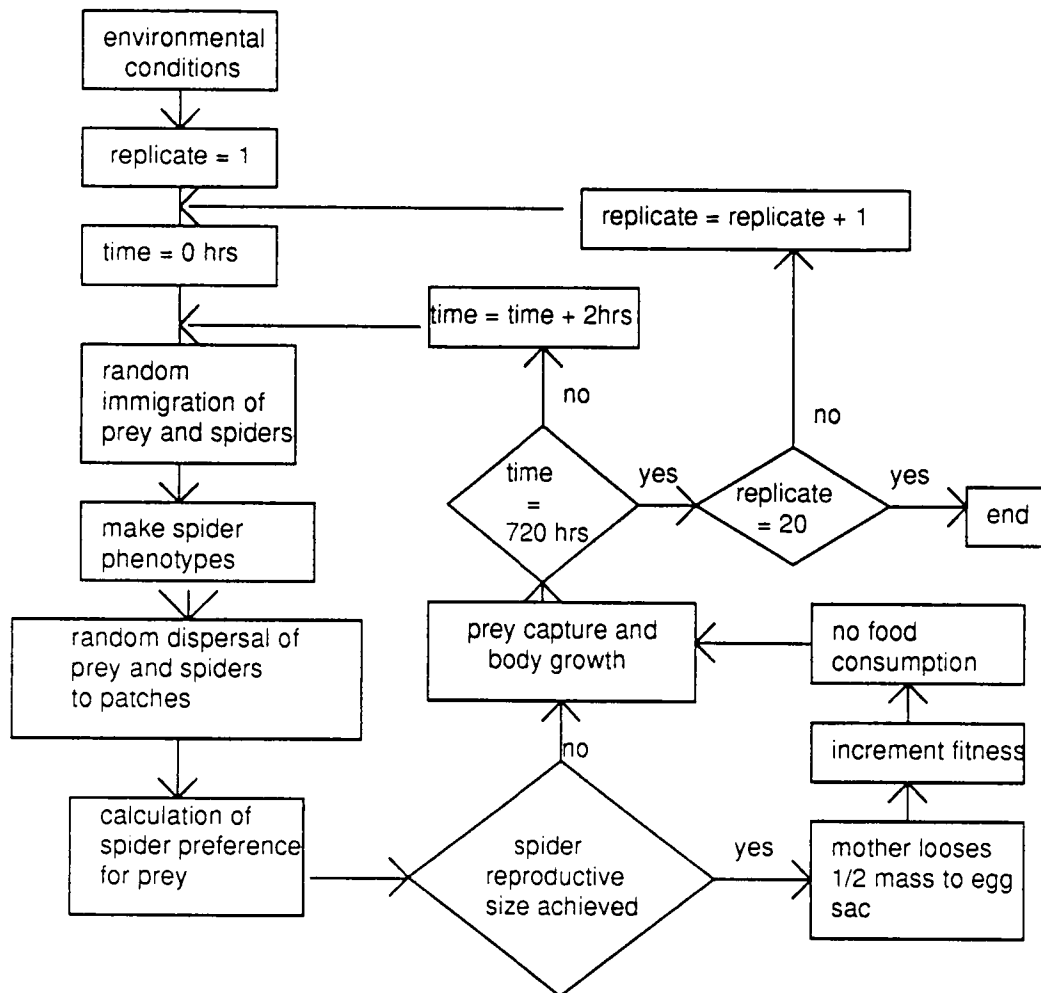


Figure 4.1. General flow chart of the individual based computer model of prey limitation by spiders.

Table 4.1. Definition and values of variables and parameters used in Monte-Carlo simulations of individual spiders of a single species feeding on prey species assemblages in a patchy habitat.

Code	Description	Value
Used		
m	no. of spider species	1
k	no. of patches in a 20 m ² habitat	1, 5
n	no of species of prey	2, 5
X_{ji}	no. of individuals of prey species j in patch i	variable
r_j	maximum population growth rate of species j/2 hour interval	$r_1 = 1.09$ $r_{j=2,n}=1.01$
c_j	average mass of an individual prey of species j in mg.	$c_1 = 10$ $c_{j=2,n} = 200$
er	pseudo-random uniform number	$0 \leq er < 1$
u_j	average no. of individual prey immigrating into a 20 m ² habitat/2 hours	$u_1 = 12$ $u_{j=2,n} = 2$
—	dispersal rate of prey	0.001
—	average no. of spiders of a species immigrating into a 20 m ² habitat/2 hours	12 ^c else: 1
y_j	prey mass captured (mg) of species j by a spider	variable

(Table 4.1 continued)

f	food ingested (mg) by a spider	variable
a	food (mg) assimilated by a spider	variable
e	body weight (mg) of a spider	variable
U_j	indicator function measuring spider activity	$\{0, 1\}$
α_j	capture rate of prey species j (mg/mg/time) by an individual spider	0.25^c
p_j	spider preference for prey species j	$0 \leq p_j < 1$
dd_j	no. of prey of species j potentially eaten by other spiders during 2 hour interval	$\max = 2$
$w(f)$	capture cost function	$0 \leq w(f) \leq 1$
ag	spider level of aggression towards other spiders	$\{0, 1/2, 1\}$
q	quality of a spider's territory	
g_j	availability (mg) of prey species j to a spider	

^{c} : denotes a constant at time $t = 0$. All other values have a variance.

between $0 \leq e_r < 1$ simulating the stochastic effect of weather on insect growth, y_{jab} is the quantity of food captured (mg) of prey species j by an individual spider b (L_a is the total number of spiders in the population of species a), and u_j is a random variable representing the number of immigrants of prey species j colonizing the 20m^2 area of crop. Note that emigration is absent from the model, although dispersal is simulated. The first part of equation (1) is a time varying, stochastic logistic equation. There are two time variant components (first and second negative terms in the parentheses). The second negative term increases the rate of growth of the local insect population over time, assuming that as the annual plants grow in the system, more food and space are available to the grazing insects. Hence, competition between prey decreases linearly with time. However, the rate of insect population growth is decreased by the number of prey species competing for food and the number of patches in the habitat (a space constraint). Interspecific competition between prey is not incorporated in the model, although decreasing the carrying capacity by the number of prey species was a means to partially include this under the model specific assumption of equal immigration rates of prey species. The absence of prey interspecific competition should make prey limitation by spiders more difficult to achieve. The mortality due to predation is obtained by dividing the biomass of prey species j killed in that patch at time $t-1$ by the mean biomass per prey item (c). The last term of equation (1) represents net dispersal for which I used a dispersal rate of 1 individual leaving a patch per thousand individuals at each 2 hour interval. At the same time all patches

receive $0.001/k$ of the dispersers moving among the patches. Hence, dispersal leads to mixing of the prey species.

During the first 10 days of the simulations, sub-adult spiders immigrate at random into the crop system (the early spring immigrants). The choice of a patch was given by $\text{int}(k * e_r + 1)$, where e_r is as stated above. After this initial period, immigrating spiders are assumed to be juveniles. In the simulations, individual spiders move between patches only after having suffered a 10% loss in body mass in a given patch. I used the set of differential equations developed by Nakamura (1982) for wolf spider growth to describe the growth of individual spiders in my simulation. Some modification of the equations was necessary to correct errors in the initial model and to adapt it to the multi-species prey system investigated here. In the simulation, individual spiders are assumed to be actively foraging for 16 hours/day. The system of differential equations describing spider growth is solved numerically within 2 hour intervals:

$$\dot{y}_{jrs} = U_{rs} \alpha_{jrs} p_{jrs} \min\{1, e_{rs}/c_j\} (kc_j X_{ji}/20 - c_j d_{jrs} - y_{jrs}) \\ (0.25e_{rs} - f_{rs} + a_{rs}) \quad (2a)$$

$$\dot{f}_{rs} = 0.7 \sum_{h=1}^n y_{hrs} \quad (2b)$$

$$\dot{a}_{rs} = 0.94(f_{rs} - a_{rs}) \quad (2c)$$

$$\dot{e}_{rs} = \dot{a}_{rs} - (0.024 + 0.6 w(f_{rs}) + 0.0032 \dot{f}_{rs}) e_{rs}^{0.71} \quad (2d)$$

where y_{jrs} is the mass (mg) of prey species j captured by individual r of spider species s , f represents the mass of food consumed (mg), a is the food assimilated (mg) and e denotes the spider's body weight (mg). The mathematical constraints imposed on equations 2a-d are

$$\begin{aligned}
& y, f, a, e \geq 0, \\
& y, f, a, e = 0 \text{ if } e < \text{time varying critical size}, \\
& \text{if } X_{jit} = 0, y_{jrs} = 0, \\
& \text{if } U = 0, y = 0
\end{aligned}$$

where

$$U = \begin{cases} 0 & \text{if spider is inactive or laying eggs} \\ 1 & \text{if spider is active and not laying eggs,} \end{cases}$$

and $w(f_{rs}) = 1 - 1/(1 + \max\{0, f_{rs}\})$ (My addition to Nakamura's (1982) model of *Lycosa lenta* growth to equate capture costs with 0 during periods of inactivity. Without this correction, body growth is always negative when used in the simulations.)

Equation (2a), the functional response, contains 3 terms that require explanation. These are α_j , dd_j , and p_j which are, respectively, the capture rate for prey species j , density-dependent resource depletion by other spiders of prey species j , and the preference for prey species j . The capture rate, α is initially set at 0.25 (value within the range proposed by Nakamura [1982]), but then may decrease as a result of interference by other spiders that have a biomass of > 0.8 of that of the focal spider. Hence,

$$\alpha_{irst} = \alpha_{irs(t-1)} \text{freq}(\text{no injury}) \quad (3)$$

where

$$\text{freq}(\text{no injury}) = 1 - e^{-\text{rate}}, \quad (4)$$

$$\text{rate} = q_{rs} * ag_{rs} * \sum_{v=1}^L ag_{vs} \quad (5)$$

and ag_{rs} is the level of aggressiveness individual r of species s exhibits towards other spiders in general $\{0, 0.5, 1\}$, ag_{vs} is the level of aggression of each of the other spiders in the patch that are potential competitors for food with rs , and $q_{rs(t+1)}$ represents the quality of the foraging site of individual r at time $t+1$,

$$q_{rs(t+1)} = \sum_{h=1}^n y_{hrst}/c_h/X_{kht} + \pi^{t-v-1} \prod_{j=v}^{t-1} (q_{rsj} + \sum_{h=1}^n y_{hrs}^{j/t}/c_h/X_{khj}) \quad (6)$$

where v is the first time interval after changing site, t is the present time interval, and $\pi = 23/24$ (an arbitrary constant < 1). Note that the quality of the foraging site is based on a weighted sum of the amount of food captured such that the most recent foraging period has more weight than the next most recent and so on. Foraging site quality is also relativized by dividing the weighted cumulative amount of prey captured by the biomass of prey available in the patch. Thus if food is generally plentiful within a patch, the value of individual sites is lessened. (The difference between a patch and an individual's hunting site is only that the food captured in a site is as viewed differently by each spider, whereas the food in a patch is absolute.) The function q_{rst} is not a conventional, negative exponential time discounting function (e.g., as in Stephens and Krebs 1986: 27). However, equation (6) behaves as a conventional time discounting function (with respect to discounting the past instead of the future), since $q_{rst} \propto \pi^{t-v-1} q_0 + \epsilon_{t-1}$, where $0 \leq q_0 \leq 1$ is the quality of the new territory after a move and $0 \leq \epsilon_{t-1} \leq 1$ is the relativised food intake.

Density dependent prey depletion, dd , is an upper estimate of the numbers of prey captured to the focal spider/2 hrs due to the foraging activity

of other spiders in the patch. I used the lesser of the two values, the mass of 2 prey items or the mass accommodated by the space remaining in the gut, to estimate this parameter. (From personal observation of *Lycosa* foraging, I assumed that spiders cannot handle and consume more than one prey/hr.)

$$dd_j = \min\{2, \text{space}_j\} \quad (7)$$

and

$$\text{space}_j = p_{jrs} [1 + (0.25e_{rs} - f_{rs} + a_{rs})/c_j] . \quad (8)$$

The most complex section of the model deals with spider behavior: aggression towards other spiders and diet choice. These behaviors are incorporated into the spider's feeding rate. There are 3 levels of aggression (explained above) and 6 types of prey selection, which in a crossed fashion account for 18 generalist phenotypes.

Many factors contribute to the diet of the generalist predator. Important among these is the means by which individual spiders choose to attack certain prey over others. I chose a set of pure strategies (decision processes) for the sake of clarity; in the real world, spiders may actually use a mix of these strategies. The strategies included in the simulations were: random, sequentially random, proportional, specialist, statistical, and sequentially statistical. Each prey choice strategy is described below. It is important to understand that the determination of preference for prey at time $(t + 1)$ is calculated at time t ; indeed, I do not assume spiders to be omniscient. Because the spider is guessing the future one time step ahead, the prey selection strategy can fail and natural selection may act differently upon phenotypes. Note that prey availability has been scaled everywhere by the factor $k/20$, which follows from the assumption that a spider's

perceptive range is one m². The actual size of the perceptive range is not so critical as the fact that it must be reduced to a common size for all individuals.

1) The selection of a prey type may be random for a spider, which means that the probability of choosing any prey type per time interval is on average 1/(number of prey species) and recalculated every two hours,

$$p_h = er_h / \sum_j^n er_j, \quad (9)$$

where er is a uniform pseudo-random number $0 \leq er < 1$. These preferences will be independent of prey numbers.

2) A spider chooses randomly one prey type per time interval (sequentially random), which is also recalculated every two hours,

$$p_h = 1, \text{ h is a randomly chosen integer in } \{1, 2, \dots, n\} \quad (10)$$

3) A spider could choose prey species according to their relative biomass per time interval (proportional selection),

$$p_h = g_h / \sum_j^n g_j \quad (11)$$

where

$$g_h = \min\{e_{rst}/c_h, 1\} \times c_h \times X_{ijt}/20 \text{ (prey availability in mg)}. \quad (12)$$

(Note that random, sequentially random and proportional selection are three different types of density-independent selection.)

4) A spider could specialize on the most profitable (largest and present in the patch at the previous time interval t , in the case of this simulation) prey type present in the patch during the previous time interval (specialist),

$$p_h = 1, \text{ for which } c_h = \max_{j=1,n}\{c_j\} \min\{e_{rst}/c_h, 1\}. \quad (13)$$

5) I assume that the spider has a memory and bases future foraging decisions on experience with previous levels of prey availability (as in Bayesian time series analysis). I refer to this foraging strategy as statistical. I used the Kalman Filter (Bennett 1979) in modeling the "statistical" foraging strategy. The input variables (available biomasses of prey encountered during the previous 3 time intervals) were assumed to be normal but not necessarily stationary. My choice of only the 3 previous time intervals was arbitrary since I assumed an immediate memory lasting that long. The "memory" of the Kalman filter, however, goes to the beginning of the time series regardless of the chosen lag. Briefly, the Kalman filter time series method uses Baye's theorem to update the variance-covariance matrix of input variables and to make predictions about the value of output variables. Thus, the technique incorporates the whole history of the system as viewed by the individual spider, while weighting the recent past most heavily. The Kalman filter consists of 9 equations (eqs. 15 - 23), for which I will specify the meaning of vectors and matrices involved. The notation $\mathbf{P}_{t|(t-1)}$ presented below designates the estimate of $\mathbf{P}$ at time t given its value at time $t-1$ and so on for the other variables, whereas $\mathbf{P}^T$ is the transpose of $\mathbf{P}$.

$$p_h = Y_{h,(t+1)} / \sum_j^n Y_{j,(t+1)} \quad (14)$$

$$\mathbf{Y}_{(t+1)} = \mathbf{g}_{(t+1)} \theta_{(t+1)|t} \quad (15)$$

$$\theta_{(t+1)|t} = \mathbf{F} \theta_t \quad (16)$$

$$\theta_t = \theta_{t|(t-1)} - \mathbf{K}_t [\mathbf{g}_t^T \theta_{t|(t-1)} - \mathbf{Y}_t]^{-1} \quad (17)$$

$$\mathbf{P}_{(t+1)|t} = \mathbf{F} \mathbf{P}_t \mathbf{F}^T + \mathbf{Q} \quad (18)$$

$$\mathbf{P}_t = \mathbf{P}_{t|(t-1)} - \mathbf{K}_t \mathbf{g}_t^T \mathbf{P}_{t|(t-1)} \quad (19)$$

$$\mathbf{K}_t = \mathbf{P}_{t|(t-1)} \mathbf{g}_t^T [\mathbf{I} + \mathbf{g}_t^T \mathbf{P}_{t|(t-1)} \mathbf{g}_t^T]^{-1} \quad (20)$$

$$\mathbf{Y}_t = \mathbf{g}_t^T \theta_{t|(t-1)} \quad (21)$$

$$\mathbf{P}_{t|(t-1)} = \mathbf{F} \mathbf{P}_{(t-1)} \mathbf{F}^T + \mathbf{Q} \quad (22)$$

$$\theta_{t|(t-1)} = \mathbf{F} \theta_{(t-1)} \quad (23)$$

where $\mathbf{Y}$ is the predicted $\{n \times 1\}$ vector of output variables (prey abundances), $\mathbf{g}$ is the $\{w \times w\}$ ($w = n \times \text{number of time lags}$) matrix of input variables of all prey species, which can be viewed as $\{n \times n\}$ diagonal matrix where each entry is a $\{1 \times 3\}$ vector (3 is the number of time lags), θ represents the predicted $\{w \times 1\}$ parameter vector (the equivalent of regression coefficients in ordinary least square regression), $\mathbf{F}$ codes for a $\{w \times w\}$ diagonal transition matrix which changes both the parameter vector and variance-covariance matrix, $\mathbf{K}$ is the kalman gain $\{w \times n\}$ matrix which measures the decrease in the variability of prediction of output variables, $\mathbf{P}$ is the $\{w \times w\}$ variance-covariance matrix of lagged input variables, $\mathbf{I}$ represents the $\{n \times n\}$ identity matrix, and $\mathbf{Q}$ codes for a $\{w \times w\}$ diagonal variance-covariance matrix whose entries are the time-lagged ratios of body

growth between time intervals, $e_{rs(t-L-1)}/e_{rs(t-L)}$, where L is the time lag. The $\mathbf{Q}$ matrix plays an important role in that it keeps the filter from 'closing' by the addition of internal variability to the variance-covariance matrix $\mathbf{P}$. It is well known in time series analysis that variance-covariance terms tend to zero with increasing numbers of time periods (sample size). The internal variability corresponds here to the spider's changing view of its available resources that results from the different energetic states it is in. The matrix $\mathbf{F}$ is diagonal with non-null entries $0 \leq F \leq 1$ given arbitrarily by $\text{cov}[\mathbf{Yg}]/\max\{\text{cov}[\mathbf{Yg}]\}$. My choice of these transition coefficients was justified by behavioral considerations: I wanted strong covariance terms to dominate the spider's memory. The input matrix $\mathbf{g}$ is composed of the prey availability values

$$g_{hL} = \min\{e_{rs}/c_{hL}, 1\}kc_{hL}X_{hLj}/20$$

where h is the species index and L is the time lag $\{1, 2, 3\}$. Two important details to mention are the initial values of θ and $\mathbf{P}$. For θ , I used the ordinary least square estimate which is $[\mathbf{gg}^T]^{-1}\mathbf{Yg}$. For $\mathbf{P}$, the initial estimate was $\mathbf{gg}^T$.

6) This prey selection strategy is identical to the statistical one, except that spiders specialize on the prey type predicted to be most abundant (sequentially statistical),

$$p_h = 1, Y_h = \max_{j=1,n}\{Y_j\}. \quad (24)$$

The last part of the model deals with the dynamics of reproduction. When a spider reaches a critical body mass, it incorporates 1/2 of this mass into eggs (Hammerstein and Riechert 1988) from which offspring emerge immediately. The number of offspring produced fluctuates around a mean

value determined by $1/2$ the parent's weight divided by the realized weight of the offspring (random variable with mean of 3 mg). The mother's fitness, which I define here as the cumulative number of offspring produced, is incremented at egg laying. The offspring inherit in a haploid fashion the phenotype of the mother. The offspring do not feed on prey during the first time interval, but do contribute to prey limitation and assume body growth after that initial period.

Tests and statistical methodology

Because of the many stochastic elements of the model, I replicated the results 20 times by Monte-Carlo simulation. Replication was performed within the crossed factorial combinations (Sokal and Rohlf 1981) defining the environment and the genotypes. The factors were aggression (3 levels), prey selection (6 levels), the number of patches (2 levels), and the number of prey species (2 levels). In addition to these factors, I conducted control simulations, which had no spiders, crossed with the number of prey species and patches. I limited the respective habitat factors to 2 levels because the model was extremely long to simulate as such, even when performed on a supercomputer in parallel and vector modes, because of the time required to solve numerically the spider growth equations. I also limited the number of predator species to one in this Part: multi-species predator system simulation results are presented in Part 5. It is also important to remember that an increase in the number of prey species does not increase the total number of individuals immigrating; I kept that value fixed.

In the analysis of the system I first determine the best and worse phenotypes by competing them. I then compare the life time capture successes, rates of growth and reproductive outputs these two strategies produce. Finally, I conduct their pure phenotype simulations for the best and the worse foraging strategies, and compare their overall prey regulation effect as a test of the hypothesis that better phenotypes lead to greater prey limitation. There was no computational differences between the mixed and pure phenotype simulations, except that of constraining all spiders to one phenotype in the pure case.

I applied the randomization test by computer simulation (Sokal and Rohlf 1981) to test for effects of the number of patches, number of prey species, spider aggression level, and prey selection behavior on spider fitness and prey control. This was the appropriate test given the presence of 0 fitness scores for some of the foraging strategies across all replicates (Zero values cause null variance, which leads to infinitely heteroscedastic data that is thus not testable with parametric statistics.) Further, the independence of observations required for both parametric and non-parametric statistics was not met because the phenotypes competed. Thus, there was potential statistical dependence between individuals constituting a given phenotype. The statistic retained for the randomization test by simulation was the F ratio. The test is simple. First, one calculates the F ratios of all 15 treatment effects (main and interaction effects) of the observed data. The replicates of the observed data are then randomly reshuffled 2000 times to all factorial combinations. For each reshuffle, the F ratios are calculated. Thus, at the end of the simulation there are 2001 F

ratios per treatment effect which are then ranked from smallest to largest. Treatment effects are significantly ($P \leq 0.05$) different from zero if the observed F ratio is greater than the first 95% of the ranked F ratios obtained through the randomization process just described. I validated the simulation program by comparing the calculated sum of squares to those obtained with SAS (1985); they were equivalent.

I tested by MANOVA the effects of number of patches and number of prey species on prey biomass (prey control effect) and on spider numbers. (numerical response effect). I used the average biomass of prey in the analysis to eliminate the problem of comparing prey numbers between systems consisting of different numbers of prey species. Between prey species differences in individual body weight and rates of growth necessitated comparisons of variance as well. Because these variances were high, the analyses were completed on their natural logarithms. The effect of spiders was tested on the mean and the variance of prey biomass in a separate MANOVA.

I also completed a MANOVA on the effect of the number of patches, prey selection strategies and aggression (none, or high) on the the pure phenotype context. The test was a 2 X 2 crossed factorial design.

RESULTS

Competing phenotypes.

Spider performance. The main effects of number of patches, number of prey species, and spider foraging strategy on the number of prey captured by spiders, spider body masses and spider fecundities were highly

significant ($P < 0.0005$) (Table 4.2). There was no significant main effect of spider level of aggression on these parameters. Several second order and third order interactions were significant for all variables. It is interesting that aggression, though not a significant main effect, was a significant interaction effect with foraging strategy (aggression*prey choice strategy) for all parameters excepting the total numbers of prey captured. These results indicate that spider foraging success was dependent on the interaction of environmental and genotypic conditions (Figs. 4.2 - 4.4).

Spiders belonging to any phenotype achieved reproduction only (one exception) in the presence of the higher number (5) of prey species. The fecundity data are presented for the 5 prey species runs in Fig. 4.2. Inspection of figure 4.2 reveals that the phenotype which achieved the highest fecundity was the sequentially statistical foraging strategy with high aggressiveness exhibited towards other spiders, whereas the least successful phenotype was the sequentially random foraging strategy with no aggressiveness exhibited towards other spiders. These two phenotypes, were then run in subsequent pure phenotype simulations.

The effect of the number of patches on spider fecundity and body weight is clearly seen in figures 4.2 and 4.3. That the foraging strategy offering the greatest fitness in mixed phenotypic systems potentially can regulate prey is shown by inspection of the data on total prey captured by individual spiders using the different foraging strategies (Fig. 4.4). The sequentially random and specialist phenotypes achieved the lowest total prey captures whereas the sequentially statistical phenotype realized the highest total prey captures especially at the highest aggression level which

Table 4.2. Randomization tests for the effects of patchiness, prey species numbers, prey selection strategy, and aggressiveness on average spider body mass, fecundity, and food capture in computer simulations of spider predation of associated prey populations. Pa = number of patches, Ps = number of prey species, Sb = prey selection behavior, Ag = level of aggression.

Body Mass

source	df	SS	P[F > F _d]
Pa	1	2825499.82	0.000
Ps	1	336692.31	0.000
Sb	5	914465.10	0.000
Ag	2	21451.83	0.334
Pa*Ps	1	63862.54	0.013
Pa*Sb	5	182763.73	0.003
Pa*Ag	2	1522.07	0.932
Ps*Sb	5	63087.59	0.257
Ps*Ag	2	21347.76	0.329
Sb*Ag	10	209959.47	0.015
Pa*Ps*Sb	5	47960.66	0.441
Pa*Ps*Ag	2	2026.23	0.900
Ps*Sb*Ag	10	89000.81	0.535
Pa*Sb*Ag	10	72411.36	0.682
Pa*Ps*			
Sb*Ag	10	102811.27	0.414
ERROR	1368	14819169.11	

(Table 4.2. continued)

Fecundity

source	df	SS	P[F > F _d]
Pa	1	1814.09	0.000
Ps	1	2794.43	0.000
Sb	5	1243.59	0.000
Ag	2	55.31	0.078
Pa*Ps	1	1844.65	0.000
Pa*Sb	5	787.72	0.000
Pa*Ag	2	48.05	0.083
Ps*Sb	5	1276.47	0.000
Ps*Ag	2	348.05	0.113
Sb*Ag	10	188.86	0.043
Pa*Ps*Sb	5	760.21	0.000
Pa*Ps*Ag	2	58.85	0.061
Ps*Sb*Ag	10	198.61	0.041
Pa*Sb*Ag	10	141.69	0.204
Pa*Ps*			
Sb*Ag	10	133.69	0.241
ERROR	1368	14503.46	

(Table 4.2. continued)

Total Numbers of Prey Captured

source	df	SS	P[F > F _c]
Pa	1	14443847.328	0.000
Ps	1	524783.413	0.000
Sb	5	6508438.148	0.000
Ag	2	20224.141	0.794
Pa*Ps	1	347662.688	0.009
Pa*Sb	5	1953030.984	0.000
Pa*Ag	2	131876.117	0.254
Ps*Sb	5	179698.084	0.586
Ps*Ag	2	104494.674	0.323
Sb*Ag	10	679302.166	0.144
Pa*Ps*Sb	5	320067.391	0.227
Pa*Ps*Ag	2	7340.330	0.918
Ps*Sb*Ag	10	814170.661	0.069
Pa*Sb*Ag	10	295392.009	0.785
Pa*Ps*			
Sb*Ag	10	642173.884	0.189
ERROR	1368	69030666.393	

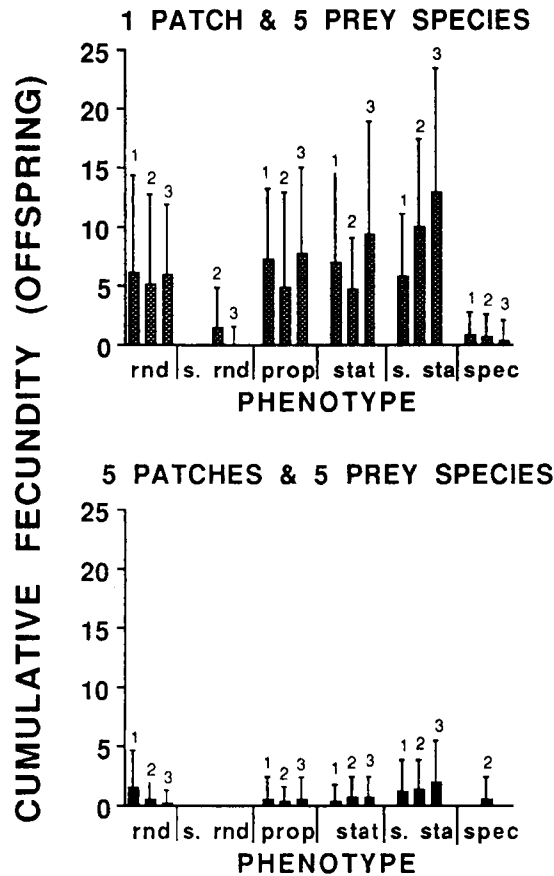


Figure 4.2. Cumulative fecundity of the 18 spider phenotypes in mixed phenotype simulations. We present only those factorial combinations for which offspring production was not null, except the case where the aggressive specialist reproduced once in the one patch and two prey species combination. The numbers 1, 2, and 3 code respectively for no, half, and complete aggression. The prey selection behaviors are: RND = random, S. RND = sequentially statistical, PROP = proportional, STAT = statistical, S. STA = sequentially statistical, SPEC = specialist. The error bars represent one standard error of 20 replicates.

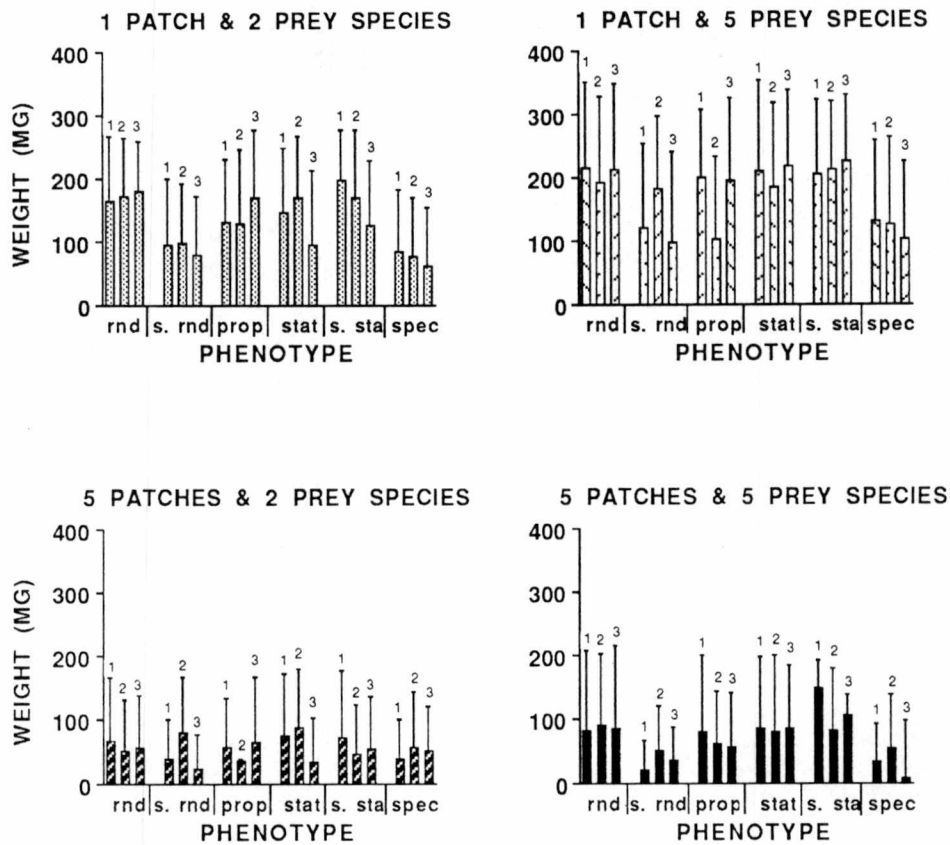


Figure 4.3. Weight of the 18 spider phenotypes in mixed phenotype simulations. The numbers 1, 2, and 3 code respectively for no, half, and complete aggression. The prey selection behaviors are: RND = random, S. RND = sequentially statistical, PROP = proportional, STAT = statistical, S. STA = sequentially statistical, SPEC = specialist. The error bars represent one standard error of 20 replicates.

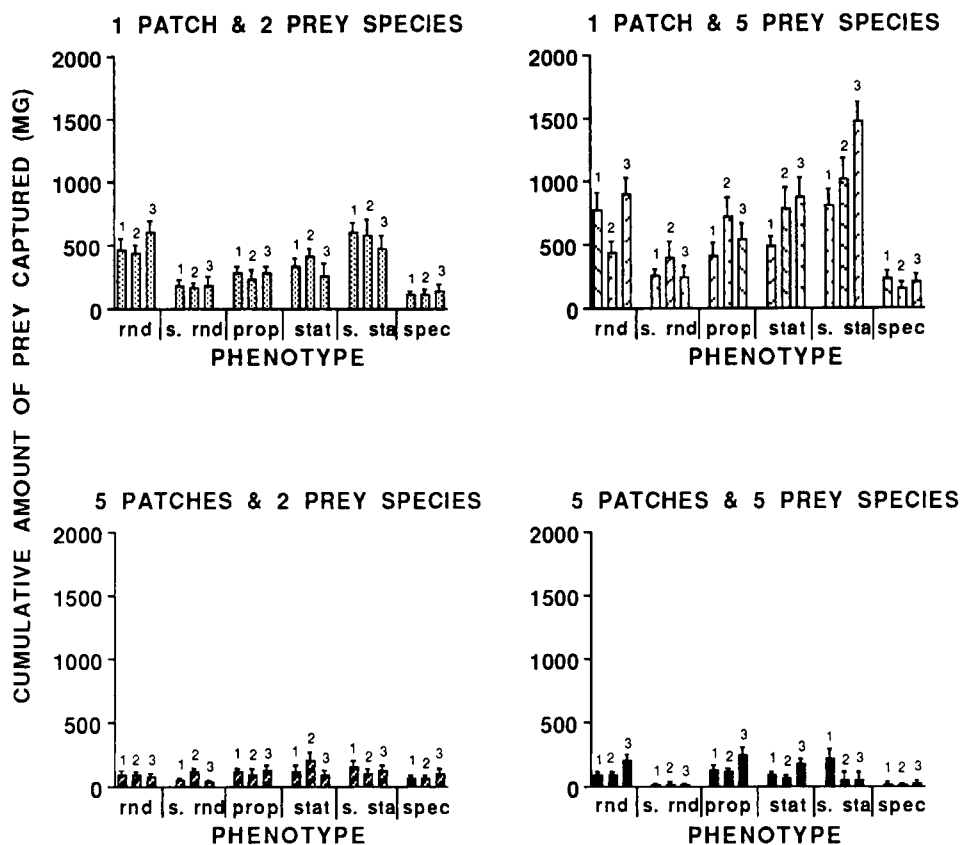


Figure 4.4. Cumulative amount of prey captured by the 18 spider phenotypes in mixed phenotype simulations. The numbers 1, 2, and 3 code respectively for no, half, and complete aggression. The prey selection behaviors are: RND = random, S. RND = sequentially statistical, PROP = proportional, STAT = statistical, S. STA = sequentially statistical, SPEC = specialist. The error bars represent one standard error of 20 replicates.

also corresponds to the highest levels of spider fecundity. Note that as for the measures of spider fitness, the pattern was observed only in the simple system: increasing the heterogeneity of the habitat by shifting from a patch number of 1 to 5 resulted in a general loss of both spider fitness and total numbers of prey captured (Fig. 4.5).

The effects of number of patches and number of prey species on both average biomass of prey and spider numbers present were significant, as were their interactions ($P \leq 0.0001$: Table 4.3A). Increased patchiness was the most significant factor in the simulations: it decreased average prey biomass in the same manner that it decreased spider weight and fecundity (Figs. 4.2 & 4.3 compared to Fig. 4.5). It also decreased the among species variance in prey biomass and spider numbers (Figs. 4.6 & 4.7). The main effect of the number of prey species was not consistent with respect to average prey biomass and spider numbers, but it did effect among prey species variance in biomass (remember that these are natural logarithmic values). This result is counter-intuitive since increased sample size (n) should have decreased this variance. It suggests that spider foraging strategies may cause increased among prey species variance. The effect of spider foraging was significant, as were all its interactions ($P < 0.0001$: Table 4.3B). As expected, the absence of spiders resulted in a greater average biomass of prey (Fig. 4.5) and a slight increase in the inter-specific variance of prey biomass (Fig. 4.6). The major cause of the significant interactive effects appears to be a disproportionately greater decrease of prey biomass due to spiders in the "one patch & two prey species" treatment than in the "one patch & five prey species" treatment (Fig. 4.5).

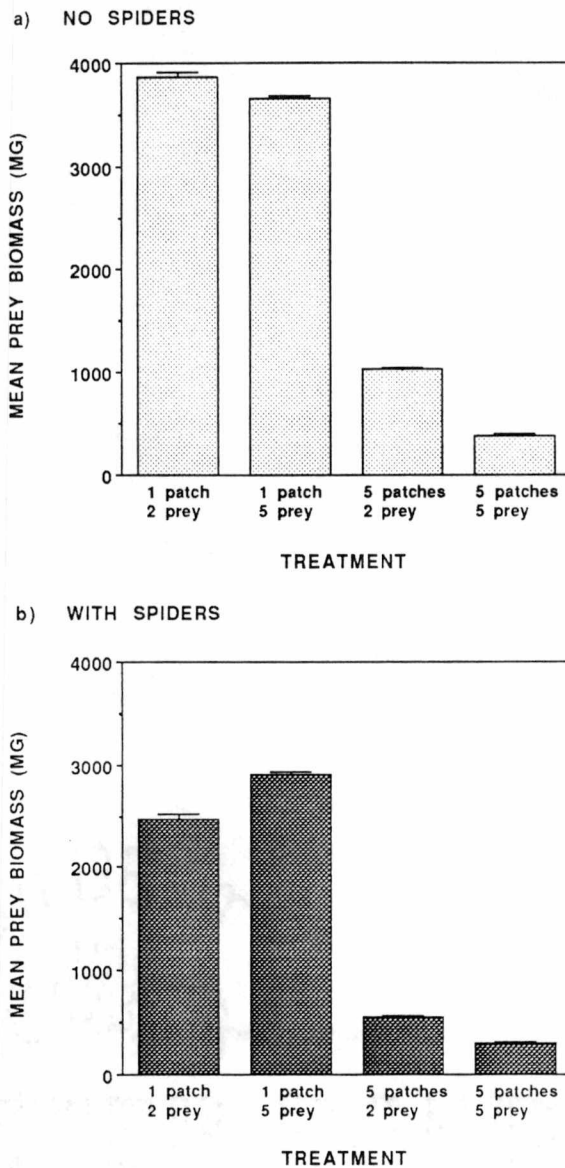


Figure 4.5. Response of mean prey biomass to the number of patches and prey species, and to the presence of spiders in mixed phenotype simulations. Error bars are one standard error.

Table 4.3. MANOVA of the effects of spiders, patch and prey species number on average prey biomass and the number of spiders in model mixed phenotype systems. Twenty replicates per factorial combinations.

A. Effect on prey and spiders				
source	Wilks' lambda	F	df/df	P
patch	0.017	2871.15	3/154	0.0001
prey	0.187	222.177	3/154	0.0001
patch*prey	0.426	69.07	3/154	0.0001
B. Effect on prey (control)				
spider	0.112	595.0.2	2/151	0.0001
patch	0.007	10287.4	2/151	0.0001
prey	0.112	1575.482	2/151	0.0001
spider*patch	0.129	506.235	2/151	0.0001
spider*prey	0.464	87.074	2/151	0.0001
patch*prey	0.224	260.71	2/151	0.0001
spider*				
patch*prey	0.687	32.813	2/151	0.0001

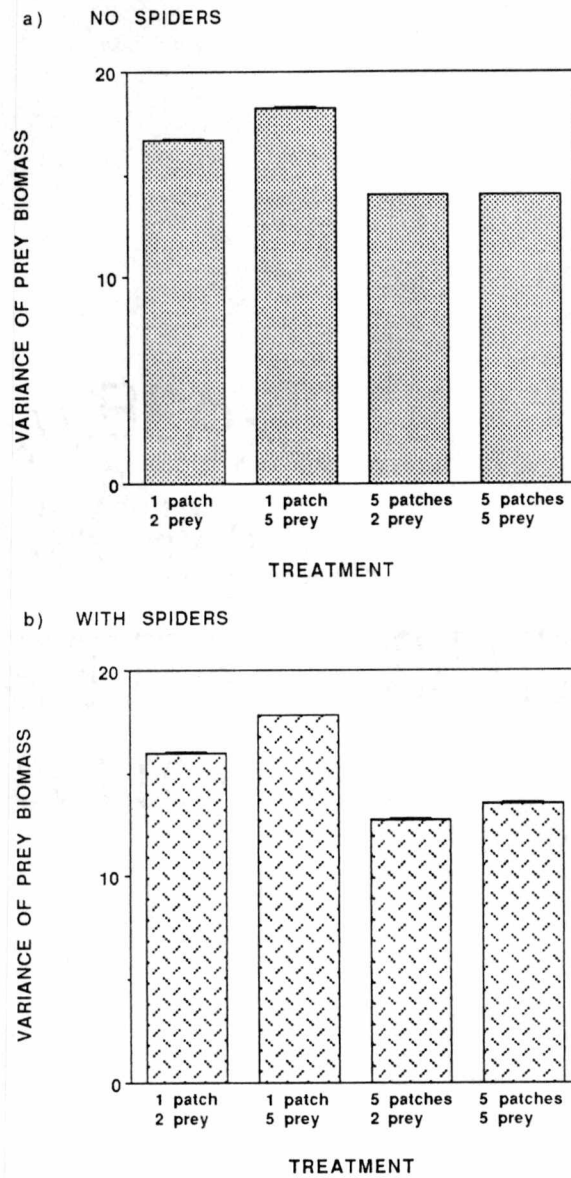


Figure 4.6. Response of the inter-specific variance in prey biomass to the number of patches and prey species, and to the presence of spiders in mixed phenotype simulations. Error bars are one standard error.

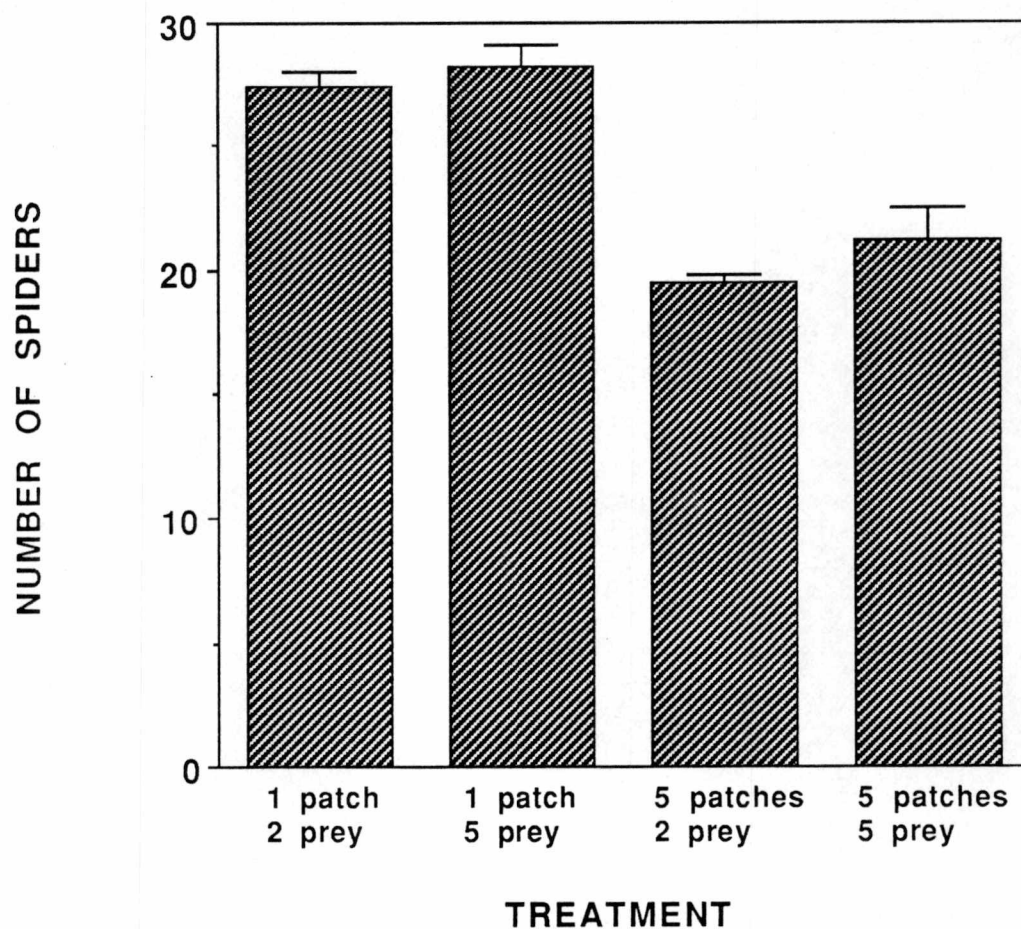


Figure 4.7. Response of the number of spiders to the number of patches and prey species, and to the presence of spiders in mixed phenotype simulations. Error bars are one standard error.

Prey regulation with pure phenotypes.

The two retained phenotypes for the pure phenotype runs were the sequential statistical foraging strategy with high aggression exhibited towards other spiders versus the sequential random foraging strategy with no aggression exhibited towards other spiders. The former was the "superior" phenotype in mixed simulations. The results of the pure phenotype simulations are that level of aggression exhibited towards other spiders has no effect ($P = 1.0$) on spider numbers in the system nor on prey biomass. Foraging strategy and patch number and their interaction, however, all showed significant effects ($P < 0.0001$) (Table 4.4). A decrease in the number of patches increased by four times at least the average biomass of prey (Fig. 4.8). The random foraging strategy caused a greater reduction in prey biomass and increase in spider numbers than did the statistical behavior at both patch levels. This effect was more marked at the lower level of patchiness (2 patches). Patchiness had the surprising effect of reversing the fitness superiority of the foraging strategies. In the two patch system, the random strategy produced on average two times more offspring to a spider than the statistical strategy, whereas the reverse prevailed in the five patch system for which the statistical strategy produced 5 times more offspring.

DISCUSSION

The results of these simulations indicate that there are conditions under which generalist predators can limit associated prey populations, since I observed cases for which model spiders kept prey as low as 2

Table 4.4. MANOVA of the effects of the best and worst spider phenotypes at two and five patches on the average and the variance of prey biomass, and the numerical response of spiders in model pure phenotype systems. These analyses exclude aggression because of the absence of variance for that effect.

MANOVA

<u>source</u>	<u>Wilk's lambda</u>	<u>F</u>	<u>df/df</u>	<u>P</u>
phenotype	0.037	632.849	3 / 74	0.0000
patch	0.021	1145.184	3 / 74	0.0000
phenotype*patch	0.162	127.082	3 / 74	0.0001

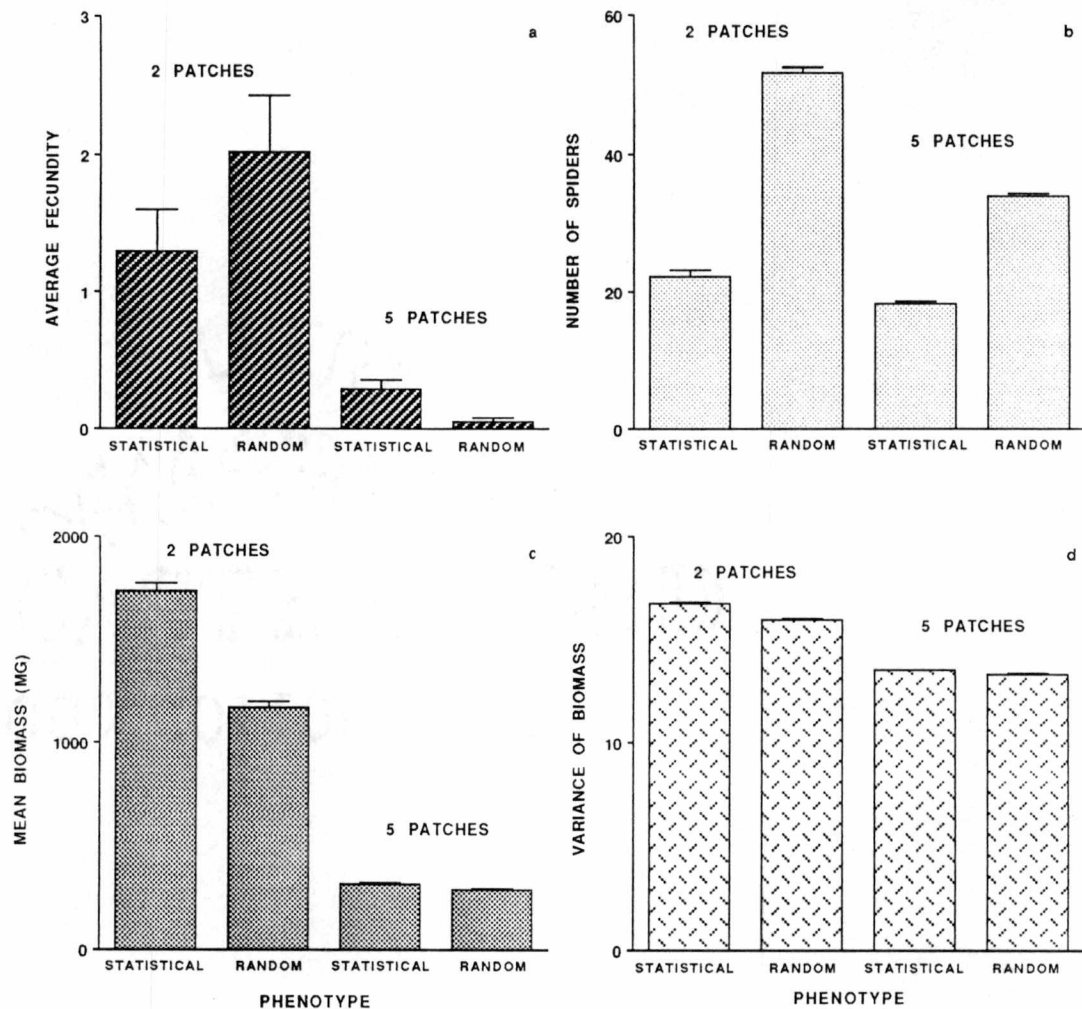


Figure 4.8. Response of fecundity and numbers of spiders, mean prey species biomass and its variance to the effects of patchiness and the random and statistical specialist behaviors in pure phenotype simulations. The effect of aggression was not presented since there was none. Sub-figures are: (a) average offspring production, (b) numbers of spiders, (c) mean prey biomass, and (d) the among species variance of prey biomass. Errors bars are one standard error.

individuals (200 mg each) per m^2 in pure systems. In the absence of spiders, the numbers of prey were nearly twice as large (Fig. 4.5). The environmental or extrinsic components of the systems (patchiness and the number of prey species) largely governed prey levels which in turn determined spider fitness. It is well known that patchiness influences population dynamics (Huffaker 1958, Murdoch et al. 1985, Chesson 1978, Kareiva 1986, Reeve 1988); in this model, increased patchiness led to smaller prey subpopulations which suffered relatively more from the negative contribution of random environmental effects and from local predation (Eq. 1). The simulated spider predators actually decimated prey subpopulations in the multiple patch system.

The effect of the number of prey species on predator fitness or prey biomass has been less well studied. I observed that an increase in the number of prey species increased spider fitness. I think that the greater number of prey species reduced prey depletion through a partitioning of spider feeding which may be targeted on single species in low species systems. The recent work by Heller (1980) and Juliano (1989) suggests that polyphagous consumers can benefit from increased numbers of prey types by consuming less preferred ones as the numbers of the preferred type diminish. When variability is present in the prey supply, a predator that takes everything or that temporarily specializes while having a statistical knowledge of this variability (sequentially statistical) will do better than a pure specialist or random specialist. This is what I observed with competing phenotypes. I also confirmed that greater spider fecundity was associated

with higher feeding rates (total number of prey captured) which fits the empirical data for spiders (e.g., Riechert & Tracy 1975).

The hypothesis that more competitive phenotypes (from mixed phenotype simulations) will consume more prey, thus increasing regulation was not supported in pure phenotype simulations. However, the phenotype which produced the most offspring in the pure phenotype, low patchiness system (random behavior) did achieve significantly the greatest prey control. Thus, the hypothesis is supported in that context, but I realize that results drawn from mixed phenotypes cannot be carried over to pure phenotype systems. For instance, patchiness did not affect the relative superiority of phenotypes in mixed systems, but reversed it in pure phenotype systems. These observations point to the key role of competition between and within phenotypes. The only reason I can advance for the lower spider numbers and prey control of the statistical specialist in pure systems is that the best competitor of such an individual is another of its kind. Intraspecific competition (i.e., resource depletion) was probably more intense among statistical specialists due to their common response to capturing the most profitable prey species during any time interval, whereas random specialists did not have such focused preferences because individual behavior was not uniform. Hence, the statistical specialist would "beat" the random specialist when the food supply is either low or very patchy. The same reasoning could also explain the observed increase in the variance of prey biomass with increased numbers of prey species in mixed systems. The deterministic and statistical specialist would have focused on particular prey species. This led to reductions in the selected prey species numbers and a

consequent higher among species variance of prey biomass. In two prey species systems, there is less room for choice, thus less room for heterogeneity, than in a five species system. Figure 4.8d confirms that the statistical specialist was associated with more among prey species variance than the random specialist.

The results presented here have consequences for the practice of biological control. First, prey control may be achieved by manipulating habitat patchiness and quality (Riechert and Bishop 1990). The practice of intercropping is one example of a technique for increasing patchiness and prey species richness (Strong et al. 1984, Provencher and Vickery 1988). Since patchiness reduces prey numbers, generalist predators such as spiders may still reproduce in polycultures because of greater prey species richness. I initially thought that a selective program which reduced spider aggression (territoriality and cannibalism) would be the most beneficial strategy, but model results have shown that the main effect of aggression not to be a significant factor of prey limitation (but see below) and that the superior phenotype achieving greatest prey limitation was the most aggressive. Since immigration cannot be prevented in field conditions, I must conclude that the role of pure phenotypes may be of limited value and, as a result, research should be focused on competitive strains of predators that maximize their fitness in patchy habitats.

Model limitations. Although the stochastic, mechanistic and individual based model is more realistic and testable than many deterministic and aggregated models (Huston et al. 1988), I am aware of its present limitations. I have not included predation on spiders, emigration,

molting, and time lags between the formation of the egg sac and the eclosion of offspring in it. Most importantly, the behavioral dynamics of the system are not spatially explicit. Many, if not all, of the behaviors that distinguish generalist predators are very local, especially aggressive behaviors and their associated costs. For instance, there can be severe energetic and behavioral consequences for a territory resident to fight against a larger or smaller adversary (Hammerstein and Riechert 1988). The notion of territory itself is spatially defined and highly tuned to local resource quality (Riechert 1981). Preference for prey types is also a very local phenomena because spiders have very short distance detection ranges (e.g., vibratory and olfaction <1 m, vision often a few cm centimeters [Witt & Rovner 1982]). What happens more than 1 meter away is expected to be of no consequence to a spider. Hence, I am not surprised that the aggression results did not stand out in the analysis; aggression was not spatially explicit. Future improvement of the model will have to address these issues.

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PART 5

THEORETICAL TEST OF THE BIOLOGICAL CONTROL EFFECT OF ASSEMBLAGES OF SPECIES OF SPIDERS IN VARIABLE ENVIRONMENTS

INTRODUCTION

Riechert and Lockley (1984) proposed that generalist predators should exert more control on associated prey populations if present in multi-species assemblages than as single species. The greater impact of many generalist predator species would be caused by the broader range of predator body sizes and foraging behaviors present which increase the probability that prey of different size classes and species will be killed by predators (Riechert and Lockley 1984, Riechert and Bishop 1990).

In this study I test whether increasing the number of predator species in a system while holding the total number of individual predators constant increases the control of associated prey populations. Note that associated with the increase in predator species number, I also model increases in prey and spider body size variability. I view a generalist predator as a foraging phenotype that has the potential to select prey from an array of sizes and species, to compete with other predators, and to exhibit aggressive behaviors. In the situation of multispecies assemblages of generalist predators, I envision that patchiness of prey, the number of predator species and the range of body sizes of these predators would form the predator's environment. In order to have an understanding of the results while respecting the complexity of individual based dynamics, I explicitly modeled individual predators operating in a patchy and stochastic environment. The tested hypothesis requires an individual based approach (Huston et al. 1988) precisely because variability of body sizes can better be accounted for in such a manner than through a model with size aggregation. I chose

spiders as the model predators because they are typical generalist predators (Riechert and Lockley 1984) on which good physiological data and growth functions have been published (Nakamura 1982).

SIMULATION MODEL

The computer model used here is nearly identical to the one presented in Part 4. The following parameter values differ: the mean weight of prey and spider species, the maximum rate of increase of the prey species, and the minimum weight of reproduction of the spiders. In the previous Part, one of the prey species was much smaller than the others in order to have food available for juveniles. In the present case, I am more concerned with spiders of varying body sizes consuming prey of varying sizes, which is a central idea of the hypothesis proposed by Riechert and Lockley (1984, Riechert and Bishop 1990). Hence, I created systems in which the average size of prey and spiders span more evenly from large to small around a grand average of 100 mg. Hence, the smaller prey species reproduced at a faster rate and smaller spiders reproduced at a smaller minimum size. The variability of body sizes was distributed between low and high values by simply spreading the means of each species less or more, respectively. The smaller the species, the smaller the variability in body sizes around its species mean. The algorithms which determined the body sizes of prey were,

$$c_j = (200. - W_1(n-j) + W_2 j/n)(0.5 - er),$$

$$r_j = 1. + 0.5/c_j$$

where low variability of prey body sizes consists of $W_1 = 10$, $W_2 = 2$, high variability is obtained with $W_1 = 45$, $W_2 = 40$, and er is a pseudo-random number uniformly distributed (DURAND subroutine, E.S.S.L. 1988). The parameter W_1 governs the magnitude of interspecific variability, whereas W_2 influences intraspecific variability. The algorithm for spiders is,

$$e_{rs} = U_t(200. - (s - 1)Z_1) + (1 - U_t)(10. - (s - 1)Z_2) \\ + 20(0.5 - er)/((1 + (1 - U_t))^2)$$

where $U_t = \begin{cases} 1 & \text{for } 1 \leq \text{day} \leq 10 \\ 0 & \text{for } 10 < \text{day} \end{cases}$,

low variability of spider body size being obtained by setting $Z_1 = 10$, $Z_2 = 0.1$, and high variability is achieved with $Z_1 = 30$, $Z_2 = 0.5$. These two parameters have the same significance as the ones for prey variability. The variables and parameters used in the simulations are presented in Table 5.1.

Tests and Statistical Methodology

Because of the many stochastic elements of the model, I replicated the results 20 times by Monte-Carlo simulation. Replication was performed within the crossed factorial combinations (Sokal and Rohlf 1981). The factors were the number of predator species (0, 1, 4), the interspecific variability between prey body size (low, high), and the interspecific variability between spider body sizes (low, high). Interspecific variability of body sizes was either high or low (see above) around a general average body size of 100 mg for spiders and prey. Each species had its own average body size

Table 5.1. Definition and values of variables and parameters used in an individual based Monte-Carlo simulations of spider multi-species assemblages feeding on associated prey species in a patchy habitat.

CODE	DESCRIPTION	VALUE
m	no. of spider species	1, 4
k	no. of patches in a 20 m ² habitat	2
n	no of species of prey	4
t	time interval	
X_{ji}	no. of individual prey of species j in patch i	variable
r_j	maximum population growth rate of species j/2 hours	$1.09 \leq r_1 \leq 1.01$
c_j	average weight of an individual prey of species j (mg)	$10 \leq c_j \leq 200$
er	pseudo-random uniform number	$0 \leq er < 1$
u_j	average no. of individual prey immigrating into a 20 m ² habitat/2 hours	$2 \leq u_j \leq 12$
—	dispersal rate of prey	0.001
—	average no. of spiders of a species immigrating into a 20 m ² habitat/2 hours	12^c or 1
y_j	food captured (mg) of prey species j by a spider	variable
f	food ingested (mg) by a spider	variable
a	food (mg) assimilated by a spider	variable

(Table 5.1. continued)

e	body weight (mg) of a spider	variable
U_j	indicator function measuring spider activity	$\{0, 1\}$
α_j	capture rate of a spider for prey species j (mg/mg/time)	0.25^c
p_j	spider's preference for prey species j	$0 \leq p_j < 1$
dd_j	no. of prey of species j potentially eaten by other spiders during 2 hours	$\max = 2$
$w(f)$	capture cost function	$0 \leq w(f) \leq 1$
ag	level of aggressiveness a spider exhibits towards others	$\{0, 1/2, 1\}$
q	quality of a spider's territory	
g_j	prey availability (mg) of species j to a spider	variable

^{c} : denotes a constant at time $t = 0$.

with variance around that value. Both the average and the variance were arbitrary, although correlated as previously mentioned. I fixed the number of prey species at four and the number of patches at two to ensure a moderate reproduction of spiders (known from the results presented in Part 4). Note that the simulations incorporated spider prey selection strategies and aggressiveness towards other spiders distributed randomly to individuals.

I selected four dependent variables to measure the system's response. These were the among species average and variance of prey biomass, the number of spiders, and the (among individual and species) average cumulative amount (mg) of food captured by all spiders. The independent variables were the number of predator species, and prey and spider interspecific variability of body sizes. For these analyses I deleted the control (0 spiders), since in the absence of spiders there can be no spread of their body sizes, no survivorship of spiders, and no prey captured. I used MANOVA to account for treatment effects given the potential correlations between the response variables (SAS 1985, PROCEDURE GLM). I tested the effect of the absence versus the presence of spiders on mean prey biomass and its variance through a contrast within the MANOVA.

RESULTS

The main overall effect of the number of spider species was significant ($P < 0.0001$; Table 5.2). A greater number of spider species decreased the mean among species prey biomass, and the among species variance of prey biomass, and increased the number of spiders and the cumulative amount of prey captured by all spiders (Figure 5.1 - 5.4).

Table 5.2. MANOVA of the effects of the number of spider species, and interspecies variability in predator and prey body sizes on the average and variance of prey biomass, the number of spiders, and the cumulative amount of prey captured by spiders in multi-species simulated systems. SP = no. of predator species, PY = interspecies variability in prey body size, PD = interspecies variability in predator body sizes.

source	Wilks' λ	F value	df / df	P > F
SP	0.2720	99.664	4 / 149	0.0001
PY	0.1880	160.827	4 / 149	0.0001
PD	0.6921	16.572	4 / 149	0.0001
SP * PD	0.9535	1.812	4 / 149	0.1293
SP * PY	0.8303	7.613	4 / 149	0.0001
PY * PD	0.9898	0.381	4 / 149	0.8217
SP * PY * PD	0.9984	0.056	4 / 149	0.9940
CONTRAST:				
NO SPIDERS				
VS. SPIDER				
SPECIES	0.574	86.318	2 / 233	0.0001

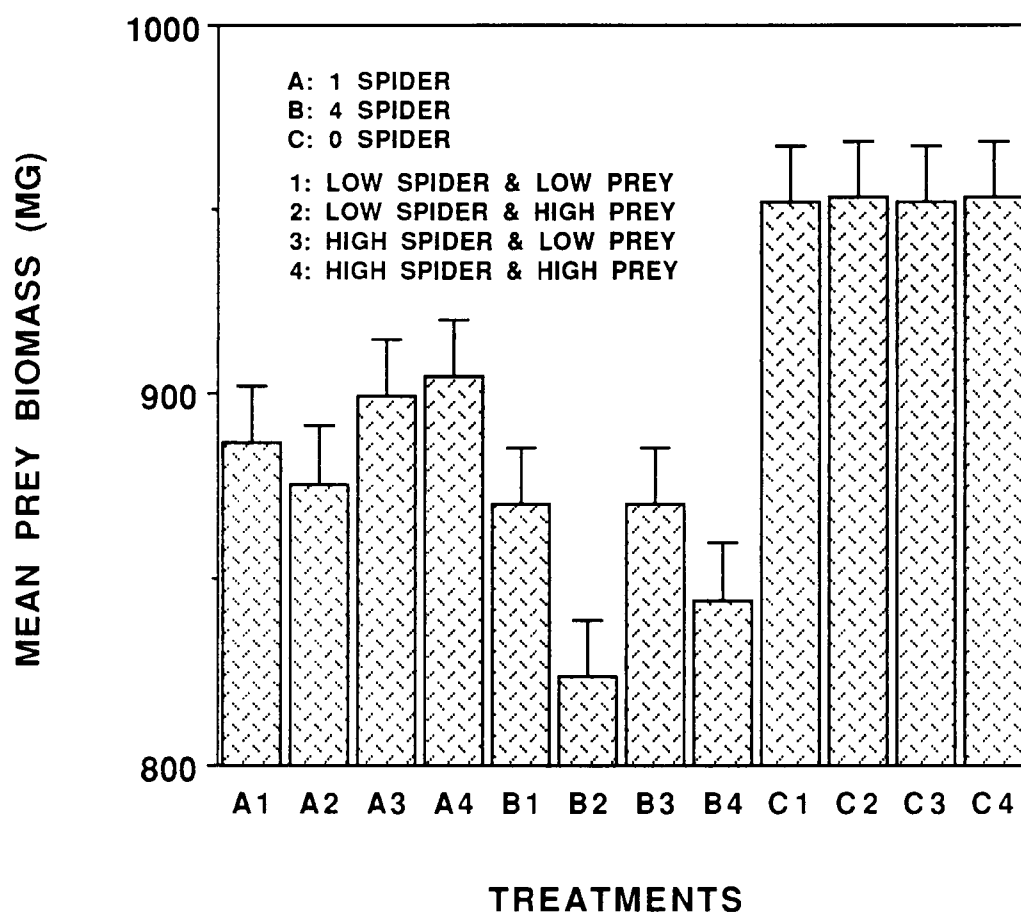


Figure 5.1. Mean prey biomass at varying number of spider species and inter-specific spider and prey body size variability in spider multi-species assemblages simulations. The mean is taken over species over the whole habitat. Results were obtained from Monte-Carlo simulation results ($n = 20$). The absence of difference between controls (C) is due to the absence spiders, thus the absence of spider body size variability. Error bars are one standard error.

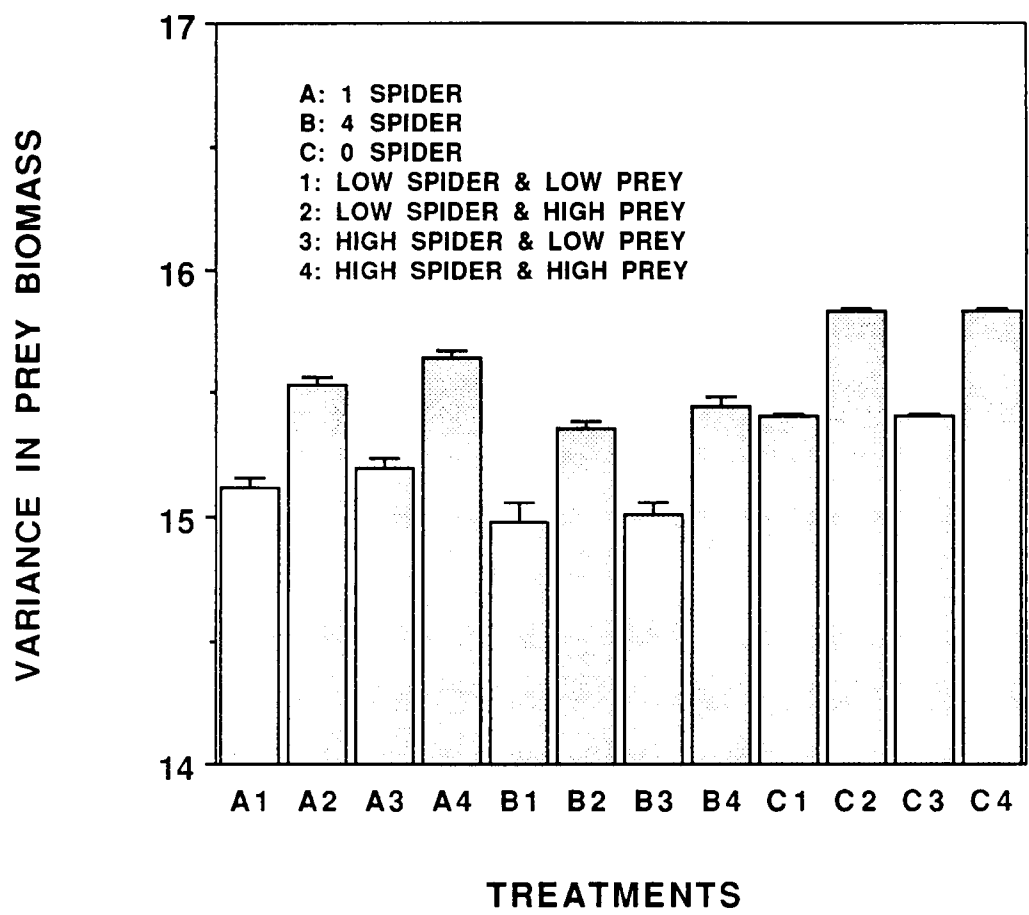


Figure 5.2. Among-species variance of prey biomass at varying number of spider species and inter-specific spider and prey body size variability in spider multi-species assemblages simulations. Error bars are one standard error.

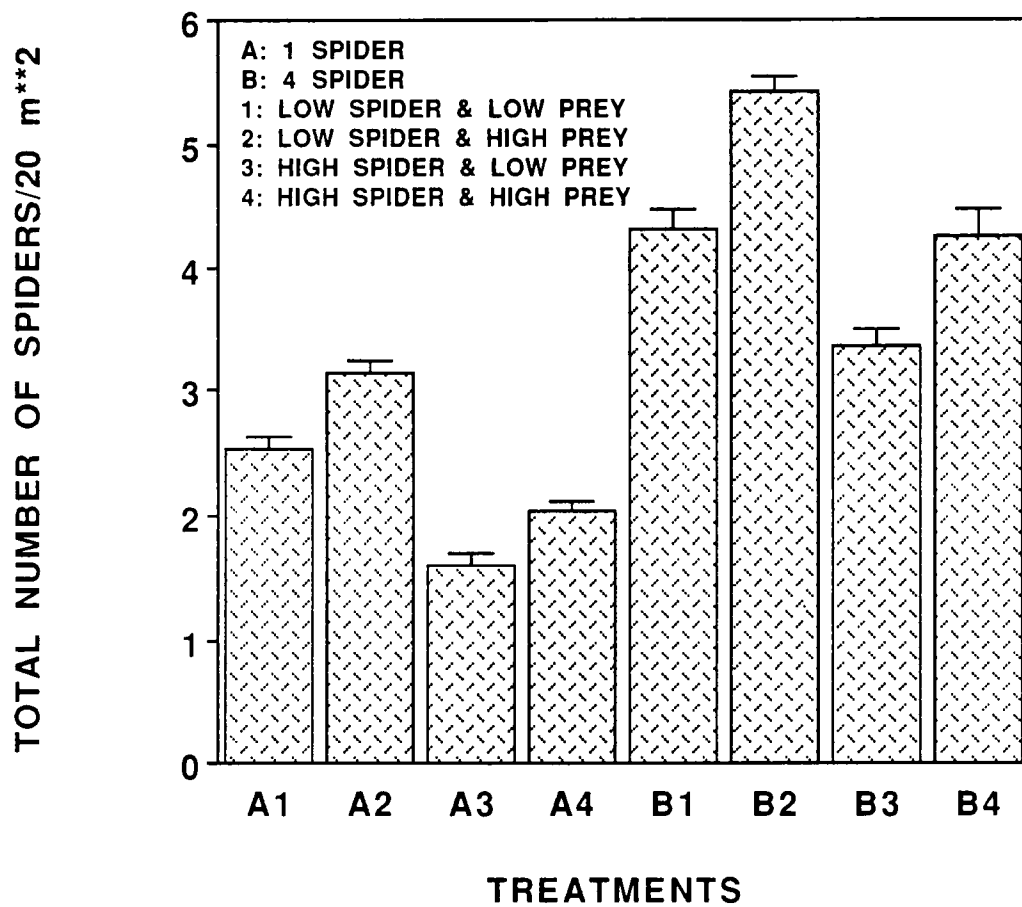


Figure 5.3. The number of spiders at varying number of spider species and inter-specific spider and prey body size variability in spider multi-species assemblages simulations. Error bars are one standard error.

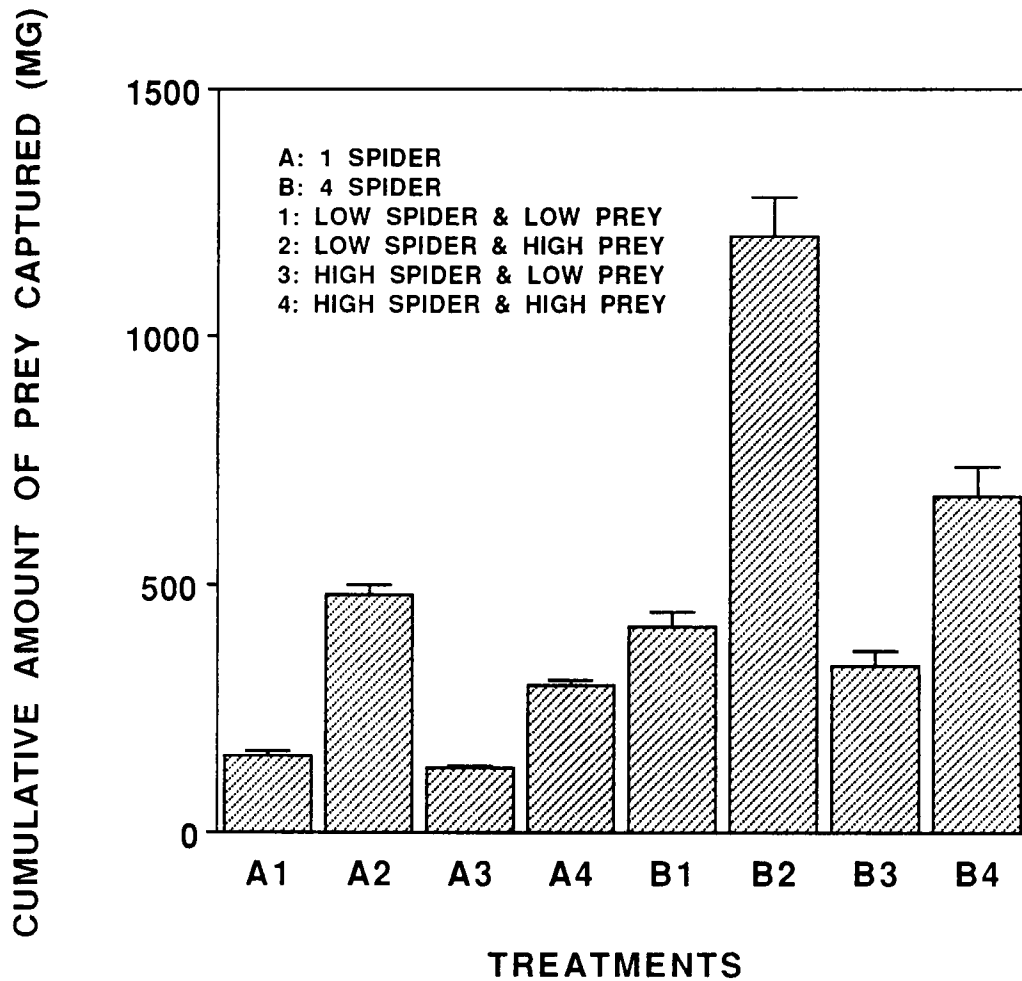


Figure 5.4. The cumulative amount of prey captured by spiders at varying number of spider species and inter-specific spider and prey body size variability in spider multi-species assemblages simulations. The amount of prey captured is cumulative over an individual's lifetime, then averaged among individuals and spider species. Error bars are one standard error.

Although significant and consistent, this overall effect of spider species was not strong, except for the cumulative amount of prey captured. Controls (0 spiders) lead to greater numbers of prey ($P < 0.0001$; Table 5.2), yet the greatest decrease in prey biomass due to spiders was slightly over 100 mg relative to the 950 mg observed in the absence of spiders (Fig. 5.1). The overall main effects of prey and spider interspecific variability of body sizes were both significant ($P < 0.0001$; Table 5.2). The effect of the interspecific variability of prey body sizes was the strongest of the two. Greater variation in prey species body sizes increased slightly the number of spiders and the among species variance of prey biomass. It also greatly increased the cumulative amount of prey captured while its effect on mean prey biomass was opposite and weak (Figure 5.1 - 5.4). Greater variation of spider body sizes was associated with slightly higher mean prey biomasses and among species variances, but with fewer spiders and the cumulative amount of prey they captured. The only significant ($P < 0.0001$) overall interaction was for the number of spider species crossed with prey body size variability.

DISCUSSION

The simulation results confirmed, in part, the hypothesis proposed by Riechert and Lockley (1984) that species assemblages of generalist predators may limit assemblages of prey species better than a single generalist predator species. The observed effects, although consistent and significant, were not strong for all response variables. It could be that four predator species are not enough to have produced a stronger effect. Spider species numbers are in the tens to hundreds in most temperate systems

(Gertsch and Riechert 1976). It is not uncommon in unmanipulated agrosystems to find at least 10 spider species (and several more non-spider predators) per m². Alternatively, spider survivorship was generally poor in the simulations (Fig. 5.3), thus controls and non-controls may have behaved similarly without the immigration of spiders. This happens if the average weight of an individual prey is too low relative to the average size of spider, which was sometimes the case in these simulations. The prey do not support the spiders in the system when spiders have depleted the larger prey species or if the variability of the body sizes of prey is low relative to their mean weight.

Not surprisingly, I found that a large interspecific variance of prey biomass increased biocontrol, and the survivorship of spiders. I expected this effect since increased variability of prey body sizes would result in larger numbers of large prey, which upon their consumption by spiders would lower the average biomass of prey. Larger prey items were the preferred ones for spiders large enough to capture them. The one effect which was not predicted, although small, was that increased interspecific variance of spider body sizes would have detrimental effects on biocontrol and on spider survivorship. My experience with the simulation model makes me believe that increased competition between spiders underlies this effect (see Part 4). Hence, a greater spread in spider body sizes may have eliminated the smaller predator species. I know from previous computer simulations that smaller spiders generally survive less well than large ones. This is possible since all spiders were given randomly the same set of behavioral strategies; behavioral similarity would have increased competition through

local resource depletion. This happens since larger spiders may capture large and small prey, but smaller spiders can only capture small prey. In spider assemblages, an increase in the number of species is usually accompanied by an interspecific spread of body sizes and a greater variety of very distinct foraging strategies, which could reduce competitive effects. For example, web-building spiders may capture flying insects which would otherwise be unavailable to wandering spiders and vice-versa. Moreover, insect prey would fall victim during different life stages to spiders using fundamentally different capture strategies. It is fairly difficult to model such dynamics because they require the explicit incorporation of spatial, three-dimensional variables and behaviors. A more complete test of the hypothesis will require adding spatial dynamics to the simulation model.

Two of the three factors examined in this paper could be used for biological control; the number of species of spiders and the interspecific variability of their body sizes. The composition of prey body sizes is a field condition one has to cope with, so manipulation of prey body sizes is a less feasible option. One might consider increasing the richness of prey by adding companion plants to agroecosystems (see review in Strong et al. 1984). Spiders can be manipulated in two ways; through introductions to crops or by habitat manipulations. Since most spiders must be reared in isolation and provided variable live prey, mass releases of laboratory reared animals probably is not economically feasible. However, spiders continuously invade habitats by ground and aerial dispersal (Turnbull 1973, Bishop 1989). Bishop's (1989) work indicates a constant influx of spiders throughout the early-mid growing season in east Tennessee and spiders

were less successful in late crops which coincided with the end of immigration. Hence, fostering their numbers and richness is more a matter of managing the environmental features of habitats to prevent emigration by using mulch which provides shelter (Riechert and Bishop 1990). The finer details of habitat management could further add some control to varying the interspecific spacing of body sizes. For example, certain plants may only harbor small web-spiders, whereas broad leaved crops or wide spacing between crop rows would favor large ground spiders. Greenstone (1984) has shown that spider richness is correlated with the structural diversity of plants.

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PART 6

VALIDATION EXPERIMENT OF AN INDIVIDUAL BASED MODEL OF PREY LIMITATION BY SPIDERS

INTRODUCTION

In seeking environmentally safe alternatives to the present practice of pest control, one should first propose methods easy to implement. Usually these methods involve habitat management. For instance, crop rotation, crop timing, and many forms of polycultures belong to that type. These practices result either in the pest being deprived of its preferred food type at a critical time in its development or having its preferred food type associated with plants that are repellent to the pest (Root 1973, Strong et al. 1984). It is more difficult, however, to manage habitats to enhance the impact of predators on prey because the mechanisms are indirect and less well understood. Riechert and Bishop (1990) have shown that biological control by spiders can be greatly increased if garden plots are covered with mulch, which protects spiders from unfavorable weather conditions and may supply them with alternative prey. Kareiva (1986) demonstrated experimentally that the increased patchiness of goldenrods favored aphid outbreaks because the dispersal of their predator, a ladybird beetle, was hindered by greater patchiness. This result is somewhat opposite to the classic findings obtained of Huffaker (1958).

I investigated theoretically aspects of predation by spiders in order to seek and understand factors which could be used for pest control. An individual based computer model of predation by spiders has shown that both environmental and behavioral factors significantly influenced the numbers of prey in a habitat (Parts 4 and 5). By far, the environmental factors should prove easier to manipulate than behavioral ones. The latter factors are likely to be genetically based and may, thus, require a great

amount of research demonstrating their feasibility in applied pest control and dependability (heritability). Hence, I summarized only the predictions emerging from such environmental factors as habitat patchiness. An increase in the number of patches in a habitat made prey subpopulations relatively more vulnerable to stochastic weather effects, and local predation. It also decreased the carrying capacity of the habitat for the pest, resulting in their lower numbers. Both the weather effect and carrying capacity effects were built in the model. The effect of changing the numbers of prey species on prey numbers increased spider foraging success and reproductive effort. It is thus supposed that this factor increased prey availability to these predatory generalists and, as a result, encouraged the consumption of prey. Similarly, increasing the number of species of spiders resulted in a larger total amount of prey captured. Among more subtle factors was the interspecific variation in the body sizes of prey; a greater variation in prey body sizes resulted in a significant reduction of prey numbers.

In order to verify the robustness of the model, I conducted a field test of some of its qualitative predictions. The behavioral factors of spiders (e.g., aggressiveness, foraging strategy) were not tested because such an undertaking was beyond the scope of this research. I included three of the model's simplest predictions; the effects of the number of patches, the number of prey species, and the number of spider species. I did not consider the body size effects because they were more difficult to reproduce in the field and three factors complicated sufficiently the logistics of the experiment.

METHODS

The experiment was conducted in a clover-fescue pasture in Knox County of east Tennessee between August 28 and September 11, 1990. The experimental design consisted of 24 uniformly spaced enclosures in a 15 m X 15 m area. Each enclosure had a 2 m X 2 m square frame made of a wood frame base. It was 0.6 m in height and the above ground structure consisted of no-see-emTM netting covering a crossed polyethylene pipe support structure (the pipe ends were nailed into opposite corners of the enclosure). The floor of enclosures consisted of mowed pasture vegetation and wood mulch. The number of patches assigned to an enclosure determined which type was used. Two types of enclosures were used; single chambered and four chambered. The four chambered enclosure was partitioned through the use of a "+"-shaped board frame with a "v" in the middle of each board segment to permit spider and prey movement between patches. All enclosures had an opening in the netting which was kept shut with a paper clamp. Spiders and prey were introduced through this opening. The netting frames were held with hooks and eyes to, and nailed to, the buried frames. Strips of foam was stapled on the inner sides of the two frames to seal the enclosure.

The design was a completely randomized 2 X 2 X 3 factorial experiment (Sokal and Rohlf 1981). The factors were the number of patches {1, 4}, the number of species of prey {1, 3}, and the number of species of spiders {0, 1, 3}. Each factorial combination was replicated twice. (Initially I

conducted two temporal blocks. The results of the first one, however, were not used because enclosures failed to be escape-proof. This problem was corrected for the second block.)

Prior to starting the tests, I removed manually all arthropods found in the enclosures and then sprayed the enclosures with insecticide (RAIDTM). The removal effort was not totally successful since non-introduced arthropods were observed later on. A week later, spiders were introduced and then constant numbers of prey were introduced on each of six days. From day 7 to the end of the experiment on day 15, the enclosures were left untouched. On day 15, all prey and spiders were counted in the enclosures.

The three prey species used were a wild cricket (*Gryllus pennsylvanicus*), a katydid (*Orchelimum vulgare*), and a grasshopper (*Melanoplus femur-rubrum*). The average weight of crickets was 0.08 g (+/- 0.09, n=8). Katydid and grasshoppers were larger than crickets and weighed on average 0.13 g (+/- 0.10, n=5) and 0.16 g (+/- 0.06, n=5), respectively. The cricket was the prey chosen for the one species treatment. Ten individuals per day were introduced in the enclosures. The three prey species treatment consisted of 3 crickets, 2 katydids, and 2 grasshoppers added daily to appropriate enclosures. This combination assured that ten crickets would approximately equal the weight of the three species together.

The three spiders used were, in decreasing order of adult weight, *Lycosa rabida* (Lycosidae), *Trochosa pratensis* (Lycosidae), and *Agelenopsis kastoni* (Agelenidae). Lycosids do not build webs and the species I used were active all day. *Agelenopsis kastoni* is largely nocturnal and builds a flat, non-sticky sheet-web with an attached funnel. *Trochosa*

was the species designated for the one species treatment. Nine of them were introduced to each of the one spider species enclosures. (This density seemed to be within the range of the species in the field.) *Trochosa* approximated 1 cm in length and weighed on average 0.29 g. For the three species treatment, I introduced one *Lycosa* (0.6 g), three *Trochosa*, and three *Agelenopsis* (0.2 g). I assumed that one *Lycosa* equaled three *Trochosa* or three *Agelenopsis*.

RESULTS

The statistical analysis was a balanced three-way ANOVA with fixed effects. The response variable was a linear combination of numbers of prey given by: $1 \times (\text{number of crickets}) + 1.69 \times (\text{number of katydids}) + 2.11 \times (\text{number of grasshoppers})$. The constants 1.69 and 2.11 were the ratios of the average weights of katydids to crickets, and grasshoppers to crickets, respectively. This linear combination was termed a prey biomass equivalent. All of the main effects were found to be highly significant (Table 6.1). The strongest effect was the number of species of spiders, the weakest being the number of patches. Only two of the four interactions were significant and both involved the number of species of spiders interacting with the number of prey species or the number of patches. Contrasts within the spider treatments revealed that the large spider species effect was caused by the control containing generally more prey than the other spider treatments ($P < 0.0001$; Figure 6.1). This difference between the one and three spider species effect was marginally significant ($P < 0.0561$). Hence, the significant interactions were probably caused by the control. An

Table 6.1. Factorial ANOVA of the effect of the number of patches and of the number of species of prey and spiders on combined prey numbers from a field experiment. All factorial combinations were replicated twice. The patch, prey, and spider effects have, respectively, 2, 2, and 3 levels.

source	df	SS	F value	P > F
patch	1	220.948	10.37	0.0073
prey	1	556.0363	26.10	0.0003
spider	2	1456.328	34.18	0.0001
patch*prey	1	1.260	0.06	0.8119
patch*spider	2	387.2452	9.09	0.0040
prey*spider	2	164.807	3.87	0.0505
patch*prey*patch	2	4.095	0.10	0.9090
contrasts:				
control vs. spiders	1	1276.172	68.87	0.0001
1 vs. 3 spiders	1	78.766	4.25	0.0561
error	12	255.637		

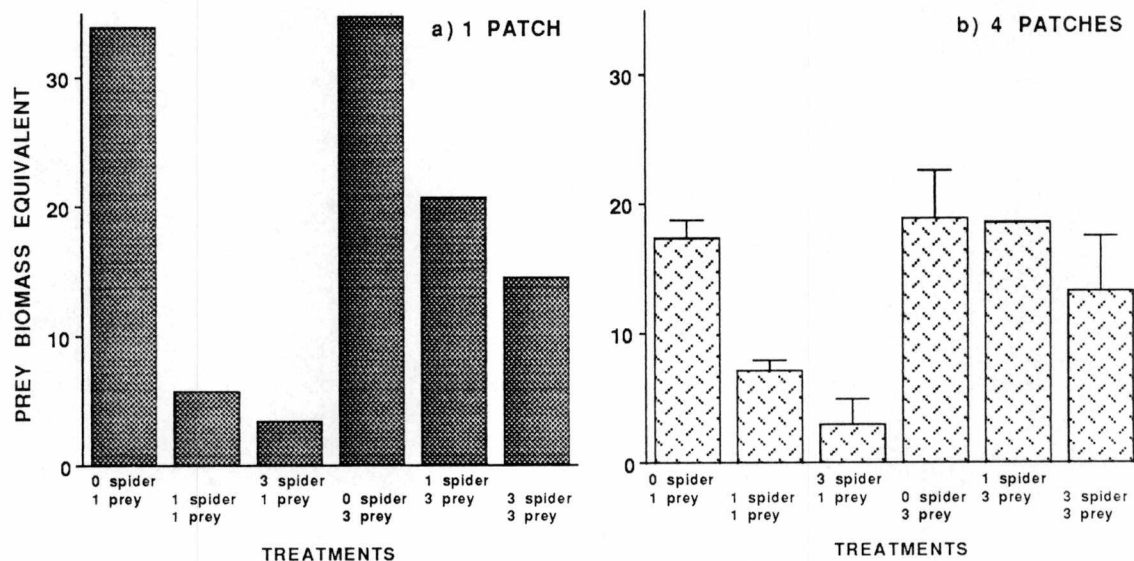


Figure 6.1. The effect of patchiness, and the number of species of prey and spiders on the prey biomass equivalent in a factorial field experiment. A prey biomass equivalent was calculated by the linear combination $1 \times (\text{number of crickets}) + 1.69 \times (\text{number of katydids}) + 2.11 \times (\text{number of grasshoppers})$. One species of prey = crickets, three species of prey = (crickets + katydids + grasshoppers), one species of spiders = *Trochosa*, three species of spiders = (*Lycosa* + *Trochosa* + *Agelenopsis*). Error bars are one standard error ($n = 2$). The absence of error bars on some columns indicates very weak errors.

increase in the number of patches mainly decreased the biomass of prey in the controls (0 spiders), whereas a greater number of prey species increased their biomass, except in controls (Figure 6.1). Although marginally significant, the biomass of prey was consistently smaller in the one spider species treatment than in the three species one.

DISCUSSION

The results of this experiment qualitatively support the model predictions, although some of the mechanisms responsible for treatment effects may differ between field and model results. Increases in prey biomass with increases in the number of prey species is the easiest effect to explain. Large prey items present only in the three species treatments may have been unavailable to most spiders, except *L. rabida*. Hence, in the absence of larger spiders, as in 2/3 of factorial combinations, larger prey probably suffered only from mortality that was independent of spider predation. Even if *Lycosa* were present, it may have preferred easier prey, such as crickets and katydids, to grasshoppers. The large-spider effect could also explain the effect of a larger number of species of spiders on prey biomass. *Lycosa* was only present in the three species enclosures

The effect of patchiness, observed mainly in the controls, is not explained by differential rates of predation. Patchiness hence affected the non-spider mortality of prey. It could be that smaller insect netting domes increased the temperature inside the 4-patch enclosures, thus causing prey to dehydrate faster. Temperature effects were not checked nor suspected, but since the deep wood mulch and vegetation provide shelter against the

heat, I assumed that microclimate conditions were not affected by dome size. (In the model, weather effects are independent of patchiness.) Secondly, the frequency of encounters between prey and non-introduced predators may have been higher in 4-patch enclosures because of the greater wood surface on which both prey and predators were commonly found. However, it is doubtful that the few non-introduced predators could have produced a nearly twofold decrease in prey numbers. The third and more interesting alternative is that herbivore prey sensing a lesser amount of food available in a small patch may have attempted to disperse. Such dispersal would be an upward movement, obviously stopped by the netting and during which time prey would dehydrate and not feed. Although this is an enclosure effect, it actually would be mimicing correctly emigration in response to increased patchiness. The role of patchiness here is thus different from the one built in the computer model. In the model, it is the population growth rates of the smaller subpopulations which are impacted by negative stochastic effects and carrying capacity. Population growth did not have time to occur in the experiment and emigration was not included in the model nor planned for in the field test. However, both model and experiment shared the localized effect of predation.

The treatments presented in this experiment are not beyond application to garden or crop management. Creating patchiness would consist of introducing islands or barriers of vegetation through intercropping, for example. Since some insects may not cross through certain types of plant species or plant architecture (Strong et al. 1984, Kareiva 1986), whereas ground spiders would move freely with respect to vegetation, the

effect of patchiness obtained in the experiment could be reproduced in a crop. Intercropping has the added benefit of depressing prey numbers, while usually increasing species richness of both prey and predators (Tahvanainen and Root 1972, Root 1973, Strong et al. 1984). To further encourage the build-up of predator numbers and richness, which contributes to biological control, one could make habitats more hospitable to predators by such simple practices as mulching (Riechert and Bishop 1990) and shallow plowing.

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PART 7

SUMMARY AND CONCLUSIONS

In this research, I examined theoretically and experimentally the processes by which spiders may regulate associated prey populations. The general hypothesis was that spiders, as individual generalist predators, may regulate prey populations if their foraging phenotype at least maximizes their relative fitness, since increased reproductive output usually requires a greater consumption of prey. To analyze this general hypothesis it was necessary to adopt a phenotypic view of generalist predators which would account for the contributions of behavioral traits and environmental factors to fitness and predation.

Theoretical tests were performed with an individual based, stochastic computer model simulating individual spiders feeding on prey subpopulations in a patchy habitat. I first examined the foraging success and offspring production of spiders, as well as prey biomass remaining in the system under different environmental and behavioral treatments. At this point, I sought to identify a generalist phenotype which would remain competitive under different combinations of environmental conditions. Of the two traits forming the foraging strategy, the level of aggressiveness exhibited towards other spiders and the prey selection strategy, only the latter proved significant, but their interaction was significant. The most competitive (i.e., which achieved the highest fecundity in mixed phenotype simulations) phenotype of the 18 tested was highly aggressive towards other spiders and consisted of a multivariate, Bayesian statistical prey selection behavior which specialized for one time interval on the prey species predicted to be most available within the spider's patch. The poorest strategy corresponded to specialization for one time interval on a randomly chosen prey species

with no aggressiveness exhibited towards conspecifics. Although specialization can increase the probability of failure to find sufficient, or any, preferred prey in a variable environment, it may be, however, an efficient strategy if the forager can make estimates of future prey availability and if other assumptions are met (e.g., the prey are not too variable). The competitive behavior discussed here was a fairly sophisticated application of a time series model, which may not reflect real animal behavior. It is noteworthy though to mention that the simpler and maybe more realistic prey selection behaviors also modeled performed nearly as well as the statistical one. This was the case with a proportional prey selection strategy. In conformance to the hypothesis, the phenotypes achieving the highest fecundity also captured the most biomass of prey. These results were maintained even though the number of patches, and the number of species of prey varied. Increased patchiness decreased strongly average prey biomass and spider foraging success, whereas an increased in the number of species of prey had the opposite effect.

Secondly, I computer tested the hypothesis that multi-species assemblages of spiders would better regulate associated prey populations than a single species. To achieve this, the number of species of spiders, and interspecific variation of prey and spider body sizes were tested in a crossed factorial design. A greater number of species of spiders and an increase in the body size of prey significantly enhanced predation and spider survivorship, but greater variation in spider body sizes had an opposite, significant effect. Hence, simulation results partly corroborated the species assemblage hypothesis. The effect of spider body size suggested

that it may not be the variability of body size which is important, but the richness of behavioral capture strategies which would prevent too much competitive diet overlap. This behavioral diversity was not built in the simulations. Alternatively the number of predator species and variation in their sizes was small compared to the real world situation.

A series of experiments was devised to test model assumptions and to validate some predictions emerging from the model. Model assumptions were that (1) hunger influences the foraging behavior and predation of spiders, (2) spiders switch between prey types, and (3) spiders can "forecast" prey numbers. First, it was established that hunger had no effect on the activity of, and predation by, *Tetragnatha laboriosa* or on choices made by the spider *Lycosa rabida*, but that more food deprived spiders gained weight very rapidly compared to satiated ones once exposed to prey. In a choice experiment, where *L. rabida* was offered a simultaneous choice between three different patterns of covariability formed by two prey species, spiders generally avoided the prey variability treatment presenting the greatest probability of food deprivation, although all treatments had the same average prey availability. Spider switching and forecasting were examined in a third and complex experiment with *Lycosa rabida*. Spiders generally switched positively between two prey types, and, to a lesser extent, showed no switching. Positive switching means that spiders captured disproportionately more of the more abundant prey type. Cases of negative switching were rare, yet their occurrence on days when the relative abundance of prey was reversed suggested that spiders may have used a weighted average of prey abundance to form preferences for prey. The

weighted average appeared more sensitive to low prey numbers and more recent values of prey numbers. Forecasting tests revealed that *Lycosa* significantly exhibited preferences indicating a dependence on past numbers of prey. Thus, spiders chose prey species according to decisions taken in the past 10 days.

The final experiment was a field validation of three of the model's qualitative predictions concerning the number of patches, and the number of species of prey and spiders. I limited my tests to these factors for logistic reasons and because the behavioral aspect of the model was far too difficult to test. As predicted from the model, decreased patchiness increased the numbers of prey only in the absence of spiders from field enclosures, but a greater number of prey species increased the biomass of prey only in the presence of spiders. The weaker, but consistent effect of increased spider species was to decrease prey biomass. I believe that greater patchiness caused prey to emigrate but which, in this case, caused mortality (dehydration and/or lack of food while sitting on the netting). In the presence of spiders, this effect may have been reduced simply because spiders consumed the prey. Both the spider and prey effects were apparently caused by the presence or absence of the larger species of spider which could capture the larger prey species.

In conclusion, spiders, as generalist predators, have shown features fostering their ability to regulate prey. Theoretical evidence certainly indicates that spiders can decimate prey subpopulations that have growth rates permitting them to double their numbers in one day. Field experiments detected switching and forecasting behavior in the spider *L. rabida*. These

two behaviors may be complementary and necessary for successful spider foraging and prey limitation. Finally, prey regulation and spider foraging success were determined to be sensitive to combinations of environmental and phenotypic factors both in field and model tests.

VITA

Louis Provencher was born in Montreal, Canada, on June 3, 1961. From birth to six years of age, he lived successively in Montreal, Winnipeg, Toronto, and, again, in Montreal where he remained from 1967 to 1986. Following graduation from high school in 1978, Louis completed a two year program in pure sciences at The College Edouard MonPetit. He then worked for one year, and thereafter became a biology major at McGill University in Montreal. Louis left McGill after one semester and joined the department of biological sciences of The University of Quebec in Montreal. He graduated in biology with a specialization in ecology in 1984. Louis remained at The University of Quebec in Montreal to work on a Master's with Daniel Coderre. His masters thesis was an evaluation of spider predation effects on aphids in corn crops. In 1986, Louis left Canada to start a doctorate with Susan E. Riechert at The University of Tennessee in Knoxville. His dissertation work included modeling and experiments addressing the problem of biological control with spiders. During his graduate years, Louis visited the Rocky Mountains, hiked parts of The Appalachian Trail in New Hampshire and Tennessee, travelled to Belize and Guatemala, canoed the cypress swamps of Louisiana, and explored many parts of the deserts of the southwestern United States. He received his Ph.D in Ecology in December of 1990. In 1990, he was awarded a post-doctorate fellowship from the Natural Sciences and Engineering Research Council of Canada to conduct two years of research in Seattle with Peter Kareiva.